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CHECK LIST OF RECENT CORAL RECORDS
FROM ALDABRA (INDIAN OCEAN)

by Brian Roy Rosen

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INTRODUCTION

The purpose of this check list is to bring together all records
of corals at Aldabra since no proper listing and bibliography exist
at present.   I have also taken this opportunity to make several
revised identifications and to add some depth data which were not
available when I presented my earlier list (Rosen 1971a).   It is in
fact possible to extract partial depth information for the species
in this earlier list from the accompanying account by Barnes *et al.*
(1971, especially their Table 2).   I have incorporated this
information here, and therefore only cited Bellamy's MS figures where
they supplement the published information.   I should like to express
my thanks to Dr. David Bellamy (University of Durham) for allowing me
to use this information.   I should also like to thank Professor John
Wells (Cornell University) for permission to use and refer to a
manuscript currently in preparation.   Dr. Michel Pichon (James Cook
University) and Ms Zena Dinesen (James Cook University) kindly checked
the taxonomic list, and Dr. C.G. Adams (British Museum (Natural History))
offered helpful criticisms of the manuscript.

COLLECTIONS AND LITERATURE

Table 1 analyses known coral collections made at Aldabra and
related publications.   It therefore serves as an Aldabra coral
bibliography, and extends the information given in the more general
bibliographies by Stoddart (1971), and by Peters & Lionnet (1973).

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It is undoubtedly true that published coral records from Aldabra are based on less than half of the total amount of coral material which has actually been collected there. The present check list therefore provides only a partial picture of Aldabra's coral fauna. Large coral collections were evidently made by Voeltzkow and by Fryer (Sladen Expedition), but only a fraction of their material has ever been studied. Stoddart (1971) has given an account of these earlier expeditions. He points out, however, that until the visits by the *Calypso* Expedition (Cousteau, Cherbonnier) and by J.L.B. Smith, both in 1954, no specialist marine collections had been made at Aldabra. Cherbonnier collected corals and other groups, and Smith collected fishes. The Cousteau-Cherbonnier coral collection has recently been identified by Dr. Michel Pichon (James Cook University of North Queensland) and myself, and an account is currently in preparation.

The next most important period of coral collection is the most recent. This is represented by the series of phases of the Royal Society Expedition to Aldabra, and associated visits, reconnaissance, etc., which began in 1966. Only the corals from Phase VI have so far been identified. Drew (1977) recently published a few photographs of the ecological transects carried out by the Phase VI party, and I have included a few identifications that were possible from the photographs.

There remain the Phase I, II and V collections. The corals from the first two of these Phases were collected by Dr. John Taylor (British Museum (Natural History)), and together with the Phase VI corals constitute the most important of the Aldabra coral collections. Unfortunately, only the sight records for corals from Phases I and II have so far been published. For Phase V, Brander *et al.* (1971) mentioned a few names, but presumably a more extensive collection awaits published identifications. A number of identifications of both Fryer's and Taylor's material were incorporated in an account of coral zoogeography in the Indian Ocean (Rosen 1971b, see tables), but in that paper, Aldabra was considered together with neighbouring islands ("Aldabra-Glorioso group") and the information in the tables cannot therefore be quoted here. All but two possible generic records in that list however are covered in the present check list. The opportunity is also taken here to give the register numbers of specimens of Aldabra material but only where authors have previously published them.

Finally it may be noted that of all the coral material from Aldabra, only six genera (Döderlein, 1902, Matthai, 1914, 1928) have ever been fully described.

REMARKS ON THE CORAL FAUNA

Fifty five coral genera* have so far been described or listed.

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* subgenera are counted as separate genera in this discussion

Of these, 4 are non-scleractinians, and 4 are ahermatypic scleractinians one of which is only a sight record (*Paracyathus*). Of the remaining 47 (hermatypic) genera, one (*Stylocoeniella*) is only a sight record. In addition to the corals listed here, two further genera may be present at Aldabra: *Merulina* and *Plerogyra*, since they appear in the Aldabra-Glorioso group list (Rosen 1971b). On the other hand, two genera (*Physophyllia* and *Gyrosmilia*) in the present check list require verification by re-examination of the original specimens. The figure of 46 hermatypic coral genera seems therefore to be a reasonable interim working total.

This figure differs from the 50 given by Rosen (1971b, table 1, line b) for the Aldabra-Glorioso group. Three genera in that tabulation required confirmation, two of these being the genera discussed above and also listed here. The third however, *Anomastraea*, has now been re-examined and is in fact a *Coscinaraea* (see check list for details). *Plesioseris* in the earlier lists is now no longer regarded as a distinct subgenus of *Psammocora* (see below), and finally there are the two genera (*Merulina* and *Plerogyra*) known from elsewhere in the Aldabra-Glorioso group but not as yet from Aldabra itself. Four genera may therefore be subtracted from the Aldabra-Glorioso list in order to make it comparable with the present one, and this leaves 46 hermatypic genera, i.e., one fewer than here. This does not however signify the addition of a new generic record as the new name, *Gardineroseris* appears by reason of synonymy changes affecting *Agariciella* and *Leptoseris*.

It is less easy to be precise about numbers of coral species at Aldabra, even if the perennial problem of what constitutes a coral species is disregarded. There are 95 named species here, taking all "cf." forms as distinct. In addition, there are 8 genera for which there are only unnamed species records ("sp.", "spp.", etc.), or no mention of species at all. I have arbitrarily counted all these records as one species for each genus concerned, so bringing the total to 103 species. (Note that in the list which follows, unnamed species records have been treated as genus records. See next section). Of the 103 species reckoned in this way, 6 are non-scleractinians and a further 4 are ahermatypes, leaving a total of 93 hermatypes. Two of these require verification. Sight records include 1 ahermatype, 5 hermatypes.

By comparison with other Indian Ocean reef regions, the above figures suggest that few new scleractinian genera will be added by further work on Aldabra corals, but that many more species (or "species") may well be recorded. On the first point, Rosen (1971b) interpolated only a further 5 genera, 3 of them fungiids, for the Aldabra-Glorioso group. *Verrillofungia*, *Ctenactis*, *Halomitra*, *Alveopora* and *Oulophyllia*. For non-scleractinians, there is a good possibility of more hydrocoral genera and of species, because in various works by Boschma there are species known from nearby islands not as yet recorded from Aldabra.

Because of the Cousteau-Cherbonnier list currently in preparation, it is not useful to discuss zoogeographical aspects here, except perhaps to draw attention to "shrinkage" in the Indian Ocean distribution of *Anomastraea*, following its elimination from Aldabra (see Rosen 1971b, fig.8).

NOTES ON THE PRESENTATION OF THE CORAL RECORDS

The list gives all known scleractinian records, together with the usual coralline reef octocorals and hydrozoans. The corals are set out in Treatise order (Wells 1956) but with the octocorals and hydrocorals at the end.

Square brackets have been used for both species and generic records to indicate names now placed in synonymies and records which are otherwise incorrect for Aldabra. Their current names, where applicable are also given in the appropriate places in the list, and pairs of names affected in this way are cross referenced. For the most part the synonymies of more recent works, where they affect Aldabra records, have been accepted uncritically because the present list is primarily intended as a compilation. Generic names which have been used in the past, but which are now widely regarded as synonyms, are given in square brackets immediately beneath the currently valid names (e.g. *Platygyra* and [*Coeloria*]).

The status of each record can be assumed to be a formal taxonomic treatment (check list, description, etc.) unless additional information is given:

SR - sight record

TC - citation of taxon in a text account, e.g. in diagrams or non-taxonomic tables.

Plate and figure numbers have been given for species only where the coral illustrated is indicated in an author's caption as being from Aldabra.

Specimen numbers are quoted only if authors have published them. Abbreviation used: BM(NH) - British Museum (Natural History), Dept. of Zoology.

Depth data for species follow each author's record and consist only of the actual depths stated by individual authors. No interpolated depth ranges have been given. For generic depth ranges, all the depth records for each genus and its species are brought together, and again, no interpolations are made except in the topmost 5m. Here "surface" records have been taken to be 0m and extended down to the next recorded depth which falls within the range 0-5m. For depths given as "Bellamy MS", see the Introduction.

Genera and species. Records of unidentified species are listed
directly under the generic name, even when an author has distinguished
several such "sp." names by number, or given a "spp." indication.
There is no way of knowing whether more than one "sp." record within
a genus represents one or more species (see remarks on the species
totals in the previous section).

PUBLISHED CORAL RECORDS FOR ALDABRA

1. *Stylocoeniella* Yabe & Sugiyama, 1935   Recorded depth range:
                                                    surface
                    Price 1971, 150   SR TC surface

2. *Psammocora* Dana, 1846   Recorded depth range: 18m

        Psammocora haimeana Edwards & Haime, 1851
                    Voeltzkow 1902, 565

        Psammocora nierstraszi van der Horst, 1921
                    Rosen 1971a, 109   Bellamy MS: 18m

3. *Stylophora* Schweigger, 1819   Recorded depth range: 0-5m
                    Brander *et al.* 1971, 417, 423, 424 TC   less than 5m
                    Fryer 1911, 411   SR TC
                    Price 1971, 166   SR TC surface

        S. mordax (Dana, 1846)
                    Barnes *et al.* 1971, 101, 102 TC 1-2m
                    Brander *et al.* 1971, 423, 425 TC less than 5m
                    Rosen 1971a, 110

        S. pistillata (Esper, 1797)
                    Barnes *et al.* 1971, 103   TC   2m
                    Rosen 1971a, 110

4. *Seriatopora* Lamarck, 1816   Recorded depth range:
                                               surface, 12m, 27m, 33m
                    Barnes *et al.* 1971, 103   TC 12m
                    Fryer 1911, 411   SR TC
                    Rosen 1971a, 110   Bellamy MS: surface

        [*S. hystrix* Dana, 1846]
                    Barnes *et al.* 1971, 97, 103 TC 27, 33m
                                             (probably should be *S.* cf.
                                             hystrix as in Rosen 1971a).

S. cf. *hystrix* Dana, 1846
      Rosen 1971a, 110   Bellamy MS: surface
                       (see also *S.* *hystrix*, Barnes
                          et al.)

5. *Pocillopora* Lamarck, 1818   Recorded depth range: surface
                                to 18m, 21, 27, 33m
      Brander *et al.* 1971, 417, 423, 424 TC less than 5m
      Drew 1977, pl.1a (BRR)
      Fryer 1911, 411, 412 SR TC
      Price 1971, 150   SR TC surface

    P. damicornis (Linnaeus, 1758)
      Barnes *et al.* 1971, 103 TC 1m
      Rosen 1971a, 110

    P. danae Verrill, 1864
      Barnes *et al.* 1971, 103   TC 21, 27, 33m
      Rosen 1971a, 110   Bellamy MS: 20-27m

    P. cf. *danae* Verrill, 1864
      Price 1971, 166   SR TC surface

    P. eydouxi Edwards & Haime, 1860
      Barnes *et al.* 1971, 102   TC 3, 5, 8-10, 12, 15, 17m
      Brander *et al.* 1971, 423   TC less than 5m
      Rosen 1971a, 110   Bellamy MS: 5-18m

6. *Acropora* Oken, 1815   Recorded depth range:
                                surface to 33m

  [*Madrepora* auctt. (non Linnaeus, 1758)]
      Barnes *et al.* 1971, 93, 94, 102, 103 (including
                       spp. nos. 2, 3, 4) TC 1-3,
                       5, 7, 12, 17m
      Bellamy *et al.* 1969, 103   SR TC dead
      Drew 1977, pls 1a, 1b, 1c, 3a, 3b (BRR)
      Fryer 1911, 410, 411 (as *Madrepora*) SR TC
      Rosen 1971a, 110 (spp. "Nos. 1-4"),
                       Bellamy MS: surface to 15m

    A. cf. *cuneatus* [sic] (Dana, 1846)
      Price 1971, 166   SR TC surface

    A. digitifera (Dana, 1846)
      Price 1971, 150   SR TC surface

A. cf. *digitifera* (Dana, 1846)
        Price 1971, 166   SR TC   surface

A. cf. *diversa* (Brook, 1891) "No.1"
        Barnes *et al.* 1971, 103   TC 9m
        Rosen 1971a, 110   Bellamy MS: 2-8m

A. cf. *diversa* (Brook, 1891) "No.2"
        Barnes *et al.* 1971, 103   TC 2m
        Rosen 1971a, 110

A. glochiclados (Brook, 1893)
        Barnes *et al.* 1971, 101, 102, 107   TC 1-2m
        Rosen 1971a, 110

A. irregularis (Brook, 1892)
        Barnes *et al.* 1971, 102 TC 1m
        Price 1971, 166   SR TC surface
        Rosen 1971a, 110

A. monticulosa (Brueggemann, 1879)
        Barnes *et al.* 1971, 103 TC   13m
        Rosen 1971a, 110   Bellamy MS: surface

A. palifera (Lamarck, 1816)
        Barnes *et al.* 1971, 102   TC   1-3, 5-7m
      ?Drew 1977, pl.1c, 3b (BRR)
        Brander *et al.* 1971, 417, 423, 424 TC less than 5m
                   (sometimes as "*Acropora A*")
        Rosen 1971a, 110   Bellamy MS: 1-8m
        Voeltzkow 1902, 565 as *Madrepora palifera* Lamarck

A. spicifera (Dana, 1846)
        Barnes *et al.* 1971, 103   TC 1, 5-6, 20, 28m
        Rosen 1971a, 110   Bellamy MS: 1-33m

A. tubicinaria (Dana, 1846)
        Brander *et al.* 1971, 417, 423, 424, 425 TC less than 5m
                   (sometimes as "*Acropora B*")

A. variabilis (Klunzinger, 1879)
        Barnes *et al.* 1971, 103 TC   15, 28, 33m
        Rosen 1971a, 110   Bellamy MS: 13m

7. *Astreopora* Blainville, 1830
        Fryer 1911, 411   SR TC Recorded depth range:
                          3-7m

   Astreopora myriophthalma (Lamarck, 1816)
        Barnes *et al.* 1971, 101, 102 TC   2-3, 5-6m
        Rosen 1971a, 110   Bellamy MS: 3-7m

8. *Montipora* Quoy & Gaimard in Blainville, 1830 Recorded depth range:
                                                surface to 39m
                Barnes *et al.* 1971, 97, 103 (as "*Montipora* sp.2")
                                                TC 28, 35, 39, 43m
                Fryer 1911, 411   TC   SR
                Rosen 1971a, 110 (Spp "Nos. 1, 2"). Bellamy MS: 6-39m
                Taylor 1971b, 192   TC   SR   surface
                ?Drew 1977, pl.2a, 3e   (BRR)

    Montipora elschneri Vaughan, 1918
                Barnes *et al.* 1971, 103 TC   11m
                Rosen 1971a, 110   Bellamy MS: 8m

    [*Montipora erythraea* von Marenzeller, 1907]
                Barnes *et al.* 1971, 103 TC 10-12, 20, 22, 27m
                            (probably should be *M.* cf. *erythraea*
                            as in Rosen 1971a)

    Montipora cf. *erythraea* von Marenzeller, 1907
                Rosen 1971a, 110   Bellamy MS: 8-23m
                            (see also *M.* *erythraea*, Barnes *et al.*)

    Montipora cf. *punctata* Bernard, 1897
                Barnes *et al.* 1971, p 103   TC   12m
                Rosen 1971a, 110   Bellamy MS: 10m

    [*Montipora tuberculosa* (Lamarck, 1816)]
                Barnes *et al.* 1971, 102   TC 1-3, 5-8, 10, 12m
                            (probably should be *M.* cf. *tuberculosa*
                            as in Rosen 1971a)

    Montipora cf. *tuberculosa* (Lamarck, 1816)
                Rosen 1971a, 110   Bellamy MS: 1-8m
                            (See also *M. tuberculosa*, Barnes *et al.*)

    Montipora verrucosa Lamarck, 1816)
                Barnes *et al.* 1971, 102 TC   2-3, 5-6, 10, 17m
                Rosen 1971a, 110   Bellamy MS: 3-15m

9. *Pavona (Pavona)* Lamarck, 1802   Recorded depth range: 4-27m

    Pavona (P.) clivosa Verrill, 1869
                Rosen 1971a, 110   Bellamy MS: 5m

    Pavona (P.) explanulata (Lamarck, 1816)
                Barnes *et al.* 103   TC   12m
                Rosen 1971a, 110   Bellamy MS: 4m

Pavona (P.) frondifera Lamarck, 1816
       Rosen 1971a, 110   Bellamy MS: 7m

Pavona (P.) gardineri van der Horst, 1922
       Rosen 1971a, 110   Bellamy MS: 23m

Pavona (P.) cf. *minor* Brueggemann, 1879
       Rosen 1971a, 110   Bellamy MS: 6m

Pavona (P.) praetorta (Dana, 1846)
       Rosen 1971a, 110   Bellamy MS: 4m

Pavona (P.) varians Verrill, 1864
       Barnes *et al.* 1971, 103 TC 10-12, 18, 27m
       Rosen 1971a, 110   Bellamy MS: 8-27m

10. *Pavona (Pseudocolumnastraea)* Yabe & Sugiyama, 1933
                          Recorded depth range 18, 20m
       Barnes *et al.* 1971, 103 TC   20m
       Rosen 1971a, 111   Bellamy MS: 18m

11. *Leptoseris* Edwards & Haime, 1849   Recorded depth range 22, 25m

Leptoseris columna Yabe & Sugiyama, 1941
       Rosen 1971a, 111   Bellamy MS: 25m

[*Leptoseris? mycetoseroides* Wells, 1954]
       Barnes *et al.* 1971, 97, 103 (as *L? mycetoserioides*
                   [sic] TC 27,33m
       Rosen 1971a, 111
   (This species is a synonym of *Agariciella minikoiensis*
   Ma, 1937 according to Wells MS (1977)).

Leptoseris tubulifera Vaughan, 1907
       Rosen 1971a, 111   Bellamy MS: 22m

12. *Agariciella* Ma, 1937   Recorded depth range 27, 33m

Agariciella minikoiensis Ma, 1937
       Barnes *et al.* 1971, 97, 103 (as *Leptoseris?*
                   mycetoserioides [sic]
                   Wells, 1954). TC 27,33m
       Rosen 1971a, 111 (as *L? mycetoseroides*)
   (*L? mycetoseroides* Wells 1954 is a synonym of present
   species according to Wells MS (1977)).

[*Agariciella ponderosa* (Gardiner 1905)]
        Barnes *et al.* 1971, 103, 106   TC 28, 33m
        Rosen 1971a, 111
(This species is a synonym of *Gardineroseris planulata*
(Dana, 1846) according to Scheer & Pillai (1974) and
Wells MS (1977)).

13.   *Gardineroseris* Scheer & Pillai, 1974 Recorded depth range 28-33m

    Gardineroseris planulata (Dana, 1846)
        Barnes *et al.* 1971, 103, 106 (as *Agariciella*
               ponderosa Gardiner, 1905))
               TC 28, 33m Bellamy MS: 28-33m
        Rosen 1971a, 111 (as *A. ponderosa* (Gardiner))
    (*Agariciella ponderosa* (Gardiner, 1905) is a synonym of
    present species according to Scheer & Pillai (1974) and
    Wells MS (1977)).

14.   *Pachyseris* Edwards & Haime, 1849. Recorded depth range: 15, 18,
                                           20-22m

    Pachyseris laevicollis (Dana, 1846)
        Barnes *et al.* 1971, 97, 103, 106   TC 15, 18, 20-22m
        Rosen 1971a, 111

    Pachyseris rugosa (Lamarck, 1816)
        Rosen 1971a, 111

  [*Anomastraea* von Marenzeller, 1901]

    [*Anomastraea (A.) irregularis* von Marenzeller, 1901]
        Barnes *et al.* 1971. 103 TC (with "?") 10-11m
        Rosen 1971a, 111

    (Subsequent examination by BRR and MP of the particular
    specimen on which these records are based shows that
    it is actually *Coscinaraea columna* (Dana, 1846)).

15.   *Coscinaraea* Edwards & Haime, 1848   Recorded depth range: 9-28,
                                          33m
        Barnes *et al.* 1971, 103 (as *C.* sp. No.1) TC 11, 28m
                      Bellamy MS: 11-27m

        Rosen 1971a, 111 (as *C* spp. Nos. 1, 2).
                      Bellamy MS: 18m

Coscinaraea columna (Dana, 1846)
        This MS - after re-determination of the specimen on
        which previous records of *Anomastraea (A.)*
        irregularis von Marenzeller, 1901 were based (see
        above). TC 10-11m   Bellamy MS: 9m

Coscinaraea monile (Forskål, 1775)
        Barnes *et al.* 1971, 103 TC 11, 28, 33m
        Rosen 1971a, 111

16. *Cycloseris* Edwards & Haime, 1849   Recorded depth range: 7, 10-11m

Cycloseris cyclolites (Lamarck, 1816)
        Barnes *et al.* 1971, 103 TC 10-11m
        Rosen 1971a, 111   Bellamy MS: 7m

Cycloseris distorta (Michelin, 1843)
        Döderlein 1902, 44, 74, pl.3, figs. dd, ee, ff,
          pl.5, figs. 3, 3a. (as *Fungia distorta* f. *Cycloseris*).

        Voeltzkow 1902, 565 (as *Fungia distorta*).

Fungia Lamarck, 1801   Recorded depth range: 3-12,
        Drew 1977, 3   15, 17, 19-20m

[*Fungia distorta* Michelin, 1843]
        Voeltzkow 1902, (see *Cycloseris distorta*, above)

[*Fungia distorta* Michelin, 1843 f. *Cycloseris*]
        Döderlein 1902 (see *Cycloseris distorta*, above)

[*Fungia fungites* (Linnaeus, 1758) var. *confertifolia* Dana, 1846
        Döderlein 1902, 44, 155, pl.23, figs 2, 2a
        Voeltzkow 1902, 565
        (see *Fungia (F.) fungites*, below)

[*Fungia scutaria* Lamarck, 1801 var. *placunaria* Klunzinger, 1879]
        Döderlein 1902, 44, 93, 96 (see under *Fungia*
                        (Pleuractis), below)

[*Fungia scutaria* Lamarck, 1801 var *tenuidens* Quelch, 1886]
        Voeltzkow, 1902, 565 (see under *Fungia (Pleuractis)*
                       below)

17. *Fungia (Danafungia)* Wells, 1966   Recorded depth range: 19-20m

        Rosen 1971a, 111   Bellamy MS: 19-20m

18. *Fungia (Fungia)* Lamarck, 1801   Recorded depth range: no
                                                    information
        Doderlein 1902, 44, 155, pl.23, figs 2, 2a (as *F.*
                    fungites var. *confertifolia*).

        Voeltzkow 1902, 565 (as *F. fungites* var.
                              confertifolia)

19. *Fungia (Pleuractis)* Verrill, 1864   Recorded depth range: 3-12,
                                            15, 17m

    Fungia (Pleuractis) paumotensis Stutchbury, 1833
        Barnes *et al.* 1971, 102 TC 3, 5, 9, 12, 15m
        Rosen 1971a, 111   Bellamy MS: 3-12m

    Fungia (Pleuractis) scutaria Lamarck, 1801
        Barnes *et al.* 1971, 102 TC 3, 5, 10, 17m
        Döderlein 1902, 44, 93, 96 (as *F. scutaria* var.
                      placunaria)
        Rosen 1971a, 111   Bellamy MS: 6-10m
        Voeltzkow 1902, 565 (as *F. scutaria* var.*tenuidens*)

20. *Herpolitha* Eschscholtz, 1826   Recorded depth range: 20-23,
                                              27m

    Herpolitha limax (Esper, 1797)
        Barnes *et al.* 1971, 103, 106 TC 21, 27m
        Rosen 1971a, 111   Bellamy MS: 20-23m

21. *Podabacia* Edwards & Haime, 1849   Recorded depth range: 18, 22,
                                              27m
        Barnes *et al.* 1971, 97, 103, 106 TC 22, 27m
        Rosen 1971a, 111   Bellamy MS: 18m

22. *Goniopora* Blainville, 1830   Recorded depth range: 1m

    Goniopora stokesi Edwards & Haime, 1860
        Rosen & Taylor, 1969 TC   1m

    Porites Link, 1807   Recorded depth range: surface
                                         to 22m
        Brander *et al.* 1971, 417, 424 TC less than 5m
        Fryer 1911, 410, 411 SR   TC
        Ma 1958, 10   TC
        Ma 1959, 33   TC
        Price 1971, 166   SR   TC   surface
        Taylor 1971b, 181, 186, 188, 190-2, SR TC surface

23. *Porites (Porites)* Link, 1807   Recorded depth range: surface
                                                                 to 22m

        Porites (P.) andrewsi Vaughan, 1918
                Barnes *et al.* 1971, 101, 102 TC 2, 5-6, 8m
                Rosen 1971a, 111   Bellamy MS: 3-8m

        Porites (P.) lichen Dana, 1846
                Barnes *et al.* 1971, 97, 103, 106 TC 20, 22m
                Rosen 1971a, 111   Bellamy MS: 18m

        Porites (P.) lutea Edwards & Haime, 1851
        Porites lutea Edwards & Haime, 1851
                Barnes *et al.* 1971, 102   TC 2-3, 5-7m
                Price 1971, 166, 169   SR TC surface
                Rosen 1971a, 111   Bellamy MS: 2-7m
                Taylor 1971b, 183   SR TC surface
                Voeltzkow 1902, 565

        Porites (P.) nigrescens Dana, 1846
        Porites nigrescens Dana, 1846
                Barnes *et al.* 1971, 102 TC 5, 8-9, 11-12, 15, 17-18m
                Brander *et al.* 1971, 423 TC less than 5m
                Rosen 1971a, 111   Bellamy MS: 2-22m
                Taylor 1971b, 192   SR TC surface

24. *Porites (Synaraea)* Verrill, 1864   Recorded depth range: 1m

        Porites (Synaraea) iwayamaensis Eguchi, 1938
                Barnes *et al.* 1971, 103   TC 1m
                Rosen 1971a, 111

25. *Plesiastrea* Edwards & Haime, 1848   Recorded depth range: 27-28,
                                                                 33m
                Barnes *et al.* 1971, 103, 106 TC 28, 33m
                Rosen 1971a, 111   Bellamy MS: 27m

        Plesiastrea versipora (Lamarck, 1816)
                Rosen 1971a, 112   Bellamy MS: 27m

26. *Favia* Oken, 1815   Recorded depth range: surface
                                                                 to 33m
                Barnes *et al.* 1971, 103 TC 7m
                Fryer 1911, 411   SR TC
                Price 1971, 150, 166   SR TC surface
                Rosen 1971a, 112
                Taylor 1971b, 183, 186,   SR TC surface

[*Favia* acropora (Linnaeus, 1767)]
          Matthai 1914, 102 (1 specimen)
(Matthai's *F.* acropora is a synonym of *F. stelligera* (Dana,
1846); see Vaughan 1918, 101).

[*Favia bertholleti* Valenciennes MS]
          Ma 1958, 12   TC
          Ma 1959, 42   BM(NH) Reg. Nos. 1927.5.12.6,
                                   and 1927.5.12.49 [Matthai's
                                   material] TC
          Matthai 1914, 95 pl.24, fig.1   (2 specimens, above)

(Matthai's (and hence Ma's) *F. bertholleti* is a synonym *F.
favus* (Forskål, 1775); see Rosen (1968, 343)).

Favia favus (Forskål, 1775)
          Rosen 1968, 330 (*F. bertholleti* of Matthai (1914)
          BM(NH) Reg. Nos. 1927.5.12.6, and 1927.5.12.49)

[*Favia halicora* (Ehrenberg, 1834)]
          Matthai 1914, 106 (2 specimens)

(Matthai's *F. halicora* is a synonym of *Favites abdita* (Ellis
& Solander, 1786); see Wijsman-Best (1972, 33)).

Favia pallida (Dana, 1846)
          Barnes *et al.* 1971, 102 TC 2,5-6,9,11-12,15,17-18,
                                          20-22,28,33m
          Rosen 1971a, 112   Bellamy MS: 2-33m

Favia stelligera (Dana, 1846)
          Barnes *et al.* 1971, 103 TC 9m
          Matthai 1914, 102 (as *F.* acropora) (1 specimen)
          Rosen 1971a, 112

[*Favia vasta* (Klunzinger 1879)]
          Matthai 1914, 108, pl.27 fig.6   (1 specimen)

(Matthai's *F. vasta* is a synonym of *Favites virens* (Dana, 1846);
see Vaughan (1918, 111); but see also Chevalier (1971, 229)
who regards Matthai's *F. vasta* as *Favites vasta*).

27. *Favites* Link, 1807   Recorded depth range: surface
                                                              to 21m
     [*Prionastrea* Edwards & Haime 1857]
          Barnes *et al.* 1971, 103 (as "*F.* sp." following a
               Favites species, but should probably be *Favia* sp.
               as in Rosen 1971a, 112) TC 6m.
          Fryer 1911, 411 (as *Prionastrea*)   SR   TC

     Favites abdita (Ellis & Solander, 1786)
          Barnes *et al.* 1971, 102 TC 2-3, 5-8, 10-11, 17m

Matthai 1914, 106 (as *Favia halicora* (Ehrenberg, 1834) (2 specimens)
Rosen 1971a, 112   Bellamy MS: 2-33m

Favites cf. *pentagona* (Esper, 1794)
Barnes *et al.* 1971, 103   TC   3, 7, 21m
Rosen 1971a, 112   Bellamy MS: 3-21m

Favites virens (Dana, 1846)
[*Favites vasta* (Klunzinger, 1879)]
Matthai 1914, 108, pl.27, fig.6 (as *Favia vasta* (Klunzinger, 1879. See under *Favia vasta*, above) (1 specimen).

28.   *Goniastrea* Edwards & Haime, 1848 Recorded depth range: surface, 9-33m
Taylor 1971b, 183, 188, 190   SR   TC surface

[*Goniastrea incrustans* Duncan, 1889]
Barnes *et al.* 1971, 97, 103   TC   27, 33m
Rosen 1971a, 112   Bellamy MS: 23-33m
(The specimen on which these records are based was mistakenly identified. It should be *Goniastrea palauensis* (Yabe & Sugiyama, 1936)).

Goniastrea palauensis (Yabe & Sugiyama, 1936)
Barnes *et al.* 1971, 97, 103 (as *G. incrustans*) TC 27, 33m
Rosen 1971a, 112 (as *G. incrustans*) Bellamy MS: 23-33m

Goniastrea pectinata (Ehrenberg, 1834)
Barnes *et al.* 1971, 102 TC 9-11, 15, 18, 20-22, 27, 33m
Price 1971, 166   SR   TC   surface
Rosen 1971a, 112   Bellamy MS: 9-33m

Goniastrea retiformis (Lamarck, 1816)
Barnes *et al.* 1971, 103   TC   11m
Ma 1958, 14
Ma 1959, 48 B.M.(N.H.) Reg. No. 1927.5.4.186
[Matthai's material]   TC
Matthai 1914, 118 (2 specimens)
Rosen 1971a, 112   Bellamy MS: 11-19m

29.   *Platygyra* Ehrenberg, 1834 Recorded depth range: surface to 33m
[*Coeloria*, Edwards & Haime, 1848]
Fryer 1911, 411 (as *Coeloria*). SR   TC
Price 1971, 166   SR   TC   surface

Platygyra astreiformis (Edwards & Haime, 1849)
Ma 1958, 15   TC
Ma 1959, 53 BM(NH) Reg. No. 1928.4.18.599 "Eldabra"
TC

Platygyra daedalea (Ellis & Solander, 1786)
          Ma 1958, 15   TC
          Matthai 1928, 24 (as *Coeloria daedalea*) (2 specimens)

Platygyra lamellina Ehrenberg, 1834
          Barnes *et al*. 1971, 102 TC 2-3,5-7,9-10,12,15,17-18,
                                           20-21,33m
          Rosen 1971a, 112   Bellamy MS: 2-33m

[*Platygyra phrygia* (Ellis & Solander, 1786)]
          Matthai 1928, 112   2 specimens

(Matthai's "*Platygyra*" is actually *Leptoria*; see Crossland
(1952, 150)).

30. *Leptoria* Edwards & Haime, 1848   Recorded depth range: surface
     [*Platygyra*, Matthai 1928, only]   to 12m
          Brander *et al*. 1971, 417, 423-5 TC less than 5m
          Price 1971, 166   SR TC surface

Leptoria phrygia (Ellis & Solander, 1786)
          Barnes *et al*. 1971, 102 TC 1-2, 5, 9, 12m
          Matthai 1928, 112 (as *Platygyra phrygia* (Ellis &
                   Solander, 1786)) (2 specimens)
          Rosen 1971a, 112   Bellamy MS: 2-12m

31. *Hydnophora* Fischer, 1807   Recorded depth range: surface
                                                  to 3m, 15-33m
          Fryer 1911, 411   SR TC

[*Hydnophora contignatio* (Forskål, 1775)]
          Matthai 1928, 155, pl.46, fig.2 (1 specimen, BM(NH)
                   Reg. No. 1928,3.1.56).
     (*H. contignatio* is a synonym of *H. exesa* (Pallas, 1766); see
     Wijsman-Best, 1972, 51)

Hydnophora exesa (Pallas, 1766)
          Barnes *et al*. 1971, 103 TC ?2, 15, 27-28, 33 (This
                   species appears twice in the table on p.103,
                   the second time at 2m. Is this second
                   record meant to be *H. microconos*?)

          Matthai 1928, 140 (2 specimens)
          Matthai 1928, 155, pl.46, fig.2, (as *H. contignatio*
                   (1 specimen, BM(NH) Reg. No. 1928.3.1.56)
          Rosen 1971a, 112   Bellamy MS: 15-33m

Hydnophora microconos (Lamarck, 1816)
          ?Barnes *et al*. 1971, 103 (see under *H. exesa*, above)
          Price 1971, 166   SR TC surface   TC 2m
          Rosen 1971a, 112 Bellamy MS: 2-3m

32. *Diploastrea* Matthai, 1914　　　　Recorded depth range: no
　　　　　　　　　　　　　　　　　　　　　　　　information

　　　　Diploastrea heliopora (Lamarck, 1816)
　　　　　　　Rosen 1971a, 112

33. *Leptastrea* Edwards & Haime, 1848　　Recorded depth range: 2-22m

　　　　Leptastrea immersa Klunzinger, 1879
　　　　　　　Barnes *et al.* 1971, 103　TC　2m
　　　　　　　Rosen 1971a, 112　　　　Bellamy MS: 2-11m

　　　　Leptastrea purpurea (Dana, 1846)
　　　　　　　Barnes *et al.* 1971, 102　TC　9, 11-12, 20, 22m
　　　　　　　Rosen 1971a, 112　　　　Bellamy MS: 9-22m

34. *Cyphastrea* Edwards & Haime, 1848　　Recorded depth range: surface
　　　　　　　　　　　　　　　　　　　　　　　　　to 33m
　　　　　　　Taylor 1971b, 183, 186, 192　SR　TC　surface

　　　　Cyphastrea chalcidicum (Forskål, 1775)
　　　　　　　Barnes *et al.* 1971, 103　TC　3, 7, 21, 28m
　　　　　　　Rosen 1971a, 112　　　　Bellamy MS: 3-33m

35. *Echinopora* Lamarck, 1816　　　　　Recorded depth range: 2-39m

　　　　Echinopora gemmacea (Lamarck, 1801)
　　　　　　　Barnes *et al.* 1971, 102　TC　2, 5-6, 9, 11, 15, 18,
　　　　　　　　　　　　　　　　　20-22, 27, 33m
　　　　　　　Rosen 1971a, 112　　　　Bellamy MS: 2-39m

36. *Oulangia* Edwards & Haime, 1848　　Recorded depth range: 18m
　　　　　　　Rosen 1971a, 112　　　Bellamy MS: 18m

　　　[*Madrepora* Linnaeus, 1758]
　　　　　　　Fryer 1911, 410, 411 (this record is almost
　　　　　　　　　　　　certainly *Acropora*).　SR　TC

37. *Galaxea* Oken, 1815　　　　　　　Recorded depth range: surface
　　　　　　　　　　　　　　　　　　　　　　　to 13m, 15m
　　　　　　　Fryer 1911, 411　　　SR　TC

　　　　Galaxea fascicularis (Linnaeus, 1767).　Recorded depth range:
　　　　　　　　　　　　　　　　　　surface to 13m, 15m
　　　　　　　Barnes *et al.* 1971, 102　TC　2-3,5,7,10,15m
　　　　　　　Matthai 1914, 59 (6 specimens)
　　　　　　　Rosen 1971a, 112　　　Bellamy MS: 2-13m

38. *Blastomussa* Wells 1968   Recorded depth range: 24m

         Blastomussa merleti Wells, 1961
                    Rosen 1971a, 112   Bellamy MS: 24m

39. *Acanthastrea* Edwards & Haime, 1848   Recorded depth range: surface,
                                               20-23, 27, 33m
                    Fryer 1911, 411   SR   TC
                    Price 1971, 166   SR   TC   surface

         Acanthastrea echinata (Dana, 1846)
                    Barnes *et al.* 1971, 103   TC   21-22, 27, 33
                    Rosen 1971a, 112   Bellamy MS: 20-23m

40. *Lobophyllia* Blainville, 1830   Recorded depth range: 5-23,
                                               27-28,35,39,43m

         Lobophyllia corymbosa (Forskål, 1775)
                    Barnes *et al.* 1971, 102, TC 5-6,10,15,27m
                    Rosen 1971a, 113   Bellamy MS: 5-23m

         Lobophyllia hemprichii (Ehrenberg, 1834)
                    Barnes *et al.* 1971, 103   TC   21, 27-28,35,39,43m
                    Rosen 1971a, 113

41. *Symphyllia* Edwards & Haime, 1848   Recorded depth range: 20-21,
                                                                        27m

         Symphyllia nobilis (Dana, 1846)
                    Rosen 1971a, 113   Bellamy MS: 20m

         Symphyllia valenciennesii Edwards & Haime, 1849
                    Barnes *et al.* 1971, 103, 106   TC   21,27m
                    Rosen 1971a, 113   Bellamy MS: 20m

42. *Echinophyllia* Klunzinger, 1879   Recorded depth range: 18-33m

         Echinophyllia aspera (Ellis & Solander, 1786)
                    Barnes *et al.* 1971, 103, 106 TC   21, 27m
                    Rosen 1971a, 113   Bellamy MS: 18-33m

43. *Mycedium* Oken, 1815   Recorded depth range: 18-33m

         Mycedium tenuicostatum Verrill, 1901
                    Barnes *et al.* 1971, 103 TC   18,22,28m
                    Rosen 1971a, 113   Bellamy MS: 18-33m

Mycedium tubifex (Dana, 1846)
    Barnes *et al.* 1971, 103 TC 18,21,28,33m
    Rosen 1971a, 113 Bellamy MS: 18-27m

44. ?*Physophyllia* Duncan, 1884   Recorded depth range: 26m

  ?*Physophyllia ayleni* Wells, 1934
    Rosen 1971a, 113 Bellamy MS: 26m

45. *Pectinia* Oken, 1815   Recorded depth range: 12,18,
                   20,26m
    Barnes *et al.* 1971, 103 TC 27m
    Rosen 1971a, 113

  Pectinia lactuca (Pallas, 1766)
    Barnes *et al.* 1971, 103 TC 12, 18m
    Rosen 1971a, 113 Bellamy MS: 20m

46. *Paracyathus* Edwards & Haime, 1848 Recorded depth range: surface
    Taylor 1971b, 192 SR TC surface

47. *Physogyra* Quelch, 1884   Recorded depth range: 10-28,33m
    Barnes *et al.* 1971, 103 TC 10, 12, 18,20-22,28,33m
    Rosen 1971a, 113 Bellamy MS: 10-28m

48. ?*Gyrosmilia* Edwards & Haime, 1851 Recorded depth range: 15,17-
                   33m

  ?*Gyrosmilia interrupta* (Ehrenberg, 1834)
    Barnes *et al.* 1971, 103 TC 17-18, 27m
    Rosen 1971a, 113 Bellamy MS: 15, 18-33m

49. *Dendrophyllia* Blainville 1830 Recorded depth range: surface
                   to 5m
    Barnes *et al.* 1971, 93 106 TC
    Bellamy *et al.* 1969, 103 SR TC
    Brander *et al.* 1971, 400 TC less than 5m
    Fryer 1911, 411   SR TC
    Taylor 1971b, 192, 204 SR TC surface

  (Some of these records are probably *Tubastrea*)

  Dendrophyllia cf. *florulenta* van der Horst 1922
    Rosen 1971a, 113 Bellamy MS: surface

[*Dendrophyllia micrantha* (Ehrenberg, 1834)]
Barnes *et al.* 1971, 94,97,103   TC   39, 41-44m
Rosen 1971a, 113   Bellamy MS: surface to 44m +

(This species is now regarded as a *Tubastraea*)

50.   *Tubastraea* Lesson, 1834   Recorded depth range: surface
      [*Dendrophyllia*, in part]   to 44m +
                Taylor 1971b, 190, 192   SR TC surface
                see also *Dendrophyllia*, above

      Tubastraea micrantha (Ehrenberg, 1834)
                Barnes *et al.* 1971, 94, 97, 103 (as *Dendrophyllia*
                                  micrantha) TC   39, 41-44m

                Rosen 1971a, 113 (as *D. micrantha*), Bellamy MS:
                                  surface to 44m +

51.   *Turbinaria* Oken, 1815   Recorded depth range: 20-33m
                Barnes *et al.* 1971, 103   TC   21, 27, 33m
                Rosen 1971a, 113   Bellamy MS: 20-33m

52.   *Tubipora* Linnaeus, 1758   Recorded depth range: surface
                                                                 to 1m
                Fryer 1911, 410 SR TC

      Tubipora musica Linnaeus, 1758
                Barnes *et al.* 1971, 103   TC   1m
                Rosen 1971a, 113   Bellamy MS: surface

53.   *Heliopora* Blainville, 1830   Recorded depth range: surface
                Fryer 1911, 410   SR   TC
                Stoddart 1967, 17, 18 SR TC (as sediment component)
                Stoddart *et al.* 1971, 50 SR TC (as sediment
                                                   component)

      Heliopora coerulea (Pallas, 1766)
                Rosen 1971a,   113   Bellamy MS: surface
                Voeltzkow 1902, 565

54.   *Millepora* Linnaeus, 1758   Recorded depth range: surface
                                                                 to 12m
                Brander *et al.* 1971, 417, 423, 424 TC less than 5m
                Drew 1977, pl.1a, 3a (BRR)
                Fryer 1911, 410-412 SR TC
                Price 1971, 166, 169 SR TC surface
                Taylor 1971b, 192   SR TC surface

[*Millepora* cf. *clavaria* Ehrenberg, 1834]
        Voeltzkow 1902, 565

(*M. clavaria* is a synonym of *M. exaesa* Forskål, 1775; see
Boschma (1948, 28)).

Millepora exaesa Forskål, 1775
        Barnes *et al.* 1971, 101, 102, 107   TC 3,5-7,9m
        Rosen 1971a, 114   Bellamy MS: 2-9m
        ?Voeltzkow 1902, 565 (as *M.* cf. *clavaria*).

Millepora platyphylla Hemprich & Ehrenberg, 1834
        Barnes *et al.* 1971, 102 TC 1-2,5-6,12m
        Brander *et al.* 1971, 423,425 TC less than 5m
        Rosen 1971a, 114   Bellamy MS: 1-11m
        Taylor 1971b, 183   SR TC surface

55. *Distichopora* Lamarck, 1816   Recorded depth range: surface
                                                   to 2m

Distichopora fisheri Broch, 1942
        Barnes *et al.* 1971, 103   TC 2m
        Rosen 1971a, 114   (forma *alpha* Wells, 1954)
                        Bellamy MS: surface

Distichopora violacea (Pallas, 1766)
        Rosen 1971a, 114   Bellamy MS: surface

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genus or species name, or provide photographs from which such names
may be inferred. These works form the basis for the present check list.
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Table 1

Collections and studies of corals of Aldabra

Abbreviations: BM(NH)DZ - British Museum (Natural History), Department of Zoology.

SMEM - Station Marine d'Endoume, Marseille

UDDB - University of Durham, Department of Botany

SR - Sight records

The number of identifications is based on those actually listed by individual works, no allowance being made for validity, synonyms, etc. 'Identifications' here includes all levels of taxonomic study.

COLLECTION/EXPEDITION	Voeltzkow
DATE	1895
COLLECTION CURRENTLY DEPOSITED AT:-	?
COMPLETENESS OF STUDY OF MATERIAL	Identifications presumed in-complete
GENERA IDENTIFIED	5
SPECIES IDENTIFIED	7

AUTHORS	STATUS OF IDENTIFICATIONS	GENERA IDENTIFIED	SPECIES IDENTIFIED	
Barnes et al. 1971	Ecological account using names in Rosen 1971a	43	79	
Bellamy et al. 1969	General account. Sight records in text	2	–	
Brander et al. 1971	Ecological account, records in text	7	7	
Döderlein 1902	Monograph on the genus *Fungia*	1	3	X
Drew 1977	Discussion of transect method. Corals named from plates by BRR in present list	5	1	
Fryer 1911	General account. Sight records in text	17	–	
Ma 1958	Coral growth account based on many regions. Lists of specimens for numerous species	4	5	
Ma 1959		4	4	
Matthai 1914	Monograph of faviid species	3	4	
Matthai 1928	Monograph of meandrine coral species	2	5	
Pichon & Rosen (in prep.)	Check list with remarks			
Price 1971	Ecological account. Sight records in text	12	17	
Rosen 1968	Taxonomic revision of some faviid genera	1	1	
Rosen 1971a	Check list	50	101	
(Rosen 1971b, Table 1, line e)	Generic list for Aldabra-Glorioso group	(53)	–	(X)
Rosen & Taylor 1969	Reproduction in *Goniopora*, at Aldabra	1	1	
Stoddart & Wright 1967	General account. Sight record in text	1	–	
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Voeltzkow 1902	Check list, partly after Döderlein 1902	5	7	X

Fryer-Sladen	Cherbonnier - Cousteau	ROYAL SOCIETY EXPEDITION TO ALDABRA				
		Reconnaissance	Phase I	Phase II	Phase V	Phase IV
1908-9	1954	1966	1967	1967	1968	1968-9
BM(NH)DZ	SMEM	?	BM(NH)DZ	BM(NH)DZ	?	BM(NH)DZ UDDB
Identifications of only a small part	Identifications in hand	Identifications not yet made on collected material	Identifications not yet made on collected material except Phase V in part			Identifications complete
12 SR + 8		1 SR	20 SR + 1		7	50
14		-	19 SR + 1		7	101
						X
						X
					X	
						X
X						
X						
X						
X						
X						
	X					
			X			
X						
						X
	(X)		(X)			(X)
			X			
		X				
			X		X	
			X		X	

RÉCIFS CORALLIENS, CONSTRUCTIONS ALGUAIRES,
ET ARRIÉCIFES À LA GUADELOUPE,
MARIE GALANTE ET LA DÉSIRADE

par R. Battistini et M. Petit

LISTE DES FIGURES

RÉCIFS CORALLIENS, CONSTRUCTIONS ALGUAIRES, ET ARRIÉCIFES À LA GUADELOUPE, MARIE GALANTE ET LA DESIRADE

par R. Battistini et M. Petit

Certaines régions des Caraïbes possèdent une vie corallienne florissante : ainsi sur le Banc d'Argent en face de Porto-Rico, dans les Iles Vierges, ou au large des côtes du Yucatan.   Si nous considérons les "petites Antilles", et plus spécialement les îles françaises, on constate le peu d'intérêt que ces formations ont suscité jusqu'à présent.

Le but de cet article[1] est de faire un court inventaire des récifs de la Guadeloupe et de ses deux dépendances, Marie Galante et la Désirade, et surtout de dégager les caractères très originaux des formes que l'on y observe.   La morphologie des "récifs" guadeloupéens résulte en effet de la combinaison, à des degrés variables, de trois types de formations tout à fait différentes :

1.   les coraux proprement dits
2.   les constructions alguaires
3.   les arrécifes.

L'exposition joue un rôle déterminant dans la répartition des récifs, et dans leur morphologie.   Dans la région considérée, les vents dominants viennent des secteurs NE, E et SE (voir la figure n° 2), les côtes W et NW étant au contraire en position d'abri.

Ainsi que cela est habituel, c'est dans les secteurs les plus exposés que les constructions alguaires prennent leur développement maximum : ainsi sur la côte orientale de la Grande Terre de la Guadeloupe, sur la côte orientale et méridionale de Marie Galante, et sur la côte sud-est de la Désirade.   On s'attendrait à trouver dans ces secteurs exposés de larges platures coralliennes émergeant légèrement à basses mers, comme c'est le cas par exemple dans l'Océan

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Indien : or il n'en est rien.   Seuls subaffleurent d'étroits segments
de constructions alguaires, larges de quelques mètres, sur lesquels
brisent les grands déferlements.

Paradoxalement, c'est en situation relativement abritée, dans le
Petit et le Grand Culs de Sac Marin, que l'on trouve les éléments de
platures coralliennes de beaucoup les plus étendus, en face de Goyave
et de Petit Bourg, et dans la barrière qui ferme le Grand Cul de Sac.

Sur la côte orientale de la Grande Terre de la Guadeloupe
(secteur de Moule en particulier), coraux et algues calcaires ne font,
sans doute, qu'habiller un système d'arrécifes, constitué par 4 à 5
alignements d'anciens grès de plages décollés du rivage, et donnant
autant de lignes de déferlements.   On trouve donc ici une morphologie
comparable à celle décrite par Ottmann (1960 et 1963) et Laborel (1965)
sur la côte nord-est du Brésil.

Les côtes occidentales et méridionales de Basse-Terre ne possèdent
pas de récifs coralliens, sans qu'on en sache la raison, à l'exception
d'un récif frangeant embryonnaire à l'Ilet Pigeon.

LA GUADELOUPE

La côte orientale de la Grande Terre est ourlée de bancs discontinus,
étroits, donnant autant de brisants.   A l'Anse Maurice, au Moule, à
l'Anse à l'Eau ainsi qu'à la Gourde, apparaît l'importance de telles
constructions linéaires et étroites, de nature essentiellement alguaire.
Les algues calcaires qui les construisent sont d'une étonnant vitalité
et d'une grande diversité.   Ces éléments massifs, longs de plusieurs
mètres, sont séparés entre eux par des sillons perpendiculaires à la
côte : il ne s'agit donc en aucun cas de véritables barrières continues.
Ces constructions alguaires incluent de nombreux pâtés coralliens morts
ou vivants.   Les principales espèces répertoriées (*Porites astreoides*,
Favia, Diploria, Montastrea et *Siderastrea*) sont essentiellement
massives ; rares sont les formes tubulaires, branchues ou palmées du
type *Acropora*[1].

Le long du rivage, il existe à peu près partout une ou deux lignes
de grès de plage affleurant à basse mer, présentant la disposition
classique en micro-cuestas hautes de quelques dizaines de centimètres à
front tourné vers la plage.   Certains de ces bancs de grès décollent
complètement du rivage, comme à l'Anse de la Gourde, ou à l'Est de Moule,
et se perdent vers le large (fig. 3).

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[1] Nous remercions très vivement Monsieur J.P. Chassaing, de l'INRA de
Guadeloupe, qui a bien voulu nous initier à la détermination des
principales espèces coralliennes et qui nous a accompagné lors de
certaines plongées.

Nous pensons que plus au large, les lignes de brisants successives correspondent à de telles lignes de grès de plage encore davantage décollées, qui ont servi de support aux constructions coralliennes et alguaires.   C'est dans le secteur compris entre Moule et la Pointe de la Couronne qu'apparaît le mieux la réalité de ces "arrécifs" (photographies aériennes verticales, mission 006-100 n°s 293 à 296). L'aspect rigide, rectiligne, des différentes lignes de brisants décalées les unes par rapport aux autres, ne peut avoir d'autre origine.

<u>Le littoral méridional de la Grande Terre</u> est plus simple, sans succession rythmique de bancs à l'entrée des anses.   Si les constructions demeurent étroites et parfois plus localisées, leur nature change radicalement.   Nous sommes ici en présence de récifs frangeants classiques quasiment morts.   Le platier, de quelques dizaines de mètres de largeur maximum, est constitué presque exclusivement de grandes feuilles ou de fragments d'*Acropora palmata* et de débris de *Porites porites* Pallas sur lesquels végètent quelques touffes de corail vivant parmi lesquels dominent toujours l'*Acropora palmata* mais aussi des formes branchues, fragiles, telles que l'*Acropora prolifera*, les *Porites porites* Pallas, et les *Millepora*.

Comme sur la côte Est, la faible profondeur exclut l'existence de tombant et permet un ennoiement rapide de la construction sous ses propres débris sableux.

Un chenal d'embarcations, d'une centaine de mètres de largeur, peut passer à un véritable lagon, comme au droit de Saint François ou de Sainte Anne, couvert par une étroite prairie à Cymodocées.   Enfin la plage révèle de rares grésifications, généralement tendres et de faible développement comme aux Raisins Clairs, à l'entrée de Saint François, ou à l'anse du Mancenillier plus à l'Est.

<u>La côte Ouest de la Grande Terre</u> rappelle, par bien des aspects, le littoral méridional : les récifs frangeants s'étendent de l'Anse Laborde au Nord jusqu'à Port Louis au Sud.   La proportion de corail mort est toujours très importante et les espèces peu variées avec prédominance d'*Acropora palmata* et *Porites porites*.   Actuellement, la vie corallienne serait plus active que sur le littoral méridional ; l'*Acropora palmata* domine, ainsi que la forêt naine de *Millepora complanata* et les énormes *Diploria strigosa* et *D.clivosa*.   Notons la déformation des *Acropora palmata,* fortement dissymétriques, le plateau se développant essentiellement vers l'intérieur, perdant leur belle platitude pour prendre l'aspect de longs tuyaux d'orgues.   Ces faits sont certainement à mettre au compte des conditions nautiques et de l'action des houles d'Ouest.

Les grès de plage prennent une réelle importance de la pointe d'Antigues à l'Anse Bertrand où les lignes de brisants se succèdent. L'Anse Bertrand, largement ouverte, abrite trois alignements successifs, phénomène unique sur l'ensemble de ce littoral occidental et méridional.

Ainsi la Grande Terre se caractérise-t-elle par une ceinture étroite, discontinue, de faible épaisseur, et sans véritable tombant, de platures coralliennes frangeantes au Sud et à l'Ouest passant à des constructions alguaires sans doute ancrées sur des arrécifes à l'Est.

Ces récifs plus ou moins vivants se localisent systématiquement au large d'anciennes constructions coralliennes soulevées à +4 ou +5 m , riches en *Diploria,* et probablement d'âge pré-flandrien (datations en cours à Gif-sur-Yvette) : il existe donc une certaine constance dans la répartition géographique de la vie corallienne depuis un Quaternaire encore non précisé.

Les "Culs de Sac Marins"

De part et d'autre de l'isthme reliant Grande et Basse Terre s'étendent d'importantes platures dans une position abritée, mais en eau souvent trouble, surtout lors des fortes houles.   Toutefois il est remarquable d'observer l'indigence de la vie corallienne sur la côte Ouest de Basse Terre, liée peut être au trouble des eaux occasionné par l'apport alluvial des torrents qui descendent de la montagne proche. Cependant une exception importante doit être signalée avec l'îlet à Pigeon, en face de Malendure, où les constructions vivantes descendent à -48 m[1].

Depuis l'îlet Fajou, dans le Grand Cul de Sac Marin au Nord, jusqu'au droit de Sainte Marie, au Sud, au delà du Petit Cul de Sac Marin, les récifs s'étendent considérablement.   Ils atteignent 200 à 300 mètres de largeur sur une distance d'une quinzaine de kilomètres d'Ouest en Est, à l'entrée du Grand Cul de Sac.   Ils s'interrompent au niveau de deux profondes passes correspondant probablement à un ancien écoulement fluvial pré-flandrien, contemporain d'un bas niveau marin. Le platier massif porte des îlots (cayes) sablonneux sur la bordure Nord, argileux et marécageux à l'arrière, colonisés par les palétuviers (îlets Fajou et Caret).   Le vaste lagon est parsemé de pâtés et pinacles de coraux vivants, émergeant d'un fond sableux.   Les principales espèces répertoriées sont *Acropora palmata*, *Porites porites*, *Oculina, Mussa angulosa*.   A l'accore, il semble que la morphologie du récif prenne une structure en peigne avec éperons et sillons ; comme dans les récifs d l'Océan Indien ou de la Mer Rouge, la crête alguaire reste de dimension restreinte[2].   En fait, les îlots sont accrochés à un ancien récif envasé, émergé d'une quarantaine de centimètres.   On distingue une première auréole corallienne vivante accrochée au rivage où dominent *Porites porites*, *Porites divaricata* et *Millepora alcicornis*,

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[1] Communication orale de J.P. Chassaing

[2] Voir l'étude de A. Guilcher, sous-presse.

puis une large plage sableuse, propre, où prolifèrent les *Acropora palmata,* enfin le récif barrière proprement dit où foisonnent les espèces.   Notons qu'il s'agit toujours de têtes et de pâtés dispersés, jamais de constructions massives.   Toutefois le secteur se distingue par l'abondance des formes vivantes.

Le petit Cul de Sac Marin est également riche en constructions vivantes qui se disloquent en redans successifs que séparent de profonds chenaux, dans l'alignement strict du drainage continental actuel.   Si cette série de platures s'apparente à celle du Nord, on ne distingue plus cependant la morphologie à cayes[1], ni l'accore à éperons et sillons.   Parmi les espèces les plus fréquentes nous relevons[2] : *Siderastrea, Madracis mirabilis, Stephanocoenia intercepta, Agaricia agaricites, Colpophyllia, Acropora cervicornis, Dendrogyra cylindrus, Meandrina meandrites.*   Il s'agit en fait d'une colonisation des anciens interfluves flandriens aujourd'hui immergés ; les passes profondes, dans le prolongement du drainage continental, même indigent, pourraient être interprétées comme d'anciens axes d'écoulement pré-flandrien.

Ainsi nous relevons de profondes différences dans les diverses constructions récifales frangeant la Grande Terre ou barrant le Grand Cul de Sac ; ces disparités sont-elles à mettre en relation avec l'agitation de l'eau, les fortes houles étant plus favorables aux algues calcaires encroûtantes, les littoraux protégés s'avérant plus aptes au développement de la vie corallienne ? La zone intermédiaire aurait-elle connu dans un passé récent une vie corallienne plus florissante étouffée ensuite par la prolifération des algues ? Les quelques renseignements sur la direction, la force des vents au sol et de la houle ne sont pas décisifs (fig 2).   Il serait d'un grand intérêt d'étudier également les conséquences, au niveau des constructions vivantes, des vents destructeurs qui accompagnent les cyclones comme cela a déjà été entrepris dans le golfe du Mexique.

LA DESIRADE

La petite île de la Désirade possède quelques constructions généralement immergées sur son littoral méridional (fig 4), dans l'Anse de Baie Mahault, de l'Anse Petite Rivière à la pointe du Désert, et dans l'inflexion, largement ouverte, de Grande Anse.   Ce littoral rappelle celui de la côte orientale de la Grande Terre avec ses grès de plage qui se dégagent des sables calcaires blancs de la plage, un étroit herbier à Cymodocées qui n'existe pas partout, un chenal d'embarcations à pâtés de corail vivant, et enfin des constructions alguaires peu massives, discontinues, qui se dédoublent localement, fortement battues

[1] Le terme local de caye est vidé de son sens morphologique.

[2] détermination et récolte de J.P. Chassaing.

par une houle à peu près constante.   Seule la plature barrant l'entrée
de Grande Anse est largement percée par deux passes dans l'alignement
d'un ancien drainage.

Ce littoral méridional est bordé par un récif soulevé à 4-5 m ;
les plus beaux témoins s'étendent à la pointe des Colibris, à l'Ouest,
mais à l'Est ils couvrent l'ensemble de la Pointe Gros Rempart sur une
profondeur de 300 m.   Comme à la Grande Terre, il y a donc ici aussi
une certaine correspondance entre la localisation de la vie corallienne
actuelle et celle des coraux anciens.

En face du Souffleur, où nous l'avons examinée, la crête alguaire
se présente sous la forme de petits éléments à sommet relativement
plat, de quelques mètres à une vingtaine de mètres d'allongement, et
larges de 3 à 5 mètres en moyenne, grossièrement alignés et séparés
les uns des autres par de profondes coupures.   Le sommet, qui émerge
à mer basse, de 50 cm en moyenne, entre les déferlements des vagues,
est couvert par des algues brunes, dont des Sargasses, et par des
Ulves.

Du côté du large, ces éléments discontinus qui constituent la
crête alguaire sont limités par un tombant brutal, parfois avec
apparence d'encorbellement, entièrement tapissé par des algues
calcaires encroûtantes de couleur rose.   Vers le lagon, le tombant
est moins marqué : le calcaire alguaire est de ce côté troué de
multiples loges d'oursins.   Il y a aussi quelques têtes de corail
vivant, mais il apparait nettement que ce corail ne joue pratiquement
aucun rôle dans la construction de la crête.   Par contre dans le
lagon, profond de 3 à 5 mètres, il existe de nombreuses grosses
patates isolées de corail sur fond de sable.

MARIE GALANTE

Cette île, aux contours massifs, possède aussi sur presque tout
son pourtour un récif corallien ancien à 4 ou 5 mètres d'altitude, qui
localement (Folle Anse) pénètre à plus de 3 km à l'intérieur des terres.
Ce vieux récif est absent du Nord de l'île, qui correspond à un
compartiment affaissé, dominé par un escarpement de faille
morphologiquement bien net : c'est là un argument péremptoire pour un
âge pré-flandrien de ce vieux récif.

Un récif frangeant actuel n'existe que sur les façades W, S.W et
Sud de l'île, depuis l'Anse Piton jusqu'à Grand-Bourg.   Comme sur la
côte orientale de la Grande-Terre et à la Désirade, les constructions
alguaires jouent ici aussi un rôle essentiel, et ce sont elles qui
constituent tous les points hauts sur lesquels se produisent les
déferlements.   Comme à la Désirade, ces déferlements sont séparés de
la ligne de rivage par un chenal d'embarcations mais qui ne dépasse
pas ici 3 mètres de profondeur.

A la vision stéréoscopique sur photographies aériennes verticales,
les éléments constituant la crête alguaire apparaissent souvent avec

une forme en S ou en crochet (fig. 5) ; la crête alguaire elle-même peut se dédoubler en deux ou même trois alignements parallèles, comme en face de la Plaine des Galets au Nord de la Caye à Facheux (fig 5).

Les plages de sable fin calcaire se terminent par un trottoir de grès à la fois épais, très dur, et en forte pente ; mais cette grésification n'appartient qu'au littoral oriental. Les lagons sont occupés par un maigre herbier à Cymodocées auquel succède rapidement un platier mort, blanchâtre, de *Porites porites* Pallas, où vivent quelques souches aux moignons fragiles et quelques formations encroûtantes de *Porites astreoides*. Face au large se développent les *Acropora palmata* morts, puis le platier encroûté, propre, dénué de blocs basculés, qui se termine par une levée alguaire. Ce banc alguaire est sillonné de chenaux de 2 à 3 m de profondeur, à fond sableux vers l'intérieur, s'enrichissant en galets vers le large. Ces sillons fréquemment réunis, soudés, déterminent des tunnels où se réfugient poissons et langoustes. Les pâtés ont généralement un profil en champignon, avec plateau sommital horizontal, alvéolé, envahi par les algues courtes et dévoré par une infinité de petits oursins lithophages qui y ont creusé des loges ; les flancs, en encorbellement, sont tapissés de plaques d'algues brunes ou vertes, le pied est enfoui dans le sable calcaire. Au-delà succède un paysage d'une grande désolation, champ de ruines figées d'*Acropora* morts, cassés, parmi lesquels s'accrochent quelques bouquets vivants qui se font de plus en plus nombreux vers le large (fig. 6).

Cette description du littoral, valable de la caye à Facheux au Nord à la Pointe des Basses au Sud, est particulièrement caractéristique au niveau de la caye à Tonnerre. Ces constructions alguaires, communes aux littoraux orientaux étudiés, face à l'Océan, prennent un beau développement et se présentent ici d'une manière schématique. On observe nettement en plongée le passage progressif de la formation corallienne à *Acropora palmata* morts au platier construit par encroûtement des algues qui prennent appui sur les ruines ; puis les *Porites porites* Pallas se multiplient à l'arrière. On observe également la coalescence des différents pâtés coralliens par les algues qui jettent des ponts, respectant les couloirs initiaux, lesquels deviennent alors des chenaux étroits où croissent *Porites asteoides*, *Agaricia agaricites*, *Diploria strigosa* et *D. clivosa,* enfin *Isophyllia*. L'aspect général en S ou en crochet est illusoire : la vue d'avion révèle des constructions en pâtés successifs, individualisés : il y a une juxtaposition plutôt qu'une véritable coalescence. L'aspect continu, que donne la carte au 1/20 000 e, est une interprétation abusive du dessinateur.

Le dédoublement de la crête alguaire en deux ou même trois alignements parallèles pose un problème. L'hypothèse la plus vraisemblable est qu'ici aussi, comme sur la côte orientale de la Grande Terre, l'ossature est fournie par des lignes de grès de plage qui donnent le dessin d'ensemble des brisants. Ces grès de plage ne seraient plus apparents, car complètement habillés et recouverts par des constructions coralliennes et alguaires auxquelles ils ont servi de socle.
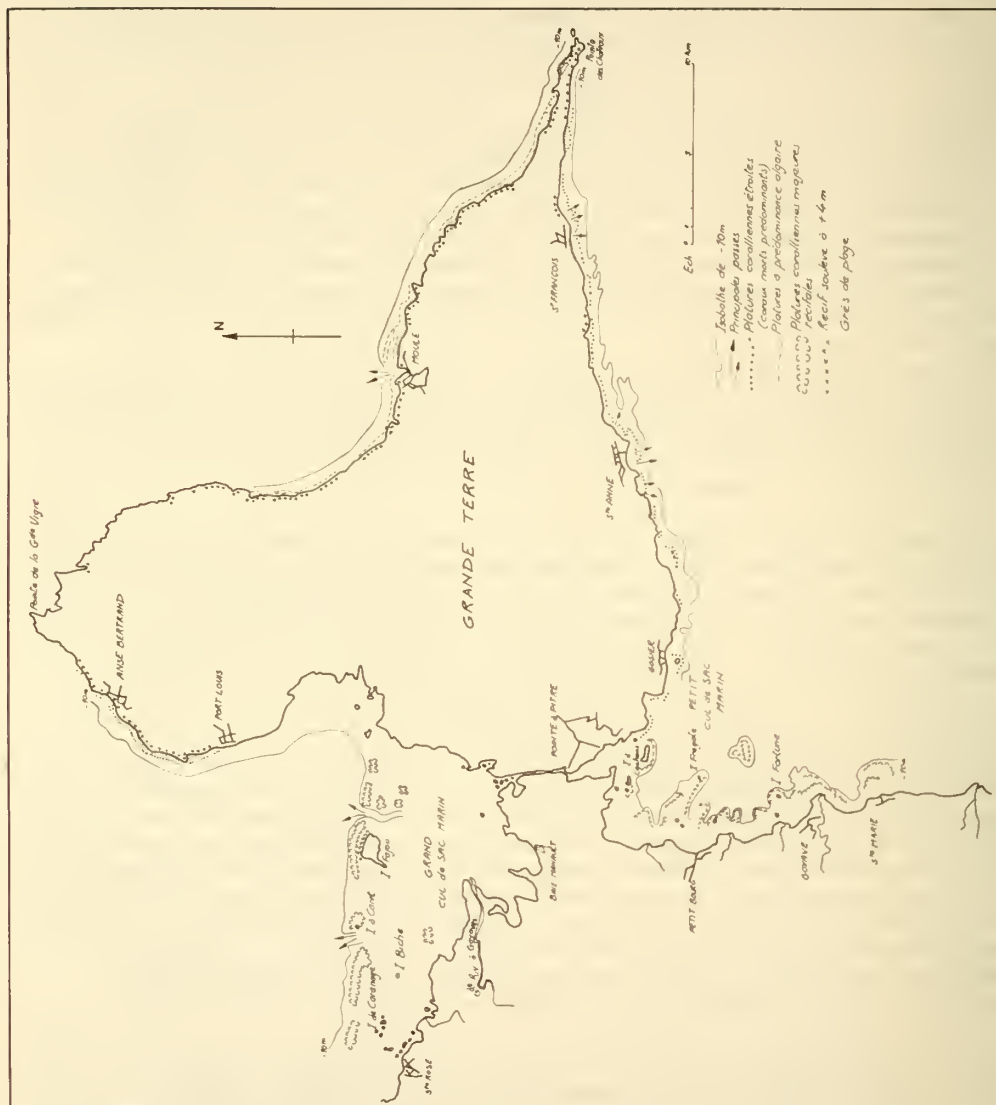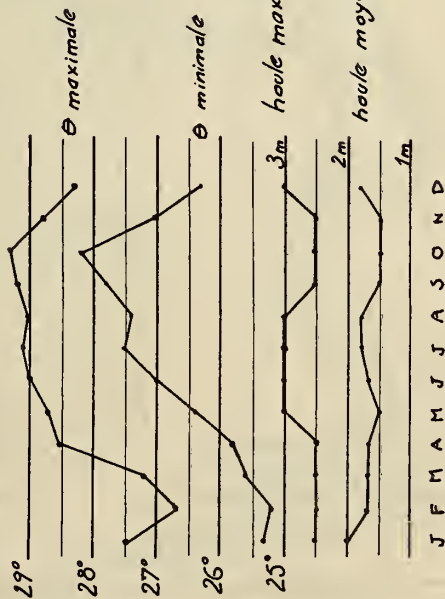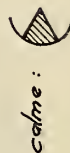
Fig. 2. Température de l'eau de surface, houle et vent. La Désirade 1971-1974.
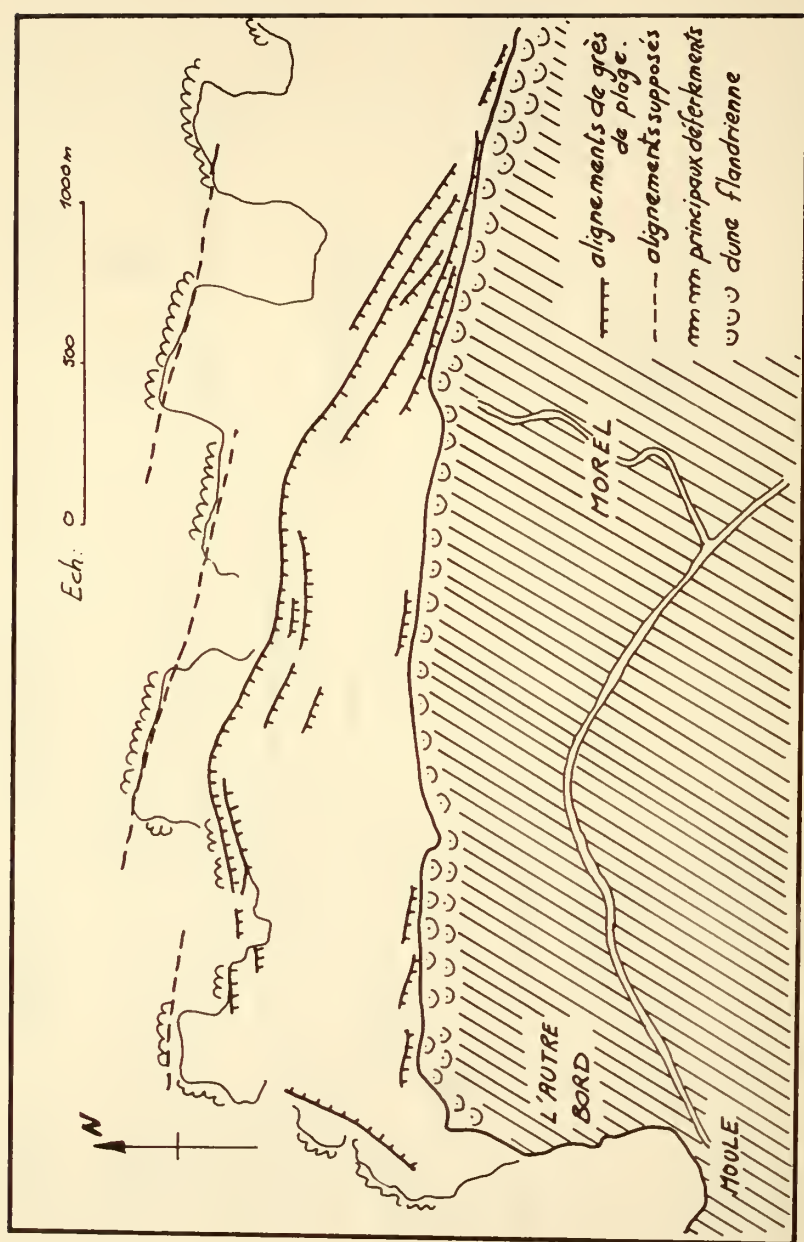
Fig. 3. Grès de plage formant des arrécifes à l'Est de Moule (Grande-Terre).
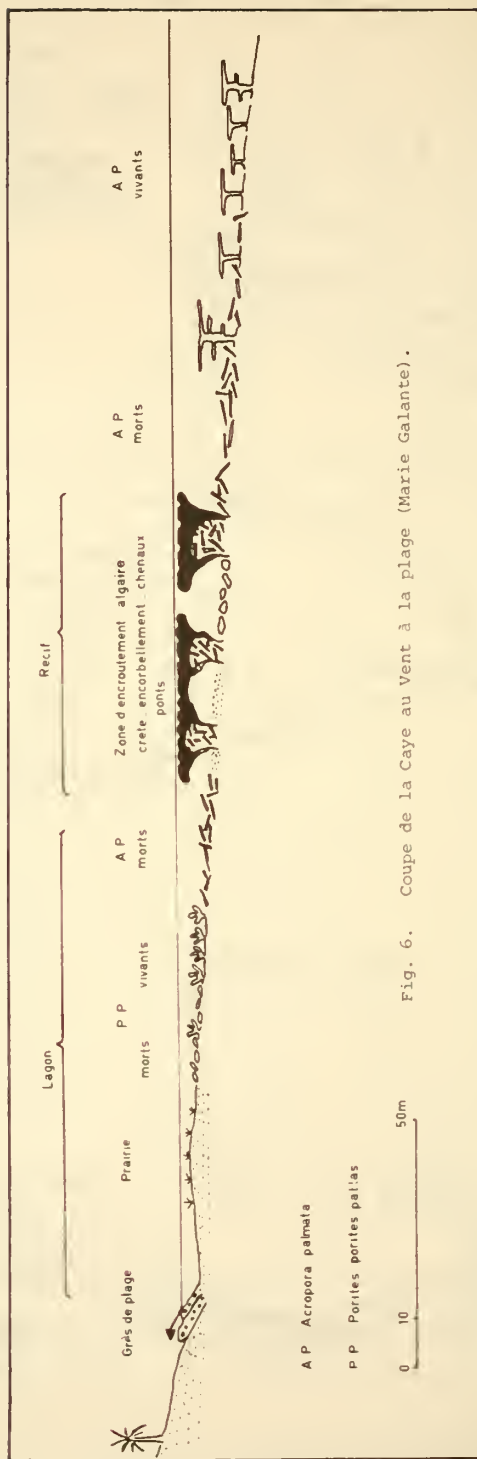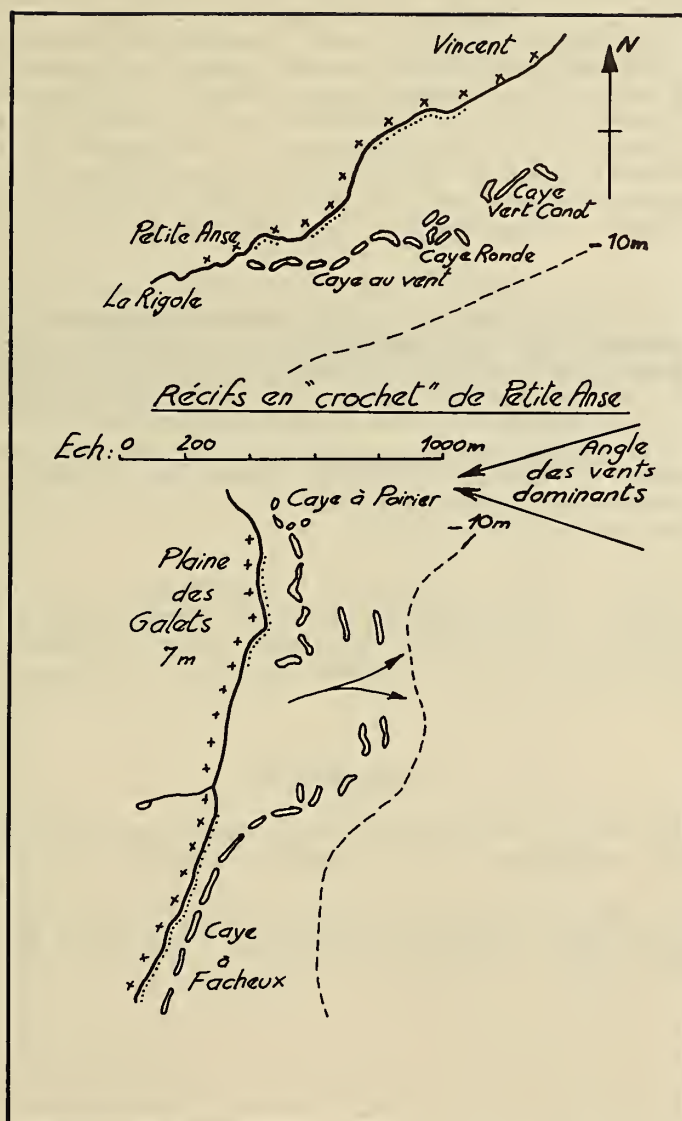
Fig. 4.   Marie Galante et Désirade.

Fig. 6. Coupe de la Caye au Vent à la plage (Marie Galante).

Fig. 5. "Récifs en crochet" de Petite Anse et "récifs en S" de Facheux à Marie Galante.

CONCLUSION

Comparée aux fonds si riches de Porto Rico, d'Haïti ou du golfe
du Mexique, la vie corallienne paraît peu active sur la bordure
orientale de la mer Caraïbe.   Pourtant les conditions écologiques
semblent favorables au premier abord (températures, clarté et agitation
des eaux sont amplement satisfaisantes) comme l'indiquent les quelques
relevés effectués par la météorologie nationale à la Désirade.   Si la
vie corallienne a été plus exubérante dans le passé (vieux récifs),
pourquoi l'est-elle si peu actuellement ? Une modification du climat
et des courants marins ne peut être envisagée localement sans imaginer
une répercussion autour des îles plus septentrionales qui sont encore
plus exposées.   La pollution ne peut être non plus invoquée.

Mais le fait essentiel demeure l'extrême vitalité des constructions
alguaires dans les secteurs les plus exposés à la houle.   La crête
alguaire constitue le trait morphologique majeur de ces récifs.   Elle
détermine aussi largement leur évolution, en gênant en particulier le
transit des matériaux coralliens morts vers le rivage : peut être
est-ce la cause essentielle d'une différence majeure avec la morphologie
des récifs de l'Océan Indien, qui eux sont caractérisés par
l'affleurement à basse mer de larges éléments de plature, alors qu'ici
il y a généralement plusieurs mètres d'eau entre la plage et les
déferlements de la pente externe.

Un autre caractère important est le rôle que jouent les bancs de
grès de plage.   On peut supposer qu'en de nombreux endroits, ce sont
eux qui constituent l'ossature de l'ensemble, et qui déterminent, sous
leur habillage de corail et d'algues calcaires, le dessin général des
brisants.

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SYSTEMATICS AND ECOLOGY OF THE LAND
CRABS (DECAPODA: COENOBITIDAE, GRAPSIDAE
AND GECARCINIDAE) OF THE TOKELAU ISLANDS,
CENTRAL PACIFIC

by J.C. Yaldwyn and Kasimierz Wodzicki

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SYSTEMATICS AND ECOLOGY OF THE LAND CRABS (DECAPODA: COENOBITIDAE, GRAPSIDAE AND GECARCINIDAE) OF THE TOKELAU ISLANDS, CENTRAL PACIFIC

by J.C. Yaldwyn[1] and Kazimierz Wodzicki[2]

ABSTRACT

The Tokelau Islands consist of three atolls (Atafu, Nukunonu and Fakaofo) approximately 500 km north of Western Samoa. Their numerous islets are formed mainly of coral sand and rubble with no standing freshwater. Sixty-one plant species have been recorded, 13 of these being introduced and 10 being adventives. There are three vegetation zones, the beach, the beach-crest, and the interior coconut/fern zone with the physiognomy of a humid tropical forest. Marine invertebrates have not been studied. One hundred and fifty insect species in 83 families have been recorded with most being widely distributed South Pacific species including several introduced agricultural pests, e.g. Rhinoceros Beetle. Some marine fishes have been listed and 7 species of lizards are known from the group. Twenty-six bird species (15 sea birds, 8 shore birds and 3 land birds) are known but none are endemic races. Domestic pigs, cats, man and the Polynesian Rat (*Rattus exulans*) are the only mammals. *R. exulans* is an economic pest as it causes considerable damage to the coconut crop and assists in the spread of filariasis.

Ten species of "land crabs" are identified from the Tokelaus, 4 being terrestrial hermit crabs of the anomuran family Coenobitidae (3 *Coenobita* spp. and *Birgus latro*) and 6 being terrestrial crabs of the brachyuran families Grapsidae (2 *Geograpsus* spp., a *Metopograpsus* and a *Sesarma*) and Gecarcinidae (2 *Cardisoma* spp.). Eight of these species have been recorded before from the Tokelaus under one name or another but two, *Geograpsus grayi* and *Metopograpsus thukuhar*, are new records for this group of atolls. The total of 10 land crab species

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from the Tokelaus can be compared numerically with 15 species on one atoll (Arno) in the Marshall Islands, 9 on one atoll (Kapingamarangi) in the Carolines and 7 from one atoll (Raroia) in the Tuamotus. All the land crab species from the Tokelaus (except for *Sesarma ?gardineri* known elsewhere only from New Guinea and southern Micronesia) are wide-ranging Indopacific forms known from at least the western Indian Ocean to the eastern central Pacific.

Fourteen different crab names in the Tokelau language are recorded and identified. Vernacular names for common land crabs such as *uga (Coenobita brevimana), ugauga (Birgus latro), paikea (Cardisoma rotundum)* and *kalamihi (Geograpsus crinipes)* are used with minor modifications for similar species in Samoa, Niue and the Cook Islands. A traditional story about the *kaviki* (the shore crab, *Ocypode ceratophthalma*) recorded by Dr. Judith Huntsman of the University of Auckland, is given in translation.

All land crab species on the Tokelaus are nocturnal scavengers. Population counts of *Coenobita brevimana* and *C. perlata* together, *Birgus latro, Cardisoma rotundum, C. carnifex,* and *Geograpsus crinipes* give a combined density of about 560 crabs per 5000 sq. m. This figure can be compared to approximately the same land crab density figure on Kapingamarangi Atoll in the Carolines (Niering, 1956) but is in dramatic contrast to counts of approximately 30,000 *Cardisoma planatus* per 5000 sq. m on Clipperton Atoll in the eastern tropical Pacific (Ehrhardt, 1968).

The numerous land crabs on the Tokelaus have an indirect effect on rat control programs and a direct effect on *R. exulans* themselves. Crabs interfere with rat traps and poison baits, eating both warfarin and zinc phosphide. The effect of the anticoagulant warfarin on crabs is unknown, but quadrat counts show that crabs are severely affected by zinc phosphide. The slight risk to humans of secondary poisoning from eating affected crabs can be virtually eliminated by banning crab collecting in poisoned areas for periods after poison baiting, and by putting poison baits in aluminium tubes of a diameter small enough to exclude large and sought-after species such as *Birgus latro* and the two *Cardisoma* spp. Large land crabs presumably prey on young rats, thereby forcing rats to nest above ground level, and compete with rats for at least one of their important foods, the coconut meat available in man-opened and abandoned nuts.

INTRODUCTION

There is no comprehensive information on the systematic status and biology of "land crabs" (both terrestrial hermit crabs and terrestrial true crabs) on islands in the central and south Pacific. Holthuis (1953) in his enumeration of crustacean species from coral atolls in the Marianas, Marshalls, Gilberts and Tuamotu Islands lists, but does not comment on, seventeen species of land crab in the families

Coenobitidae (land hermit crabs), Grapsidae and Gecarcinidae (true crabs). Niering (1956: 16-18) recorded nine land crab species of these families from Kapingamarangi Atoll in the Carolines and gives a general, but vivid, description of their habits. An extensive summary of the published information on the general ecology of land crabs on Pacific atolls is given in the excellent review of atoll environment by H.J. Wiens (1962: 432-439).

One of us (K.W.) visited the atolls of the Tokelau group on four separate occasions (November 1966 - February 1967 and April - June 1968, Nukunonu Atoll; July - September 1971, Fakaofo Atoll; December 1972 - February 1973, Atafu Atoll) working on the problem of rat damage to coconuts (Wodzicki, 1968a, 1968b, 1969a, 1970, 1972a, 1972b, 1973a, 1973b, 1973c; Mosby and Wodzicki, 1972; Mosby, Wodzicki and Shorland, 1974; Mosby, Wodzicki and Thompson, 1973). During his early visits he made incidental collections of land crabs and was surprised at both the systematic variety and the abundance of these animals. On the suggestion of J.C.Y., he made a special collection of land crabs during his last trip concentrating on obtaining a coverage of the different species present, particularly those with "specific" Tokelauan names. The 1972/73 visit to Atafu Atoll produced a list of seven different land crab species and these have already been recorded in a preliminary report on this visit (Wodzicki, 1973c).

K.W. had previously recorded that land crabs seriously interfere with snap and live-trapping of rats on the Tokelaus (Wodzicki, 1968a: 56) and then added details of interference with ground-placed poison baits (1973c: 21,29). As the coconut crab (*Birgus latro*) and to a lesser extent other land crabs are a part of the Tokelauan diet, he was aware that the use of acute poisons in rat control, such as zinc phosphide, might create the danger of secondary poisoning of humans. During a concurrent survey (Wodzicki, 1969b) of rat ecology and damage on Niue Island, an isolated raised atoll south-east of Samoa, K.W. made similar collections of land crabs and these will be the subject of a future study.

The purpose of the present paper is to provide a detailed account of the systematic status and local names of the ten land crabs on the Tokelau Islands, to comment on their ecology and significance in these atolls, and to discuss the local problem of rat-crab relationships.

ENVIRONMENT AND NATURAL HISTORY

Situation and Climate

The Tokelau (or Union) Islands consist of three atolls, named from west to east Atafu, Nukunonu (sometimes misspelt "Nukunono", see Wodzicki and Laird, 1970: 247) and Fakaofo. Their eighteenth and nineteenth century European names, not now used, are Duke of York,

Duke of Clarence and Bowditch Islands respectively. The Tokelaus are
bounded by latitudes 8°S and 10°S and by longitudes 171°W and 173°W.
The atolls are approximately 500 km to the north of Western Samoa;
Nukunonu is about 90 km south and east of Atafu and Fakaofo is about
65 km east of Nukunonu. They are typical atolls, each being surrounded
by a coral reef with an inner lagoon. The numerous islets (or motus)
of each atoll vary in number and size but do not rise more than 3 to 5
metres above sea level. The total land area of the Tokelaus is about
11.5 sq.km and the areas of the three atolls are approximately as
follows (revised 1975 figures, N.Z. Ministry of Foreign Affairs):

	Total land area (sq. km)	Area largest islet (sq. km)	Area of lagoon (sq. km)
Atafu (fig. 1)	3	1.5	19
Nukunonu (fig. 2)	4.5	1.5	109
Fakaofo (fig. 3)	4	1	59

The mean annual temperature is about 28°C, with July or August
being the coolest months and April or May the warmest. The rainfall
is heavy but inconsistent and a daily precipitation of 8 cm or more
can be expected at any time of the year. The highest mean annual
rainfall is 2829 mm at Fakaofo for the years 1958-74. The islands
lie in the zone of the south-easterly trade winds but from November
to February north-easterly and northerly winds predominate (Kennedy,
1966). The Tokelaus are within the hurricane belt and severe tropical
storms occur irregularly. Further details of daily temperatures and
annual rainfall provided by the New Zealand Meteorological Service
(J.D. Coulter, *in litt.*) are given in tables I and II.

People

The Tokelau atolls are in a border area between Micronesia and
Polynesia, and are inhabited by about 1600 Polynesians. Although the
islanders retain linguistic and cultural ties with Samoa, Tokelauan
culture is of composite origin including elements from both eastern
and western Polynesia (Macgregor, 1937). It is distinctly moulded
by the atoll environment. The population has shown a significant
decline over recent years due to emigration to New Zealand (fore-
shadowed by Doumenge, 1966, and documented by Hooper and Huntsman,
1973). The islands are within the political boundaries of New
Zealand and the Tokelauans are New Zealand citizens (Annual Report,
1974; Kennedy, 1966). Nearby Swains Island (or Olosenga), regarded
by some authors as geographically part of the Tokelau group (see
Krauss, 1970) is about 200 km south of Fakaofo and about 300 km north
of Samoa. It is United States territory and is excluded from the
present study. Bibliographies of the Tokelau Islands and of Swains
Island have been compiled by Krauss (1969, 1970).

Table I   Surface temperature in the Tokelau Islands ($^{\circ}$C)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
ATAFU (1929-1941)													
Mean daily maximum	30.0	30.0	30.5	30.5	30.5	30.0	29.5	30.0	30.0	30.0	30.0	30.0	30.0
Mean daily minimum	26.0	25.5	26.0	26.0	26.0	26.5	26.0	26.0	26.0	26.0	26.0	26.0	26.0
Daily mean	28.0	28.0	28.5	28.5	28.5	28.5	28.0	28.0	28.5	28.0	28.0	28.0	28.5
ATAFU (1969-1974)[1]													
Mean daily maximum	31.0	31.1	31.3	31.3	31.2	30.7	30.7	30.5	31.0	31.6	31.8	31.3	31.1
Mean daily minimum	25.1	25.5	25.7	25.9	26.1	26.2	25.3	25.2	25.6	25.5	25.8	25.4	25.6
Daily mean	28.1	28.3	28.5	28.6	28.7	28.5	28.0	27.0	28.4	28.6	28.8	28.3	28.4
FAKAOFO (1969-1974)[2]													
Mean daily maximum	30.8	31.2	31.3	31.5	30.9	30.3	29.8	29.8	30.2	30.9	31.1	31.1	30.7
Mean daily minimum	25.0	25.1	25.3	25.8	25.9	25.9	25.4	25.4	25.4	25.3	25.7	25.5	25.5
Daily mean	27.9	28.2	28.3	28.7	28.4	28.1	27.6	27.6	27.8	28.1	28.4	28.3	28.1
NUKUNONU (1969-1974)[3]													
Mean daily maximum	29.8	30.1	30.7	31.4	31.4	31.5	31.2	30.9	30.9	30.9	30.8	30.3	30.8
Mean daily minimum	23.3	24.1	23.7	24.1	24.1	24.2	24.3	24.1	24.2	24.2	24.7	24.6	24.1
Daily Mean	26.6	27.1	27.3	27.8	27.8	27.9	27.7	27.5	27.6	27.6	27.7	27.4	27.5

1 Actual period 1969, 1971-1972, 1974
2 Actual period 1969-1972, 1974
3 Actual period 1969-1972, 1974

Table II   Mean rainfall in the Tokelau Islands (mm)

	Period of record	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
ATAFU	1929-1953	294	343	269	211	195	223	241	213	185	267	236	360	2911
	1958-59,1971,1974	398	154	218	140	179	142	187	193	203	219	133	386	2552
FAKAOFO	1958-60, 1970-74	383	305	200	125	196	193	236	175	206	284	201	325	2829
NUKUNONU	1958-60, 1971-71, 1974	352	235	221	169	133	157	208	195	217	267	158	379	2691

Soils and Vegetation

The islets of the three atolls are, with a few local exceptions, composed entirely of decaying organic matter, coral sand and rubble. There is no natural standing freshwater and the islanders use sub-surface sources and roof catchment systems.

The plant cover of the islets has not been greatly modified by man and despite centuries of human intrusion, and the ubiquitous introduction of the coconut palm, the vegetation of the Tokelaus still remains in a state of natural equilibrium.

The relative paucity of plant species (61, of which 13 are introduced cultivated plants and 10 are adventives) is another important characteristic of the vegetation of the Tokelau atolls (Parham, 1971). It is appropriate to consider the vegetation of each atoll islet as a single unit, a comparatively simple ecosystem, composed of three main zones: (1) the lower beach or foreshore of sand with more stable areas of coral rubble or beachrock; (2) the beach-crest, and (3) the interior strip on relatively flat stable coral sand. The characteristics and the principal plants of these three zones have been described by Parham (1971: 587-593, figs 4-8) in some detail and can be summarised here. The narrow foreshore zone of either the ocean or lagoon side of the islet is "practically devoid of vegetation" probably due to the unstable nature of this unprotected beach area. A creeping sand-binder, a grass and sedge occasionally occur as pioneers on recently-modified beaches. The beach-crest zone, as the name indicates, stands about 3 to 5m above the high tide level and may extend 10 to 20 m inland. There are four distinct plant associations including the *Messerschmidia argentea* facies which is characteristically seen on exposed sea-side frontages. Other distinctive shrubs and trees found in this zone are the windbreak-forming *Scaevola taccada*, the tall straggling shrub *Pemphis acidula*, the screwpine *Pandanus* (probably *P. tectorius*) and the tree *Guettarda speciosa*.

The interior strip or central zone of the islets is typically occupied by a dense coconut/fern (*Cocos nucifera/Asplenium nidus*) forest with a closed 20 m or more high canopy formed by coconut palms with an understory of other trees including *Cordia subcordata, Pisonia grandis, Guettarda* and *Pandanus* spp. The luxuriant character is enhanced by low shrubs and a dominant crowded ground cover of ferns, including *Nephrolepis hirsutula, Phymatodes scolopendria* and *Psilotum nudum* in addition to *Asplenium*, as well as mosses, lichens and fungi. This plant association has the general physiognomy of a humid tropical forest.

Human existence on the Tokelaus is still largely based on fishing and coconuts. All vegetated islets of any significant size carry coconuts planted by man. The eastern islets of each atoll carry more coconut palms to the ground area than the western and southern islets,

and are reputed to provide larger returns of copra per comparative area.
Other introduced cultivated plants are only found on the village motu
of each atoll which in all three cases is a western islet.   These
cultivated introductions are mainly used for food or as ornamental
plants.   The interior forest zone of certain eastern islets and areas
such as Olopuka, Natama, Te Ahaga and Laualalava on Atafu Atoll (see
fig. 1), Long Motu on Nukunonu Atoll (fig. 2), and Fenualoa and Lefu
on Fakaofo Atoll (fig. 3) appears to be denser and more luxuriant than
the forest zone of western and southern islets.   This luxuriance in
plant growth may have some connection with the predominence of easterly
trade winds.   Observations by K.W. and reports from local inhabitants
would indicate that coconut crabs (*Birgus latro*), and possibly other
land crabs, are significantly more abundant on these uninhabited
eastern islets.

     In addition to coconut palms, two other plants in the coconut/fern
forest zone are of especial importance to the Tokelauans.   The *kanava*
(*Cordia subcordata*) is the only timber tree used for canoe hulls on
these atolls and the *lau mea* fern (*Asplenium nidus*) is extensively
used as a green vegetable (K.W., personal observation;   Parham, 1971:
603-604).

Invertebrate Animals

     There is a rich fauna of corals and other marine invertebrates
around the Tokelau Islands, not yet studied.   Reef and lagoon crabs,
and other crustaceans are well represented.   Small collections of
marine crabs made by K.W. are in the National Museum of New Zealand
and Tokelauan names of a few species are recorded below.   Hinds (1971)
in a report to the South Pacific Commission mentions the presence of
the Crown-of-Thorns starfish at these islands and discusses van Pel's
observations (1958) on the possibility of transplanting pearl oysters
and trochus shells to the lagoons.   Although a recent issue of
Tokelau Islands stamps features selected corals (September 1973) there
is no published record of the actual occurrence of these forms in the
area.   A stamp issue featuring named cowrie shells (November 1974) is,
however, based on species recorded from one of the atolls (Ingam, 1940).

     The terrestrial invertebrates of the Tokelaus have been the
subjects of several studies.   Laird (1956) recorded some freshwater
protozoans, Hoyt (in Wodzicki, 1968a) listed an unidentified earthworm,
Laird (1956) listed several unidentified entomostracan crustaceans,
while Dale (1959) identified three widely distributed isopods.   Land
crabs are listed by Laird (*Sesarma* sp. only), Hoyt, Hinckley (1969)
and Wodzicki (see below).   Insects have been treated in some detail
by Dale (1959), Hoyt (in Wodzicki, 1968a) and Hinckley (1969).   The
latter records a total of 150 insects in 83 families most being widely
distributed South Pacific species including several introduced
agricultural pests.   The most important of these introductions is
obviously the Rhinoceros Beetle (*Oryctes rhinoceros*) accidentally
brought in from Western Samoa and still well established on Nukunonu
Atoll in spite of a planned programme of eradication sponsored by the

United Nations Development Program/South Pacific Commission Rhinoceros Beetle Control Project. Arachnids have been recorded by Marples (1955), who found 13 spiders all known from Samoa, Hoyt (in Wodzicki, 1968a), who added two mites and a scorpion, and by Hinckley (1969) who listed further mites. Centipedes and millipedes have been listed by Hoyt and by Hinckley. Additional collections of terrestrial arthropods made on the Tokelau atolls by K.W. are in the Entomology Department of the National Museum of New Zealand, but have not as yet been studied.

Three terrestrial molluscs, all known from other Pacific islands, are recorded by Dale (1959). Finally the Tokelau Islands were selected as the site of a WHO supported research project on the control of mosquitos as carriers of filariasis and the results of this project have been reviewed by Laird (1966).

The geographic relationship of the Tokelau Island terrestrial invertebrates can be summarized in the words of Hoyt (in Wodzicki, 1968a) "It is doubtful if any of the species of land inhabiting invertebrates are endemic to the Tokelaus and probably a few of the species come and go from time to time. In general most of the insects (and spiders) appear to have come from Samoa, although many are widely distributed throughout the South Pacific." In contrast to the Central Pacific atolls of Canton (Phoenix Group), Palmyra (Line Islands) and Johnston, which have faunas mainly derived from Hawaii, "the Tokelaus have obtained most of their fauna from the south and much of it from Samoa."

Vertebrate Animals

There is a rich and varied lagoon and offshore fauna of marine fishes still undocumented and fishing remains the mainstay of the Tokelauan way of life. Van Pel (1958) and Hinds (1971) give lists of many edible fishes taken by local fishermen. A stamp issue featuring named reef fishes was issued in November, 1975.

Seven species of Pacific Island lizards (4 skinks and 3 geckos) have been recorded from the Tokelaus (Wodzicki, 1968a: 69; Whitaker, 1970). The commonest species is the blue-tailed skink, *Emoia cyanura*, found practically everywhere within coconut plantations and near human habitation. Four marine turtles have been identified from local reports (Wodzicki, 1968a: 67) and it appears that the Green Turtle (*Chelonia mydas*) nests on some of the islets of the group but is subjected to considerable human predation.

A recent survey (Wodzicki and Laird, 1970) revealed a relatively rich avifauna of at least 26 species (15 sea birds, 8 shore birds and 3 land birds). Of these, seven sea birds and one land bird (the Pacific Pigeon, *Ducula pacifica*) are known to breed on the Tokelaus and the populations of these eight species are at present on the decline as they are being taken for food by the islanders. All 26 bird species are known widely on other Pacific islands and no endemic

races have been described from the Tokelaus.   Most have been recorded
from nearby central Pacific island groups such as the Gilbert and Ellice
Islands and the Samoan Archipelago.   All but one of the shore birds
and two of the land birds (a duck, ? *Anas super-ciliosa*, and the Long-
tailed Cuckoo, *Urodynamis taitensis*) are migratory which demonstrates
the importance of these atolls as mid-Pacific stepping stones.

Apart from domestic pigs, which are retained in enclosures or on
small islets, cats (almost entirely kept as pets, rarely feral), and
man, the Polynesian Rat (*Rattus exulans*) is the only other mammal found
in the Tokelau Islands (Kirkpatrick, 1966; Wodzicki, 1972b).
Fortunately no other rodents are found on these atolls but the
Polynesian Rat inflicts considerable damage to coconuts, thereby
affecting both the local food supply and copra production (Wodzicki,
1968a, 1972a).   Rat damage is restricted to immature green coconuts
on the palm (Laird, 1963) and rats do not attack unopened nuts on the
ground (Wodzicki, 1972a: 311).   The Polynesian Rat gnaws a small pit
or an opening in the fibrous exterior of the green nut near the
peduncle.   A few days later the damaged nut drops to the ground and
lies unused until eventual disintegration.   These damaged nuts provide
ideal habitats for the larvae of the diurnal mosquito (*Aedes
polynesiensis*), carrier of filariasis (caused by the nematode *Wucheria
bancrofti*), which breed in either the water-filled, rat-gnawed pits or
in the decaying interior of the nuts (Laird, 1963, 1966).

MATERIAL AND METHODS

All specimens in the "Material examined" lists given below were
collected by K.W. unless otherwise stated.   All examined material is
in the collection of the National Museum of New Zealand.   Measurements
of both hermit crabs and true crabs are middorsal carapace lengths in
millimetres.

SYSTEMATICS OF THE LAND CRABS

CRUSTACEA
Order DECAPODA
ANOMURA
Family COENOBITIDAE

Coenobita Latreille, 1825

Coenobita Latreille, 1825: 276. Alcock, 1905: 139-141 (key to
    Indian supp.), 192-193 (world checklist).   Fize and Serène,
    1955: 2-7 (key to South East Asian spp.).   Gordan, 1956: 311-312
    (bibliography 1905-1954).

Three species of terrestrial hermit crabs were found on the
Tokelau Islands.   These can be recognized as belonging to the
characteristic terrestrial hermit crab genus *Coenobita* by their

habitat, by their shell-bearing habit, and by the compressed eye stalks with the cornea both terminal and lateral.   Their generic identity can be confirmed by the twisted, asymmetrical abdomen bearing uropods but lacking paired pleopods and by the peduncle of the antennule (antenna 1) being as long as, or longer than, the carapace and ending abruptly (i.e. lacking a flagellum).   All three are typically nocturnal species and can be specifically identified using the key given by Alcock (1905; translated into French by Fize and Serène, 1955).

<div align="center">

Coenobita brevimana Dana, 1852
(Tokelau name - *uga*)

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Coenobita clypeata Latreille, 1826: 277.   [Not *C. clypeatus* Herbst,
    1791 = *C. diogenes* of various authors, from the West Indies.]
Coenobita clypeata; Dana, 1852: 473;   1855: pl.30 fig. 4a.
Coenobita clypeata var. *brevimana* Dana, 1852: 473;   1855: pl.30 fig. 4b.
Coenobita clypeatus; Alcock, 1905: 142, pl.15 figs. 1, 1a.
Coenobita brevimanus; Rathbun, 1910: 314 (synonymy with *C. clypeata*
    Latreille).
Coenobita hilgendorfi Terao, 1913: 388 (replacement name for *C. cylpeata*
    Latreille used by some authors).
Coenobita brevimanus; Holthuis, 1953: 36.
Coenobita clypeata; Fize and Serene, 1955: 7, figs. 1 A-C, pl.1 fig. 1

Material examined:

<div align="center">Atafu Atoll</div>

7 Feb. 1973, Nauta, 1 male 27mm, 2 females 25mm (1 ovigerous).
14 Feb. 1973, Te Hepu, 1 damaged male, 3 females 25-28mm.
19 Feb. 1973, Vao islet, 2 males 19-20mm, 25 females 20-29 mm.
    (collected with *C. perlata*).

<div align="center">Fakaofo Atoll</div>

1 Aug. - 19 Sept. 1970, 4 males 19-44mm.

Remarks:

This characteristic purplish species can be readily identified as "*C. clypeata* Latreille" from Alcock's 1905 key by the reduced antennal scale not being fused with the 2nd segment of the antennal peduncle, by the slightly (rather than "strongly") compressed eyestalks, and by the presence of a "bunch of hairs" on the inner surface of the right palm only.

The form of the large (left) hand in the larger specimens from Fakaofo and Nautua is as shown in Fize and Serène, 1955: fig. 1B.   The lower border is long and relatively straight.   The lower border of the large hand in the smaller specimens from Fakaofo and in the Atafu collections of 14 and 19 February differs from that shown by Fize and Serène in being relatively short and more convex in outline (cf. the characters given for Dana's so-called variety *brevimana* by Fize and Serène, 1955: 11).

We have not followed Fize and Serène (1955) in their use of the
name "*C. clypeata* Latreille" for this species.   Rathbun (1910)
accepted that the name "*C. clypeata*" was pre-occupied by *C. clypeata*
Herbst, 1791, used for a West Indian species of this genus.   She
applied the name *C. brevimana* Dana, originally used for a variety of
C. clypeata Latreille, to this well known Indopacific species and was
followed in this usage by Edmondson (1923) and Holthuis (1953).   The
name *C. hilgendorfi* Terao, 1913, has been used by some authors for this
species, e.g. Forest (1954).

The mollusc shells used by this species and retained with the
above collections belong to three genera.   The commonest was *Turbo
(Marmarostoma) argyrostoma*, and the other two were *Mancinella armigera*
and *Casmaria ponderosa*.

Colour notes:

Carapace, hands and legs purplish in life and colour retained in
alcohol.

Distribution:

Widely distributed in the Indopacific ranging from the East
African coast and Madagascar through the Indian Ocean and the
Indonesian Archipelago to the Marshall Islands (Holthuis 1953),
Ellice Islands (Whitelegge, 1897), Line Islands (Edmondson, 1923),
Tahiti and the Tuamotu Archipelago (Holthuis, 1953; Forest, 1954).
This species was first recorded from the Tokelau Islands by Hinckley
(1969), and later (under the name *C. clypeata*) by Wodzicki (1973c).

Coenobita perlata H. Milne Edwards, 1837
(Tokelau name - *uga kaifala*)

Coenobita perlata H. Milne Edwards, 1837: 242.
Coenobita perlatus; Alcock, 1905: 145, pl.XIV figs 2, 2a.
Coenobita perlatus; Holthuis, 1953: 37.
Coenobita perlata; Fize and Serène, 1955: 24, figs 3C, 4A-C; pl.1
    fig. 2.

Material examined:

Atafu Atoll
31 Dec. 1972, Motu-ite-Fala, 1 female 31mm.
16 Jan. 1973, Nautua, 1 female 29mm.
26 Jan. 1973, Olopuka, 1 male 28mm.
10 Feb. 1973, 1 male 26mm.
19 Feb. 1973, Vao islet, 1 male 21mm (collected with *C. brevimana*).

Fakaofo Atoll
1 Aug. - 19 Sept. 1970, 3 males 8-30mm.

Remarks:

The striking red colouring allows immediate visual recognition of this species in its natural habitat. It can be readily identified as *C. perlata* from Alcock's 1905 key by having the reduced antennal scale fused with the 2nd segment of the antennal peduncle, by the strongly compressed eyestalks, by the presence of a "brush of hairs" on the inner surface of both palms, by the presence of an oblique stridulating row of laminar teeth on the upper part of the outer surface of the left palm, and by having the outer surface of the propodus of the 3rd left leg (2nd walking leg) convex and not sharply separated from the anterior surface. In mature males the coxa of the 5th right leg is produced into a long curved tube (the vas deferens), considerably longer than the short vas deferens tube of the left coxa.

Specimens of this species were taken in shells of the mollusc *Turbo (Marmarostoma) argyrostoma*.

Colour notes:

As mentioned above, the characteristic colour of the carapace and legs of this species is red, varying in the specimens examined from a pale to a vivid red. The juvenile specimen with a carapace length of 8mm was creamy-white in general colour with red bands on the wrists of chelae and walking legs.

Distribution:

Widely distributed in the Indopacific ranging from the Red Sea and Madagascar through the Indian Ocean and the Indonesian Archipelago to the Marshall Islands (Holthuis, 1953), Samoa and the Tuamotu Archipelago (Holthuis, 1953; Forest, 1954). This species was first recorded from the Tokelau Islands by Hinckley (1969), and later by Wodzicki (1973c).

Coenobita rugosa H. Milne Edwards, 1837

Coenobita rugosa H. Milne Edwards, 1837: 241.
Coenobita rugosus; Alcock, 1905: 143, pl.XIV figs. 3, 3a.
Coenobita rugosus; Barnard, 1950: 469, fig. 86.
Coenobita rugosa; Holthuis, 1953: 40.
Coenobita rugosa: Fize and Serène, 1955: 12, figs. 2A-C, 3A; pl.1 figs. 3, 5, 7-10.

Material examined:

Atafu Atoll
5 Dec. 1972-20 Feb. 1973, 2 males 9-12mm, 2 females 7.5-9.5mm.

Remarks:

    These small specimens were identified as this species from
Alcock's 1905 key by having the reduced antennal scale fused with the
2nd segment of the antennal peduncle, by the strongly compressed
eyestalks, by the presence of a "brush of hairs" on the inner surface
of both palms, by the presence of an oblique stridulating row of lamina
teeth on the upper part of the outer surface of the left palm, and by
having the outer surface of the propodus of the 3rd left leg flat and
separated from the anterior surface by a well defined crest.   In
mature males the coxa of the 5th right leg is produced into a curved
vas deferens tube but this is only slightly longer than the vas
deferens tube of the left coxa.

Colour note:

    The colour of these small specimens was creamy-white with light,
orange-brown marks on hands and walking legs.

Distribution

    Widely distributed in the Indopacific ranging from Natal and East
Africa (Barnard, 1950), through the Indian Ocean and the Indonesian
Archipelago to the Marshall and Gilbert Islands (Holthuis, 1953),
Ellis Islands (Whitelegge, 1897), Line Islands (Edmondson, 1923),
Tahiti and the Tuamoto Archipelago (Holthuis, 1953; Forest, 1954);
apparently recorded from the west coast of the Americas (Barnard, 1950).
This species was first recorded from the Tokelau Islands by Wodzicki
(1968a).

Birgus Leach, 1815

Birgus Leach, 1815: 337.   Alcock, 1905: 148.

    The genus *Birgus* is monospecific.   The general appearance and
habits of the distinctive Robber or Coconut Crab, *B. latro*, are well
known from numerous general accounts and illustrations that have been
published in the semi-popular literature on Indopacific animals.   The
place of this large land "crab" in the general ecology of coral atolls
has been summarized by Wiens (1962: 432-434).

Birgus latro (Linnaeus, 1767)
(Tokelau name - *ugauga*)

Cancer latro Linnaeus, 1767 (not "1758" as given by Gordan, 1956): 1049.
Birgus latro; Henderson, 1888: 50 (synonymy).
Birgus latro; Alcock, 1905: 150, pl.XVI fig. 1.
Birgus latro; Reyne, 1939: 283 (habits and distribution).
Birgus latro; Gordan, 1956: 304 (bibliography 1905-1954).

Material examined:

Atafu Atoll
8 Jan. 1973, Nautua, 2 females 62-74mm.

Fakaofo Atoll
1 Aug. - 19 Sept. 1970, 1 male 33mm.

Remarks:

Although many specimens of this large and readily identified land crab were seen by K.W. during his visits to the Tokelau Islands only three small specimens were brought back for the systematic collections. Larger specimens were collected during rat poisoning trials on Atafu in 1973 and have been used for chemical analysis.

Distribution:

Widely distributed on islands in the Indian Ocean; not recorded from the Malaysian-western Indonesian area, but ranging from the eastern Indonesian Islands and the Philippines, through northern New Guinea, to the Marshall Islands (Holthuis, 1953), Ellis Islands (Whitelegge, 1897), Niue Island (Yaldwyn, 1970), Line Islands (Edmondson, 1923), Tahiti and the Tuamotu Archipelago (Holthuis, 1953; Forest, 1954). Recorded from Swains Island just to the south of the three atolls of the Tokelau group by Dana (1852: 474; 1875). Dana visited Swains Island during the United States Exploring Expedition 1838-42 and recorded that "Great numbers of Birgi (large Crustacea) were burrowing over the island, some of which were six inches in breadth" (Dana, 1875: 160). First recorded from the Tokelau Islands by Wodzicki (1968a) and Hoyt (in Wodzicki, 1968a), and later by Hinckley (1969).

BRACHYURA
Family GRAPSIDAE
Subfamily GRAPSINAE

Geograpsus Stimpson, 1858

Geograpsus Stimpson, 1858: 101. Rathbun, 1918: 231 (American and eastern Pacific sp.). Tesch, 1918: 74 (Indo-West Pacific spp.). Banerjee, 1960: 157 (key to Indo-West Pacific spp.).

Two species of the land crab genus *Geograpsus* were collected on the Tokelau Islands. These can be readily recognised in the field as belonging to this distinctively terrestrial grapsid genus by the obvious toothed plate on the chelipeds. This feature is a prominent, plate-like expansion of the inner distal margin of the merus (arm). It is found in some other members of the subfamily Grapsinae, such as the intertidal genera *Grapsus* and *Pachygrapsus*, the semi-terrestrial and distinctively-shaped genus *Metopograpsus* (see below) and the

temperate genus *Leptograpsus*. The generic identity of the Tokelau material dealt with here can be confirmed by the following features: the carapace is quadrate and dorsally flattened with the front (the interorbital margin) wider than either orbit but less than half the carapace width; the pterygostomial region of the carapace (on either side of the mouth-field) is neither reticulated nor "hairy"; the fingers of the chelae are distally acute and not spoon-shaped, and there is an opening into the gill chamber fringed with setae between the bases of the 3rd and 4th legs (see Barnard, 1950: 9, 76, 111).

Both species of *Geograpsus* recorded here can be specifically identified using the key given by Banerjee (1960).

<div align="center">

Geograpsus crinipes (Dana, 1851)
(Tokelau name - *kalamihi*)

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Grapsus crinipes Dana, 1851: 249.
Grapsus crinipes Dana, 1852: 341, pl.XXI fig. 6.
Geograpsus crinipes; Alcock, 1900: 396 (synonymy).
Geograpsus crinipes; Edmondson, 1959: 162, fig. 4a.
Geograpsus crinipes; Banerjee, 1960: 163, figs. 1e, 3q, 3r, 4a-c.

Material examined:

<div align="center">Atafu Atoll</div>

8 Jan. 1973, Nautua, 1 male 48mm.
4 Feb. 1973, from house in Atafu village, 1 male 40.5mm.
14 Feb. 1973, Kokoloa, 1 female 30mm.
  May 1976, coll. P.C. Cotton, 2 females 23.5-31mm.

<div align="center">Nukunonu Atoll</div>

26 Dec. 1966, Teahua Motu, 1 female 41mm.
8 Feb. 1967, Avelau, Long Motu, 1 female 38mm.
26 May, 1968, 1 male 45.5.mm.

<div align="center">Fakaofo Atoll</div>

1 Aug. - 19 Sept. 1970, Fenualoa, 1 female 38mm.
1 Aug. - 19 Sept. 1970, 3 females 26-45mm.

Remarks:

This was the commoner of the two species of *Geograpsus* found on the Tokelau Islands. It can be identified as the relatively light-coloured, large species *G. crinipes*, from Banerjee's key (1960: 158). It has the lateral margins of the carapace parallel and not converging posteriorly, keeled throughout their lengths; the cardiac and intestinal regions of the carapace have a series of transverse irregular striae; the suborbital border between the external orbital angle and notch is dentate; the upper border of the buccal cavern is straight; the sternite of the chelipeds is not pubescent, and the lower margins of the meri of the walking legs are only very weakly dentate distally.

Although most of the twelve specimens available showed no trace of pubescence on the sternite of the chelipeds, two large females had some faint low pubescence on the anterior part of this sternite. Even the smallest specimens, two females from Fakaofo and a female from Atafu, all with immature triangular abdomens (carapace lengths 26, 27 and 23.5mm respectively), show the characteristic features of this species as listed above, including the fully keeled lateral margins of the carapace (cf. the small females identified below as *Geograpsus grayi*).

Colour notes:

Three more or less different colour patterns were recorded in the preserved material. These differences could not be related to sex or size. Pale coloured individuals were straw or creamy-orange above and paler below. Intermediate coloured individuals were pale to dark grey above, often with darker or more orange frontal and gastric regions, and paler below. A dark individual had a dark brown carapace with the chelipeds, walking legs and sternites paler but with brown patches.

Distribution:

Widely distributed in the Indopacific ranging from the Red Sea, through islands in the Indian Ocean and the Indonesian Archipelago to the Marshall Islands (Holthuis, 1953), Ellis Islands (Whitelegge, 1897), Line Islands (Edmondson, 1923), Hawaiian Islands (Edmondson, 1959), Tahiti and the Tuamotu Archipelago (Holthuis, 1953), extending to Easter Island in the eastern Pacific (Garth, 1973). The species was first recorded from the Tokelau Islands by Wodzicki (1973c), though the "*Geograpsus grayi*" records from the Tokelaus given by Hinkley (1969) probably refer to this common species of *Geograpsus*.

Geograpsus grayi (H. Milne Edwards, 1853)

Grapsus grayi H. Milne Edwards, 1853: 170.
Geograpsus grayi; Alcock, 1900: 395 (synonymy).
Geograpsus grayi; Banerjee, 1960: 159, figs. 1f, 3n-p.

Material examined:

Nukunonu Atoll
Nov. 1966 - Feb. 1967, 1 female 24mm.

Fakaofo Atoll
1 Aug. - 19 Sept. 1970, 1 female 19mm.

Remarks:

Two small female specimens of *Geograpsus* from the Tokelaus with unkeeled posterolateral margins on the carapace are tentatively identified as *G. grayi*. Following Banerjee's key (1960) they have the lateral margins of the carapace more or less parallel (*but not*

noticeably converging posteriorly) and keeled anterolaterally but not keeled posterolaterally; the epistome is poorly developed; the suborbital border between the external orbital angle and notch *is very slightly dentate*, and the sternite of the chelipeds bears a distinct irregular patch of pubescence. Though the underlined features do not agree with Banerjee's key to *G. grayi*, the unkeeled posterolateral carapace margin and the pubescence on the sternite separate these small specimens from the other species of *Geograpsus*.

The two females identified by us as *G. grayi* have rounded abdomens of the mature type at carapace lengths of 19 and 24mm. The Fakaofo specimen of *G. grayi* was collected in the same period and on the same atoll as the smallest available specimens of *G. crinipes*, two females of 26 and 27mm. These female *G. crinipes* at that larger size have abdomens in the immature (triangular) abdominal stage as described above. We consider this to be additional evidence that two species of *Geograpsus* are present on the Tokelau Islands. Mature male specimens of this second species would be needed to confirm this tentative specific identification.

Colour notes:

The Nukunonu female after preservation was pale creamy-orange above and below, while the Fakaofo female was dark brown on the anterior part of the carapace and pale brown on the posterior part of the carapace, the chelipeds, walking legs and sternites. The hands of the latter specimen were slightly iridescent on the outer surface.

Distribution:

Widely distributed in the Indopacific ranging from the Red Sea area, through islands in the Indian Ocean and the Indonesian Archipelago to the Marshall Islands (Holthuis, 1953), Wake Island and Fiji (Banerjee, 1960), Niue Island (Sendler, 1923; Yaldwyn, 1970), Cook Islands (Sendler, 1923), Tahiti and the Tuamotu Archipelago (Holthuis, 1953). This is probably a new record for the Tokelau Islands as the "*Geograpsus grayi*" records from these atolls given in Hinckley (1969) are considered by us to refer to the commoner species *G. crinipes*.

Metopograpsus H. Milne Edwards, 1853

Metopograpsus H. Milne Edwards, 1853: 164. Tweedie, 1949: 466 (key to spp.). Banerjee, 1960: 172 (key to spp.).

The species of the genus *Metopograpsus* are not generally regarded as typical "land crabs" as the few references to habitat published usually record them from mangrove swamps or intertidal sand flats (e.g. Macnae and Kalk, 1962: 27; Macnae, 1966: 80; McNeill, 1968: 80). One species of the genus was collected for K.W. on Atafu Atoll by Dr. Iuta Tinielu during work on rat control and forwarded to us with a

collection of land crabs.

Metopograpsus as a genus is characterized as follows: the carapace is quadrangular with the posterior margin narrower than the anterior margin; the front (i.e. the anterior margin between the orbits) is wider than half the carapace width; weak striations are present laterally, but absent medially, on the dorsal surface of the carapace; the anterolateral surfaces of the carapace on each side of the mouth field (the pterygostomial regions) are smooth rather than reticulate; and the third maxillipeds lack an oblique setose ridge on their outer surfaces (see Barnard, 1950).

The species of *Metopograpsus* from Atafu was readily identified as *M. thukuhar* using the key given by Banerjee (1960).

Metopograpsus thukuhar (Owen, 1839)
(Tokelau name - *lala*)
Grapsus thukuhar Owen, 1839: 80, pl.24 fig. 3.
Metopograpsus thukuhar; Tesch, 1918: 80 (synonymy).
Metopograpsus thukuhar; Banerjee, 1960: 186, figs. 6f, 6g.
Metopograpsus thukuar (sic) Forest and Guinot, 1961: 155, figs. 162, 167.
Metopograpsus thukuhar; Crosnier, 1965: 25, figs. 20-22, 27.

Material examined:

Atafu Atoll
Dec. 1973, coll. Iuta Tinielu, 2 males 15-18mm, 2 females 13-15mm.

Remarks:

Dr. Tinielu sent a small collection of crabs from Atafu to K.W. in December 1973 in answer to a request for "land crabs". This consisted of two species of *Cardisoma*, a species of *Sesarma* and the four specimens of *Metopograpsus* listed above. He commented (*in litt.* 14 Dec. 1973) on the latter as follows "The lala are darkish in colour small in size."

From Banerjee's key the following features were found to be diagnostic for *M. thukuhar*: no tooth on lateral margin of carapace posterior to external orbital angle; free edges of postfrontal lobes rounded and blunt, postfrontal region with ridges and markings (cf. Crosnier, 1965: fig. 21); suborbital tooth blunt and not keeled from tip to base (cf. Crosnier, 1965: fig. 27); base of antenna thickly pubescent; no "pubescent areas" on anterior surface of propodi of 1st to 3rd walking legs, no "linear fringe" of setae on upper margin of propodus of 4th walking leg; male abdomen with 6th segment (penultimate) slightly longer than 5th; male 1st pleopod with terminal chisel-like chitinous projection (i.e. chitinous projection not T-shaped or apically concave, see Forest and Guinot, 1961: fig. 162; Crosnier, 1965: fig. 20), and female oviducal aperture partly obstructed with a blunt lobe rather than a chitinous projection (cf. Forest and Guinot, 1961: fig. 167).

Distribution:

Widely distributed in the Indopacific ranging from the east coast
of Africa and Madagascar, through islands in the Indian Ocean and the
Indonesian Archipelago to Japan, Australia, Fiji and Samoa (Banerjee,
1960), Hawaii (Edmondson, 1959; Banerjee, 1960) and Tahiti (Forest
and Guinot, 1961). This is the first record of this species from the
Tokelau Islands.

<div align="center">
Subfamily SESARMINAE
Sesarma Say, 1817
</div>

Sesarma Say, 1817: 76. Tesch, 1917: 128 (synonymic list of spp.),
234 (key to Indopacific spp.). Crosnier, 1965: 46 (key to
subgenera). Serène and Soh, 1970: 387 (generic and subgeneric
subdivision of Sesarma s.l.).

Members of the tropical and subtropical genus Sesarma s.l. are
commonly referred to as "marsh crabs" and most species are recorded
as living in mangrove swamps, mud flats or saline marshes. Even in
the absence of mangroves and true marshes (cf. Parham, 1971: 592), a
species of Sesarma s.l. occurs on the Tokelau Islands. This is
regarded by us as a "land crab" as all specimens taken were collected
on kanava trees (Cordia subcordata) or coconut palms at a distance from
the beach. This Sesarma has already been recorded from the Tokelau
Islands by Laird (1955, 1956). His specimen was taken with mosquito
larvae from a "rot-hole" in a puka tree (Hernandia peltata) on
"Motusanga" (Motuhaga), Nukunonu in June 1953.

There are over one hundred species of Sesarma s.l. in the
Indopacific area (Serène and Soh, 1970). This multiplicity of species
has made classification difficult both at the specific and generic
level. Recently the genus Sesarma in its wide sense has been broken
up into a number of new genera and subgenera by Serène and Soh (1970)
as a step towards the ultimate revision of this whole group of allied
species. The Tokelau Sesarma belongs to the new genus Labuanium as
defined in this reclassification. In our essentially faunal study we
will take a conservative systematic view and use Labuanium Serène and
Soh, 1970, in a subgeneric sense.

<div align="center">
Sesarma (Labuanium) ? gardineri Borradaile, 1900
(Tokelau name – ataata o hiliao)
Fig. 4
</div>

References to S. gardineri:
Sesarma gardineri Borradaile, 1900: 593, pl. XLII fig. 8.
Sesarma gardineri; Nobili, 1905: 497.
Sesarma gardineri; Tesch, 1917: 194 (in synonymy of S. rotundatum
Hess, 1865).

Material examined:

Atafu Atoll

16 Jan. 1973, Nautua, 1 male 28mm.
Dec. 1973, coll. Iuta Tinielu, 3 males 26-28mm.
May 1976, coll. P.C. Cotton, 1 female 33.5mm.

Nukunonu Atoll

18 Feb. 1967, 1 male 30mm.

Remarks:

This relatively uncommon, pinkish orange, tree-climbing crab is
readily recognizable as a species of *Sesarma* s.l. by its lateral
carapace margins being nearly straight rather than strongly convex,
by the distinctly reticulate nature of the pterygostomial region, by
the front of the carapace being bent downwards almost at right angles
to the dorsal surface of the carapace with strong postfrontal lobes at
this angle, by the basal segment of the antenna being in communication
with (i.e. not excluded from) the orbit, and by the absence of teeth
on the posterior edge of the walking leg meri (cf. Barnard, 1950;
Crosnier, 1965).   In Tesch's (1917: 235) or Crosnier's (1965: 47)
subdivision of the genus the Tokelau species would be placed in the
subgenus *Sesarma* as it has two teeth on the lateral border of the
carapace behind the external orbital angle, and the upper border of
the hand has only one or two simple longitudinal ridges (and no
pectinated crest).

In Tesch's key (1917: 238) to the Indopacific species of *Sesarma*,
subgenus *Sesarma*, the Tokelau material can not be identified as *S.
rotundatum* Hess in couplet 46 as the sides of the carapace are
posteriorly divergent and not regularly convex, nor as *S. trapezoidea*
Guérin in couplet 49 as the upper border of the male movable finger is
not "regularly and transversely milled".

Using Serène and Soh's (1970) key to genera and subgenera of the
Sesarma complex the Tokelau species has the following diagnostic
features (in addition to those listed above): basal segment of
antennule somewhat swollen and about as broad as long, walking legs
long with anterior and posterior borders of meri subparallel for most
of segment, breadth of front just a little shorter (regarded as
"subequal" for the key) than breadth of posterior border of carapace,
postfrontal lobes strongly ridged anteriorly, carapace lateral border
slightly diverging posteriorly and almost concave, walking leg dactyls
about half length of propodi, male abdomen relatively narrow and
elongate.   Thus it can be placed in *Labuanium* though the lateral
borders of the carapace are not "slightly convex".   Serène and Soh
list eight Indopacific species in their *Labuanium* group.   Serène
(*in litt.*, 10 June 1975) considers that the species of this group are
probably all palm-tree dwellers.

Following correspondence and discussions with Dr. Serène in 1975-76 on the identity of this *Sesarma* species, we now regard it as conspecific with the species recorded as the "red tree-crab" and described from Funafuti (in the Ellice Islands) and Rotuma (north-west of Fiji) as *Sesarma gardineri* by Borradaile in 1900. *S. gardineri* has been synonymized with *S. rotundatum* Hess by Rathbun (1907: 33) and Tesch (1917), consequently it was not listed as a separate species under *Labuanium* by Serène and Soh in 1970.

Using an unpublished key to the species of *Labuanium* provided for us by Serène, the Tokelau specimens are identified as "*L. gardineri*" from the following characters: frontal margin of carapace with a weak median concavity, anterior margin of postfrontal lobes not strongly crested and armed with blunt (rather than sharp) tubercles, lateral border of carapace diverging somewhat from behind external orbital angle and nearly straight rather than medially convex, innder surface of male palm with scattered granules arranged neither in vertical nor in transverse rows, upper borders of male palm with a finely granulate longitudinal line, upper border of male free finger (cheliped dactyl) with irregular longitudinal row of 13-15 acute conical tubercles, lower border of fixed finger with acute tubercles, walking leg dactyls about half length of propodi and thickly tomentose on both borders. As the status of *S. gardineri* vis-a-vis *S. rotundatum* is not at all clear we have followed Serène's advice and used this specific name with a question mark. It would appear that the nearly straight (though diverging) lateral carapace margins and the walking leg dactyls being at least half the length of the propodus may serve to distinguish Borradaile's species from *S. rotundatum* with its medially convex carapace margins and walking leg dactyls less than half propodi. *S. rotundatum* was originally described from Sydney in eastern Australia but this temperate locality is probably incorrect as the species has not been recorded from Australia since. The correct nomenclature and relationship of these oceanic island, tree-climbing *Sesarma* must await a complete revision of the whole group.

Note on arboreal habits:

This *Sesarma* was seen only on overgrown eastern islets, such as Nautua and Te Ahaga, of Atafu Atoll (see fig. 1) by K.W. in 1973. It was observed on rainy days running on coconut trunks or on kanava branches and sometimes on the ground. Laird took his specimen (1955) on a puka tree at Nukunonu, and Holthuis (1953: 33) recorded what was probably the same *Sesarma* from a "hole in live coconut trunk" on Ujae Atoll in the Marshalls.

Colour notes:

As mentioned above this crab on the Tokelau was recorded as being "pinkish orange in life". Borradaile's specimens (1900) were described as "red", while Holthuis (1953) noted that his specimen from Ujae was "orange-gray".

Distribution:

Sesarma gardineri has been recorded in the Indopacific from New Guinea, the Ellice Islands, Rotuma and the Tokelaus.   It was first recorded from the Tokelau Islands by Laird (1955, 1956) and later by Wodzicki (1973c).

S. rotundatum has been recorded from the Nicobar Islands in the Indian Ocean, Java, New Guinea, Duke of York Island near New Britain, the Caroline and Marshall Islands in Micronesia, Samoa and Hawaii (Tesch, 1917).

The Duke of York Island between New Britain and New Ireland, recorded as a locality for S. rotundatum by Miers (see Tesch, 1917), is not the same as the older European name (Duke of York Island) for Atafu Atoll in the Tokelaus.

Family GECARCINIDAE

The typical land crab family Gecarcinidae is represented on the Tokelau Islands by two species.   These crabs on the Tokelaus are easily recognised in the field by their distinctive shape, appearance and colour.   They have a deep, transversely oval body with the lateral borders tumid and strongly arched owing to the expanded gill chambers. The anterior margin, including the wide orbits is considerably more than half the greatest width of the carapace, the eyes are large, and the general colour of these crabs is usually dark.   Mature males of one of the species occurring on the Tokelaus (Cardisoma carnifex) can be very large and have one cheliped conspicuously enlarged.

Türkay (1974: 224) gives a useful key to the genera of gecarcinid land crabs found in the Indopacific area.   This key is given here in translation for the convenience of Pacific research workers.   (In both keys used here the references, e.g. 1(2), are alternatives. Where there is no agreement with 1, refer to 2.   Where the agreement is with 2, then proceed to the next number, i.e. 3, etc.).

Key to gecarcinid land crab genera in Asia and Oceania

1(2) Pterygostomial regions without "hairs" -
                 Gecarcoidea H. Milne Edwards, 1837
                 (2 spp. in Asia and Oceania).
2(1) Pterygostomial regions with a thick tomentum of "hairs".
3(4) A suborbital crest present beneath the lower margin of the
     orbit at the same level as the upper margin of the mouth field -
                 Epigrapsus Heller, 1862
                 (2 spp. in Asia and Oceania)
4(3) No suborbital crest present - Cardisoma Latreille, 1828
                 (4 spp. in Asia and Oceania)

The wide anterior margin of the carapace (frontorbital border), the setose patches on the anterolateral surface of the carapace on each side of the mouth field (the pterygostomial regions) and the lack of a suborbital crest place both Tokelauan gecarcinid species in the genus *Cardisoma* (see Alcock, 1900; Türkay, 1974).

<center>*Cardisoma* Latreille, 1828</center>

Cardisoma Latreille, 1825-28: 685 [pp.345-832 were published in 1828].
    Bright and Hogue, 1972: 16 (synopsis of world spp.; list of
    arthropod burrow associates). Türkay, 1974: 224 (key to Asian
    and Pacific spp.).
Cardiosoma (sic) Alcock, 1900: 444 (synonymy).

Indopacific land crabs of this genus can be identified from Türkay's up-to-date key to the four species found in this area. This key, somewhat modified by us, is also given here in translation.

Key to the species of Cardisoma in Asia and Oceania

1(2) Tomentose area on pterygostomial region longer (i.e. higher) than
    width at base. Corneous endpiece of male 1st pleopod
    asymmetrical; suture on lateral side of endpiece (Türkay,
    1973a: fig. 4a-b; 1974: fig. 3). Female genital opening with
    lateral margin strongly produced (thickened and expanded), median
    margin distinctly produced but to a lesser extent than the lateral
    margin (Türkay, 1973a: figs. 2, 11) -

<center>*C. carnifex* (Herbst, 1796)</center>
(Indopacific from East African coast to the Tuamotu Archipelago).

2(1) Tomentose area on pterygostomial region together with that on
    exopod of 3rd maxilliped about as long as width at base.
    Corneous endpiece of male 1st pleopod symmetrical; suture on
    median side of endpiece. Female genital opening with lateral
    margin distinctly produced, but median not produced at all and
    hardly noticeable.

3(4) Distance between external orbital tooth and eqibranchial tooth
    (first lateral tooth) on margin of carapace equal to or less
    than one third width of orbit. Under surface of corneous
    endpiece of male 1st pleopod not visible from "above" (Türkay,
    1974: fig. 2). Expanded lateral margin of female genital
    opening extending out from sternum and leaning over aperture
    towards midline in ventral view (Türkay, 1974: fig. 13) -

<center>*C. hirtipes* Dana, 1851
(Indopacific from Bay of Bengal to Hawaii).</center>

4(3) Distance between external orbital tooth and epibranchial tooth
    equal to or greater than half width of orbit. Under surface
    of corneous endpiece of male 1st pleopod visible from "above".

Expanded lateral margin of female genital opening extending out from sternum parallel to line of sight and not leaning towards midline in ventral view (Türkay, 1974: fig. 10, *C. longipes*; 1973a: fig. 12, *C. rotundum*).

5(6) Surface of carapace granulated over much of its area and with a distinctly granulated postfrontal crest. The 4th pereiopod (3rd walking leg) is twice or more than twice width of carapace. Corneous endpiece of male 1st pleopod distally pointed, a little longer than width at base (Türkay, 1974: fig. 4a-b) -

> *C. longipes* (A. Milne Edwards, 1867)
> (Indopacific, known only from New Caledonia,
> Ocean Island in the Gilberts, Kandavu Island
> in Fiji, Niue, and Makatea in the Tuamotus)

6(5) Surface of carapace granulated only on hepatic regions, no postfrontal crest present. The 4th pereiopod is a little longer than width of carapace but never approaching twice width. Corneous endpiece of male 1st pleopod distally broad and blunt, not as long as width at base (Türkay, 1974: fig. 1) -

> *C. rotundum* (Quoy and Gaimard, 1824)
> (Indopacific from Indian Ocean to Hawaii).

> *Cardisoma carnifex* (Herbst, 1796)
> (Tokelau name - *tupa*)
> Fig. 5

Cancer carnifex Herbst, 1796: 163, pl.41 fig. 1.
Cardisoma obesum Dana, 1852: 375, pl.24 fig. 1.
Cardisoma carnifex; Boone, 1934: 187, pls 97, 98.
Cardisoma carnifex; Miyaki, 1939: 188, 220, pl.15(5) fig. 2.
Cardisoma carnifex; Türkay, 1973a: 89, figs. 2,4,9-11.
Cardisoma carnifex; Türkay, 1973b: 108, figs. 7-8.
Cardisoma urvillei; Türkay, 1973c: 969, fig.b, pl.1 figs 1-2
    (=*C. carnifex*).
Cardisoma carnifex; Türkay, 1974: 224-229, figs. 3,11 (synonymy; distribution map).

Material examined:

Atafu Atoll
8 Jan. 1973, Nautua, 1 male 68mm (det. M. Türkay).
14 Feb. 1973, Te Hepu, 1 female 60.5mm (det. M. Türkey).
    Dec. 1973, coll. Iuta Tinielu, 1 female 64mm.

Fakaofo Atoll
1 Aug. - 19 Sept. 1970, 1 male 73mm.

Remarks:

Though not the commoner of the two *Cardisoma* species found on the
Tokelaus, *C. carnifex* can usually be recognised in the field by the
greater size they can reach (cf. *C. rotundum*, carapace length up to at
least 55mm) and by the gross disparity in size in the male chelipeds.
This asymmetry increases with increase in size of the male crab.   The
Nautua male collected on 8 January 1973 with a carapace length of 68mm
had the propodus (palm and fixed finger) of the enlarged chela
measuring 80.5mm while that of the small chela measured 54.5mm.   On
the other hand the Fakaofo male of 1970 with a carapace length of 73mm
had the propodus of the enlarged chela measuring 99mm while that of the
small chela measured 62mm.   Females have unequally sized chelipeds but
do not have this asymmetry developed to the same extent as in mature
males.

Following Türkay's key (as given here) to the species of *Cardisoma*,
these specimens have the tomentose area on the pterygostomial region
considerably longer than wide at the base, the corneous tip of the male
1st pleopod asymmetrical, the female genital opening with its lateral
margin strongly thickened and expanded into a round protuberance, and
with its medial margin thickened into a low rim of uniform height.
Thus this material is clearly referable to *Cardisoma carnifex*.

Miyake (1939: 189) in discussing the species of *Cardisoma* present
in the Micronesian area listed a series of differences between *C.
carnifex* and *C. hirtipes*, but did not include *C. rotundum* in his
discussion.   Our specimens from the Tokelaus show the features listed
by Miyake as characteristic of *C. carnifex*.   These are as follows: 1,
the epibranchial tooth on the anterolateral margin of the carapace is
placed very close to the external orbital angle; 2, the width of the
orbit is greater than the width of the front; 3, the lateral margin
of the carapace bulges outwards prominently behind the epibranchial
tooth; 4, the granulated ridge marking the anterolateral border of
the carapace extends posteriorly behind the level of the
gastrocardiac suture; 5, the postfrontal lobes of the carapace are
reasonably distinct but are rounded anteriorly, other carapace regions
are not clearly delineated; 6, the width of the tormentose area of
each pterygostomial region is equal to half the width of the buccal
cavity (note: Miyake compares the width of *both* tomentose
pterygostomial areas to the full width of the buccal cavity); 7, the
lower orbital border meets the lateral orbital border at a right angle,
and 8, the meri of the walking legs carry setae at the distal end of
the anterior margin only (note: Miyake uses the term "posterior margin"
of merus, but a reading of Alcock, 1900: 446, indicates that "distal
end of merus" was probably what Miyake intended).

In addition we note (following Edmondson, 1962: 25) that *C.
carnifex* does not have, behind the level of the posterior end of the
granulated anterolateral ridge of the carapace, the 3 to 5 short
curved striae running obliquely over the branchial margin onto the
upper surface of the carapace so characteristic of the other species

of *Cardisoma* (compare figs. 5 and 6).

Colour notes:

    Two of our specimens were dull, dark reddish-brown in general colour with some paler mottling. Another specimen was somewhat shiny (with a micropunctate carapace surface) and dark reddish-brown in colour with a broad, transverse, very dark, crescent-shaped mark at the gastrocardiac suture on the carapace. The largest male, in contrast, was orange-yellow, with the hands and ventral surface dirty white in colour, and the setae on the propodi and carpi of the walking legs jet black and very obvious.

Distribution:

    Widely distributed to the Indopacific ranging from the east coast of Africa and Madagascar, through islands in the Indian Ocean, the east coast of India and the Indonesian Archipelago to the Ryukyu Islands, Gilbert Islands (Holthuis, 1953; Türkay, 1974), Ellis Islands (Türkay, 1974), Line Islands (Edmondson, 1962), Samoa (Türkay, 1974), Cook Islands (Edmondson, 1962; Türkay, 1974), Tahiti and the Tuamotu Archipelago (Holthuis, 1953; Türkay, 1974). This species was first recorded from the Tokelau Islands by Hoyt (in Wodzicki, 1968a), with later records by Wodzicki (1973c) and Türkay (1974).

    A review of the natural history and utilization by man of *Cardisoma carnifex* in the Indopacific is given by Guinot (1967).

<div align="center">

Cardisoma rotundum (Quoy and Gaimard, 1825)
(Tokelau name - *paikea, tupa*)
Fig. 6

</div>

Thelphusa rotunda Quoy and Gaimard, 1825: 527, pl.77 fig. 1.
Cardiosoma (sic) *hirtipes* Alcock, 1900: 447 (part only, *C. rotundum* is included under *C. hirtipes*).
Discoplax pagenstecheri Sendler, 1923: 24, pl.20 (also numbered 5) fig. 2.
Cardisoma hirtipes; Edmondson, 1962: 23 (part).
Cardisoma rotundum; Türkay, 1973a: 92, figs. 5,12-14.
Cardisoma frontalis; Türkay, 1973c: 971, fig. 1a, pl.1 figs. 3-4 (=*C. rotundum*).
Cardisoma rotundum; Türkey, 1974: 234, figs. 1,14 (synonymy; distribution map).

Material examined:

<div align="center">

Atafu Atoll

</div>

21 Jan. 1973, from house in Atafu village, 1 female 31mm (det. M. Türkay).
14 Feb. 1973, Te Hepu, 1 female 51.5mm (det. M. Türkay).
  Aug. 1973, coll. Iuta Tinielu, 3 males 44-51mm, 3 females 48-51mm (det. M. Türkay).

Dec. 1973, coll. Iuta Tinielu, 2 males 34-46.5mm.

Nukunonu Atoll

29 Nov. 1966, Long Motu, 1 male 47mm.
23 Dec. 1966, Motuakea, 2 males 50-51mm.
26 Dec. 1966, Teahua Motu, 1 male 47mm, 1 female 47.5mm.
   Dec. 1966, Village Motu, 3 males 41-50mm, 3 females 39-45.5mm.
8 Jan. 1967, Lalo, Long Motu, 2 males 34-47mm.
7 Feb. 1967, Avelau, Long Motu, 1 ovigerous female 55mm.
   April-June 1968, 2 males 34-37mm.

Fakaofo Atoll

1 Aug. - 19 Sept. 1970, Fenualoa, 1 male 36.5mm, 2 females 41-54mm.
1 Aug. - 19 Sept. 1970, 1 male 48mm, 1 female 48mm.

Remarks:

   C. rotundum appears to be more common on the Tokelau Islands than
the larger *C. carnifex* (31 specimens of *C. rotundum* in the present
collections compared with only four *C. carnifex*).   *C. rotundum* is not
only the smaller of the two species but has symmetrically-sized
chelipeds both in males and in females.

   The specimens listed above can be identified from Türkay's key
to the species of *Cardisoma* (as given here) by having the tomentose
area on the pterygostomial region about as long as wide at the base;
the distance between the external orbital tooth and the epibranchial
tooth greater than one third and usually greater than one half the
width of the orbit; the postfrontal lobes distinct but not developed
into a crest; the surface of the carapace granulated only on the
hepatic regions, and the 4th pereiopod longer than the width of the
carapace but never twice as long.   In addition the corneous tip of
the male 1st pleopod is symmetrical, broad and blunt, while the female
genital opening has its lateral margin strongly thickened and expanded
out from the sternum, but not leaning over the aperture towards the
midline, and does not have its medial margin produced at all.   This
combination of features firmly identifies the smaller Tokelau
Cardisoma as *C. rotundum*.

   For many years *C. rotundum* has been confused with, and often
included in the synonymy of, the virtually sympatric species *C.
hirtipes*.   Türkay (1973a, 1974) showed clearly that two species were
involved, separated them in his key and provided a short table (1974:
233) of additional differences between these two similar forms.   Our
specimens from the Tokelaus have the features tabulated as
characteristic of *C. rotundum* by Türkay but show somewhat greater
variability than Türkay allowed for.   Thus the distance between the
epibranchial tooth and the external orbital tooth in our material is
sometimes *less than half* the width of the orbit, but always greater
than one third of this width.   (Note: one specimen from Nukunonu had
a second, less developed, epibranchial tooth on one margin of the
carapace).   Türkay describes the central part of the epistome in

C. hirtipes as granulate and that of *C. rotundum* as smooth. However, some specimens in our material of *C. rotundum* have a very few tubercles on the central part of the epistome (but never as many as shown in material of *C. hirtipes* available to us from other areas) and all have an obvious row of tubercles along the ventral edge of the epistome. The subdistal tooth on the meri of the walking legs of our specimens is indeed not noticeable ("wicht wahrnehmbar") as described by Türkay.

As discussed above under *C. carnifex*, Miyake (1939: 189) listed a series of differences between that species and *C. hirtipes* (presumably including specimens of *C. rotundum*). Difference number 6 indicates that the combined width of the tomentose areas of both pterygostomial regions is much greater than the width of the buccal cavity. In our material of *C. rotundum* the width of the tomentose area on each pterygostomial region is subequal to the width of the buccal cavity as well as being subequal to the length of the tomentose area itself.

Finally we must mention an extremely useful preliminary distinguishing feature which we used in the initial separation of *C. rotundum* from *C. carnifex* in our Tokelau collections. This was the presence or absence of a series of short curved striae running obliquely over the branchial margin onto the dorsal surface of the carapace behind the level of the posterior end of the granulated anterolateral carapace ridge. As mentioned by Edmondson (1962: 25) these striae are absent (or hardly developed) in *C. carnifex*, but present in *C. rotundum* (3 to 5 in our material) and in the two other species of this genus (*C. hirtipes* and *C. longipes*).

Colour:

There was considerable variation in the colour patterns seen in the preserved material available of this species from the Tokelau Islands. The colour patterns recorded could be grouped into four different categories.

1. The commonest pattern (19 specimens) observed was varying degrees of dark purplish-black, usually with some purple mottling on the walking legs and occasionally purple mottling on the posterior part of the carapace. Hands were distinctly paler, sometimes purple dorsally, the sternum was pale. Many of these specimens had the margins of the movable sutures in the chelipeds and walking legs (particularly the carpomeral suture) distinctly and obviously reddish in colour.

2. A less common pattern (5 specimens) varied from pale to dark purplish-brown with purple mottling on the carapace and walking legs. Hands distinctly pale, sometimes tinged with orange. The dactyls (claws) of the walking legs in one specimen were of a contrasting pinkish-orange.

3. An equally common pattern (5 specimens) varied from pale orange-yellow to a darker orange-brown with in some cases dark markings on the carapace or reddish mottling on the walking legs. As in the other patterns described the hands were distinctly paler.

4. Two specimens only were somewhat different from category 3 above. These were pale tan in colour over the dorsal surface of the carapace and limbs with pale grey hands and a pale sternum.

No relationship could be found linking these colour differences with the sex, age, or atoll distribution of these crabs.

Distribution

Widely distributed in the Indopacific (but less widely than *C. carnifex*) ranging from islands in the Indian Ocean to the Ryukyu Islands, Marshall Islands (Holthuis, 1953; Türkay, 1974), Ellis Islands (Türkay, 1974), Cook Islands (Türkay, 1974) and Tikahau in the Tuamotu Archipelago (Türkay, 1974). Türkay (1974) records a specimen from Hawaii, but Edmondson had concluded in 1962 (p.25), with the Bishop Museum collections in front of him, that there was "no record to justify the inclusion of any member of the genus *Cardisoma* among the Hawaiian fauna at the present time."

C. rotundum was first recorded from the Tokelau Islands by Wodzicki (1968a: 68), with later records by Wodzicki (1973c) and Türkay (1974).

TOKELAU NAMES FOR LAND CRABS

Introductory Remarks

Other than a short vocabulary (Boardman, 1969) and a preliminary dictionary (Kilifi and Webster, n.d.), there are no published dictionaries of the Tokelau language and no official lists of animal and plant names are available. Tokelau names for plants are listed in Macgregor (1937) and in Parham (1971), the latter based on collections made by K.W. on Nukunonu in 1966-67 and in 1968. Some crab names are listed in Wodzicki (1973c) and a complete list of bird names are given by Wodzicki and Laird (1970). The Tokelau vocabulary has many cognates with that of Samoa. The orthography used and pronunciation of consonants are discussed in Macgregor (1937) and more recently in Sharples (1970, 1976).

The land crab names, and the names of some crabs collected in the lagoon, given here were acquired in the field by K.W. from Tokelauans as the crabs were actually collected. They have been checked with two social anthropologists at the University of Auckland - Dr. Antony Hooper and Dr. Judith W. Huntsman. Our thanks go to

these two scientists for their continued help over the years with matters Tokelauan.   Additional comments on crabs were provided by Dr. Hooper (*in litt.*, 3 September 1973) from notes made by him on Fakaofo.   These have been freely quoted here.   The following comments (based on Wodzicki and Laird, 1970: 250) incorporate information provided by Dr. Huntsman (*in litt.*, 16 September 1977) and explain the orthography adopted in this paper for Tokelau vernacular names. There is an "official" orthography of Tokelauan, and linguistic analysis of the language has been undertaken by Dr. Peter Sharples (1976).   In Tokelauan, as in other Polynesian languages, vowel length is phonemic.   The phonemically distinct long vowels are indicated by macrons, *f* is a voiceless bilabial fricative and *h* is a glottal fricative which occurs palatised before back vowels. Following Samoan, the sound *ng* as in the English "sing" is rendered by the letter *g*.   The Tokelau sound unit (or phoneme) written as *h* is the reflex of the Samoan phoneme written as *s*, and the Tokelau phoneme written as *k* is the reflex of the Samoan glottal stop written as ' (c.f. *kalamihi* and *'alamisi* in table III).

Alphabetical List of Crab Names recorded from the Tokelau Islands

Ataata o hiliao, the name applied on Atafu to the small, orange, long-legged "marsh crab" (*Sesarma ? gardineri*) known for its habit of climbing trees.

Kaifala, see *uga kaifala*

Kalamihi, used for the land crab *Geograpsus crinipes*.   These are described by Hooper as living inland, under stones and other debris, they are not known to dig their own burrows.   They are eaten but are reputed to cause constipation.

Kamakama, name recorded by Hooper for a two-inch wide (about 5 cms) edible, grey or mottled crab found on rocks close to the lagoon edge.   Probably a species of *Grapsus*.

Kaviki, used for the marine ghost crab (*Ocypode ceratopthalma*) of the sandy beaches.   Dr. Hooper records that these large white or pale brown crabs reach up to about 5 cms in width and dig holes down into the sand mainly on the ocean side of the islets. These burrows do not appear to reach water level.   *Kaviki* are used in local medicines and a tale about this crab recorded and translated by Dr. Huntsman is given in a later section.

On Fakaofo, Hooper reports that three kinds of *kaviki* are recognised.   The *kaviki mataloloa* with "long legs", the *kaviki pukupuku* with "short legs" and a third kind known to some as *uliuli taigole* which are "small and black" and are found in soft muddy sand. [It would appear that the latter two names would not refer to species of *Ocypode*.]

Lala, used for the crab *Metopograpsus thukuhar* on Atafu. Presumably
  equivalent to the name *paikea lala* recorded by Hooper (see below
  under *paikea*).

Paikea, used on all three atolls for the smaller of the two *Cardisoma*
  species, *C. rotundum*, though sometimes the name *tupa*, usually
  applied to the larger *C. carnifex*, is used as a general name for
  both species of *Cardisoma*.

  Dr. Hooper records that on Fakaofo there was always some confusion
when Tokelauans were talking about the different kinds of *paikea*.
Some informants distinguished more colour varieties than others.
There appeared to be three main kinds:
(a) The *paikea* which are normally eaten.   These are brown in colour
and up to about 5 cms in width.   Specimens from the village islet
tend to be more yellow in colour and are called *paikea hehega*.   They
burrow or shelter under rocks or other ground debris.   In addition to
their use as human food they are also collected for feeding to pigs.
[These are variously coloured forms of *Cardisoma rotundum*, see our
discussion under this species in the "Systematics" section.]
(b) The "black" *paikea*.   Sometimes called *paikea uli* (*uli* meaning
"black") or *paikea lala*;   these are found under rocks and are usually
not eaten.   [Probably these are *Metopograpsus thukuhar* already
discussed under the name *lala*.]
(c) The "red" *paikea*.   These are described as red in colour, about
2.5 cms in width and having long legs.   They are called *paikea fala*
and are described as living on *fala* trees (*Pandanus* spp.) or in rain
water-filled *tugu*, which are natural or man-made water storage holes
in palms or other trees (see Wodzicki, 1968a: fig.10).   They are not
eaten.   [Presumably these are *Sesarma ? gardineri*, already listed
under the name *ataata o hiliao* as recorded on Atafu.]

Paka, according to Hooper used as a general name for "sea crabs" as
  distinct from land crabs.   There are several different kinds
  recognised by their differing colour and size.

Tapako, the name supplied to K.W. for a small swimming crab, *Portunis*
  sp., taken in the lagoon at Natama islet, Atafu.

Tapolalau, used for specimens of the common marine Indopacific box
  crab, *Calappa hepatica*, taken in the lagoon at Olopuka, Atafu.

Tupa, used for both species of *Cardisoma*, but usually applied to the
  larger species with asymmetrically-sized chelae, *C. carnifex*.
  Dr. Hooper describes these as living in burrows on Fakaofo and
  taken as food.   He also records the interesting observation
  that "they come up out of their holes in hurricanes."

Uga, used as a general name for land hermit crabs of the genus
  Coenobita.   One of us (K.W.) recorded the unqualified name

uga in wide use on Atafu for the purplish species *Coenobita brevimana*, while the name *uga kaifala* was applied to the red species *C. perlata*.

Dr. Hooper recorded the names *uga uli* and *uga fala* in use on Fakaofo for the purple and red species of *Coenobita* respectively.

Uga kaifala, used for the red species *Coenobita perlata* on Atafu.

Ugauga, used on all three atolls for the coconut crab, *Birgus latro*, though colour variations occur.

Comparative List of Crab Names from Samoa, Niue and the Cook Islands

It was felt that a comparative table of vernacular names for the land crabs, and some of the obvious shore crabs, as used in the Tokelau Islands, Samoa, Niue Island and the Cook Islands would be of general interest to those working on ecology and environmental studies in this area of the South Pacific. Some knowledge of local names is the key to working in the Pacific on large and edible animals.

The Samoan crab names in table III were obtained from the extensive list of vernacular names published with their systematic identifications in Kramer (1903: 412-413). These names have been checked with the most recent Samoan dictionary (Milner, 1966). In Samoan the sound *ng* (as in the English "sing") is represented by the letter *g*. The unaspirated voiceless glottal stop is written as an inverted comma ('). We thank Mrs. Seni Neich of Wellington for help in the interpretation of the Samoan crab names.

The Niuean crab names were obtained on Niue Island by J.C.Y. in 1971 and 1972. The orthography used is that adopted in the standard Niuean dictionary (McEwen, 1970). Unlike in written Tokelauan and Samoan the sound *ng* in Niuean is written in McEwen as *ng*, although *g* will be found in older texts. The syllable written as *te* is pronounced *se* in Niuean (thus *tautea* = *tausea*).

The Cook Island crab names were obtained from the only dictionary of Cook Island Maori known to us (Savage, 1962). The sound *ng* is written as *ng* in this dictionary of the Rarotongan dialect. Some additional crab names were supplied by Mr. R. Powell of Rarotonga (*in litt.* October 1976) through Mr. J.M. Campbell of the Plant Diseases Division, D.S.I.R., Auckland. The latter names are indicated by an asterisk in table III, and not all of these appear in Savage (1962). Powell informs us that the coconut crab is called *unga ono* on Rarotonga (cf. *unga – 'onu* for an unspecified land crab in Savage, 1962), *kavo* on the northern atoll of Penrhyn. He also records that coloured forms of *unga* (*Coenobita* spp.) are referred to as *teatea* (white), *muramura* (red), and *kerekere* (black).

We have not attempted to search for and list crab names from other Polynesian island groups. However, we note in passing that Whitelegge (1897) records the following names from Funafuti Atoll in the Ellice Islands (about 890 km west of Atafu): *ounga ouri* for *Coenobita clypeata* (= *C. brevimana*), *ounga koula* for *Coenobita olivieri* (possibly *C. spinosa*, see Fize and Serène, 1955: 5), and *keibea* for *Cardisoma "hirtipes"* (presumably *C. rotundum,* see Turkay, 1974); and that Tinker (1965, supported by Pukui and Elbert, 1957) records the Hawaiian names *'ohiki* for *Ocypode ceratophthalme* and *'a'ama* for *Grapsus grapsus*. Churchward's Tongan dictionary (1959) gives *paka* as a general name for crabs, *'unga* for hermit crabs, and the names *kalamihi, kamakama, keviki, tafola, teitei, tupa, tupaolelangi, 'ū'ū* (all similar to names in table III) are listed among other unidentified crab names.

A Traditional Story of the Kaviki or Ghost Crab

Dr. Judith W. Huntsman recorded the following tale on Nukunonu Atoll and has kindly allowed us to include her translation here.

This is the story of Kaviki, a beauty of the Tokelau Group

This story is about the kinds of creatures that crawl on the ground and live there. The creatures like *ugauga* (coconut crab), *tupa* (large land crab), *paikea* (medium sized land crab), *Kalamihi* (greyish small land crab), *kaviki* (sand crab) etc. and all their various kinds of judging on their colour.

Now *Kaviki* lives in the village. (The kind of *kaviki* that has its eyes placed at the very top of its head and lives in the sand, where it buries itself). He makes up his mind one day that he will go and wander around the world to look for a wife. *Kaviki* is very handsome. The news of his beauty spreads far and wide.

Kaviki now goes to where he wants to go. He goes towards inland, to the bush; and when he gets to the bush the women *kalamihi*, the kind that are greyish, call like this:

"*Kaviki*, you are so beautiful. *Kaviki*, you are so handsome."

Kaviki replies to them: "What are your feelings." The woman *kalamihi* calls him: "Come here and we will be wed." *Kaviki* answers her: "Ach! Who do you think admires you, you hairy-legged, greyish-skinned creature." So the woman *kalamihi* is shamed.

Kaviki goes on, he goes to Alofi [western side of Nukunonu]. When he goes there, the women *paikea* (the white *paikea*) of this place call: "How beautiful *Kaviki* is." *Kaviki* replies: "What do you feel [meaning: is it true what you say]; *Kaviki* is a chief's son. He is very handsome and very beautiful."

Table III Comparative list of crab names from the Tokelau Islands, Samoa, Niue and the Cook Islands

Scientific name	Tokelau name	Samoan name	Niuean name	Cook Island name
Land crabs:				
Coenobita spp. (dark coloured)	uga	uga	ungamea	unga
Coenobita sp. (reddish)	uga kaifala	?	ungafala	unga muramura
Birgus latro	ugauga	ūū	unga	(unga-kaveu (unga ono*
Geograpsus crinipes	kalamihi	'alamisi	tautea	?
Geograpsus grayi	—	?	kalahimu	?
Metopograpsus thukuhar	lala	?	—	?
Cardisoma carnifex	tupa	tupa	—	tupa
Cardisoma rotundum	tupa, paikea	pa'atea	—	?
Cardisoma longipes	—	—	kalavi	—
Shore crabs:				
Ocypode ceratophthalma	kaviki	av'i	—	papaka*
Grapsus spp.	kamakama	'ama'ama	kamakama	?
Calappa spp.	tapolalau	tāpola	?	pakapaka*
General name for crabs	paka (sea crabs)	pa'a	paka (edible sea crabs)	papaka*

Legend to tabe III

— indicates species not present or, in the case of *G. grayi* on Tokelaus, species not named.
? name not available to us.
* name from Mr. R. Powell, Rarotonga.

A woman *paikea* calls: "Come here and we will be wed." *Kaviki* replies to her: "Ach! Who would admire you, greyish-skinned, skinny-legged creature." That woman *paikea* is also shamed.

He goes on to another place. When he arrives there the women *ugauga*, (the kind that is black) call to him: "Look! How beautiful *Kaviki* is." *Kaviki* replies: "What again are your feelings? *Kaviki* is handsome, *Kaviki* is beautiful?" The black woman *ugauga* says to him: "Come here and we will be wed." *Kaviki* answers her: "Ach! Who admires you, you are dark black!" He insults her like this and the black woman *ugauga* is shamed.

Kaviki keeps on going and he comes to Tokelau [north east corner of Nukunonu atoll]. The women *ugauga* of this place see *Kaviki* approaching and call out: "Look! *Kaviki* is very beautiful and very handsome!" *Kaviki* again replies: "What are your feelings? *Kaviki* is very beautiful!" The red woman *ugauga* crab calls to *Kaviki*: "Come here and we will be wed." *Kaviki* answers her. "Ach! Who wants you, fat-legged thing!" So this red woman *ugauga* is shamed.

Kaviki carries it on like this. He goes around until all the islets of the atoll are covered in his walk. Down he goes and goes and he arrives at Lalō and Nataulagā [eastern side of Nukunonu atoll]. The large *tupa* of this place call: "Look! *Kaviki* is beautiful! He is very handsome." *Kaviki* replies: "What are your feelings? *Kaviki* is beautiful? He is handsome?" The woman *tupa* calls out: "Come here and we will be wed." *Kaviki* replies: "Ach! Who admires you? Long-legged thing, and skinny and hairy creature!" So the woman *tupa* is also shamed.

But look now, all the kinds of creatures like this; the coconut crabs, the large land crabs, the medium sized land crabs, the small greyish land crabs etc. all come down and follow him persistently to find out where he will get a wife for himself. They come down and wait for him at Tepuka [islet on south western side of Nukunonu]. They all gather together in this place, and wait until *Kaviki* arrives as he is going round the islets of Atumotu [southern side of Nukunonu].

Now *Kaviki* comes down, he arrives at the point and the women of that place, the *kaviki toga* (the southern *kaviki*) call out: "Look! Kaviki is very beautiful! He is very handsome!" *Kaviki* answers them: "But what are your feelings? *Kaviki* is very beautiful? *Kaviki* is very handsome?" The southern woman *kaviki* says to him: "Come here and we will be wed." *Kaviki* replies: "Ach! Who admires you ugly people."

This is the exact place where *Kaviki* gets *kaviki toga* (southern *kaviki*). *Kaviki* is now chased away from there. The women mock him. The women call him names to shame him and he calls back to shame them. All the different kinds of *ugauga, paikea, tupa, kalamihi* etc. shout out: "Look here *Kaviki*! Who do you think wants you? The skinny-legged thing with your eyes sticking up on the very top of your head."

Unfortunately *Kaviki* is ashamed.   The women again shout at him: "You there, your eyes sticking out at the very top."

Kaviki stands up, and runs fast.   He runs away because he is ashamed.   All the different kinds of women chase him.   He runs away and climbs up a pandanus tree.   The very pandanus tree on which *kaviki toga* is.   That is the *kaviki* whom *Kaviki*, the son of a chief, loves. The kind of *kaviki* which are red, and are found on the pandanus tree. They are also on coconut trees and inside the *tugu* [holes in coconut trees to collect rainwater].   So the greyish *kaviki* and the red *kaviki* now live on the pandanus.   They are wed.

So ends the story of *Kaviki*.

(Comment by J.C.Y. and K.W.: we wonder if the *kaviki toga* of the story are equivalent to the tree-climbing *ataata o hilia* of Atafu?).

NOTES ON THE ECOLOGY OF THE LAND CRABS

Introductory Remarks

Eighty years ago Charles Hedley summarized so dramatically the place of land crabs in the atoll ecosystem that any discussion on this subject could start no better than with his actual words — "The dominant note in the life of a coral atoll, as expressed by the Funafuti [Ellice Islands] fauna, struck me as the abundance and ubiquity of Crustacea.   The Avifauna were but sea fowl, the indigenous Mammalia but rats, the Reptilia only a stray scink and gecko, while insects and land mollusca...were barely represented.   Into the vacant places swarmed Crustacea.   Not an inch of the atoll world is secure from them.   The *Coenobita* wander across from shore to shore and dispute any stray edibles with the rats..."   (Hedley in Whitelegge, 1897: 127-128).

The effect of land crabs on atoll life is discussed by Wiens (1962: 432-439) and can be briefly stated as follows: land crabs are nocturnal scavengers eating any available organic material such as dead animals, coconut meat, and other vegetable matter such as twigs, leaves and fruit; they play a major role in the incorporation of organic matter into the soil and their burrowing activity aids in soil aeration.   Where burrowing is not practical because of the lack of soil, land crabs shelter under piles of coconut husks, amongst tree roots, in cavities in coral rubble, or in crevassed coral limestone.

Observations in the Tokelaus

On the Tokelau atolls burrowing by land crabs was not obvious except in a few sandy bays on the lagoon side of the islets.   Land crabs were not observed during daylight, except when freshly opened coconuts were discarded on the ground.   These would usually attract some *Coenobita* during the day but would be covered with land crabs

(mainly *Coenobita*, but including *Geograpsus, Cardisoma* and *Birgus*) at night. All the land crabs recorded on the Tokelaus were observed living on the ground although some species were good climbers. *Birgus latro* was often observed at night feeding on rat baits nailed to palm trunks up to two metres above ground, but was not observed climbing to the crowns of palms. The common *Coenobita brevimana* also climbed to rat baits, while *Sesarma ? gardineri* was often seen running along coconut or kanava trunks.

Land Crab Numbers

To obtain some idea of the relative effect of land crabs on the ecosystem of the Tokelaus, K.W. decided to make a preliminary estimate of their numbers during field work on Atafu Atoll in 1972-73. As part of his project on rat ecology and control he had established 14 quadrats on a representative series of islets on various sides of the Atafu lagoon (Wodzicki, 1973c). Each quadrat was a 50 metre square with a total of 2500 square metres. A two to three metre wide strip around each quadrat was cleared of ground vegetation. Five of these quadrats on properties showing severe rat damage to coconuts were selected on three different islets for estimating crab numbers. All five quadrats were situated in coconut/fern forest on the following properties: Laualalava (containing 102 coconut palms and 25 other trees), Te Ahaga (115 palms, 8 other trees), Nautua (117 palms, 8 other trees), Olopuka (132 palms, 23 other trees), and Fenualoa (100 palms, 22 other trees) — see fig. 1. At each quadrat on various dates (see table IV) eleven baits of halved mature coconuts were spaced around the cleared strip at about 12-metre intervals between 1700 and 1800 hours. After about two hours the quadrats were revisited by a team of three people carrying bright lights and all crabs found on or in the vicinity of each bait were identified and counted. In two quadrats, Laualalava and Te Ahaga, it was possible to repeat the baiting and counts on later dates (14 days later at the former and 6, 7, 1 and 1 day later at the latter). In these two quadrats the crabs found on each date were individually marked with a spot of paint of a different colour for each visit.

The result of these nocturnal land crab counts are listed in table IV and can be summarized as follows. The hermit crabs of the genus *Coenobita* are, as expected, the most numerous land crab species on Atafu Atoll with a total of 1266 individuals (i.e. about 96%) out of 1319 different land crabs counted in all five quadrats. The other species in decreasing numerical significance are *Birgus latro* (37), *Cardisoma rotundum* (11), *Geograpsus crinipes* (4) and *C. carnifex* (1). At the two quadrats where counts were repeated on later dates, it was found that there was a much larger *Coenobita* population than that indicated at the first count in each quadrat. Thus 84 *Coenobita* were counted at Te Ahaga on the first night, but the total number of different individuals seen had risen to 383 after the fourth count 15 days later. Similarly, at Laualalava there were 333 *Coenobita* counted on the first night, but the total number of different individuals after the second count 14 days later was 551. The coloured marking at these

Table IV. Numbers of land crabs in five quadrats on Atafu Atoll, January - February 1973.

Quadrat	Date of count	Coenobita spp.		Birgus latro		Cardisoma rotundum No. of crabs at baits	Cardisoma carnifex No. of crabs at baits	Geograpsus crinipes No. of crabs at baits	Total No. of crabs seen on each visit	Total No. of different crabs seen at quadrat
		No.of crabs unmarked	No.(& %) at baits	No.of crabs unmarked	No.(& %) at baits					
Laualalava	25-1-73	333	-	0	-	0	1	1	335	
	8-2-73	234	218(93%)	1	-	3	0	1*	239	558
Te Ahaga	23-1-73	84	-	3	-	0	0	0	87	
	29-1-73	109	91(83%)	13	11(85%)	0	0	0	122	
	5-2-73	107	89(83%)	8	7(86%)	1	0	0	116	
	6-2-73	141	91(65%)	3	1(33%)	4*	0	2	150	
	7-2-73**	35	28(80%)	0	-	1*	0	0	36	413
Nautua	5-2-73	208	-	3	-	0	0	0	211	211
Olopuka***	12-2-73	5	-	5	-	2	0	0	12	12
Fenualoa	2-2-73	119	-	6	-	0	0	0	125	125

Legend to table IV

   * Unmarked crabs, not seen at previous count.

  ** Count made at 1000 hours, i.e. in daylight.

*** Area poisoned with zinc phosphide on 22-1-73 (i.e. 21 days before count).

two quadrats was done on the mollusc shell of the *Coenobita* and on the carapace of the other species. No attempt was made at these subsequent counts, and in the assessment of numbers, to allow for shell change in the hermit crabs or moult in the other crabs. The marking and recapture figures at the Laualalava and Te Ahaga quadrats suggest either very large populations or considerable mobility of land crabs, especially the *Coenobita* populations. Although *Coenobita* are usually nocturnal as indicated by the large numbers seen at night, a count taken at Te Ahaga on the morning of 7 February 1973 showed that 35 *Coenobita* (i.e. a quarter as many as counted the night before) were still feeding on what little remained of the baits at 10 a.m.

These population counts can be compared to those given by Niering (1956: 17) and Ehrhardt (1968) for land crab numbers on Kapingamarangi Atoll in the Caroline Islands and on Clipperton Atoll in the eastern tropical Pacific off southern Mexico. Niering's figures are the only counts we have found of land crab populations on an Indopacific atoll. He recorded a total of 526 hermit crabs, true crabs and coconut crabs in a 40,560 square foot strip transect by counting individual land crabs found under surface vegetation and debris, and adding the number of crab holes seen. Niering's count was presumably made in daylight. K.W.'s highest total count for an Atafu quadrat of 2500 square metres was 558 land crabs at Laualalava. Making an arbitrary assumption that K.W.'s baits were attracting land crabs from an area *twice* that of the quadrat around which the baits were placed, his highest count gave a figure of about 560 crabs per 5000 square metres in the Tokelaus. Niering's figure is of the same order being about 530 crabs in an area of 4500 odd square metres in the Carolines.

Ehrhardt set out to make a census of the gecarcinid land crab *Gecarcinus planatus* on isolated Clipperton Atoll, which has a land area of 1763 square kilometres. He did a synchronized series of counts of adult crabs in selected sectors at 1800 hours (one hour after observed crab emergence) and arrived at a density for the different sectors ranging from 1.4 crabs to 12.6 crabs per square metre, with an estimated average of 6 crabs per square metre over the whole land surface of the Atoll. This average gives a total population of about 11.5 million land crabs on Clipperton Island. The average figure of 6 crabs per square metre on Clipperton gives a total of 30,000 land crabs in an area of 5000 square metres compared with 560 on Atafu and somewhat more than 530 on Kapingamarangi.

Crab-Rat Relationships

It has been reported from other Pacific Atolls that land crabs seriously interfere with rat trapping (Storer, 1962: 46,57) and poison baiting (Smith, 1969: 56,70). Similar interference on the Tokelaus has been described by Wodzicki (1968a, 1973c). As the coconut crab, *Birgus latro*, and to a smaller extent the other land crabs are a part of the diet of the Tokelauans, it has been thought that the use of acute poisons, such as zinc phosphide, in rat control may create a danger of secondary poisoning in humans. In addition, it has been

suggested that under certain atoll conditions predatory land crabs may have a direct effect on rat population.

In the Tokelau atolls snap trapping for the Polynesian Rat (*Rattus exulans*) was considerably handicapped by the dense populations of land crabs of all types and also to a lesser degree by lizards. The degree of interference is best illustrated by examples from trapping on various islets on Nukunonu (Wodzicki, 1968a: 56). It was found, when trap lines were visited every two hours, that during daylight interference was mainly due to lizards. From dusk onwards increasing numbers of land crabs began to appear, usually before most of the rats began to move. Thus when the rats appeared on the scene a large percentage of the traps were no longer available as crabs had already taken the bait or been caught. During one night's trapping on a low lying part of Long Motu with a high crab population and numerous rats present a grid of 50 ground-laid traps caught six crabs and had 42 traps sprung with the bait taken, but not a single rat was caught. On Atafu (Wodzicki, 1973c: 21) serious crab interference also occurred with traps nailed at about 1.8 metres above ground level on coconut palms. *Coenobita* spp. and *Birgus* were the observed culprits.

Wodzicki (1973c: 21) found that land crabs on Atafu also ate both zinc phosphide baits and anticoagulant warfarin baits laid for rats. He found *Coenobita* spp. regularly inside aluminium tubes (70-80mm in diameter) containing grated coconut with 2.5% zinc phosphide and these land crabs were without doubt responsible for the disappearance of many of the poison baits. Partly or fully grown *Birgus latro* was too large to enter the poison tubes, but indentations made by the claws of *Birgus* on both ends of several tubes showed that these large land crabs had tried to reach the baits inside. From later crab baiting in areas poisoned with zinc phosphide on Atafu, it is clear that this poison adversely affects (presumably "kills") *Coenobita* spp. (see table IV, Olopuka quadrat).

Warfarin cake baits on Atafu were also greedily eaten by *Coenobita* spp. and *Birgus*, particularly when this bait was laid on the ground. These land crabs were also seen taking rat cake nailed at about 1.8 metres above ground level on coconut palms, and on one occasion a dozen *Coenobita* and one *Birgus* were observed around a single bait on a palm trunk. No information was obtained on the affect of this anticoagulant on land crabs on Atafu.

To guard against the possibility of secondary poisoning of humans during zinc phosphide baiting for rats, the *Fono Toeaina* (Council of Elders) on Atafu ban visits to, and the collecting of land crabs on, properties poisoned for a fortnight after the laying of such baits (Wodzicki, 1973c: 22). In the Olopuka quadrat trial, zinc phosphide in grated coconut was presented (as described above) in aluminium tubes which prevented the entry of *Birgus latro* and *Cardisoma* spp. Only 5 *Coenobita* were counted at crab baiting 21 days later compared with counts ranging from 84 to 333 per visit on unpoisoned quadrats (see table IV). The counts of *Birgus* and *Cardisoma*, however, were

approximately the same as the counts made in the unpoisoned quadrats.
Thus, as zinc phosphide affects *Coenobita* spp., it probably affects
other land crabs, however, the use of poison tubes prevents the larger
(and more sought after by the islanders) *Birugs* and *Cardisoma* spp. from
having access to this poison.   If such precautions are taken there
should be little or no risk to the Tokelau people of secondary
poisoning from zinc phosphide during future rat control programs.
Smith (1969: 67-68) conducted zinc phosphide poisoning trials on caged
land crabs and Ship Rats *(R. rattus)* in the Gilbert Ialands and was able
to demonstrate that land crabs appear to have "a considerable
resistance to zinc phosphide".   He could not secondarily poison rats
with zinc phosphide-fed crabs.   He concluded that the "risk of any
secondary poisoning to human beings would appear to be negligible".

We assume that the ubiquitous presence of land crabs on the Tokelau
atolls probably affects the Polynesian Rat population in two ways.   The
large species, particularly *Birgus latro,* presumably prey on rats,
especially on young in the nest, while the movement of swarms of land crabs
of all sizes may force rats to take up an arboreal existance.   These
assumptions are undirectly supported by the fact that no rat nests were
found at ground level by K.W. during his four visits to the Tokelau
Islands.   The only rat nests seen were in the tops of coconut palms and,
in one case, in the hollow top of a one-metre high palm stump.   Presumably
crabs also compete, to a certain extent, with rats for available coconuts
split open by islanders and abandoned (compare Hedley's comments at the
beginning of the section on "Ecology").   As already described, such
opened coconuts on the ground attract large numbers of land crabs at
night and the presence of these crabs could interfere with rats feeding
on this coconut meat.   Mosby, Wodzicki and Thompson (1973) demonstrate
that the coconut meat forms an important part of the rat diet on the
Tokelaus.   *Rattus exulans* is presumably too small to attack crabs,
except in their juvenile stages, and this assumption is supported by the
almost complete lack of crustacean remains in the 312 rat stomachs from
all three Tokelau atolls analysed by Mosby *et al.*

Predation

The two main predators of land crabs in the Tokelaus are man and
pigs.   As stated above in the list of Tokelau crab names, most of the
larger land crabs are actively collected and eaten by the islanders.
Thus *ugauga (Birgus latro)*, *tupa (Cardisom carnifex)*, *paikea (C.
rotundum)*, *kalamihi (Geograspus crinipes)* to a lesser extent, and
presumably the larger *uga (Coenobita* spp.) are all food items for man.
On Atafu Atoll edible land crabs are known to be more abundant on the
eastern islets as already mentioned.   K.W. was informed that certain
of these eastern islets were reserved for crab collecting and were left
undisturbed for periods of time to allow larger harvests of *Birgus* and
other species to be made at spaced intervals.

Pigs on Pacific islands are notorious eaters of land crabs. Although
pigs are kept on the Tokelaus in enclosures or on small islets, Dr. Hooper
has reported that *paikea* in particular are collected specifically for

feeding to penned pigs. Occasional escapee pigs are known to have reached isolated areas and to have survived, presumably partly on land crabs, for considerable periods.

SUMMARY

As each section above has been followed by a separate discussion, the main findings brought out by the present contribution can be summarized as follows:

1.   Ten species of "land crabs" are recorded from the Tokelau Islands. They belong to six genera placed in three families. Four of these species are terrestrial hermit crabs (Anomura) and six are terrestrial true crabs (Brachyura).   These ten species are listed here with their most commonly used Tokelauan names.

Coenobitidae

Coenobita brevimana Dana, 1852   *uga*
Coenobita perlata H. Milne Edwards, 1837   *uga kaifala*
Coenobita rugosa H. Milne Edwards, 1837
Birgus latro (Linnaeus, 1767)   *ugauga*

Grapsidae

Geograpsus crinipes (Dana, 1851)   *kalamihi*
Geograpsus grayi (H. Milne Edwards, 1853)
Metopograpsus thukuhar (Owen, 1839)   *lala*
Sesarma ? gardineri Borradaile, 1900   *ataata o hiliao*

Gecarcinidae

Cardisoma carnifex (Herbst, 1796)   *tupa*
Cardisoma rotundum (Quoy and Gaimard, 1825)   *paikea*

Eight of these species have already been recorded from the Tokelau Islands but two, *Geograpsus grayi* and *Metopograpsus thukuhar*, are new records for this group of atolls.

2.   The number of land crab species on the Tokelau Islands (10) can be compared with Holthuis's (1953) figure of 15 land crab species on Arno Atoll in the Marshall Islands, and 11 species on Ujae Atoll in the same Micronesian group.   Holthuis gives a combined total of 16 land crab species for the Marshall Islands in the western central Pacific and seven for Raroia Atoll in the Tuamotu Archipelago, eastern Polynesia.   Another recent record for Micronesia is Niering's (1956) figure of nine land crab species on Kapingamarangi Atoll in the Caroline Islands.

3.   All the land crab species recorded from the Tokelau Islands, except for the poorly known *Sesarma ? gardineri*, are widely

distributed species in the Indopacific known from the East African coast or the Indian Ocean islands eastwards to the Society Islands or the Tuamotu Archipelago.   *S. ? gardineri* is at present known with certainty only from New Guinea, southern Micronesia and the Tokelaus.

4.   Quadrat counts and relative numbers in collections indicate that *Coenobita brevimana, Birgus latro, Cardisoma rotundum* and *Geograpsus crinipes* are the most numerous species (in decreasing order of abundance) on the Tokelau Islands.

5.   Fourteen different crab names in the Tokelau language are listed and their identity discussed.   The most abundant species as listed immediately above, are called *uga, ugauga, paikea* and *kalamihi*.   These names and some others listed are used with minor modifications for similar species in Samoa, Niue and the Cook Islands.

6.   All the land crab species in the Tokelau Islands are nocturnal scavengers.   Population counts on Atafu Atoll in the Tokelaus give a density of about 560 land crabs per 5000 square metres, and this can be compared with approximately the same figure given for land crab density on Kapingamarangi Atoll in the Caroline Islands by Niering (1956).   This is in dramatic contrast to a figure of approximately 30,000 land crabs per 5000 square metres obtained by Ehrhardt (1968) on Clipperton Atoll off southern Mexico in the eastern tropical Pacific.

7.   The presence of numerous land crabs on the Tokelau Islands has an indirect effect on rat control programs and (presumably) a direct effect on rats themselves.   Land crabs interfere with snap traps, both ground laid and fixed to trees, and with poison baits.   Both warfarin and zinc phosphide baits are eaten by these crustaceans.   The effect of the anticoagulant land crabs in the Tokelaus is unknown, but it is clear from poison trials in quadrats that crab numbers were severely affected by the acute poison zinc phosphide.   The very slight risk of secondary poisoning of humans can be virtually eliminated by following recommended precautions.

Land crabs directly affect Polynesian Rats in two different ways. Large species can presumably prey on rats, especially young, thus forcing rats to nest above ground level, mainly in coconut palms. Land crabs also compete with rats for the coconut meat available in nuts opened by Tokelauans and abandoned.

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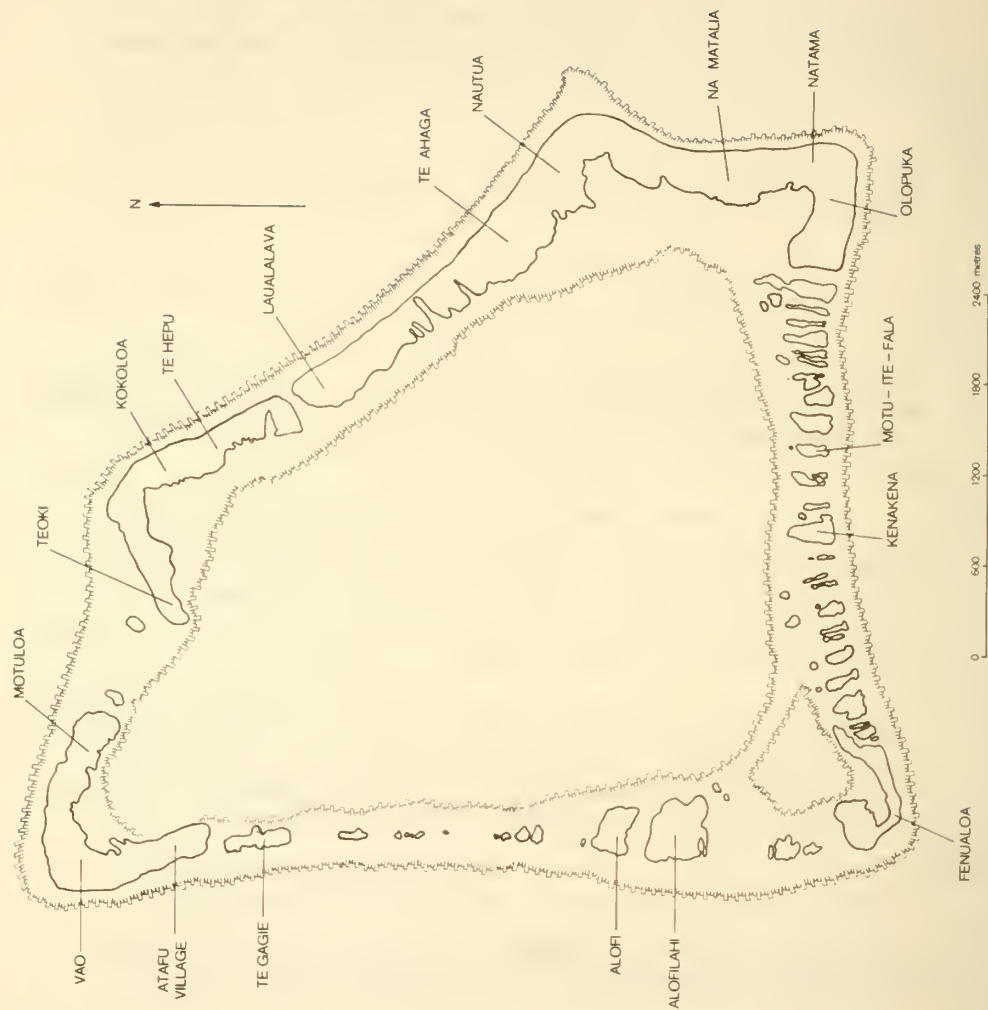
Fig. 1. Map of Atafu Atoll, based on N. Z. Lands and Survey Department
Aerial Plan No. 1036/7A (1974).
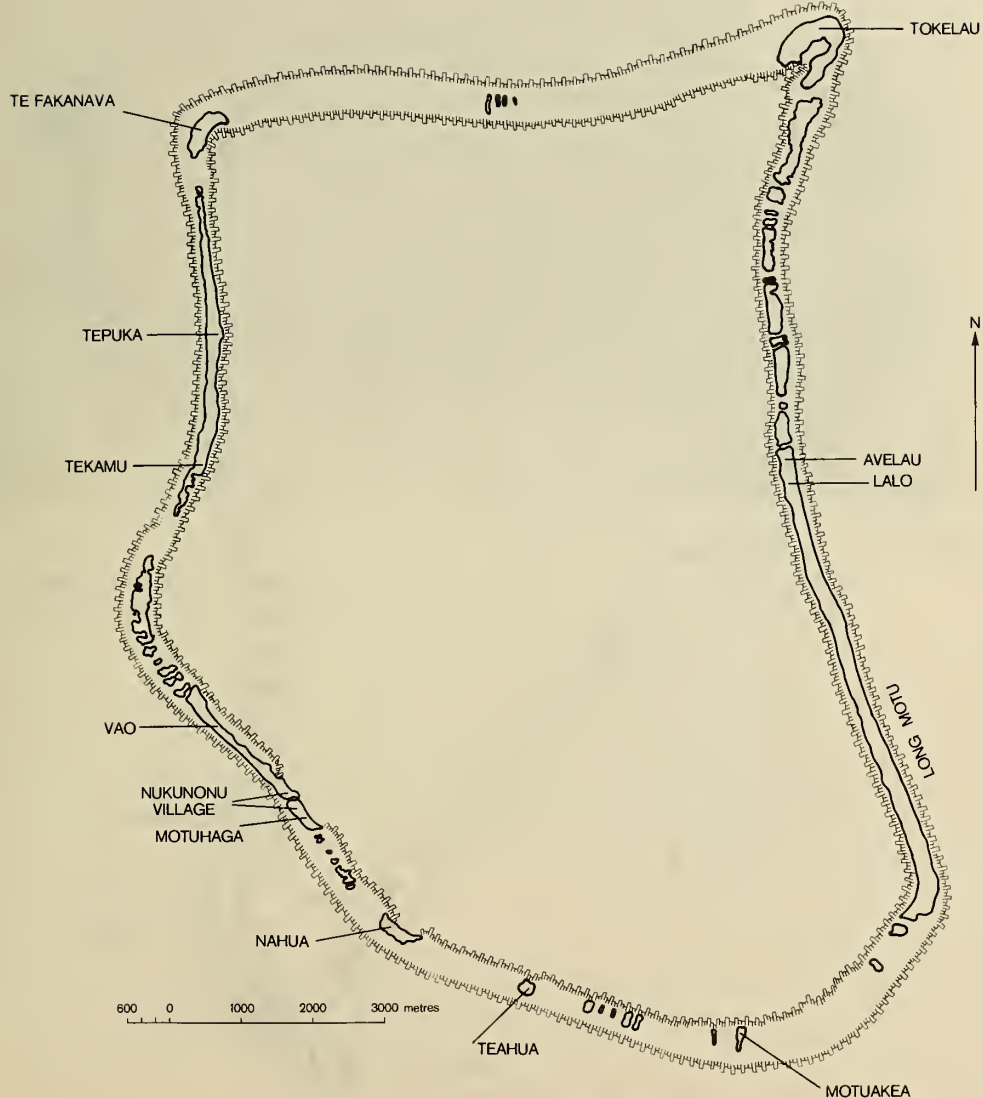
Fig. 2. Map of Nukunonu Atoll, based on N. Z. Lands and Survey Department
Aerial Plan No. 1036/7B sheets 1 and 2 (1974).

MULIFENUA

LEFU

MATAGI

FENUAFALA

FAKAOFO
VILLAGE

TETIALAU

SAUMAFATAGA

SAKEA

FENUALOA

N

600   0   1000   2000   3000 metres
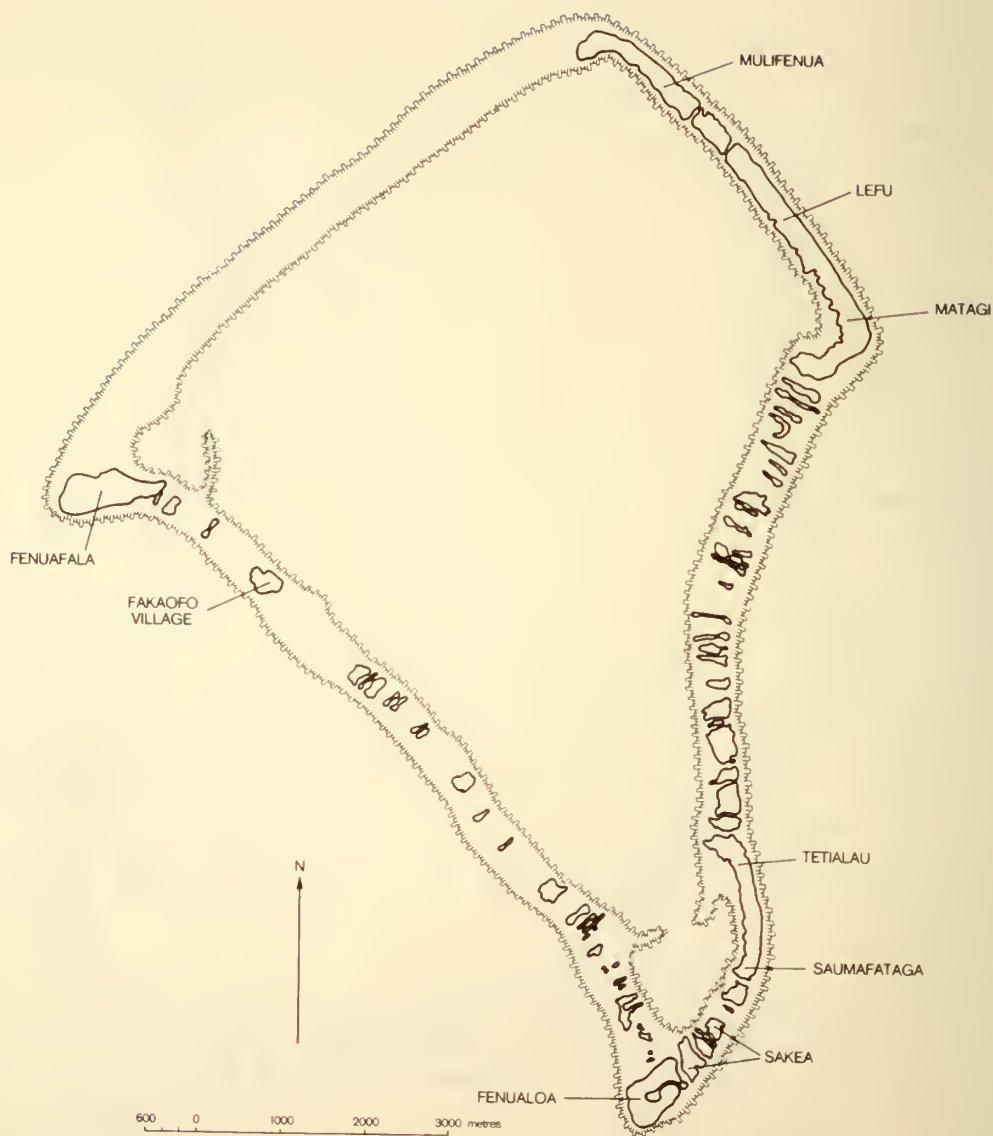
Fig. 3.   Map of Fakaofo Atoll, based on N. Z. Lands and Survey Department
          Aerial Plan No. 1036/7C (1974).
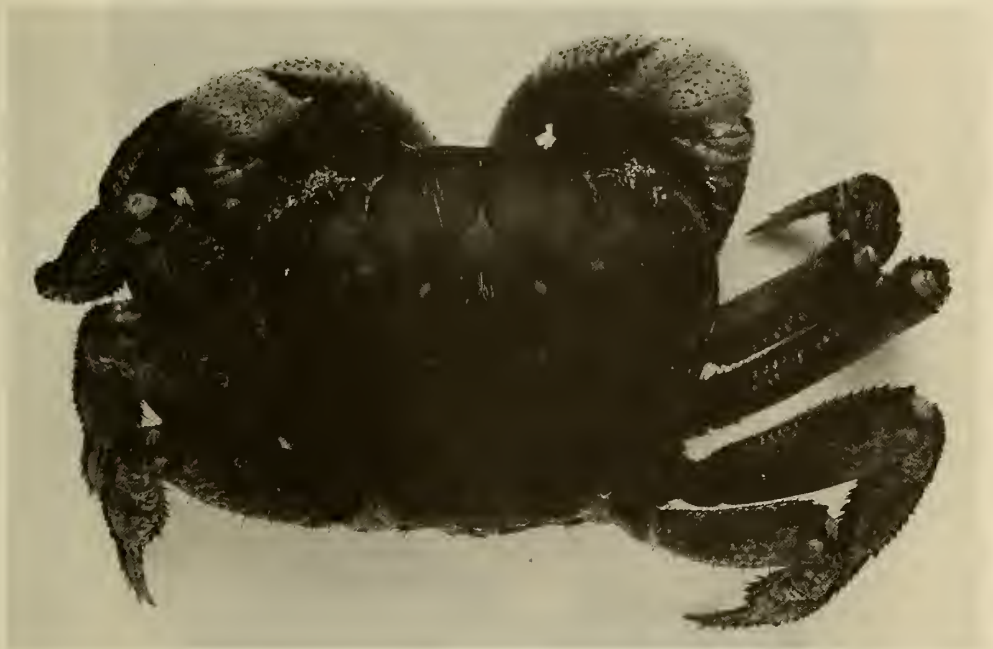
Fig. 6.   *Cardisoma rotundum*.   Dorsal view of male, carapace length 41.5 mm
         from Village Motu, Nukunonu.
         (<u>Photo</u> T.R. Ulyatt)

Fig. 4. *Sesarma (Labuanium) ?gardineri*. Dorsal view of male, carapace
length 28 mm from Nautua, Atafu.
(Photo T.R. Ulyatt, National Museum of N.Z.)

Fig. 5. *Cardisoma carnifex*. Dorsal view of female, carapace length 64 mm
from Atafu.
(Photo R.R. Ulyatt)

SOME ASPECTS OF THE ECOLOGY OF REEFS SURROUNDING ANEGADA, BRITISH VIRGIN ISLANDS

by R.P. Dunne and B.E. Brown

THE VIRGIN ISLANDS

Scale of Miles

Heights in Feet

Longitude West of Greenwich

ATLANTIC

OCEAN

ANEGADA

The White Horse

Pelican Point
East Pt
White Bay
Settlement
Cooper Rock
Little Anegada
Soldier Pt
Windlass Bight
Wells
Keel Pt
West End
Ruffling Pt
Pomato Pt

Necker I
Prickly Pearl
Virgin Sound
Mosquito I
Gorda Sd
South Sound
1370
VIRGIN GORDA
Pajaros Pt
Copper Mine Pt
Fallen Jerusalem
Round Rock
Round Rock Passage
Ginger I
Seal Dogs
George Dog
Gt Dog
West Dog
1960
Cooper I
Carvel I
Tow Rock
Scrub I
Beef I
Bull
Dead Chest
Blonde Rock
Salt I
Peter I
Salt I Passage
SIR FRANCIS DRAKE CHANNEL
Gt Camanoe I
Guana I
Rough Pt
TORTOLA
1270
1200
Road Town
1780 Harbour
Sage Mtn
Norman I
Pelican I
Flanagin I
Carrot Shoal
Santa Monica Rock
Leduck I
Eagle Shoal
Ram Head
ST JOHN
1192
Narrows
Windward Passage
Congo Cay
Lovango Cay
Pillsbury Sound
St James Is
Dog Rock
Thatch Cay
Grass Cay
Great Thatch I
Little Thatch I
Cut
Thatch I Cut
Green Cay
Sandy Cay
1010
1070
Gt Harbour
Jost Van Dyke
Little Van Dyke
Great Tobago I
Little Tobago I
Mercurius Rock
King Rock
Middle Passage
ST THOMAS
U.S.B.

ATLANTIC OCEAN
Anguilla
Virgin Is
Barbuda
St Kitts
Nevis
Antigua
Redonda
Guadeloupe
Dominica
Martinique
St Lucia
St Vincent
Barbados
Grenada
Tobago
Trinidad
Windward Is
Leeward Is
CARIBBEAN SEA
Puerto Rico
VENEZUELA

SOME ASPECTS OF THE ECOLOGY OF REEFS SURROUNDING ANEGADA, BRITISH VIRGIN ISLANDS

by R.P. Dunne[1] and B.E. Brown[2]

Introductory Description

Anegada is a most unique island from many aspects. Northernmost of the American and British Virgin Islands and easternmost of the Greater Antilles, it is a flat limestone island, 17 km long and 4 km wide with a total area of about 14.94 square miles (9,567 acres 54 sq km). It is set aside from the other British Virgin Islands, being some 19 km from Virgin Gorda, its closest neighbour. It lies in distinct contrast to the volcanic and mountainous landscapes of the Virgin Group, with a maximum elevation of only 8 metres. To the north and east (windward side) the island is edged by extensive reefs beyond which stretches the Atlantic Ocean. On the leeward side, a shallow sea (2 to 8 m) separates Anegada from the main Virgin Island Group.

History

Schomburgk (1832) is the earliest authority on the island, having visited it in 1831 when he completed a most extensive survey. He writes: 'Of its history little is known; there is no likelihood that it was settled early. Père Labat, the only early writer who speaks of the Lesser West India islands, observes, that aborigines used it as an occasional rendezvous, where they procured great quantities of conchs (Strombus gigas); and large piles of these shells are still to be seen at the east end of the island, but nowhere else; which seems to prove decidedly that it was not permanently occupied, but merely resorted to from time to time.' One of these heaps was again reported by Krieger (1938) during his visit to the Virgin Islands in 1937. Gross (1975) notes that for these conch the technique that has been used to extract the animal from its shell is distinctly aboriginal; quoting de Booy (1919) as the authority. Certainly it is not a technique used by the modern West Indian conch fisherman. Gross has also obtained radio carbon dates of AD 1245 +/- 80 for two samples of the conch shells.

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1.   2.
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                                   Cullercoats,Tyne & Wear, England
    (Manuscript received June 1977--Eds.)

Schomburgk continues: 'At a later period the retired bays of the island served as a lurking place to buccaneers, Kirke and Bone being said to have especially frequented it: and the latter has bequeathed his name to a creek on the northern side, which appears to have been his favourite resort. Ultimately as the trade among the West Indian islands became more frequent, and repeated shipwrecks in this quarter held out hopes of advantage to those who might be in the neighbourhood to profit by them, settlers took up their permanent residence on the island, and were, at one time, more numerous than they are now. They found that the loose ground which covered it was capable of bearing provision crops, and even cotton; while the rearing of stock and sale of the underwood, which was progressively cleared away and which, being very full of gum, had a preference in the market of St. Thomas, furnished a further resource. The great object, however, always was and still is, the wreck of vessels.'

In their bibliography of the Shipwrecks of the Virgin Islands (1523-1825), Marx and Towle list some 82 recorded wrecks on Anegada. Schomburgk himself records 53 wrecks on the island between the years 1803-1833. It is clear, therefore, from these facts alone that the Island has been the unfortunate site of many wrecks, which have both served to support and add to the community.

In 1832 Schomburgk reported this community to number 11 white and 21 coloured families. It is fair to say that the total population of the island was about 132. Since then, the population has rarely risen above 300. The 1970 Census indicated a population of 271 people living on Anegada.

In the latter years this population has remained low because of the lack of any form of industrial development, and with fishing and agriculture on a small scale only, Anegadians have had to look elsewhere for employment. As the other major islands in the British Virgin Islands have not been experiencing full employment, Anegadians have tended to emigrate, mostly to the USA and in particular to New York, where today there exists an Anegada Progressive League. This League has some 100 members, but there are thought to be up to 800 Anegadians in New York. In many cases, whole families have departed and in others the working age element only. This has left a population that comprises mainly children, teenagers and elderly people.

Recent History

The latter days of Anegada's history are perhaps the more interesting.

In 1967 the Government entered into an agreement with a development company, called the Development Corporation of Anegada (DEVCAN), whereby the whole island, with the exception of 1,500 acres, was leased to the Corporation for 199 years. They would be permitted to develop the Island as they wished as a major tourist resort and

commercial area.

Concern was subsequently expressed on the social and economic implications of the concessions granted to the corporation, particularly in relation to the extent to which the hands of future governments would be tied virtually indefinitely and the way in which the existing residents were being confined to a relatively small area around their village. Eventually, a commission of enquiry was held under the Chairmanship of Sir Derek Jakeway KCMG OBE which reported in November 1969 on both the Anegada and Wickhams Cay Agreements.

The report found that there were certain conditions in the agreements which could be regarded as unfair in national terms and suggested they should be renegotiated.

This solution proved unacceptable to the government and it was decided that the interests of all the companies concerned should be purchased. Agreement was finally reached in July 1971, for a price of $ 5.8 millions, of which $ 2.127 millions was attributable to interests held in Anegada.

Subsequent to the withdrawal of DEVCAN, the island was proposed as an oil storage and refining complex for the Virgin Islands Refinery Corporation. The Government rejected this proposal for several reasons. Firstly the company required a very large acreage at the West End; secondly, the Government were asked to sign an agreement before details of the proposal were known; and thirdly, the company wished exclusive right on all its activities. (British Virgin Islander, January 1974). The Government had also become cautious in its dealings over Anegada, and particularly felt that in this case insufficient steps had been taken to ensure protection of the environment.

In May 1973 preliminary discussions were held in Tortola between members of the Government and representatives of the Sterling Bank and Trust Company Ltd., of Grand Cayman concerning the future development of Anegada. As a result, the Government welcomed and approved a proposal by Sterling Bank to set up a Study Group whose purpose would be to investigate the feasibility of developing the western part of Anegada as a low density tourist/residential project aimed at supplying the needs of both the local and international markets. The Government's approach was cautious and no agreement had been signed before the unexpected overnight collapse of the Sterling Bank in late 1974. As a result all further work on Anegada has ceased and there is at present no likelihood of a continuation.

Since that date no further proposals have arisen and it seems unlikely that any further development schemes will arise for some time to come.

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ISLAND STRUCTURE

Introduction

Like many low limestone islands in tectonically active areas
Anegada does not have an easily defineable history.   The Island is
an elevated coral reef, orientated parallel to the incoming wave
trains like its modern counterpart.   The mechanism which has caused
this emergence provides a complex problem entailing at least two
principal factors either alone or in combination.   The discussion
presents evidence in an attempt to identify the factors and mechan-
isms which have occurred.

Geological Origin of the Virgin Islands

The naturalist Schomburgk (1832) first discusses the origin of
Anegada and the Virgin Islands.   He states: 'The surface of the
island is the production of the industrious tribe of lithophytae,
based (it may be presumed) as usual on a submarine elevation; and,
as it has been supposed that the West Indies have been detached from
the Floridas by an eruption of the ocean, the whole may be considered
as a chain of mountains projecting from the American Continent.'

Today we are naturally able to be more authoritative than
Schomburgk about Anegada's structure and origin.   Geologically the
Virgin Islands belong to the Greater Antilles (Cuba, Hispaniola,
Puerto Rico and Jamaica).   They rise from a continental platform,
the Puerto Rican Shelf, which is about 65 metres below sea level.
Only the island of St. Croix is separated from the rest of the archi-
pelago by the greater depths of the Anegada Passage, which is up to
4,500 metres deep.   According to Blume (1974) the islands are com-
posed of folded Cretaceous sedimentary rock as well as metamorphic
and volcanic rocks and have a dome shaped or mountainous relief.

Heatwole and MacKenzie (1967) are the most recent authority on
the geological origin and describe events in their chronological
account (Fig. 1).

'The Puerto Rican Shelf resulted from vulcanism during the
Cretaceous (Meyerhoff, 1933) and became emergent largely through
orogenic movements in the lower Eocene.   Subsequent sea flooding
occurred in the Oligocene followed by raising during a middle
Miocene orogenesis.'

According to one view, there was then a Pliocene upheaval
(Butterlin, 1956).   A tilting to the northeast then supposedly
occurred which permitted the Atlantic and Caribbean to inundate part
of the shelf, separating the Virgin Islands from Puerto Rico
(Mitchell, 1954).   Mitchell also suggests that the Anegada Passage,
which separates St. Croix from the other islands, was formed in the
Quaternary.   He claims that at least one major subsidence, followed
by emergence, occurred in the Pleistocene, with minor vertical
oscillations into recent times.

Recent evidence indicates that the Caribbean area has been more stable in the late Tertiary and Quaternary than the above summary would suggest. Weaver (1961) suggests that vertical differential movements have been negligible in the Caribbean since the Miocene and that the stage by stage emergence of Puerto Rico resulted from eustatic sea level lowering rather than movements of land masses. Proceeding from the premise that Caribbean land masses have been relatively stable since the Miocene, Heatwole and MacKenzie constructed a paleogeographic map of the Puerto Rican Island Shelf for different periods using sea level curves (Fig. 2).

According to this analysis, Anegada has been connected to the Virgin Islands and Puerto Rico by a land bridge until between 10,000 - 8,000 BP (Before Present) and was subsequently of much greater area until between 8,000 - 6,000 BP when its present shape was attained. In their subsequent investigation of faunal similarity and endemism the results further suggest that this land bridge has existed until fairly recently. Carey (1972) concurs with this model in his investigations on the herpetofauna of Anegada. If these conclusions on the geological evolution and faunal similarity are correct, then it is clear that the island as it exists today was above sea level at least 8,000 years ago.

Topography

Anegada has a surface area of 9,567 acres (14.94 sq. miles; 33 sq km: Survey Department, Tortola). Topographically it is flat, with a maximum elevation of about 26 feet above mean level near the Settlement and on the northwestern shore at Cow Wreck Bay (Directorate of Overseas Surveys). In the past there has been much disagreement over the true height; Schomburgk (1832) mentions a height of 60 feet at the East End, Britton (1916) suggests 30 feet, Howard (1970), Carey (1972) and LaBastille (1973) all quote heights of between 24 and 27 feet, D'Arcy (1971) on the other hand reports that the greatest elevation today seems to be less than 15 feet with much of the island less than 10 feet above sea level. Actual authorities for these heights are unclear, and it would thus seem that the greatest reliance can be put on the Directorate of Overseas Surveys work in 1971 (Fig. 3).

Physiography

The island is described by Howard (1970). He notes that the island is composed entirely of limestone. Bedrock is exposed over 60% of the island and typically is characterised by a modified karst topography. Solution pits and sinkholes are abundant with maximum diameters of three feet and depths greater than eight feet (Plate 2). The western 40% of the island is mantled by loose carbonate sands with a moderate vegetative cover. He concludes that the island can be divided into five physiographic subdivisions: 1. Bedrock Ridge, 2. Bedrock Flat, 3. Stabilised Dune and Beach Ridge complex, 4. Salt Ponds, 5. Mangrove Marsh. (Fig. 3.) A further description of the island by Evans (1974) states that the western end is sand, stabilised dunes and internal ponds, to the east is upraised coral

limestone with some loose rock, but very little eroded.   Stabilised
sand dunes run in storm ridges on the West End and all along the north
coast at heights of 12 - 16 feet.

Geology

Howard states that Bedrock on the island is composed entirely
of blue grey to dark grey limestones which range in nature from
rudaceous biocalcarenite to arenaceous calcilutite.   All exposures
which he examined were highly recrystallised.   Evidence of pre-
modern sub aerial exposure was found in two localities where packets
of highly oxidised silt containing terrestrial gastropods were
preserved in solution sinks.   D'Arcy (1975) records examination of
samples yielded by recent quarrying to a depth of 20 - 30 feet on the
limestone plain, and refers to the rock as bioclastic partially
recrystallised limestone containing the foraminifer Archaias, which
ranges in age from the Eocene to the Recent.

On the basis of lithologic and paleontologic variations
Howard (1970) has delineated two distinct facies:

1. A high energy reef front.

2. A quiet water, relatively protected reef platform.

He describes the reef front as generally orientated N30 W,
parallel to modern prevailing wave trains, with a series of irregular
projections with a general orientation of N 70 E and which appear
from aerial photographs to parallel modern spur and groove structures
directly seaward of the ridge (Plate 1).   Fossil remains from the
reef front inland of Pelican Point (Fig. 3) show species of Montastrea
and Diploria (Plate 3).   Howard also notes the presence of the
whelk Citarium pica.   Further back on the reef platform remains of
Acropora cervicornis are found (Plate 4) and Howard additionally notes
the fossils of mollusca Codakia and Olivella, and corals Millepora,
Diploria and Montastrea.   Here the fossil corals are normally
concentrated in relatively small areas which he interprets as
representing small patch reefs developed locally on the platform.

Age

Sample dates have not been obtained for the Anegada limestone
and estimates of age of the fossil reef are based on observations of
previous workers.   Howard (1970) classifies it as exclusively late
Cenozoic limestone possibly of Pleistocene age.   Further evidence to
suggest that the reef is of the late Cenozoic era is furnished by the
fact that during the late Mesozoic and early Tertiary the Atlantic and
Pacific Oceans were connected through what is now central America; as
a result, reef genera in both oceans were closely related, the closing
of the Isthmus of Panama that occurred in the Miocene and the number
of Atlantic genera decreased to less than 20 while Pacific genera
increased to more than 80. (Milliman, 1973).   Since the visible
fossil evidence from Anegada is clearly a Caribbean fauna, the last

reef growth has undoubtedly occurred since the Miocene segregation. Additionally, on the geological evidence of Heatwole and MacKenzie (1967) the Puerto Rican Shelf would have been in existence post the Miocene and possibly provided a shallow enough base for reef formation, although the water depths over this part of the shelf are probably not quite as clear cut as their model of sea level changes suggests.

Tectonics or Sea Level Stands

Anegada's emergence could have occurred as a result of two possible events, (1) tectonic activity causing local uplift, or (2) reef growth during the high sea level stands of the inter glacial. The evidence supporting these two postulates will now be examined.

Blume (1974) observes that low lying limestone plateaux in the Caribbean are frequently partly dissected marine abrasion platforms of Pleistocene age which have been uplifted by recent tectonic activity. Furthermore recent plate tectonics have established Anegada's position in a potentially active area, on the edge of the Caribbean plate under which the Atlantic plate is forced (Horsfield and Bennet Stone, 1972). If the origin is indeed tectonic uplift then by the results of faunal similarity (Heatwole and MacKenzie, 1967) it is probable that the reef would have been uplifted at some time before 10,000 BP in order for the land bridge to have existed.

The second possible mechanism is that of sea level change. Stoddart (1969) notes that evidence from marine terraces, especially in Europe, indicates a general Quaternary sea level regression from an early Pleistocene level 180 m above the present. Successively lower terraces correspond to successive inter glacial sea levels in this scheme. Reefs, therefore, could presumably have been built to higher levels than the present during each of these interglacials. In the western Atlantic, Broecker and Thurber (1965) have calculated dates from Bahaman and Florida Key limestones which indicate that periods of marine limestone formation existed at about 85,000, 130,000, and 190,000 years ago, and imply that the surface of the ocean was then slightly higher than at present. Stoddart (1969) also points out that slightly elevated reefs and lithified deposits of reef origin are common throughout the reef seas, and some of these exposures have been correlated with emergent terraces on Pacific high islands and referred to Holocene high stands of the sea. Uranium series dating of elevated coral limestones in the Indian and Pacific Oceans has given a date as last interglacial (circa 130,000 BP). He is cautious, however, to take account of certain cases where elevated deposits are attributable to local storm action, as in Micronesia (Shepard et al., 1967), or of local tectonic emergence, as on Guam. The former of these cautions is unlikely in the case of Anegada where both orientation and apparent zonation is in support of an entire elevated reef rather than rubble beds containing fossil corals.

Howard (1970) has apparently committed himself to an opinion that Anegada owes its existence to previous high sea level stands by suggesting that the emergent portion represents the maximum elevation attained by a series of periodically re-established barrier reef - carbonate platform complexes. Evidence for this is not forthcoming and remains unsubstantiated.

The problem in defining Anegada's emergence thus remains, until further light is cast by more detailed investigations.

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REEF STRUCTURE OF ANEGADA, BRITISH VIRGIN ISLANDS

The ecology of reef systems within the Northern Caribbean has now been extensively studied, particularly as a result of the work of Newell (1959); Newell et al (1951, 1959); Goreau (1959a, 1959b, 1966); Goreau and Wells (1967); Goreau and Goreau (1973); and Glynn (1973a and b). In a comprehensive survey of work in this area, Milliman (1973) states that the most distinctive difference between coral reef studies in the Caribbean and those in the Pacific has been the direction of emphasis. The most recent investigations in the Caribbean have centred around sedimentological and geological aspects of reef and bank environments whereas Pacific studies have had an essentially biological theme.

This difference in scientific approach is exemplified by work which has been carried out to date on the reefs around Anegada, one of the most northerly islands of the British Virgin Group. A brief mention of the geology of the island is recorded by Martin Kaye (1959) but more recently a reconnaissance of the geology of the island was carried out by Howard (1970). This paper describes the geological structure of Anegada and presents evidence for the origin of the island and its surrounding reefs. A recent paper by Adey and Burke (1976) on the Holocene bioherms of the Eastern Caribbean also includes a brief description of the reefs around Anegada. Although not specific to Anegada, this paper is also primarily concerned with the origin of Caribbean reef structures.

The following investigation is an attempt to describe the reefs surrounding Anegada from a biological standpoint. Because of the nature of the study, descriptive methods were adopted that were essentially similar to those used by Goreau (1959) in his original survey of the Ocho Rios reef off north-east Jamaica. In this way a semi-quantitative measure of diversity and abundance of coral species was obtained together with descriptions of unusual growth forms and distribution patterns.

SITE DESCRIPTION

Windward Shore

Along the windward shore of the island four main sites were selected. These were West End, Jack Bay, Loblolly Bay and East End (Fig. 4). In addition, Cow Wreck Bay and Bone Bay were also included in a preliminary reconnaissance survey and observations on these areas are included in the text.

Leeward Shore

Along the leeward shore nine patch reefs were studied in detail. The position of the selected study areas is shown in Fig. 4.

METHODS

Initially a brief preliminary survey of sites around the island was carried out in an attempt to ascertain which areas would benefit from more detailed study.

Windward Shore

At each selected site on the northern shore, an area approximately ½ km wide, was mapped from the shore, seawards across the reef. The shore was first mapped by theodolite and Tellurometer and temporary stations triangulated into the Directorate of Overseas Survey network. The seaward zone was mapped using an inflatable with echo sounder and reflective prisms for the Tellurometer instrument. A snorkel diver provided underwater information, which was recorded along with station fixes, by the boatman. The information obtained in this way correlated extremely well with detail taken from aerial photographs and also provided additional information about substrate type which enabled better interpretation of the photographs.

Transects were then laid from the shore across the reef as far as proved physically possible. In some cases transect length exceeded 600 m. The transect line was marked at 10 m intervals with buoyant coded tags and was aligned by the use of shore transect markers. Depth soundings were then taken at each tag marker along the full length of the transect and these later corrected by the use of simple tidal data recorded on the shore. A profile was then drawn by two divers swimming the transect and noting coral species, colony size and any other notable physical features. Detailed observations were also made on the dominant algae and the presence of gorgonids and sponges noted. The profiles were then employed to define any zonation on the reef. The zonation system chosen was based upon that used by Goreau and Goreau (1973), although not all zones were represented at the sites chosen on Anegada. Generally the following zones were recognised - Lagoon, Rear reef, Reef top and Buttress. At two sites - Jack Bay and East End it was necessary to include an inshore zone within the zonation scheme.

Within these zones the abundance of recorded coral species was noted. A system similar to that used by Goreau (1959) was adopted, in which relative abundances were assessed using the following notation:

Rare

Scarce

Common

Abundant

Working from the transect line within a zone, the area investigated fell in the range of vision from that marker. Underwater photographs were taken in representative areas and particular note was

made of any unusual growth forms encountered during searches. Specimens of unidentified coral species were collected and returned to the field laboratory for later identification.

Leeward Shore

On the southern shore where discrete patch reefs are found, work concentrated on a total description of the patch together with an estimation of the abundance of observed coral species.

OBSERVATIONS

A notable feature of the windward shore reef is its continuity. Only at a few points along the 11 mile shoreline is it broken by narrow channels and only at one place does it appear to be absent - Deep Bay. Along its length there is considerable variation in the shoreline to reef distance (Fig. 4 and Plate 1). Starting at West End the main reef lies approximately 500 m offshore; at Windlass Bight 2 km; at Jack Bay only 200 m, and at Pelican Point the distance increases up to 3 km as the reef leaves the easternmost point of the island to form Horse Shoe Reef. At one location, Soldier Point, the reef comes within several metres of the shoreline.

The main reef system consists of a mixture of coral and algal ridge systems; the dominant coralline algae being crustose species such as Lithophyllum spp., Porolithon spp., and Neogoniolithon spp. One outstanding feature of the main reef system on the north-eastern side of Anegada is the patchiness of the Acropora palmata dominated rear reef, much of which is dead, extensively bored and coated by crustose coralline algae. Another significant feature of the reef structure is the lack of any 'drop-off' beyond the buttress zone. As noted earlier by Adey and Burke (1976) this region consists of a coralline dominated spur and groove fore-reef. Maximum depths, at the base of the spurs, are approximately 10 - 15 m, the bottom sloping away gently seawards. It has been suggested by Adey that a shallow bench exists at 10 - 15 m, sloping from west to east, upon which the reefs and ridges of Anegada are built.

There follows a general description of the main reef system of Anegada in terms of the zones described earlier for the windward shore, and comparative descriptions for selected patch reefs on the leeward shore.

Windward Shore

i) Inshore Zone

An inshore zone could only be defined at two locations along the windward shore of Anegada - at transect 2 in Jack Bay and Transects 5 and 9 at East End (Plates 16 and 18).

The profile for transect 2 at Jack Bay shows an inshore area of beach rock. This structure extended approximately 1 km along the western shore of Jack Bay but as the profile indicates, was limited

in its extent seaward. The beach rock had abundant algal cover in the tidal pools, the dominant species being Turbinaria turbinata. Also recorded in this habitat were large numbers of the chiton Acanthopleura granulata (Gmelin).

In contrast, at the East End of the island the inshore zone was found to consist of a fringing reef (Plate 18). The structure extended approximately 2 km east of Pelican Point, around the eastern tip of the island, and approximately 400 m to the west of the Point - its seaward extent being approximately 50 - 100 m.

Profiles of this zone are illustrated in Fig. 11 where it can be seen that the structure may be divided into three areas: i) An inshore sand bottom, colonised by algae and spermatophytes (the dominant species being Penicillis capitatus, Halimeda incrassata and Syringodium filiforme and Thalassia testudinum respectively), ii) a coralline algae dominated section, and iii) an outer living coral region.

At a distance which varied between 10 - 15 m from the shore, two coralline algae species (identification still to be confirmed) became dominant. Thalassia, Halimeda and Penicillis were still present but were not as abundant as before.

At approximately 20 - 25 m from the shoreline small amounts of the coral Porites porites var. divaricata were found. Most of the coral found at this point was living and interspersed with coralline algae and sparse Thalassia. Beyond this distance along the profile, large amounts of Porites appeared to be dead (ratio live:dead approximately 1:3) and encrusted by coralline algae. Within this habitat, considerable numbers of echinoids were found, in particular Echinometra lucunter.

The components of the outer living edge of the inshore fringing reef varied, depending on the site chosen for study. East of Pelican Point and actually extending around the east end of the island, the outer rim of the reef consisted of Porites porites var. divaricata (ratio live:dead 1:1) which then gave way to Acropora palmata in the deeper waters (0.5 - 1.0 m) of the edge of the structure.

West of Pelican Point the outer part of the 'fringing' reef consisted predominantly of living Porites (Plate 6), which provided an excellent habitat for many small reef fish. Water depths at the base of the Porites bank were also in the range 0.5 - 1.0 m.

The inshore fringing reef was only found around the east end of Anegada. Both Almy and Carrion Torres (1963) and Glynn (1973a) have also described Porites divaricata Leseuer forming either separate colonies or a continuous cover at 0.5 - 1.0 m depths close to the coastline around Puerto Rico. Roos (1971) reports pavements of Porites porites var. divaricata in very shallow water at Arashi, Aruba.

ii) Lagoon Zone

          The lagoon zone was the most extensive of all zones to be
described on the windward shore.   As mentioned earlier the reef
distance from the shoreline varied considerably along the windward
coast so that the lagoon may vary in its leeward extent from 50 m
to 1.5 km.   A comparison of the profiles drawn on the windward
shore illustrates this well.   Towards the west end of the island,
i.e., West End, Cow Wreck Bay, Bone Bay, Windlass Bight, where the
lagoon was at least 250 m wide, patch reefs were found which were up
to 15 - 20 m diameter.   At both Cow Wreck Bay and Bone Bay there were
large numbers of well developed patch reefs.   The depth of the lagoon
at these two sites ranged between 2 - 4 m.   Generally the inshore
patch reefs supported little live coral growth, consisting of a dead
coral base surrounded by sand and algae.   Moving out across the
lagoon towards the main reef, the percentage live coral cover increased;
dominant encrusting species such as Porites astreoides, Siderasterea
siderea, Siderasterea radians, and Diploria clivosa being replaced by
Acropora palmata, Montastrea annularis and Diploria spp. as massive
dominants in deeper water.   It was noted that a large proportion of
Acropora palmata, found on patch reefs in the outer lagoon, was dead.

          A brief count of Strombus gigas, by a visiting scientist from
the West Indies Laboratory, yielded 11 individuals/200 sq. m (Imsand -
pers. comm.) in the lagoon of Bone Bay.   This mollusc was found on a
sand bottom, colonised by Thalassia and Halodule, at a depth of 2 - 3 m.

          Tubastrea coccinea was recorded on the sheltered seaward edge of a
patch reef in Bone Bay at a depth of 0.5 m.

          Table 1 summarises the coral species found at sites around the
island and also indicates the relative abundance of these species in
each zone.   The coral Manicina areolata, was recorded at only two
sites along the windward shore, one of these being the lagoon zone at
West End where it was noted as scarce.   At West End the most notable
feature of the lagoon was the extensive sandy areas covered by
vascular plant species and algae.   These included; Thalassia
testudinum, Syringodium fileforme, Halimeda incrassata, Penicillis
capitatus and Udotea flabellum.   A species list for the area is given
on page

          At Jack Bay (transects 1 and 2) and Loblolly Bay (transect 3)
where the lagoon was less extensive than in the above areas, i.e.,
60 - 170 m seaward extent, less established patches of coral were
found, ranging from individual coral heads to coral patches 10 - 20 m
diameter.   Generally the ratio of live to dead coral was low - 1:3,
the dominant species being encrusting forms and those resistant to
sedimentation.   Acropora palmata, Montastrea annularis, Montastrea
cavernosa, Porites porites and Acropora cervicornis were represented
although their distribution was patchy.   The live corals tended to
be based on dead coral substrate which was colonised by algae species
such as Padina sanctae-crucis, Codium spp., Turbinaria tricostata,
Halimeda monile and Sporochnus pedunculatus.

At the east end of the island the lagoon area separated the main
reef from the shore by a considerable distance - in excess of 1.5 km.
From aerial photographs the lagoon at East End would appear to be an
area in which there is considerable transport of sediment by currents,
much of this material being deposited on the leeward side of the
island.   Within the lagoon area worked, similar features were noted
as observed at West End.   Such similarities included extensive areas
of coralline derived sand colonised by Thalassia and Syringodium,
interspersed by Penicillis, Halimeda and Udotea; also predominantly
barren inshore areas with dead coral substrate covered by sand and
algae.   Two 90 m transects confirmed these general observations
(Plate 18).   Transect 6 was laid over an area covered by Thalassia
with patchy and sparse coral cover.   The most significant feature
at this site was the abundance of Strombus gigas over a complete size
range.   At previous sites only large individuals had been noted
within the lagoon (Bone Bay, Loblolly Bay).   Also at East End several
large specimens of the King Helmet shell, Cassis tuberosa, were
recorded close to the shore at Pelican Point.

A second 90 m transect, approximately 1 km from the shore,
traversed an area in which there were several well developed, isolated
patches of Diploria labyrinthiformes, Montastrea annularis, Acropora
cervicornis and Acropora palmata.   Many specimens of Acropora palmata
were actually detached from the original coral base but were still
continuing to survive.   Particular note was made of the non-hermatypic
coral species, Tubastrea coccinea, which was recorded in several seaward
facing overhangs of Montastrea annularis.

No quantitative measurements were made on the abundance of Diadema
antillarum; most individuals were seen in the lagoon zone but at no
site did numbers appear to equal the density of animals reported on the
rear reef at Taque Bay, St. Croix.   (Ogden et al. 1972).

iii) Rear Reef

The rear reef, at the major sites visited on the windward coast
(West End, Jack Bay, Loblolly Bay and East End) extended between 70 - 100
m beyond the lagoon to the reef top.   Depths of water over the rear
reef ranged between 1-2 metres, with depths of 2-3 metres in sandy
areas between the coral growths.   Characteristically the rear zone was
an area in which the dominant corals were Acropora palmata and to a
lesser extent, Montastrea annularis.

Although as many as 27 coral species, out of a maximum of 31
recorded for the entire island, were noted in this zone, the distribution
of coral was again very patchy with considerable amounts of dead coral
and coral rubble interspersed between live specimens.   The extent of
dead coral within the rear reef is well illustrated in Figures 7, 8, 9
and 10, showing profiles of the windward shore.   The sea-fan Gorgonia
flabellum, and the sea-whips Pseudopterogorgia americana and Plexaura
spp. were relatively common in the rear zone, particularly in Jack
Bay and Loblolly Bay (Plate 7).

At West End the rear reef contained substantial dense patches
of Thalassia (up to 900 sq. m), which was growing upon sand that had
accumulated on dead coral substrate.   Generally there was a paucity
of live coral in this region; the majority of species being small
specimens of encrusting forms such as Porites astreoides, Porites
porites, Siderasterea radians, Siderasterea siderea, Diploria
strigosa, Diploria clivosa, Agaricia agaricites, and Millepora
squarrosa.

At East End there was a marked patchiness in the rear zone where
much of the substrate consisted of dead coral rubble, particularly
Acropora cervicornis.   Colonies of live coral, however, were well
established in contrast to the West End, and included Acropora
palmata, Montastrea annularis and Acropora cervicornis.   The relative
abundance of Acropora cervicornis within this area was quite marked;
large colonies (0.5 - 2 m diameter) of Diploria labyrinthiformes were
also common.

Tubastrea coccinea was recorded in a particularly high energy
environment - as indicated by extensive growth of Millepora squarrosa
nearby (Plate 8) - at the seaward limit of the rear zone where it
merged with the reef top.   The coral was found in an overhand formed
within a dead Acropora palmata colony.   Several specimens were
recorded in a similar situation in the area and although localised,
the species was relatively common here.

iv)   Reef Top

Division between rear reef and reef top was quite arbitrary at
some points along the windward shore.   At certain sites, such as
West End, Jack Bay (transect 1), Loblolly Bay and East End there were
zones which could quite easily be defined as reef top - however other
sites such as Jack Bay (transect 2), Cow Wreck Bay, and Bone Bay did
not appear to exhibit any clearly defined reef top zone.

The general water depth over the reef top of the former sites
was relatively consistent, ranging from 0.1 - 0.5 m.   At times of
low diurnal tides, many colonies of Acropora palmata were fully
exposed.   This was particularly noticeable at West End and Jack Bay.
Again this zone, like those described previously, was a region in
which dead coral predominated - living colonies being mainly encrusting
species.   Table 1 gives full details of all species recorded in the
area.   Acropora palmata was again the dominant species, the ratio of
live:dead being 1:5.   One particularly outstanding feature of the
reef top zone at Jack Bay was the existence of a coralline ridge
composed of at least three coralline algae species (identification
still to be confirmed). (Plates 9 and 10).   This ridge, already
identified by Adey and Burke (1976) is described as forming algal
ridge lobes or 'cup-reefs' on the sides of grooves which extend land-
ward into the reef-ridge system of the northeastern shore of the island.
The coralline algal ridge supports numerous fleshy algae species including
Dilophus guineensis which is particularly abundant, Dictyopteris delicatula,

Polysiphonia sp., _Hypnea_ spp. and _Ceramium_ sp.   The ridge also creates shelter for a diverse 'in-fauna' including molluscs (Gastropoda: _Acmaea_ sp., _Cremides barbadensis_ Gmelin., _Lucapina_ sp., _Tricolia thalassicola_ Robertson, Amphineura: _Choneplax lata_., _Isnochiton_ sp.) echinoderms (_Echinometra lucunter_), sipunculid worms, and amphipod and decapod crustacea.

Inshore of this region the reef top at Jack Bay consisted of dead _Acropora palmata_ which had been consolidated by the encrustations of coralline algae species and also extensively 'bored' (Plates 11 and 12).   One of the organisms responsible for this effect is likely to be the rock boring bivalve, _Lithophaga nigra_ Orbigny - specimens were collected from samples of coral returned to the field laboratory. Also found within the cavities created by boring were the bivalve mollusc _Barbaitia pulchella_ Reeve and large numbers of _Isnochiton_ sp.

Another feature of the reef top along the windward shore was the presence of a _Millepora squarrosa_ ridge at two sites - at Loblolly Bay (transect 3) and also at East End (transect 8).   At both sites _Tubastrea coccinea_ was found;   at Loblolly Bay the specimen was detached but at East End the coral was established upon dead _Acropora palmata_.

More abundant algal cover was again noted at West End where the dominant species recorded on the reef top was _Turbinaria turbinata_ - other species noted were _Padina sanctae-crucis_, _Halimeda incrassata_, _Udotea flabellum_, and _Dictyosphaeria cavernosa_.

v)   Buttress Zone

The 'buttress' or 'spur and groove' fore-reef was much more marked towards the west end of the island.   Aerial photographs support this observation and together with mapping by the Expedition indicate that the spurs and grooves are aligned at an angle of 60° to the shoreline, on a bearing N - S.

Observations of the 'buttress' zone at Jack Bay, Cow Wreck Bay and West End were quite extensive but at Loblolly it proved physically impossible to swim over the _Millepora_ high energy region.   Observations at East End were similarly limited although snorkellers did gain access to one section of the fore-reef.

At the West End site, the buttress zone did not appear to be so well developed as at sites a few km further east, i.e., West End - Cow Wreck Bay.   On transect 4 the fore-reef sloped gently away to a maximum depth of approximately 4 m.   On this slope dead coral pre-dominated although it was not extensively bored.   Dominant corals in the region were typically those characteristic of a buttress zone, namely _Diploria clivosa_, _Diploria strigosa_, _Acropora palmata_, and _Millepora squarrosa_.   Another marked feature of the slope was the abundance of gorgonians (_Gorgonia flabellum_ and _Pseudopterogorgia americana_) and algae (_Tubinaria turbinata_, _Stypopodium zonale_ and _Dictyopteris justii_).

The transect at West End (Plate 17) passed over the spur and groove system in a region where the maximum height of the spurs was only 1-2 m; the spurs consisted of dead coral and the grooves between them were filled by sand.

Further East at Cow Wreck Bay, a more developed spur and groove system (particularly to the West of the Bay) was again characterised by the dominant corals, Montastrea annularis, Acropora palmata, Millepora squarrosa and large colonies of Diploria spp. - Diploria strigosa colonies measuring up to and > 1 m.   The corals, Millepora squarrosa, ('boxwork form' Stearn and Riding 1975) and Agaricia agaricites, var. crassa were particularly abundant at the edge of spurs where the water depth was approximately 1 m.   These spurs measured up to 4-5 m in height and ranged from 4-10 m in width. Beyond this zone the bottom sloped gently away at 6-8 m with no marked drop off seaward.

In contrast to the previous areas, the buttress zone of Jack Bay (transects 1 and 2) yielded a much greater proportion of live coral together with a greater variety of coral species (Table 1).   The spur and groove effect, however, was not as evident at Jack Bay as at sites towards the west end of the island.   At the seaward end of transect 1 the dominant corals were similar to those quoted in the previous paragraph.   Particular note was made of the growth form of Acropora palmata which was encrusting as opposed to branching. Species such as Isophyllia multiflora and Isophyllastrea rigida were recorded in the buttress zone but were limited in their abundance.

The buttress zone of transect 2 was particularly significant in terms of the presence of the plate-like form of Montastrea annularis and also the abundance of Agaricia agaricites, the more typical form with thick leaf-like outgrowings and corallites on all sides of the colony.   Also on this transect, at a depth of 10 m, a record of Mussa angulosa was obtained - this was the only site at which the coral was recorded.

Beyond the buttresses formed by Montastrea annularis, the bottom levelled off at approximately 12 m, with evidence of an 'old' spur and groove formation at this depth.   These spurs were aligned similarly to those recorded at West End, although their origins were not investigated by coring.   The height of the spurs was 0.5 - 0.8 m above the sand filled grooves between them - the spurs themselves being covered by sand and algae, particularly Turbinaria spp.   From the final marker on transect 2, snorkellers swam offshore, beyond the reef, for a distance of 1 km.   The bottom was similar in type to that area just beyond the buttress zone, with intermittent large pillars of Montastrea annularis arising out of a sand substrate which was traversed by 'tongues' of rock outcrops covered by sand and algae. The depth gradually increased to 15 m about 2 km offshore at this point.

Leeward Shore

   The southern and western patch reefs border on the shallow waters
(2-8 m) of Gorda Sound.   Charts of the area show a considerable number
of coral heads breaking surface, for a distance of up to 3 km from the
southern shore of the island, and patch reef development is quite
extensive (Plates 1 and 13).   The size of the patches varies from
between 3-4 m diameter to over 100 - 200 m diameter.   Profiles of the
patch reefs are shown in Fig. 13.

   The limited amount of time available for study resulted in the
detailed description of only a small number of areas.   Eight patch
reefs were studied in all; their position relative to the island is
shown in Fig. 4.   Of those patch reefs investigated, the majority
showed an essentially similar structure, independent of their size,
apart from patch reefs III and IX which were situated in shallow
waters (1-2 m) and were much closer inshore than the other sites
visited.   The basic structure of most of the patch reefs consisted of
a central core of Acropora palmata surrounded on the outer edges by
Montastrea annularis heads and large colonies of Diploria spp.   The
latter corals formed discrete heads which were based on sand in depths
of water ranging from 5-6 m.

   A comparison of the profiles obtained for each patch reef
illustrates the similarity in basic structure.   The dominant coral on
all patches was Acropora palmata and was frequently dead and encrusted
by coralline algae.

   Generally both the abundance and diversity of coral species was
greater on the leeward side of the island than on the windward shore
(Table 1) with a maximum of 22 species recorded on patch reef II.
The abundance of Acropora prolifera was particularly noticeable on the
leeward shore especially on patch reefs II, VII and IX.   In each case
the colonies were all localised on the shoreward facing side of the
patch.

   Acropora cervicornis was also relatively abundant - particularly
on patch reefs VI, VII and VIII.   A notable feature on patch reef VIII
was an intermediate form of Acropora palmata and Acropora cervicornis,
in which cervicornis-like protuberances projected from Acropora palmata
branches.   Similar growth forms have been noticed by Roos (1971) on
Bonaire and St. Martin and obviously such observations cast doubts
about the species distinction.

   A variety of growth forms of other corals were noted, e.g., on
patch reef II and IV, two forms of Porites astreoides were observed -
the typical encrusting form and also a plate-like variety (Plate 14).
Roos (1967) has already shown that in localities where light is
limiting the coral shows a conspicuous flattening in response to
ambient light conditions.

Agaricia agaricites var. crassa and var. fragilis were also
recorded on patch reef II.   Generally Agaricia agaricites var.
fragilis was restricted to overhangs and gullies and var. crassa to
shallow water on top of the patch reef.   Millepora also displayed
several forms on this patch reef (Plate 15).   In this example both
the bladed Millepora complanata and the branching Millepora alcicornis
are illustrated, in a water depth of 3 m.

At only one site did Montastrea annularis exhibit a vertical
plate form similar to that recorded in the buttress zone of Jack Bay -
this growth form is characteristic of the species when growing on
shadowed vertical surfaces (Roos 1971).

Coral species which were either absent or rare at sites visited
on the leeward side of the island included Mycetophyllia lamarkana,
Isophyllastrea rigida, Tubastrea coccinea and Manicina areolata.
The latter species, however, was rated as common on patch reef VI
where detached specimens were found on the sand at 3-4 m water depth,
between the pillars of Montastrea annularis surrounding the patch.

In general Gorgonids were abundant at all sites - the dominant
species being Gorgonia flabellum, Pseudopteryogorgia americana and
Plexaura spp.

Apart from patch reefs III and IX, relatively few algae species
were recorded on the other patch reefs visited.   Calcareous species
noted in sand around the reefs included Halimeda opuntia, Penicillis
capitatus and Udotea flabellum.   The Queen conch, Strombus gigas,
was recorded around patch reef IV (approximate density 8 per 200 sq. m.)
and also around patch reef VI (5 per 200 sq. m.).

Patch reefs III and IX were unlike other sites visited on the
leeward shore of the island since they were in much shallower water
(1-2 m) and as a result were colonised by many algae species.   Patch
reef III at Pomato Point was located only 50 m from the shore and
consisted of mainly dead Acropora palmata which had been encrusted
and consolidated by coralline algae and also extensively bored.
Coral species, resistant to sedimentation such as Siderasterea radians
and Diploria clivosa were common.

Patch reef IX consisted of similar dominant coral species and
was also covered by abundant algal growth with dense Thalassia between
coral outcrops.   A complete list of dominant algae species collected
at these sites can be found in Table 2.

SUMMARY

Altogether 31 species of coral were recorded on Anegada - that is including sites visited on both the windward and leeward sides of the island. This figure compares with 37 species from Cuba (Duarte Bello 1961); 34 species from Puerto Rico (Almy and Carrion Torres 1963); 34 species from Barbados (Lewis 1960); 29 species from Curacao (Roos 1964); 62 species from Jamaica (Goreau and Wells 1967) and 46 Scleractinian species from Bonaire (Scatterday 1974). All these collections involved the use of similar skindiving/snorkelling techniques. However, as Goreau and Wells state in their paper on the shallow water Scleractinia of Jamaica, it is important to define the depth range in which these studies were carried out, e.g., Lewis worked to 10 m; Roos and Scatterday to 30 m, Goreau to 96 m, while other workers restricted their collections to depths of less than 10 m in areas that were mainly on the inner lagoon side of reefs. The maximum depth worked around Anegada by members of the Expedition was 10 m.

The apparent absence of Madracis decactis may be accounted for by the worked depth of only 10 m, since this species is usually restricted to deeper water, the shallowest record from material examined in the Netherland Antilles being 9.4 m (Roos 1971). Scatterday (1974) however reports abundant Madracis decactis colonies in well concealed cavities in shallow waters on the Kralendyk reefs of the Netherland Antilles.

Of those species noted on Anegada, the largest number recorded on the windward shore occurred within the rear zone of Jack and Loblolly Bay. Up to 24 species were observed here and these figures compare well with the numbers of coral species recorded on individual patch reefs on the leeward shore (17 - 24). The number of corals recorded on the reef top and buttress zone however was relatively low at all sites on the windward shore. Goreau (1973) describes similar results, in part, for the Jamaican north coast reefs where he shows that the rear zone is an area containing a varied Scleractinian community (i.e., 9 families: 17 genera: 29 species) and the reef flat Scleratinian fauna is impoverished (7 families: 10 genera: 22 species). However, in addition, the buttress zone is described as the richest habitat of the reef with 41 species of 23 genera of hermatypic Scleractinia and 2 species of Hydrocorallina. Certainly this is not the case in Anegada where the maximum number of species recorded within the buttress zone of Jack Bay was 15 (6 genera) as compared with the more diverse rear reef. There may be several reasons for this marked difference in observations: firstly, the buttress zone on Anegada is found in relatively shallow water, certainly not in excess of 10 m whereas similar zones in Jamaica extend down to depths of 20 m.

Secondly, the north coast of Jamaica may not be exposed to the same physical forces ensuing from wave action as the windward reef of Anegada where there is a considerable amount of dead and broken coral within the mixed coral/algal ridge system. The effect of wave action

is quite obvious, particularly at East End, where branches of
Acropora palmata are found detached from their original bases.   As
reported by other workers (D'Arcy 1975) a 'ground-sea' during the
winter months increases wave action considerably on the exposed
northern shores of the island.

Thirdly, hurricane damage is quite possible, as noted elsewhere
in the Caribbean (Stoddart 1963, 1974).   The most recent hurricane to
affect Anegada has been Hurricane Donna in 1960 which removed many
houses from their foundations in the 'Settlement'.   As a point of
interest in this context, a severe tropical storm (later to become
Hurricane Elouise) hit the island during the late summer of 1975 after
the completion of the current survey.   The resemblance of the Anegada
rear reef to sites affected by hurricane damage on the British
Honduras reefs is quite marked (Stoddart pers. comm.).

Although it is not perfectly clear why the buttress zone of the
windward reef is so depauperate in terms of coral species, it should
be mentioned that in a survey of Grand Cayman reefs, Roberts (1974)
describes the upper fore-reef terrace of the northern fringing reef
(water depths 5-10 m) as a 'barren plain'.   He believes that the
intense energy of the waves is dissipated in this zone and as a
result only encrusting and low relief growth forms of coral are found
here.

In terms of dominant coral species the most evident must surely
be Acropora palmata which dominates both the rear reef and reef-flat
on the north-eastern reef and also constitutes the central core of
many of the leeward patch reefs.   Such findings are in line with the
observations of Milliman (1973) who states that although Acropora
palmata may be the dominant coral in Northern Caribbean reefs (Newell
et al. 1951, 1959; Ginsburg 1956; Shinn 1963; Logan 1969) and
Montastrea annularis the dominant on south-western Caribbean atolls
(Milliman 1969a) this generalisation does not always hold.   For
instance Acropora palmata has also been shown to be the dominant coral
at St. Croix (V.I.) even though the climate resembles the southern
rather than the northern Caribbean (Milliman 1973).   With regard to
the considerable amounts of dead Acropora palmata noticed on the
windward reef of Anegada, it has been previously suggested by Shinn
(1963) that dead Acropora on the Florida reefs is the result of
'over-crowding':   Roos (1971) however does not attribute this cause to
the death of colonies in Bonaire.   In a more recent review of reefs
around Bonaire Scatterday (1974) notes that prolific growth of this
species is often limited to areas with heavy wave action (Goreau 1959;
Storr 1964; Hoffmeister and Multer 1968).   In Bonaire as in Anegada
healthy Acropora palmata may be found on both the seaward margins of
the reef as well as along channels (presumably there is sufficient
wave action along channels to promote growth).   According to
Scatterday a similar situation exists in the windward reefs of the
Caribbean Gulf of Mexico where parts of the colonies in more shore-
ward locations are killed as a result of being forced into a position
where wave action is diminished to an intolerable level, in the lee
of other colonies that are established seaward.

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Further detailed observations obviously need to be obtained around Anegada, particularly on the leeward side of the island and along Horse Shoe Reef where patch reefs abound. In terms of coral growth, patch reefs in the lee of the island showed not only a relatively good diversity of coral species but also a relatively greater abundance of these species when compared with the northern reef - particularly large colonies of the following species being found: Acropora cervicornis, Acropora prolifera, Diploria labyrinthiformes and Diploria strigosa. Scatterday (1974) also reports vigorous reef growth in leeward areas of Bonaire. This is in contrast to many other Caribbean reef systems where reefs located on the leeward sides of islands are poorly developed when compared to those found on the exposed windward coasts (Milliman 1973).

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ERA	PERIOD	Epoch	Sea level change
CENOZOIC	QUATERNARY	Pleistocene 1	Stability
		Pliocene 10	Raising
	TERTIARY	Miocene 15	
		Oligocene 10	Sea flooding of shelf
		Eocene 19	Shelf becomes emergent
		Paleocene 15	
MESOZOIC	CRETACEOUS	60 million years	Vulcanism results in formation of Puerto Rican Shelf

Holocene

present

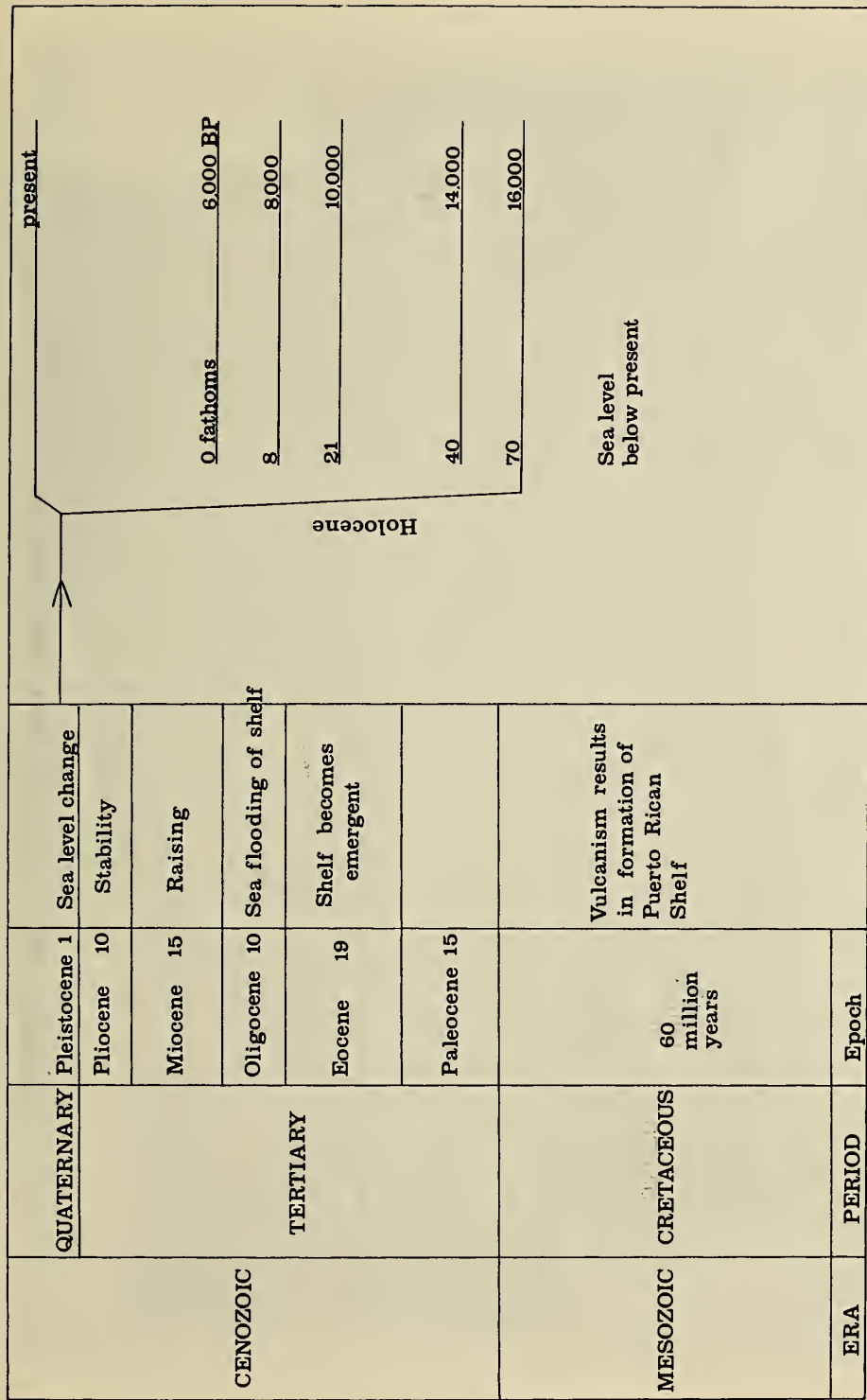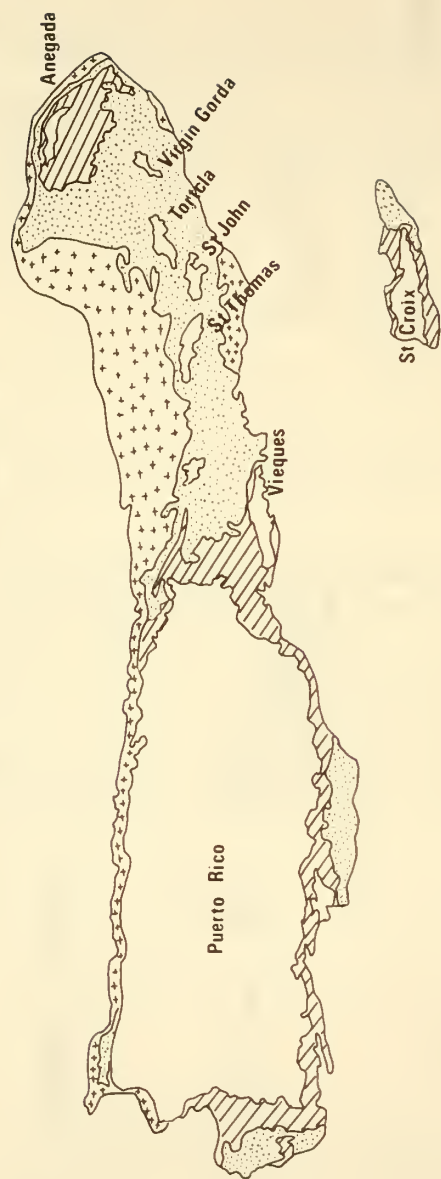|	
0 fathoms	6,000 BP
8	8,000
21	10,000
40	14,000
70	16,000

Sea level below present

Fig 1 Origin of the Puerto Rican Shelf

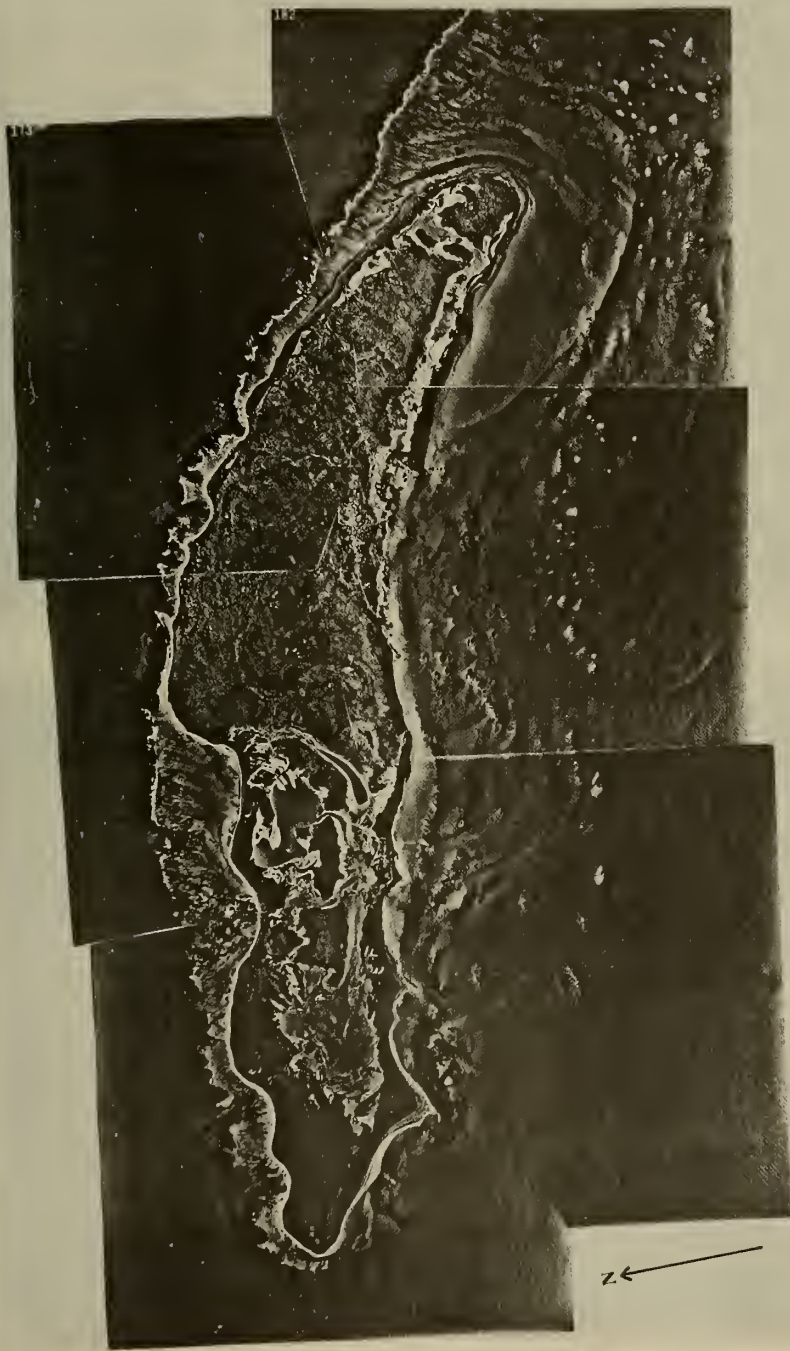Largest outline — max sea level lowering during Pleistocene

areas submerged 14,000 — 10,000 BP

10,000 — 8,000

8,000 — 6,000

Smaller islands omitted for clarity

Fig 2   Paleogeographic Map of the Puerto Rican Shelf   (after Heatwole and MacKenzie, 1967)

ANEGADA

Plate   1.   Aerial Mosaic: composed from 1959 USAF photos.
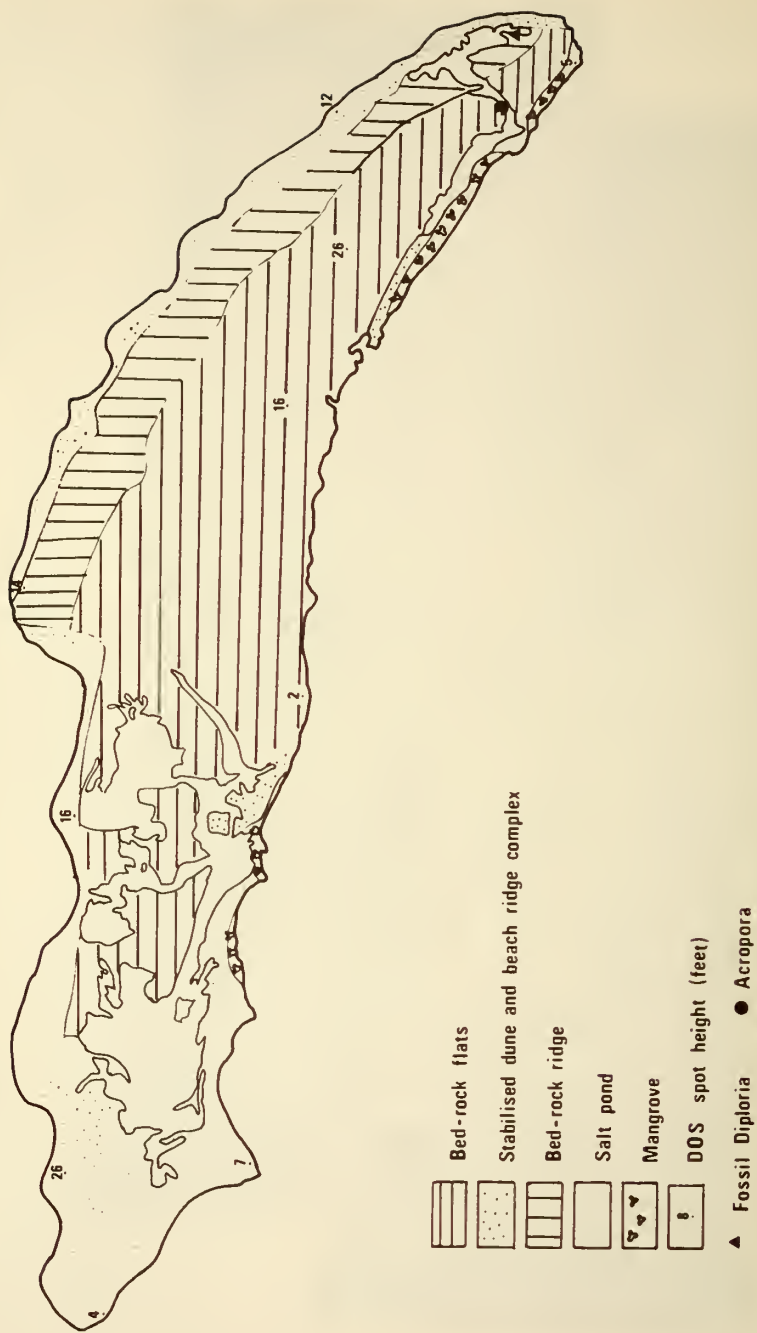
Fig 3   Physiographic subdivisions (after Howard, 1970)

Bed-rock flats

Stabilised dune and beach ridge complex

Bed-rock ridge

Salt pond

Mangrove

DOS spot height (feet)

▲ Fossil Diploria   ● Acropora

Plate 2   Potholes in Limestone: East End.
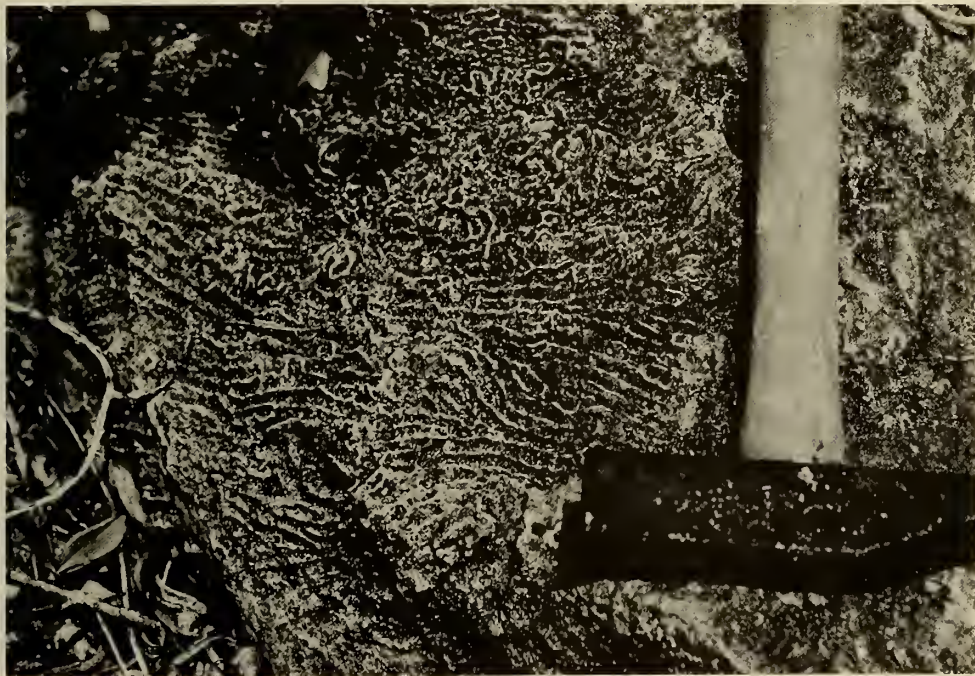

Plate 3   Fossil _Diploria_: Pelican Point.
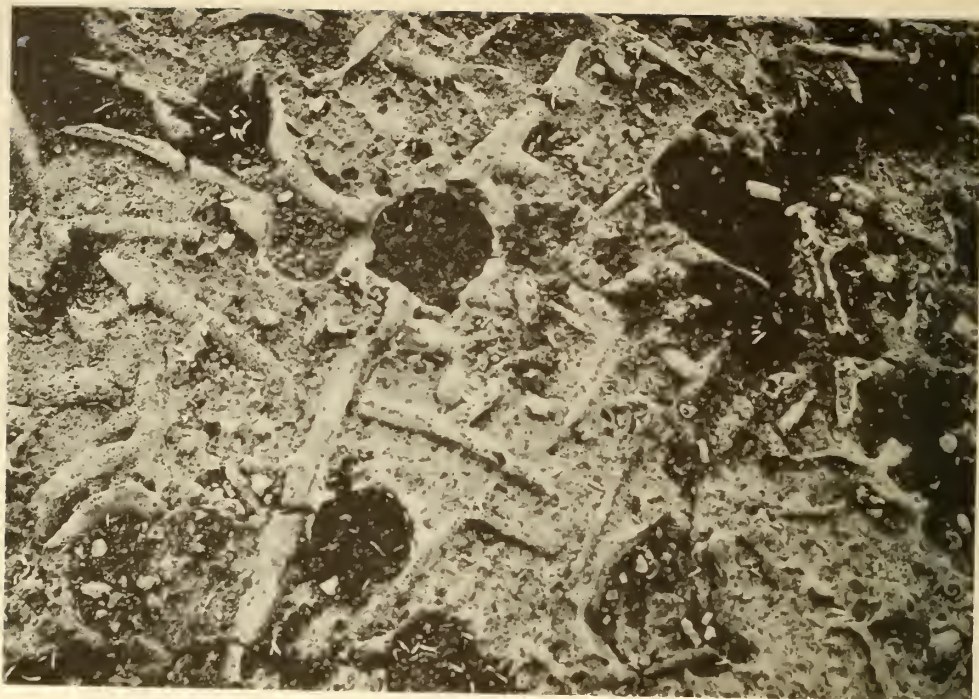
Plate 4   Fossil _Acropora cervicornis:_ Pelican Point.

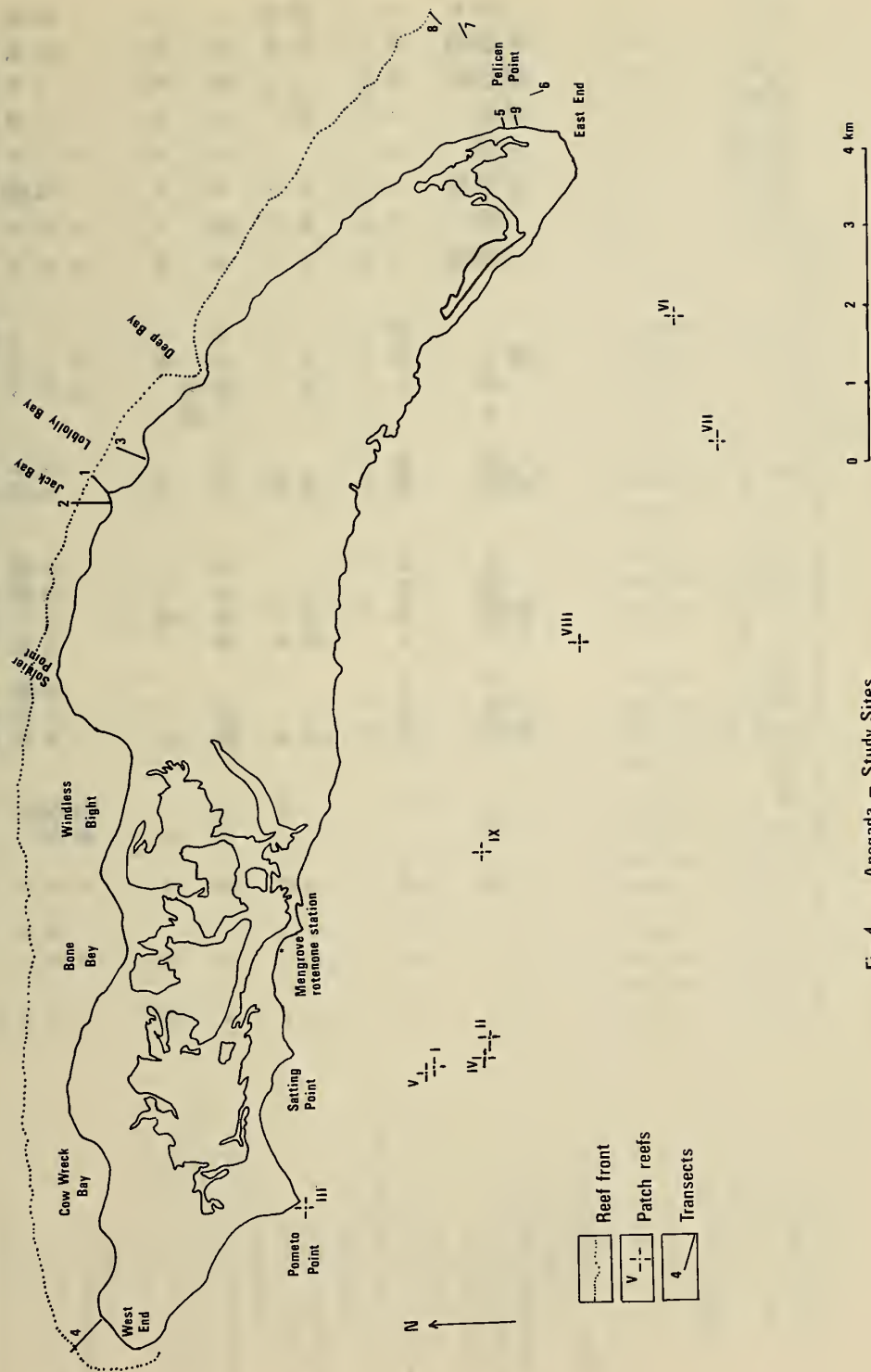Plate 5   Anegada from East End.

Fig 4   Anegada — Study Sites

TABLE 1 LIST OF CORAL SPECIES AND THEIR ABUNDANCE : ANEGADA, BRITISH VIRGIN ISLANDS.

SPECIES	WEST END Lagoon	WEST END Rear Zone	WEST END Reef Top	WEST END Buttress	COW WRECK BAY Lagoon	COW WRECK BAY Rear Zone	COW WRECK BAY Reef Top	COW WRECK BAY Buttress	WINDWARD SHORE JACK BAY TRANSECT 1 Lagoon	Rear Zone	Reef Top	Buttress	JACK BAY TRANSECT 2 Lagoon	Rear Zone	Reef Top	Buttress	LOBLOLLY BAY Lagoon	Rear Zone	Reef Top	EAST END Inshore	Lagoon	Rear Zone	Reef Top	PATCH REEFS II	III	IV	V	VI	VII	VIII	IX

ANTHOZOA SCLERACTINIA

ACROPORIDAE
Acropora cervicornis
Acropora palmata
Acropora prolifera

AGARICIIDAE
Agaricia agaricites (var. crassa)
Agaricia agaricites (var. fragilis)

SIDERASTREIDAE
Siderastrea radians
Siderastrea siderea

PORITIDAE
Porites astreoides
Porites porites (var. divaricata)
Porites porites (var. clavaria)
Porites porites (var. furcata)

FAVIIDAE
Favia fragrum
Diploria clivosa
Diploria strigosa
Diploria labyrinthiformis
Montastrea annularis
Montastrea cavernosa

WINDWARD SHORE LEEWARD SHORE

SPECIES

Column groups:

- WEST END: Lagoon, Rear Zone, Reef Top, Buttress
- COW WRECK BAY: Lagoon, Rear Zone, Reef Top, Buttress
- JACK BAY TRANSECT 1: Lagoon, Rear Zone, Reef Top, Buttress
- JACK BAY TRANSECT 2: Lagoon, Rear Zone, Reef Top, Buttress
- LOBLOLLY BAY: Lagoon, Rear Zone, Reef Top
- EAST END: Inshore, Lagoon, Rear Zone, Reef Top
- PATCH REEFS: II, III, IV, V, VI, VII, VIII, XI

FAVIIDAE cont.
Colpophyllia breviserialis
Colpophyllia amaranthus
Colpophyllia natans
Manicina areolata

TROCHOSMILIIDAE
Dichocoenia stokesii

MUSSIDAE
Scolymia lacera
Mussa angulosa
Isophyllastrea rigida
Isophyllia multiflora
Mycetophyllia lamarckana

CARIOPHYLLIDAE
Eusmilia fastigiata

DENDROPHYLLIIDAE
Tubastrea coccinea

HYDROZOA MILLEPORINA

MILLEPORIDAE
Millepora alcicornis
Millepora squarrosa
Millepora complanata

KEY :   Rare ·   Scarce ●   Common ●   Abundant ●

Fig. 5   Number of coral species recorded on A.) the Windward shore
and B.) the Leeward shore of Anegada.
Key: 1   Inshore Zone   3   Rear Reef
       2   Lagoon Zone   4   Reef Top
                             5   Buttress Zone

A.

ZONE: 1 2 3 4 5   1 2 3 4 5   1 2 3 4 5   1 2 3 4 5   1 2 3 4 5   1 2 3 4 5   1 2 3 4 5
AREA: WEST END   COW WRECK   JACK BAY   JACK BAY   LOBLOLLY   EAST END
                    BAY   TRANSECT 1 TRANSECT 2   BAY

NO. OF SPECIES   25 20 15 10 5 0

B.

NO. OF SPECIES   25 20 15 10 5 0

         II   III   IV   V   VI   VII   VIII   IX
                                 PATCH   REEF
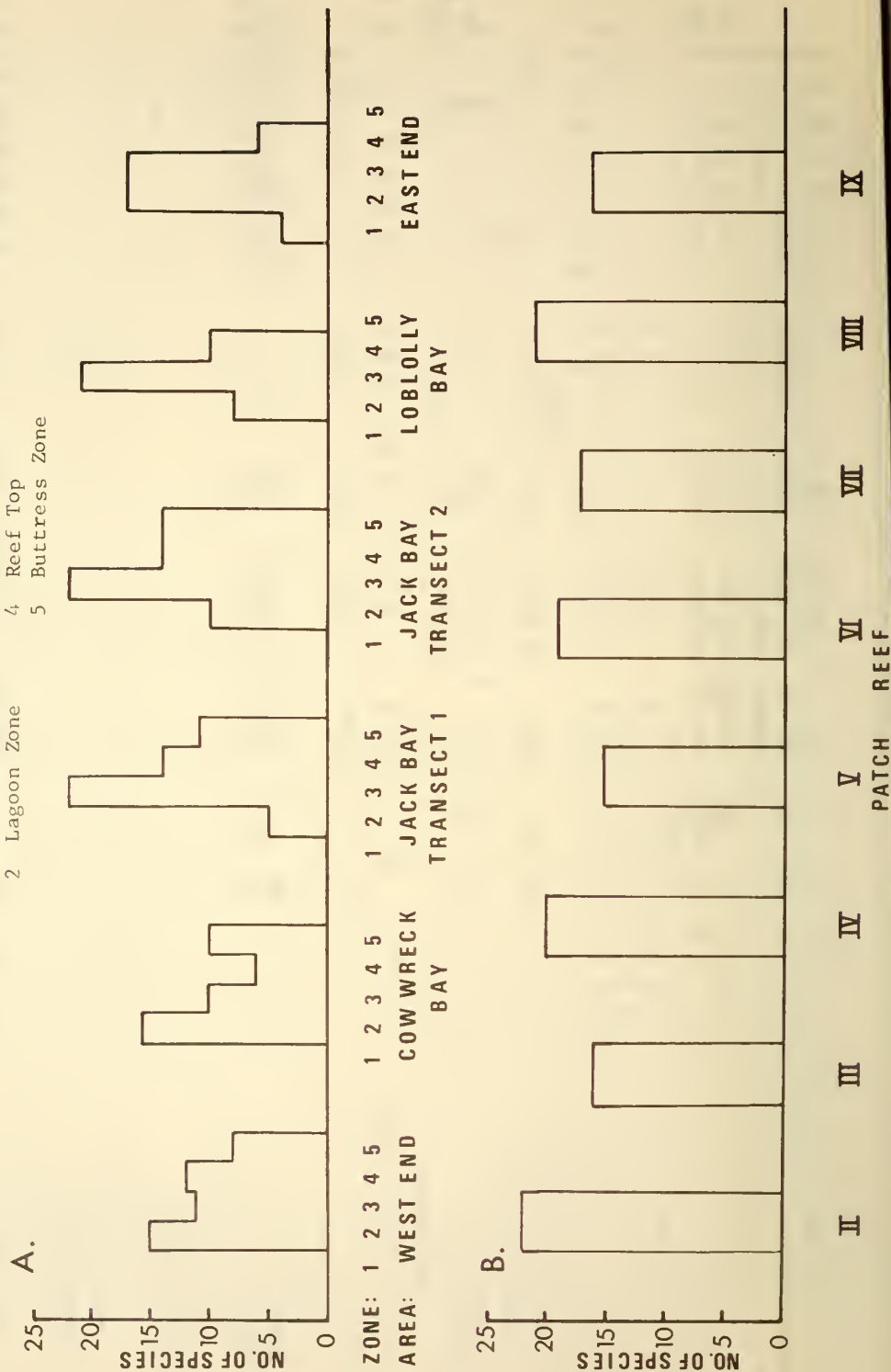
Plate 6   End of inshore transect: Pelican Point. <u>Porites</u> <u>porites</u> var. divaricata.

Plate 7   Sea-whips <u>Plexaura</u> spp. and <u>Pseudopteragorgia</u> <u>americana</u> in Jack Bay.

Plate 8   <u>Millepora</u> <u>squarrosa</u> on reef top at East End.

Plate 9   Algal ridges on seaward side of reef at Jack Bay.

Plate 10   Specimen of algal ridge, Porolitheae.

Plate 11   Extensively bored <u>Acropora</u> <u>palmata</u> on reef top at
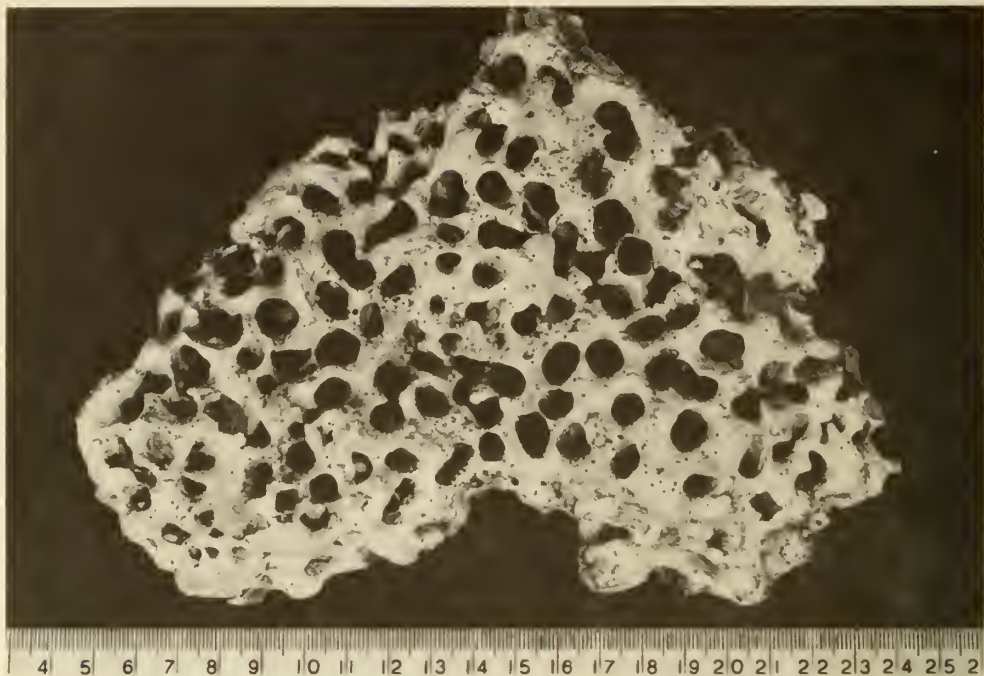   Jack Bay.

Plate 12   Specimen of bored <u>Acropora</u> <u>palmata</u>.

Plate 13   Patch reefs on leeward shore of Anegada (Virgin
Gorda can be seen in the background).

Plate 14   Plate like growth of <u>Porites</u> <u>astreoides</u>.

Plate 15   Bladed <u>Millepora</u> <u>complanata</u> and branched <u>alcicornis</u>
    on Patch Reef II.

Plate 16   Jack and Loblolly Bays; showing position of
Transects 1, 2 and 3.

LOW WATER

Legoon

Rear Zone

FINE SAND

Reef Top

DEAD BRANCHING CORAL - EXTENSIVELY BORED & POTHOLED

SAND

SAND

Buttress

SAND

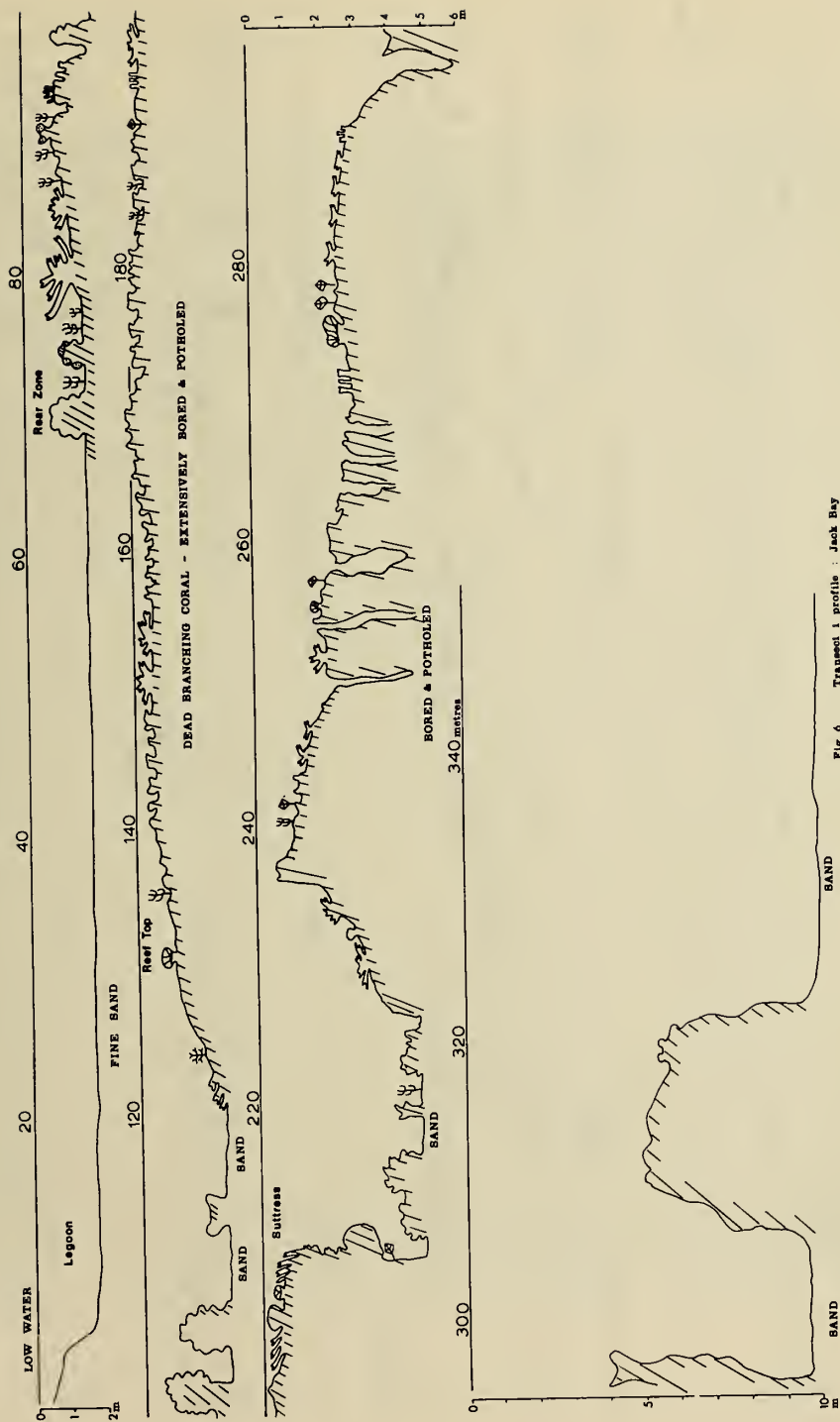BORED & POTHOLED

SAND

SAND

BAND

Fig 6   Transect 1 profile : Jack Bay
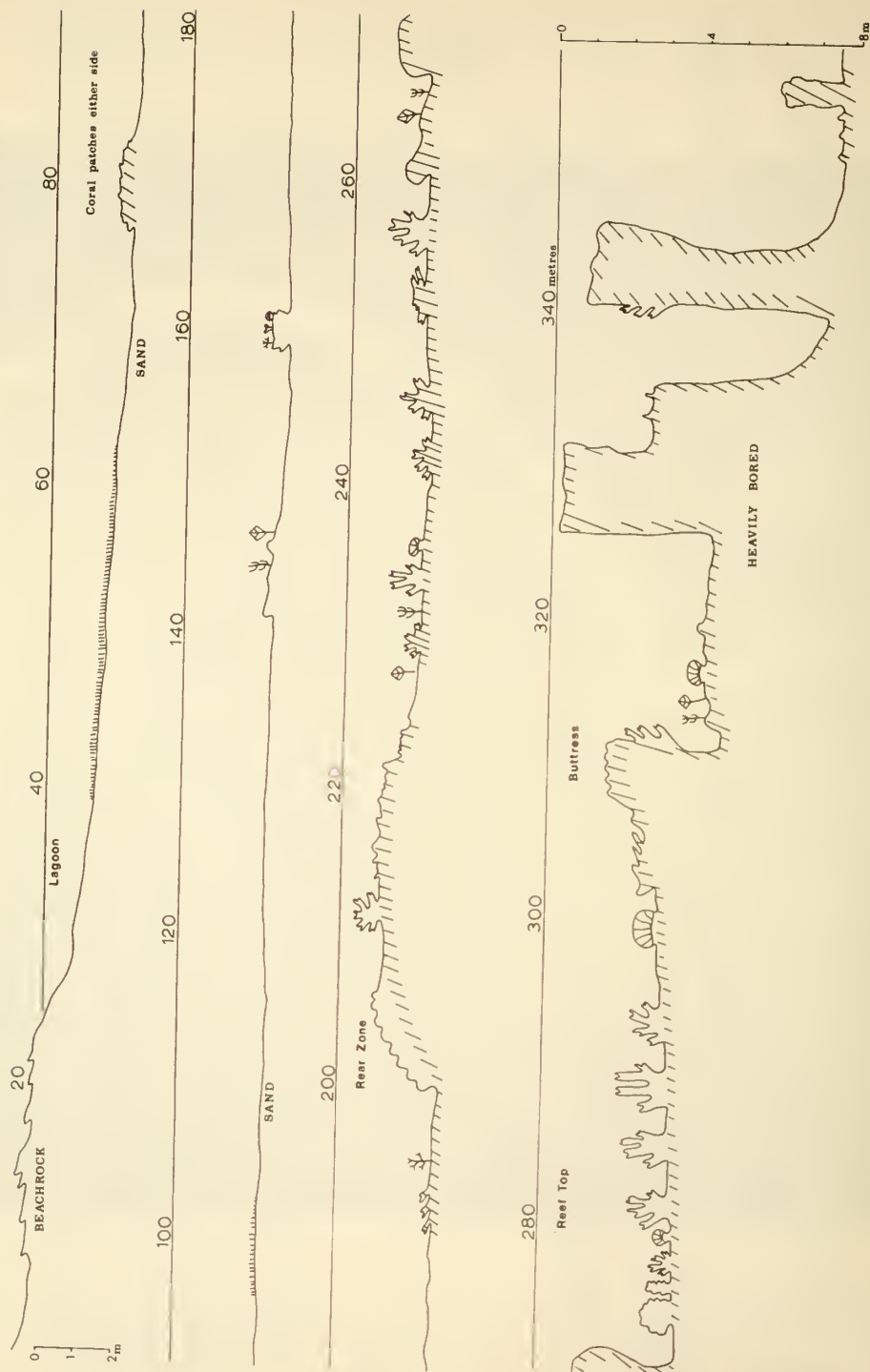
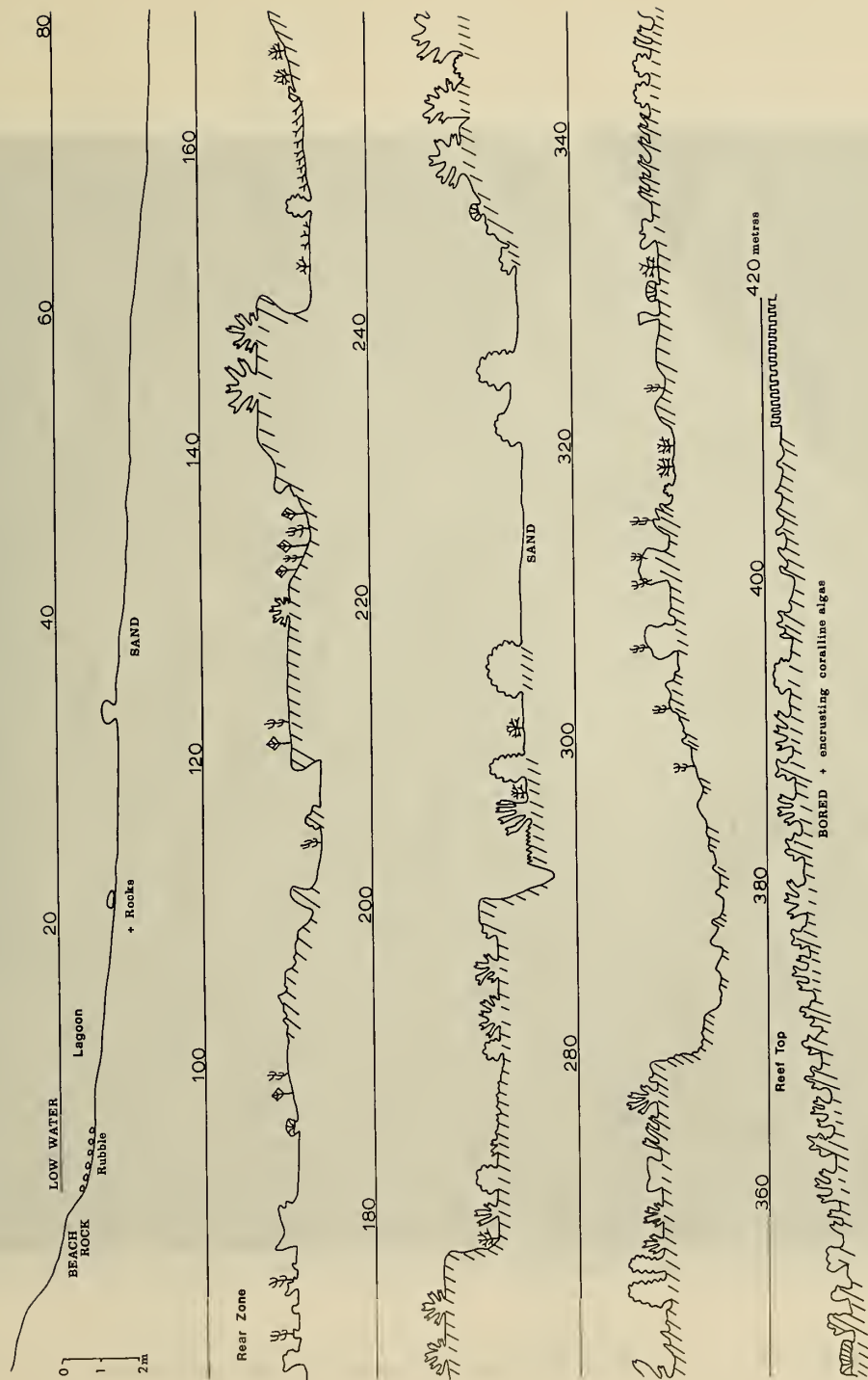Fig 7   Transect 2 profile   Jack Bay

Fig 8   Transect 3 profile : Loblolly Bay

Plate 17   West End; showing position of transect 4.
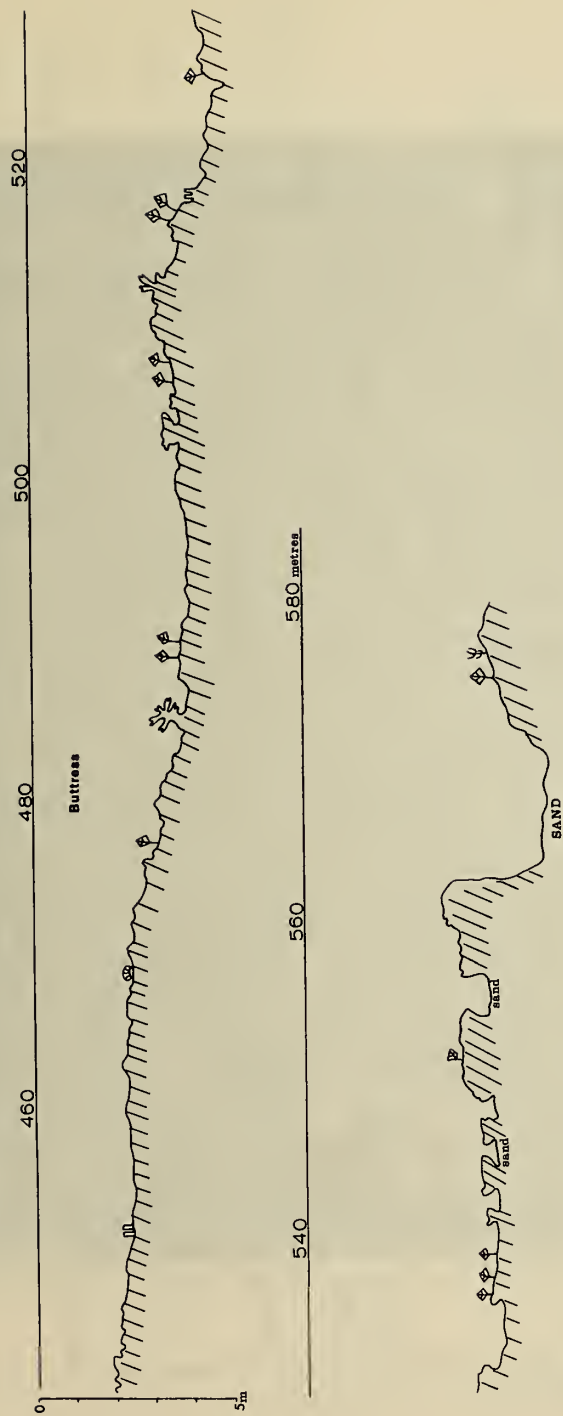
Fig.9   Transect 4 profile : West End

Plate 18   East End; showing position of Transects 5, 6, 7, 8 and 9.
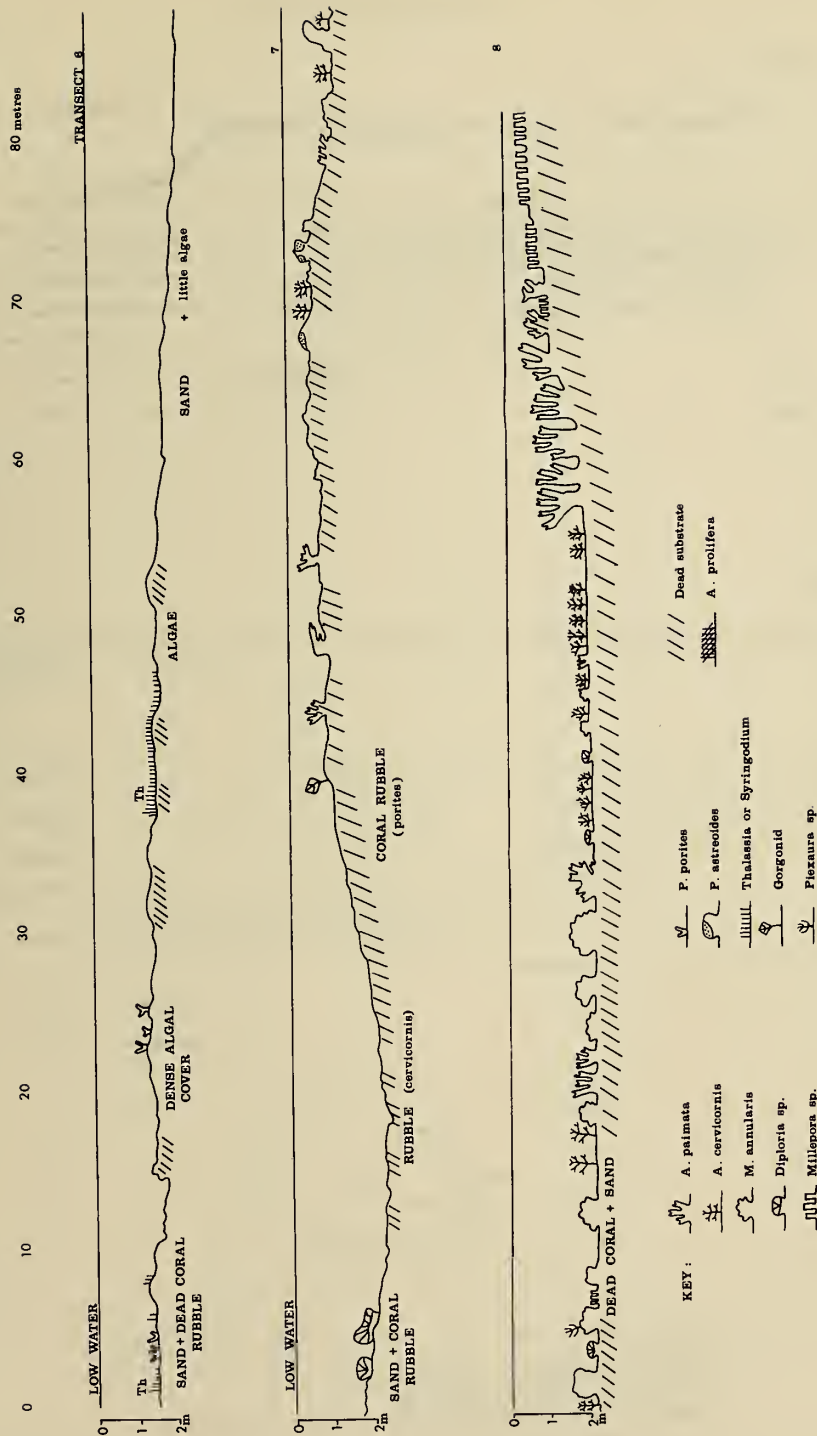
Fig 10   Transect profiles 6, 7 and 8 : Pelican Point, East End
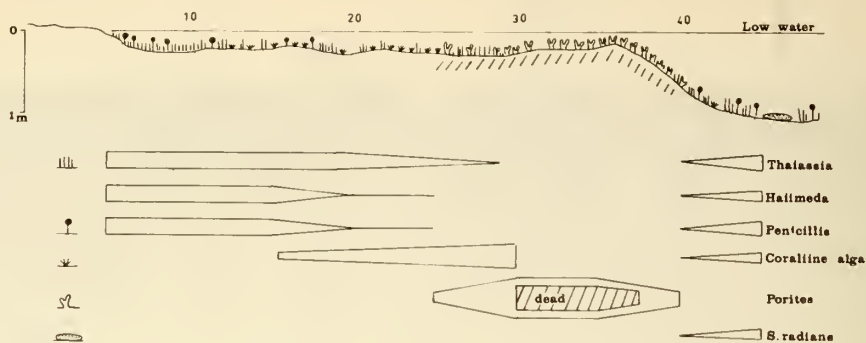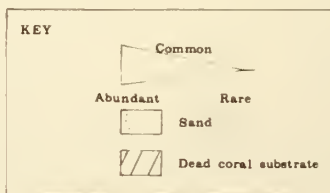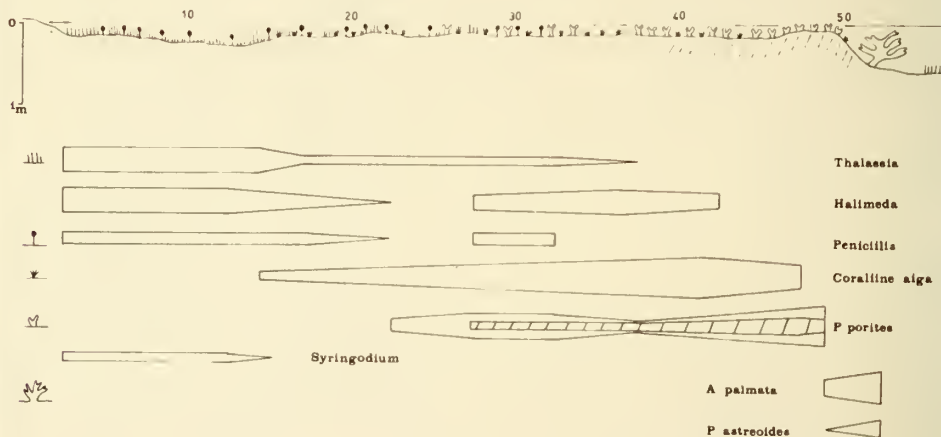
Fig. 11 Profiles of the inshore fringing reef at East End, Anegada, showing zonation and abundance
of the dominant species.

SPERMATOPHYTA · Thalassia testudinum, Syringodium filiforme

ALGAE · Penicillis capitatus, Halimeda incrassata

SCLERACTINIA   Acropora palmata, Porites poritea var divaricata, Porites astreoides,
Siderastrea radians.

Fig 12   PATCH REEF PROFILES

The profiles are presented in an order corresponding to a
geographical distribution running from West to East, see fig.4
        Patch Reef I was only used for a fish rotenone station
and is not therefore represented here.   Transects were not
possible on Patch Reef III due to poor visibility but a plan
view is available.

PATCH REEF II

Profile A

Profile B

Plan

PATCH REEF IX

Profile A

Profile B

Plan

PATCH REEF VII

Profile A

Profile B

PATCH REEF V

Profile A

0 1 2 3m

Profile B

0 1 2 3m

Plan

N

Sand

A

B

Sand

0 30 m

10 20 30 40

PATCH REEF III Plan

Sand

Coral Patch

Sand 0.7

Thick Halimeda & Syringodium 0.15

Sand 0.3 m

Pomato Point

N

0 30 m

PATCH REEF IV

Profile A

0
1
2m

bored

10 20 30 40 50 60

Plan

approx boundary of shallow reef

A

N

0 80m

Plan

A

B

60 m

0

N

Plan

N

A

B

60 m

0

Profile A

10   20   30   40   50   60   70   80   90   100

A palmata 50 m in extent

40 m

Profile B

0   10   20   30   40   50   60   70   80

8

PATCH REEF VIII

7 m

0

Profile A

10   20   30   40   50   60   70   80   90

25 m

Profile B

0   10   20   30   40   50   60   70   80

25 m

6 m

0

PATCH REEF VI

7 m

0

NOTES ON THE ALGAE OF ANEGADA, BRITISH VIRGIN ISLANDS

The marine algae of the Virgin Islands have been extensively studied by Borgesen (1913-20). The most useful recent reviews include the manuals of Taylor (1967) and Chapman (1961, 1963), and both these works have been used in the identification of algae species collected on Anegada. More recently Earle (1972) has listed 154 species of plants from Lameshur Bay, St. John, including 26 species that were new records for the Virgin Islands.

The collection made is not intended as a comprehensive survey of the island's marine algae - only dominant species were collected along the transect lines and therefore the species list (Table 2) is certainly not exhaustive nor complete. A total of 46 species are recorded from 14 families. The data is presented in tabular form so that it can be readily used as both a total species list and for area reference.

Algae were mounted and preserved for taxonomic reference as dried specimens. The collection is now held for reference by the Cambridge Anegada Expedition, c/o Dr. B.E. Brown, Dove Marine Laboratory, University of Newcastle upon Tyne, Cullercoats, Northumberland.

TABLE 2

ALGAE and SPERMATOPHYTAE SPECIES LIST

SPECIES	WEST END	JACK & LOBLOLLY BAY	EAST END	PATCH REEF III	PATCH REEF IX
CHLOROPHYCEAE					
Cladophorales Family : Cladophoraceae					
Chaetomorpha sp.	-	+	-	-	-
Cladophora crispula Vickers		+			
Siphonocladiales Family : Dasycladaceae					
Acetabularia crenulata Lamouroux	+				
Family : Valoniaceae					
Dictyosphaeria cavernosa (Forsskål) Børgesen	+		+	+	+
Siphonales Family : Caulerpaceae					
Caulerpa cupressoides var. mamillosa (Montagne) Weber-van Bosse			+		
Caulerpa sertularioides var. brevipes (J. Agardh) Svedelius			+	+	+
Caulerpa racemosa var. clavifera (Turner) Weber-van Bosse	+				+
Caulerpa racemosa var. occidentalis (J. Agardh) Børgesen				+	
Family : Codiaceae					
Avrainvillea (longicaulis) (Kutzing) Murray and Boodle			+		
Udotea conglutinata (Ellis and Solander) Lamouroux				+	
Udotea flabellum (Ellis and Solander) Lamouroux	+		+	+	
Penicillis capitatus Lamarck	+		+	+	+
Penicillis dumetosus (Lamouroux) Blainville	+			+	
Halimeda opuntia (Linnaeus) Lamouroux	+	+			
Halimeda tuna (Ellis and Solander) Lamouroux				+	
Halimeda incrassata (Ellis) Lamouroux	+		+	+	
Halimeda monile (Ellis and Solander) Lamouroux		+	+	+	
Codium (isthmocladium) Vickers		+			
PHAEOPHYCEAE					
Dictyotales Family : Dictyotaceae					
Dilophus guineensis (Kützing) J. Agardh		+			
Dictyota dichotoma (Hudson) Lamouroux	+				
Dictyota divaricata Lamouroux	+			+	
Dictyota indica Sonder in Kützing			+		
Dictyopteris justii Lamouroux	+				
Dictyopteris delicatula Lamouroux			+		
Stypopodium zonale (Lamouroux) Papenfuss	+				
Lobophora variegata (Lamouroux) Papenfuss	+		+		
Padina sanctae-crucis Børgesen		+			+
Sporochnales Family : Sporochnaceae					
Sporochnus pedunculatus (Hudson) C. Agardh		+			

ALGAE and SPERMATOPHYTAE SPECIES LIST

SPECIES continued	WEST END	JACK & LOBLOLLY BAY	EAST END	PATCH REEF III	PATCH REEF IX
Fucales Family : Sargasseae					
Sargassum platycarpum Montagne				+	
Turbinaria tricostata Barton		+	+		
Turbinaria turbinata (Linnaeus) Kuntze	+	+	+		
RHODOPHYCEAE					
Cryptonemiales Family : Corallinaceae Sub Family : Melobesieae					
Lithothamnion sp.	+	+	+	+	
Lithophyllum sp.	+	+	+	+	
Goniolithon sp.		+	+		
Porolithon sp.		+	+		
Amphiroa fragilissma (Linnaeus) Lamouroux			+		
Amphiroa rigida Lamouroux var. antillaria Børgesen				+	
Gigartinales Family : Hypneaceae					
Hypnea sp.		+			
Family : Gracilariaceae					
Gracilaria sp.	+				
Rhodymeniales Family : Champiaceae					
Coelothrix irregularis (Harvey) Børgesen				+	
Cermiales Family : Ceramiaceae					
Ceramium nitens (C. Agardh) J. Agardh		+			
Ceramium sp.		+			
Family : Rhodomelaceae					
Polysiphonia sp.		+			
Bryothamnion triquetrum (Gmelin) Howe	+				
Acanthophora spicifera (Vahl) Børgesen			+		
Laurencia poitei (Lamouroux) Howe	+		+		
SPERMATOPHYTA					
Halophila baillonis Ascherson	+		+		
Syringodium filiforme Kutzing	+		+		
Thalassia testudinum Konig	+		+		

Acknowledgements

    We are indebted to Nancy Ogden of the Fairleigh Dickinson West Indies Laboratory at St. Croix, for checking and correcting our identifications of the algae.

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CORAL REEF FISH OF ANEGADA, BRITISH VIRGIN ISLANDS

The first mention of the abundant fish life around Anegada is that
of Schomburgk (1832), but it was not until 1973 that any attempt was
made to assess the fisheries and mariculture potential of the island
(Iversen et al). During the latter survey a brief dive was carried
out on patch reefs off East Point, Anegada and 30 species of reef fish
were recorded.

Approximately 185 species (55 families) were recorded in the present
survey at sites on both the windward and leeward sides of the island.

METHODS

Collection of information involved firstly, fishwatching to obtain
estimates of easily visible fish on the reef; rotenone collections in
selected areas to capture cryptic species and thirdly, photography of
fish species so collected as a record and aid to later identification.

Fishwatching was carried out at selected sites. These included
Jack Bay, Loblolly Bay, West End and East End on the northern shore and
nine patch reefs on the southern shore. Brief surveys of Cow Wreck Bay
and Bone Bay are also included in the summary of results.

At each site particular habitats were chosen that were representative
of features in a zone, e.g., in the lagoon zone at East End such habitats
included a sand substrate, a sand and algae region and an inshore fringing
reef. Within these areas three pairs of divers would fishwatch for 60
minutes, noting not only the presence of fish species but also their
abundance. The following scoring scheme was adopted for the survey:

<u>Number of individuals</u>

Species allocated	1
to one of 6 groups	2-5
according to numbers	6-10
seen.	11-30
	31-100
	100+

During the 60 minute fishwatch, the first 20 minutes were spent in a
general swim of the area; the second and third 20 minute periods were
spent examining a relatively small area (approximately 10 m in extent)
paying particular attention to cryptic and retiring fish species. Thus
a general overall impression of relative abundance in the area was
obtained.

Results obtained in the field from each pair of divers appeared to
show surprisingly good agreement for each site visited. Note was also
made during fishwatches of the presence/absence of juvenile fish and
their abundance on the reef.

Several night dives were carried out both on the northern shore and on patch reefs on the leeward shore, in an attempt to describe any changes that might occur in the fish population on the reef after dark.

By assessing abundances in this way, factors such as time of day, state of tide, meterological conditions, etc., are likely to play an important role in determining numbers of fish on the reef at any one time. In this preliminary survey it was impossible to standardise all these factors and this limitation must be borne in mind in interpretation of the final results.

'Rotenone' or fish poison stations were carried out at a limited number of sites according to methods described by Randall (1963). Rotenone is an alkaloid with an empirical formula of $C_{23}H_{22}O_6$ and its effect upon fishes is to cause vasoconstriction of the capillaries of the gills (Hamilton 1941) and hence respiratory impairment. Powdered rotenone, however, has relatively little effect upon invertebrates except the groups Cephalopoda and Turbellaria.

In the present study rotenone was used in the form of derris powder (3-6% rotenone). The powder was mixed with water immediately before use, in the following proportions, for dispersal in approximately 10^3 m^3 seawater:

1.2 Kg derris powder/2.5 litres water

A pair of divers first selected the site of the poison station and then estimated the strength and direction of currents using fluoroscein dye. Appropriate quantities of the poison were released by the divers, and on its dispersal two additional pairs of divers assisted in the collection of fish by netting both on the surface and on the bottom. The specimens were then returned to the boat, moored nearby, where the collection was sorted and fish species placed in appropriate tanks of seawater before immediate return to the field laboratory on completion of the station. Time spent on each site varied between 3-4 hours. At patch reef I, the first poison station attempted, subsequent visits indicated that fish returned to the patch within 24 hours of application and dispersal of the poison.

On return to the laboratory the specimens were prepared for photography, according to methods used by Randall (1961). Each specimen was pinned out in a wax-bottom dissecting dish and the fins fixed in an erect position before applying formalin with a fine paint brush to the fins and other parts of the body such as the gill covers etc. A few minutes later the specimen was removed and covered with a small amount of water in a perspex container - a photographic record was then made. All specimens collected at rotenone or poison stations were weighed (net wt.), measured (standard length) and preserved in 10% formalin.

The fish collection is now housed at the British Museum (Natural History), Cromwell Road, South Kensington, London SW7.

Identification of specimens was made using Bohlke and Chaplin (1968); Randall (1968) and Chaplin and Scott (1972).

OBSERVATIONS

All results are contained in the species list (Table 3) for the island, where abundances are recorded for each habitat visited. Information is based on fishwatches during the day.   The key at the end should provide a guide to information on the abundance of juvenile species; specimens collected in rotenone stations, etc.

TABLE 3

LIST OF FISH SPECIES ANEGADA. BRITISH VIRGIN ISLANDS

SPECIES / Substrate Type	WEST END A Sand / Sand + Grass / Coral Patches	WEST END C	WEST END D	COW WRECK D	BONE BAY A Coral Patches	JACK BAY A Sand	JACK BAY B Palmata	JACK BAY C Algal Ridge	JACK BAY D	LOBLOLLY A Sand	LOBLOLLY B Palmata	LOBLOLLY C	EAST END Sand	EAST END A Sand + Algae	Fringing Reef	EAST END B Palmata	EAST END D	1	2	3	4	5	6	7	8	9
ORECTOLOBIDAE *Ginglymostoma cirratum* (Bonnaterre) Nurse shark			•		P												•									
CARCHARHINIDAE *Carcharhinus springeri* (Bigelow and Schroeder) Reef shark					P												•									
Carcharhinus limbatus (Valenciennes) Blacktip shark																	•									
Negaprion brevirostris (Poey) Lemon shark					P												•									
DASYATIDAE *Dasyatis americana* Hildebrand and Schroeder Southern stingray		•		•		•				•	•		•	•					•							
MYLIOBATIDAE *Aetobatus narinari* (Euphrasen) Spotted Eagle Ray			•					•	•								•									
ELOPIDAE *Megalops atlantica* Valenciennes Tarpon		•																								
CLUPEIDAE *Harengula humeralis* Cuvier Redear sardine						•							•											•		

Substrate Type

	WEST END					COW WRECK	BONE BAY	JACK BAY				LOBLOLLY				EAST END					LEEWARD SHORE PATCH REEFS
SPECIES	A Sand	Sand + Grass	Coral Patches	C	D	D	A Coral Patches	A Sand	B Palmata	C Algal Ridge	D	A Sand	B Palmata	C	D	Sand	A Sand + Algae	Fringing Reef	B Palmata	D	1 2 3 4 5 6 7 8 9

SYNODONTIDAE

Synodus synodus (Linnaeus) Red Lizardfish

Synodus foetens (Linnaeus) Inshore lizardfish

Synodus intermedius (Agassiz) Sand diver

Trachinocephalus myops (Forster) Snakefish

MORINGUIDAE

Moringua edwardsi (Jordan and Bollman) Spaghetti eel

XENOCONGRIDAE

Chilorhinus suensoni Lütken Seagrass eel

Kaupichthys hyoproroides (Strömman) Reef eel

MURAENIDAE

Enchelycore sp. Chestnut moray

Gymnothorax funebris Ranzani Green moray

Gymnothorax moringa (Cuvier) Spotted moray

Muraena miliaris (Kaup) Goldentail moray

Anarchias yoshiae Kanazawa Pygmy moray

Substrate Type

Also found at mangrove rotenone
station

SPECIES	WEST END A Sand	A Sand + Grass	Coral Patches	C	D	COW WRECK D	BONE BAY A Coral Patches	JACK BAY A Sand	B Palmata	C Algal Ridge	D	LOBLOLLY A Sand	B Palmata	C	EAST END Sand	A Sand + Algae	Fringing Reef	B Palmata	D	1	2	3	4	5	6	7	8	9
OPHICHTHIDAE																												
Myrichthys oculatus (Kaup) Goldspotted eel		(1)																										
Ahlia egmontis (Jordan) Key worm eel											(1)																	
Myrophis punctatus Lütken Speckled worm eel																												
BELONIDAE																												
Strongylura notata (Poey) Redfin needlefish					•								•	•														
Tylosurus crocodilus (Peron and LeSueur) Houndfish								●														•	•			•	•	
Strongylura timucu (Walbaum) Atlantic needlefish																							•					
HEMIRAMPHIDAE																												
Hemiramphus brasiliensis (Linnaeus) Ballyhoo				•									•						•									
Hyporhamphus unifasciatus (Ranzani) Halfbeak																•												
ATHERINIDAE																												
Atherinomorus stipes (Müller and Troschel) Hardhead silverside					•									•		•											•	
HOLOCENTRIDAE																												
Holocentrus ascensionis (Osbeck) Longjaw squirrelfish		•	•	•			P									•	●	•			●	●	●	●	●			•
Adioryx coruscus (Poey) Reef squirrelfish	(2)	(4)														(1)	●				•	•						•

Chart — Fish species distribution by location and substrate type

Column group headers (left to right):

- **WEST END** — A (Sand), A (Sand + Grass), C (Coral Patches), D
- **COW WRECK** — C, D
- **BONE BAY** — A (Coral Patches)
- **JACK BAY** — A (Sand), A (Palmata), B (Algal Ridge)
- **LOBLOLLY** — A (Sand), B (Palmata), C, D
- **EAST END** — A (Sand), A (Sand + Algae), A (Fringing Reef), B (Palmata), D
- **LEEWARD SHORE / PATCH REEFS** — 1, 2, 3, 4, 5, 6, 7, 8, 9

Substrate Type

SPECIES

Adioryx vexillarius (Poey) — Dusky squirrelfish

Plectrypops retrospinis (Guichenot) — Cardinal soldierfish

Holocentrus rufus (Walbaum) — Squirrelfish

Myripristis jacobus Cuvier — Blackbar soldierfish

BROTULIDAE
Ogilbia sp.

OPHIDIIDAE
Parophidion schmidti (Woods and Kanazawa) — Dusky cusk

AULOSTOMIDAE
Aulostomus maculatus Valenciennes — Trumpetfish

SYNGNATHIDAE
Corythoichthys brachycephalus (Poey) — Crested pipefish

Syngnathus dunckeri Metzelaar — Pugnose pipefish

Syngnathus elucens Poey — Shortfin pipefish

SPHYRAENIDAE
Sphyraena barracuda (Walbaum) — Great barracuda

Sphyraena picudilla Poey — Southern sennet

Selected annotations on the chart:
- Circled numbers under WEST END Coral Patches: 20 (*Holocentrus rufus*), 3 (*Myripristis jacobus*)
- Circled numbers under EAST END Fringing Reef: 48 (*Holocentrus rufus*), 4 (*Myripristis jacobus*)
- "P" markers under BONE BAY (Coral Patches) for *Holocentrus rufus*, *Myripristis jacobus*, *Aulostomus maculatus*, and *Sphyraena barracuda*
- Note: Collected off Setting Point and at mangrove rotenone station

Species distribution matrix (sites vs. species).

Column group headers (left to right): WEST END · COW WRECK · BONE BAY · JACK BAY · LOBLOLLY · EAST END · LEEWARD SHORE PATCH REEFS

Substrate Type labels:
- WEST END: A (Sand), A (Sand + Grass), A (Coral Patches), C, D
- COW WRECK: D, D
- BONE BAY: A (Coral Patches)
- JACK BAY: A (Sand), B (Palmata), C (Algal Ridge), D
- LOBLOLLY: A (Sand), B (Palmata), C
- EAST END: A (Sand), A (Sand + Algae), A (Fringing Reef), B (Palmata), D
- LEEWARD SHORE PATCH REEFS: 1 2 3 4 5 6 7 8 9

SPECIES

MUGILIDAE
Mugil trichodon Poey — Fantail mullet

BOTHIDAE
Bothus lunatus (Linnaeus) — Peacock flounder
Bothus ocellatus (Agassiz) — Eyed flounder

APOGONIDAE
Apogon maculatus (Poey) — Flamefish
Apogon binotatus (Poey) — Barred cardinalfish
Apogon conklini (Silvester) — Freckled cardinalfish
Apogon pigmentarius (Poey) — Dusky cardinalfish
Astrapogon stellatus (Cope) — Conchfish

SERRANIDAE
Cephalopholis fulva (Linnaeus) — Coney
Petrometopon cruentatum (Lacépède) — Graysby
Serranus tigrinus (Bloch) — Harlequin bass
Hypoplectrus unicolor (Walbaum) — Hamlet
Epinephelus striatus (Bloch) — Nassau grouper

Fish species distribution by substrate type and locality.

SPECIES	WEST END — Sand	WEST END — Sand + Grass (A)	WEST END — Coral Patches	WEST END — C	WEST END — D	COW WRECK — D	BONE BAY — Coral Patches (A)	JACK BAY — Sand (A)	JACK BAY — Palmata (B)	JACK BAY — Algal Ridge (C)	JACK BAY — D	LOBLOLLY — Sand (A)	LOBLOLLY — Palmata (B)	LOBLOLLY — C	LOBLOLLY — D	EAST END — Sand + Algae (A)	EAST END — Fringing Reef	EAST END — Palmata (B)	EAST END — D	LEEWARD 1	LEEWARD 2	LEEWARD 3	LEEWARD 4	LEEWARD 5	LEEWARD 6	LEEWARD 7	LEEWARD 8	LEEWARD 9
Epinephelus adscensionis (Osbeck) Rock hind		①																	•								•	•
Epinephelus guttatus (Linnaeus) Red hind			•						•				•			•	②		•		•			•	•	•		
Mycteroperca bonaci (Poey) Black grouper				•							•						①											
Chorististium rubre (Poey) Swissguard basslet					•						•				•													
GRAMMISTIDAE																												
Pseudogramma bermudensis (Kanazawa) Foureye basslet																												
GRAMMIDAE																												
Gramma loreto Poey Fairy basslet			②	•	•	•					•			•			①		•		•			•	•		•	
PRIACANTHIDAE																												
Priacanthus cruentatus (Lacépède) Glasseye snapper			•	•		•							•	•		•		•	•		•	•	•	•	•	•	•	
Priacanthus arenatus Cuvier Bigeye				•					•																			
PEMPHERIDAE																												
Pempheris schomburgki Müller and Troscel Glassy sweeper																		•										
BRANCHIOSTEGIDAE																												
Malacanthus plumieri (Bloch) Sand tilefish				•				•								•				①								

Species distribution matrix (columns grouped by locality and substrate type; ● = large dot, • = small dot, P = present; circled values shown in parentheses).

SPECIES	WEST END Sand	WEST END A Sand+Grass	WEST END Coral Patches	WEST END C	WEST END D	COW WRECK D	COW WRECK D	BONE BAY A Coral Patches	JACK BAY A Sand	JACK BAY B Palmata	JACK BAY C Algal Ridge	JACK BAY D	LOBLOLLY A Sand	LOBLOLLY B Palmata	LOBLOLLY C	LOBLOLLY D	EAST END Sand	EAST END A Sand+Algae	EAST END Fringing Reef	EAST END B Palmata	EAST END D	PR 1	PR 2	PR 3	PR 4	PR 5	PR 6	PR 7	PR 8	PR 9
CARANGIDAE																														
Caranx ruber (Bloch) Bar jack	•		•	•	•	•	•	P	●	•	•	●	●	•	•	●	●	•	•	•	•		•	•	•	•	•	•	•	•
Caranx fusus Geoffroy Saint-Hilaire Blue runner				•	•				•		•		•				•	•						•			•			
Caranx latus Agassiz Horse-eye jack				•	•				•																					
Trachinotus goodei Jordan and Evermann Palometa	•			•	•				•																					
LUTJANIDAE																														
Lutjanus mahogoni (Cuvier) Mahogany snapper			•	•	•	•	•	P				•	•	•	•	•	•		•	•	•		•	•	•	•	•	•	•	•
Lutjanus jocu (Bloch and Schneider) Dog snapper								P																•			•	•	•	
Lutjanus apodus (Walbaum) Schoolmaster			•	•	•	•	•	P	•	•	•	•	●	●	●	•	•		●	●	•		•	•	•	•	•	•	•	•
Lutjanus griseus (Linnaeus) Grey snapper			•	•	•				•						•															
Ocyurus chrysurus (Bloch) Yellowtail snapper			•	•	•	•	•	P	•	•	•	•	•			•	•			•			•	•	•	•	•	•	•	•
Lutjanus synagris (Linnaeus) Lane snapper																	•							•						
POMADASYIDAE																														
Haemulon aurolineatum Cuvier Tomtate	(15)	(4)	•	•	•	•	•	P	•			•	•	•	•	•	•	●	(6)	•	•		●	•	•	•	•	•	•	●
Haemulon flavolineatum (Desmarest) French grunt		(17)	•	●	•	•	•	P	•								•		●	•	•		•	●	●	●	●	●	●	●

Substrate Type

Table of fish species distribution by station and substrate type.

Column groups (stations): WEST END · COW WRECK · BONE BAY · JACK BAY · LOBLOLLY · EAST END · LEEWARD SHORE PATCH REEFS

Substrate Type (sub-columns):
- WEST END: Sand (A) · Sand + Grass · Coral Patches (C)
- COW WRECK: D · D
- BONE BAY: Coral Patches (A)
- JACK BAY: Sand (A) · Palmata (B) · Algal Ridge (C) · D
- LOBLOLLY: Sand (A) · Palmata (B) · C
- EAST END: Sand · Sand + Algae (A) · Fringing Reef · Palmata (B) · D
- LEEWARD SHORE PATCH REEFS: 1 · 2 · 3 · 4 · 5 · 6 · 7 · 8 · 9

SPECIES	WEST END Sand (A)	W.E. Sand+Grass	W.E. Coral Patches (C)	COW WRECK D	COW WRECK D	BONE BAY Coral Patches (A)	JACK BAY Sand (A)	JACK BAY Palmata (B)	JACK BAY Algal Ridge (C)	JACK BAY D	LOBLOLLY Sand (A)	LOBLOLLY Palmata (B)	LOBLOLLY C	E.E. Sand	EAST END Sand+Algae (A)	E.E. Fringing Reef	EAST END Palmata (B)	EAST END D	PR 1	PR 2	PR 3	PR 4	PR 5	PR 6	PR 7	PR 8	PR 9
Haemulon album Cuvier — Margate	•	•																		•	•	•		•			
Haemulon chrysargyreum Gunther — Smallmouth grunt	•	•		•				•					•							•	•	•	•	•		•	•
Haemulon plumieri (Lacépède) — White grunt			•																								
Haemulon carbonarium Poey — Caesar grunt													•								•						
Haemulon sciurus (Shaw) — Bluestriped grunt	•	●			●	P		•	•	•	•	•	•		●	③	•		•	●	●	●	•		●	●
Anisotremus virginicus (Linnaeus) — Porkfish		•		•																•	•		•				
Anisotremus surinamensis (Bloch) — Black margate			•							•																	
Haemulon macrostomum Gunther — Spanish grunt				•									•										•		•		
SPARIDAE																											
Calamus bajonado (Bloch and Schneider) — Jolthead porgy			•				•	•	•		•		•					•				•		•			•
GERREIDAE																											
Gerres cinereus (Walbaum) — Yellowfin mojarra			•	•		●		•			•												•			•	•
Eucinostomus gula (Quoy and Gaimard) — Silver jenny	•																										
Eucinostomus jonesii Günther — Slender mojarra						P	•				•																
Eucinostomus argenteus Baird and Girard — Spotfin mojarra																		•		•							

Collected at mangrove rotenone station

Distribution table of fish species across Bermuda reef sampling sites.

	WEST END					COW WRECK	BONE BAY	JACK BAY				LOBLOLLY			EAST END					LEEWARD SHORE PATCH REEFS								
Substrate Type	Sand	Sand + Grass	Coral Patches	C	D	D	Coral Patches	Sand	Palmata	Algal Ridge	D	Sand	Palmata	C	Sand	Sand + Algae	Fringing Reef	Palmata	D	1	2	3	4	5	6	7	8	9
SPECIES	A					D	A	A	B	C	D	A	B	C		A		B	D									

SCIAENIDAE

Equetus punctatus (Bloch and Schneider) — Spotted drum

MULLIDAE

Mulloidichthys martinicus (Cuvier) — Yellow goatfish

Pseudupeneus maculatus (Bloch) — Spotted goatfish

KYPHOSIDAE

Kyphosus sectatrix (Linnaeus) — Bermuda chub

EPHIPPIDAE

Chaetodipterus faber (Broussonet) — Atlantic spadefish

CHAETODONTIDAE

Holacanthus tricolor (Bloch) — Rock beauty

Holacanthus ciliaris (Linnaeus) — Queen angelfish

Pomacanthus paru (Bloch) — French angelfish

Pomacanthus arcuatus (Linnaeus) — Grey angelfish

Chaetodon capistratus (Linnaeus) — Foureye butterflyfish

Chaetodon striatus Linnaeus — Banded butterflyfish

POMACENTRIDAE

Microspathodon chrysurus (Cuvier) — Yellowtail damselfish

LEEWARD SHORE
PATCH REEFS

9 8 7 6 5 4 3 2 1

WEST END · COW WRECK · BONE BAY · JACK BAY · LOBLOLLY · EAST END

Substrate Type

WEST END: A Sand · Sand + Grass · Coral Patches · A C D
COW WRECK: D
BONE BAY: A Coral Patches
JACK BAY: Sand · A Palmata · B · C Algal Ridge · D
LOBLOLLY: Sand · A · B Palmata · C · D
EAST END: Sand · Sand + Algae · A · Fringing Reef · Palmata · B · D

SPECIES

Eupomacentrus partitus (Poey)
Bicolor damselfish

Eupomacentrus dorsopinicans (Poey)
Dusky damselfish

Eupomacentrus planifrons (Cuvier)
Threespot damselfish

Eupomacentrus variabilis
(Castelnau)
Cocoa damselfish

Eupomacentrus sp.
Honey damselfish

Eupomacentrus leucostictus
(Müller and Troschel)
Beaugregory

Abudefduf saxatilis (Linnaeus)
Seargeant major

Chromis multilineata (Guichenot)
Brown chromis

Chromis cyanea (Poey)
Blue chromis

CIRRHITIDAE
Amblycirrhitus pinos (Mowbray)
Redspotted hawkfish

LABRIDAE
Bodianus rufus (Linnaeus)
Spanish hogfish

Bodianus pulchellus (Poey)
Spotfin hogfish

Thalassoma bifasciatum (Bloch)
Bluehead

Halichoeres maculipinna (Müller
and Troschel)
Clown wrasse

SPECIES

Substrate Type

WEST END — Sand, Sand + Grass, Coral Patches, A, C, D
COW WRECK — D
BONE BAY — Coral Patches, A
JACK BAY — Sand, Palmata, Algal Ridge, A, B, C, D
LOBLOLLY — Sand, Palmata, A, B, C
EAST END — Sand, Sand + Algae, Fringing Reef, Palmata, A, B, D
LEEWARD SHORE — PATCH REEFS — 1, 2, 3, 4, 5, 6, 7, 8, 9

Halichoeres poeyi (Steindachner)
Blackear wrasse

Halichoeres bivittatus (Bloch)
Slippery dick

Halichoeres pictus (Poey)
Painted wrasse

Halichoeres garnoti (Valenciennes)
Yellowhead wrasse

Halichoeres radiatus (Linnaeus)
Puddingwife

Hemipteronotus novacula (Linnaeus)
Pearly razorfish

Hemipteronotus splendens (Castelnau)
Green razorfish

SCARIDAE

Scarus vetula Bloch and Schneider
Queen parrotfish

Scarus taeniopterus Desmarest
Princess parrotfish

Scarus coeruleus (Bloch)
Blue parrotfish

Scarus guacamaia Cuvier
Rainbow parrotfish

Scarus coelestinus Valenciennes
Midnight parrotfish

Sparisoma rubripinne (Valenciennes)
Yellowtail parrotfish

Sparisoma chrysopterium (Bloch and Schneider)
Redtail parrotfish

SPECIES — Substrate Type

LEEWARD SHORE PATCH REEFS: 1 2 3 4 5 6 7 8 9

WEST END: Sand (A), Sand + Grass, Coral Patches, C, D
COW WRECK: C, D
BONE BAY: Coral Patches (A)
JACK BAY: Sand (A), Palmata (B), Algal Ridge (C), D
LOBLOLLY: Sand (A), B, Palmata, C
EAST END: Sand, Sand + Algae (A), Fringing Reef (B), Palmata (D)

Sparisoma radians (Valenciennes)
  Bucktooth parrotfish

Sparisoma aurofrenatum
  (Valenciennes)
  Redband parrotfish

Scarus croicensis Bloch
  Mottlefin or Striped parrotfish

Sparisoma viride (Bonnaterre)
  Stoplight parrotfish

DACTYLOSCOPIDAE
Leurochilus acon Böhlke
  Smoothlip stargazer

Dactyloscopus tridigitatus Gill
  Sand stargazer

Dactyloscopus crossotus Starks
  Bigeye stargazer

Gillellus rubrocinctus Longley
  Saddle stargazer

CLINIDAE
Labrisomus haitiensis Beebe
  and Tee-van
  Reef blenny

Labrisomus bucciferus (Poey)
  Puffcheek blenny

Labrisomus gobio (Valenciennes)
  Goggle-eye blenny

Labrisomus nuchipinnis (Quoy and
  Gaimard)
  Hairy blenny

Malacoctenus versicolor (Poey)
  Barfin blenny

Paraclinus fasciatus (Steindachner)
  Banded blenny

Substrate Type

	WEST END					COW WRECK	BONE BAY	JACK BAY			LOBLOLLY				EAST END					LEEWARD SHORE PATCH REEFS									
SPECIES	Sand	Sand + Grass A	Coral Patches	C	D	D	Coral Patches A	Sand A	Palmata B	Algal Ridge C	Sand A	Palmata B	C	D	Sand	Sand + Algae A	Fringing Reef	Palmata B	D	1	2	3	4	5	6	7	8	9
Labrisomus guppyi (Norman) Mimic blenny																				③								
Malacoctenus macropus (Poey) Rosy blenny																				①								
Paraclinus cingulatus (Evermann and Marsh) Coral blenny																												
Malacoctenus gilli (Steindachner) Dusky blenny												●					③											
Acanthemblemaria maria Böhlke Secretary blenny		①										④																
Chaenopsis ocellata Poey Bluethroat pikeblenny																												
TRIPTERYGIIDAE																												
Enneanectes pectoralis (Fowler) Redeye blenny		①										㉙																
Enneanectes atrorus Rosenblatt Blackedge triplefin												⑫																
BLENNIIDAE			●	●	●	●	P	●	●	●		●	●	●	●	●	●		②	●	●	●						
Ophioblennius atlanticus (Valenciennes) Redlip blenny		●	●																					●		●	●	●	
Blennius cristatus Linnaeus Molly Miller	●		●	●																								
GOBIIDAE																												
Coryphopterus glaucofraenum Gill Bridled goby		③ ●												●	●	●	●		⑦	●	●	●	●	●	●	●	●	●
Gobiosoma genie Böhlke and Robins Cleaning goby		② ③	●												●	●	④	●					●		●	●	●	●
Gobiosoma gemmatum (Ginsburg) Frecklefin goby		①													●	●	①	●							●			
Quisquilius hipoliti (Metzelaar) Rusty goby																				①								

SPECIES

Bathygobius soporator
(Valenciennes)
Frillfin goby

Coryphopterus alloides Böhlke
and Robins
Barfin goby

Gnatholepis thompsoni Jordan
Goldspot goby

Coryphopterus dicrus Böhlke
and Robins
Colon goby

Gobiosoma evelynae Böhlke and
Robins
Sharknose goby

Gobionellus boleosoma (Jordan
and Gilbert)
Darter goby

SCORPAENIDAE
Scorpaena inermis Cuvier
Mushroom scorpionfish

ACANTHURIDAE
Acanthurus coeruleus Bloch
and Schneider
Blue tang

Acanthurus chirurgus (Bloch)
Doctorfish

Acanthurus bahianus Castelnau
Ocean surgeon

BALISTIDAE
Balistes vetula Linnaeus
Queen triggerfish

Canthidermis sufflamen
(Mitchill)
Ocean triggerfish

Substrate Type

WEST END
A Sand
   Sand + Grass
   Coral Patches
C
D

COW WRECK
D

BONE BAY
A Coral Patches

JACK BAY
A Sand
B Palmata
C Algal Ridge
D

LOBLOLLY
A Sand
B Palmata
C

EAST END
A Sand
   Sand + Algae
   Fringing Reef
B Palmata
D

LEEWARD SHORE
PATCH REEFS
1 2 3 4 5 6 7 8 9

Collected at mangrove rotenone station

Collected at mangrove rotenone station

LEEWARD SHORE PATCH REEFS

EAST END

LOBLOLLY

JACK BAY

BONE BAY

COW WRECK

WEST END

Substrate Type

Zone numbers: 1 2 3 4 5 6 7 8 9

EAST END — D, B (Palmata), A (Fringing Reef), A (Sand + Algae), Sand

LOBLOLLY — C, B, A (Palmata), Sand

JACK BAY — D, C (Algal Ridge), B (Palmata), A (Sand)

BONE BAY — A (Coral Patches)

COW WRECK — D

WEST END — C, D, A (Coral Patches), Sand + Grass, Sand

SPECIES

Melichthys niger (Lacépède)
Black durgon

Cantherhines pullus (Ranzani)
Orangespotted filefish

Aluterus scripta (Osbeck)
Scrawled filefish

OSTRACIIDAE
Lactophrys triqueter (Linnaeus)
Smooth trunkfish

TETRAODONTIDAE
Sphoeroides spengleri (Bloch)
Bandtail puffer

Canthigaster rostrata (Bloch)
Sharpnose puffer

DIODONTIDAE
Diodon hystrix Linnaeus
Porcupinefish

GOBIESOCIDAE
Arcos rubiginosus (Poey)
Red clingfish

KEY:

Number of individuals
1
2 – 5
6 – 10
11 – 30
31 – 100
100+

P — species noted but no abundance record made

(8) — rotenone station with number of specimens collected

ZONE LETTERS

A. Lagoon
B. Rear Zone
C. Reef Top
D. Buttress

ADDENDUM TO FISH SPECIES LIST

Species	Site

SERRANIDAE

Hypoplectrus puella (Cuvier and   Patch Reef 2
                    Valenciennes)
Barred hamlet

Hypoplectrus nigricans (Poey)   Patch Reef 6
Black hamlet

Mycteroperca tigris (Valenciennes)   East End
Tiger grouper   Area D

  LUTJANIDAE

Lutjanus analis (Cuvier)   Patch Reef 9
Mutton snapper

  LABRIDAE

Clepticus parrai (Bloch and   Patch Reef 6
                  Schneider)
Creole wrasse

  OSTRACIIDAE

Lactophrys bicaudalis (Linnaeus)   Patch Reef 2
                                         Patch Reef 7
Spotted trunkfish   Patch Reef 9
                                         Bone Bay

Species changes at night

Observations at night indicated that a marked difference in distribution of fish on the reef occurred after dusk.

Although abundant during the day, members of the family Pomadysidae were strikingly absent from the reef at night as a 'fish watch' on patch reef V would indicate. Table 4 shows the relative abundance of reef species during the day (mid-day fishwatch) and at night (fishwatch during and immediately after the evening change-over) and the contrast in the number of species present is quite clear. Similar observations have already been recorded in some detail by members of the Tektite Program (Collette and Talbot 1972). During the evening change-over period the snappers (Lutjanidae) and the grunts (Pomadysidae) leave the reef, some in schools and some alone, for the sandflats and seagrass areas where they feed. It was also noticed that the grunts were accompanied in their excursions over the sand by the holocentrids, Holocentrus rufus and Holocentrus coruscus. Myripristis jacobus does not appear to move far away from the reef at night.

Results depicted in the Table also indicate the replacement of diurnal species by nocturnal species such as Apogon maculatus, Apogon binotatus and Pempteris schomburgki and such findings are in general agreement with the work of the Tektite Program in Lameshur Bay, St. John, U.S. Virgin Islands.

The mangrove area

Other interesting observations were made on a mangrove area, also on the leeward side of the island, approximately 1.5 km east of Setting point. Here, on a discrete mangrove patch (measuring approximately 25 m by 15 m in extent and situated in a depth of water of 1 m) a rotenone station yielded 22 species of fish (Fig. 13), the majority of which were juveniles. Paricularly abundant were the French grunts Haemulon flavolineatum, the Silver jenny Eucinstomus gula, the Ballyhoo Hemiramphus brasiliensis and the Yellowfin mojarra Gerres cinereus. As Fig. 14 shows, the mangrove area can be regarded as a 'nursery' with large numbers of juvenile fish recorded. Indeed, mangroves are known to be highly productive areas which also serve as shelters to young reef fish (Ogden, Yntema and Clavijo 1975).

SUMMARY

A total of 185 species (55 families) of reef fish were recorded on Anegada. A similar study on Tague Bay Reef, St. Croix, U.S. Virgin Islands, yielded 125 species (44 families) - Ogden et al (1972), although the total number of marine species for the entire island was estimated at 300 by Ogden, Yntema, and Clavijo (1975). Randall (1968), in 'Caribbean Reef Fishes', cites 300 common reef fish which may be found on reefs and sandflat/seagrass communities in the Caribbean - this figure

does not include many of the cryptic species which would be collected in a rotenone station.

Similar trends in the distribution of reef fish were observed on the northern shore of Anegada as those recorded in the Taque Bay study, St. Croix; with relatively greater numbers of species being found in the rear and buttress zones as compared to the shallow reef flat or reef top (Fig. 15). The increased number of species in these areas is probably due in part to the greater water depth and diversity of habitat provided by the regions. The highest number of species of reef fish recorded on the northern shore of Anegada was at West End in the buttress zone where 70 species were recognised. Particular note was made at this site of the spadefish Chaetodipterus faber and the tarpon, Megalops atlantica.

As is to be expected, generally lower numbers of fish species were recorded over the sand and sand/grass areas. Numbers of species ranged from 18-28 in the sandy lagoons of sites on the northern shore - predominant species including the jacks, (Carangidae); the mojarras (Gerridae); and the sanddivers (Synodontidae). In an area extensively colonised by algae, in the lagoon at East End, up to 40 species were noted; also at East End 44 species were recorded on the inshore fringing reef. The french grunt Haemulon flavolineatum, the reef squirrelfish Holocentrus coruscus, the bluehead Thalassona bifasciatum, and the striped parrotfish Scarus croicensis were particularly abundant at the latter site and a small rotenone station yielded 21 species, including large numbers of the dusky squirrelfish Holocentrus vexillarius, redtail parrotfish Sparisoma chrysopterium, striped parrotfish Scarus croicensis, ocean surgeon Acanthurus bahianis, freckled cardinalfish Apogon conklini and the chestnut moray Enchelycore sp.

On the leeward side of the island the number of species recorded varied between 54 - 78 on the nine patch reefs visited. The highest number of species was recorded on patch reef VI at the east end of the island. The most outstanding feature on the patch reefs was the general abundance of the Pomadsyidae - particularly Haemulon flavolineatum and Haemulon sciurus, both species being found shoaling in stands of Acropora prolifera and Acropora palmata.

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SPECIES	ABUNDANCE	
	DAY	NIGHT
SYNODONTIDAE		
Synodus intermedius (Inshore lizardfish)	*	*
BELONIDAE		
Strongylura notata (Atlantic needlefish)	*	
Tylosurus crocodilus (Houndfish)	*	*
HDLOCENTRIDAE		
Holocentrus coruscus (Reef squirrelfish)		***
Holocentrus ascensionis (Longjaw squirrelfish)	***	
Holocentrus rufus (Squirrelfish)	**** (local)	**
Myripristis jacobus (Blackbar soldierfish)	**	**
AULOSTIMIDAE		
Aulostomus maculatus (Trumpetfish)	**	**
SPHYRAENIDAE		
Sphyraena barracuda (Barracuda)	**	
APDGDNIDAE		
Apogon maculatus (Flamefish)		****
Apogon binotatus (Barred cardinalfish)		****
SERRANIDAE		
Cephalophilis fulva (Coney)	**	
Epinephelus adscensionis (Rock hind)	*	
PRIACANTHIDAE		
Priacanthus cruentatus (Glasseye snapper)	***	
PEMPHERIDAE		
Pempheris schomburgki (Glassy sweeper)		****
CARINGIDAE		
Caranx ruber (Bar jack)	**	
LUTJANIDAE		
Lutjanus mahogoni (Mahogony snapper)	**	
Lutjanus jocu (Dog snapper)	*	
Lutjanus apodus (Schoolmaster)	***	
Lutjanus griseus (Grey snapper)	** (off reef)	
Dcyurus chrysurus (Yellowtail snapper)	**	
POMADASYDAE		
Haemulon aurolineatum (Tomtate)	**	
Haemulon flavolineatum (French grunt)	***** (local)	*
Haemulon sciurus (Bluestriped grunt)	***	
Haemulon plumieri (White grunt)	***	
Haemulon macrostomum (Spanish grunt)	**	
Anisotremus virginicus (Porkfish)	**	
SPARIDAE		
Calamus bajonado (Jolthead porgy)	* (near reef)	
GERRIDAE		
Gerres cinereus (Yellowfin mojarra)	**	
Eucinostomus gula (Silver jenny)		**
MULLIDAE		
Mulloidichthys martinicus (Yellow goatfish)	**	
KYPHDSIDAE		
Kyphosus sectatrix (Bermuda chub)	***	
CHAETDDONTIDAE		
Holacanthus ciliaris (Queen angelfish)	*	
Pomacanthus paru (French angelfish)	*	
Chaetodon capistratus (Foureye butterflyfish)	**	
Chaetodon striatus (Banded butterflyfish)	**	
PDMACENTRIDAE		
Microspathodon chrysurus (Yellowtail damselfish)	**	*
Eupomacentrus dorsopunicans (Dusky damselfish)	***	**
Eupomacentrus variabilis (Cocoa damselfish)	***	
Eupomacentrus sp. (Honey dameelfish)	**	
Eupomacentrus leucostictus (Beaugregory)	**	
Abudefduf saxatilis (Seargeant major)	**	*

SPECIES	ABUNDANCE	
	DAY	NIGHT
LABRIDAE		
Thalassoma bifasciatum (Bluehead wrasse)	***	
" " (" juvenile)	**	
Halichoeres poeyi (Blackear wrasse)	*	
Halichoeres radiatus (Puddingwife)	**	
Halichoeres garnoti (Yellowhead wrasse)	**	
SCARIDAE		
Scarus vetula (Queen parrotfish)	**	
Scarus taeniopterus (Princess parrotfish)	**	
Scarus coelestinus (Midnight parrotfish)	**	*
Sparisoma rubripinne (Yellowtail parrotfish)	**	*
Sparisoma chrysopterum (Redtail parrotfish)	**	
Sparisoma aurofrenatum (Redband parrotfish)	*	
Scarus croicensis (Striped parrotfish)	***	
Sparisoma viride (Stoplight parrotfish)	**	*
BLENNIDAE		
Dphioblennius atlanticus (Redlip blenny)	**	
ACANTHURIDAE		
Acanthurus coerulus (Blue tang)	***	**
Acanthurus chirurgus (Doctorfish)	**	
Acanthurus bahiansis (Ocean surgeon)	**	**
DSTRACIIDAE		
Lactophrys triqueter (Smooth trunkfish)	*	*

TOTAL SPECIES	**55**	**20**

Key: *   1   ***   6-10
      **   2-5   ****   11-30   *****   31-1D0

Table 4   Relative abundance of reef fish on patch reef V by day and by night.

Fig. 13   Coral reef fish species list and numbers of individuals
collected at a rotenone station - a mangrove patch on the
leeward shore of Anegada.
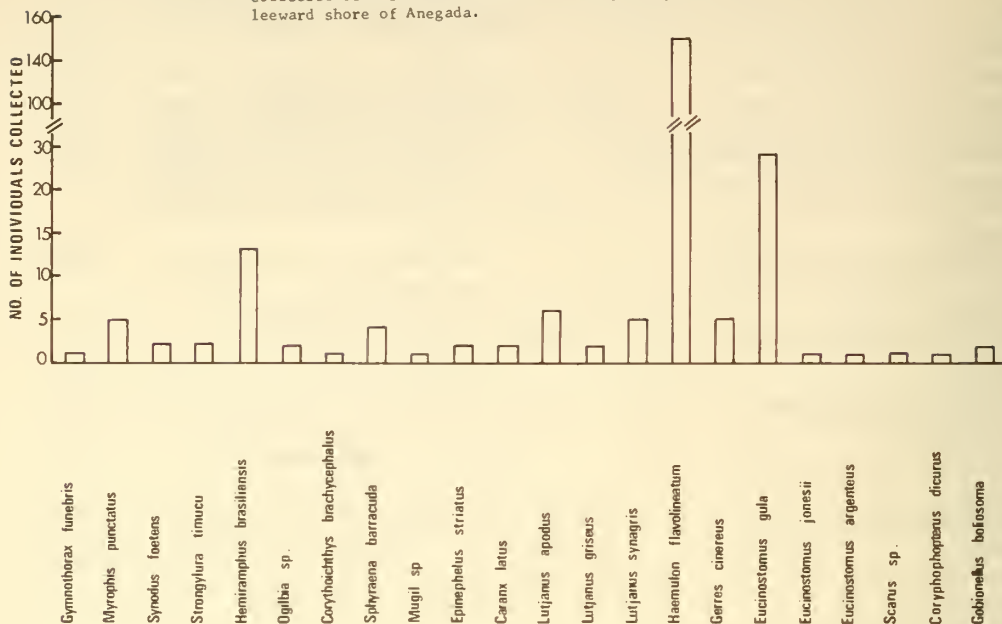
Fig. 14   Length - frequency distribution of the French Grunt
Haemulon flavolineatum at a rotenone station - a mangrove
patch on the leeward shore of Anegada.
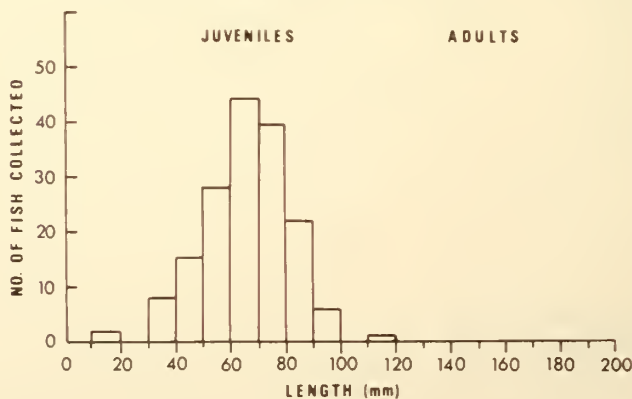
Fig. 15 Number of coral reef fish species recorded on A.) the Windward shore and B.) the Leeward shore of Anegada.
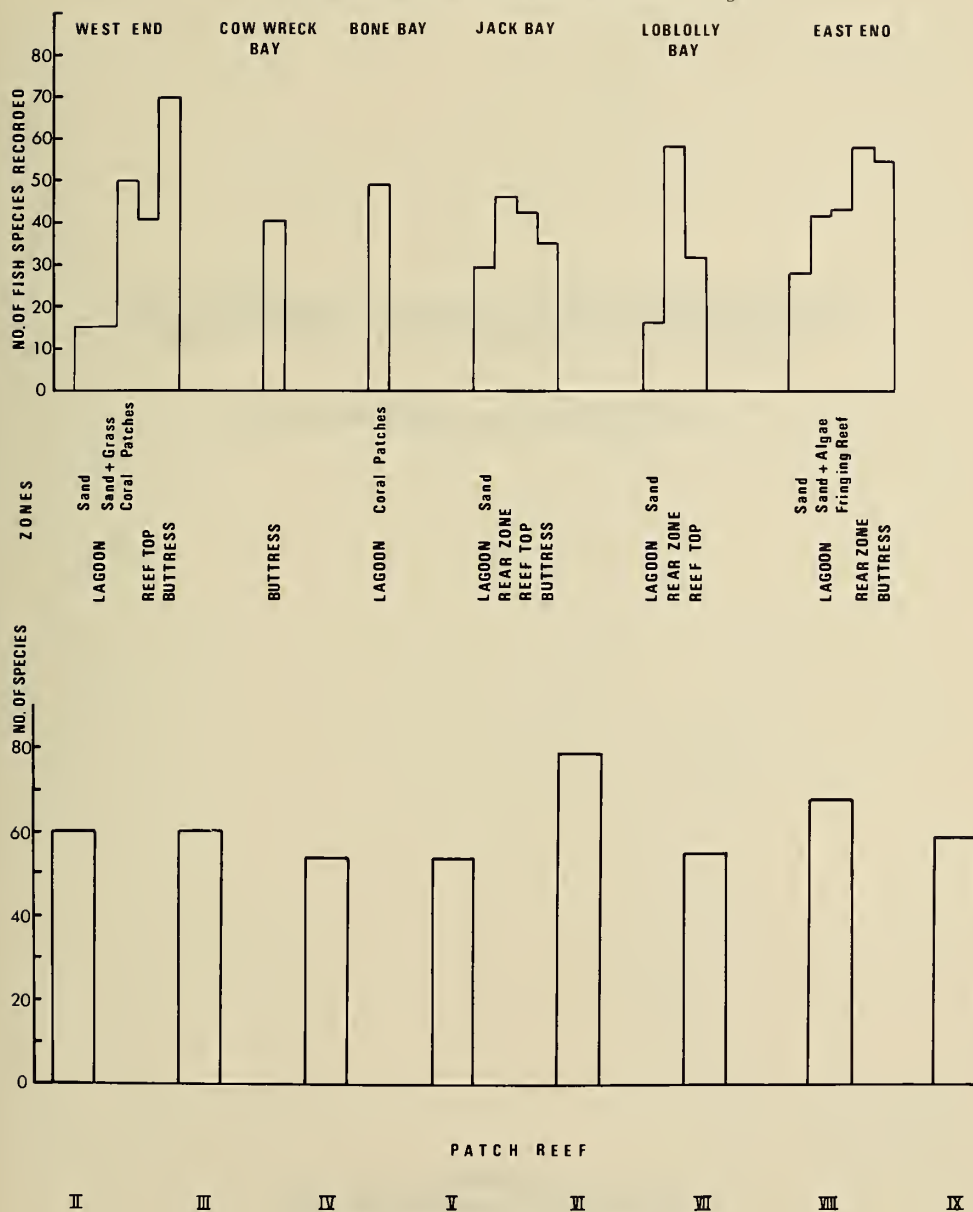
THE INTERTIDAL ALGAE OF THE MAINLAND COAST IN THE VICINITY OF TOWNSVILLE, QUEENSLAND

by Yinam Ngan and Ian R. Price
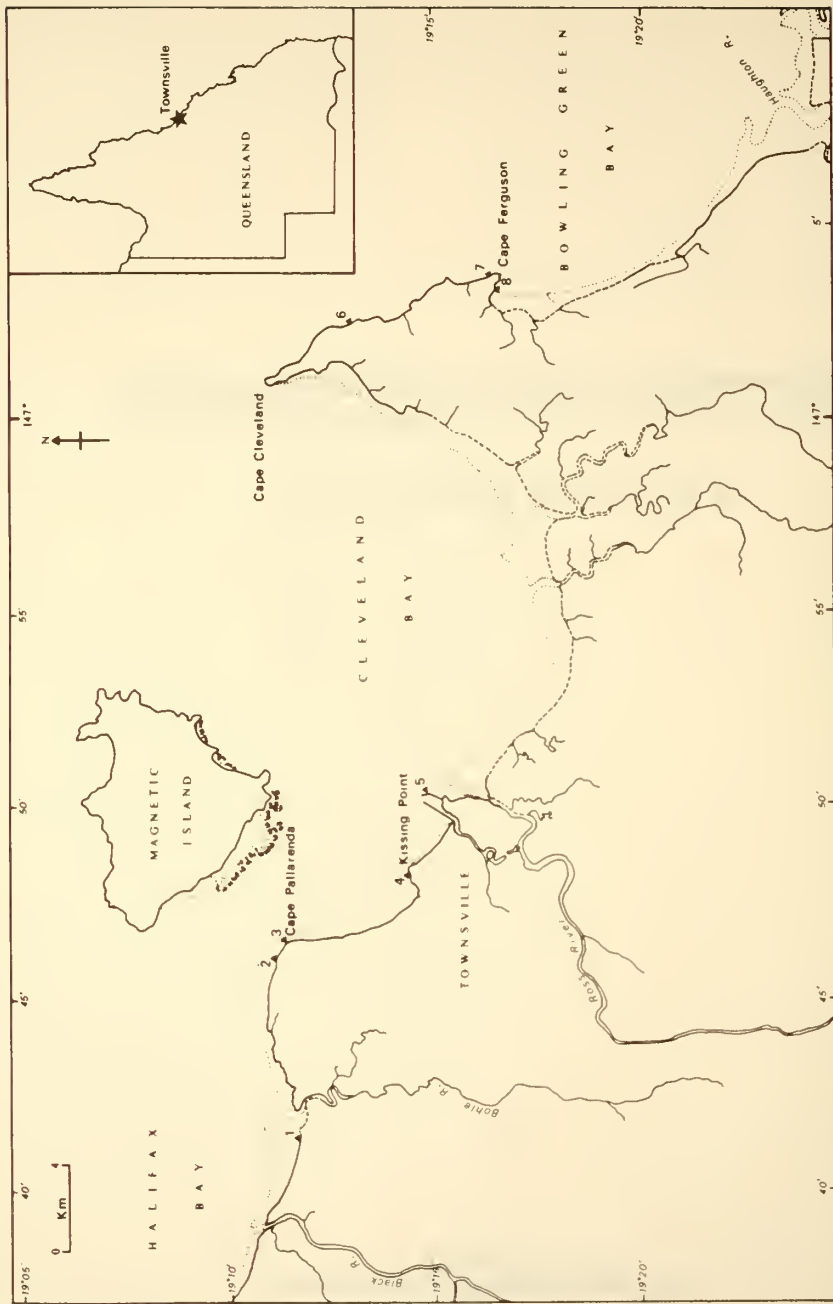
Fig. 1. Map of Townsville region showing location of collecting stations. 1 - Station I, Saunder's Beach; 2 - Station II, NW of Cape Pallarenda; 3 - Station III, Cape Pallarenda; 4 - Station IV, Kissing Point; 5 - Station V, Eastern Breakwater; 6 - Station VI, SE of Cape Cleveland; 7 - Station VII, Cape Ferguson, Turtle Bay; 8 - Station VIII, Cape Ferguson, Ticklebelly Bay.

THE INTERTIDAL ALGAE OF THE MAINLAND COAST IN THE VICINITY OF TOWNSVILLE, QUEENSLAND

by Yinam Ngan and Ian R. Price[1]

ABSTRACT

One hundred and thirty-nine taxa of intertidal marine algae are recorded from eight stations in the vicinity of Townsville, on the north-east tropical coast of Australia. The flora comprises 25 species of Chlorophyta, 19 of Phaeophyta, 89 of Rhodophyta, and 6 of Cyanophyta, most of which are new records for the area.

INTRODUCTION

The benthic marine algal flora in the Townsville region has remained virtually unstudied to the present time. Only three algal species have been reported previously (Endean *et al.*, 1956). However, some collections and studies have been made in Queensland waters to the north (see Lucas, 1931; Cribb, 1961; Price *et al.*, 1976) and also further south (see Lucas, 1931; May, 1951; Cribb, 1954, 1956, 1958a, 1958b, 1960, 1965a, 1965b, 1966, 1969, 1971, 1972, 1973, 1975). Earlier references relating to the marine algae of north-east Queensland are included in Cribb (1954).

The following list of species includes references to published descriptions and illustrations, which should facilitate and stimulate further studies of the algal flora in tropical Australia. The list includes many widely distributed tropical Indo-West Pacific taxa, and will enable more detailed biogeographical comparisons with other regions.

The check-list relates chiefly to rocky intertidal areas along the mainland coast. It is based on collections at eight different stations (Fig. 1) over a two-year period (February 1975 – November 1977), as part of a detailed ecological study of the intertidal algal communities. Stations III, IV, V and VII were sampled monthly throughout this period.

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A total of 139 taxa, comprising 25 Chlorophyta, 19 Phaeophyta, 89 Rhodophyta and 6 Cyanophyta, is reported. The arrangement of orders and families in the Divisions Chlorophyta, Phaeophyta, Rhodophyta, and Cyanophyta generally follows those of Womersley and Bailey (1970), Papenfuss (1951), Kylin (1956), and Desikachary (1973) respectively. In each family, genera and species are listed in alphabetical order.

Voucher specimens of all species listed are deposited in the Herbarium of the Botany Department, James Cook University of North Queensland, Townsville, Queensland, Australia (JCT), and an incomplete set of duplicates is housed in the Herbarium of the Botany Department, University of Queensland, Brisbane, Queensland, Australia (BRIU). Voucher specimen numbers (YN...) are given in parentheses in the station listing for each taxon.

LOCATION AND DESCRIPTION OF THE STATIONS

The study area is located approximately midway along the eastern coast of the State of Queensland, between latitudes 19°10' and 19°17' S, and longitudes 146°37' and 147°04' E (Fig. 1). This dry tropical zone fits essentially into the Aw category in the Köppen scheme (Dick, 1975), with a prolonged and intense drought in the low-sun period of the hemisphere, followed by substantial rainfall during the warmer part of the year (December to March).

The shoreline consists generally of alternating granitic rocky headlands and sandy beaches, and includes the estuaries of rivers such as the Bohle, Ross and Haughton. Mangrove vegetation occurs at numerous places along the coast. The study area is sheltered from oceanic swell from the south-west Pacific Ocean by the Great Barrier Reef system.

The tides are semi-diurnal with significant diurnal inequality (Easton, 1970). The mean tidal range is 2.5m at spring and 0.8m at neap periods (Queensland Department of Harbours and Marine, 1977).

The south-east trade winds prevail for much of the year. The occasional passage of tropical cyclones in summer is generally accompanied by torrential rain, storm surge, and high wave energy.

Station I (Saunder's Beach): Gently sloping sandy beach with occasional patches of pebbles and shell-fragments; the latter is the only type of substratum available to larger algae in this unstable habitat. Algae were also collected in the neighbouring estuary of Saunder's Creek.

Station II (NW of Cape Pallarenda): Rocky point with frequent sand and silt covered boulders at higher intertidal levels. A very gently sloping sand flat occurs at lower intertidal levels.

Station III (Cape Pallarenda): Similar to station II, but the shore
   densely covered with boulders except at the lowest intertidal
   levels.

Station IV (Kissing Point): Rocky point consisting in the intertidal
   of a mass of sediment covered boulders and rocks, with a sandy
   floor at the lowest intertidal levels. The Point is bounded to
   the east by a sandy beach, and to the west by a small, shallow,
   muddy bay containing sparse mangrove vegetation near the shore-
   line and extensive lag gravels at lower levels.

Station V (Eastern Breakwater): Artificial harbour wall consisting of
   relatively smooth granitic rocky surfaces at higher intertidal
   levels, and irregular boulders at lower levels. Conditions inside
   the breakwater are sheltered (and heavily silted) in comparison
   with the exposed outer face.

Station VI (SE of Cape Cleveland): Steeply sloping rocky shore
   consisting of sediment free boulders above and pebbles below.

Station VII (Cape Ferguson, Turtle Bay): Steeply sloping rocky shore
   consisting mostly of large boulders providing numerous shaded
   situations, with some sandy patches at lower levels.

Stations VIII (Cape Ferguson, Ticklebelly Bay): Rocky shore varying
   from large boulders to a gently sloping muddy beach with
   occasional boulders, and adjacent to extensive mangrove
   vegetation.

   The stations listed above may be divided into two groups. The
area between Capes Cleveland and Ferguson, which includes Stations VI
and VII, is characterized by steeply sloping sandy beaches and rocky
outcrops, higher wave energy, and generally less turbid water. In
contrast, stations to the west of Cape Cleveland (I, II, III, IV and
V) and to the south of Cape Ferguson (VIII) generally slope more gently,
are more sheltered, and the water is usually more turbid. These
differences in environmental conditions are reflected in the composition
of the intertidal algal flora of these two groups of stations, as will
be discussed in detail in a subsequent publication.

DIVISION CHLOROPHYTA

Order ULOTRICHALES

Family Ulvaceae

Enteromorpha clathrata (Roth) J. Agardh. Bliding 1963: 107, fig. 67.
　　Station IV (YN 12).

E. flexuosa (Wulfen ex Roth) J. Agardh. Bliding 1963: 73, fig. 38.
　　Station II, III, IV (YN 373), V, VI, VII (YN 93).

E. ralfsii Harvey. Bliding 1963: 43, fig. 18.
　　Station IV (YN 390).
　　Occasional lateral proliferations are present as in
　　E. chaetomorphoides Boergesen (1913: 5, fig. 1), but the cells
　　contain 2-4 pyrenoids.

Ulva rigida C. Agardh. Bliding 1968: 546, figs. 6-10.
　　Stations III, IV (YN 112, YN 367), V, VI, VII.

Order CLADOPHORALES

Family Cladophoraceae

Chaetomorpha antennina (Bory) Kuetzing. Boergesen 1913: 16, figs.
　　4-5; 1940: 37. Cribb 1954: 17, pl. 1, fig. 6. Dawson 1954: 386,
　　fig. 6*l*.
　　Stations III, IV, V, VI (YN 155), VII.

C. spiralis Okamura 1912: 162, pl. 95. Segawa 1968: 11, fig. 49.
　　Stations IV, VII (YN 389).
　　Comparison with authentic Japanese material is required.

Chaetomorpha sp.
　　Stations III, IV (YN 393).

Cladophora fascicularis (Mertens ex C. Agardh) Kuetzing 1853: 26,
　　pl. 90, fig. 2. Boergesen 1940: 34, fig. 10. Pham-hoang 1969:
　　433, fig. 4.38.
　　Stations III, IV, V, VI, VII (YN 94).

C. rugulosa von Martens. Okamura 1910: 103, pl. 80, figs. 1-7.
　　Sakai 1964: 67, figs. 31-2, pl. 15, fig. 1. Pham-hoang 1969:
　　431, fig. 4.36.
　　Stations III, IV, V, VI (YN 151), VII.

Rhizoclonium capillare Kuetzing. Cribb 1965b: 262, pl. 1, figs. 1-8.
　　Stations III (YN 272), IV.
　　Cribb considers that the transfer of *R. capillare* to *Chaetomorpha*
　　by Boergesen (1925: 45, fig. 13) on the basis of the number of
　　nuclei is not justified.

R. implexum (Dillwyn) Kuetzing. Cribb 1965b: 264.
  R. kochianum Kuetzing. Boergesen 1913: 19, fig. 7.
  Stations III (YN 309), IV.

R. riparium (Roth) Harvey. Taylor 1960: 76. Dawson 1964: 11, pl. 8,
    figs. B-E. Pham-hoang 1969: 413, fig. 4.18.
  Stations III (YN 296), IV, VII, VIII.

Family Anadyomenaceae

Microdictyon okamurai Setchell. Yamada 1934: 40, figs. 6-7.
    Taylor 1950: 46, pl. 27, fig. 1. Dawson 1956: 32, fig. 11a.
    Pham-hoang 1969: 439, fig. 4.43.
    Station VII (YN 313).
    The cell wall thickness is about 2 μm and shows little variation.

Order SIPHONOCLADALES

Family Valoniaceae

Valonia aegagropila C. Agardh. Egerod 1952: 348, pl. 29, fig. b.
    Dawson 1954: 388, fig. 8j. Cribb 1960: 13.
    Station IV (YN 320).

Family Siphonocladaceae

Cladophoropsis herpestica (Montagne) Howe. Dawson 1954: 390, fig. 8h.
    Cribb 1960: 10, pl. 4, figs. 5-6.
    Station IV, V, VI (YN 154), VII.

Family Boodleaceae

Boodlea composita (Harvey) Brand. Boergesen 1940: 21, fig. 6;
    1946: 15, fig. 5. Dawson 1954: 390, fig. 9c-d. Cribb 1960: 14
    Station VII (YN 392).

Struvea anastomosans (Harvey) Piccone & Grunow ex Piccone.
    Boergesen 1913: 54, fig. 39. Dawson 1954: 390, fig. 8g.
    Cribb 1960: 13.
    Stations III, IV, V, VI (YN 153), VII.

Order CODIALES

Family Bryopsidaceae

Bryopsis indica Gepp & Gepp 1908: 169, pl. 22, figs. 10-11.
    Boergesen 1953: 6, fig. 1. Cribb 1954: 18. Dawson 1956: 34,
    fig. 14.
    Stations IV (YN 27), V.

Order CAULERPALES

Family Caulerpaceae

Caulerpa lentillifera J. Agardh. Weber-van Bosse 1898: 380, pl. 34,
    figs. 1-2. Cribb 1958b: 213, pl. 4, figs. 1-4, pl. 5, figs. 1-17.
    Station VII (YN 260).

C. racemosa var. *laetevirens* (Montagne) Weber-van Bosse 1898: 366,
    pl. 33, figs. 8, 16-22. Cribb 1958b: 212, pl. 3, figs. 1-7.
    Stations III, IV (YN 69), V, VII.

C. taxifolia (Vahl) C. Agardh. Boergesen 1913: 131, figs. 104-105.
    Cribb 1958b: 210, pl. 1, figs. 8-11, pl. 2, figs. 1-5.
    Stations III, IV, V, VII (YN 95).

C. verticillata J. Agardh. Weber-van Bosse 1898: 267, pl. 20, figs.
    7-10. Boergesen 1913: 121, figs. 95-98. Dawson 1954: 392,
    fig. 10b.
    Station V (YN 409).

Family Udoteaceae

Chlorodesmis hildebrandtii Gepp & Gepp 1911: 16, 137, figs. 74-75.
    Ducker 1967: 164, pls. 6, 16.
    Station III (YN 391).
    Ducker (1967: 163) queried the occurrence in Queensland of this
    species, which occupies an intermediate position between *C. major*
    and *C. fastigiata* (given as *C. comosa*, but see Ducker 1969: 17).

Udotea flabellum (Ellis & Solander) Howe. Gepp & Gepp 1911: 131,
    pl. 3, figs. 26-28. Lucas 1931: 49. Durairatnam 1961: 25,
    pl. 20, fig. 2.
    Stations III (YN 399), IV.

Order DASYCLADALES

Family Dasycladaceae

Acetabularia calyculus Quoy & Gaimard. Valet 1969: 617, pl. 44,
    figs. 7-9.
    Stations III, IV (YN 72).

DIVISION PHAEOPHYTA

Order ECTOCARPALES

Family Ectocarpaceae

Bachelotia antillarum (Grunow) Gerloff   1959: 37. Cardinal 1964: 10.
    Pylaiella antillarum (Grunow) De Toni. Blomquist 1958: 25, figs. 1-17.
    Station V (YN 407).

Feldmannia irregularis (Kuetzing) Hamel 1939: XVII, fig. 61f.
     Cardinal 1964: 54, fig. 29.
     Ectocarpus irregularis Kuetzing. Boergesen 1941: 23, figs. 8-11.
     Dawson 1954: 398, fig. 14e-f.
     Station III (YN 297).

Giffordia mitchellae (Harvey) Hamel 1939: x, fig. 61c.
     Ectocarpus mitchellae Harvey. Boergesen 1941: 7, figs. 1-5.
     Dawson 1954: 400, fig. 14c-d.
     Stations III, IV (YN 117), VII.

Family Ralfsiaceae

Ralfsia sp.
     Stations II, III, IV (YN 413), V, VI, VII.

Order SPHACELARIALES

Family Sphacelariaceae

Sphacelaria furcigera Kuetzing 1855: 27, pl. 90, fig. 2. Dawson
     1954: 400, fig. 14g.
     Stations III (YN 292), IV, VII.

S. tribuloides Meneghini. Boergesen 1941: 41, fig. 18. Dawson 1954:
     400, fig. 14i-j.
     Station VII (YN 281)

Order DICTYOTALES

Family Dictyotaceae

Dictyopteris delicatula Lamouroux. Boergesen 1914: 60, figs. 40-41.
     Yamada 1950: 187, figs. 5-6. Pham-hoang 1969: 333, fig. 3.32.
     Station VII (YN 256).

D. woodwardii (Brown ex Turner) Schmitz. Durairatnam 1961: 35, pl. 23.
     Misra 1966: 151, fig. 79.
     Haliseris woodwardii (Brown) J. Agardh. Kuetzing 1859: 22, pl. 53,
     fig. 2.
     Station VII (YN 331).

Dictyota bartayresii Lamouroux. Cribb 1954: 20. pl. 3, fig. 6.
     Stations III, IV (YN 397), V, VII.
     Some specimens are similar to *D. bartayresii* Lamouroux *sensu*
     Vickers (see Jaasund 1970: 72, figs. 1D, 2C).

D. ciliolata Kuetzing. Womersley 1958: 148, pl. 1. Taylor 1960: 223,
     pl. 32, fig. 3, pl. 59, fig. 1. Jaasund 1970: 76, fig. 2A.
     Stations III, IV, V (YN 249), VII.

D. dichotoma var. *intricata* (C. Agardh) Greville. Cribb 1954: 20,
     pl. 3, fig. 4.
     Stations III (YN 395), IV.

Lobophora variegata (Lamouroux) Womersley 1967: 221. Womersley &
     Bailey 1970: 292.
     Pocockiella variegata (Lamouroux) Papenfuss 1943: 467, figs. 1-14.
     Dawson 1954: 400, fig. 14k.
     Stations IV, VII (YN 97).

Padina tetrastromatica Hauck. Boergesen 1930a: 172, fig. 10, pl. 2;
     1935: 35. Gaillard 1967: 447, figs. 1-6.
     Stations III, IV (YN 113), V, VII.

Spatoglossum asperum J. Agardh. Boergesen 1935: 35, pl. 5; 1937b: 313;
     1941: 48. Durairatnam 1961:34. Misra 1966: 160, fig. 85.
     Station VII (YN 335).

Order DICTYOSIPHONALES

Family Punctariaceae

Colpomenia sinuosa (Roth) Derbès & Solier. Okamura 1907b: 86, pl. 19,
     figs. 11-12, pl. 20, figs. 10-12. Boergesen 1914: 20, fig. 12.
     Clayton 1975: 187, figs. 5-7, 12-13.
     Stations III, IV (YN 414), V, VII.

Rosenvingea orientalis (J. Agardh) Boergesen 1914: 26; 1930a: 168;
     1937a: 25. Cribb 1954: 24, pl. 2, fig. 3. Misra 1966: 126.
     Station IV (YN 396).

Order FUCALES

Family Cystoseiraceae

Cystoseira trinodis (Forsskål) C. Agardh. Papenfuss & Jensen 1967: 21,
     figs. 1-2. Jaasund 1976: 53, fig. 108.
     Stations IV (YN 400), V, VII.

Family Sargassaceae

Sargassum oligocystum Montagne. Womersley & Bailey 1970: 299, fig. 8,
     pl. 25, fig. 16.
     S. binderi Sonder ex J. Agardh. Sonder 1871: 11. J. Agardh 1889:
     87, pl. 26, fig. 2. Jaasund 1976: 57, fig. 112, pl. 4.
     Stations IV, V, VII (YN 372).
     The specimens show many of the characters described for
     S. oligocystum by other authors, although the branches are only
     slightly compressed. Spines occur on the very short leaf petiole.

Sargassum sp.
     Station VII (YN 401).
     The material shows a number of the features of *S. polycystum*
     C. Agardh as described by Durairatnam (1961: 46, pl. 10, figs.
     14-18) and Jaasund (1976: 57, fig. 115), for example muricate
     branches, but fertile specimens have not been found.

DIVISION RHODOPHYTA

Order NEMALIALES

Family Helminthocladiaceae

Liagora sp.
    Station VII (YN 354).

Family Chaetangiaceae

Galaxaura oblongata (Ellis & Solander) Lamouroux. Boergesen 1927: 71,
    figs. 39-41. Chou 1947: 7, pls. 2-3, 9. Papenfuss & Chiang
    1969: 310, fig. 5.
    Stations IV (YN 394), VII.

Scinaia moretonensis Levring 1953: 509, figs. 39-40. Womersley 1958:
    153.
    Stations IV, VII (YN 356).

Family Bonnemaisoniaceae

Asparagopsis taxiformis (Delile) Trevisan.
    Boergesen 1919: 352, fig. 347-351. Dawson 1953: 57.
    Station IV, V (YN 415).

Falkenbergia hillebrandii (Bornet) Falkenberg. Boergesen 1919: 331,
    figs. 332-333. Dawson 1954: 414, fig. 25*l*.
    Stations IV, V (YN 46).

Order GELIDIALES

Family Gelidiaceae

Gelidium corneum (Hudson) Lamouroux. Boergesen 1920: 114, fig. 124.
    Sreenivasa Rao 1970: 71, fig. 5A-E, pl. 2, fig. h. Taylor 1928:
    142, pl. 28, fig. 2.
    Stations IV, V (YN 342), VII.
    Further comparative studies are required to confirm this
    identification.

G. crinale (Turner) Lamouroux. Feldmann & Hamel 1936: 240, fig. 22.
    Station III (YN 277; YN 370).
    The vegetative and reproductive (cystocarpic and tetrasporic)
    structure fits that described by Feldmann and Hamel.

G. crinale var. *perpusillum* Piccone & Grunow. Weber-van Bosse 1921:
    225. Dawson 1954: 421, fig. 31e-f.
    Stations II, III (YN 337), IV.

G. heteroplatos Boergesen 1934: 3, fig. 3. Jaasund 1976: 73, fig. 145.
    Stations III, IV (YN 202), V, VII (YN 279).

Certain specimens referred to this species show some features of *G. spathulatum* (Kuetzing) Bornet (see Pham-hoang 1969: 123, fig. 2.53).

G. pusillum (Stackhouse) Le Jolis. Boergesen 1924: 279, fig. 26, Dawson 1954: 420, fig. 31a-c. Taylor 1960: 354, pl. 45, fig. 4. Stations III, IV (YN 119), V, VII (YN 161).

Gelidium sp. 1
   Station V (YN 411).
   The shape and arrangement of the cystocarps, and the anatomy of the thallus are similar to those described for *G. heteroplatos*. However the rather short and somewhat terete thalli and the form of the tetrasporangial stichidia seem distinct.

Gelidium sp. 2.
   Station IV (YN 198, YN 326).
   The specimens superficially resemble those referred to *Gelidium corneum* , but they are more slender and less cartilaginous. Rhizines are confined to the inner cortex, but as female material has not been collected the generic relationships remain uncertain.

Order CRYPTONEMIALES

Family Rhizophyllidaceae

Chondrococcus hornemannii (Lyngbye) Schmitz. Weber-van Bosse 1921: 255. Womersley & Bailey 1970: 305.
   Desmia hornemannii Lyngbye. Kylin 1956: 166, fig. 113.
   Station VII (YN 374).

Family Hildenbrandtiaceae

Hildenbrandtia prototypus Nardo. Dawson 1953: 95, pl. 7, fig. 4; 1954: 424, fig. 36a-b.
   Stations II, III, IV, V. VI (YN 152), VII, VIII.

Family Corallinaceae

Amphiroa fragilissima (Linnaeus) Lamouroux. Weber-van Bosse 1904: 89, pl. 16, figs. 1-2, 5. Dawson 1954: 430, fig. 40g-h. Taylor 1960: 403, pl. 47, figs. 1-2.
   Stations III, IV (YN 118), V. VII.

Cheilosporum spectabile Harvey ex Grunow. Weber-van Bosse 1904: 106. Boergesen 1935: 51, fig. 23. Pham-hoang 1969: 146, fig. 2.75. Womersley & Bailey 1970: 314, fig. 22, pl. 26.
   Station VII (YN 378).

Jania adhaerens Lamouroux. Boergesen 1917: 195, figs. 184-7. Pham-hoang 1969: 142, fig. 2.71. Jaasund 1976: 77, fig. 154.
   Stations IV, V, VII (YN 416).

Jania sp.
   Station VII (YN 255).

The conceptacle morphology is identical to that described for
J. rubens (Linnaeus) Lamouroux by Kuetzing (1857: 40, pl. 84,
figs. 2-3) and Pham-hoang (1969: 140, fig. 2.68). The branching
pattern is very variable in our material and further confirmation
is required.

Family Grateloupiaceae

Grateloupia divaricata Okamura 1915: 55, pls. 116, 117, figs. 12-18;
    1942: 99.
    Stations III (YN 307), IV (YN 196), V, VII (YN 162).
    The morphology of this species is highly variable. Comparison
    with authentic Japanese material is required.

Order GIGARTINALES

Family Gracilariaceae

Ceratodictyon spongiosum Zanardini. Okamura 1909: 1, pls. 51-52.
    Dawson 1954: 438, fig. 48c.
    Stations III, IV (YN 408).

Gelidiopsis scoparia (Montagne & Millardet) Schmitz. Boergesen 1952:
    26, figs. 13-14; 1954: 22, fig. 7. Pham-hoang 1969: 178, fig. 2.108.
    Station VII (YN 376).

G. variabilis (Greville ex J. Agardh) Schmitz. Weber-van Bosse 1928:
    426. Pham-hoang 1969: 177, fig. 2.107. Jaasund 1976: 87, fig. 176.
    Station IV (YN 357), VII.

Gracilaria crassa Harvey ex J. Agardh. Boergesen 1936: 86, fig. 8.
    Dawson 1954: 438, fig. 48b. Ohmi 1958: 25, fig. 11, pl. 5,
    figs. D-E. Jaasund 1976: 85, fig. 170.
    Stations III, IV (YN 115), V, VII.

G. edulis (Gmelin) Silva. Ohmi 1958: 16, fig. 6, pl. 3, fig. B.
    Durairatnam 1961: 62, pl. 14, figs. 4-5. Jaasund 1976: 85,
    fig. 172.
    Stations IV (YN 199), V, VII (YN 310).

G. purpurascens (Harvey) J. Agardh. Weber-van Bosse 1928: 437.
    Ohmi 1958: 30, fig. 14, pl. 6, figs. C-D.
    Stations IV (YN 365), VII (YN 375).

G. rhodotricha (Dawson) Papenfuss 1966: 100.
    Gracilariopsis rhodotricha Dawson 1949: 47, pl. 19, figs. 3-7.
    Ohmi 1958: 47, fig. 23, pl. 10, figs. A-B.
    Stations III (YN 193, YN 371), IV.
    Papenfuss includes *Gracilariopsis rhodotricha* in the genus
    Gracilaria. The similarity of our material to the descriptions
    given by Dawson and Ohmi is striking. However, the plants from
    this area are smaller and more slender, and male reproductive
    organs have not been found.

G. textorii (Suringar) De Toni. Weber-van Bosse 1928: 438. May 1948:
41. Ohmi 1958: 40, figs. 20-21.
Stations III, IV (YN 350), VII (YN 96).

G. verrucosa (Hudson) Papenfuss. Dawson 1954: 438, fig. 49. Ohmi
1958: 6, figs. 1-2, pl. 1, figs. A-D.
Stations III (YN 192), IV.
This species is often difficult to distinguish from
G. rhodotricha in the field, but can be recognized by the three-
layered cortex, the hemispherical cystocarps with numerous
nutritive filaments, and the many-layered pericarp.

Family Sphaerococcaceae

Caulacanthus ustulatus (Mertens) Kuetzing 1868: 3, pl. 8. Boergesen
1933b: 115; 1950: 19, figs. 5-6. Feldman & Hamel 1936: 256,
figs. 31-33.
Stations III (YN 274), IV (YN 203), V (YN 351), VII.
A very variable species in this area, and may include *C. indicus*
Weber-van Bosse (1921: 222, fig. 67).

Family Solieriaceae

Sarconema filiforme (Sonder) Kylin 1932: 22. Papenfuss & Edelstein
1974: 31, figs. 1-3, 13, 20-25.
Station IV (YN 321, YN 369).

Solieria mollis (Harvey) Kylin 1932: 20, pl. 6, fig. 12. Segawa 1968:
84, fig. 397. Pham-hoang 1969: 189, fig. 2.121.
Rhabdonia mollis Harvey 1863, synop.: 41.
Stations III (YN 269; YN 301), IV.
The specimens agree well with the original description given by
Harvey and appear to be distinct from *S. robusta*.

S. robusta (Greville) Kylin 1932: 18. Boergesen 1950: 13.
Jaasund 1976: 93, fig. 188.
Stations III (YN 270), IV.

Family Rhabdoniaceae

Catenella nipae Zanardini. Tseng 1942: 143, fig. 2. Dawson 1954: 443,
fig. 52f.
Stations II, III (YN 276), IV (YN 157), VII, VIII.

Family Hypneaceae

Hypnea boergesenii Tanaka 1941: 233, figs. 6-8, pl. 53, fig. 1.
Dawson 1954: 436, fig. 46K.
Stations III, IV (YN 346), VII.

H. cenomyce J. Agardh. Tanaka 1941: 250, fig. 21. Pham-hoang 1969:
197, fig. 2.129
Stations V, VI (YN 165).

H. cervicornis J. Agardh. Tanaka 1941: 240, fig. 13. Pham-hoang 1969:
     192, fig. 2.123.
     Stations III (YN 340), IV (YN 347), VII.

H. cornuta (Kuetzing) J. Agardh. Tanaka 1941: 242, fig. 14.
     Dawson 1954: 436, fig. 46c. Jaasund 1976: 99, fig. 200.
     Station IV (YN 360).

H. esperi Bory. Kuetzing 1868: 9, pl. 26, figs. A-C. Tanaka 1941:
     243, fig. 15. Dawson 1954: 436, fig. 46h-j.
     Stations III, IV (YN 345), VII.

H. pannosa J. Agardh. Kuetzing 1868: 9, pl. 27, figs. i-k.
     Weber-van Bosse 1928: 445, fig. 193. Tanaka 1941: 247, fig. 20.
     Jaasund 1976: 97, fig. 196.
     Stations V, VII (YN 384).

H. valentiae (Turner) Montagne. Dawson 1954: 436, figs. 46*l*, 47.
     H. charoides Lamouroux. Kuetzing 1868: 8, pl. 22, figs. a-b.
     Stations IV (YN 344), VII.

Family Dicranemaceae

Dicranema rosaliae Setchell & Gardner 1924: 745, pl. 22, fig. 6.
     Dawson 1957: 115, figs. 22a, 23a.
     Station VII (YN 304).
     Our specimens, like those of Setchell and Gardner and of Dawson,
     are sterile.

Family Phyllophoraceae

Gymnogongrus griffithsiae (Turner) Martens. Kuetzing 1869: 24,
     pl. 65, figs. e-g. Gayral 1958: 398, pl. 107. Pham-hoang 1969:
     206, fig. 2.138.
     Stations IV (YN 13), V, VII.

G. pygmaeus J. Agardh. Kuetzing 1869: 24, pl. 64, figs. c-d. Dawson
     1954: 440, fig. 51c.
     Stations III, IV (YN 349), V (YN 250), VII.

Family Gigartinaceae

Gigartina sp.
     Stations IV, V (YN 383), VII.

Order RHODYMENIALES

Family Rhodymeniaceae

Coelothrix indica Boergesen 1944: 14, figs. 9-11; 1950: 40, figs.
     20-21.

Stations IV (YN 377), VII.
Dawson (1957: 115) suggests that *C. indica* is conspecific with
C. irregularis Boergesen (1920: 389, figs. 373-4), but our
specimens agree better with Boergesen's description of the
Mauritius species.

Rhodymenia leptophylla J. Agardh. Weber-van Bosse 1928: 461.
Kylin 1931: 20, pl. 6, fig. 16. Chapman & Dromgoole 1970: 134,
pl. 44.
Station VII (YN 282).
This species has been considered endemic to New Zealand
(Chapman & Dromgoole, 1970). However, Dawson (1941: 144, pl. 20,
fig. 18; pl. 27, fig. 39) described *C. leptophylloides* as a very
closely related and possibly identical species from Hawaii.

Family Lomentariaceae

Champia parvula (C. Agardh) Harvey. Boergesen 1920: 407, figs. 392-393.
Dawson 1954: 443, fig. 52C. Womersley & Bailey 1970: 321.
Stations III, IV, VII (YN 353).

Order CERAMIALES

Family Ceramiaceae

Centroceras clavulatum (C. Agardh) Montagne. Dawson 1954: 466, fig.
54h. Womersley & Bailey 1970: 323.
Stations III, IV, V, VI (YN 147), VII.

Ceramium fastigiatum (Roth) Harvey. Boergesen 1918: 241, fig. 231.
Taylor 1928: 191, pl. 27. Nakamura 1965: 129, fig. 4. Pham-
hoang 1969: 237, fig. 2.169.
Station III (YN 363).

C. gracillimum var. *byssoideum* (Harvey) Mazoyer. Dawson 1954: 448,
fig. 55e-f. Nakamura 1965: 136, fig. 6. Itono 1972: 76,
figs. 2-3.
Stations III, IV (YN 380), V, VII.

C. maryae Weber-van Bosse 1923: 324, figs. 117-118. Dawson 1954: 448,
fig. 56g-i.
Station IV (YN 364).

C. mazatlanense Dawson 1950: 130, pl. 2, figs. 14-15; 1954: 448,
fig. 55g-j. Itono 1972: 82, fig. 11 B-C.
Station VII (YN 379).

Ceramium sp.
Station VII (YN 352).
The specimens have forcipate tips, cortical bands with a central
whorl of larger periaxial cells, and whorled tetrasporangia.
They approach *C. marshallense* Dawson (1957: 20, fig. 27a-b), but
differ in their broader branches (200 μm), unequal dichotomies,
and wider cortical bands (130 μm).

Griffithsia sp.
    Station VII (YN 382).

Pleonosporium sp.
    Station IV (YN 319), V (YN 412).
    Rhizoids occur on the lower parts of the main axes, and
    polysporangia are present.

Spyridia filamentosa (Wulfen) Harvey. Boergesen 1917: 233, figs.
    222-6. Dawson 1954: 444, fig. 54i. Jaasund 1976: 111, fig. 224.
    Station IV (YN 381).

Family Delesseriaceae

Caloglossa bombayensis Boergesen 1933b: 127, figs. 10-12.
    Stations II, III, IV (YN 280).
    The status of this species in relation to *C. ogasawaraensis*
    Okamura has been discussed by Tseng (1945: 163) and Post (1943:
    139; 1955: 371).

C. leprieurii var. *hookeri* (Harvey) Post 1943: 127, figs. 3-5, 24.
    Taylor 1960: 544.
    Stations I, II, III, IV (YN 158), V, VI, VIII.

Family Dasyaceae

Heterosiphonia multiceps (Harvey) Falkenberg 1901: 654.
    Dasya multiceps Harvey. Kuetzing 1863: 27, pl. 77.
    Station IV (YN 368).

H. wurdemanni var. *laxa* Boergesen 1919: 324, figs. 327-8.
    Dawson 1956: 57, fig. 60; 1963: 404, pl. 129, fig. 1.
    Station IV (YN 325).

Family Rhodomelaceae

Acanthophora muscoides (Linnaeus) Bory. Okamura 1907a: 38, pl. 8,
    fig. 8-10. Taylor 1960: 619, pl. 72, fig. 3. Jaasund 1976: 137,
    fig. 278.
    Stations III (YN 191), IV, VII.

A. spicifera (Vahl) Boergesen 1918: 259, figs. 235-8. Weber-van Bosse
    1923: 347, figs. 131-2. Dawson 1954: 456, fig. 61a-b.
    Stations III (YN 190), IV (YN 110), V, VII.

Acrocystis nana Zanardini. Okamura 1907a: 23, pls. 6-7. Dawson 1954:
    461, fig. 63b-c. Jaasund 1976: 143, fig. 291.
    Station VII (YN 334).

Bostrychia binderi Harvey 1847: 68, pl. 28. Tseng 1943a: 177, pl. 1,
    figs. 7-8.
    Stations III (YN 317), IV (YN 159), VII, VIII.

B. kelanensis Grunow ex Post 1936: 20; 1955: 356; 1957: 90.
Tseng 1943a: 169, pl. 2, figs. 1-5.
Station IV (YN 402).

B. radicans (Montagne) Montagne. Post 1936: 13. Tseng 1943a: 168,
pl. 1, figs. 1-3. Dawson 1954: 452, fig. 59d-e. Jaasund 1976:
127, fig. 257.
Stations I, II, III, IV (YN 156, YN 252), V, VII, VIII.

B. tenella (Vahl) J. Agardh. Boergesen 1918: 300, figs. 299-303.
Tseng 1943a: 176, pl. 1, fig. 6. Jaasund 1976: 127, fig. 258.
Stations III (YN 275), IV.

Chondria dasyphylla (Woodward) C. Agardh. Taylor 1928: 170, pl. 34,
fig. 1. Jaasund 1976: 135, fig. 274, pl. 9.
Stations III (YN 303), IV.

C. rainfordii Lucas 1927, 560, pls. 45, 47, fig. 2.
Stations III (YN 189), IV.

Chondria sp. 1.
Station VII (YN 386).
The specimens superficially resemble *C. dasyphylla,* although
cystocarpic and tetrasporic plants are only 1-2 cm tall.
Branch tips are truncate, but with a projecting apical region.
The walls of internal cells are markedly thickened over their
whole surface.

Chondria sp. 2.
Station VII (YN 385).
The specimens show good agreement with the descriptions of
C. collinsiana Howe given by Taylor (1960: 617) and Jaasund
(1976: 135, fig. 275), except that the pericentral cell walls
are strongly thickened over their whole surface.

Herposiphonia insidiosa (Greville ex J. Agardh) Falkenberg.
Okamura 1930: 25, pl. 264, figs. 10-16. Dawson 1954: 452,
figs. 58h-i.
Station VII (YN 362).

H. tenella forma *secunda* (C. Agardh) Hollenberg 1968: 556.
H. secunda (C. Agardh) Falkenberg. Boergesen 1918: 469,
fig. 428.
Stations III, IV (YN 404), V, VII.

Laurencia dotyi Saito 1969: 154, figs. 9 A-C, 10 A-B.
Station VII (YN 257).

L. gracilis Hooker & Harvey. Yamada 1931: 212, fig. M, pl. 12,
fig. b.
Stations IV (YN 358), VII.

L. majuscula (Harvey) Lucas 1935: 223. Saito & Womersley 1974: 819,
figs. 1A, 6.
Station VII (YN 92, YN 283, YN 329).

L. nidifica J. Agardh. Yamada 1931: 202. Boergesen 1945: 47, figs.
21–24. Cribb 1958a: 168, pl. 5, fig. 12, pl. 6, figs. 1–3.
Saito 1969: 152, fig. 5.
Stations III, IV (YN 253), VII.

L. papillosa (C. Agardh) Greville. Yamada 1931: 190, pl. 1, figs. a–b.
Dawson 1954: 458, fig. 61i. Cribb 1958a: 169. pl. 7, figs. 6–8.
Saito 1969: 158.
Stations III (YN 146), IV, VII.

L. perforata (Bory) Montagne. Kuetzing 1865: 18, pl. 49, figs. e–g.
Boergesen 1930b: 69, fig. 26. Yamada 1931: 193, figs. A–B, pl. 3,
fig. b. Cribb 1958a: 164, pl. 3, figs. 1–2.   ,
Stations IV (YN 201), VII (YN 287).

L. pygmaea Weber–van Bosse 1913: 122, pl. 12, fig. 6. Dawson 1954: 458,
fig. 62k. Cribb 1958a: 166, pl. 4, figs. 1–6.
Stations IV (YN 70), V, VII.

L. succisa Cribb 1958a: 163, pl. 1, figs. 1–3. Saito 1969: 157.
Stations VII (YN 288, YN 327, YN 359).

L. tenera Tseng 1943b: 200, pl. 1, fig. 6, pl. 2, figs. 5–6.
Dawson 1954: 458, fig. 62b–c. Cribb 1958a: 167, pl. 5, figs.
1–10. Saenger 1973: 25, figs. 12–13.
Station VII (YN 289, YN 333).
The specimens agree very well with the detailed descriptions of
the sterile and tetrasporic materials given by Tseng. However,
no peripheral haptera are present in our specimens.

Laurencia sp.
Station VII (YN 388).
This species belongs to the subgenus Chondrophycus (see Saito
1969: 148), and approaches *L. cartilaginea* Yamada (1931: 230,
fig. 0, pl. 19a) in anatomy (see Saito 1967: 53, fig. 43).
However, our material appears to be more slender (to 1 mm broad
at the base), more or less cylindrical throughout, and the
ultimate branchlets are not densely arranged on the upper branches.

Leveillea jungermannioides (Martens & Hering) Harvey. Falkenberg 1901:
392, pl. 6, figs. 1–13, pl. 14, figs. 18–27. Dawson 1954: 461,
fig. 63a.
Station VII (YN 355).

Polysiphonia coacta Tseng 1944: 71, pl. 2. Pham–hoang 1969: 258,
fig. 2.189.
Station IV (YN 361), VII (YN 343).

P. fragilis Suringar. Okamura 1929: 7, pl. 255. Dawson 1954: 452, fig.
      60a-b.
      Station III (YN 338).

P. subtilissima Montagne. Kuetzing 1863: 10, pl. 28, fig. 1a-e.
      Tseng 1944: 70, pl. 1. Pham-hoang 1969: 255, fig. 2.185.
      Stations III (YN 300), IV, V, VII.

Tolypiocladia glomerulata (C. Agardh) Schmitz. Falkenberg 1901: 177,
      pl. 21, figs. 27-29. Dawson 1954: 452, fig. 59b-c.
      Roschera glomerulata (C. Agardh) Schmitz. Weber-van Bosse 1923:
      359.
      Stations III, IV (YN 403), VII.

Vidalia fimbriata (R. Brown) J. Agardh. Falkenberg 1901: 430, pl. 7,
      fig. 19. Boergesen 1945: 44, fig. 20. Jaasund 1976: 133,
      fig. 269.
      Station VII (YN 330).

DIVISION CYANOPHYTA

Order NOSTOCALES

Family Oscillatoriaceae

Lyngbya majuscula (Dillwyn) Harvey ex Gomont. Dawson 1954: 380,
      fig. 3d. Umezaki 1961: 54, pl. 8, fig. 3.
      Stations II, III, IV (YN 299), V, VII (YN 295), VIII.
      Drouet (1968: 263) refers this taxon to *Microcoleus lyngbyaceus*
      (Kuetzing) Crouan.

Microcoleus chthonoplastes Thuret ex Gomont. Desikachary 1959: 343,
      pl. 60, figs. 7-9. Umezaki 1961: 37, pl. 5, fig. 2. Pham-hoang
      1969: 22, figs. 1-16.
      Stations III, IV (YN 291), V.
      Drouet (1968: 109) refers this taxon to *Schizothrix arenaria*
      (Berkeley) Gomont.

Family Rivulariaceae

Calothrix crustacea Thuret ex Bornet & Thuret. Dawson 1957: 127, fig.
      31e. Umezaki 1961: 95, pl. 17, fig. 2, pl. 18, fig. 1.
      Stations II, III (YN 286), IV, V, VI, VII, VIII.

C. pilosa Harvey. Dawson 1954: 379, fig. 3e. Umezaki 1961: 97, pl. 18,
      fig. 2.
      Stations III, IV, V, VIII (YN 398).

Kyrtuthrix maculans (Gomont) Umezaki 1961: 85, pl. 14, fig. 1.
      Stations II, III, IV (YN 406), V, VI, VII, VIII.

Order STIGONEMATALES

Family Mastigocladaceae

Brachytrichia quoyi (C. Agardh) Bornet & Flahault. Dawson 1954: 380,
    fig. 3k-1. Umezaki 1961: 82, pl. 13.
    Stations III, IV (YN 298), V, VII.

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BLUE-GREEN ALGAE (CYANOBACTERIA) OF
THE OCEANIC COAST OF ALDABRA

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ABSTRACT

An account is given of the blue-green algae of the oceanic coast of Aldabra, from the supralittoral to the sublittoral at 40 m depth. These algae are most conspicuous in the supralittoral and upper littoral. Here they form an almost complete cover on rocks, usually with both epilithic and endolithic layers, and on beachrock sometimes also a distinct chasmolithic layer some 3 to 5 mm inside the rock. Lower in the intertidal their distribution is patchy, though sometimes there occur visually conspicuous films of various Oscillatoriaceae or *Nodularia* on sediments or tiny colonies of *Calothrix crustacea* on rocks. Of all regions on the atoll with a dense photosynthetic cover, the uppermost 15 m of the sublittoral probably has the fewest obvious growths of blue-green algae, but these become more frequent at greater depths. Conspicuous blue-green algal populations below 15 m are all dominated by forms of *Lyngbya*. At one site, at a depth of 40 m, there occurred branched tubular structures made up of filaments of *L. sordida*, and closely associated with shrimps which apparently live inside the tubes. Although a similar association has been noted elsewhere in shallow tropical waters, this is the first record for deep waters.

INTRODUCTION

Observations made during the Phase VI Royal Society expedition to Aldabra Atoll, Indian Ocean, showed that blue-green algae (Cyanobacteria) are widespread and often very abundant. It was therefore decided to attempt to produce a comprehensive account of the types and roles of these organisms. Descriptions have since been made of these algae in terrestrial and freshwater environments (Whitton, 1971; Donaldson & Whitton, 1977) and the intertidal region of the lagoon (Potts & Whitton,

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in press). There has not so far been an opportunity to make a systematic study on the outside of the atoll, but many scattered observations have been included at the same time as other studies. They are brought together in the present paper to help complete the general picture of blue-green algae on this one atoll.

There is now a considerable literature on Aldabra. The volume edited by Westoll and Stoddart (1971) includes accounts of the shallow sublittoral marine vegetation (Price, 1971) and zonation of intertidal animals (Taylor, 1971). More recent data on geology are given by Braithwaite *et al.* (1973), and Braithwaite (1975), climate by Stoddart and Mole (1977) and intertidal animals by Hughes and Gamble (1977). Trudgill (1976) and Taylor and Way (1976) deal with aspects of marine erosion, including some comments on the role of endolithic algae. Data on pH and Eh given by Potts and Whitton (1979a) include environments on the oceanic coast, while Potts and Whitton (in press) describe a pink endolithic prokaryote in the supralittoral of an oceanic cliff. These authors also review the marine literature.

METHODS

Interpretation of zones on shore

The use of zonal terminology proved difficult, because many observations were made on single visits at a particular time. Taylor (1971) used the terminology of Lewis (1964), with littoral fringe, eulittoral and sublittoral zones. Potts and Whitton (in press) followed Womersley and Edmonds (1952) when describing the distribution of blue-green algae in the lagoon, with a supralittoral, upper, mid and lower littoral and sublittoral. In the present account we do not feel sufficiently confident of our interpretation of zonation to use one terminology and suggest the equivalents in other systems. We use the terms supralittoral, upper littoral and sublittoral where the zones appear to be equivalent to those described for the lagoon; in situations where there is a distinct barnacle zone (the upper limit of the eulittoral in Lewis's system), reference is also made to this.

Dates and locations

Observations on the blue-green algae of the atoll have been made during three periods: December 1968 — January 1969 by B.A.W.; November 1972 — June 1973 by B.A.W. (part) and A. Donaldson; November 1974 — June 1975 by B.A.W. (part) and M.P. Observations outside the reef ridge in deeper waters were made only during the first visit, on the western end of the north coast; materials were collected down to 40 m using SCUBA (diving). Detailed observations on endoliths in the supralittoral and upper littoral were made only during the third period. Brief general observations were included on the oceanic coast opposite the locations of the 13 transects studied in the lagoon (Potts & Whitton, in press). Visits were made also to the only area of mangrove forest outside the lagoon (Au Parc) and the most exposed coast, the eastern extremity of Point Houdoul.

Naming of blue-green algae

The methods used here for naming blue-green algae are the same as those described in detail by Potts and Whitton (in press). They involve the classical botanical approaches to allocating binomials by authors such as Frémy (1933) and le Campion-Alsumard (1969), with one important modification. Where species have been delimited in the past almost entirely on rather arbitrary size ranges, the records made here are based on standardized ranges *e.g.* cells > 2 ≤ 4 μm, > 4 ≤ 8 μm wide etc. In the floristic list, records are given first for the actual categories used, and then the most appropriate binomial added.

RESULTS

Rocks in the supralittoral and upper littoral

Blue-green algae are present on almost all rock surfaces in the supralittoral and the upper part of the littoral. The nearer a true terrestrial environment, the more frequent is *Tolypothrix byssoidea,* the thinner any continuous endolith layer and the more scattered any true chasmolithic growths. Below the zone of *T. byssoidea,* but above the barnacle zone, the surface of most rocks may appear steel-blue, grey or almost black. The paler colours are due to *Hyella balani,* which grows both at the surface and endolithically. A bright green layer of chasmoliths is sometimes present, composed of forms resembling *Pleurocapsa.* In the same zone (below *Tolypothrix byssoidea* and above barnacles) *Scytonema* sp. forms small olive-green tufts in depressions in the champignon; it was found at every location studied, usually with many epiphytes *e.g. Xenococcus* spp., *Dermocarpa* spp. Slightly lower down the shore *Calothrix* and *Rivularia* are widespread on the north coast, and *Isactis* and *Rivularia* on the south coast.

Areas of beachrock on Île Picard (near the settlement) were studied more intensively. The rock is smooth, rounded and slopes towards the sea at an angle of about 10-15°. It has a blue-grey colour due to *Hyella balani,* and when fractured, a chasmolithic layer about 2 mm thick is visible at a depth of about 3-5 mm. Cells resembling *Pleurocapsa* and fungal hyphae are also present. In small cracks and crevices slightly further down the shore, but still holding water after the tide has receded, accumulated sand supports thin films of *Lyngbya martensiana* and *Schizothrix calcicola,* with some *Nodularia harveyana.* On passing down the shore from the blue-grey rocks, the colour changes to brown at about the level that barnacles appear. The brown colour is due to the sheaths of *Calothrix crustacea* and *C. contarenii,* which form a thin epilithic layer over *Hyella balani.*

After a period of particularly high tides and stormy seas, an extensive area of supralittoral beachrock became exposed due to the removal of sand deposits several metres thick which had been present for at least six months (and probably longer). The newly exposed rock appeared pale yellow, lacking the characteristic steel-blue colour of adjacent rocks. Examination of the surface of the beachrock showed no obvious blue-green algal communities. Patches of pale blue were

just discernable after 5 days, while the whole rock had light steel-blue colour within 2 weeks.   Visually the rock was indistinguishable from other rocks after 5 weeks, but the green chasmolithic layer had not yet appeared.

Several species were recorded only in particular parts of the atoll, although this may well be simply a consequence of insufficient sampling elsewhere.   *Scytonema endolithicum* grows in the upper supralittoral of Île Picard.   The closely appressed filaments bore as much as 1200 μm into the rock; the cells are bright blue-green and the sheaths yellow-brown.   When chips of rock with this alga were placed on agar (high CaCO$_3$ — seawater medium), filaments also developed above the surface, growing vertically, in small tufts, and reaching heights of 1000 — 2000 μm.   At Dune d'Messe, inspection of black rocks showed that lichens are frequent higher up, while the endoliths *Brachytrichia* sp. and *Solentia stratosa* become more frequent lower down.   A zone of lighter coloured rocks below these black rocks showed *Mastigocoleus testarum* to be the dominant endolith here.   Rocks elsewhere on the south coast (*e.g.* Dune Jean Louis) showed a similar vertical colour zonation, with a blue-black zone above a paler one.   *Brachytrichia* sp., *Solentia stratosa* and *Mastigocoleus testarum,* but apparently not *Scytonema endolithicum,* are all widespread on cliffs of the lagoon shore.

Reef-flat and reef-ridge on Île Picard

In general it appears that the longer rocks are covered by water each tidal cycle, the less conspicuous are the blue-green algae; however small areas of *Lyngbya* or colonies of *Calothrix crustacea* are not uncommon both in the area of the reef-flat and on the reef-ridge. Occasional patches of blue-green algae occur on the sediments between the shore and reef-ridge on Île Picard.   These consist usually either of *Nodularia* or mixed populations of *Lyngbya* and other Oscillatoriaceae. Blue-green algal patches are apparently most frequent on sediments near the research station, in the same region that pink colourations due to phototrophic bacteria occur at some spring tides (Potts & Whitton, 1979b; in press).   The Oscillatoriaceae here include *Spirulina*.

Sublittoral

Visually obvious growths of blue-green algae are only occasional, or even rare, in the upper 10 m, but become slightly more frequent at greater depths (down to 45 m, the maximum depth surveyed).   The great majority of samples consist largely or entirely of *Lyngbya,* apart from the endolith *Plectonema terebrans* and occasional epiphytes, but *Calothrix* films also accur in the upper 10 m.   *Lyngbya* trichomes show a wide range of widths, from about 5 to 40 μm, with no easy separation into distinct species, though many fall into the size range of *L. sordida* (14 — 31 μm).   Conspicuous growths of the broadest forms (*L. majuscula*) were found only down to 20 m.   Trichomes range in colour from green through olive to pink.   Down to about 20 m examples occur of all colours, but by 40 m all are pink.   Some of the best developed growths of *L. sordida* at 40 m were found to cover the surface of a sponge, itself red in colour (when viewed in daylight).   A particularly

interesting population of *L. sordida* was found at this depth off Île Malabar, not far from Passe Gionnet. The alga formed branched structures attached at various points to dead coral and a dead clam; in at least some cases the alga formed distinct tubes. This population was closely associated with several shrimps, which apparently live inside the alga structure.

LIST OF SPECIES

Durham computer number	Category used for records	Equivalent binomial, where applicable
010801	*Brachytrichia* sp.	
010918	*Calothrix contarenii* Bornet et Flahault	
010919	*C. crustacea* Thuret	
011560	*Chroococcus,* > 8 ≤ 16 μm, sheath not striated	*C. turicensis* (Nägeli) Hansgirg
018201	*Calmatella buaensis* Ercegović	
012005	*Dermocarpa leibleiniae* (Reinsch) Bornet et Thuret	
012006	*D. olivacea* (Reinsch) Tilden	
012008	*D. sphaerica* Setchell et Gardner	
012009	*D. minima* Geitler	
012050	*Dermocarpa* sp.	
012201	*Entophysalis granulosa* Kütz.	
013403	*Hormathonema violaceo-nigrum* Ercegović	
013604	*Hyella balani* Lehmann	
013605	*H. tenuior* Ercegović	
018750	*Isactis* sp.	
014204	*Lyngbya confervoides* Ag.	
014205	*L. digueti* Gomont	
014206	*L. epiphytica* Hieronymus	
014211	**L. martensiana* Menegh. ex Gomont	
014212	*L. norgardii* Wille	
014219	*L. majuscula* Harvey	
(014238)	*L. sordida* (Zanard.) Gom.	
014501	*Mastigocoleus testarum* Lagerheim	
014801	*Microcoleus chthonoplastes* Thuret ex Gomont	
014903	*Microcystis reinboldii* (Richter) Forti	
015101	*Nodularia harveyana* Thuret	
015103	*N. spurnigeria* Mertens	
015814	*Plectonema terebrans* Bornet et Flahault	
015932	*Pleurocapsa* > 4 ≤ 8 μm	*P. fuliginosa* Hauck
015933	*Pleurocapsa* > 8 ≤ 16 μm	*P. crepidinum* Collins
015934	*Pleurocapsa* > 16 μm	
016101	*Pseudanabaena catenata* Lauterborn	

Durham computer number	Category used for records	Equivalent binomial, where applicable
016572	*Rivularia* sp. D	
016602	*Schizothrix arenaria* (Berk.) Gomont	
016604	*S. calcicola* (Ag.) Gomont	
016732	*Scytonema endolithicum* Ercegović	
016754	*Scytonema* > 16 μm	*Scytonema* sp.
018602	*Solentia stratosa* Ercegović	
016901	*Spirulina subsalsa* Oersted	
016951	*S. subtilissima* Kütz.	
017602	*Tolypothrix byssoidea* (Berk.) Kirchner	
018401	*Trichodesmium erythraeum* Ehrenberg ex Gomont	
018402	*T. thiebautii* Gomont	
018052	*Xenococcus* > 2 ≤ 4 μm	*X. laysanensis* Lemmermann
018053	*Xenococcus* > 4 ≤ 6 μm	*X. kerneri* Hansgirg
018054	*Xenococcus* > 6 ≤ 8 μm	*X. schousboei* Thuret

Lyngbya martensiana may perhaps be a misidentification of *L. semiplena* Ag. The latter, in contrast to the former possesses a calyptra; *L. semiplena* has been reported elsewhere from marine environments much more often than *L. martensiana*.

DISCUSSION

Blue-green algae are equally abundant in the supralittoral of oceanic and lagoon shores of Aldabra, but there is a marked contrast in their behaviour further down the shore. On the oceanic side they become less frequent the longer surfaces are covered by water during each tidal cycle; this contrasts with the lagoon where large areas of the lower littoral are covered by mats of *Microcoleus chthonoplastes* (Potts & Whitton, in press).

Of all regions on the atoll with a dense photosynthetic cover, the uppermost 15 m of the sublittoral probably has fewer obvious growths of blue-green algae than any other. As ropes and buoys often developed *Lyngbya* tufts rapidly, it seems likely that the intensive grazing by animals is the main reason for the poor development of blue-green algae in the upper part of the coral zone. The importance of grazing by fish in suppressing algal growth on a shallow reef has been documented in some detail for Curaçao by Wanders (1977) and van den Hoek *et al.* (1978). Too few observations have been made of the sublittoral in the lagoon to compare it with the ocean.

Deeper in the ocean attached blue-green algae become slightly more frequent, in some cases being closely associated with a red sponge or with shrimps. The latter is apparently a similar association to that recorded by Cowles (1913) who summarized earlier data, Taylor (1950) for the Marshall Islands and Newhouse (1954) for Raroia. The previous

records are all from shallow waters, but otherwise the present
association appears very similar.   Cowles described the blue-green
alga as *Plectonema,* but Newhouse identified his material as *Lyngbya
sordida,* the same species as recognized for Aldabra.

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NO. 239

VEGETATION OF ALDABRA, A REASSESSMENT

by R.J. Hnatiuk and L.F.H. Merton

VEGETATION OF ALDABRA, A REASSESSMENT

by R. J. Hnatiuk[1] and L.F.H. Merton[2]

INTRODUCTION

Aldabra's vegetation has been described and communities or types of vegetation distinguished for a part or all of the atoll on several occasions (Fryer, 1911-12; Vesey-Fitzgerald, 1942; Stoddart & Wright, 1967; Stoddart 1968b; Fosberg, 1971; and Grubb, 1971). The classifications of Vesey-Fitzgerald and Stoddart & Wright are essentially modifications of that of Fryer (1911-12, p 414) who recognized four major units: Mangrove Swamp, *Pemphis* Bush, Varied or Open Bush, and Shore Zone (table 1). Vesey-Fitzgerald (1942, p 7) added a "Spray Zone Community" and a "Herb Mat Community" while Stoddart and Wright (1967, p 26) included "Man induced vegetation". Stoddart (1968b, Fig. 1) included *"Casuarina"* as a separate unit. He also made important distinctions within the shrub dominated communities by using what appears as a combination of floristic and geomorphologic criteria. However, in his descriptions of the "Platin with open woodland" he did not specifically note the occurrence of tortoise turf although reference to *Dactyloctenium pilosum* and *Eragrostis* sp. clearly indicates he was aware of its presence.

Grubb (1971, p 351) produced a detailed map of the east end of Grande Terre showing 10 "vegetation types" as distinguished on aerial photos with some ground control, but since he includes units called "champignon" and "mud flats", he is concerned with "habitats" and not only "vegetation". However, he has come closer to understanding the complexity of the scrub types than many of the other workers have. Fosberg's (1971) classification is by far the most detailed to date, recognizing 63 vegetation types almost exclusively on the basis of vegetation and floristic criteria. Only in the distinction of "swamp" does he overtly use habitat data in his definition of a type (Fosberg

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Table 1. A comparison of classifications of the vegetation of Aldabra.

FRYER (1911)	VESEY-FITZGERALD (1942)	STODDART & WRIGHT (1967)	GRUBB (1971)	FOSBERG (1971)	HNATIUK & MERTON (this paper)
Mangrove Swamp	M. Communities	M. Communities	Avicennia Swamp	15,16,17,18,19, 35,36,38,47,48	(4) M. Vegetation
Pemphis Bush	P. Thicket	P. Thicket	P. Scrub	21,46	(3) P. Scrub
Varied & Open Bush	Mixed Scrub	Mixed Scrub	Mixed Scrub / Scrub Forest / Coastal Woodland	2,3,4,5,7,8,9, 11,12,13,23,25, 30,32,34,39,42, 43,45,50	(6) Mixed Scrub / (1) Casuarina Groves
			Pool Vegetation	6,20,31,37,52, 53,58	(Lumnitzera-Thespesia populneoides Scrub / (10) Bacopa-Mollugo Meadows.
			Grass Sedge Swards	33,44,45,50,51, 54,56,57	(9) Tortoise Turf
Shore Zone	Psammophilous Associations / Spray Zone Communities / Dune Scrub	Psammophilous Associations	Sporobolus Swards (Coastal Woodland)	10,14,22,29,43a, 57,59,60,61,62	(7) Sclerodactylon Tussock Grassland / (8) Sporobolus virginicus Coastal Turf / (11) Pioneer Vegetation of Beaches
	Man-induced Vegetation			24,28,40	(1) Casuarina Groves / (2) Coconut Groves / (13) Gardens
Herb Mat Community					(12) Herbaceous Meadows of Lagoon Islets
				27,41,63	(15) algal
				49	(14) Acrostichum Stands
				26,55 (Submerged marine meadows)	

1967, p 120).

Four vegetation maps, or maps which at least portray vegetation units, for the whole of the atoll are known to exist (Baker, 1963, Stoddart 1968a, b, and Directorate of Overseas Surveys D.O.S. 6001 Vegetation Overlay, 1969). All maps appear to be drawn from an interpretation of aerial photographs taken in 1960. Baker's map was primarily intended as a geological map with some vegetation notes appended and thus criticism of his vegetation notes need to be tempered with this in mind. Both the D.O.S. map and Baker's suffer from what appears to be lack or insufficient use of ground control. Because of certain errors in photo-interpretation found on these maps caution is advised in attempting to use them. Stoddart's 1968b map clearly shows the distribution of the major landforms and some vegetation units for Aldabra. The only major unit missing on the scale of his map is dense shrub on medium champignon.

Fosberg has applied the classification scheme which he devised for the International Biological Program (Fosberg, 1967). It is a general purpose scheme that is able to be applied in many places of the world. It uses a heirarchical structure so that, for instance, his 63 ultimate units on Aldabra may be grouped into 24 units at the next highest and six units at the top of the classification.

With so much work already done on the vegetation of the 155 square kilometres of dry land on Aldabra, why is yet another study necessary? The reason is, that despite the past work, there is still only a rudimentary understanding of the atoll's vegetation. The earliest works gave the basic outline of much of the vegetation but did not specifically consider several important units such as the "tortoise turf" (Grubb 1971, p 359) or "mixed orthophyll 'tortoise pastures'" (Fosberg 1971, p 223). Grubb's work was not intended to be comprehensive for the atoll, and certain specific problems, treated below, have limited the use of Fosberg's classification. It is the objective of the current work to present both a comprehensive classification and a synthesis of Aldabra's vegetation such as has not been possible before.

Before discussing our classification it is instructive to make a closer examination of Fosberg's detailed classification (1971). His primary subdivision criterion of "spacing" of plants, and his ultimate criterion of "floristic" composition have made it difficult to use on Aldabra. Of lesser importance but still contributing to the overall difficulty of use are the criteria of leaf size, and evergreenness. These latter two criteria have been found to be dependant upon the amount of water available during a particular year or growing season. Thus the plants on one piece of ground may appear "evergreen" and "mesophyllous" one year but the same plants deciduous and "microphyllous" another year, because of the unpredictable and very variable climatic regime found on Aldabra (see Stoddart & Mole, 1977). Such a characteristic is undesirable in a vegetation classification and the solution (of Asprey & Loveless 1958) to a similar problem encountered in Jamaica, that of using the phenological state prevailing under "average"

Table 2. A vegetation classification for Aldabra based upon canopy plants

WOODY	HERBACEOUS	ALGAL
Single-Species Dominant	Monocot Herbs	15. "Cyanophycean film and boring algae vegetation" (little studied but see Fosberg 1971, p 224; also A. Donaldson, Botany Dept. Durham has worked on these communities (unpublished).
(1) Coconut Groves	Single-Species Dominants	
(2) *Casuarina* Groves	(7) *Sclerodactylon* Tussock Grassland	
(3) *Pemphis* Scrub	(8) *Sporobolus virginicus* Coastal Turf	
Species-Groups Dominant	Species-Groups Dominant	
(4) Mangrove Vegetation	(9) Tortoise Turf	
(5) *Lumnitzera-Thespesia populneoides* Scrub		
(6) Mixed Scrub	Dicot Herbs (Species Group)	
variants:	(10) *Bacopa-Mollugo* Meadows	
a. Dune Scrub	(11) Pioneer Vegetation of Beaches	
b. Beach Scrub	(12) Herbaceous Meadows on Lagoon Islets	
c. *Sideroxylon* Scrub	Mixed woody & herbaceous Community (man induced)	
	(13) Gardens	
	Other	
	(14) "*Acrostichum* stands" (of limited extent, see Fosberg 1971, p 222).	

conditions is not feasible because the "average" condition on Aldabra is not known (Hnatiuk & Merton, 1979).

The use of spacing of plants as the primary basis of division in classification (Fosberg, 1967, p 69) may appear at first sight to be a straightforward description of a feature of the plants, independent of the surrounding physical environment. "Closed" vegetation poses little problem but the "open" and "sparse" spacing groups used by Fosberg (1967, 1971) include space which on Aldabra is not part of the individual plants making up the vegetation. The unoccupied space between plants is part of the physical environment that Fosberg wishes to exclude from the classification criteria. Such a distinction may appear as "hair splitting" but two fundamentally different situations are being grouped under Fosberg's application of his "spacing" criteria. To take the extreme case of sparse vegetation in which there is more than twice the individual plant diameter between plants (Fosberg 1967, p 79), on the one hand plant cover may be sparse but the actual place where each plant grows in the sparsely vegetated area is usually assumed to be independent of the substrate (i.e. the plants could grow at any site within the area). On the other hand plant cover may be sparse because the sites where the plants can potentially grow are themselves sparsely distributed in a matrix of uninhabitable space. If plant cover is "closed" in the habitable areas then the vegetation should be seen as closed even though the "habitat" is open. The situation is somewhat analagous to plants growing in soil in pots on a bench. The spacing of plants is then easily seen as a two-level characteristic dependent upon firstly how close together plants can grow in a pot and secondly upon how closely spaced are the pots. We believe that it is the first of these levels of spacing which should be considered on Aldabra where this two-level distinction is to be found, for example at the east end of Grande Terre and along much of the south coast of Grande Terre inland of the "8-metre ridge".

Floristic data have often been effectively used to define vegetation units because the presence or abundance of particular species or species groups are known to be good indicators of environmental conditions. Studies of species distribution patterns on Aldabra (S. & R. Hnatiuk, unpublished) have suggested that colonization patterns may be a prominent feature of the atoll's plants, and these patterns are made complex through the interaction of developing interspecific and species-environment interactions leading to establishment of species niches. Fosberg (1971) has been generally cautious in his use of floristics as criteria for classification, but even so he has used such units as *Acalypha* scrub, *Guettarda* scrub, and *Scaevola* scrub that subsequent observations have found to be too heterogeneous to be called single types. Fosberg's classification may thus indicate the potential vegetation that could develop on Aldabra, but it does not adequately portray the present vegetation.

Our classification has been based upon features of the canopy plants only, understorey plants are not considered in the classification but are noted in the descriptions. Plant nomenclature follows that of Fosberg and Renvoize (1979).

(1) COCONUT GROVES

Location: planted at many sandy places but particularly on the west coast of the atoll, on Ile Esprit and Ile Michel. Small groves can be found on other beaches.

Vegetation: the coconut palm, *Cocos nucifera* is the dominant plant. It is evergreen and often reaches over 20 m, but also much less in poor sites. *Casuarina* is frequently found with and usually somewhat taller than the palms. The cover of the coconut palm canopy varies from greater than 75% in densely reproducing groves to less than 25% where planting was sparse. The largest plantation with over 1000 trees is found at Settlement while small plantings of less than a dozen trees can be found at Grande Cavalier. The distribution patterns of mature plants often reflects the ordered rows of the original planting. The understorey is variable depending somewhat upon the degree and recentness of maintenance of the groves. Thus the better maintained groves tend to have a grass understorey about 5-20 cm high. The grass species are usually either *Eragrostis sub-aequiglumis, Paspalum distichum,* or *Sporobolus virginicus*. The sedges *Cyperus ligularis, Cyperus niveus,* and *Fimbristylis cymosa* may also occur in locally dense patches. In some groves there may be much self seeding of coconuts resulting in very dense groves as on parts of Ile Michel. The Anse Mais grove is developing similarly (R.J.H. unpublished work). Species from the Mixed Scrub (6) are commonly found in the understorey of the neglected groves.

Soil: The calcareous mineral arenaceous soil of Trudgill (1979), also called the Farquhar Series(Piggott 1968), is the most common soil found, but sand of the Shioya Series (Piggott 1968) may be found in parts of the Ile Esprit Grove.

Phenology: Seasonal changes in the coconut trees are limited to a reduction in crown size and a slowed development of leaves, flowers and fruit during the dry season, at which time the understorey herbs also become brown and dry. Flowering of understorey plants is largely restricted to periods of sufficient rain.

Notes: The coconuts are not thought to be native to Aldabra and primarily occur in areas where they were introduced by man, although now they have become naturalized in some areas. Whereas formerly, maintenance of the groves kept the understorey clear of scrub and coconut regeneration, now that maintenance has essentially lapsed, except for sections of the Settlement grove, scrub species can be found invading some parts of groves, while in other places the development of coconut thickets with litter accumulations exceeding 1.5 m deep is occurring. There are no indications as yet that the groves will spread beyond the areas of deep sandy soil, though they may be extending into a few formerly scrub-dominated areas with sandy soil on the west coast of Grande Terre. It appears from simple transplant studies with *Carica papaya,* that competition for water may be an important limiting factor for the vegetation of these plantations.

(2) *CASUARINA* GROVES

Location: *Casuarina* Groves are found primarily on the north and west sea coasts of Aldabra, and on some lagoon-facing sandy beaches.

Vegetation: The canopy is evergreen and dominated by *Casuarina equisetifolia* that may reach more than 20 m above ground. The *Casuarina* may occur together with *Cocos* and the vegetation type may then be referred to as "*Casuarina* and *Cocos* Grove". The understorey of *Casuarina* Groves is various and can be *Cocos,* Mixed Scrub (tall or low), grass, or barren.

Soil: Two soil types have been found under *Casuarina:* Farquhar Series (Piggot, 1968), and organic brown calcareous soils (Trudgill, 1979). Occasionally a shallow, rendzina-like soil consisting largely of organic matter with a small amount of sand over rock is all that is found. In most places, the soil under *Casuarina* has a thick (2-10 cm) layer of *Casuarina* 'needles'.

Phenology: There is still some doubt about how *Casuarina* reached Aldabra. Fryer (1911, p 416) and Fosberg (1971, p 215) believe *Casuarina* to be definitely introduced by man, but Ridley (1930, p 316-17) believes it to be widely distributed by the sea. Wickens (1979) gives further information. What ever may have been its method of introduction, it is now well established and apparently spreading (as are other species) as seen in the small, dense groves of young saplings and seedlings at the periphery of some groves (e.g. west end of Passe Houareau grove, and south of Anse Var). Young plants are to be seen growing up through Mixed Scrub on both sides of Passe Houareau. The effect of the overtopping of scrub by *Casuarina* is variable. In some instances it appears that the scrub may either die out (Fosberg 1971, p 216) or may continue to thrive apparently little affected by the *Casuarina* as for example just north of Settlement. In some areas *Acalypha claoxyloides* is found to form a dense understorey shrub stratum to *Casuarina* (e.g. between Anse Owen and Anse Grande Poche, north west end of Ile Polymnie, part of the grove on the west side of Passe Houareau) as also does *Plumbago aphylla*. We would repeat Fosberg's statement that this is a "good problem for an ecological investigation" (1971, p 216).

Heavy infestations of *Casuarina* by the woolly coccid, *Icerya seychellarum,* are associated with reduction in photosynthetic canopy, reduced or halted growth, and, in small plants at least, death.

(3) *PEMPHIS* SCRUB

Location: *Pemphis* Scrub is one of the widespread and common vegetation types found on the atoll.

Vegetation: *Pemphis* Scrub as defined here includes those areas where *Pemphis acidula* grows in pure or virtually pure stands, and excludes those areas where *Pemphis* is merely one of many scrub species — such latter areas being classed Mixed Scrub (6). Most of the *Pemphis* in

the *Pemphis* Scrub occurs as multi-stemmed plants although large, single-stemmed, tree-like *Pemphis* also occur. Other plant species are rare in this type but the most common include *Vernonia grandis, Acalypha claoxyloides,* and *Scaevola taccada*. Certain Mixed Scrub species are often found growing in a mosaic with *Pemphis* Scrub, and it appears from observations that two vegetation types are involved (see notes below and discussion on 'Mosaics').

The height of *Pemphis* Scrub ranges from about 0.5 m to more than 6 m. Mature *Pemphis* growing in nearly pure stands less than 1 m high, is common along parts of the trade-wind-exposed, south coast of Grande Terre. There is some evidence (D. Lewis, pers. comm.)that such plants may be genotypically dwarfed and often prostrate. That they have only been found on the seaward edge of scrub may suffice to distinguish them as a sub-type, which is part of Fryer's "Shore Zone" (Table 1).

The canopy of tall *Pemphis* is very deep, often reaching 4 to 5 m. The "surface" of the canopy is very irregular with narrow, conical branches that are leafy to near their bases. Foliage density does not appear to be exceptionally high and direct sunlight penetrates to the ground; however, there is virtually no understorey development.

Soil: The soil appears very poorly developed. It may consist of "shallow organic soil" (Trudgill, 1979) over solid rock (and is thus a very shallow rendzina-like soil) or no soil may be visible at all. Surface feeding roots may be abundant in the small pockets of organic accumulation but all that is generally visible is the tops of roots that pass down into crevices in the otherwise barren rock.

Phenology: *Pemphis* is evergreen, its stems form no resting buds, and it can grow throughout the year, producing leaves, flowers, and fruits. Growth may decline or cease in periods of severe drought, particularly in plants that do not appear to have direct contact with sea water. Leaf fall is stimulated by the onset of dry conditions and by heavy infestations of the woolly coccid, *Icerya seychellarum*.

Notes: As noted by Fosberg (1971, p 221) past estimates of the abundance of *Pemphis* have been exaggerated. This is particularly noticeable in the maps of Baker (1963) and the Directorate of Overseas Surveys (Vegetation overlay 6001, 1:25,000, 1969) where Mixed Scrub and *Pemphis* Scrub have been misinterpreted from the aerial photographs (see notes under Mixed Scrub (6)).

The correlation between the occurrence of *Pemphis* Scrub and very rough limestone (champignon) has been noted since the earliest reports, but caution is necessary in using this relationship. For example, Braithwaite *et al.*, (1973, p 337) found a high correlation between '*Pemphis* dominated scrub' on the D.O.S. vegetation map and the occurrence of 'dissected areas of the Takamaka limestone' and used this correlation in their extrapolation of geological boundaries from interpretation of vegetation as seen on aerial photographs. The geological map is probably a fair representation of the surface geology, but the designation "*Pemphis* dominated scrub" is very much in error in several

large areas.   In our experience it would appear that *Pemphis* is the
dominant plant on sites where the surface is sufficiently dissected to
allow salt water to penetrate into the rooting zone, and also to prevent
any substantial amount of soil from accumulating at the surface.
Areas such as this can extend over several square kilometres (e.g. parts
of south west Grande Terre) but most of the *Pemphis* Scrub occurs in a
mosaic with a subdivision of the Mixed Scrub.   *Pemphis* Scrub occupies
the low ground, while Mixed Scrub occupies the knolls that rise 0.5 to
1.0 m above the low ground.   These knolls may be only 5 to 10 m across
so that if a larger unit of area is taken as the basis of study, the
distinction between these types disappears.   However, it appears useful
in understanding the vegetation to recognize the elements as separate
vegetation types because there does not seem to be a dynamic,
vegetational relationship between the two types — each occurs in its own
distinct habitat.

From circumstantial evidence, it seems that *Pemphis* may be able to
utilize salt water as a water source: live roots are often seen
extending into the tidally inundated portions of pot holes; the canopy
is evergreen with somewhat succulent leaves; measurements show growth
to be continuous throughout the dry months on sites apparently devoid
of soil when other shrub species nearby have long lost their leaves.

The dynamic status of *Pemphis* Scrub is not clear.   Seedling and
sapling size individuals are very rarely reported for *Pemphis*.   As
noted above, a few large, tree-like individuals with diameters of about
0.3 m and extending above ground for 2 to 2.5 m before branching, can be
found throughout the atoll, but most *Pemphis* occurs as a prolifically,
low-branching shrub.   Until more is known about this species, further
interpretation of these observations would be premature.   The autecology
and population structure of *Pemphis* is another good problem for
ecological research.

(4)   MANGROVE VEGETATION

Location: around most of the lagoon coast including on many of the
numerous islets in the lagoon, and occasionally at isolated, inland
places.

Vegetation: The four most common species are *Avicennia marina*,
Bruguiera gymnorrhiza, Ceriops tagal, and *Rhizophora mucronata*.
Three less abundant species of mangrove are *Sonneratia alba, Xylocarpus
granatum* and *X. moluccensis*.   The trees range in height from 1 m to
greater than 10 m, and canopy cover ranges from less than 25% to
virtually 100%.   A zonation of mangrove species relative to distance
inland or nearness to tidal streams is not obvious on Aldabra as it is
in continental areas (Macnae, 1971).   Without knowing more about the
reason why the mangrove species are distributed as they are on Aldabra,
division of this vegetation on floristic bases seems premature.
Macnae recognized two variants on the basis of the height of the trees:
'high forests' (greater than about 6 m) being found mostly on the north,
west and east lagoon shores and only sporadically on the south, while

the second 'thickets and low forests' being 1 to 6 m high predominate
on the south shore of the lagoon.

Soil: ranges from light grey, silty marl with only stunted mangrove
(e.g. Dune Jean Louis landing) to deep, highly organic muds with tall
mangrove forests (e.g. Cinq Cases Creek) (Macnae, 1971).

Phenology: The trees are evergreen and for *Bruguiera, Ceriops* and
Rhizophora, flowers and fruits can be found at all times of year, but
not necessarily on the same plant at all times.   The cycle of events
for an individual is not known.   *Avicennia* appears to have a seasonal
response and to be more synchronized for all populations than are the
former three species.   Generally it appears that *Avicennia* produces
leaves during the wet season, and flowers and fruits during the dry
season but more observations are needed.

Notes: The mangroves, especially the tall ones, have been cut for
timber at many places and regeneration is abundant in some places and
absent in others.   Macnae (1971) comments on the relatively old trees
on the north lagoon shore of Grande Terre where soils are poor and the
trees, though stunted, have large root systems.   The detailed dynamics
of this vegetation are not known and would repay study.

(5) *LUMNITZERA-THESPESIA POPULNEOIDES* SCRUB

Location: appears restricted to the east end of the atoll, in and
around summer-flooded basins.

Vegetation: The major canopy species are *Lumnitzera racemosa* and
Thespesia populneoides.   *Pandanus tectorius* occurs around some of the
basins, forming large dense clumps.   These three species commonly
occur in pure stands but may be inter-mixed.   Canopy cover ranges
from 100% beneath closely growing shrubs to less than 25% where shrubs
are few and branches not numerous.   The canopy ranges in height from
about 1.5 m to more than 5 m above ground.

The understorey is generally barren of plants but tussocks of the
sedge *Fimbristylis ferruginea* are common beneath breaks in the shrub
canopy and are largely, but not exclusively restricted to these sites.
Cyperus ligularis is also occasionally found here.

Soil: The soil is classed as mineral sediments: SM in Trudgill's
system (1979).   The soil is light to dark grey, fine-textured, saline,
and commonly contains mollusc shells.   The surface may have a litter
layer and organic matter appears well mixed into the upper layers.
Water logging is common during the rainy season, whilst during the dry
months, the water table may fall below soil surface allowing the surface
soil to become quite dry and powdery.   The extent of the drying is
dependent upon the amount and distribution of rainfall in any
particular year.

<u>Phenology</u>: *Lumnitzera* and *Pandanus* are essentially evergreen but the quantity and size of leaves present appears to be much greater during the wet season than during the dry. *Thespesia* may lose most if not all leaves during prolonged dry season drought. Flowers can be found at most times of year on *Lumnitzera* but they become very scarce during drought periods and very abundant with the return of the rainy season. Flowers on *Thespesia* and *Pandanus* are largely confined to the late wet season although occasional exceptions do occur. Ripe fruits are common in late wet and early dry season, and become more scarce as the dry season advances.

<u>Notes</u>: It appears that *Lumnitzera* occurs most abundantly and luxuriantly beside pools and in soils that are more saline than those favoured by *Thespesia,* while *Pandanus* is at its best in the least saline conditions. However, the species are often found intermixed at one and the same site. Although *Pandanus* often occurs near fresh water pools (*cf.* Stoddart & Wright 1967, p 27) it is found sufficiently often in equally large and luxuriant groves or as isolated individuals in locations far from such pools (e.g. Anse Var, coastal scrub east of Passe Gionnet, Passe Houareau camp, and Point Vacqua) that the general value of *Pandanus* as an indicator of fresh water pools or of a particular vegetation type is largely restricted to the east end of Grande Terre.

The dynamic status of this vegetation type is not known. However, it appears to have experienced change as evidenced by the apparently uniform size of most individuals around a pool although different pools appear to have different populations. About 1.3 km south west of Takamaka Grove, conspicuously "two-aged" stands of *Lumnitzera,* as judged by shrub height and stem diameter, are to be found but the reasons for this structure are not known.

(6)   MIXED SCRUB

<u>Location</u>: widespread throughout the atoll.

<u>Vegetation</u>: No single taxon characterizes this community, but some of the most common ones are: *Apodytes, Canthium, Erythroxylum, Euphorbia pyrifolia, Ficus* spp., *Maytenus, Mystroxylon, Ochna, Polysphaeria, Sideroxylon,* and *Terminalia boivinii.* Less abundant or locally common taxa are: *Acalypha claoxyloides, Allophyllus, Clerodendrum, Dracaena, Flacourtia, Guettarda, Jasminum, Operculicarya, Pandanus tectorius, Phyllanthus casticum, Margaritaria cheloniphorbe, Scaevola, Scutia, Secamone, Tarenna trichantha, Tarenna supra-axillaris, Tricalysia,* and *Triainolepis.* Many other taxa also occur. The understorey is generally barren, but dense to open patches of *Cyperus niveus* or *Lomatophyllum aldabrense* locally occur.

The Mixed Scrub varies greatly in height from site to site. It is at its greatest in Takamaka Grove, reaching about 12 metres and at its least (less than 1 m) in some of the areas of shallow soil. In some of the most extensive areas of Mixed Scrub (e.g. west of Bassin Frigate) the height is about 3-5 m.

Soil: The Organic Brown Calcareous Soil (CMD) (Trudgill, 1979) is the
most common found under Mixed Scrub.   It often occurs in pits 5-20 cm
deep and in some areas is overlain by leaf litter or even several
centimetres of arthropod frass (mostly from a millepede).   The latter
is called a Shallow Organic Soil, Pellet Type (OSP) by Trudgill.

     In some areas the soil is sandy and belongs to the Farquhar Series.
In a few places, sand has become mixed with the upper layers of the CMD.
Shallow Organic Soil (OS) (Trudgill, 1979) may also be found.

Phenology: With such a large number of species, the phenological status
of this type is complex at any time of year.   However, certain
generalizations are possible.   Firstly, there are evergreen and
deciduous species and a few which are neither entirely one nor the other
depending upon just how dry it becomes.   Flowering and fruiting is in
general most prolific during the rainy season.   For any particular
species the peak may be at the start, middle or end of the wet period.
A very few species flower most profusely during the dry months (e.g.
Capparis cartilaginea).   Some taxa are very opportunistic, flushing
new leaves and flowers after any moderate rainy period and just as
rapidly losing them when it dries up (e.g. *Allophyllus, Erythroxylum*).

Notes: This vegetation type is perhaps the most complex on Aldabra and
the one about which the least is known.   As a type it extends into a
wide variety of habitats defined on species dominance, canopy height,
plant spacing, and substrate type.   For the time being it is being
left as a single, heterogeneous unit although variants are recognised
below as sub-types on the basis of certain conspicuous features.
However, the status of these sub-types is very uncertain and requires
detailed study.

          sub-type   a.   Leeward Scrub

                    Recognised primarily by its location in the lee of the
                    trade winds on or at the base of dunes.

                    Location: mostly associated with the large dunes on the
                    south coast of Grande-Terre.

                    Notes: As a habitat it is extensively used by both
                    tortoises and birds as a cool, shadey place to avoid the
                    heat of midday.   As a vegetation category, it is
                    essentially an extension of the Mixed Shrub.

          sub-type   b.   Dune Scrub

                    Recognised by its location on dunes and by floristic
                    composition.

                    Location: primarily on large dunes (e.g. Dune Jean
                    Louis).

Vegetation: dominated by woody plants from 1 metre to about 7 m high in open or closed communities. Understorey plants usually absent. The common species are *Tournefortia argentea, Scaevola taccada,* and *Thespesia populnea.*

Notes: The species are characteristically, widespread, coastal, tropical taxa.

sub-type   c.   Beach Scrub

Recognised by its location and floristic composition.

Location: at the head of small beaches.

Vegetation: as for Dune Scrub but the common species are usually *Cordia subcordata, Casuarina equisetifolia, Hibiscus tiliaceus, Scaevola taccada, Suriana maritima,* and *Tournefortia argentea.*

Notes: Resembles Dune Scrub closely, but the nearness to the sea and less deep sandy soil may account for the somewhat different species composition. Otherwise the two sub-types have much in common.

sub-type   d.   *Sideroxylon* Scrub

Recognised primarily on the basis of species composition.

Location: Generally on knolls of limestone rising 0.5 to 1.0 m above the surrounding rough champignon terrain.

Vegetation: *Sideroxylon inerme* dominates these knolls as relatively large single-stemmed plants with broadly spreading crowns and fairly dense, evergreen canopy. *Maytenus* and *Scutia* may be common associates in the canopy while *Cyperus niveus* often occurs in the understorey.

Notes: This sub-type is one of the important variants of the Mixed Scrub in that it is common and widespread in a mosaic with the extensive areas of *Pemphis* Scrub. Because *Sideroxylon* Scrub occurs consistently in habitats distinct from those of *Pemphis* Scrub, although in a fine mosaic with it, it seems valid and useful to classify the *Sideroxylon* Scrub separately from the *Pemphis* Scrub.

The dynamic status of the sub-type is not clear. Most *Sideroxylon* on Aldabra are large and no seedling or sapling individuals have been reported despite prolific fruit production that is known to be fertile at least in part. How this sub-type relates to Mixed Scrub is not clear, as the two merge imperceptibly in some areas.

The distribution patterns of Mixed Scrub in some areas of Aldabra are very conspicuous, particularly when seen on aerial photographs. In the present classification, the various distinct patterns are not classified separately, but some comments seem pertinent because of the very different habitats they create.

Firstly, there is a conspicuous arrangement of shrubs in rows oriented more or less north west to south east. Fosberg (1971, p 218, and Grubb 1971, p 357) have suggested that the prevailing south east trade wind may be involved in the origin of this pattern. The present day trade winds may be ruled out as the immediate cause by noting that several areas of pronounced row-pattern are sharply demarcated from surrounding scrub which shows no such pattern. Examination on the ground showed that shrubs in areas of row-pattern are almost always growing in pits, depressions or on broken ground separated by smooth to undulating regions with very shallow pits and virtually no soil. The smaller the depression in which the shrubs grow, the more dwarfed were the shrubs. Thus the immediate cause of the rows would appear to be patterning of the habitable substrate and not to the direct influence of the wind. It is noteworthy that very similar patterns can be seen on aerial photo 42 SY 15 no. 031 where they occur not only on dry land but also on the wave cut platform of the south east coast of Grande Terre. The trade winds do result in regular die-back of the previous seasons growth on shrubs. This die-back is most pronounced on the windward sides of shrubs and eventually may result in very windswept crowns. Some plants with such crowns do lean down wind, but whether this tilt is directly caused by the force of the wind or the stress resulting from the very asymmetric crowns is not clear, but this situation of wind shaping of crowns is not directly related to that of arranging the positions of individuals into a pattern of parallel rows.

The second conspicuous pattern is that of "clumps" of shrubs throughout large areas of platin and pavé at the east of Grande Terre. Field observations again have shown the shrubs to be associated with patches of rough ground in an otherwise little broken terrain of limestone. The rough ground may be (as noted by Grubb 1971, p 357) in the form of depressions or sump holes. Such places accumulate soil and thus hold moisture, providing adequate rooting conditions for shrubs, or they may be local patches of moderately deeply pitted champignon or fissured rock. In all cases it seems that where adequate rooting by shrubs is possible, they occur, and where sufficient rooting conditions are not met, there is only low vegetation or bare rock. Takamaka Grove is the superlative development of one such shrub clump on Aldabra. The distribution of space habitable by shrubs in these areas relates to the origins of the substrate pattern Hnatiuk & Merton (1979).

(7) *SCLERODACTYLON* TUSSOCK GRASSLAND

Location: primarily around the sea coasts of the whole atoll although its greatest extent is along the south coast of Grande Terre. Occasional patches can be found well inland (e.g. 1.3 km south west of Takamaka Grove).

<u>Vegetation</u>: One species, *Sclerodactylon macrostachyum* dominates this vegetation type.   This grass grows in tussocks from 0.05 m in height where grazing is heavy to over 0.5 m in height where grazing is absent. The crowns of the tussocks usually interdigitate with each other and produce virtually 100% canopy cover, but where grazing occurs, cover may be considerably less.   There is no understorey vegetation, but a variant with *Cyperus ligularis* as dominant may occur (see notes below).

<u>Soil</u>: The sandy Farquhar Series (CMA of Trudgill, 1979), is the most common soil found in this vegetation type, but stoney soils and occasionally the fine Organic Brown Calcareous soil (Trudgill, 1979) form the substrate of the tussocks.

<u>Phenology</u>: Seasonal changes are slight.   The tussocks are evergreen and individual leaves appear to remain green throughout their length and then die rapidly, thus the canopy never appears brown from dead leaf tips as occurs in some tussock grasses.   The leaves do turn pale grey from salt and fine calcareous deposits during long dry spells with strong onshore winds and ocean swell.   Flowering occurs almost exclusively during the rainy season and can be prolific.

<u>Notes</u>: The dynamic status of the community is complex.   It would seem that under heavy grazing pressure and shade seeking activity of tortoises, the tussocks are killed and replaced by *Sporobolus virginicus* (Hnatiuk *et al.*, 1976).   Where extensive stands of *Sclerodactylon* occur, the plants often appear to belong to distinct clones, 10 to 50 m across, being distinguished on the basis of leaf colour (blue, brown, light green).   In some places that are little disturbed by grazing, the *Sclerodactylon* grow. in a mosaic, closed-canopy community with low, coastal Mixed Scrub on rocky, shallow, soil.   *Cyperus ligularis* also forms tussocks and dense, one-species stands in habitats identical to those of the *Sclerodactylon*.   The *Cyperus* appears to be an invasive species of disturbed habitats.   It is only grazed by tortoises when it is producing new growth.   Its loose tussocks and flexible leaves are not as susceptible to mechanical damage from trampling as are tussocks of *Sclerodactylon*.   Until more is known about the sedge, it seems best not to classify it as a separate vegetation type.

(8) *SPOROBOLUS VIRGINICUS* COASTAL TURF

<u>Location</u>: Widespread on sandy deposits around the sea coast of the atoll, but most abundant along the south and east coast of Grande Terre.

<u>Vegetation</u>: One species, *Sporobolus virginicus,* dominates this vegetation type, but several other species also are to be found: *Euphorbia stoddartii, Fimbristylis cymosa, Launaea sarmentosa, Lepturus repens, Portulaca mauritiensis,* and *Sida parvifolia*.   All but *Lepturus* occur most frequently with the *Sporobolus* where tortoise grazing is intense; *Lepturus* tends to be found on stonier soil than is *Sporobolus*. The short turf of *Sporobolus* (less than 1 to 2 cm in height) with cover of less than 50% in places, found under intense grazing conditions,

becomes a tall sward (10 - 20 cm in height) with 100% cover and with a dense accumulation of litter (Hnatiuk *et al.*, 1976).

Soil: The type appears largely restricted to the Farquhar Series sand (CMA of Trudgill, 1979) of the low perched beaches but in some places Shioya sand is the substrate.

Phenology: *Sporobolus virginicus* is evergreen.   It produces most new growth during the rainy season.   It appears to flower most prolifically during the late wet and early dry season, but relatively heavy rains during the dry season can stimulate sporadic flowering.   The leaves may become grey on the windward trade coast from fine, air-borne, calcareous deposits during the trade wind season.   The vegetation takes on a brownish cast during the dry months as the leaves begin to slowly die back from the apex.

Notes: The dynamics of this vegetation type appear to be closely linked with that of the *Sclerodactylon* Tussock Grassland.   The *Sporobolus virginicus* Coastal Turf may at some time in the past have been confined to unstable sandy soil at beach crests but appears to have become widespread through the feeding and shade seeking activity of tortoises at the expense of both low Mixed Scrub and the Tussock Grassland.   However, having once become established over large tracts, it seems to persist (Hnatiuk *et al.*, 1976).   Its long term status in these places is not known.

(9)   TORTOISE TURF

Location: primarily on the platin and pavé terrain at the east end of Grande Terre although rather small, often poorly developed patches are found on Ile Picard (e.g. Back Path, near Bassin Cabri, and near Anse Var) and on Ile Polymnie.

Vegetation: Tortoise Turf is an assemblage of many species that change in relative dominance from place to place.   The following dwarf grasses and sedges are most common: *Bulbostylis basalis, Dactlyoctenium pilosum, Eragrostis decumbens, Fimbristylis cymosa, Panicum aldabrense, Cyperus pumilus,* and *Sporobolus testudinum.*   The most common dicot herbs are *Euphorbia stoddartii, Phyllanthus maderaspatensis, Sida parvifolia,* and *Tephrosia pumila.*   A thallose liverwort, *Riccia,* is common on heavily grazed ground.   The intensely grazed turf is mostly less than 1 or 2 cm in height and the canopy cover less than 20%.   In lightly grazed conditions, cover can approach 100% and height, depending upon which species is dominant, can reach 10 - 15 cm.   There does not appear to be any development of strata within the community.

Soil: The Organic Brown Calcareous Soil (Trudgill, 1979) is almost all that is found in this type.   The soil is only a pale coloured representative of this soil type, perhaps because the dark horizon only forms under a shrub canopy or perhaps the former, darker horizon has been eroded in recent years (Merton *et al.*, 1976).

Phenology: The summer rains bring a slow greening of the turf and the onset of dry conditions brings a gradual browning as many of the plants die.   Flowering and fruiting is largely done during the late rainy period and early dry period.   Most of the species appear to be short lived perennials or facultative annuals during years of severe drought. Seed production can be high judging from the abundance of seedlings that can be found once the wet season is well established.

Notes: Tortoise Turf, first named by Grubb (1971, p 359), is a community that appears well developed to withstand moderate to intense grazing.   In fact, its species richness may in part be possible because grazing keeps the more vigorously growing members from overtopping the less vigorous ones.   Exclosure plots have only recently been set up but strong species interactions appear to be possible as the various species grow to much greater stature when not or little grazed than when heavily grazed.   The Tortoise Turf has been seen to be invaded by the large sedge *Cyperus ligularis* where grazing has been restricted.   It does not appear that the turf survives under a shrub canopy.   Thus where shrubs are prevented from growing by continual browsing and abrasion as for example with *Ficus* spp., and *Ochna,* the Turf thrives where it would otherwise be shaded out.   In the absence of at least moderate grazing, the Tortoise Turf could well become much less extensive than it is today.

        The status of broad leaf herbs in the Turf is not clear.   They are all readily eaten by the tortoises and some of these herbs are restricted to pits and crevices where the tortoises cannot reach. Many of these herbs appear capable of growing more rapidly and much larger than most of the dwarf grasses and sedges in the Turf.   Thus, whether the dicot herbs would completely dominate the Turf if grazing were reduced is a matter of conjecture.

        Two sub-types may be recognized:

        sub-type   a.   Herbaceous pasture

                It is characterized by a dominance of broad leaved herbs.
                It occurs in areas little grazed by tortoises (e.g. pits
                in champignon near Cinq Cases, on the 8 m ridge south of
                Anse Var, along part of Back Path, and near Bassin Cabri).
                The major taxa vary with geographic location but include:
                *Asystasia, Euphorbia stoddartii, Evolvulus, Hypoestes,
                Lagrezia, Nesogenes, Hedyotis, Portulaca mauritiensis,
                Ruellia,* and *Tephrosia.*   Although quite distinct
                communities of Herbaceous Pasture can be found, because
                it grades into Tortoise Turf in some places, it here
                will be only distinguished as a sub-type.

        sub-type   b.   *Fimbristylis cymosa* Turf

                It is dominated by a single species and occurs over
                extensive areas of platin and pavé.   It does not appear
                to be as readily grazed by tortoises as the other Turf

species although exclosure sites indicate that there must
be some degree of grazing of new leaves and inflorescences
during the rainy season. *Fimbristylis cymosa* appears
somewhat more abundant in the northern part of the
platin-pavé at the east end of Grande Terre while the
other monocot Turf community is more common further
south, but the two ranges overlap considerably. Until
more is known about the interrelationships of the various
Turf communities, it seems best to recognize only sub-
types of the main Tortoise Turf vegetation.

(10) *BACOPA-MOLLUGO* MEADOWS

Location: It has been found only at the east end of Grande Terre on
summer flooded basins.

Vegetation: The dwarf, succulent herbs, *Bacopa monnieri* and *Mollugo
oppositifolius,* are the most common species found. They generally
grow as very prostrate plants, less than 1.5 cm high and rooting at the
nodes. Where protected from grazing *Mollugo* has been found to grow
very much larger, reaching 20 cm in height, but *Bacopa* does not respond
so vigorously. Cover is variable from greater than 75%, to less than
10% where grazing is intense or soil sparse.

Soil: A "mineral sediment (SM)" of Trudgill, (1979). It is a fine
grey, generally saline silt, that may crack on drying. Algal sediments
(SA of Trudgill, 1979) may also occur here. An algal surface layer is
not uncommon. The soil is periodically submerged when the basins fill
after rain, and then slowly dries out. Depending upon the extent of
the droughts each dry season, the soil may or may not completely dry
out.

Phenology: The plants are short lived perennials that remain green for
as long as there is sufficient moisture available. Several weeks
innundation does not halt either leaf or flower production although
competition from algal blooms may eventually retard their growth. When
the water recedes, the herbs flourish. Flowering and fruiting can
thus occur at any time of year when moisture conditions permit.

Notes: *Bacopa-Mollugo* Meadows are closely associated with *Lumnitzera-
Thespesia* Scrub. However, since the former does not grow under the
latter nor are they always present at the same basin, it seems best to
classify these two very different structural units as separate
vegetation types.

The particular conditions favoured by each of the two dominant
herbs is not clear. *Bacopa* may be more common in shallow soil and
rock crevices while *Mollugo* may be more common on the deeper soil of the
basin, but more observations are needed.

sub-type   a.   *Bryodes* Meadow

> A dicot herb community dominated by one species, *Bryodes micrantha*.   It appears to form in some places, a zone which is transitional between *Bacopa-Mollugo* Meadow and Tortoise Turf.   The soil is often innundated by water during the wet season, but as the colour of the soil is brown, the duration of water logged conditions must be brief.   The *Bryodes* community is ephemeral, appearing for a brief period only after prolonged rainy periods and dieing out as the soil dries out.   Flowering and fruiting occur readily during this brief, active season. If artificially watered, the individual plants can live at least a year.   Because only a very few patches of this community have been seen, its status is uncertain.

   The pools occupied by both *Bacopa-Mollugo* Meadow and *Lumnitzera Thespesia populneoides* Scrub are found in depressions with impeded drainage in the hardened platin and pavé.   The basins may fill with 0.5 m to 1.5 m of water during the rainy season, and slowly dry during the trade wind season.   A complex succession of algae parallels the seasonal changes in water levels (A. Donaldson pers. comm.), and fish are occasionally to be found in the flooded pools.   When pools dry out they are left with a hard, cracked crust that is matted by algae, or may be colonized by *Bacopa* and *Mollugo*.

(11) PIONEER VEGETATION OF BEACHES

Location: at the crest of most beaches around the atoll.

Vegetation: A mixture of herbs common on the strand line throughout much of the tropics forms this type.   The most common species are *Cyperus conglomeratus, Dactyloctenium ctenoides, Ipomoea pes-caprae,* and *Sporobolus virginicus*.   The community may consist of several or only one of these species.   The canopy height is dependent on the species but is usually less than 0.2 m except for *Cyperus* which rises to 0.6 m.   The canopy cover is generally less than 25% but locally denser patches do occur.

Soil: The soil is undeveloped beach sand.

Phenology: Vegetative growth, flowering, and fruiting are prolific during the wet season and much reduced or halted during the dry months.

Notes: This vegetation type is a pioneer on disturbed beach crests. It can vanish overnight if the beach is eroded by a storm, or may gradually disappear as tall woody plants of the Mixed Scrub sub-type Beach Scrub become established on places of extended stability.

(12) HERBACEOUS MEADOWS ON LAGOON ISLETS

Location: on some of the islets in the lagoon, particularly off the north shore of Grande Terre (e.g. Champignon des Os).

Vegetation: The dominant species are different on different islets and even on different parts of the same island.   But taken as a whole they form an assemblage quite distinct from anything else on the atoll and therefore they are recognized as a separate vegetation type.   The commonest species are *Achyranthes aspera, Boerhavia* sp., *Dactyloctenium pilosum, Lagrezia oligomeroides, Lepturus repens, Portulaca oleracea, P. mauritiensis, Sida parvifolia,* and more rarely *Sesuvium portulacustrum.*   The shrubs *Acalyphya claoxyloides* and *Pemphis acidula* are not uncommonly present though in a stunted form.   Cover is generally high (greater than 75% during the wet season).   Average height to the top of the canopy is less than 0.75 m and often less than 0.3 m.

Soil: Generally very little and composed of coarse sand with a few silty patches presumably both blown or washed up from the lagoon floor by wind and wave action.   Bird dung and remains are locally abundant and in such areas the soil may be of the Desnoeufs Series (the organic soil, guano variety, OSG of Trudgill, 1979).

Phenology: Vegetative growth, flowering and fruiting are largely confined to the wet season and early dry season until fresh water supplies are exhausted and then most of the community goes dormant. These islands can thus be bright green in January to March, and dull brown in August to November.

Notes: The dynamic status of this vegetation is uncertain but since some islets are currently used as roosts and nesting sites, while others appear to have been so used in the past, they may have been modified from shrub to herb cover by the activities of the birds. Some dead shrubs can be seen on some of the islets which are now entirely covered by Herbaceous Meadow.

(13) GARDENS

Location: near current or old sites of habitation, primarily at Settlement but also near Anse Var, Anse Mais, Anse Malabar, Ile Michel and Passe Houareau camp.

Vegetation: Many species of both cultivated and "weed" status are used to define this type.   The commonest cultivated species are *Ipomoea batatas, Moringa oleifera, Capsicum frutescens, Phaeseolus* sp., *Datura metel, Tamarindus indicus, Cymbopogon, Solanum melongena, Carica papaya, Panicum maximum, Cucurbita* spp., *Agave sisalana,* and *Pedilanthus tithymaloides.*   Common weeds and ornamentals are *Stachytarpheta jamaicensis, Tridax procumbens, Synedrella nodiflora, Catharanthus roseus,* and *Sida acuta.*

Canopy height and cover is very variable depending upon the degree of cultivation, disturbance, and species composition.

<u>Soil</u>: Primarily of the Farquhar Series although some phosphate rich soil has been reported (Baker, 1963, p 107).

<u>Phenology</u>: Variable, depending upon the species concerned.   However, most of the species are active during the wet season and early dry season, becoming dormant during the driest months.   Some species such as *Carica* produce most leaves during the rains, and ripen their fruits only during the mid to late dry season.

<u>Notes</u>: Although the vegetation can be recognized on the basis of its floristic composition, certain special features can be noted.   The species are all probably either deliberately or accidentally introduced by man.   Some of the species do not appear able to spread either because all viable seed seems to be eaten by animals (e.g. *Moringa*), or no flowers are produced and vegetative spread is extremely limited (e.g. *Cymbopogon, Bambusa*).   Other species have become naturalized and are spreading into the native vegetation (e.g. *Stachytarpheta, Passiflora, Agave*).

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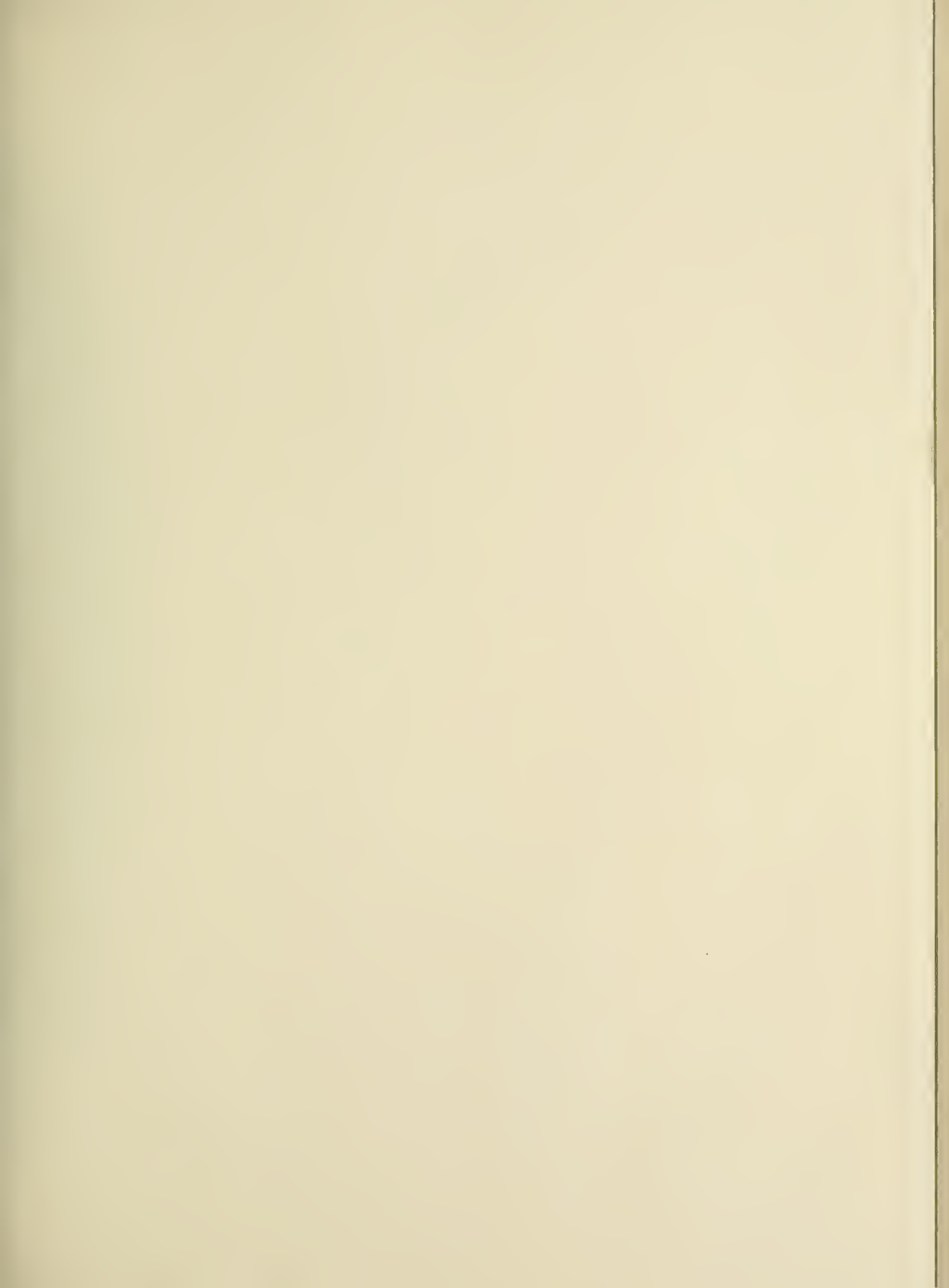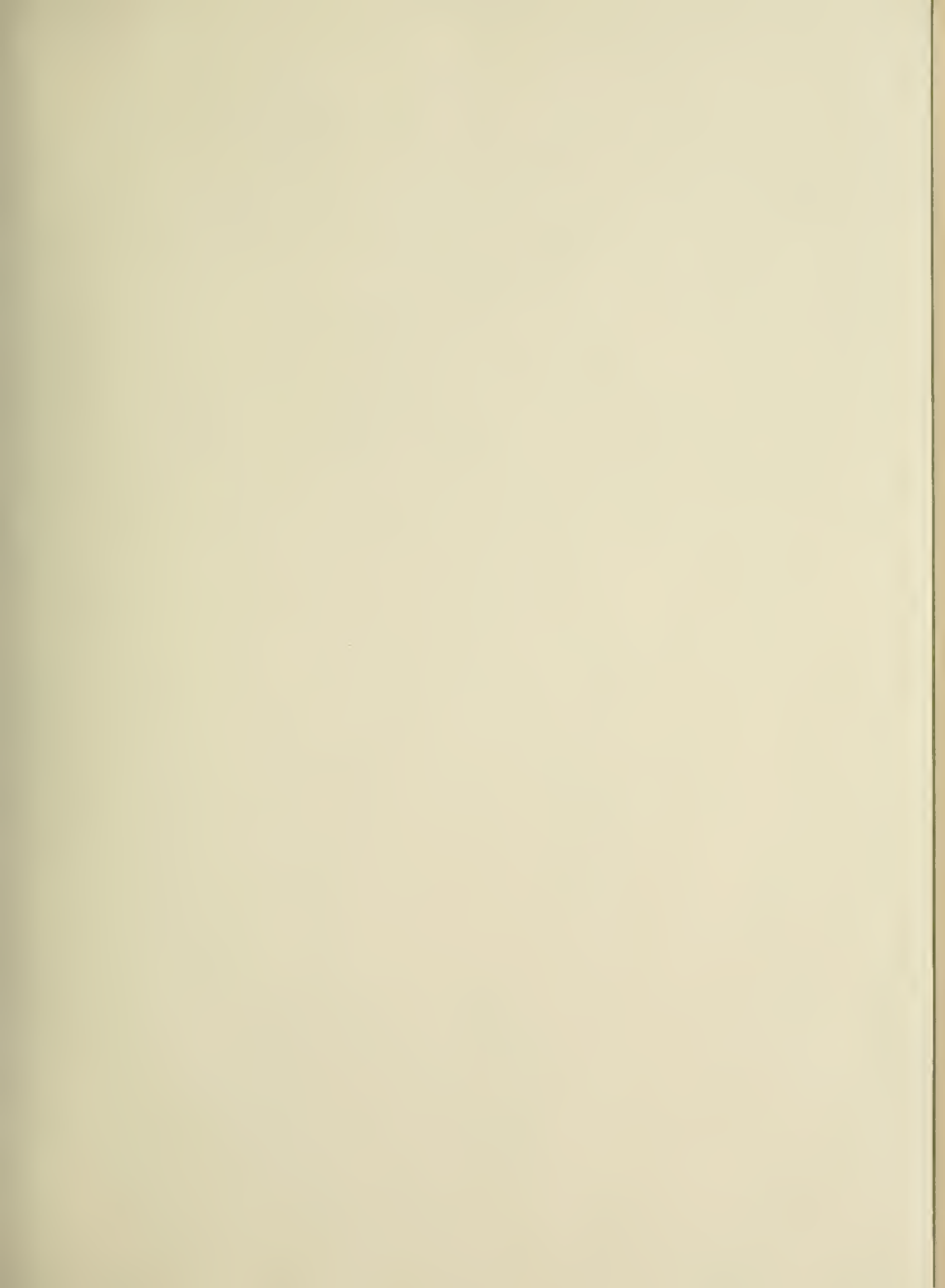
ATOLL RESEARCH BULLETIN

240. *Man and the Variable Vulnerability of Island Life.*
A Study of Recent Vegetation Change in the Bahamas
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MAN AND THE VARIABLE VULNERABILITY OF ISLAND LIFE.
A STUDY OF RECENT VEGETATION CHANGE IN THE BAHAMAS

by Roger Byrne

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MAN AND THE VARIABLE VULNERABILITY OF ISLAND LIFE.
A STUDY OF RECENT VEGETATION CHANGE IN THE BAHAMAS

by Roger Byrne[1]

I. INTRODUCTION

A question of increasing concern to scientists and lay-
men alike is to what extent plant and animal communities can
withstand disturbance by man. In this context the histori-
cal biogeography of small islands is especially relevant.
Island life has proved to be particularly vulnerable to
human disturbance. In the brief period of human settlement
faunal extinction rates have been proportionally much higher
on islands than on the continents. For plants the situation
is less clear. Few island studies have dealt in detail with
the consequences of man's impact and as a result the vulner-
ability of insular plant communities is poorly understood.
It was with this general problem in mind that the present
study was undertaken.

More specifically, an attempt was made to determine the
extent to which man has modified the vegetation of Cat
Island, a small island in the Bahamas. Originally, it was
intended to deal with the vegetation of the island as a
whole, but for several reasons the detailed analysis was
limited to the mixed evergreen-deciduous woodland, or "cop-
pice" as it is locally known. The woodland covers more than
90 percent of the island and has been intensively disturbed
by man. On a theoretical level the question was considered
as to whether or not the vegetation of offshore islands such
as Cat is vulnerable in the same way as that of the Hawaiian
Islands or the Galapagos. The choice of Cat Island was to a
certain extent fortuitous. As a low-limestone island it
provided a comparatively simple setting, it was reasonably

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accessible, and like the Bahamas as a whole its vegetation was virtually unexplored.

Field work was carried out during three visits: July to October 1967, June to August, 1968 and June to September 1970. In addition short visits were made to three other Bahamian islands: Bimini, Mayaguana, and New Providence. Historical evidence was gathered in London during the spring of 1968. Particular attention was paid to the manuscript collections at the Public Records Office, the British Museum, the British Museum of Natural History, and the Royal Botanical Gardens at Kew. This text represents a revised version of a doctoral dissertation submitted to the University of Wisconsin in 1972 (Byrne, 1972).

II. THE THEME: MAN AND THE VULNERABILITY OF ISLAND LIFE

The idea that island life is inherently vulnerable to disturbance by man was first proposed by Charles Darwin as supporting evidence for his theory of natural selection. Since Darwin's time, however, the whole question of insular vulnerability has been variously interpreted and as yet there is no consensus.

Early Interpretations

During his voyage on the Beagle (1831-1836), Darwin was particularly impressed by the extent to which man had disturbed the plant and animal life of so many remote islands. On St. Helena, for example, the woodland had been virtually removed by the combined effects of selective cutting and grazing, and the native plants had been apparently replaced by introduced species.

> The many imported species must have destroyed some
> of the native kinds; and it is only on the highest
> and steepest ridges that the indigenous flora is
> now predominant (Darwin, 1839: 485).

In his account of the voyage, Darwin made no attempt to explain why the plants and animals of remote islands should have been so vulnerable to disturbance. His explanation was to come twenty years later in The Origin of Species. Here he suggested that continental species have a competitive advantage over insular species because the struggle for existence is more severe on continents than on islands. Islands, because of their small size and inaccessibility, have fewer species and consequently the competition among those present is less vigorous. To support this idea he pointed out how relict floras and faunas had survived on islands long after they had become extinct on the mainland.

> On a small island the race for life will have been
> less severe, and there will have been less modifi-
> cation and less extermination. Hence, we can
> understand how it is that the flora of
> Madeira...resembles to a certain extent the
> extinct tertiary flora of Europe (Darwin, 1859:
> 108).

This view of islands as natural museums in which plants and animals are preserved by isolation was generally accepted by the great nineteenth century naturalists.

Wallace, for example, agreed with Darwin that species from continental areas, particularly Europe, were more aggressive than insular types. Like Darwin, he noted how the native flora and fauna of St. Helena had been drastically changed during the few hundred years of European settlement.

> When first visited by civilized man it was in all probability richly stocked with plants and animals, forming a kind of natural museum or vivarium in which ancient types, perhaps dating back to the Miocene period, or even earlier, have been saved from destruction which has overtaken their allies on the great continents (Wallace, 1902: 308, 309).

Darwin's close friend Joseph Dalton Hooker was also impressed by the vulnerability of island life. He wrote at length on the success of European weeds on oceanic islands, and like Darwin attributed it to their supposedly superior competitive ability (Hooker, 1860, 1865, 1867a, 1867b).

In general terms, Darwin, Wallace, and Hooker were all agreed that island life was inherently vulnerable. What was not clear was the detailed nature of this vulnerability and to what extent it was due to man. The nineteenth-century naturalists were limited in their thinking by the typological species concept, and because of this they reduced the intricacies of competition to a battle in which the length of species lists assumed an inordinate importance. This is not to say that they were entirely unaware of the significance of man's role. Wallace (1902: 306), for example, emphasized that European weeds could not have successfully invaded New Zealand had man not disturbed the native vegetation first.[1]

Before reviewing more recent views of the vulnerability of island life, mention should be made of the important role oceanic islands played in the development of the theory of natural selection. In The Origin of Species Darwin argued strongly against the then popular land-bridge theory that had been used to account for the origin of insular floras and faunas. Oceanic islands, he maintained, had never been connected to the continents and consequently were poor in species of both plants and animals; furthermore, many important taxa were not represented at all. This impoverishment, he argued, was further evidence against the doctrine of independent creation.

1. Allan (1936), in his critique of the hypothesis of insular vulnerability, failed to give Wallace credit for this observation.

> He who admits the doctrine of the creation of each
> separate species, will have to admit that a suffi-
> cient number of the best adapted plants and
> animals were not created for oceanic islands; for
> man has unintentionally stocked them far more
> fully and perfectly than did nature (Darwin, 1859:
> 370).

This argument reinforces his earlier conclusion that
the inhabitants of oceanic islands are inherently vulnerable
to disturbance. Both Hooker and Wallace emphasized the
difference between continental and oceanic islands; the
former having at some time been connected by land bridges to
the continents, whereas the latter had always been isolated.
Wallace elaborated on the distinction and defined oceanic
islands as follows:

> Islands of volcanic or coralline formation, usu-
> ally far from continents and always separated from
> them by very deep sea, entirely without indigenous
> land mammalia or amphibia, but with a fair number
> of birds and insects, and usually with some rep-
> tiles (Wallace, 1902: 243).

Recent Views

In the present century the broad approach of the
natural scientist has generally been abandoned in favor of
narrow specialization.

Botanists have been divided on the question as to
whether or not insular plants are inherently vulnerable to
disturbance. One school of thought has held that Darwin's
interpretation was basically incorrect. Allan (1936), for
example, argued that continental plants are not inherently
more aggressive than insular types. According to Allan, in
New Zealand the introduced species owe their success to
prior disturbance of the natural vegetation by man and his
domesticated animals. Much the same conclusion was reached
by Egler in his review of the status of alien plants in
Hawaii.

> In the absence of anthropic influences, the evi-
> dence strongly favors the view that most of the
> aliens will be destroyed by the indigenes, such
> aliens surviving only in greatly reduced numbers
> and as very subordinate members of the resulting
> ecosystem (Egler, 1942: 23).

At the same time, Egler argued against the need for any general theory to account for the processes involved, and suggested that the history of each alien species should be looked at individually.

A somewhat different view of insular vulnerability has been presented by Fosberg (1936, 1965, 1972). Fosberg has argued that the ecosystem concept provides an especially useful means of evaluating the significance of man's impact on island life. In essence, he has restated the Darwinian hypothesis in modern terms. In his introduction to the symposium <u>Man's Place in the Island Ecosystem</u>, he characterizes the island ecosystem as follows:

> Limitation in organic diversity; reduced inter-species competition; protection from outside competition and consequent preservation of archaic, bizarre, or possibly ill-adapted forms; tendency toward climatic equability; extreme vulnerability, or tendency toward great instability when isolation is broken down (Fosberg, 1965: 5).

In another paper on this theme, Fosberg emphasized the contrast between old continental ecosystems and young island ecosystems. The former, he suggests, are floristically and faunistically diverse, well-balanced, rarely invaded by aliens, and quick to recover after disturbance. The latter are poor in species, often imbalanced, often invaded, and slow to recover after disturbance (Fosberg, 1963: 557-561). The ecosystem concept has been of considerable value in guarding against too narrow a view of man's impact on island life.

Another botanist who has emphasized the idea that island life is inherently vulnerable is Carlquist (1965, 1970). Like Darwin and Wallace, Carlquist has suggested that islands have been refugia for species that have become extinct on the continents. In his recent book on the natural history of Hawaii, he devoted a chapter to a consideration of the loss of competitiveness in native plants, (Carlquist, 1970: 173-179). He notes that the flora is especially poor in poisonous, strongly-aromatic, or spiny plants and concludes that this reflects the lack of any grazing pressure from mammals. He also points out that few Hawaiian plants are weedy and that most species are less competitive than their continental counterparts. These factors, together with inbreeding, small population sizes, and highly specialized habitat requirements, have made the Hawaiian species especially vulnerable to disturbance. Unfortunately, Carlquist avoids the subject of man's impact. His main concern is the fate of the rare endemics, and

introduced species are dismissed as uninteresting weeds, whose story could "only have been a catalogue of sorts" (Carlquist, 1970: viii). This attitude has been characteristic of many island botanists. Rare endemics and remote virgin forests have attracted much more attention than cosmopolitan weeds and secondary woodland.

Unlike botanists, zoologists have rarely questioned the idea that island life is inherently vulnerable to disturbance. Simpson and Mayr, for example, have accepted the vulnerability thesis and have tried to place it in the framework of modern evolutionary theory.

Simpson (1953: 306) suggested that islands, particularly small, strongly isolated islands, are "evolutionary traps," in which the possibilities of further evolution are extremely restricted. The organisms reaching such islands become specifically adapted to a small number of niches, and thereafter a rather static, closed ecological situation persists. Populations are likely to be small, with little genetic variability available for change. If invasion occurs, the native organisms are particularly subject to rapid extinction. On the other hand, he rejects the idea that islands are ephemeral features and therefore unlikely to be very old.

Mayr (1963: 74-76) has likewise noted that insular faunas are particularly vulnerable to competition from introduced species. In general terms he accepts the idea that species from large areas have a competitive advantage over species from small areas.[2] At the same time he cautions against the acceptance of any sweeping generalizations and points out that there are many exceptions to the rule.

Another zoologist who has been concerned with the consequences of the invasion of islands by alien species is Wilson (1965). From a statistical analysis of Hawaiian bird faunas he concluded that there was no evidence to suggest that continental species were intrinsically superior to insular species. His approach, however, involving as it did only faunal lists, could hardly be expected to provide any conclusive answers.

A broader approach to the whole problem of insular vulnerability has been advocated by Elton. In The Ecology of Invasions by Animals and Plants he devoted a whole chapter to a consideration of "The Fate of Remote Islands" (1958:

2. Mayr expressed the same idea in his concluding remarks to the symposium on The Genetics of Colonizing Species (Baker and Stebbins, 1965: 559).

77-93). Having documented the drastic changes on islands
such as Juan Fernandez and Hawaii, he repeats the argument
that insular plant and animal communities are vulnerable to
invasion because of their comparative simplicity.

> Natural habitats on small islands seem to be more
> vulnerable to invasion than those on the con-
> tinents. This is especially so on oceanic islands
> which have rather few indigenous species (Elton,
> 1958: 147).

The idea that species diversity can be directly corre-
lated with stability has since become a canon of the conser-
vation movement. In essence it is a restatement of the
Darwinian hypothesis put forward nearly a hundred years ear-
lier. Unfortunately, Elton does not explain on just why
small islands are so vulnerable or, more particularly, to
what extent man is responsible for this vulnerability. As
Elton himself admits, this is a poorly-researched topic and
ecologists have in general avoided such complicated ques-
tions.

Geographers who have explored this theme have rarely
been intimidated by the complexities of island life. In
most cases they have taken an holistic approach which has
included plants, animals, and man. A pioneer study of this
kind is Clark's The Invasion of New Zealand by People,
Plants, and Animals (1949). Here, however, the main concern
was with the invaders, particularly man, and the changes in
the native flora and fauna are only briefly described.

More recently, Harris (1965) has explored a similar
theme in his Plants, Animals, and Man in the Outer Leeward
Islands. This study involved a detailed review of the his-
torical evidence for man's impact on the plant and animal
communities of Antigua, Barbuda, and Anguilla. Harris's
conclusions were much the same as Elton's, namely, that
small oceanic islands are particularly vulnerable to inva-
sion by alien plants and animals, especially man. The plant
and animal communities of the Outer Leewards are highly
vulnerable because they lack the "ecological resistance" of
more complex communities, and although the number of species
that have become extinct since man first settled the islands
is not known, it is thought to be large (Harris, 1965: 141).

In another publication, Harris (1962) reviewed Darwin's
hypothesis in the light of his research in the Outer Lee-
wards. Like Allen and Egler, he emphasized the point that
without prior disturbance by man, alien plants would make up
only a small proportion of the total plant cover. In other
words, alien plants are not inherently more aggressive than

the native species. A very similar conclusion was reached by Watts (1966, 1970) in his study of man and vegetation change in Barbados. Having shown that alien species had not been able to invade areas of comparatively undisturbed vegetation, Watts concluded that alien species were dependent for their success on prior disturbance by man.

In a similar study Kimber (1969) analysed the history of recent vegetation change in Martinique, a small volcanic island in the Lesser Antilles. Although her approach was primarily historical, it was strongly influenced by the ecosystem concept. The question of insular vulnerability was not considered as such, but the evidence presented clearly shows that the vegetation of the island has been disturbed drastically by man. In her conclusion she states that the island ecosystem of Martinique is out of balance and that the plant cover has been degraded and simplified by man's interference (Kimber, 1969: 599).

A somewhat different approach to the problem has been taken by J.D. Sauer (1960, 1967). Unlike Clark, Harris, Watts, and Kimber, Sauer combined the historical approach with detailed analyses of the contemporary vegetation. His research on the coastal vegetation of Mauritius and the Seychelles is especially relevant to the present study insofar as it shows that the native species were inherently well-adapted to withstand the impact of disturbance by man. These findings do not necessarily mean that Darwin's hypothesis should be rejected. They do mean that coastal species with their cosmopolitan distributions are not typically insular. Significantly, the inland vegetation on both Mauritius and the Seychelles has been extensively modified by man.

Unresolved Issues

In general terms Darwin's hypothesis has withstood the test of empirical research rather well, although it must be admitted that few biologists or geographers have concerned themselves with a detailed analysis of insular vulnerability. In some cases vulnerability is easily understood. Flightless birds without fear of predators are obvious candidated for extinction. For plant populations the situation is less clear.

With a few notable exceptions, such as Egler, Fosberg, and J.D. Sauer, botanists have tended to ignore the subject, and have concerned themselves with systematic studies or with the analysis of undisturbed vegetation. Several biogeographers have explored the theme but for the most part

have restricted themselves to the historical approach.
Unfortunately, the historical record alone is rarely
detailed enough to allow for anything more than a very qual-
itative reconstruction of vegetation change. For some
islands it has been possible to establish the chronology of
introductions and extinctions, but these in a sense
represent only the first and last chapters of the story.
The complex processes of vegetation change that have been
started by man on small oceanic islands are still only
poorly understood.

On a different level, the question as to what extent
islands vary in their vulnerability remains unanswered.
Theoretically, one would expect that the vegetation of inac-
cessible islands such as the Hawaiian Islands or the
Galapagos would be more vulnerable to disturbance than that
of off-shore islands such as the Bahamas. The former are
inhabited by rare endemics, the latter by wide-ranging
species. Somewhat unexpected, therefore, are the conclu-
sions reached by Harris (1965), Watts (1966), and Kimber
(1969), which suggest that the plant and animal life of the
Lesser Antilles is vulnerable in much the same way as that
of the Hawaiian Islands. If this is indeed the case, the
plant and animal life of the Bahamas might also be expected
to be vulnerable.

With these questions in mind, it was decided to study
in some detail man's impact on the vegetation of one small
island in the Bahamas, Cat Island. More specifically, the
study attempts to determine to what extent cutting, burning,
browsing, and the introduction of alien plants and animals
have brought about changes in the native vegetation.

Although Cat Island is an oceanic island in the sense
that it has never been joined to the continent, it is
clearly less isolated than remote islands such as Hawaii or
the Galapagos. As an offshore island with a lesser degree
of insularity, it provides an interesting test for the
hypothesis of insular vulnerability.

III. THE SETTING: A LOW LIMESTONE ISLAND

In spite of their early discovery, the Bahamas are still in many respects unknown. Wallace (1902:5), in his introduction to Island Life, briefly commented on the remarkable contrasts in flora and fauna between peninsular Florida and the Bahamas, only 50 miles to the east (Figure 1). The differences, he argued, could not be explained by existing conditions, as the climate and soil of the two areas were the same. The Bahamas were different, he implied, because they were islands. Unfortunately, although he went on to discuss, with the aid of many examples, "the complex causes of insular floras and faunas," the Bahamas were not referred to again. Then, as now, very little was known about them. Unlike the formerly prosperous sugar islands to the south, the Bahamian environment has attracted little attention from scientists.[1]

This has been particularly true for remote "Out Islands"[2] such as Cat Island (Figure 2). Apart from some botanical exploration at the beginning of the present century (Britton, 1907) and a study of land snails in the 1930s (Clench, 1938), virtually no scientific research of any kind had been carried out on Cat Island before the present study was started in the summer of 1966. Lind's study of coastal landforms began shortly afterwards and his findings have since been published (1969).

Cat Island provides a comparatively simple setting for a study of man and vegetation change. It is only 250 square kilometers in area and has a subdued relief, the highest elevation being just over 60 meters. Because of its small size and low elevation it is climatically more or less uniform. The differences that do exist are due to differences in exposure; the eastern and southern coasts face the trade winds, while the western coast is comparatively sheltered. As far as bedrock geology is concerned, again there is little variation; the entire island is composed of virtually pure calcium carbonate. There is, however, some local variation in lithology which in large part reflects the degree to which the limestone has become indurated by exposure to the atmosphere. Also, there is considerable local variation

1. This is not strictly true in certain areas of biology and geology, as a lengthy bibliography compiled by Gillis et al. (1976) indicates.
2. The term "Out Island" in the Bahamas refers to islands other than New Providence, the seat of the capital, Nassau.
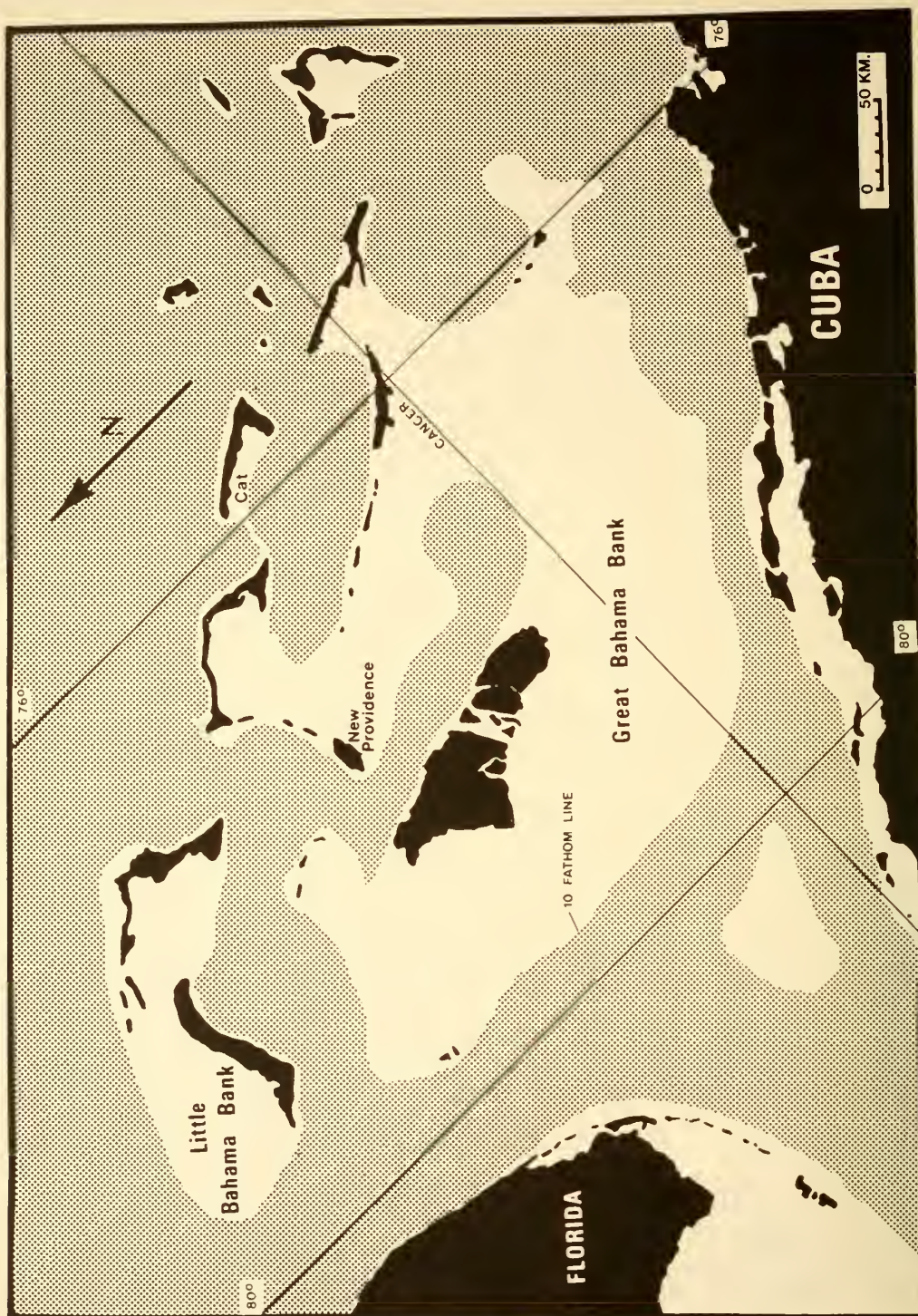
Figure 1.   Map of the Bahama Islands

in the degree to which the limestone surface has been
dissected by solution. In some areas there are numerous
potholes, in others the surface is still more or less
intact. These local differences in lithology and relief
have an important influence on the composition and structure
of the vegetation.

Insularity

Cat Island is located in the east central part of the
Bahamian archipelago, less than a hundred miles north of the
Tropic of Cancer (Figure 1). Like most Bahamian islands it
fringes the windward margin of a shallowly submerged bank.
Together the island and the bank form an easterly arm of the
Great Bahama Bank which projects out into the deep water of
the Atlantic. Off the northern, eastern and southern coasts
precipitous slopes descend to depths of more than 2,500
fathoms. To the west ten miles of bank lie between the
island and the comparatively shallow Exuma Sound, only 1000
fathoms deep. To the northwest a narrow submarine ridge
connects Cat Island with Eleuthera and the Great Bahama
Bank. There is, however, no evidence of any geologically
recent land connection between the Great Bahama Bank and
either Florida or Cuba, so in this sense, Cat Island is an
oceanic island.

On the other hand, the sea level fluctuations of the
Pleistocene drastically changed the relative areas of land
and sea. A fall in sea level of only 10 fathoms, such as
occurred several times during the Pleistocene, would double
the present land area of the island and make it a peninsula
of the Great Bahama Bank (Figure 1). For the Bahamas as a
whole it would increase the land area from 5,400 to 60,000
square miles and would make the minimum salt water distance
to Cuba only 10 miles and to Florida 50 miles. Clearly, Cat
Island's insularity has varied significantly in the recent
geological past; even today this is not an oceanic island to
the same degree as remote islands such as the Hawaiian
islands or the Galapagos. Cat Island's insularity is also
qualified by the proximity of other islands in the archi-
pelago.

Geology and Geomorphology

The shallow water of the Bahama banks provides an ideal
environment for the accumulation of a great variety of car-
bonate sediments, and borehole data indicate that similar
sediments have been accumulating in the area since at least
the Early Cretaceous and possibly the Palaeozoic (Lynts,
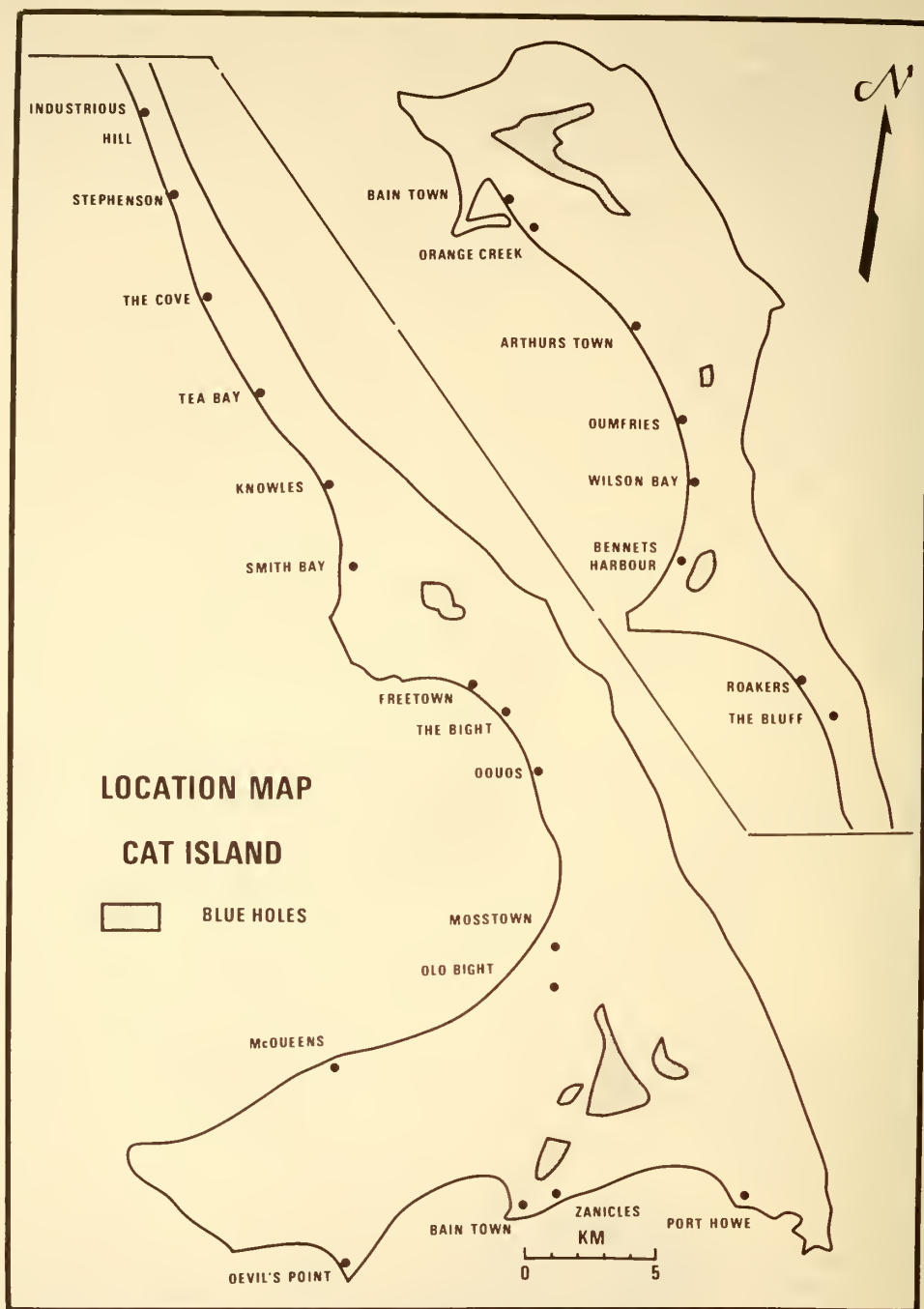
Figure 2. Location Map of Cat Island

1970: 1227). This accumulation has been made possible by a long-continued subsidence, and indicates that the Bahamian environment has in the long term been a remarkably stable one (Newell and Rigby, 1957).

Even so, the present Bahamian islands are in a geological sense very young. The surface rocks are aeolianites and shallow- water marine sediments of late Pleistocene or Holocene age. On Cat at least three age-surfaces can be identified. They are easily recognized in the field by the degree to which the limestone has been indurated and potholed. Because of the homogeneous nature of the bedrock, differences in surface characteristics are important in determining the character of the vegetation. For this and other reasons that will be discussed later it was decided to use landform types as a framework within which to analyse vegetation change. Although some of the details of the origins of Bahamian landforms are still unclear, the general pattern seems plain; furthermore, it is a pattern that repeats itself on all the larger islands.[3] What follows here is a brief account of the sequence of landform types observed on Cat Island. Figure 3 represents a geomorphological cross-section of the island and Figure 4 shows the distribution of the more important habitat-types.

Dune Ridges.

On the windward side of the island three discontinuous dune systems run sub-parallel to the present coast. The oldest lies furthest inland and is usually higher than the other two, reaching just over 60 meters in places. The aeolianite is indurated to an unknown depth, and its surface is pockmarked with potholes. Although no dates are available for the age of these dunes, they may have been formed during the Yarmouth or early Sangamon interglacial. That they were partly submerged prior to the present sea level rise is shown by a wave-cut bench at about 1 meter above the present high tide mark. Fossil coral was occasionally observed at about the same elevation, although nowhere was it as common as on other Bahamian islands, such as Andros and Mayaguana. Isotope dates for presumably synchronous corals on the Florida Keys range between 80,000 and 150,000 years (Broecker and Thurber, 1965; Newell, 1965).

A mile or so to the east of the older dunes is a dune system of intermediate age.[4] These dunes are generally

3. Doran (1955) has provided a useful account of the landforms of the southeastern Bahamas.
4. In some areas, as for example behind the northern coast of the island, the intermediate-age dunes have overridden the older dunes.
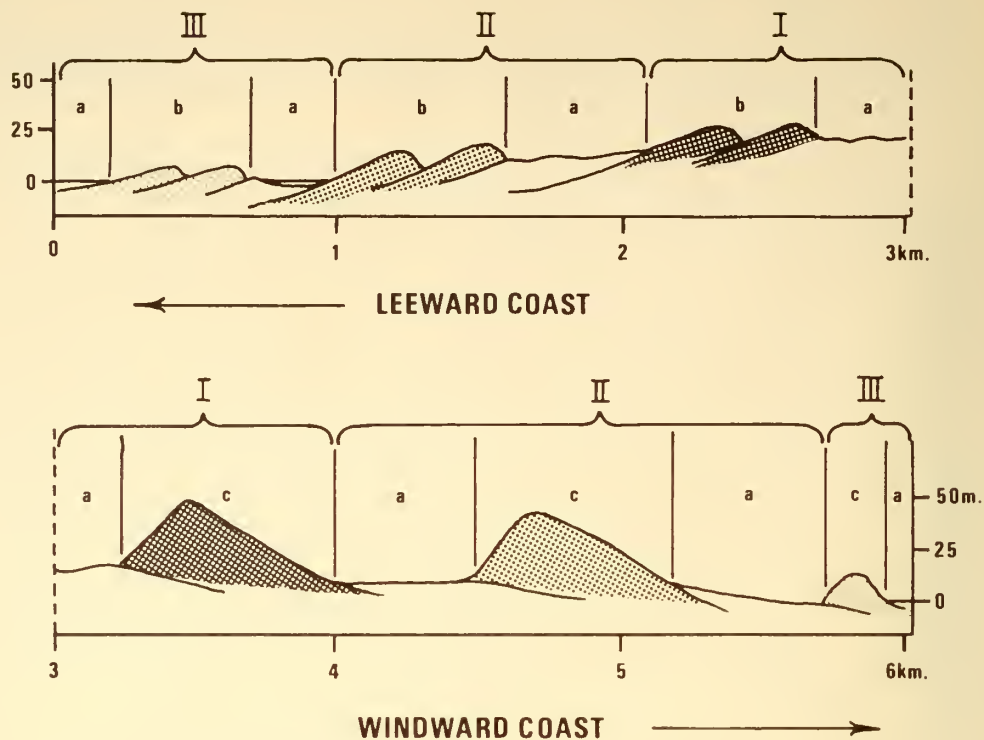
Figure 3
A Geomorphological cross-section of Cat Island

	AGE		LANDFORM TYPE	HABITAT TYPE
III	Holocene	a	Marine Beds	Offshore
		b	Beach Ridges	Whiteland
		c	Dune Ridges	Whiteland
II	Young Pleistocene	a	Marine Plains	Flatland
		b	Beach Ridges	Blackland
		c	Dune Ridges	Blackland
I	Old Pleistocene	a	Marine Plains	Flatland
		b	Beach Ridges	Blackland
		c	Dune Ridges	Blackland

%

**MAJOR
HABITAT TYPES**

WHITELAND
FLATLAND
BLACKLAND
SAVANNA
MANGROVE

KM.

0   5
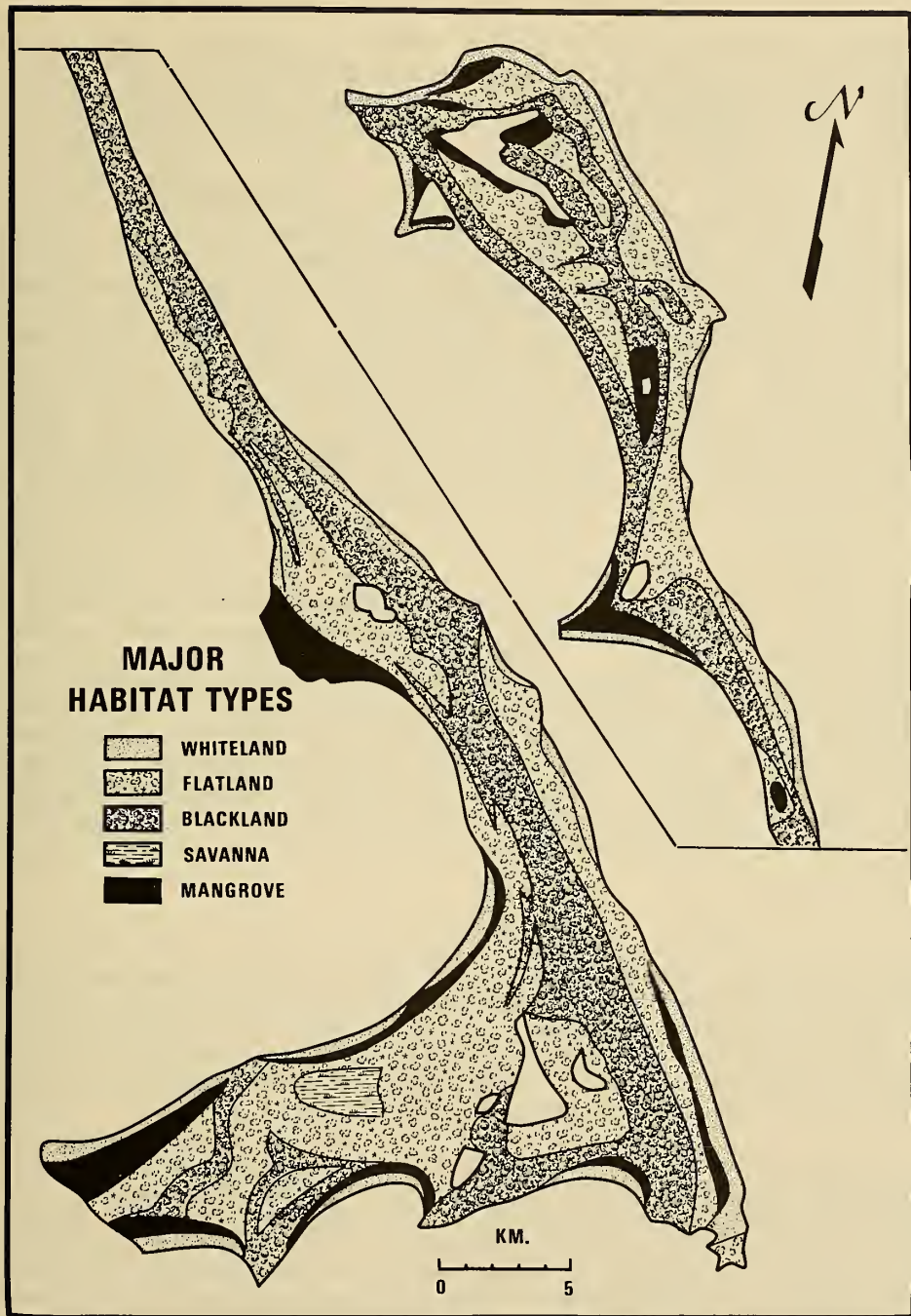
Figure 4.   Map of Cat Island showing Major Habitat Types

between 15 and 30 meters high. Their surfaces are also indurated, but lack the numerous potholes of the older dunes. In localized areas the limestone is loosely consolidated and breaks down to produce a sandy soil. On the ground, the intermediate dune system has a comparatively fresh appearance, with steep lee slopes and gentle dip slopes easily distinguished. Also Pleistocene in age, they do not show any evidence of marine erosion apart from that which has accompanied the recent rise in sea level. Directly behind the windward coast is the youngest dune system. These dunes rarely reach more than 15 meters in height and are usually around 6 meters high. The lime sand has been only shallowly indurated and is easily kept loose by cultivation. Like the two older dune systems, the younger dunes are fossil landforms, and erosion rather than dune formation characterizes the present coast. These Holocene dunes were studied in detail by Lind, who obtained dates for them of between 4,000 and 500 years (Lind, 1969: 126).

Casual inspection with a hand lens suggested, all three dune systems are composed of similar carbonate sediments. Oolites are particularly important, with fragments of shell, coral, and calcareous algae also being common. Fossils are not abundant, although in certain layers shells of the land snails Cerion and Cepolis can be found. The differences in the surface characteristics of the three dune systems are important as far as the cultivation of crops is concerned and as a consequence they are recognized locally as distinctive habitat-types. The two Pleistocene dune systems are known collectively as "the blackland," while the Holocene dunes are called "the whiteland".

Beach Ridges.

On the leeward side of the island, water has been a more important depositional agent than wind, and here beach ridges are the most prominent land form. They curve round in multiple series independent of whatever was the prevailing wind direction at the time they were being formed. Their distribution has apparently been influenced by the movement of currents in the lee of the dunes.

Again three age surfaces can be distinguished, each one corresponding to a dune system on the windward side of the island (Figure 3). Collectively they differ from the dunes both in their lower elevation and in the symmetry of their cross profiles. In terms of surface characteristics, each beach ridge system is much the same as its equivalent dune system, and to this extent offers similar opportunities for plant life. This is true of cultivated as well as wild plants, and as a result the local people make the same

distinction between the younger, older, and intermediate-
aged surfaces as they do on the dunes. The former is known
as "the whiteland," the other two "the blackland".

Lagoonal Plains.

        Between the dunes, and between the dunes and beach
ridges, are two comparatively level surfaces. Their origin
is indicated by the marine shells they contain, including
the conch Strombus. Apparently they are of different ages.
The higher surface at about 6 meters above sea level is rid-
dled with potholes, whereas the lower one, only a few meters
above sea level, is comparatively intact. The higher sur-
face is probably the same in age as the oldest dune/beach-
ridge system while the lower surface corresponds to the
intermediate dune/beach-ridge system. A third surface,
corresponding to the youngest dune/beach-ridge system, can
be seen below present sea level at an average depth of about
3 fathoms.

        Unlike the cross-bedded aeolianite that makes up the
dunes, these marine sediments have bedding planes that are
close to horizontal and as a result the land surface tends
to be much smoother. Especially level areas are known
locally as "platey land" and, as will be shown later, have a
distinctive vegetation cover. The plains are not entirely
flat, being characterized by low undulations with wave-
lengths in the order of 1 x 10 meters. The proximity of the
water table in low-lying areas means that slight changes in
elevation can produce sharp changes in vegetation.

                            Soils

        The soils of the island are thin and discontinuous.
For the most part they vary according to the age of the land
surface and the extent to which it has been disturbed by
man.   Mooney (1905), in the only comprehensive account of
Bahamian soils yet available, lists four soil types as being
present on Cat: (1) Coral sand, (2) Bahama Black Loam, and
(3) Bahama Red Loam, (4) Bahama Marl.

        The coral sand type refers to the soil found on the
Holocene sand dunes and ridges, or in local terms, the
whiteland. The term "coral sand" is a misnomer since coral
fragments form only a very small percentage of these sedi-
ments. The whiteland soil type is immature in the sense
that there is little profile development. The A1 horizon is
very thin, rarely more than a few inches thick if it is
present at all.   In most parts of the island, cultivation
has disturbed whatever profile had developed in the pre-

agricultural period.[5] According to Mooney (1905: 157), this soil is quite rich in potash, phosphates, and nitrates. However, a more recent government report states that the whiteland soil is poor in nutrients and too droughty for successful agriculture (Anonymous, 1960).

The Bahama Black Loam is the most widespread soil type on the island. It covers all but a few areas of the indurated Pleistocene surfaces. Like the whiteland soil it has been severely disturbed by cultivation and is rarely more than a few inches thick. During cultivation it collects in pockets and crevices in the limstone surface, leaving large areas of bare rock exposed. According to Mooney (1905: 158), it is a residual soil derived from the underlying limestone by weathering. An alternative explanation would be that it consists of broken-down organic matter. Because of the capillary rise of water through the underlying limestone, this soil type is less droughty than the whiteland soils (Anonymous, 1960: 2). It is recognized as the most productive soil type on the island and is therefore frequently cultivated.

The Bahama Red Loam has a restricted distribution on Cat Island. It is found on the older dune and beach ridge systems and in the land-locked depressions between them. This red soil is almost certainly a fossil soil that formed under different weathering conditions during the Pleistocene. Similar fossil soils have been described in several areas of the West Indies (Ruhe et al., 1961; Kaye, 1959). It is a lateritic soil rich in iron and aluminum and has been derived from the underlying limestone by weathering. Although it appears to be a loam in the field, particle size analysis has shown it to be a clay (Ahmad and Jones, 1969). This is also indicated by the way in which it floods after rain and becomes hard and compacted when dry. According to Mooney (1905: 166), it is rich in nutrients, particularly phosphates, nitrates, and potash, It has a slightly lower pH than the Bahama Black Loam (7.0-7.5 cf7.5-8.0) and probably because of this has been especially favored for pineapple cultivation (Anonymous, 1960: 2).

Mooney's fourth soil type, the Bahama Marl has a very restricted distribution on Cat Island, being found only in small areas of low ground east of McQueens settlement (Mooney, 1905: plate XXXI). Basically it is a freshwater marl overlying decayed organic material. Its proximity to the water table makes cultivation precarious, and as a result it has only been used for grazing in recent years.

5. Lind (1969) failed to take this into account in his study of the coastal landforms of the island.

The importance of soil differences as far as the composition of the wild vegetation is concerned is not clear. The whiteland is a distinctive habitat-type, but not because of its soil characteristics. The boundary between the Black Soil and Red Soil is usually distinct, but as Mooney reported (1905: 165), it does not appear to have any significance as far as wild vegetation is concerned. The Bahama Marl is too localized to be of major importance. For the island as a whole it is probably a safe assumption that soil differences per se are not an important cause of variation in the structure and composition of wild vegetation.

Climate

As might be expected from its location, Cat Island has a seasonally wet and dry sub-tropical climate (Table 1).

TABLE 1

CLIMATIC DATA 1952-1962
THE BIGHT, CAT ISLAND
Bahamas Dept. of Agriculture, cited in Lind (1969: 10)

	Temperature		Rainfall	
	F	C	inches	mm.
Jan	72	22.2	1.2	30.5
Feb	74	23.3	1.2	30.5
Mar	73	22.8	1.6	40.6
Apr	75	23.9	4.5	114.3
May	78	25.6	3.9	99.1
Jun	81	27.2	1.9	48.3
Jul	82	27.8	3.8	96.5
Aug	83	28.3	5.0	127.0
Sep	82	27.8	9.1	231.1
Oct	80	26.7	9.1	231.1
Nov	76	24.4	3.6	91.4
Dec	77	25.0	2.1	53.3
Total			39.2	995.7
Mean	78	25.6		

The basic climatic control is the north Atlantic sub-tropical high pressure cell. In winter the cell moves south and intensifies, limiting convection and reducing rainfall. Occasional outbreaks of modified polar air bring cloudy

weather from the north and temperatures fall as low as the 60s, but for the most part the sky is clear and temperatures average in the 70s. In summer the high pressure cell moves north, convection is stronger, and trade wind cumulus clouds may tower as high as 50,000 feet. This is the rainy season, during which sporadic convectional showers provide most of the total precipitation. Afternoon temperature may reach the low 90s in July and August, although the comparatively cool trade winds keep the averages in the 80s.

As far as plants are concerned, perhaps the most important aspect of Cat Island's climate is its mildness. Separated from the continent by the warm waters of the Gulf Stream and under the influence of the trades for most of the year, the island has a truly oceanic climate. Wallace (1902: 5) underestimated this oceanicity when he argued that differences in plant and animal life between Florida and the Bahamas could not be explained by climate. Frost is virtually unknown in the islands, and because of this many plants are able to grow that could never survive for long on the mainland. To the northerner Bahamian vegetation is very definitely tropical.

In a negative sense rainfall is a more important climatic variable than temperature. Although the data presented in Table 1 do not show it, summer droughts are a common occurrence in the Bahamas. In some years no rain may fall for several months and at such a time plant life is dependent upon either the formation of dew or the upward movement of water through the limestone by capillary action. A visitor to Cat Island from the West Indies or Central America would see few plant species that were new to him, but he would probably be surprised by the generally stunted nature of the vegetation. Early students of the Bahamas flora were especially impressed by the many morphological adaptations to drought shown by Bahamian plants, for example, hairiness and small leathery leaves (Coker, 1905: 215). Deciduousness is also a response to the seasonally-dry climate, and during the "winter" many trees and nearly all the shallow-rooted bushes lose their leaves.

A phenomenon closely related to the occurrence of drought is fire. Unfortunately, the significance of natural fires as far as Cat Island vegetation is concerned is difficult to assess. According to local informants, no lightning fires were known to have occurred within living memory. Even so, the possibility remains that they could occur, especially in the seasonally-flooded savannah. The evergreen woodland could also burn naturally if there were enough dry fuel available on the ground. This is rarely the case today, although it may have been more common in the

past. The significance of natural fires in the Everglades area of South Florida has been recently emphasised by Craighead (1971) and Robertson (1962).

Another important aperiodic climatic variable is the frequency of hurricane strength winds. In 186 years, 12 hurricane eyes have passed over the island, an average of one every 16 years (Lind, 1969: 132). Although no studies have been done on the effects of hurricanes on Bahamian vegetation, the conclusions drawn from studies in similar areas elsewhere are probably applicable (Craighead, 1962, 1964; Stoddart, 1965; Sauer, 1962; Wadsworth and Englerth, 1959). Native species are usually quick to recover after the storm. Flexible trunks and branches, bushy habits, photosynthetic bark, and deep root systems are characteristic of many Bahamian species.

Hydrology

The porosity of the limestone exaggerates the droughtiness of the surface, but on the other hand it means that rainfall is not quickly lost as run-off. In the indurated Pleistocene dunes, the water table may be at a considerable depth below the surface. At the Devils Point settlement, for example, deep wells are required to reach fresh water. In the summer of 1970 the water table was 12 meters below the ground surface and only 3 meters above sea level. Plant life on these hills must therefore rely upon water from the unsaturated zone. In the loosely-consolidated younger dunes and beach ridges the water table is very close to sea level.

Although there are no permanent fresh water streams on the island, several low-lying, land-locked depressions are flooded after heavy rains in the summer and autumn. This flooding makes tree growth impossible and means that slight changes in elevation can cause sharp changes in vegetation. In these areas the location of the water table has an important influence on the character of the vegetation.

The Environment as a Whole

A low, limestone island such as Cat appears to provide a rather difficult environment for plant life. Droughts, hurricanes, and an apparently infertile limestone surface all combine to place limitations on plant growth, and at first acquaintance it is somewhat surprising that anything can grow here, wild or cultivated. Yet, paradoxically, the island is floristically rich. In an area of only 250 square kilometers, probably a thousand species of vascular plants

are present.[6] In large part this diversity must reflect the fact that the low, limestone island is an ancient environment. In the area that is now the Bahamas, islands similar to Cat have probably been discontinuously present since at least the early Cretaceous. Plants and animals have therefore had a long time to adapt to this sort of setting. It is interesting to note here that of 60 genera identified in the Wilcox Flora of the Southeastern United States, which dates to the early Eocene (Berry, 1930), roughly 40 percent are living in the Bahamas today. This is not to suggest as the nineteenth-century authorities might have done, that Bahamian vegetation has survived undisturbed since the early Tertiary. The Bahama islands as they are today are geologically young. Furthermore, the sea level oscillations of the Pleistocene must have caused drastic changes in hydrological conditions and corresponding changes in vegetation independent of any changes in regional climate. On a shorter time scale, natural disturbance, in the form of dune formation and erosion, flooding by salt and fresh water, hurricanes, and lightning fires, has undoubtedly played an important role in the development of Bahamaian vegetation. How this vegetation has been able to withstand the new types of disturbance introduced by man is the main concern of the present study.

6. This estimate is based on the Bahama Flora (Britton and Millspaugh, 1920:vii), which lists 995 spermatophytes and 33 pteridophytes for the archipelago as a whole. These totals, however, only include cultivated species such as have shown "a strong tendency to become spontaneous."

IV. THE PRESENT VEGETATION: A GENERAL VIEW

Ideally, a study of man and vegetation change would begin with the vegetation as it was before man arrived and then trace the changes that have occurred as a result of his presence. In practice, even for recently settled islands, this is rarely possible. The problem, of course, is that there are so few accurate accounts of aboriginal vegetation. Certainly for Cat Island there is nothing. The Arawaks left no written record, and the early European accounts are disappointingly vague. An alternative approach was therefore called for. The one that is followed here is similar to that used by Harris in his study of the Outer Leeward Islands (1965). The present vegetation is described first in general terms. This general account then provides the basis for the later, detailed analysis of man's impact.

In most respects, the vegetation of Cat Island is similar to that of the rest of the Bahamas and indeed to that of similar environments in the New World subtropics as a whole.[1] A low, largely evergreen woodland covers all but the lowest ground, where it gives way to either salt-tolerant vegetation or seasonally-flooded savanna. Because of the island's small size and low relief, climate is not an important cause of variation in the composition or structure of the vegetation. The differences that do exist can largely be attributed to disturbance by man or to differences in topography, lithology and drainage. For purposes of general description, therefore, the vegetation was classified indirectly on the basis of landform or habitat- types. The resulting classification is shown in Table 2. It has the advantage that it avoids the arbitrary problem of classifying vegetation itself and at the same time provides a coherent framework within which to study the processes of vegetation change.

The Original intention, was to study man's impact on the vegetation of the entire island. However, it soon became clear that such a broad approach would have to be of limited depth and it was therefore decided to restrict the study to an analysis of man's modification of the evergreen woodland, or "coppice" as it is locally known. Unlike the vegetation of salt water habitats and seasonally-flooded

[1]. It differs from several Bahamian Islands (New Providence, Abaco, Andros, Grand Bahama, Caicos) in that the Caribbean pine (Pinus caribaea) is not present. There is no obvious explanation for the anomalous distribution of pine in the Bahamas.

TABLE 2
VEGETATION AND HABITAT TYPES
A. SALT WATER HABITATS

ASPECT	COASTAL		INLAND	
HABITAT TYPE	Holocene dunes and beach ridges	Pleistocene dunes and beach ridges	Holocene marine sands	Pleistocene marine limestones
LOCAL NAMES	Strand	Scrub	Tidal Flats	Lagoons
VEGETATION	Strand	Scrub	Mangrove	Mangrove

B. FRESH WATER HABITATS

DRAINAGE	SEASONALLY-FLOODED		WELL-DRAINED		
HABITAT TYPE	Holocene marls	Pleistocene marine limestones	Holocene dunes and beach ridges	Pleistocene dunes and beach ridges	Pleistocene marine limestones
LOCAL NAMES	Marsh	Savanna	Whiteland	Blackland	Flatland
VEGETATION	Marsh	Savanna	Woodland	Woodland	Flatland

areas, the woodland occupies ground on which cultivated
crops can be grown, and as a result it has been drastically
disturbed by man. In the general account that follows, the
comparatively undisturbed vegetation of the uncultivated
areas is described first, since it provides the background
for the later discussion of the woodland.[2] Figures 5 through
15 illustrate the general aspect of the vegetation of the
uncultivated areas.

Salt Water Habitats

Salt water is never far from the surface in the Baha-
mas. No part of Cat Island is more than 3 kilometers from
the sea, and the fresh water lens at its deepest is probably
not more than 30 meters thick. All the larger lakes are
saline and tidal. Around the margins of these lakes there
is a transitional zone of brackish water, the width of which
varies from a few meters to over a kilometer. Its extent
largely a function of topography and bedrock characteris-
tics.

The vegetation of the salt-water habitats is distinc-
tive, few of the salt-tolerant species are adapted to life
in a fresh-water environment. None of the species present
is peculiar to Cat Island and most of them are widely dis-
tributed throughout the New World sub- tropics. The differ-
ences in vegetation within the salt-water habitats are
largely to differences in parent material and exposure. The
latter is most important, and accounts for the contrast
between the vegetation of the coast and that of the tidal
flats and lagoon margins.

Coastal Environments

The coastal environment presents problems that few
species have been able to overcome. The plants that live
here are adapted to periodic flooding by salt water, salt
spray, high evaporation rates, and geomorphic instability.
Soils are thin or non-existent and the species present are
capable of growing in a raw sand or bare rock substrate.
The nature of the substrate is the main determinant of local

2. Most of the species listed in this account were col-
lected in the field. A voucher collection including
some 600 specimens has been deposited in the University
of Wisconsin herbarium, and an almost complete dupli-
cate set in the herbarium of the Arnold Arboretum, Har-
vard University. A systematic list of the species en-
countered is given as Appendix I, and a list of local
names and their scientific equivalents as Appendix II.

Figure 5. Holocene beach-ridges at North Bird Point. Mallatonia gnaphaloides is in the central foreground, Suriana maritima in the lower left. Herbaceous cover consists of Uniola paniculata and Iva imbricata. The coconuts in the background are planted.

Figure 6. Holocene dune coast east of Stevenson. Large thickets are primarily Coccoloba uvifera. In the foreground is Hymenocallis declinata together with Uniola Paniculata and Ipomoea pes caprae.

variation in floristic composition.

  Holocene Dunes and Beach Ridges. Most of the dunes and
beach ridges that fringe the coast were formed during the
postglacial rise in sea level. They are composed of a
variety of carbonate sediments that are as yet poorly conso-
lidated and are in fact being constantly eroded and redepo-
sited, especially along the exposed east coast. This is a
particularly unstable habitat and as one would expect,
herbs, vines, and shrubs are especially important.

  The zonation of species that characterizes so many
tropical coasts is not always evident on Cat Island. Dis-
turbance by waves, wind, and man usually prevents the estab-
lishment of any stable pattern. In several exposed areas
along the eastern and northern coasts the sand is virtually
bare of shrubs. Here sea oats (Uniola paniculata) and the
sea lily (Hymenocallis declinata) are common. The sand is
usually crisscrossed by trailing vines, Ipomoea pes-caprae,
Cassytha filiformis, Canavalia maritima, and the bay mari-
gold (Ambrosia hispida). several grasses (Paspalum vagina-
tum, Cenchrus tribuloides, Distichlis spicata) and succu-
lents (Sesuvium portulacastrum, Iva imbricata, Chamaesyce
mesembrianthemifolia, Cakile lanceolata). Not all of these
species are likely to be found in any one locality, but all
are common along the coast. In other areas a thicket of
evergreen shrubs reaches down to the edge of the beach.
Probably the two most common species here are the sea grape
(Coccoloba uvifera) and bay cedar (Suriana maritima). Also
characteristic of the coastal thickets are Scaevola
plumieri, Mallatonia gnaphaloides and Guilandina bonduc.

  In some areas along the comparatively quiet western
coast the Holocene sands have become partially indurated.
The harder surface offers different opportunities for plant
life and is characterized by different species combinations.
This transitional type of habitat can in fact be included in
the next sub-heading.

  Pleistocene Dunes and Beach Ridges. The indurated
Pleistocene surfaces offer a more stable habitat for plant
life and, the vines and stoloniferous grasses are less com-
mon here. Fleshy beach plants such as Sesuvium portulacas-
trum are occasionally seen but for the most part low xero-
phytic shrubs provide the only cover. Two very common
species are Strumpfia maritima and Rachicallis americana.
Suriana maritima is sometimes present as also are Antirrhea
myrtifolia, Erithalis fruticosa, Ernodea littoralis, Eugenia
longpipes, Jaquinia keyensis and Bumelia retusa. The lime-
stone surface is very droughty and even on sheltered sites
the shrubs are rarely more than 2 meters tall.

Tidal Flats and Lagoon Margins.

Along the exposed eastern coast no plants can survive for long in the inter-tidal zone. However, this is not the case along the more sheltered leeward coast. Here is an extensive area of tidal flat most of which occupied by mangroves. All four New World mangrove species are native to Cat Island, the red mangrove (Rhizophora mangle), the black mangrove (Avicennia germinans), the white mangrove (Laguncularia racemosa), and buttonwood (Conocarpus erecta). Rhizophora is by far the most common of the four, ranging from the high tide mark to the edges of the tidal channels. On the flats it rarely reaches more than a meter in height, whereas along the tidal channels it may reach 2 to 3 meters. Avicennia, more tree-like in habit and lacking the prop roots, appears to prefer a more stable substrate than lime mud. Characteristically, it is seen fairly close to the high tide mark or in an area where the limestone bedrock is close to the surface. Laguncularia is the rarest of the four and appears similar in habitat preferences to Avicennia. Conocarpus is very definitely restricted to a narrow zone just above the high tide mark. Also, salt-tolerant herbs such as Batis maritima, Salicornia perennis and Borrichia arborescens are frequently found just above the high tide mark.

Along the central axis of the island and behind the coastal dune barriers are several salt water lagoons, some narrowly connected to the sea, others completely landlocked.[3] For reasons that are not immediately apparent the lagoons vary considerably in their physical and biological characteristics. Some are comparatively clear while others have the consistency of thick soup due to the accumulation of algae. The vegetation around their margins, however,· is similar to that found along the coast or on the tidal flats. and floristic differences can be largely attributed to differences in substrate.

Unconsolidated sediments, such as cover a wide area around the Orange Creek Blue Hole (Figure 2), are usually characterized by Rhizophora and other typical tidal flat species. On the other hand, salt-tolerant shrubs such as Rachicallis, Strumpfia, and Conocarpus are more common where the shoreline is rocky.
This generalization does not always hold true, as for example along the rocky shoreline of the Blue Hole east of Dumfries, where there is a forest of pure Rhizophora, with

3. Several of the deeper lagoons are known as "blue holes." Some are thought to be inhabited by sea monsters and are therefore avoided by the local people.

Figure 7. Leeward limestone coast at Wilson Bay.   Species present are _Conocarpus erecta_,   _aevola plumierii_, _Coccoloba uvifera_, _Reynosia septentrionalis_, _Borrichia arborescens_, and _Strumpfia maritima_.

Figure 8. Exposed limestone coast south of north Bird Point.   _Suriana maritima_ showing the effects of exposure to the trade winds.

Figure 9. *Rhizophora mangle* at the Dumfries Blue Hole. Epiphytic bromeliads are the only other vascular plants present here.

Figure 10. Margin of a tidal channel south of Dumfries. *Avicennia nitida* dominates the foreground, its pneumatophores are growing in a meter of peat and marl. The most common species in the background is *Conocarpus erecta*.

trees as high as 8 meters, growing on peat that was measured to be at least 6 meters thick in places. Samples were taken from this peat for pollen analysis, but unfortunately they proved to be barren.

Man's Impact on the Vegetation of Salt-Water Habitats.

For the most part the vegetation of salt-water habitats has not been disturbed by man. Only near the settlements on the sheltered leeward coast has really significant modification taken place. Here mangrove swamps in tidal inlets have been locally cleared or filled to reduce the mosquito problem and generally improve sanitary conditions. Rhizophora is cut for charcoal, although not in sufficient quantities to affect its overall distribution. Likewise Conocarpus has not become noticeably rare around the settlements even though it is the most popular source of firewood.

A few horses are grazed on the whiteland, although it is doubtful that they have had much of an impact on the coastal vegetation as most of the common species are not really palatable. Fires were occasionally observed to have spread down to the coast from inland fields; however, their effect has probably been small in the long term.

As far as the invasion of alien plants is concerned, only the Australian Pine (Casuarina equisetifolia) has been really successful. It was introduced to the island probably less than a hundred and fifty years ago and has since spread along most of the sheltered west coast. It is planted in the settlements as an ornamental and occasionally on the whiteland as a windbreak. From these plantings it has rapidly colonized a narrow zone just above the high tide mark. Characteristically, it carpets the ground with a cover of needles that few species can cope with and has replaced the native plants over a considerable section of the leeward coast. On the windward coast it has been less successful, possibly because erosion is more active there.

Apart from Casuarina, the only other exotics that have become established are Spanish Bayonet (Yucca aloifolia) and the Mahoe (Thespesia populnea), neither of which have spread far outside of the settlements. The coconut (Cocos nucifera), although often seen in the beach drift, has for some reason failed to establish itself spontaneously on Cat Island. The same is true of the Indian Almond (Terminalia catappa).

In general, the vegetation of salt water habitats has proved remarkably resistant to disturbance by man. Except

Figure 11. Competition between <u>Casuarina equisetifolia</u> and <u>Gundlachia corymbosa</u>. The accumulation of <u>Casuarina</u> needles has somehow caused the death of the <u>Gundlachia</u> bushes. Crab holes are evident in the foreground.

on the leeward coast where Casuarina has become so impor-
tant, there is little evidence of man's intervention.

Seasonally-Flooded Freshwater Habitats

Over most of the island fresh water is quickly absorbed
at the surface. However, in low-lying areas, particularly
land-locked areas, the surface may be flooded to a depth of
several feet after heavy summer rains. The water may stand
on the ground for several days before being absorbed by the
limestone. These floods, together with drought in the dry
season, provide a combination that few perennials can with-
stand. Woody species may survive long enough to become
saplings, but in the long-term, tree growth is not possible.
The vegetation of these areas is in many respects similar to
that of the Florida Everglades and to seasonally- flooded
savannas in general.

The largest area of savanna on Cat Island is just to
the east of McQueens (Figure 2). To the north and east it
is bounded by a Pleistocene dune ridge whose fairly steep
slopes provide a sharp limit to the flooded area, whereas to
the south and west a gradual rise through a series of low
ridges produces a more broken transition. The ridges appear
as islands, or "hammocks," of evergreen woodland surrounded
by savanna. With increasing elevation the woodland
increases in area at the expense of the savanna, until the
distribution is reversed and small pockets of savanna sur-
vive in depressions surrounded by woodland. These in turn
disappear on the higher ground.

In the lower parts of the larger savannas fresh water
may be present throughout the year. These marshy areas are
characterized by Eleocharis caribaea, sawgrass (Cladium
jamaicense), and cattail (Typha domingensis). In seasonal
ponds several aquatics were collected, including Nymphaea
ampla var. pulchela, Potamogeton heterophyllus, and Pros-
perinaca platycarpa. Around the margins of these ponds
Echinodorus berteroi Jussiaea suffruticosa, Centella erecta,
Lippia stoechadifolia are commonly encountered, together
with the sedges Albilgaardia monostachya, Dichromena
colorata and Rhynchospora cyperoides. Around the edges of
the smaller, potholes the pond apple (Annona glabra) is
often found.

In the drier areas several species of herbs are charac-
teristically present; for example, Pluchea rosea, Buchnera
elongata, Eustoma exaltatum, Sabbatia stellaris, Eupatorium
villosum, Walthera indica, Cynoctonium mitreola, and Linum
bahamense. The savannas are not grasslands in the true

Figure 12. A "hammock" in the McQueen's savanna. A poison-wood (Metopium toxiferum) has become established on a small ridge. On either side are palmettoes (Sabal palmetto); in the foreground Pluchea rosea, Andropogon gracilis, and Aristida ternipes.

Figure 13. A small seasonally-flooded depression just above the McQueen's savanna. The white bracts of Dicromena colorata are visible in the foreground, as are saplings of Tabebuia bahamensis. In the background are Coccoloba uvifera and Metopium toxiferum.

sense of the word, as grasses cover only a small percentage of the total area. <u>Andropogon gracilis</u> and <u>Aristida ternipes</u> were the only grasses seen, and both were rare.

Around the edges of the savannas, pioneer shrubs and small trees often obtain temporary foothold; especially common are horsebush (<u>Gundlachia corymbosa</u>), sweet gale (<u>Myrica cerifera</u>), coco plum (<u>Chrysobalanus icaco</u>), beefwood (<u>Torrubia Longifolia</u>), and five finger (<u>Tabebuia bahamensis</u>). Palmettoes (<u>Sabal palmetto</u>) mark the upper margins of the flooded ground and in turn give way to evergreen woodland on the well-drained sites.

Man's Impact on the Seasonally-Flooded Freshwater Habitats.

As in the salt-water habitats, the growth of crops is not possible in the seasonally-flooded areas, and consequently the native vegetation has been relatively undisturbed. Fire has probably been the main cause of change.[4] All but the youngest palmettoes show scorch marks on their trunks (Figure 14). According to local information, savanna fires served no useful purpose and were simply the work of children. There were no reports of any lightning fires, but this does not mean they never occur. In the Everglades, for example, they are not uncommon events (Robertson, 1962).

Grazing by horses was observed in the more accessible areas, although what species were affected was not determined. The savannas are generally regarded as poor pasture because they dry out during the winter months.

No alien species appear to have established themselves in the seasonally-flooded areas. Casuarina, which has colonized analogous areas in the Everglades (Egler, 1952), is conspicuously absent. On the other hand, the McQueens savanna does provide a good example of man having locally extended the range of a native species. As can be seen from Figure 15, the trail through the savanna passes through an avenue of palmettoes. These have grown from berries dropped during the harvesting of palmetto inflorescences for hog feed. For the most part, however, the seasonally-flooded savannas have been of little value to man, and for this reason they have remained relatively undisturbed.

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4. There is no evidence to suggest that the area of savannas has been enlarged by repeated fires. In all cases the woodland comes down to the edge of the seasonally flooded areas.

Figure 14. Palmettoes (Sabal palmetto) recently burned by children. The palmettoes were not killed by the fire and were actually sprouting new leaves at the time the photograph was taken.

Figure 15. "Footpath distribution" of palmettoes near McQueens. The individuals alongside the trail have grown from accidentally dropped fruits, that had been gathered for hog feed.

Well-Drained Freshwater Habitats.

Most of the island is covered by a low, largely ever-
green woodland, locally known as "the coppice". And as its
local name implies, it has been drastically disturbed by
man. Seen from above it has the appearance of a patchwork
quilt, the abandoned fields of shifting agriculturalists
showing progressively darker shades of green according to
their age (Figure 16). On the ground, sharp changes in
height and floristic composition give further clues as to
the history of disturbance. It was this obviously disturbed
aspect of the woodland that made it particularly interesting
in the context of the present study

In mature woodland on the more mesic sites, the dom-
inant trees reach a height of 10 meters or so, with the
larger trees having diameters at breast height of from 20 to
30 centimeters. On dry sites, where the fresh water lens is
thin or the limestone surface is steep, the woodland degen-
erates into a cactus scrub. Here the shrubby trees are
rarely more than 3 meters tall, and the dildo cactus
(Cephalocereus millspaughii) adds to the xerophytic charac-
ter of the vegetation.

As a vegetation type the Cat Island woodland is prob-
ably equivalent to Beard's (1955) "Evergreen Bushland" and
dry "Evergreen Thicket". This kind of vegetation is fre-
quently encountered in low limestone environments throughout
the New World sub-tropics. To the northerner the woodland
is definitely tropical. The great majority of species
present range south to the Greater Antilles or beyond, and
very few are found north of the Florida Keys. Furthermore,
it is floristically rich. Coker was certainly correct when
he reported that:

As one passes through a typical Bahamian coppice,
different plants are met with at every step. The
variety seems interminable and on first acquain-
tance one is appalled with the difficulty of
becoming acquainted with them (Coker, 1905: 232).

In the present study, 120 species of trees and shrubs
were encountered during systematic sampling, and herbarium
collections were made of 30 more (Appendix I). This floris-
tic diversity is to a large extent masked by a remarkably
uniform physiognomy. Most of the woody species have small,
entire-margined and leathery leaves. This uniformity pro-
vides a classic example of convergent evolution, species
having adapted in similar ways to the problems of life on a
low limestone island.
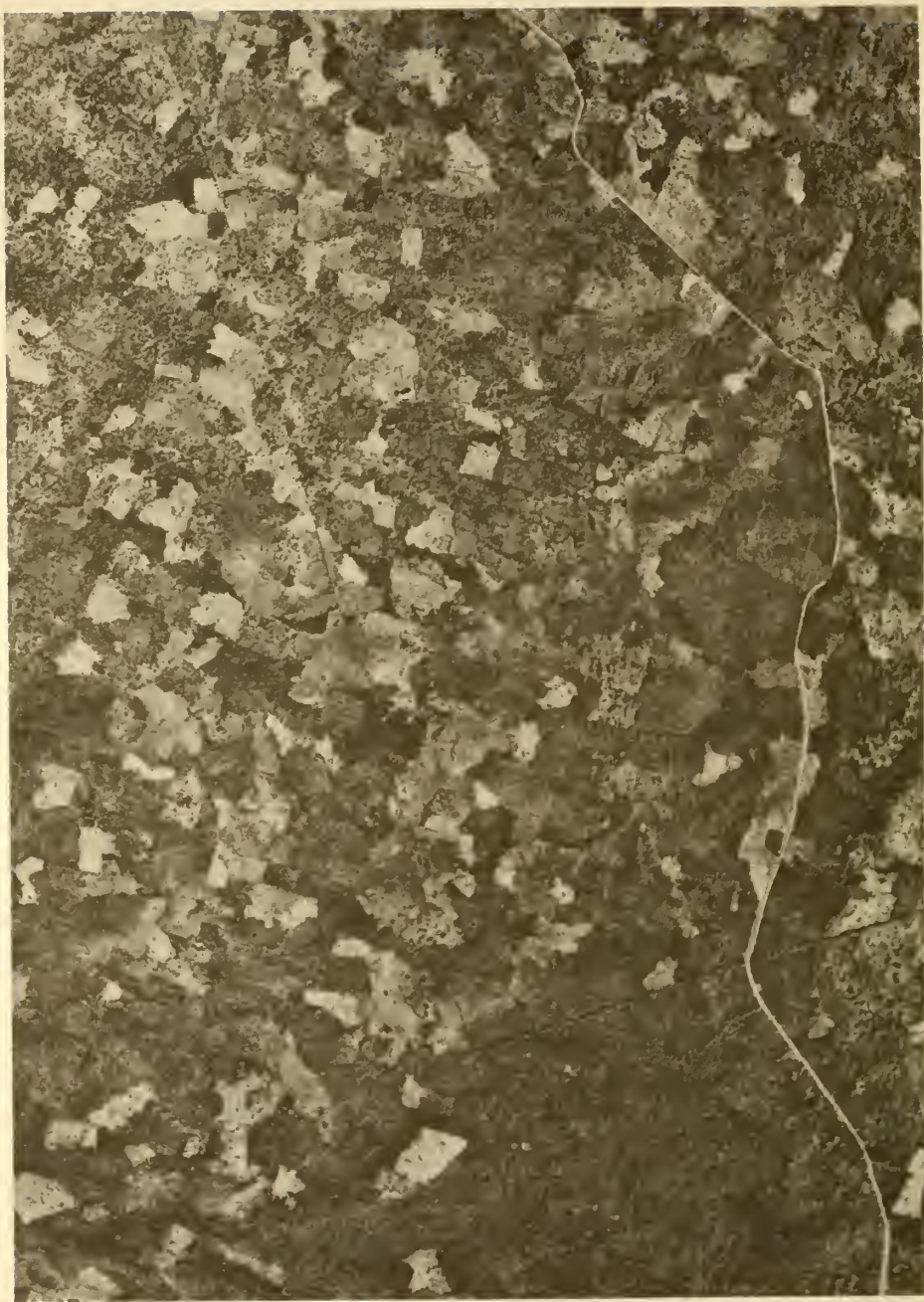
Figure 16. An aerial view of the woodland south of
Old Bight. Scale = 1:1,000
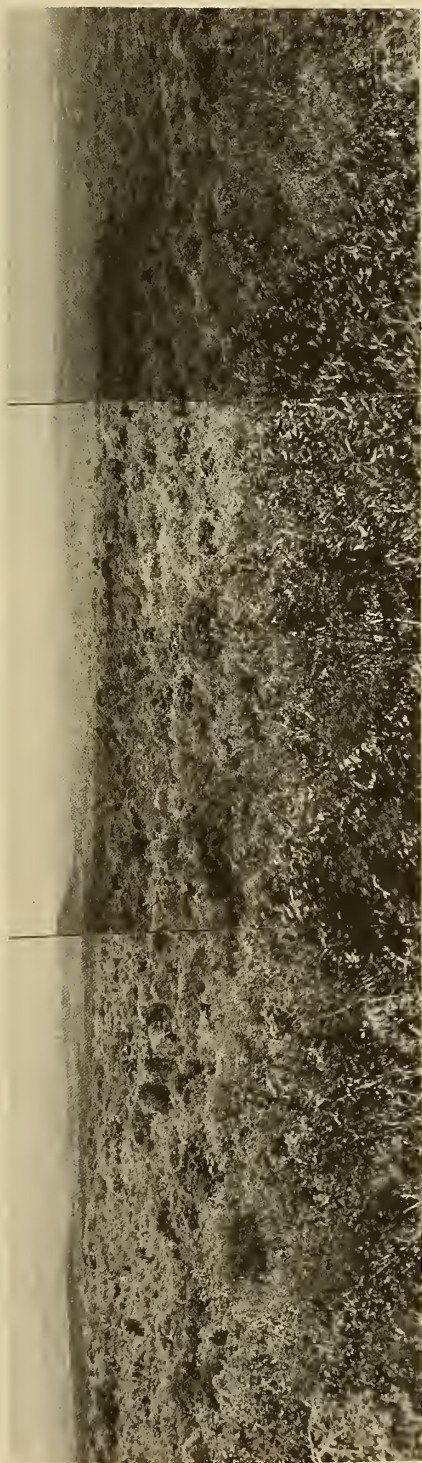
Figure 17. View of the woodland looking east from the Pleistocene dune-ridge north of Freetown. A saltwater lagoon, locally known as Red Pond, is visible to the left.

On the other hand, the woodland is not entirely uniform in structure or floristic composition. As was indicated above, both vary from place to place, largely as a function of the availability of moisture. This in turn is largely determined by the location of the water table and the nature of the substrate. Although the former was difficult to identify in the field the latter was not. Therefore it was decided to simplify the analysis by subdividing the woodland into three types on the basis of landform or "habitat" characteristics (Table 2). More specifically the three types are: (1) Holocene dunes and beach ridges; (2) Pleistocene marine plains; and (3) Pleistocene dunes and beach ridges--or, in local terminology, the whiteland, flatland, and blackland, respectively. As will become clear later, these habitat-types are not floristically distinct, as many species are present in all three. Even so, by subdividing the woodland in this way it was possible to control some of the environmental variability that would otherwise have complicated any analysis of man's impact. Figures 17 to 23 give a visual impression of the three habitat types.

The Whiteland

The largest area of whiteland on the island forms a discontinuous strip along the east coast (Figure 4). On the west coast there are localized areas near Orange Creek, Bennet's Harbour, and McQueens. Not all of the whiteland is covered by evergreen woodland. On its seaward margins it is occupied by the salt-tolerant vegetation of the coast or tidal flats, and inland by the seasonally-flooded savanna, or other varieties of evergreen woodland, depending upon the location of the water table.

The woodland is generally lower on the whiteland than elsewhere. The trees have a characteristically bushy appearance, and are rarely more than 6 meters tall. The number of species present is proportionately lower. There are probably three basic reasons for this impoverishment. First, the loose sand does not have a very high moisture-retention capacity and ground water is not able to rise very easily by capillary action (Anonymous, 1960). Second, the sand provides a rather insecure rooting-medium for trees so often subject to hurricane-strength winds. Third, and perhaps most important, the whiteland has in most areas an exposed location on the coast and evapotranspiration rates are therefore high. This is particularly significant on the southern and eastern coasts, which face the persistent trade winds.

In spite of the impoverished aspect of the whiteland vegetation, a considerable diversity of species is likely to

Figure 18.   A whiteland field, the light area in the middle
distance, is in the process of being cleared.   In this case
the fallow period has not been long enough to allow shrubs
to become established. Uniola paniculata, Chloris petraea,
Cenchrus echinatus and Bidens pilosa are common in the fore-
ground.

Figure 19.   Corchorus hirsutus dominates this whiteland
field The bushes are probably about ten years old Coccoloba
uvifera is present in the left foreground and also in the
distance.

be encountered at any one locality. Especially common in
areas of older woodland are cassina (Acacia choriophylla),
ramshorn (Pithecellobium keyense), dollen plum (Reynosia
septentrionalis, poisonwood (Metopium toxiferum), milkberry
(Bumelia retusa), and beefwood (Torrubia longifolia). On
less favorable sites sea grape (Coccoloba uvifera), coco
plum (Chrysobalanus icaco), black torch (Erithalis fru-
ticosa), and white torch (Amyris elemifera) may be present.

On exposed sites, the woodland degenerates into a coa-
stal thicket in which the area of bare sand exceeds the area
covered by vegetation. Such eas are occasionally washed
by salt water and are therefore not cultivated. Apart from
a few remote areas, as for example west of McQueens (Figure
2), the whiteland has been repeatedly cleared and burned for
agriculture during the past three hundred years. The wood-
land is in fact secondary vegetation in various stages of
recovery after clearing, burning, and grazing.

The Flatland

Between the whiteland and the Pleistocene dunes and
beach ridges is the flatland. In total area it accounts for
the largest part of the island. On its lower margins it
grades into either the whiteland, the seasonally-flooded
freshwater areas, or the saline lagoons; on higher ground it
is bordered by the Pleistocene dunes and beach ridges.

The woodland is generally higher on the flatland than
on the whiteland. In relatively undisturbed areas, trees
were seen 10 meters in height with diameters at breast
height of 20 to 30 centimeters. In contrast to the almost
impenetrable whiteland thickets, individual trees are spaced
2 to 3 meters apart . The more common species are pigeon
plum (Coccoloba diversifolia), poisonwood (Metopium toxi-
ferum), wild tamarind (Lysiloma bahamensis), kamalamay (Bur-
sera simaruba), and mastic (Sideroxylon foetidissimum). The
ground is covered with a thick accumulation of leaves, which
in turn may be covered by a dense growth of terrestrial
bromeliads. The trees themselves characteristically support
a rich growth of epiphytic orchids and bromeliads. The
woodland as a whole has a distinctly tropical appearance.

Such undisturbed areas are comparatively rare, as most
of the flatland has been repeatedly cleared and burned for
agriculture. Second-growth woodland in various stages of
recovery covers most of this habitat-type. Here a great
variety of species are present including horsebush
(Gundlachia corymbosa), granny bush (Croton linearis), jum-
bay (Leucaena leucoephala), and soap bush (Corchorus hir-
sutus). The individual trees and shrubs are closely spaced,

Figure 20. A flatland field close to the edges
of the seasonally-flooded savannah. Cultivation is
precarious here because of the risk of flooding.
Palmetto fronds have been laid out to dry before
burning.

Figure 21. Second growth on the flatland south-east
of Bennet's Harbour. The bushes are three meters tall
and probably about twenty years old. The palmetto
is the buffalo top (Thrinax microcarpa).

Figure 22. A severely burned blackland field. Note that many of the bushes in the background are still without leaves. The photograph was taken in June 1967 after an unusually dry dwinter.

Figure 23. The same field in 1970, from a slightly different angle. The field had been abandoned in 1969. Recovery is slow probably because of the deep burn. The sprout in the foreground (Coccoloba diversifolia) is one of the few to be seen.

making the woodland almost impossible to penetrate without a
machete. The canopy in thinner and as a result a luxuriant
growth of epiphytes is not possible. Vines, however, are
common, particularly the troublesome Smilax havanensis,
together with Jaquemontia cayensis, and several morning
glories (Ipomoea microdactyla, I. acuminata).

The Blackland

The Pleistocene dunes and beach ridges in a sense form
the backbone of the island, and are covered with the highest
and floristically most diverse woodland. Except in exposed
areas facing the trade winds or in areas where slopes were
excessively steep, this is the optimum habitat for tree
growth.

As on the flatland, comparatively undisturbed woodland
was hard to find because most of the blackland has been
intensively used for agriculture. However, in a few areas
trees were seen on the order of 12 meters tall with diame-
ters at breast height of around 30 centimeters. This mature
woodland has a distinctly tropical appearance not only
because of the great number of species present, but also
because of the many epiphytic orchids and bromeliads. The
dominant tree species are pigeon plum (Coccoloba diversi-
folia), poisonwood (Metopium toxiferum), hog cabbage palm

(Pseudophoenix vinifera), mastic (Sideroxylon foetidis-
simum), and madeira (Dipholis salicifolia).

In older woodland the differences between the flatland
and blackland are not too obvious. This is not the case in
the younger woodland. On the blackland the limestone sur-
face is riddled with potholes and small crevices. These
microhabitats play an important role in slowing soil erosion
and reducing evaporation. The broken surface also reduces
the severity of the fires set by the shifting agricultural-
ists. As will be shown later, the rate of succession is
more rapid on the blackland than on any other habitat-type.

V. CLEARING AND BURNING FOR AGRICULTURE

Cat Island has been discontinuously inhabited for at least a thousand years, during which time the woodland has been repeatedly cleared and burned for agriculture. The history of this disturbance is unfortunately obscure. The impact of agriculture on the woodland is only occasionally referred to in the historical record, and the record itself is understandably thin. What follows here is a brief summary of the evidence that is available. Particular attention is given not so much to the history of agriculture itself as to the way in which agricultural practises have affected the woodland.

The Island Arawak (1000 A.D.-1500 A.D.)

The first known inhabitants of the Bahamas were the Island Arawak. According to the available archaeological evidence, these people probably reached the islands about 1000 A.D., having left the South American mainland at about the time of Christ (Rouse, 1964; Hoffman, 1967; MacLaury, 1970). At the time of European contact, Arawakan-speaking peoples occupied a wide area, including Amazonia, Central America, and the Caribbean, and although detailed population figures are not known, it appears that a very large number of them, several million according to the Spanish accounts, were in the Greater Antilles, Turks and Caicos, and the Bahamas (Rouse, 1964).

The Arawak population of the Bahamas, or the Lucayas as the islands were called, was reported by Peter Martyr to be on the order of forty thousand (Craton, 1968: 39). If this estimate is correct, the number of people living on Cat Island must have been several thousand. Unfortunately, the Spanish accounts are not reliable on this point. What is certain is that less than thirty years after Columbus's landing the whole of the Arawak population had been transported to Hispaniola by Spanish slavers (Sauer, C.O., 1966; Craton, 1968).

The Island Arawak were skilled agriculturalists, with a long inventory of cultivated plants, including cassava, sweet potatoes, corn, beans, squashes, and tobacco (Sturtevant, 1961). They were also expert fishermen and obtained much of their food from the sea. They lived in settled villages ruled by hierarchies of chiefs, made good pottery, and had a relatively elaborate religion centering around the worship of deities known as Zemis (Rouse, 1964: 502).

Evidence of the former presence of the Arawaks is widespread on Cat Island. Pottery fragments and shell middens are commonly encountered, and in virtually every cave human bones have been found. Some reconnaissance archaeological work has been carried out (MacLaury, 1970), but the data uncovered tell little about Arawak subsistence or to what extent the woodland may have been cleared. The historical record is a more fruitful source of information here. Although Cat Island is rarely referred to specifically, it is possible to draw some general conclusions on the basis of accounts of Arawak populations in the Greater Antilles. The Arawak way of life was remarkably similar throughout the Bahamas and the Greater Antilles (Sauer, C.O., 1966).

It seems likely that the Arawaks practiced some form of shifting agriculture. The actual clearing of the woodland was probably done by fire as the thick accumulation of organic matter on the ground could have been easily burned during the dry season. Clearing of mature hardwood trees by felling or even girdling would have been difficult if not impossible for people equipped with only shell tools.

Arawak cultivation in the Greater Antilles involved planting in "conucos," mounds of earth surrounded by stones. After several years of cultivation fields were abandoned because of declining yields and competition from weeds. Just how much of the woodland was cleared in this way is not known. It would seem likely, however, that in five hundred years even a small population of shifting agriculturalists could have cleared a large part if not all of the woodland on a small island such as Cat. That this was in fact the case is suggested in a letter written by a loyalist who settled on Cat Island in 1784. He wrote that he had seen

> rocks piled up in little heaps by the Indians...and it plainly appears by this and other relics daily met with that the inhabitants have been very numerous, as there is none or but very little ground but what has been cleared and cultivated. Great quantities of their bones are to this day found in different cavities of the rocks (Eve, 1784).

There is an indirect suggestion in the historical record that the Arawak population of the islands at the time of contact was dangerously large. The Spanish accounts describe the Arawak as being close to starvation. Ferdinand Columbus, for example, noted that the amount a Spaniard would consume in a day would last the average Arawak a whole week (Craton, 1968: 24). In view of the crops the Arawaks had at their disposal there can be only two explanations for

this. Either the population was too large for the amount of cultivable land available, or there had been a recent crop failure due to a drought or hurricane.

Unfortunately Columbus's journal contains little information about Arawak agriculture or the vegetation of the islands. Apart from the Arawaks themselves, the Bahamas contained nothing of value to the Spanish and therefore received little attention. After the Arawaks had been taken to the mines of Hispaniola, the Bahamas were to remain uninhabited for nearly two hundred years. During this time the woodland presumably recovered to something like its natural state.

The English (1703-1834)

Although the English settled Eleuthera and New Providence in 1648 and 1666 respectively, Cat Island was at this time too vulnerable to attack from the French and Spanish to make permanent settlement worthwhile. In 1703, however, New Providence was attacked and 120 of the 150 inhabitants fled to Cat Island (Craton, 1968: 93). The exile was only a temporary one. In 1723 the Governor reported that "the people of Cat Island have lately quitted that remote place having been so often plundered and disturbed" (Phenney, 1723).

It was during this brief period of settlement that Cat Island's reputation as the best agricultural island in the Bahamas was established. In 1730 Governor Rogers reported that settlers without land on St. Christophers were keen to develop sugar plantations on Cat Island, which "all people in general agree is much the best of the Bahama Islands having large valleys of fine land and plenty of water" (Rogers, 1730). Seven years later settlers from Barbados, the Leewards, and the Virgin Islands were also expressing interest in obtaining land on Cat, whose reputation had increased further:

> Cat Island contains at least as much land fit
> to cultivate sugar cane upon as Barbados,
> besides a large quantity of ground fit to
> produce corn, cotton trees, indigo, ginger,
> and savannahs or low ground fit to raise and
> fatten cattle upon. The soil they say is
> much the same with that of Hispaniola or Cuba
> (Fitzwilliam, 1737).

In 1734 Thomas Coram petitioned the Commissioners for Trade and Plantations, advocating a settlement scheme involving Cat Island and Nova Scotia. He envisioned a trade

triangle in which the Bahamas, specifically Exuma, would provide salt for the cod fisheries in Nova Scotia. The set- tling of Cat Island would provide protection for the salt rakers from the Spaniards at Baracoa and "would otherwise be vastly advantageous to the crown" (Compston, 1918: 73). The Commissioners gave Coram every encouragement, but the settl- ment never took place, apparently because of the unsettled political situation in the Bahamas.

For the next sixty years the island was again virtually uninhabited. However, in 1783 settlement began in earnest. In that year the loyalists began to arrive to claim the land grants they had been promised in return for their support of the Crown during the American Revolutionary War. In total about two thousand loyalists came to the Bahamas from the former colonies, bringing with them nearly six thousand slaves (Dunmore, 1789). Of these about 60 loyalists and 500 slaves appear to have settled on Cat (McKinnen, 1804: 198). At this time Cat still had the reputation of being the best agricultural island in the Bahamas (Johnson, 1783), and most of the loyalists who settled on the island were experienced planters from the former colonies. Their main hope was to establish successful plantations based on cotton.

With few exceptions, the plantations were established on high ground overlooking the southern and eastern coasts. The blackland and flatland were regarded as the most produc- tive for cotton while the whiteland was used for food crops (Eve, 1784). Very quickly the woodland was cleared and large fields were planted in cotton. By 1788, 2000 acres had been planted on Cat, roughly a quarter of the total Bahamian acreage in cotton (Wylly, 1789). Initial yields were promising, but in 1788 and again in 1791 a large part of the crop was lost because of insect pests, specifically the chenille and red bug (Wylly, 1800). Clearing and plant- ing continued, but the planters were never able to recover their losses. Even before the Emancipation Act of 1834 the loyalists had left the island, leaving their slaves behind (Anonymous, 1840).

The impact of loyalist agriculture on the woodland can only be assessed in general terms. It is interesting to note, however, that the planters themselves attributed a large part of their failure to indiscriminate clearing. According to one contemporary account, the loyalists "went to work in the true American way, cleared immense fields, and laid their lands open to every wind" (Wylly, 1880). This "first and most fatal error" accelerated soil erosion and encouraged the spread of insect pests (Kelsall, 1800). Having learned from their mistakes, the planters later cleared smaller fields, but the damage had already been

done. As one Cat Island planter pointed out, by 1800 there
was little new land left to cultivate, and that which had
been "too much exhausted or burned" was slow to recover
(Eve, 1800). It seems clear that within the short period of
twenty years virtually the whole of the woodland had been
cleared. After the plantations were abandoned the woodland
must again have reasserted itself, but this time its
recovery was hindered by the activities of a now permanent
population of shifting agriculturalists, the abandoned
slaves.

The Free Negro (1834-Present)

The loyalists left behind 694 slaves and 55 free
negroes (Cameron, 1805), most of whom were given land or
allowed to farm the plantation lands on a share-cropping
basis. After the passing of the Emancipation Act in 1834,
some freed slaves bought land from the Crown in either 20-
or 40-acre lots, while others continued to rent or simply
occupied the land illegally as squatters. In the 1830s and
1840s settlements were established along the east coast of
the island. Some, such as Orange Creek and Bennets Harbour,
were located where small boats might anchor. For the rest
the availability of Crown Land seems to have been the most
important factor in determining their location.

Emancipation did not mean a sudden change in the way of
life of the Bahamian negroes, since most of them had been
largely independent for twenty or thirty years. According
to the report of a magistrate who visited Cat in the year
1836, all the freed slaves were quite satisfied with their
lot. Their only complaint was they had no means of sending
their surplus produce to Nassau (Stiles, 1836). Later
reports from the island seem to indicate that the free negro
population had become well-established. The old plantation
grounds were being kept as grazing land, and a small supply
of stock and corn was being shipped to Nassau (Anonymous,
1840). By this time (1840), the population was still only
750. Four years later the inhabitants of Cat Island, Rum
Cay, and Watlings were close to starvation. An unusually
long drought in that year led to the failure of crops and
had it not been for emergency supplies from Nassau the peo-
ple would have starved. According to Governor Mathew, the
famine was

> partly caused by the very unusual drought,
> partly by the improvidence of the people, and
> partly above all by the exhaustion of the
> scanty soil (Mathew, 1844).

The last point is significant insofar as it implies that a large part of the land had already been cleared. That this was the case is also suggested in the report of an Anglican missionary who visited the island in 1855:

> I found much difficulty in visiting the people. They are very much scattered with poor roads leading to their dwellings. They go out to their fields pretty early in the morning, which being far from their homes they do not return till sunset (Higgs, 1855).

This account suggests that all the accessible land had been already cultivated and that people were being forced to farm in remote areas of the island. A somewhat more optimistic view of life on Cat Island is given in the report of a government surveyor, Thomas Harvey. In his opinion Cat Island was by far the best agricultural island in the Bahamas, "the soil of the island is excellent and produces fine pineapples" (Harvey, 1858: 23).

The negro practice of clearing the woodland and then burning it was almost universally criticized by English and American visitors. A good example of this attitude is contained in Johnston's report on the agricultural capabilities of the islands. He visited Cat Island in September 1867 and reported:

> I was much pleased with my examination of the lands of the Poitier's estate; a portion of this tract is decidely the best land I saw in the out-islands. How this tract has escaped destruction so long I cannot conceive. But, alas! the work has begun in earnest. I saw very many patches recently cleared, burnt, and others burning, as I passed; cruel! cruel! (Johnston, 1867)

The gradual clearing of the woodland in part reflected the necessities of shifting agriculture but was also a response to the needs of a growing population. In 1861 the total number of people on Cat Island was 2,378, while only thirty years later the population had doubled to its highest total ever of just over 5,000 (Sharer, 1955: 92). Unfortunately, the historical record provides little insight into the state of the island at this time.

According to several of the older inhabitants interviewed on the island in 1970, the late nineteenth century was a time of considerable hardship. Not only had the attempt at sisal cultivation failed, but the population of

the island was too large to be supported by traditional agricultural methods. All the cultivable land had been cleared at least once and in many areas the fallow period was not long enough to allow an adequate recovery of fertility. The only alternative was emigration, and many of the islanders left Cat for Nassau or the United States. In certain parts of the island, particularly on level ground, the effects of this over-cropping can still be seen. In areas that have not been cultivated for half a century the woodland still has a degraded appearance.

During the present century the population has continued to decline. However, the practice of shifting agriculture has continued largely unchanged. An interesting commentary on conditions in the 1930s was given by the Harvard conchologist Clench (1938: 501-502). He reported that the unfortunate practice of burning the vegetation was resulting in the rapid disappearance of the soil, and predicted that within a few more generations there would be little or no agriculture possible. According to Clench, most of the woodland being cleared at that time was between 10 and 15 years old, and although the resulting fields were productive for only a year, they were usually farmed for two to five years after each burning. In spite of emigration the pressure of population on the land still appears to have been severe. That this was in fact the case was supported by the accounts of several older inhabitants interviewed on the island in 1970.

It has only been within the past twenty years or so that the intensity of shifting cultivation has declined. The development of the tourist industry in Nassau has led to further emigration from Cat and has meant a return flow of money and food to the island. As a result the acreage in cultivation has declined. Even so, shifting agriculture is still practiced in much the same way it has been for the last century and a half. As one farmer expressed it, "I work after the old peoples' dispensations, and I find myself walking in the right track."

Contemporary Agriculture

Agriculture today is probably less intensive than it has been at any time during the past hundred years. The total population in 1971 was about 3,000, most of whom were either older people or young children. Accurate statistics for acreage cultivated are not available, but a figure of four acres for a family of eight is probably a fair estimate.

The four acres would consist of five or six fields scattered across the island. One reason for this is that the chances of drought are lessened if fields are widely spaced; on a small island such as Cat, summer thundershowers can be very localized. Another important reason is that the different habitat- types are adapted to different crops. For example, the blackland, which is regarded as the best farming land is especially well-suited to sweet potatoes, cassava, peanuts, corn, benny seed, and beans. The flatland, at least in lower areas where moisture is available, is recognized as being especially good for tomatoes, melons, onions, and vegetables in general. Cultivation is, however, a precarious proposition here because of the risk of flooding. On the higher flatland areas the problem is drought, and corn and pigeon peas are the most common crops. The whiteland soils are easily worked but also tend to be droughty. Corn and sorghum were the main crops in 1970, although the latter is much less important that it formerly was. The localized areas of red soil are usually planted in pineapples, although cassava, pigeon peas, and peanuts may also be grown. The clay soil is usually too compact for sweet potatoes. The shallow potholes that are so common in certain flatland and blackland areas are commonly planted with bananas, pawpaws, yams, sugar cane, and eddoes. The variety of habitat-types is important insofar as it enables the farmer to diversify his crop combinations.

In any one year most farmers on the island cultivate two crops, a winter crop which is planted in May and June and harvested in December, and a summer crop which is planted in December and harvested in July and August. The winter crop is the most important in terms of yield, as the summer crop often fails because of droughts. A particular field is usually cultivated for two or three years and may therefore produce four or five crops before being abandoned.

The decision as to where to cultivate in any one habitat- type is usually made on the basis of what trees are present in the area. Poisonwood (Metopium toxiferum), pigeon plum (Coccoloba diversifolia), mastic (Mastichodendron foetidissimum), and horseflesh (Lysiloma leucoephala) are all regarded as an indication of good soil. On the other hand, wild tamarind (Lysiloma bahamensis), horsebush (Gundlachia corymobosa), and granny bush (Croton linearis) are all poor soil indicators. Also important is the age of the woodland. As a general rule, the older the trees, the more productive will be the soil after clearing and burning.

Clearing is done with a machete, usually during the cooler months from January to April. Apart from the question of fertility, people preferred to clear older trees

because they were more easily cut than younger bushy growth.
Most of the single women and older men hired professional
bush cutters to clear their fields. Fields cleared in this
way are distinctive in their regular, usually square, shape.
Fields are initially about a quarter of an acre in size, and
are expanded later if yields are good. If a field is a
large one, several shade trees will be spared. Character-
istically, these are mastic (<u>Mastichodendron foetidissimum</u>)
or kamalamay (<u>Bursera simaruba</u>). In nearly all fields
several trunks are left standing to provide support for the
vines. After clearing, the lighter brush is laid out on the
ground to dry, while the heavier trunks are pulled to the
side of the field, the reason for this being that the larger
pieces of wood burn at a high temperature and reduce the
fertility of the soil

Many local farmers take pride in their burning tech-
nique. The old tradition has long been criticized by Euro-
peans, but is apparently the best way to make nutrients
available to the crops. It removes debris, exposes the
soil, and has the advantage of killing crop-eating insect
larvae. Burning is usually done one or two days after rain
in May or June. If the ground is too dry, the burn will be
too hot and the productivity of the soil will be reduced.
One experienced farmer claimed that the severity of the burn
should be determined by the crop that is to be planted.
Sweet potatoes, for example, would benefit from a hot burn,
as they need more ash. Corn, on the other hand, needs a
lighter burn. A very hot burn was also thought to encourage
more weeds. On Cat Island, fires very rarely escaped from a
field into the uncleared woodland, because the living trees
are not dry enough to burn. The woodland is in fact a green
firebreak. The only situation in which a wild fire might
start would be where there was a great deal of dry litter on
the ground, as for example in an area of older woodland at
the end of a severe drought. Frequent clearing and burning
prevents the accumulation of litter and therefore reduces
the chances of wildfires.

A few days after a field has been burned, fertilizer is
added to the ashes. A few days after that, ideally just
after a rain, seeds and cuttings are planted. Planting is
done with the aid of a simple dibbling stick. As an
insurance against crop-eating insects and birds, especially
the ground dove, several seeds are dropped in each hole.
Nearly all farmers were aware of the advantages of seed
selection, but few thought it was worth the effort. For
most crops the time of planting is determined by the phases
of the moon. During the next few months weeding takes a
large part of the farmer's time. In the first year of cul-
tivation sprout-weeding is the main activity, while in the

second and third years the control of herbaceous weeds is more important. If there is no drought the winter crop is usually harvested in November or December. Yields are difficult to estimate because of the irregular methods of harvesting and widely-scattered fields. Most farmers, however, produce more than enough for their own needs and ship the surplus to Nassau.

At present a field is rarely cultivated for more than two or three years. The pressure on the land is so low that it is easier to clear a new field and start again than to farm intensively. According to local opinion, the minimum required fallow period for sustained yields is on the order of ten years. However, in recent years younger woodland has rarely been cleared, and the fallow period is normally at least fifteen years.

Conclusion

In conclusion, the three cultural groups, the Arawak, the loyalists, and the negro peasant farmers, have each had an important impact on the evergreen woodland. The consequences of Arawak settlement are unfortunately not well known, but historical evidence suggests they may have been significant. The loyalists in a period of less than twenty years cleared a large part, if not all, of the woodland. The negro population in a hundred and fifty years of shifting agriculture repeatedly cleared and burned the whole of the woodland. At present it is safe to say that all of the woodland has been cleared and burned at least once, and in the accessible areas it has been cleared and burned at least a dozen times. In this sense it is all secondary vegetation. What is not certain is just how the woodland has changed as a result of this clearing and burning, which species have become rare or extinct, and which have become more important.

VI. SELECTIVE CUTTING OF INDIVIDUAL SPECIES

Man's exploitation of individual species has had an important influence on the character of the woodland and indeed on the character of Bahamian vegetation as a whole. From the early part of the seventeenth century until the latter part of the nineteenth century the selective cutting of dyewoods, barks, and timber trees was an important activity in the Bahamas particularly during periods of econmic depression. So intensive was this exploitation that several sensitive species became rare. During the present century there has been a general decline in the demand for dyewoods, barks and native timber and many of the exploited species appear to have recovered. Fortunately, the history of selective cutting is more amenable to analysis than the history of clearing and burning. Usually the species involved can be definitely identified and in some cases there is reliable evidence as to their former distribution and abundance. Unfortunately, there are few specific refer- ences to Cat Island, and what follows therefore deals largely with the Bahamas as a whole.

Dyewoods

The most important of the native dywoods was brasiletto, a shrubby legume valued for the red dye obtained from its heartwood. Apparently three species were exported from the Bahamas under this trade name: Caesalpinia vesi- caria, C. bahamensis and C. reticulata. All three are small trees generally found on rather dry sites.[1]

Brasiletto was probably first cut by the Spanish in the sixteenth century (Craton, 1968: 58), although on what scale is not known. In the early seventeenth century English woodcutters from Bermuda were cutting Brasiletto in the Bahamas. The sailing orders for a trading voyage from Lon- don to Barbados in 1650 illustrate well the scope of these early activities. The captain was instructed to search the Bahamas for basiletto, seal oil, ambergris, and wreck goods and take what he found to Barbados or any of the Leewards from where it could be shipped to England. From Barbados he was to return to the Bahamas two, three, or even four times if necessary to make the enterprise profitable (Lefroy, 1877-79, II: 108).

1. The three names listed here are taken from the Baha- ma Flora (Britton and Millspaugh, 1920: 173).

In 1670 Simon Robinson, a Bermudan ship captain, reported to the Lords Proprietor.[2] that New Providence had only small quantities of brasiletto whereas "Egsuma had much brasiletto wood...and another island discovered last year also full of brasiletto wood" (Robinson, 1670: 473). According to another Bermudan (Carrell 1670: 475), Jamaica was at that time the chief port for the proceeds of "shalloping brasiletto, amber (Ambergris) and turtle shell". The effects of this early exploitation were quickly felt and by the 1670's the dyewood was in short supply. The Lords Proprietor were concerned about unlicensed cutting and in 1676 instructed Governor Chillingforth to prevent it (Albemarle, 1676). Catesby, who visited the islands in 1725, reported that the value of the wood had made it scarce, the biggest trees remaining not being more than 8 to 9 feet tall (1731,II: 51). By the time the loyalists arrived it was still being exported in considerable quantity (Schoepf, 1778:34). However, after the development of synthetic dyes in the 1870's and 1880's the demand for brasiletto declined, and by the end of the nineteenth century its export had virtually ceased (Coker, 1905: 201). On Cat Island in 1970 it was very seldom seen in the woodland.

Another valuable dyewood exported from the Bahamas was Logwood (Haematoxylum campechianum), although this species is not native to the islands. Bahamian woodcutters, cut it in Honduras in the late seventeenth and early eighteenth centuries and brought seeds back with them to plant at home. According to Catesby (1731, II: 65), it was introduced from the Bay of Honduras by a Mr. Spatches in 1722. Apparently it became quickly established locally as it was included by Bruce (1782: 422) in his list of valuable dyewoods growing in the Bahamas in the 1740's. However, when Schoepf (1788:35) visited the islands in 1784 it was not yet an important export. In the nineteenth century it was cut in large quantities on Exuma and to a lesser extent on Cat, New Providence, and Long Island. By 1880 it had become scarce and according to the Blue Book of that year the supply was virtually exhausted (Taylor, 1881: 55). At the end of the nineteenth century it was still being exported in considerable quantities to New York, the most important amounts coming from Andros, Exuma and Cat Island (Coker, 1905: 202). In 1970 there was still a demand for chipped logwood in London but the lack of any chipping machinery on the islands prevented its export.[3] On Cat Island in 1970 it was quite common in certain areas at the southern end of the island.

2. The first English settlement in the Bahamas was administered by a proprietary form of government.
3. Personal communication from Mr. Leonard A Roaker, a Bahamian agent for barks and dyewoods.

Another dyewood mentioned in the early accounts is yellow fustic, also known as yellow wood or satinwood. These names refer to Fagara flava a member of the citrus family. Yellow wood was initially cut as a dyewood but later became more important as a timber tree. Its fine grain made it the most valuable of all the woods exported from the island in the late nineteenth century. Again its value led to its being over-exploited and by the 1880 the supply had been largely exhausted (Taylor, 1881: 55). Yellow wood is certainly a rare species on Cat Island at present. Of all the valuable woods this is probably the most sensitive to cutting.

In 1723 the Governor reported that "Brown ebony of a strong rhodium scent" was being exported from the colony (Phenney, 1723: 54). The species referred to here is probably Dalbergia ecastophyllum, which today does not grow in the Bahamas. Theoretically this is a species that could have become extinct because of over-cutting. However, it is rarely mentioned in the accounts of the islands and on the basis of the available evidence it seems unlikely that ever grew on Cat Island.

There is a puzzling note in Governor Montfort Browne's report on the state of the islands in 1775. According to Browne (1775: 1), green ebony and bark were being exported to Britain. The trade name green ebony usually refers to the leguminous tree Brya ebenus, which is native to Jamaica and Cuba but not the Bahamas (Britton and Millspaugh, 1920: 196). Again the possibility exists that it was exploited to the point of extinction, although it seems more likely the Governor was referring to the re-export of wood imported from Jamaica.

Barks

Sweetwood bark (Croton eluteria) has long been an established Bahamian export. Its uses have been varied, although it seems to have been most important as a basic ingredient in tonic waters. Exploitation probably began in the seventeenth century. According to Stisser it was exported to England as a smoking mixture in 1686 (cited by Bacot 1869: 3). Catesby reported that it was common on most of the islands, although cutting had reduced the size of the trees. He described it as a fine aromatic bitter to be infused with wine or water (1731,II: 46). Throughout the eighteenth and nineteenth centuries sweetwood bark was exported on a fairly regular basis, although what statistics there are suggest cutting was especially important during times of economic difficulty. The preparation of the bark

is a rather time consuming operation and is only worthwhile
when money is in short supply.

By the end of the nineteenth century supplies were
"steadly diminishing" (Morris, 1896). And in the Bahama
Flora it is described as "Becoming scarce" (Britton and
Millspaugh, 1920: 223). In recent years the demand for the
bark has increased and in 1970 it was being actively cut on
Cat Island. A total of about 20 tons were exported from the
Bahamas in 1970, of which about a third came from Cat and
the rest from Acklins. Sweetwood bark reproduces vigorously
from sprouts and although it is not a common tree in the
woodland it seems unlikely that its importance has been sig-
nificantly reduced by cutting. The early accounts of it
having become rare may simpyly refer to a declime in the
size and yield of individual trees rather than an actual
reduction in range. On Cat Island there has been some small
scale cultivation of sweetwood bark and many families have a
"Bark field" close to their homes.

Another tree that has been cut for its bark is wild
cinnamon (Canella alba). Like sweetwood bark it was one of
the earliest Bahamaian exports and may in fact have been
exploited by the Spanish. However, unlike the sweetwood
bark, the demand for wild cinnamon was never very high and
it was exported only on a small scale (Coker, 1905: 206).
At present wild cinnamon is a very rare species on Cat
Island. Apparently it has been less able than the sweetwood
bark to recover from the effects of cutting. At one time it
was thought that Cinchona was native to the islands. Gover-
nor Phenny (1724: 55) reported that "the Spanish have told
several people that the Jesuit's bark abounds. But it has
not been found for want of a curious enquirer." Quite
likely the species referred to here was princewood (Exostema
caribaeum), a close reative to Cinchona and a common small
tree in the woodland. Princewood apparently was never cut
for its bark on a commercial scale, although it is used in
local medicine as febrifuge.

Timber Trees

Generally speaking, Bahamian timber has been protected
by its naturally small size and comparatively few species
have been cut for export. The most important of those that
have is mahogany (Swietenia mahagoni) Although widely intro-
duced elsewhere in the West Indies, mahagony is native to
the Bahamas. There is no record of its introduction and it
appears quite at home in the woodland. According to Catesby
it was the most valuable timber tree in the islands, being
better than oak for shipbuilding because it resisted shot

without splintering (1731, II: 81). The historical record indicates that it was extensively cut in the early eighteenth century. Governor Rogers (1730) reported that "one of the best employments the inhabitants have had of late is sawing mahogany and Madera plank to ship to Europe." At the end of the eighteenth century it was still the most important timber tree although it had become rare on New Providence and neighboring islands due to over-cutting. The demand for Bahamian mahogany declined,in the nineteenth century, presumably because of the small size of individual trees.

During the course of the present study, mahogany was occasionally seen on Cat Island, particularly in the more remote areas. It was also seen in the settlements where it has been planted on a small scale. Its bark is valued in local medicine and most trees are characteristically scarred as a result.

Horseflesh (Lysiloma leucocephala), a tall leguminous tree, has also been exported under the trade name mahogany. According to Catesby (1731, II: 42), it was the second most valuable tree in the Bahamas after Swietenia. Like the true mahogany, its export declined in the nineteenth century although it was still being exported in "considerable quantities at the beginning of the present century" (Coker, 1905: 202). Cutting has made it a rare tree on Cat Island, as it was very infrequently seen in 1970.

Lignum vitae (Guiacum sanctum, G. officinale), whose resinous gum was thought to provide a cure for syphilis, was probably first cut in the sixteenth century by the Spanish. The early English accounts boast of its presence and its exploitation appears to have continued throughout the seventeenth and eighteenth centuries. The hard wearing properties of the wood made it one of the most valuable of Bahamian timber trees. In the nineteenth century the demand for it also declined because of its small size (Coker, 1905: 203). As in the case of horseflesh, cutting has made lignum vitae a rare tree on Cat Island. It was seen growing wild only in areas remote from the settlements. On the other hand, it has been planted on a limited scale as an ornamental.

A number of other native species have been cut for timber, although not on the same scale as those mentioned above. These include: ironwood (Krugiodendrom ferreum), boxwood (Buxus bahamensis), mastic (Sideroxylon foetidissimum), and princewood (Exostema caribaeum). With the exception of princewood, all were comparatively rare on Cat Island in 1970. The posssibility exists that they were

always rare, but the fact that they are more commonly encountered in the more remote areas of the woodland suggests that selective cutting has reduced their importance.

Local Exploitation

The exploitation of native plants for local usage has long been an important part of Bahamian life. Furthermore, virtually every species in the woodland is recognized as being useful for some purpose. In the discussion that follows only those species whose importance in the woodland has been changed by exploitation are considered.

Several native fruits are gathered locally, most notably the sea grape (Coccoloba uvifera) and cocoa plum (Chrysobalanus icaco). Both are important on the whiteland and may have had their distribution patterns modified by accidental dropping of the fruits. Certainly the sea grape is commonly seen growing along the footpaths across the island although rarely in the woodland itself. The same "footpath" distribution is characteristic of the pondtop (Sabal palmetto) whose fruits are collected for hog feed. As was mentioned earlier fruits accidentally dropped in this way have produced an avenue of palmettoes through the McQueens savannah (Figure 14). The hog cabbage palmetto (Pseudophoenix vinifera) has been even more drastically affected by man's activities. Both its fruits and terminal buds have been collected for hog feed, and as a result it is now seen only in remote parts of the island. On the positive side, it has been occasionally planted as an ornamental.

In recent years, houses have been built with imported pine, although in the past they were entirely built with local wood. For support posts and beams hardwoods such as dollen plum (Reynosia septentrionalis), mastic (Sideroxylon foetidissimum), maderia (Swietenia mahogani), horseflesh (Lysiloma leucocephala), or cassada wood (Dipholis salicifolia) were used. For the more flexible cross-beams wattle (Eugenia spp.) or red mangrove (Rhizophora mangle) were preferred. Thatching would be done with the leaves of the Buffalo top Thrinax microcarpa). The traditional methods of thatching are African in origin. Only a few men in each settlement know the techniques and very likely they will soon be lost. Small fishing boats are still built locally, usually with horseflesh or mastic or if these are not available with wild locust (Lysiloma bahamensis).

The cutting of wood for fuel has probably reduced the local importance of several species. Buttonwood (Conocarpus

erecta) is generally regarded as the best firewood, while black torch (Erithalis fruticosa), dollen plum (Reynosia septentrionalis), and white torch (Amyris elemifera) are also used.

A great many native species are used in bush medicine, although it seems unlikely that many have become rare because of it. Two that might have been over-exploited are the boarhog bush (Callicarpa hitchcockii) and manroot (Vallesia antillana). Both are ingredients in popular aphrodisiacs and are rarely seen in the woodland around the settlements.

In summary, it seems clear that a great number of woodland species have been cut for either export or local use. This exploitation began in the sixteenth century and continued with varying degrees of intensity until the present. Although some cutting has always been done locally much of the activity appears to have been based in Nassau. As Schoepf pointed out in 1784, the white inhabitants of New Providence employed their slaves cutting wood wherever it could be found:

> Wood-cutting is gradually becoming more difficult and less lucarative. On the islands lying next to Providence the best wood is always cut off, and thus there must be recourse to islands lying farther away, or the woods must be more deeply gone into (Schoepf, 1778: 34).

On Cat in 1836 it was thought necessary to have a man on guard in the north eastern part of the island to prevent Eleuthera men from cutting wood (Stiles, 1836). Even so by the middle of the nineteenth century the more accessible timber appears to have been taken. The surveyor Harvey, who visited the island in 1855, reported that:

> The timber on St. Salvador (Cat) is fine and large and might be made a profitable branch of commerce; maderia, mahogany, cassada, princewood and braziletta, yellow wood and lignum vitae are found in every part but in greatest abundance on the east side (Harvey, 1858: 78).

In other words, the valuable timber was already depleted on the west side of the island that is in the areas close to the settlements. The exploitation of dyewoods and valuable timbers appears to have declined in the second half of the nineteenth century. Exploitation for local use has continued, but even here the pressure has eased because of the import of cheap pine from Nassau.

As might have been expected, the species that have been selectively cut have varied in their capacity to recover. Some like lignum vitae (Guaiacum sanctum), wild cinnamon (Canella alba), and yellow wood (Fagara flava) are still rare even though they have not been cut on any scale since the nineteenth century. Other species, such as sweetwood bark (Croton eluteria) and logwood (Haematoxylum campechianum), have recovered comparatively quickly. The differences here are probably due to inherent differences in reproductive capacities and habitat tolerances. What is surprising is that for the Bahamas as a whole not one economically valuable species is known to have become extinct. Even though the pre-settlement composition of the woodland is not known there is no evidence to suggest that any species has been exploited to the point of extinction. The species involved have in fact proved remarkably resilient.

VII. THE INTRODUCTION OF ALIEN PLANTS AND ANIMALS

The Bahamas have not been isolated from the large-scale interchange of plants and animals that has characterized the tropical world during the last five hundred years. In spite of their late settlement by Europeans and the persistent failure of commercial agriculture, a great number of plants and animals have been introduced to the islands. Unfortunately, most of these introductions are undocumented, particularly for remote out-islands such as Cat. What follows therefore is a general review which deals for the most part with the Bahamas as a whole. The discussion of plants is limited to those woody species capable of establishing themselves spontaneously within the woodland. Except where stated, the alien status of the species discussed is well established either by documentary evidence or by the artificial nature of their distribution. The only animals considered are those that have had some impact on the composition of the woodland.

Introduced Plants

It seems likely that the Arawaks brought several species of fruit trees to the Bahamas. The guava (Psidium guajava), sugar apple Annona squamosa), custard apple (A. reticulata), dilly (Manilkara zapota), and hog plum (Spondias mombin) were all cultivated in pre-Columbian times in the West Indies (Roumain, 1942). Each species is capable of spreading from cultivation, although to what extent any of them actually did is not known. Perhaps significantly the early English accounts make no mention of any "wild" fruit trees.

The question is complicated by the fact that in the seventeenth and eighteenth centuries all the Arawak fruit trees were reintroduced as were several other New World species such as the avocado (Persea americana), genip (Melicoccus bijugatus), pawpaw (Carica papaya), and cashew nut (Anacardium occidentale). At the same time, the tamarind (Tamarindus indica), Indian Almond (Terminalia catappa), pomegranate (Punica granatum), and mango (Mangifera indica) were introduced from the Old World. Commercially the most important Old World introductions were species of citrus. The most valuable Bahamian exports in the early eighteenth century were limes (Citrus aurantium), lemons (C. limon), oranges (C. sinensis), and sours (C. aurantium). They were exported to North America together with dyewoods, timber, and medicinal barks (Catesby, 1731, I: xxxviii).

To what extent any of the citrus were able to become naturalized is not indicated in the historical record, although by analogy with what had happened in other parts of the West Indies it would seem likely that some escaped from cultivation. Harris (1965: 93) has emphasized the rapidity with which the lime and bitter orange spread spontaneously in the West Indies. According to Howard (1950: 345), Citrus aurantium has become established spontaneously on Bimini, in the north western Bahamas. On Cat Island, citrus were extensively planted in the 1850s (Harvey, 1858: 76); however, no feral trees were seen in the woodland in 1970.

In 1783 a plan was formulated to establish a botanical garden in the Bahamas, with one of its proposed purposes being to test plants from the South Seas (Pownall, 1783). A shipment of live plants and seeds was sent to the Bahamas in 1799 from the botanical garden at St. Vincent (Anderson, 1802: 45). Four important fruit trees included were the Indian Almond (Terminalia catappa), the mango (Mangifera indica), the otaheite gooseberry (Phyllanthus distichus). and the bread-fruit (Arctocarpus communis). All four were successfully established in private gardens and may, with the exception of the breadfruit, have escaped locally. In the nineteenth and present centuries, the development of private gardens, particularly in Nassau, led to the introduction of literally hundreds of new species and varieties of fruit trees. However, there is little indication that any of them have been able to become established as part of the wild vegetation.

In contrast to the fruit trees, few ornamentals appear to have been introduced before the eighteenth century. Catesby, who visited several islands during his stay in the Bahamas (1725-1726), included only two introduced ornamentals in his Natural History, the red frangipani (Plumiera rubra) and the coral tree (Erythrina corallodendrum). Neither species is capable of spreading spontaneously.

The naturalist Schoepf, who visited the Bahamas in 1784, described a large silk cotton tree (Ceiba pentandra) in Nassau which presumably had been planted there early in the eighteenth century (Schoepf, 1788: 37). According to Gardner and Brace (1889: 369), this tree had originally been introduced from South Carolina and was the source of all the other silk cotton trees on New Providence. The species is included in the Bahamas Flora where it is reported as being "spontaneous after cultivation" (Britton and Millspaugh, 1920: 275). There is a large silk cotton tree at the Bight settlement on Cat Island. However, it shows no evidence of successful regeneration.

Other ornamentals mentioned by Schoepf which may have become locally naturalized are the sand box tree (Hura crepitans) and "Barbados Pride" (Poiniana pulcherrima). According to Gardner and Brace (1889: 376), the latter was introduced to New Providence in 1886 by a Mr. Sanders. This must have been a late reintroduction. Neither species was seen on Cat Island during the present study.

During the nineteenth century a great many ornamentals were introduced to private gardens, but comparatively few appear to have spread spontaneously. Exceptions have been the poinciana (Delonix regia), the Australian pine (Casuarina equisetifolia), Jerusalem thorn (Parkinsonia aculeata), Spanish bayonet (Yucca aloifolia), and the cactus-like Euphorbia lactea. All of these are included in the Bahama Flora and all were observed to have spread locally on Cat Island.

In the present century the development of landscape gardening has meant a further increase in the introduction of ornamentals. However, few if any are adapted to life in the woodland and consequently their story is not relevant to the present study.

Cotton is one of the few aliens known with certainty to have been introduced by the Arawaks. According to the early Spanish accounts, it was cultivated in the Bahamas on a considerable scale (Craton, 1968: 25). Which species was involved is not certain, as both Gossypium barbadense and G. hirsutum were cultivated in the West Indies (Sauer, C.O., 1950: 535). Cotton presumably persisted after the islands were depopulated but for how long is not known. There is no mention of wild cotton in the early English accounts.

As indicated earlier, cotton was cultivated on a small scale in the early eighteenth century, extensively in the late eighteenth century, and again on a small scale in the nineteenth century. On Cat Island it has probably not been cultivated since the American Civil War. In 1970 individual bushes were occasionally seen in the woodland. Sea island cotton (Gossypium barbadense) is weedy and has been able to persist on a small scale in disturbed sites.

Sisal (Agave sisalina) was introduced to the Bahamas from Yucatan in 1845 (Morris, 1896: 4). After a rather slow start as a commercial crop, it was widely planted throughout the islands in the years 1887-1896. However, the productive life of the plant proved to be shorter than expected, and cultivation ceased. Since then it has been planted locally on a small scale and has proved remarkably persistent in the wild.

Bowstring hemp (_Sansevieria thyrisiflora_) was intro-
duced to the Bahamas in the nineteenth century (Dyer, 1887).
It was planted commercially on Cat Island in the 1940s,
although like sisal it was not a commercial success. In
1970 it formed a thick carpet under second- growth woodland
in the Orange Creek area, where it had formerly been cul-
tivated. Presumably it will eventually be shaded out, but
is currently slowing down the regeneration of the native
species.

The "indigo weed" (_Indigofera suffruticosa_) was being
cultivated on New Providence as early as 1698 (Craton, 1968:
89), and may even have been introduced in Arawak times. It
is now widely distributed throughout the archipelago and was
seen occasionally in weedy sites on Cat Island in 1970. The
old-world indigo (_Indigo tinctoria_) was introduced in the
late eighteenth century but did not grow well in the Bahamas
(Brown, 1802: 27).

As was indicated earlier, logwood (_Haematoxylum cam-
pechianum_) was introduced to the Bahamas in 1722 from Hon-
duras. Since then it has spread widely around the islands
and has locally become important in the woodland. Another
leguminous tree that was probably introduced in the
eighteenth century is the sweet acacia (_Acacia farnesiana_).
Catesby (1731, II: 45),includes a plate of what appears to
be this species in his _Natural History_. Its original home
is not known with certainty, although it has been accepted
as native in Cuba (Little and Wadsworth, 1964:144). Its
spines make it a valuable hedge plant and probably because
of this it has been widely distributed throughout the Baha-
mas. On Cat Island it was occasionally observed in dis-
turbed habitats such as roadsides.

The divi-divi tree (_Caesalpinia coriaria_) was intro-
duced into the Bahamas in the early part of the nineteenth
century in the hope of exporting its pods for tanning (Ham-
ilton, 1836). Apparently the demand was not strong enough
to justify large- scale planting, and the tree was never
taken to the Out Islands. According to Britton and
Millspaugh (1920: 174), it has spread locally from cultiva-
tion on New Providence.

Several species were introduced in the eighteenth cen-
tury as fodder crops. The most important of these was Jum-
bay (_Leucaena leucocephala_ a leguminous shrub from Central
America. _Leucaena_ has been widely planted throughout the
archipelago, and is probably the most invasive of all the
introduced trees or shrubs. Also valued as a source of
fodder in the eighteenth century was the horseradish tree
(_Moringa oleifera_). It had been introduced to Jamaica from

the coast of Guinea in the seventeenth century (Edwards, 1819, I:481), and may have been brought from there to the Bahamas. The loyalists used it as fodder for sheep (Brown, 1802: 11). At present it is occasionally seen as an ornamental on Cat Island and is locally spontaneous.

Also used by the loyalists for fodder were _Sesbania grandiflora_ and the "Pride of India" (_Melia azaderach_). Both of these old-world species have spread spontaneously. The latter has been planted as an ornamental and is occasionally seen in the settlements on Cat Island.

Although the historical record is far from complete, it does indicate that very few aliens become firmly established as part of the wild vegetation. In spite of the fact that a considerable number of plants have been introduced to the Bahamas during the past three hundred years, comparatively few have been able to spread very far without man's help. Daniel McKinnen aptly described the situation in 1803:

> The exotics which are introduced seem feebly and
> unsuccessfully to struggle with cold winds; the
> droughts, and unfriendly seasons; while a crop of
> hereditary and worthless weeds take possession of
> the soil prepared for cultivation, and extract all
> its nourishment to administer fertility, as they
> decay, to the native and unprofitable forest trees
> succeeding them, the elemi, silver-leaved palmet-
> tos, and hungry aborigines of the rocks (McKinnen,
> 1806: 351).

Just why this should be so, in contrast to the West Indies, where aliens covered extensive areas at very early dates (Harris, 1965: 113), is not immediately apparent. The question will be raised again later when the quantitative importance of aliens in Cat Island woodland is discussed.

Domesticated Animals

The introduction of alien animals has often brought about far-reaching changes in the vegetation of oceanic islands and this has certainly been the case in the Bahamas. Goats, horses, sheep, cattle, and hogs have all had an impact on the wild vegetation of the islands, especially in the areas close to the settlements.

Whether or not the Spanish stocked the island with livestock is not known. When the loyalists arrived on Cat Island in the 1780s they found plenty of wild hogs, although no mention is made of any other animals (Eve, O., 1784).

Presumably the hogs brought about changes in the woodland, although just what these were is difficult to assess. Very likely the wild population was eliminated by hunting in the nineteenth century. Domesticated hogs have had an indirect impact on the woodland through the gathering of hog feed. The native hog cabbage palm (Pseudophoenix vinifera) has become rare because of this pressure. In 1970 most families had at least one hog in their yards. They are, however, penned and fed largely on household scraps.

During the loyalist period Cat Island had the reputation of being one of the better islands in the Bahamas for the raising of livestock. According to one source (Powles, 1888:234), thousands of head of cattle were raised on the island at this time. After Emancipation cattle were still raised, although not in the same numbers as before (Underhill, 1862: 480). In recent years the Bahamian government has made a concerted effort to develop livestock farming. Pastures were established in several settlements (Arthurstown, The Bluff, The Bight) and planted with African grasses.[1] Unfortunately the scheme has had little success.

The woodland was cleared with a bulldozer and the limestone surface hardened on exposure to the atmosphere and as a result even the drought-resistant African grasses have scarcely been able to survive.

In spite of reports of large cattle herds during loyalist times, it seems unlikely that livestock farming was ever much of a success. During the dry season the native grasses dry out and there is a general scarcity of forage. Furthermore, the broken, potholed nature of the limestone is dangerous for livestock. In 1970 only one herd of cattle was seen on the island, and this was being pastured on the whiteland near The Bluff settlement.

Horses were apparently numerous on the island during loyalist times. One Cat Island planter even imported thoroughbred stallions from England (Stark, 1891: 149). The horse population declined in the late nineteenth century, although horses continued to provide the main means of transportation on the island until automobiles arrived comparatively recently. It is doubtful whether any of the loyalist thoroughbred stock made any contribution to the present population of horses on the island. Cat island horses in

1. Three species were tested for use in the pastures: Rhodes grass (Chloris gayana), pangola grass (Digitaria decumbens), and star grass (Leptochloa plechtostachya). Three others were planted as possible fodder crops: elephant grass (Pennisetum purpureum), para grass (Panicum muticum), and Johnson grass (Sorghum halepense).

1970 were generally small and lean and had the distinct appearance of being both underfed and overworked. Both horses and cattle are mainly pastured on the whiteland where they feed on grasses and herbaceous weeds. Their main influence at present is to slow down the recovery of shrubs and trees.

Sheep were also introduced by the loyalists and were at one time quite numerous, especially at the southern end of the island. Grazing by sheep is of more interest to the present study in that it directly affects the woodland. Sheep, more so than cattle or horses, are content to browse. In the dry season when no grass is available they will eat the leaves of shrubs such a jumbay (Leucaena leucocephala ramshorn (Pithecellobium keyense) and pigeon berry (Rhacoma crossopetalum). This browsing has had a selective effect on the composition of the woodland.

The pasturing of sheep also affects the woodland in other ways. Some farmers will scatter grass seeds and jumbay before abandoning a field. When the last crop has been harvested, the field will be turned over to sheep. Grass seeds are cycled through the sheep's gut, and a thick growth of grass results. This means that soil development is accelerated but the recovery of the woody vegetation is retarded. In 1970 such effects were very localized on Cat Island, as only a few small herds of sheep were being raised. They are a white short-haired breed without horns.

Only the goat has had a really significant impact on the woodland. Unlike the other domesticates, the goat is content to browse at all times of the year. In 1970 the goat was the most numerous domesticate on the island, the total population amounting to several thousand. Cat Island goats are mostly coarse-haired, black or brown animals with short horns that curve over backwards. In recent years attempts have been made to upgrade the quality of the local breed with American stock.

This review of the history of plant and animal introductions does not entirely support the idea that alien species have a competitive advantage over insular species. Certainly as far as plants are concerned, few aliens have become well-established. On the other hand, domesticated animals have at various times been numerous on the island, and may in some cases have had a significant impact on the woodland. The nature of this impact is considered more closely in the section dealing with areal variation in the composition of the woodland.

VIII.   METHODS OF ANALYSIS

Unfortunately, the historical record provides only a very qualitative indication of the extent to which the vegetation of Cat Island has been modified by man.   It shows that for a period of at least a thousand years the woodland has been discontinuously cleared, burned, browsed, and selectively cut, but it does not show what the detailed consequences of these activities were. With this deficiency in mind it was decided to analyse the composition of the present woodland in such a way as to show in quantitative terms the extent to which it has been changed by man. More specifically the following questions were considered:

1.   What are the detailed consequences of clearing and burning?   How long does it take the woodland to recover? What species are involved and when do they become established?

2.   To what extent has the woodland been changed by selective pressures such as grazing, cutting, and the use of fire? Which species have become less important as a result of these pressures? Which have become more important?

3.   To what extent have alien plants been able to invade the woodland? Are they only a temporary feature of the vegetation or have they become permanently established?

Field Methods

Fortunately, it was possible to spend three field sessions on Cat Island: July to October 1967, June to August 1968, and June to August 1970.   In addition short visits were made to three other Bahamian islands--Bimini, Mayaguana, and New Providence. Basically the field work consisted of plant collection and identification, interviews, and vegetation analysis.

Plant Collection and Identification

The Bahamian woodland is typically tropical in that two individuals of the same species are rarely seen together. This, together with the physiognomic similarity of so many species, made the taxonomic problem a difficult one in the early stages of the study. A large part of the first field season was therefore devoted to the collection of plant specimens. In total some 600 collections were made, not counting duplicates (Appendix I). As far as possible all

the species encountered were collected. In the case of difficult genera, such as <u>Pithecellobium</u>, <u>Eugenia</u>, <u>Cassia</u>, <u>Coccoloba</u>, and <u>Lantana</u>, several collections of each species were made.

Provisional identifications were made in the field with the use of the keys in Britton and Millspaugh (1920) and Little and Wadsworth (1964). Local names provided useful if not always reliable clues as to the identity of many species. A nearly complete set of the plants collected was later sent to Dr. R.A. Howard of the Arnold Arboretum, and his determinations are the ones used in the present text.

Local Interviews

Because of the length of time spent in the field it was possible to develop close personal contacts with many of the local inhabitants, particularly in the settlements at the north end of the island. This in turn made it possible to gather a great deal of information relating to shifting agriculture, grazing, and the selective exploitation of woodland species.

Interviews were usually carried out on an informal basis without the use of any set questionnaire. A complicating factor here was the custom whereby the person interviewed usually provided the answers he or she thought were expected. This problem was avoided by not asking leading questions and by checking the reliability of the informant with questions the answers to which were already known. The older people were generally more knowledgeable since they had spent all their lives farming on the island. As far as the recent history of shifting agriculture was concerned, they were the only source of information. In general, Cat Islanders were both willing and knowledgeable informants. Furthermore, the information they provided was indispensable to the study as a whole.

Vegetation Analysis

Ultimately the success of this type of study depends on the ability of the investigator to accurately identify plants in the field. As was indicated above, the taxonomic problem was initially a difficult one; apart from a few weeds and aquatics, the Bahamian flora is very different from that of mid-latitude areas. Eventually, however, after walking through literally hundreds of miles of woodland and collecting every unknown, it became possible to identify on sight the vast majority of the species encountered. Once the flora was well-known it was possible to set up a sampling procedure that could be applied to the woodland as a whole.

In 1970 a sampling method was devised that would not only give answers to the questions posed above but would also provide a base-line against which further change could be assessed. Three hundred sampling sites were selected in different parts of the woodland, and since the entire woodland had been cultivated at one time or another, each sample site was in effect an abandoned field. The two criteria for selection were that the site could be accurately located on the available aerial photograph coverage[1] and that the vegetation appeared to be, or was known to be, of a uniform age.

The actual data collected consisted of a visual estimate of the cover within 25 x 1 meter quadrats in each field. Only woody species or succulents with a minimum cover of at least one quarter of a square meter in each quadrat were included. Herbs were omitted because of the marked seasonality of their occurrence and because a new sampling method would have been needed to deal with them adequately. In younger fields the quadrats were laid out in the form of a cross centered in the middle of the field. In the older fields, or in fields difficult to penetrate, a 25 meter belt transect was run as far into the field as possible. Measurements were made with a meter stick and a measured length of rope. The cover data were dictated into a portable tape recorder and later transcribed onto data sheets (Appendix III). For convenience each species encountered was given a code number. 120 species were encountered in the 300 fields sampled (Appendix I).

Once a field had been sampled it was given a number and classified on the basis of the following characteristics: (1) age since abandonment, (2) habitat-type, (3) height of vegetation, (4) soil-type, (5) moisture characteristics, and (6) distance from the nearest settlement. Finally, its location on the 1958 aerial photographs was fixed by means of a six-figure cross reference. Not all of the distinctions made above proved to be relevant to the present study, but the way in which they were established is as follows:

Age since abandonment. As can be seen from Figure 16, the woodland is in fact a patchwork of fields in different stages of recovery following clearing and burning. It was soon recognized that any analysis, if it were to be meaningful, would have to allow for these age differences. The age of the woodland was determined in two ways: local information on the history of land use, and tonal appearance on

1. Good quality stereoscopic coverage was available for the island at a scale of 1:12,500. The photographs were taken in 1958 by Spartan Aviation Services on contract to the Bahamian Government.

aerial photographs.

Local informants could usually provide a reasonably accurate age for fields abandoned less than 12 years ago, although beyond that memories were vague. For older abandoned fields the 1958 aerial photographs provided further clues as to age. Generally speaking, the older the woodland the darker its appearance on the aerial photographs. The reasons for this are basically twofold: (1) reflection from the limestone surface is reduced as succession takes place, and (2) pioneer species have generally lighter-colored leaves than the shade-tolerant species that replace them. This meant then that tonal differences on the aerial photographs provided a good indication the relative age of the woodland in the areas sampled, and by determining whether the area was white, light grey, dark grey or black, an approximate age-sequence was established.

Habitat type. As was indicated earlier, there is a variability in the woodland which reflects underlying differences in surface characteristics. To minimize the effects of this variability it was decided to classify the woodland on the basis of land surface or habitat characteristics. Initially all five basic landform types were used:

1. Holocene Dunes and Beach Ridges.
2. Young Pleistocene Marine Plains.
3. Young Pleistocene Dunes and Beach Ridges.
4. Old Pleistocene Marine Plains.
5. Old Pleistocene Dunes and Beach Ridges.

After analysis of the data collected, it became clear that habitat-types 2 and 4 could be combined, as also could 3 and 5. As far as the floristic composition was concerned the differences in each case did not appear to be significant. Furthermore, a low sample coverage in habitat type 4 limited its usefulness. The final breakdown therefore involved just three habitat-types:

1. Holocene Dunes and Beach Ridges.
2. Pleistocene Marine Plains.
3. Pleistocene Dunes and Beach Ridges.

In terms of local names these habitat-types are equivalent to the whiteland, flatland, and blackland respectively. In classifying the woodland indirectly by means of surface characteristics, the arbitrary problem classifying vegetation itself was avoided. Furthermore, a coherent framework was provided within which the processes of change could be analysed.

Height of vegetation. For each abandoned field sampled the average height of the vegetation was measured and recorded to the nearest meter. In most cases this was a meaningful figure, as the vegetation sampled was of a more or less uniform height. In the younger fields, sprouts which would characteristically project above the seedling-bushes by a meter or so were not included in the average.

Soil-type. Each sample site was classified as to whether the soil was white, black, or red. The main reason for making this distinction, in addition to that of habitat-type, was that the red soils are present in more than one habitat-type. Although they are mainly found in the flatland areas, they are also characteristic of the older Pleistocene dune ridges. However, the red soil areas are localized on the island and because of this only 34 red soil fields were sampled. Because of the small size of the total sample and because there was no indication that differences in soil type had any affect on the composition of the vegetation it was decided not to use the red soil fields as an independent unit. The white soils are simply equivalent to the whiteland habitat and the black soils to those Pleistocene surfaces without red soils.

Moisture class. Within the woodland there are differences that are independent of either soil or surface characteristics and are primarily due to differences in drainage conditions or exposure. In some areas, as for example on the leeward side of the Pleistocene dune ridges, the land surface is steep and any rain that does fall is quickly lost as run-off. Such areas are naturally droughty. Similarly, low-lying areas where the fresh-water lens is thin or non-existent are also droughty. The same is true of areas exposed to the full force of the trade winds; evapotranspiration rates are high and the trees are consequently stunted and slow-growing. On the other hand, in some low-lying areas, close to the seasonally-flooded savannas, the woodland is occasionally flooded.

In order to accommodate these differences, a three-fold classification was set up: xeric for droughty fields, hydric for seasonally-flooded fields, and mesic for intermediate fields. As it happened, only 15 xeric and 15 hydric fields were sampled, and visual inspection of their cover data suggested their floristic composition was not significantly different from the rest. Consequently these distinctions were ignored in the later analysis.

Distance index. Until recently few people on Cat Island had motor cars and even now most farmers walk to and from their fields along rocky footpaths. There is only one

road on the island and this joins the settlements along the western and southern coasts. For most of its length it is not surfaced, and travelling from one end of the island to the other is a major undertaking, so much so that people from the northern end rarely if ever visit the southern end and vice versa. All of this emphasizes the fact that the frictional effect of distance is strong on Cat Island. The importance of this to the present study is that man's modifications of the woodland through clearing, burning, selective cutting, and grazing decreases in intensity with distance from the settlements. In order to determine the significance of this, each sample site was classified in terms of its distance in kilometers from the nearest settlement.

Aerial photograph reference. As was indicated above, the choice of sampling locations was in large part determined by whether or not the field in question could be accurately located on the 1958 aerial photographs. This was thought to be especially important insofar as it would make possible future sampling in the same location.

The location of each field sampled was fixed by a cross-reference on a 1958 aerial photograph. A 12-figure reference was used, the first three numbers of which referred to the flight number of the photograph, the second three to the frame number. The last six figures provided the cross-reference on the photograph itself, the first three representing the distance in millimeters from the left-hand margin and the last three the distance from the bottom margin, (Figure 24). At a scale of 1/12,500, one millimeter on the photograph represents 12.5 meters on the ground, so the sample site is fixed quite accurately.

Analysis of Field Data

After returning from the field, the data gathered were organized for analysis. The analysis involved plant identification, aerial photograph analysis, and computer analysis of the plant cover data.

Plant Identification

As was mentioned earlier, a full set of the plants collected was sent to the Arnold Arboretum and the names of all the species included were determined by Dr. R.A. Howard. In addition to this, several days were spent at various herbaria comparing duplicate specimens with earlier Bahamian collections. The Field Museum of Natural History collection of Bahamian plants was especially useful here, as it included a duplicate set of all plants collected during the
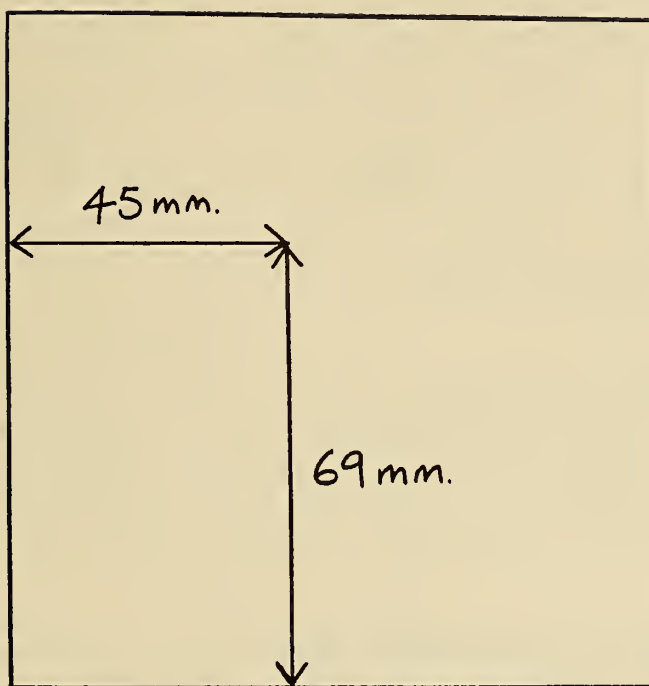
Figure 24. The aerial photograph reference grid. Each sample site was fixed by a 12-figure reference number; for example:

012 : 180 :: 045 : 069

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012 = The flight number.
180 = The frame number.
045 = Millimeters from left
        edge of photograph.
069 = Millimeters from bottom
        edge of photograph.
```

compilation of the <u>Bahama</u> <u>Flora</u> (Britton and Millspaugh, 1920).

The herbarium work had two major objectives: first, to obtain some idea of the variability present in difficult taxa such as <u>Pithecellobium</u>, <u>Eugenia</u>, and <u>Coccoloba</u>, and second, to check the dates on the collections of alien species. In the last context the early collections by Catesby and others at the British Museum of Natural History were especially useful.

<u>Aerial</u> <u>Photograph</u> <u>Analysis</u>

The 1958 aerial photograph coverage of the island was an indispensable aid to field work. The photographs made it possible to pinpoint the location of the area sampled and also provided a good indication of the age of the woodland. Having returned from the field in 1970, further aerial photograph analysis was made possible by the acquisition of aerial photographs of the island taken in 1943.[2] This further analysis consisted of two parts: confirmation of the habitat-type classification, and the establishment of time-control for the age of the woodland.

<u>Habitat-type classification</u>. As every field sampled had been accurately located on the 1958 aerial photographs, it was quite a simple procedure to check whether or not the habitat-type assigned to the ground was confirmed by the aerial photographs. Stereoscopic coverage was available for 1943 and 1958, and on both series the land surface characteristics were easily identifiable.

<u>Age determination</u>. The 1958 aerial photographs provided an approximate guide to the age of the woodland, as abandoned fields appear progressively darker with age. In spite of the time lapse between photography and sampling, this relationship appeared to be quite real on the ground, except of course for those fields cultivated and abandoned after 1958. The tonal differences, however, give only a relative time scale. It was safe to assume that a dark area of woodland was older than a light area, but the actual age difference involved could not be determined from the 1958 photographs alone.

This problem was overcome by using the 1943 photographs in conjunction with those taken in 1958. More specifically,

2. The 1943 photographs were taken by the U.S. Navy as part of a wartime defense operation. Also of quite good quality, they are available in stereoscopic coverage at a scale of 1: 30,000.

by comparing the differences in tonal density between photo-
graphs of the same area it was possible to fix with a cer-
tain degree of accuracy the age of any part of the woodland
that had not been cleared since 1958 (Table 3).

Computer Analysis

Once all the field data had been checked they were
transferred from the data sheets (Appendix III) to IBM cards
for computer analysis. Each of the categories in the age,
habitat, height, soil, moisture, and distance classes was
given a code number, and each of the species encountered was
given the same code number that had been used to refer to it
in the field (Appendix I).

Once the cards were in order programs were written to
compute basically two kinds of information. First, how did
the floristic composition of the woodland change through
time? In other words, how did the woodland recover after
clearing and burning? And second, how did the woodland vary
with distance from the settlements?

Limitations of the Data

The methods employed in gathering the data were
designed with two specific purposes in mind, namely, to
evaluate the extent to which man had changed the floristic
composition of the woodland and to provide a base-line
against which future changes could be assessed. However,
before proceeding with any discussion of the data, certain
limitations should be made clear.

Taxonomy

As has been mentioned above, several genera contain
species that are not easily distinguished in the field. For
example, in the genus Pithecellobium all the individuals
encountered were recorded as P. keyense. However, the leaf
characteristics by which this species is differentiated from
P. unguis-cati are somewhat variable and both species may
therefore be present. Similarly, in the genus Eugenia two
species, E. buxifolia and E. longipes, were quite distinct,
but three others, E. lucaya, E. myrtoides, and E. monticola,
were not, and some misidentification may have been made
here. In the Euphorbiaceae two species may have been con-
fused, Drypetes diversifolia and Savia bahamensis. Both are
similar in terms of leaf characteristics and general appear-
ance and may have been misidentified when flowers or fruit
were not available. In the genus Coccoloba, C. uvifera and
C. krugii are distinctive, but the widespread C. diversi-
folia was quite variable and may include more than one
species.

TABLE 3

AGE AND TONAL DENSITY

AGE CLASS	DATE CLEARED	APPEARANCE ON 1943 PHOTOGRAPHS	APPEARANCE ON 1958 PHOTOGRAPHS
I (<5 yrs.)	1966-1970	Not Present	Not Present
II (5-14 yrs.)	1956-1965	Not Present	Light Grey or Not present
III (15-29 yrs.)	1940-1955	Light Grey or Not Present	Medium Grey
IV (30-50 yrs.)	1920-1939	Medium Grey	Dark Grey
V (>50 yrs.)	Before 1920	Dark Grey or Black	Black

In the final analysis the taxonomic problem was not a serious one. Because of the long period of time spent in the field it was possible to identify on sight the vast majority of the species encountered. Furthermore, most of the 120 species included in the systematic sampling are quite distinctive.

Coverage

Roughly two-thirds of the sample locations are in the northern half of the island, the main reason being that the field research was based in Arthurstown. Although the road along the island is only about sixty miles long, for the most part it is simply a rough track and travelling is therefore very difficult and expensive.

This uneven coverage is probably not a significant problem as there are few obvious differences between the northern and southern parts of the island. On the other hand, it does mean that the importance of alien species in the sample is less than it might have been. Logwood (<u>Haema-toxylum campechianum</u>) was seen to be especially common around the two southern settlements of Port Howe and Old Bight.

As can be seen from Table 4, the coverage of the different age-classes is somewhat uneven. This reflects the variable character of the woodland itself. Large areas of woodland fall in the first three age-classes, whereas older woodland is comparatively hard to find. The same is true of the other variables indicated. Sample sites were chosen to give a good coverage of the woodland as a whole rather than to provide equal coverage within the different classes. This later proved to be a problem insofar as it necessitated the use of percentages in comparisons between classes with different sample coverage.

Rare Species

Even though the total sampled was large, rare species because of their very nature are not well represented. This is particularly unfortunate because it is most likely that it is the rare species have been most significantly affected by disturbance.

In spite of their limitations, the data gathered provide a comprehensive picture of

TABLE 4

THE NUMBER OF FIELDS (25 x 1m^2)
SAMPLED IN EACH CATEGORY

Age Fields	< 5 yrs. 60	5-14 yrs. 80	15-29 yrs. 83	30-50 yrs. 52	>50 yrs. 25	
Habitat Fields	Whiteland 42	Flatland 99	Blackland 159			
Soil Fields	Black 222	Red 34	White 44			
Moisture Fields	Xeric 15	Mesic 270	Hydric 15			
Distance Fields	1 km. 77	1-2 km. 73	2-3 km. 55	3-4 km. 50	4-5 km. 30	5 km. 12

the variable character of the woodland as it was in 1970.[3] As a cross-sectional sample of an uneven-aged population, they provide a basis for estimating what changes have occurred in the past and what changes are likely to occur in the future.

3. In order that the old field analysis may be repeated in the future, all the data gathered have been deposited in the Social Science Data Program Library at the University of Wisconsin. The full set of the 1958 aerial photographs may be obtained from either the University of Wisconsin Map Library; the Crown Lands Office, Nassau; or the Department of Overseas Surveys, Surbiton, England.

IX. THE IMPACT OF SHIFTING AGRICULTURE:
AGE DIFFERENCES IN THE WOODLAND

Seen from the air, the Cat Island woodland is a patchwork quilt of abandoned fields in various stages of recovery (Figure 16). It was soon recognized that any analysis of man's impact would have to include some consideration of these age differences. Not only were they significant in themselves, but they also represented an inherent variability that complicated the analysis of the whole. Fortunately, the availability of aerial photograph coverage for 1943 and 1958 made it possible to fix within certain limits the age of any part of the woodland. By sampling fields of different ages, it was possible to determine indirectly the nature of recovery following abandonment.

An analysis of succession is in many ways relevant to the hypothesis of insular vulnerability. If the hypothesis is valid, several conclusions might be expected. First, the native species would be ill-adapted to this artificial form of disturbance and would be slow to recover after clearing and burning. Second, the native species would to a large extent be replaced by aliens, especially in the earlier stages of succession. And, third, the long history of repeated clearing and burning would have brought about a marked reduction in the number of native species present.

Because of the underlying differences in land surface characteristics, the woodland was dealt with in the context of the three habitat-types: the whiteland, flatland and blackland. Figures 25, 27, and 29 show in some detail the changing floristic composition in each habitat-type at different stages of recovery. The distinction between "important" and "minor" species is arbitrarily based on whether or not the species in question accounts for more or less than 5 percent of the area sampled in any one age-class. The minor species are shown collectively according to the age-class in which they reach their maximum value. As the diagrams are largely self-explanatory, what follows here is simply an elaboration of their more important characteristics. The account of each habitat-type concludes with a discussion of a representative aerial photograph sequence.
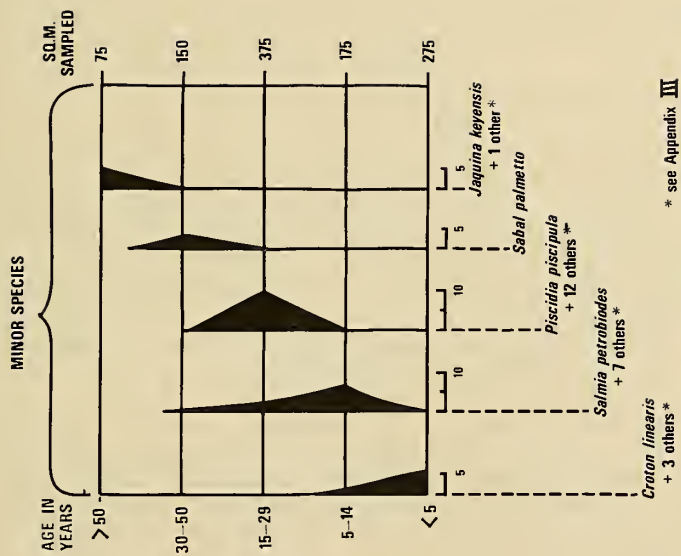

The Whiteland

The whiteland is a distinctive habitat-type and it is not surprising, therefore, that succession here is different
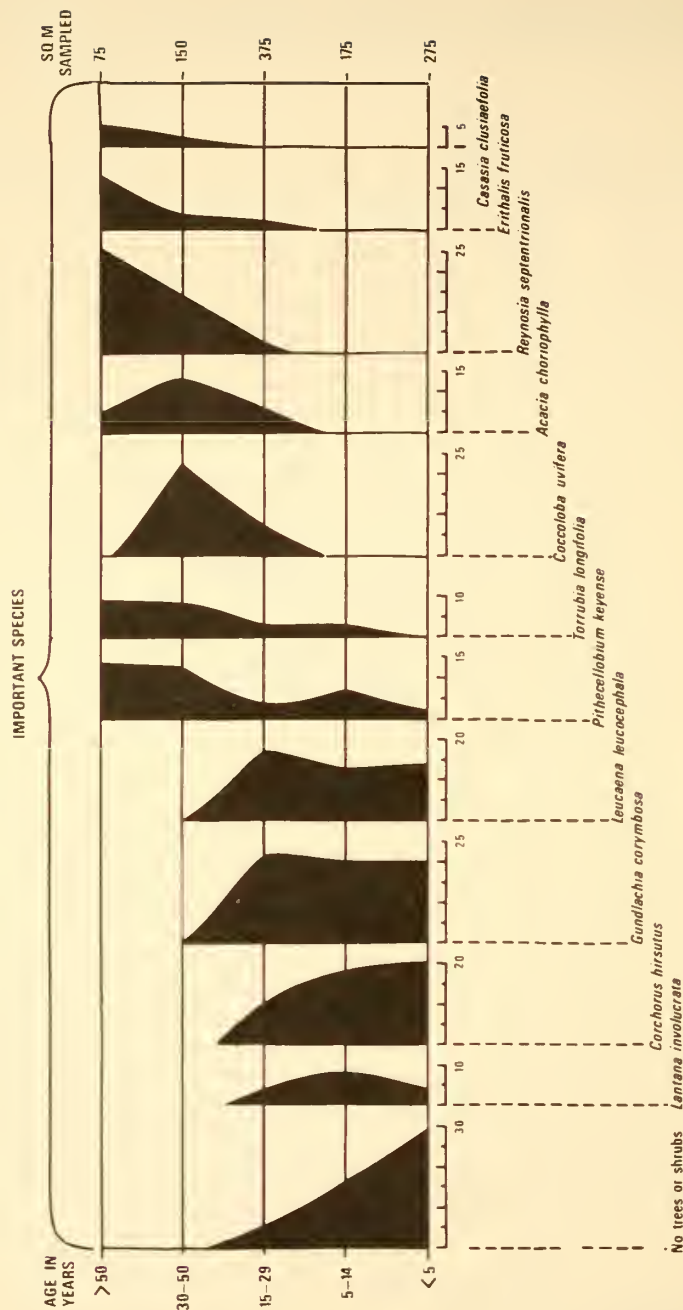
Figure 25A. Whiteland Succession Diagram (important species)

Figure 25B. Whiteland Succession Diagram (minor species)

from that on the flatland or blackland. The main difference
is that, in all age classes, a comparatively few species
account for a large part of the total cover. Gundlachia
corymbosa, Corchorus hirsutus, Leucaena leucocephala and

Lantana involucrata dominate the first three age-classes
(Figure 25A). All four are pioneer species, well-adapted to
quickly colonizing open, droughty surfaces. Any particular
field is usually invaded by only one or two of the four
species, and these will then dominate the early stages of
succession. Floristic differences between recently aban-
doned fields are probably due to chance factors, such as the
timing of abandonment, rather than to basic environmental
controls.

Gundlachia corymbosa is a shrubby composite rarely more
than 2 meters tall. It grows naturally in the low, droughty
areas around the margins of brackish ponds and salt-water
lagoons, and from here has spread rapidly into
artificially-disturbed habitats such as roadsides and aban-
doned fields. Its success can also be attributed to its
prolific seed production and efficient dispersal capacities.
Like many members of the Compositae, its seeds are dispersed
by the wind. Corchorus hirsutus appears to be very similar
to Gundlachia as far as habitat tolerances are concerned. It
grows naturally in unstable dune environments inland from
the coast. The fruit is a dehiscent capsule containing many
small wind-dispersed seeds. Leucaena leucocephala unlike
the other whiteland pioneers, is an introduced species.
Significantly, it is only found in artificially- disturbed
habitats such as roadsides and abandoned fields. Like
Gundlachia and Corchorus, its seeds are largely wind-
dispersed. However, its success can also be attributed to
its ability to reproduce from sprouts.

The only other pioneer species to reach more than 5
percent in any particular age-class is Lantana involucrata.
This aromatic shrub is somewhat smaller than the three
species discussed above, rarely reaching 2 meters in height.
It was seen growing in naturally-disturbed habitats, such as
dunes and beach ridges, and also in droughty areas surround-
ing the salt-water lagoons. Unlike Gundlachia and Cor-
chorus, Lantana depends upon birds for seed dispersal. This
species has small, fleshy fruits that are conspicuously blue
in color.

The pioneer shrubs are replaced after about 30 years by
taller bushes, particularly Pithecellobium keyense, Torrubia
longifolia, Coccoloba uvifera, and Acacia choriophylla. All
of these species, with the exception of Torrubia, grow in
dense thickets which gradually increase in area and eventu-
ally merge. The decline of the pioneers is probably in

large part due to competition from the taller, more deeply-
rooting species, although it is also possible that they are
naturally designed for only a short lifespan. Older
Gundlachia bushes, for example, were often seen to be dam-
aged by root rot and other pathogens.

Pithecellobium keyense is a leguminous shrub or small
tree that rarely reaches a height of more than 4 meters .
It grows naturally in droughty areas, such as dunes and
beach ridges, or the scrub-lands just above the salt-water
lagoons. Its seeds are covered with bright red aril, an
obvious adaptation to encourage dispersal by birds. As Fig-
ure 25 indicates, Pithecellobium is capable of colonising
recently-abandoned fields but tends to become more important
in the older age-classes.

A very similar successional pattern is shown for Torru-
bia longifolia. This small tree grows naturally in open,
droughty habitats such as sand dunes and beach ridges and
the occassionally flooded areas around the edges of the
savannas. Like Pithecellobium, its fruits are well-adapted
to dispersal by birds. A Torrubia tree in fruit is virtu-
ally covered with bright red berries.

In the penultimate age-class (30-50 years), Coccoloba
uvifera accounts for nearly 25 percent of the total cover.
According to Britton and Millspaugh (1920:116), this bushy
tree reaches 15 meters in height in certain areas of the
Bahamas. However, on Cat Island it was rarely seen to be
more than 6 meters tall. It covers extensive areas of the
whiteland, both along the coast and back into the dunes and
beach ridges. Characteristically it forms dense thickets
which gradually expand into formerly-cleared areas. As
might be expected from its wide distribution along the
coastlines of the New World tropics, its fruits are
dispersed by ocean currents. Locally, however, birds,
crabs, and man are important dispersal agents. As Figure
25A indicates, it was not encountered in the recently-
abandoned fields. Its absence suggests that its seedlings
need a certain amount of shade in order to become esta-
blished.

A similar successional pattern is shown by Acacia
choriophylla. Like Coccoloba, this small leguminous tree
was not encountered in the recently-abandoned fields. It is
not a prolific seed-producer and probably depends on birds,
crabs, and lizards as means of dispersal. Proportionally it
is more common on the whiteland than elsewhere in the wood-
land, which suggests that this may be its natural habitat.
Its thick leaves are probably an adaptation to the dessicat-
ing winds that characterize the areas close to the coast.
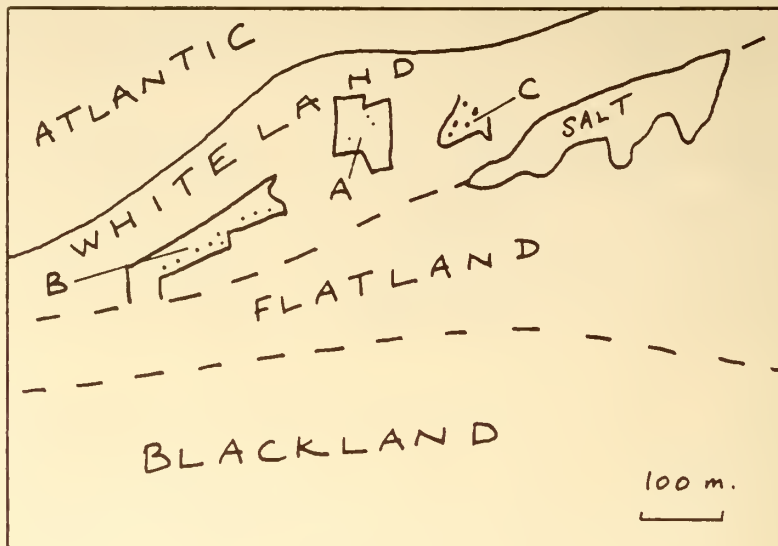
Figures 26 and 27 show a time-lapse sequence for a represen-
tative whiteland area, at south Bird Point. The most obvi-
ous difference between the two photographs is the decrease
in the area cultivated. The generally darker tone of the
whiteland on the more recent photograph does in fact
represent the recovery of the woodland.

Three general stages of recovery can be identified.
The flat grey tone, so widespread on the earlier photograph
(for example at A), represents recently abandoned fields in
which the cover is largely grasses and herbaceous weeds (see
Figure 18). In 1958 many of these areas were characterised
by a darker, fine stipple pattern, as for example at B.
This represents the low shrub cover characteristic of fields
between 5 and 15 years old (see Figure 19). The expansion
of the taller, more deeply rooted, bushes can be identified
at several locations in the older photograph (for example
C). The beginnings of this later stage are also shown in
Figure 41.

In general, the south Bird Point sequence supports the
idea of a comparatively slow recovery on the whiteland.
Several fields in cultivation in 1943 can still be identifed
on the 1958 photographs. This is rarely the case for the
other habitat types. On the other hand recovery is obvi-
ously taking place and given no further disturbance it is
not too difficult to visualise the whiteland being eventually
covered with the woodland.

Figure 26.   Whiteland, South Bird Point 1943.

Figure 27.   Whiteland, South Bird Point 1958.
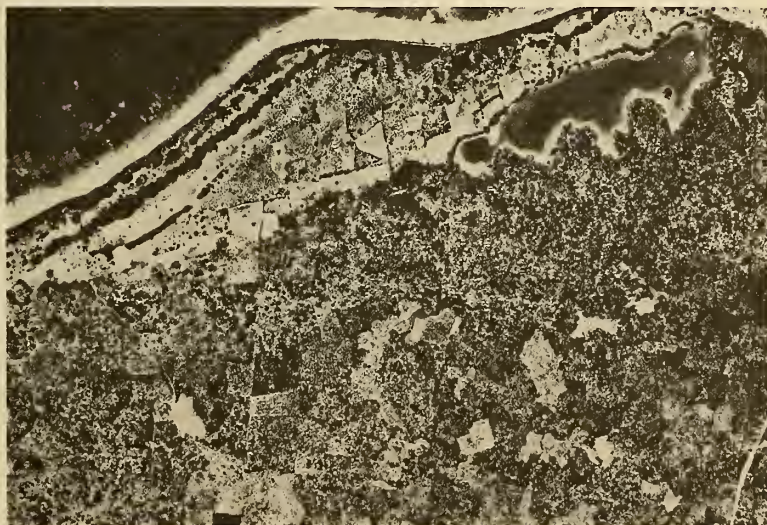
Older woodland was hard to find on the whiteland because it has been so intensively used for agriculture. Age-class 5 (more than 50 years) is therefore based on a comparatively small sample. The data do suggest, however, that the bushy character of the woodland eventually changes as trees such as Reynosia septentrionalis and Erithalis fruticosa become more important. Even so, several smaller bushes, for example, Pithecellobium, Torrubia, and Casasia, still account for a significant percentage of the total cover.

The most important species in the oldest age-class is Reynosia septentrionalis. It is also common on droughty sites on the blackland and flatland. Like most of the species discussed above its natural habitat appears to be exposed limestone ridges just inland from the coast. Its seeds are dispersed by birds and small animals such as crabs and lizards.

The last two important species on the whiteland, Erithalis fruticosa and Casasia clusiaefolia, are both members of the madder family. Erithalis is a bushy tree which rarely reaches more than 4 meters in height. It is found in the woodland throughout the island but is especially common on the whiteland. Its small purple fruits are well-adapted to dispersal by birds, although it does not become established on the recently abandoned fields (Figure 25A).

Casasia clusiaefolia, has fruits that are adapted to dispersal by ocean currents, and probably because of this it is largely restricted to the whiteland. It is a shrub with a capacity for rapid growth and is characteristically present as a minor member of the whiteland thickets. Its seeds are locally dispersed by birds, crabs, and lizards.

An account of all 28 minor species encountered on the whiteland is beyond the scope of the present discussion. As can be seen from Figure 25B, they account for only a small percentage of the total cover in every age-class. This floristic simplicity contrasts sharply with the rest of the woodland. Figures 26 and 27 show a representative time-lapse sequence for the whiteland.

The Flatland

The flatland is also a distinctive habitat-type. The land surface consists of horizontally-bedded marine limestones of Pleistocene age. The limestone is indurated-and the surface therefore tends to be droughty. This in turn
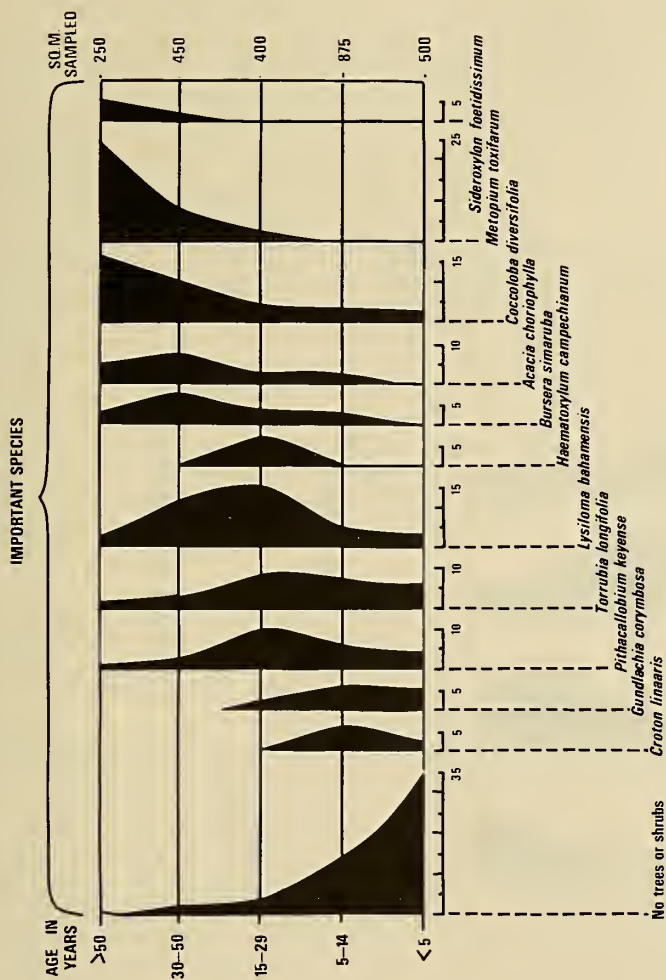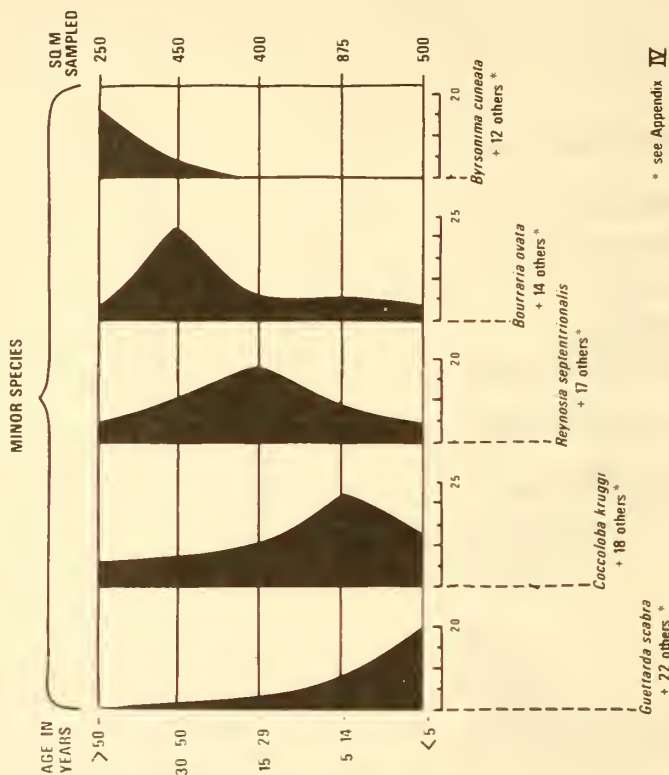
Figure 28A. Flatland Succession Diagram (important species)

Figure 28B. Flatland Succession Diagram (minor species)

means that recovery after clearing and burning is slow. As can be seen in Figure 28A, just over 34 percent of the ground in fields abandoned less than 5 years ago was bare of trees or shrubs, a slightly higher percentage than on the whiteland.

Even more important is the greater floristic diversity of the flatland. Although the number of important species is the same as on the whiteland, together they account for a much smaller percentage of the total cover. The balance is made up by 88 minor species (Figure 28B). Again, it is obviously impractical to deal individually with the minor species. The discussion that follows therefore deals largely with the dominants..

Croton linearis and Gundlachia corymbosa are the only two important species to reach their maximum cover values in the first or second age-classes. Croton linearis is a small, narrow-leaved member of the spurge family. It is not a prolific seed producer and relies primarily on birds as a means of dispersal. It grows naturally in exposed areas, for example, behind the coast, above the salt-water lagoons, and around the edges of the seasonally-flooded savanna. From these naturally droughty habitats it has invaded the recently-abandoned flatland fields. It also grows on the whiteland and blackland, but reaches its maximum cover value on the flatland.

As Figure 28A indicates, Gundlachia is clearly less important on the flatland than on the whiteland. Increased competition may be the reason for this, although environmen- tal differences between the two habitats could also be important. Even so, Gundlachia's age distribution is much the same on the flatland as on the whiteland. Like Croton linearis, it is a typical pioneer species.

In the third age-class (15-29 years), four important species reach their maximum cover values: Pithecellobium keyense, Torrubia longifolia, Lysiloma bahamensis, and the introduced dyewood Haematoxylum compechianum. Together they account for 40 percent of the total area sampled. Pithecel- lobium and Torrubia have very similar cover values in each age-class and presumably have similar ecological tolerances. Lysiloma bahamensis is a common species on the flatland. A fast-growing leguminous tree, it is well-adapted to rather droughty conditions. It has extensive, horizontal roots that run along the level limestone surface. According to Britton and Millspaugh (1920: 158), in some areas of the Bahamas it may reach 16 meters in height. On Cat Island, however, it was rarely seen to be more than 10 meters tall. It reproduces vigorously by sprouts, and is also a prolific
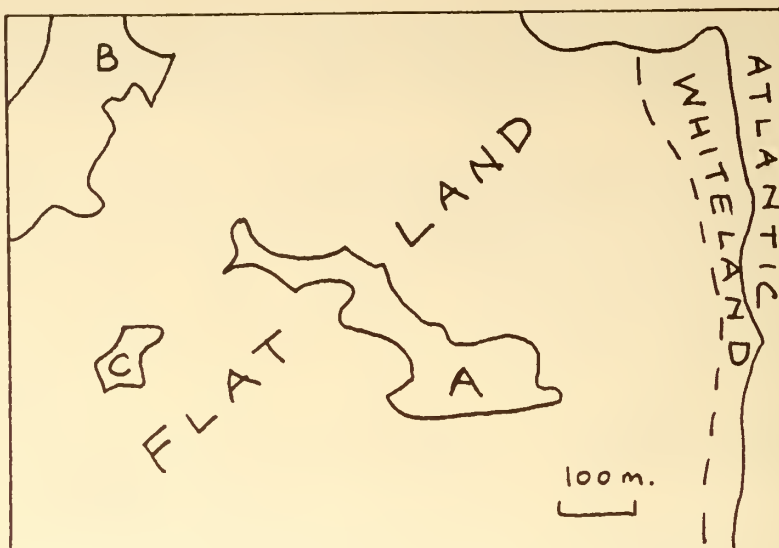
Figures 29 and 30 show a time-lapse sequence for a represen-
tative flatland area just south of Flamingo Point. This is
a particularly interesting area in that it has been rela-
tively undisturbed. It has been protected by inaccessibil-
ity, the nearest settlement being 5 kilomenters away. The
low elevation of the flatland here is indicated by the
salt-water marsh at A.

    In spite of the obvious differences in the quality of
the photographs, their tonal variation gives a good indica-
tion of the rate of recovery. The dark area on Figure 29
represents woodland that was probably over a hundred years
old. The light grey tones around its edges indicate recent
clearing. Some of these fields were abandoned shortly after
1943 because their outlines are still visible on the 1958
photograph (B). However, their tonal appearance is dif-
ferent; on the 1943 photograph they are light grey, on the
1958 photograph medium grey. This tonal change suggests
that medium grey areas on the 1943 photograph were probably
cleared around 1930.

    Another point to note is that small fields tend to
recover more rapidly than large fields. This can be seen by
comparing B and C on both photographs. The reasons for this
are undoubtedly complex but probably involve seedling supply
and microclimatic differences. In general the flatland
fields appear to recover more quickly than the whiteland
fields, recently cleared fields on the 1943 photograph being
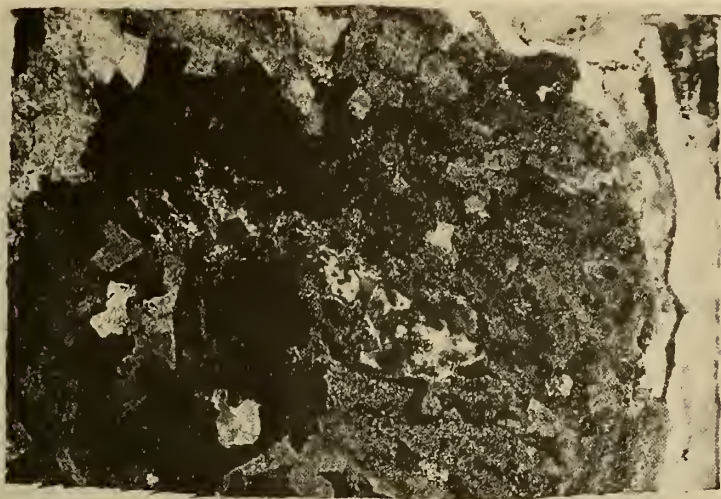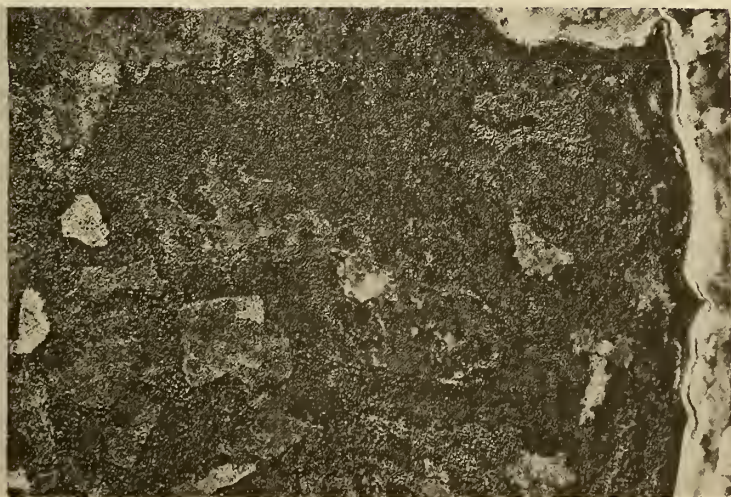rarely visible in 1958.

Figure 29.   Flatland, Flamingo Point 1943.

Figure 30.   Flatland, Flamingo Point 1958.

seed-producer. Its pods are dehiscent, the small dark brown seeds being widely dispersed by the wind. In the intermediate-age fields it effectively replaces the pioneer bushes, such as Gundlachia and Croton linearis. After thirty years, however, it in turn is replaced by other species (Figure 28A). The introduced dyewood, Haematoxylum campechianum, accounts for just over 5 percent of the cover in the intermediate age-class. Surprisingly, it is the only alien among the 11 important species in this habitat-type.

In the penultimate age-class (30 to 50 years), two important species reach their maximum cover values: Bursera simaruba and Acacia choriophylla. Bursera is a rapidly-growing tree, easily distinguished by its birch-like bark. Like many of the woodland species, it fruits prolifically and reproduces vigorously from sprouts. These characteristics have made it an important species in the woodland. As Figure 28A shows, both Bursera simaruba and Acacia choriophylla have similar age distributions. Had the area sampled on the whiteland been greater, the same would probably be true in Figure 25A. Both species have similar ecological tolerances.

In the oldest age-class (greater than 50 years), Coccoloba diversifolia and Metopium toxiferum emerge as dominants, accounting together for 45 percent of the total area sampled. Sideroxylon foetidissimum also reaches its highest value, accounting for just over 5 percent of the total. Coccoloba diversifolia is an erect fast-growing tree. On Cat Island it was rarely seen to be more than 10 meters tall. As a prolific seed-producer and efficient sprouter it is well-adapted to colonising abandoned fields. It was encountered in all age-classes on the flatland (Figure 28A). Its importance in the older woodland can probably be attributed to its ability to outgrow the more widely-branching species such as Lysiloma bahamensis, Bursera simaruba, and Acacia choriophylla. The same is probably true of Metopium toxiferum. Like the pigeon plum, Metopium is an erect fast-growing tree. It also fruits prolifically, with birds being the main means of dispersal. Unlike the pigeon plum, it was not encountered in the recently-abandoned fields. Its absence suggests that it needs a certain amount of shade in order to become established. It is also a less efficient sprouter than Coccoloba. Sideroxylon foetidissimum is clearly restricted to the older woodland. According to Britton and Millspaugh (1920: 321), it grows to 25 meters in some parts of the Bahamas. On Cat Island, however, it was never seen to be more than 12 meters tall. This valuable timber tree has been selectively cut and is probably less important now than it was in the pre-European period.

As far as the minor species are concerned, it can only be emphasized that they account for a large percentage of the total cover, over 40 percent in most age-classes. Their collective age distributions in Figure 28B are interesting in that they suggest that many of the species are present in several age-classes. Only the species reaching their maximum cover values in the older woodland have a limited age distribution. As might be expected, these are sensitive species, intolerant of the open, droughty conditions that characterize the recently-abandoned fields. Figures 29 and 30 show representative time-lapse sequences for the flatland.

The Blackland

The blackland differs from the flatland in that the limestone surface is broken and irregular. Soil erosion is therefore reduced and colonization by plants is facilitated. This is shown in the "no trees and shrubs" curve in Figure 31A. In every age-class, the area of bare ground is proportionally lower for the blackland than for the flatland. In fact, the rapidity with which succession takes place is an important reason for the early abandonment of fields on the blackland. The blackland is also floristically diverse. A total of 105 different species was encountered in the sampling, only 10 of which reached 5 percent in any one age-class.

The youngest age-class (less than 5 years) is particularly diverse. Although no important species reaches its maximum cover value here, 30 minor species do. In the second age-class (5 to 14 years), Gundlachia corymbosa, Bourreria ovata, and Pithecellobium keyense reach their maximum cover values. Of these, only Gundlachia is restricted to the younger age-classes. As on the whiteland and flatland, it was not encountered in woodland over 30 years old.

Bourreria ovata is a small tree or shrub, rarely more than 5 meters tall. It grows naturally in droughty areas close to the coast and near the salt-water lagoons; from here it has spread into the abandoned fields. Its bright red fruits are primarily dispersed by birds. It also sprouts vigorously, and because of this is commonly encountered in the recently-abandoned fields. Pithecellobium keyense has almost the same age-distribution as Bourreria. Unlike the situation on the whiteland, where it reaches its maximum cover value in the oldest age-class (more than 50 years), here it has its maximum in age-class 2 (5 to 14 years). This illustrates well the basic difference between the xeric whiteland habitat and the more mesic blackland.
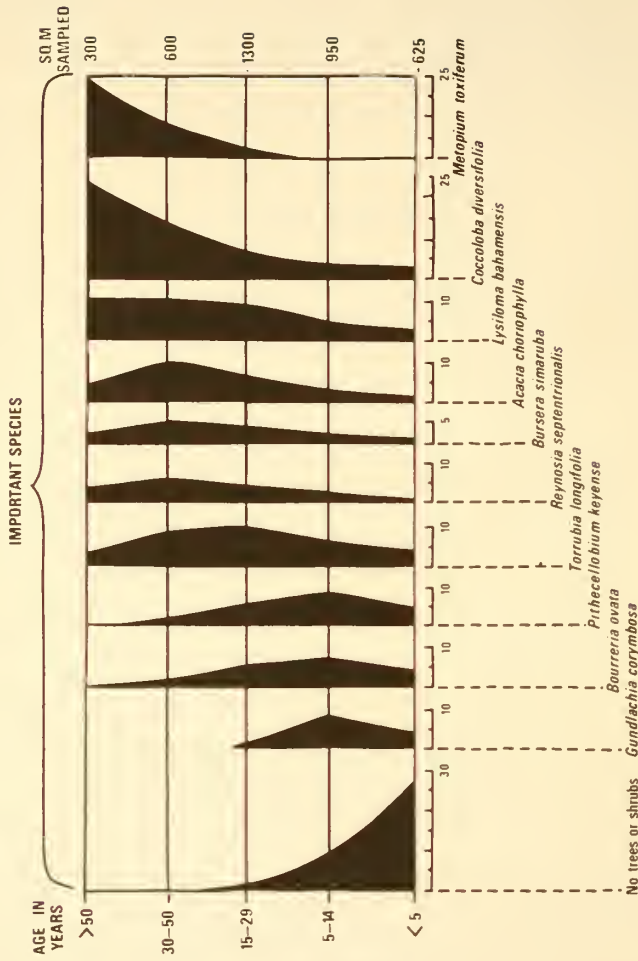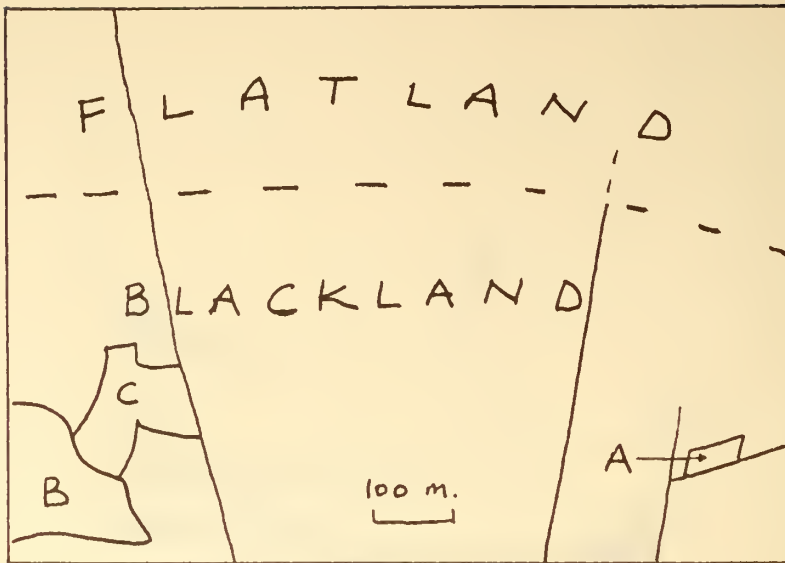
Figure 31A.   Blackland Succession Diagram (Important species)
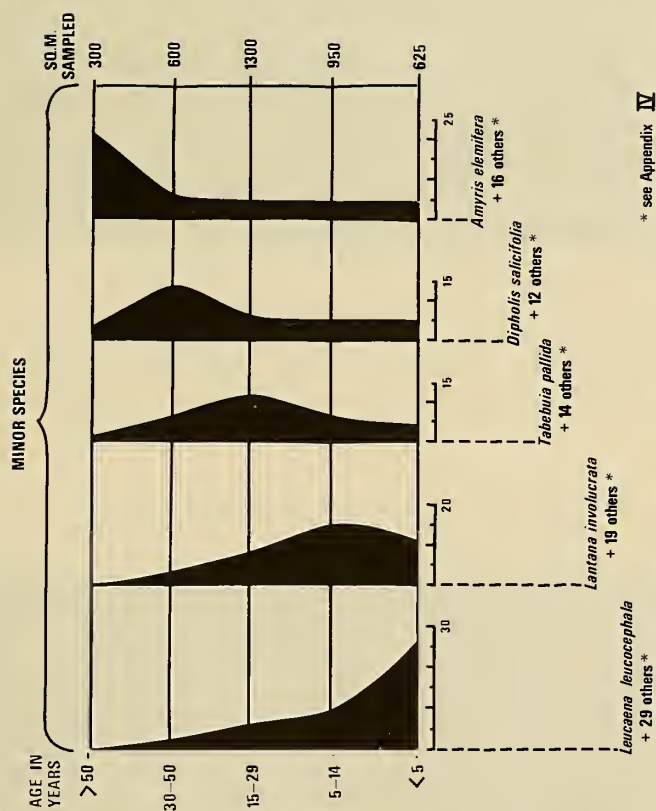
Figure 31B. Blackland Succession Diagram (minor species)

Figures 32 and 33 show a time lapse sequence for a represen-
tative blackland area near Dumfries. Unlike the whiteland
and flatland sequences discussed earlier, there was no
decrease in cultivation here between the years 1943 and
1958. The reason for this was probably accessibility. The
settlement of Dumfries is only half a kilometer away to the
west.

Again the tonal variation between the two photgraphs
gives a good idea of the age of the woodland. Only a small
area appears dark on both photographs, as for example at A.
The dark area in the lower left part of the photographs (B)
is an area of red mangrove around the Dumfries Blue Hole.
Dark areas such as A were probably at least 50 years old in
1958.

Again the change from light grey to medium grey, as for
example at C, indicates the rate of recovery. By analogy it
seems likely that the medium grey areas on the earlier pho-
tograph were cleared around 15 years before to 1943.

For the area as a whole it is interesting to note that
such a large proportion (more than 75 percent) of the wood-
land shows evidence of having been cleared within the time
span covered by the two photographs. On the other hand the
rate of recovery is obviously rapid. Few recently cleared
fields on the 1943 photograph are visible on the 1958 photo-
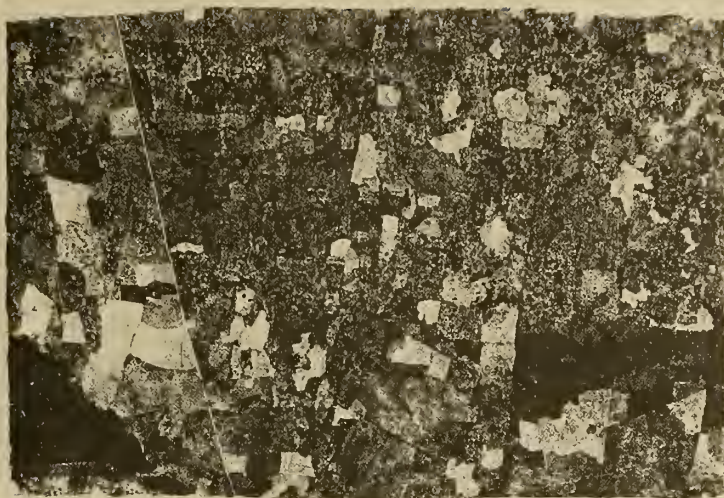graph.

Figure 32. Aerial Photograph of Blackland, 1943

Figure 33. Aerial Photograph of Blackland, 1958

The same is true of <u>Torrubia</u> <u>longifolia</u>. On the whiteland
<u>Torrubia</u> reaches its maximum cover value in the oldest age-
class (more than 50 years), while on the blackland it has
its maximum in the intermediate class (15 to 29 years).

In the penultimate age-class (30 to 50 years) , <u>Reyno-</u>
<u>sia</u> <u>septentrionalis</u>, <u>Bursera</u> <u>simaruba</u>, and <u>Acacia</u>
<u>choriophylla</u> reach their maximum cover values. All three
have been discussed above and therefore need little addi-
tional comment here. It is interesting to note, however,
that <u>Bursera</u> and <u>Acacia</u> have very similar age distributions.
This reinforces the conclusion reached earlier that both
species have similar ecological tolerances.

In the oldest age-class (more than 50 years), <u>Lysiloma</u>
<u>bahamensis</u>, <u>Coccoloba</u> <u>diversifolia</u>, and <u>Metopium</u> <u>toxiferum</u>
all reach their maximum cover values, and together account
for 55 percent of the total cover. <u>Lysiloma</u> appears to be
more persistent on the blackland than on the flatland,
although why this should be so is not immediately apparent.
<u>Metopium</u> and <u>Coccoloba</u> have very similar age-distributions
in both habitat-types.

As far as the minor species are concerned, the obvious
conclusion is that the woodland is floristically diverse in
all age-classes (Figure 31B). The implications of this are
discussed below. Figures 32 and 33 show representative
time-lapse sequences for the blackland.

The Woodland as a Whole

The old field data show quite clearly that there are
important differences in the nature of succession in the
three habitat types. Two of the variables measured, height
and floristic diversity, are shown in Figure 34. The white-
land is clearly distinctive. Compared with with the flat-
land and blackland it is floristically impoverished. An
average of less than 7 species were encountered in each
field sampled, regardless of age. Furthermore, only 12
species accounted for more than 75 percent of the total
cover (Figure 25A). The whiteland is also different in that
its rate of recovery after clearing and burning is rela-
tively slow. This can be seen from the aerial photographs
and also from the fact that pioneer species, such as
<u>Gundlachia</u> <u>corymbosa</u>, <u>Leucaena</u> <u>leucocephala</u> and <u>Corchorus</u>
<u>hirsutus</u> are more important and more persistent on the
whiteland than elsewhere. Similarly, those species that are
characteristic of the older whiteland fields, such as <u>Torru-</u>
<u>bia</u> <u>longifolia</u>, <u>Reynosia</u> <u>septentrionalis</u>, <u>Erithalis</u> <u>fru-</u>
<u>ticosa</u>, and <u>Pithecellobium</u> <u>keyense</u>, all reach their maximum

cover values in intermediate-aged fields in the rest of the woodland. There is no equivalent on the whiteland to the "highwood" that characterizes the older woodland elsewhere on the island. This pioneer aspect of the whiteland probably reflects the inherent instability of the habitat.

The whiteland vegetation is also distinctive in its generally shrubby nature. Even the older trees were on the average less than 4 meters tall (Figure 34). The stunted aspect of the vegetation is probably in large part due to its exposed location near the coast. Other physiognomic variables were not recorded, but it is probably correct to say that there is a higher percentage of evergreens on the whiteland then elsewhere.

Floristically there are no major differences between the whiteland and the rest of the woodland. A few species, such as Casasia clusiaefolia, Scaevola plumierii, and Coccothrinax argentea, are restricted to the whiteland; however, most species, are found in all three habitat-types. Differences between the the flatland and blackland are less clear. In terms of floristic diversity, the number of species encountered was, on the average, slightly higher on the blackland than on the flatland, especially in the younger age-classes (Figure 34).

The rate of recovery, at least in the earlier stages of succession, appears to be more rapid on the blackland than on the flatland. This can be seen when one compares the aerial photograph sequences (Figures 29, 30; Figures 32, 33) and when one compares the "no trees and shrubs" curves on Figures 28 and 31. Vegetation recovers more quickly on the blackland than on the flatland, for several reasons. The surface of the limestone is more broken, which means less soil erosion and a generally more mesic edaphic situation. The broken surface also reduces the severity of fire, and therefore increases the frequency of sprouting. All of this is probably responsible for the greater floristic diversity of the blackland and the greater height of the vegetation in any particular age class.

As far as the individual species are concerned, there are few major differences between the two habitat-types. Perhaps the most significant is the greater importance of Lysiloma bahamensisand Haematoxylum campechianum on the flatland. This may be a result of more droughty conditions on the flatland. The fact that the curves for individual species are generally smoother for the blackland than for the other two habitat-types is probably a reflection of differences in the area sampled in each case. The smoothness of the blackland curves is reassuring, in that it
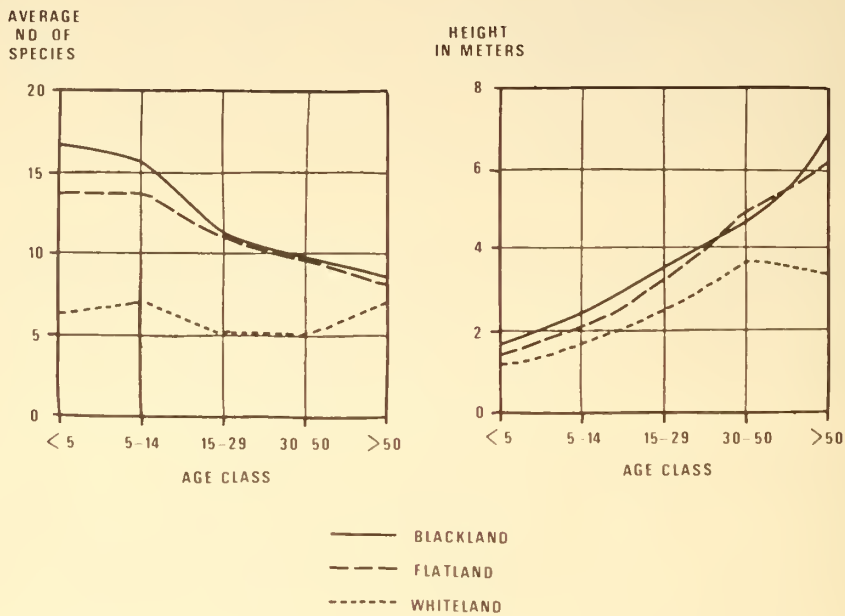
Figure 34. Graphs showing Diversity and Height against
Age, for each Habitat Type

suggests that real processes are represented.

Taking the woodland as a whole it is probably fair to say that the whiteland is quite distinctive in all the age-classes, whereas the differences between the flatland and blackland are only significant in the younger and intermediate age-classes.

The Nature of Recovery

In view of the supposed vulnerability of insular vegetation the old field data are in many respects surprising.

Perhaps the most striking characteristic of the woodland is the speed with which it recovers. As can be seen from the aerial photograph sequences, fields recently cleared in 1943 were barely visible in 1958. Although there are some exceptions (on the whiteland and in exposed areas), elsewhere woody plants very quickly colonize the limestone surface. The woodland is in fact inherently weedy. This is also shown, at least for the flatland and blackland, by the way in which most of the important species are encountered in every age-class. In other words, the recovery of the woodland does not involve the classical succession of species, each replacing the other, but rather a change in the area covered by species already present. Even the older woodland consists, for the most part, of species that are capable of colonizing recently-abandoned fields.

It is interesting to speculate whether this weediness is in itself a result of repeated clearing and burning by man with species pre-adapted to this type of disturbance having increased at the expense of the more sensitive types. Whether or not this has actually happened is impossible to determine without evidence of the composition of the pre-settlement vegetation. Fortunately, the problem can be approached indirectly. In the following section, areal variation in floristic composition is used as a clue to determine to what extent man has modified the woodland.

Another surprising aspect of the old field data is the great number of native species present in the recently abandoned fields. According to the hypothesis of insular vulnerability, very few native species would be expected to have adapted to the artificial habitats created by shifting agriculture. Yet on Cat Island, particularly on the flatland and blackland, literally dozens of native species are involved in the early stages of succession. Furthermore, the number of species encountered actually declines with age (Figure 34). This decrease in species diversity is the

opposite of what usually occurs in the early stages of suc-
cession (Loucks, 1970: 17; Odum, 1971: 256). In part, it
must be admitted, it may be an artifact of the constant area
sampled. Fewer species were encountered in the older wood-
land because the larger trees took up a greater proportion
of the area sampled. Even so, it is generally true that the
older woodland contained fewer species than the younger
woodland. As can be seen from Figures 28 and 31, two
species, Metopium toxiferum and Coccoloba diversifolia, dom-
inate the older woodland.

Again, it is interesting to speculate whether this
floristic impoverishment is in itself a result of repeated
clearing and burning and that slow-growing, shade-tolerant
species were formerly more numerous in the woodland than
they are today. This possibility is also considered in the
following section.

Another significant aspect of the old field data is the
limited importance of alien species. Only seven aliens were
encountered, and together they accounted for less than 6
percent of the area sampled. This low total was not entirely
unexpected in view of the historical evidence discussed ear-
lier, but even so it does not conform with the usual role of
alien plants on small oceanic islands. According to several
recent interpretations of insular vulnerability (Elton,
1958; Harris, 1965), alien plants have a competitive advan-
tage over native species in vegetation that has been dis-
turbed by man. The whole of the Cat Island woodland has
been drastically disturbed during the past thousand years,
and yet few aliens have been able to get established.

In summary, the analysis of age-differences in the
woodland has produced several results. First, the rate of
recovery after clearing and burning has been shown to be
surprisingly rapid. Second, the data indicate that a great
many native species are pre-adapted to withstand the effects
of clearing and burning. And third, the invasion by alien
species has had only limited success. In view of the sup-
posed vulnerability of island life all three findings were
unexpected.

X. THE IMPACT OF SELECTIVE PRESSURES:
AREAL VARIATION IN THE WOODLAND

On many small islands, woody vegetation has been virtu-
ally removed by grazing, selective cutting, and burning. On
Cat Island this has not been the case. The woodland has
survived. Even so, the question remains as to what extent
its floristic composition has been changed. As was
emphasized, the data gathered in 1970 show the nature of
vegetation change in an indirect way. Comparative analysis
of abandoned fields of different ages indicates the probable
nature of succession, but it does not show the actual
changes that have occurred in a truly historical sense.
These can only be determined from historical evidence, and
for Cat Island the historical evidence is frustratingly
thin. In spite of this deficiency, the question as to what
extent man has changed the floristic composition of the
woodland can be approached in other ways.

One approach would be to monitor future changes. If
the frequency of shifting agriculture continues to decrease,
it would seem likely that those species sensitive to clear-
ing and burning will increase in importance at the expense
of the weedy types. Just how long it would take the wood-
land to recover to its pre-settlement condition is difficult
to assess. Recovery at present may be rapid, but it is by
no means complete.

A second approach would be to analyse the areal varia-
tion within the contemporary woodland. More specifically,
by comparing disturbed areas close to the settlements with
remote, comparatively undisturbed areas, it should be possi-
ble to determine something of the selective nature of man's
impact. This was the approach taken in the present study.

As was indicated earlier, the intensity of many selec-
tive pressures decreases with distance from the settlements.
Because of this, each of the 300 sample sites was classified
in terms of its distance from the nearest settlement, so
that the nature of floristic variation with distance could
be computed. In order to simplify the analysis, the 42
whiteland sites were not included. Their floristic composi-
tion is so different from the rest of the woodland that to
include them would have introduced too many uncontrolled
variables. On the other hand, as the blackland and flatland
had been shown to be floristically similar in the age- vari-
ation analysis, they were combined in this part of the
study. The resulting 258 sample sites were classified, both
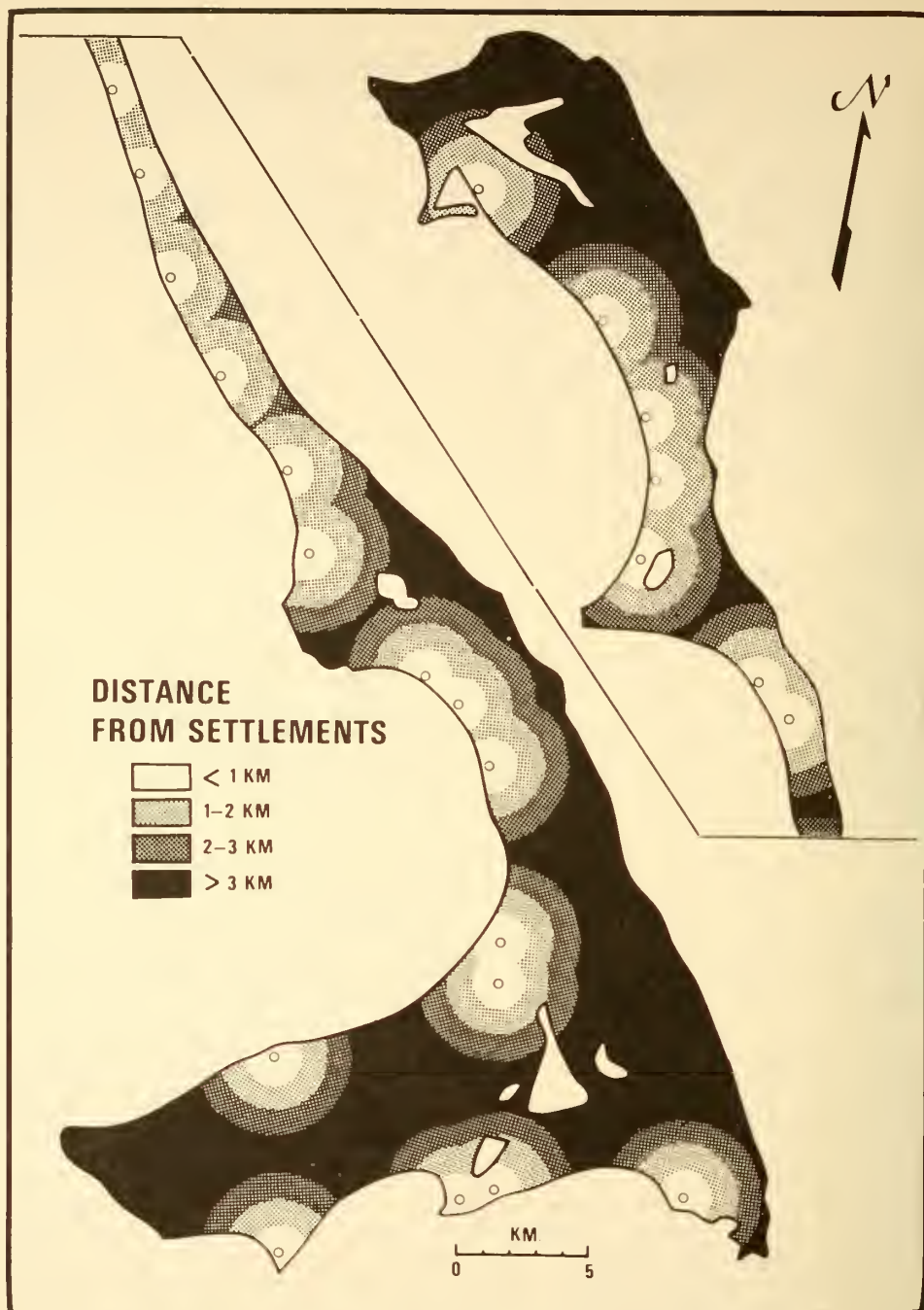as to age and to distance from the nearest settlement.

Figure 35. Map showing Distribution of Distance Classes

After initial analysis, it became clear that the fifth age-class (more than 50 years), and the fifth and sixth distance-classes (4 to 5 kilometers; 5 to 6 kilometers) did not have adequate sample coverage to make reliable interpretation possible. They were therefore combined with the fourth age-class and fourth distance-class, respectively. The areal distribution of the four distance-classes is shown in Figure 35.

Goats and the Woodland

Grazing and browsing by domesticated animals have drastically changed the vegetation of many parts of the world. Especially significant have been the changes brought about on small oceanic islands where native plants have evolved without defensive mechanisms against such pressures. On Cat Island, horses, hogs, sheep, cattle, and goats have all had an impact on the woodland. For several reasons, however, it was decided to limit the analysis to a study of the effects of grazing and browsing by goats.

Initial observations in the field suggested that of all the domesticates on the island, goats had probably had the most important influence on the floristic composition of the woodland. They were the most numerous domesticate, and unlike sheep, cattle, and horses, which only browse under duress, they are quite happy to eat the leaves of bushes and trees. They prefer young leaves, shoots, or seedlings, and in this way influence regeneration rates. A recently-grazed area has a characteristically "clean" appearance, the surface having been stripped of all herbaceous growth and seedlings (Figures 36, 37).

In order to determine the extent to which goats had modified the woodland, a working hypothesis was proferred. It was assumed that palatable species would be rarer close to the settlements than in remote areas, while the opposite would be true of unpalatable species. The first problem, then was to determine which species were palatable and which were unpalatable.

Palatable and unpalatable species.

Contrary to popular opinion, goats do have discriminating palates; some species they prefer and others they avoid. In order to determine these preferences, two approaches were used. First, local inhabitants, experienced in agricultural matters, were interviewed on the subject of goat-feeding habits. In this way, a basic check-list of preferred and

Figure 36. An area near Bennet's Harbour intensively grazed by goats. Note the Leucaena bushes in the center of the photograph have been browsed to a height of about one and a half meters. The other bushes in the foreground, Cassia bahamensis, are unpalatable to goats.

Figure 37. Another heavily grazed area near Bennet's Harbour. Cassia bahamensis is very common on the level ground where virtually no herbaceous growth has survived.

avoided species was set up. Second, the reliability of this
information was checked by offering the species in question
to hungry goats. Perhaps significantly, only five common
woodland species were found that the goats really like to
eat (Table 5). In contrast, 18 species were found that even
hungry goats refused to eat (Table 5). Most of the unpalat-
able species have strongly aromatic or poisonous leaves, the
spurge, legume, and myrtle families being well represented.

Floristic composition and distance.

        Because of the cost of wire, there are few fenced pas-
tures on the island, and as a result the goats have to be
tethered. This is necessary because of the threat they pose
to crops, and in turn means they have to be tended at least
once every other day. The goats quickly exhaust the accessi-
ble food supply and have to be moved to new areas. Also,
they have to be watered because of the lack of surface
water. Because they have to be tended so frequently, the
local people are reluctant to tether them too far from home,
and consequently the intensity of grazing pressure decreases
as a function of distance from the settlements.

        In order to determine to what extent grazing and brows-
ing had changed the woodland, the percentage cover values
for the palatable and unpalatable species were calculated at
the different distances from the settlements. The resulting
graphs are shown as Figure 38. Originally it was intended
to calculate the percentage cover values for each individual
species, but for the sake of simplicity they are presented
here as two groups.

        Reassuringly, the cover values show that, with a few
exceptions, there is a positive relationship between palata-
bility and distance, and a negative relationship between
unpalatability and distance. Furthermore, the species
included account for about 60 percent of the total area sam-
pled, so the curves can be taken as representative of the
woodland as a whole.

        In the youngest fields it is interesting to note that
the palatable species are less important than they are in
the older age-classes. This is probably due to the custom
of tethering goats in recently-abandoned fields. Just why
the unpalatable species are also less important is not easy
to explain. It may simply be due to the fact that such a
great number of species, not included in either group, are
present in the recently-abandoned fields. In spite of their
low values, the two curves show very nicely the expected
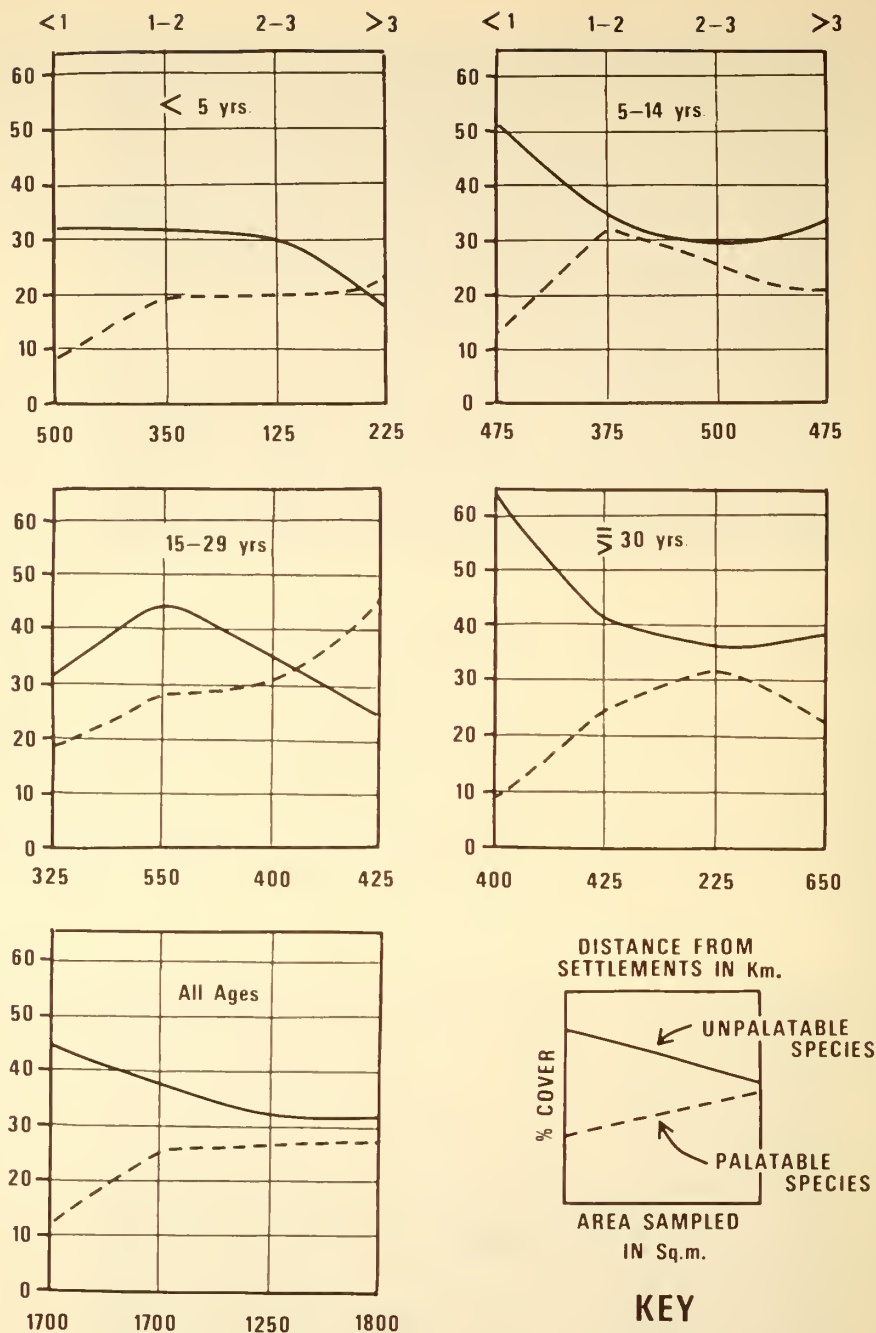relationship between grazing pressure and distance.

Figure 38. Graphs showing Age/Distance Unpalatable Species

TABLE 5

SPECIES INCLUDED IN THE ANALYSIS
OF BROWSING BY GOATS

Palatable Species

1. Torrubia longifolia
2. Acacia choriophylla
3. Leucaena leucocephala
4. Bursera simaruba
5. Pithecellobium keyense

Unpalatable Species

1. Corchorus hirsutus
2. Lantana bahamensis
3. Croton linearis
4. Gundlachia corymbosa
5. Croton bahamensis
6. Coccoloba diversifolia
7. Metopium toxiferum
8. Exostema caribaeum
9. Lantana involucrata
10. Cassia bahamensis
11. Eugenia buxifolia
12. Eugenia monticola
13. Bourreria ovata
14. Croton eluteria
15. Malphigia polytricha
16. Lysiloma bahamensis
17. Piscida piscipula
18. Croton lucidus

In the second age-class, the sample-sites less than 1 kilometer from the settlements show very definitely the expected relationship, with unpalatable species being roughly four times more important than palatable species.

However, at distances of more than 2 kilometers, the
unpalatable species show an unexpected decline, and after 3
kilometers increase again. No obvious explanation can be
offered for these changes, other than that some other vari-
able besides grazing pressure is involved.

Similarly, in the third age-class the percentage value
for the palatable species is anomalously low in the sites
closest to the settlements. This may reflect a somewhat
lower sample coverage in this category, although just how is
not clear. For the more distant sample sites, the curves
behave as expected, and suggest that the impact of grazing
is restricted to within 3 kilometers of the settlements.

For the older sample sites the curves show very well
the expected relationship in the first three distance
categories. Only in the more remote fields does the curve
for the palatable species drop unexpectedly. Again, this
must be attributed to some variable other than grazing pres-
sure, possibly increased competition from species not
included in the two groups, conceivably from species that
for other reasons are more important in remote areas, such
as economically-valuable species or species sensitive to
clearing and burning.

When all the different age-classes are combined, it is
interesting to note that the irregularities average out.
The resultant curves show a nice symmetrical arrangement,
which suggests that the impact of grazing is restricted to
within a zone less than three kilometers from the settle-
ments. At distances of more than three kilometers the aver-
age cover for the two groups is more or less constant.

The implications of the data.

The first point to be made is that the working
hypothesis was proved to be valid. Palatable species are
rarer in heavily grazed areas than in lightly-grazed areas,
while the reverse is true of unpalatable species. This
apparently obvious relationship was not immediatedly
apparent in the field, and only became clear after the
analysis of the data.

Also significant is the extent to which grazing and
browsing have modified the compostion of the woodland. The
woodland close to the settlements might be aptly described
as "goat-proof." Also, the fact that so many unpalatable
species could be identified in contrast to so few palatable
species was probably not fortuitous. Palatable species have
undoubtedly become rarer in the woodland around the

settlements. Whether or not this has actually happened can-
not be proved without historical evidence, but in view of
the data presented above, it seems more than likely that
this has been the case. Certainly if the goat population
declines it will be interesting to see how the woodland
recovers.

It is also interesting that grazing pressure is res-
tricted to a zone within 3 kilometers of the settlements.
This confirms the qualitative impression obtained in the
field, few goats being seen beyond this distance. On the
same point, it should be noted that just over two-thirds of
the sites sampled in the old field study fall within the 3-
kilometer limit. It follows, therefore, that the composi-
tion of the woodland as described in Chapter 8 has to a
large extent been determined by the goat.

The differences in the cover values between the dif-
ferent age-classes strongly suggest that the intensity of
grazing had varied in the past. For example, the palatable
species are generally more important in the 15- to 30-year
age-class than in any other age-class, even in the sample
sites more than 3 kilometers from the settlements. The pos-
sibility exists that the goat population was low during this
time period, although no local information was obtained
which suggested this had been the case.

The complicated nature of the data makes it difficult
to evaluate as far as individual species are concerned. It
is interesting to note, however, that the two dominants in
the older woodland, Coccoloba diversifolia and Metopium tox-
iferum, have very different cover values in the oldest age-
class. Even though both species are unpalatable, the former
decreases in importance away from the settlements while the
latter increases. Obviously some variable other than graz-
ing determines the importance of Metopium. For Coccoloba it
seems safe to assume that unpalatability is in large part
responsible for its variable importance in the woodland.

Other Domesticates

The goat is probably not entirely to blame for the
changes described above. Sheep, horses, hogs, and cattle
have all exerted selective pressures on the woodland,
although in each case the pressure has been different.
Sheep, for example, prefer herbs, and will only browse
reluctantly. Similarly, cattle and horses usually graze on
the whiteland, or seasonally-flooded savanna, and only
browse in the woodland during the dry season. Furthermore,
the number of woody species that horses find palatable is

limited.   The   leaves and pods of the leguminous shrub <u>Leu</u>-
<u>caena leucocephala</u>, that provide preferred   feed   for   goats
cause   horses to lose their hair and even hooves (Little and
Wadsworth, 1964).   Hogs have had an indirect impact   on   the
woodland   insofar   as the fruits and young leaves of several
palms are gathered for hog   feed.   <u>Pseudophoenix</u>   is   known
locally   as   the   "Hog-cabbage palm," and is now rare in the
woodland close to the settlements.   There were no feral hogs
on   Cat   Island in 1970, although they were reported to have
been common in the past.

Selective Cutting

Of all the pressures that man has exerted on the   wood-
land,   selective cutting was the easiest to define.   Most of
the species   involved   were   identified   in   the   historical
record, and those that were not were determined on the basis
of local information.   Out of the 120 species encountered in
the   sampling, 15 were known to have been selectively cut on
such a scale that their frequency in the woodland was   prob-
ably affected.   These consist of dyewoods, timber trees, and
species valued for fuel or fodder (Table 6).   The details of
their   use   were   discussed earlier and need not be repeated
here.   Suffice it to say that their value to   man   has   made
them vulnerable.

The selective cutting of economically valuable or   use-
ful species is basically a similar process   to   the   grazing
and   browsing of domesticated animals.   The species that are
cut decline in importance, while the species   that   have   no
value increase to take their place.   However, in the discus-
sion that follows, only the   former   are   included,   as   the
increase   in   species   that are not cut was less amenable to
analysis than was the increase in unpalatable species.   More
specifically,   it   was impossible to determine which species
increased at the expense of those that were selectively cut.
Originally it was intended to deal with each of the economi-
cally valuable species individually; however, because of the
limitations of time and space, they are here considered col-
lectively.

<u>Selective</u> <u>Cutting</u> <u>and</u> <u>Distance</u>

There are few roads on the island, and any heavy   loads
have   to be carried by horses.   Lighter loads are carried in
traditional African style, on the   head.   Either   way,   the
frictional   effect   of   distance   is strong, and as a result
remote areas of the woodland have been comparatively   undis-
turbed.   During   field   work   this   was   recognized   in   a

TABLE 6

SPECIES INCLUDED IN THE ANALYSIS
OF SELECTIVE CUTTING

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1. Caesalpinia bahamensis
2. Haematoxylum campechianum
3. Croton eluteria
4. Swietenia mahagoni
5. Lysiloma latisiliqua
6. Guiacum sanctum
7. Krugiodendrom ferreum
8. Mastichodendrom foetidissimum
9. Erithalis fruticosa
10. Pseudophoenix vinifera
11. Dipholis salicifolia
12. Amyris elemifera
13. Thrinax microcarpa
14. Callicarpa hitchcockii
15. Vallesia antillana

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qualitative way. The question remained as to whether or not the same effect would be shown in the old field data. As with the analysis of grazing and browsing, a working hypothesis was established which assumed that valuable species would be more important in remote areas of the woodland than in areas close to the settlements.

In the two youngest age-classes, the expected distribution is generally followed. The 15 species increase in importance away from the settlements. Even so, it is probably unwise to place too much weight on these curves, as the total values are so low (Figure 39).

As was the case with the palatable and unpalatable species, the third age-class (15 to 30 years) includes some anomalies. When compared with the second age-class (5 to 14 years), the first two distance-classes have increased cover values while the last two actually decline, just the opposite of what was expected. The species largely responsible for the high value in distance-class 2 is Erithalis fruticosa. Just why it should have been so important here is
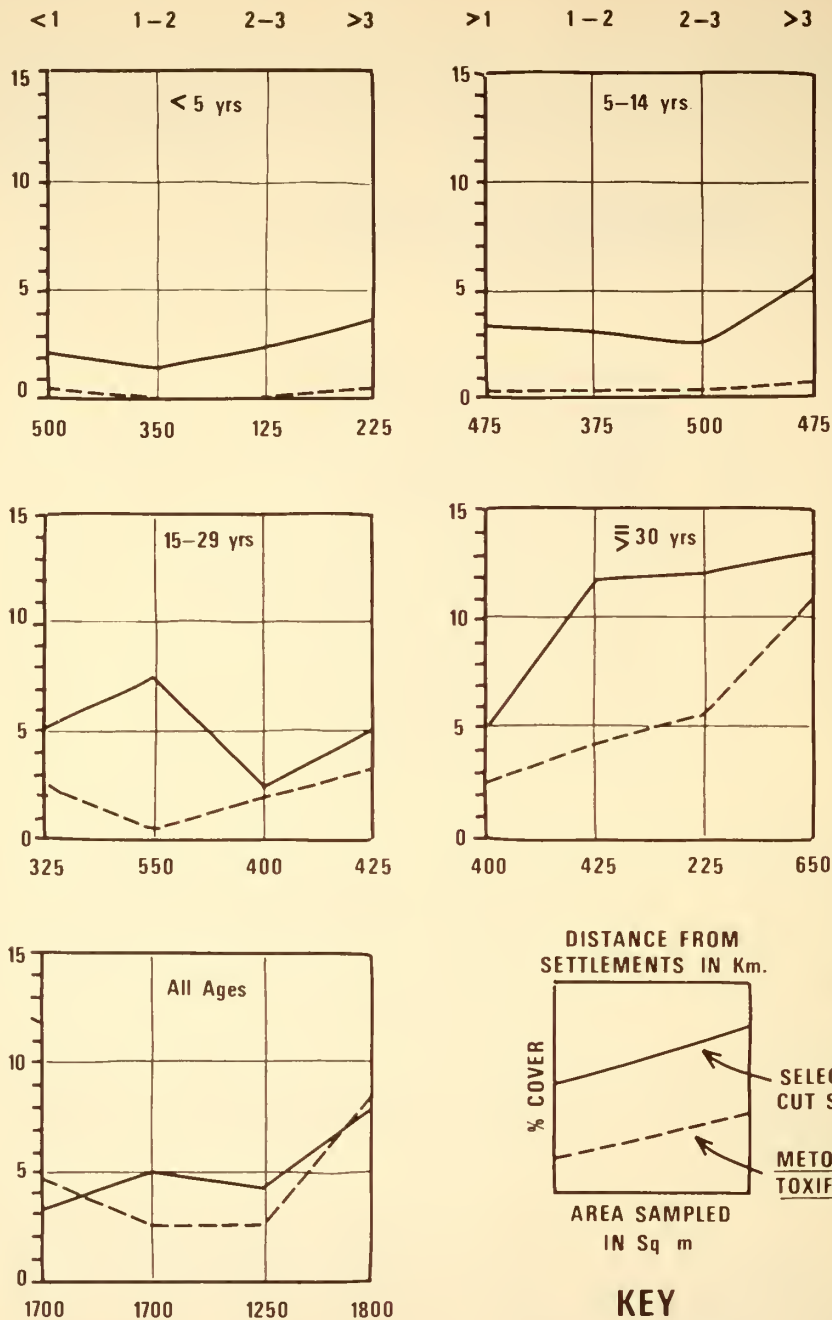
124

Figure 39.   Graphs showing Age/Distance Distributions of
              Selectively-Cut Species, and Metopium Toxiferum

not immediately apparent.

The oldest age-class very definitely shows the expected pattern. The cover-values for the sites less than 1 kilometer from the settlements are significantly lower than for the last three distance- classes. Furthermore, the cover-values for the last three classes are between 6 and 9 percent higher than in the previous age-class.

The composite curve showing all ages together shows approximately the expected distribution. However, its usefulness is questionable, because it masks what are very real differences between the different age-classes.

Implications of the Data

Again the working hypothesis was proved largely correct. The assumption that the selectively-cut species would be less common close to settlements than in remote areas is supported by the data. On the other hand, for the first three age-classes the total cover values for the 15 species are very low. This means that a relationship between distance and selective cutting cannot be clearly defined for the younger woodland.

It is interesting to speculate whether these low totals are themselves a result of selective cutting, although again without historical evidence this cannot be proved. It appears that the species involved do not have the ability to recover quickly after cutting. Certainly very few of the 15 species are common in recently-abandoned fields. In other words, they are more vulnerable to disturbance than are the common woodland species.

Somewhat surprising is the narrowness of the zone affected by selective cutting. In the oldest age-class, the impact is restricted to within a radius of 1 kilometer from the settlements. This probably reflects the general decline in demand for the 15 species during the present century.

Had the areas sampled been greater the whole question as to how significant have been the effects of selective cutting would be more easily answered. Unfortunately, many of the species that have been selectively cut are still rare, and because of this they were not encountered in the sampling. Fagara flava the dyewood, Buxus bahamensis the timber tree, and Canella alba the medicinal bark were each seen only once in the woodland. The statistical significance of rare species cannot be adequately measured in a broad survey of the kind undertaken here. In spite of their

limitations, however, the old field data do show something
of the consequences of selective cutting, and in view of the
fact that the demand for many of the species has declined in
recent years it should be interesting to monitor future
changes.

Combined Selective Pressures

Any analysis of the effect of selective pressures is
complicated by the fact that usually more than one pressure
has been involved. For example, clearing and burning, which
are non-selective in the sense that fields are established
without too much concern as to what species are present, are
selective insofar as they give an advantage to species that
can sprout or that have the ability to colonize recently-
abandoned fields. Furthermore, the frequency of clearing
and burning decreases with distance from the settlements in
generally the same way as the intensity of selective-cutting
and browsing. The net result is that several selective
pressures may be exerted on certain species at the same
time.

Originally it was hoped to analyse the impact of clear-
ing and burning in the same way as grazing, browsing, and
selective cutting, but unfortunately it was not possible to
isolate a group of species that would unambiguously show
this effect. It has only been possible to show the impact
of grazing, browsing, and selective cutting because the
species involved were known with certainty. This was not
the case with clearing and burning. Rather than avoid the
problem completely, the following discussion considers the
case of the poisonwood tree (Metopium toxiferum); as the
second most important species in the older woodland, its
distribution is worth considering.

Metopium toxiferum

Metopium, a close relative of poison ivy and poison
sumach, is characterized by a caustic sap poisonous to the
touch. It is a common tree in the older woodland, and grows
in a wide range of edaphic conditions, from the driest sites
to the wettest. As can be seen from Figure 39, it has an
anomalous distance distribution in the woodland.

In the first age-class (less than 5 years), it is rare,
and is only present in the areas closest to and furthest
away from the settlements. In the second age-class (5 to 14
years), its importance increases slightly while the same
distance pattern is maintained. In the third age-class (15

to 29 years), there is a significant increase in the cover values while again the species is more important in the first and last distance classes than in the intermediate classes. In the older age-classes (more than 29 years), there is a continued increase in cover values, although this time there is a progressive increase in importance away from the settlements. The composite age-values show the characteristic U-shaped distribution.

The variable importance of Metopium with distance from the settlements suggests several interesting possibilities. Its greater importance in the more remote areas suggests that it is sensitive to some pressure positively associated with the settlements. Metopium is cut on a small scale for its timber in certain parts of the West Indies (Little and Wadsworth, 1964: 290), although there is no evidence to suggest it has ever been exploited in the Bahamas (Coker, 1905: 205), and according to local reports it has never been cut on Cat Island. Selective cutting, therefore, does not account for the distribution.

A more likely explanation is that Metopium is sensitive to clearing and burning. Unlike many of the woodland species, it is not a prolific sprouter, and its seedlings were rarely seen in the recently-abandoned fields. Figures 28 and 31 suggest that it requires a certain amount of shade for successful germination. Assuming this to be correct, the question remains as to why the cover-values are higher in the sites closest to the settlements than they are in the intermediate classes. A plausible explanation here is that the species is unpalatable to the browsing animals. For obvious reasons it is avoided by goats and other domesticates.

The variable importance of Metopium in the woodland is therefore probably due to the interaction of at least two selective pressures. Unpalatability gives it an advantage near the settlements, while sensitivity to clearing and burning puts it at a disadvantage; in effect, each pressure is working in the opposite direction. The U-shaped distribution suggests that the unpalatability-advantage overrides sensitivity to clearing and burning near the settlements, but that the opposite is true at intermediate distances. Just why this should be so is not immediately apparent, but could easily be determined with more field work.

Obviously the combined effect of the selective pressures is going to be different for each individual species. A palatable species which happens to be economically valuable and sensitive to fire is going to be rare even in the remote areas of the island. An unpalatable species of no

use to man and with a vigorous sprouting ability is going to be common. Ideally, it would have been preferable to study the effects of selective pressures on three floristically similar islands: one that had only been grazed and browsed; one that had only been selectively cut; and one that had been cleared and burned for agriculture.   Unfortunately, three such islands do not exist.

Distance and Diversity

According to the hypothesis of insular vulnerability, the floristic composition of the woodland should have been significantly impoverished by grazing, browsing, selective cutting, clearing, and burning. The data discussed above hardly suggest that this has been the case.   In order to consider the question of impoverishment more closely, it was decided to compute the number of species present per unit area sampled in the different age and distance-classes.   The resultant totals are shown in Table 7.

TABLE 7

DIVERSITY, DISTANCE AND AGE

The average number of woody species
encountered per 25 x 1m^2 sample.

	KM. FROM SETTLEMENTS			
Less than 5 yrs.	15.70	15.21	15.00	15.20
5-14 yrs.	14.11	14.87	14.95	15.11
15-29 yrs.	11.62	10.68	11.56	10.41
30 yrs. or older	10.78	9.77	9.00	9.00
All ages	12.40	12.28	12.57	11.12

Significantly, there are no major differences in species diversity between the different distance classes. In fact, apart from the second age-class, the sample sites less than 2 kilometers from the settlements have slightly higher averages than those more than 2 kilometers away from the settlements.

The important conclusion to be drawn from this is that, although the species sensitive to selective pressures have become rare close to the settlements, they have been

replaced by a similar number of insensitive species. The discovery that so many native species are pre-adapted to withstand the impact of grazing, browsing, selective cutting, clearing, and burning was unexpected. The question as to why this is the case will be considered later.

XI. THE INVASION OF ALIEN PLANTS

Unlike the situation prevailing on remote islands such as the Hawaiian islands, comparatively few species of alien plants have become well-established in the Bahamas. Of the 120 woody species encountered during the course of the present study, only six were clearly identified as alien, and together they accounted for only 5 percent of the total cover.

The Species Involved

Leucaena leucocephala

Leucaena is a leguminous shrub with a pantropical distribution. Its original home is usually cited as Central America, although the details of its history are not clear. This is certainly so for the Bahamas. Its alien status is not confirmed by the historical record, but is strongly suggested by its localized distribution in artificially-disturbed habitats; characteristically it is a pioneer in abandoned fields, pastures, and roadsides.

It was probably introduced to the Bahamas in the early eighteenth century as a fodder crop. One of Catesby's plates (1731, II: 42) looks very much like Leucaena and is identifed as such by Britton and Millspaugh (1920: 162). However, the text clearly refers to the native Lysiloma leucocephala, so the determination remains doubtful. The naturalist Schoepf, who visited the islands in 1784, includes a Mimosa glauca in a check list of the more common plants, but gives no information as to its use or origin. Very likely the species he refers to is Leucaena leucocephala. On the other hand, there is surprisingly no mention of Leucaena in Brown's account of fodder plants in use on his plantation around the turn of the eighteenth century (1802:11). A plantation journal from Watlings Island for the year 1831 includes references to the planting of "cow bush" and "cow peas," but the identification of the species involved is not certain (Deans Peggs, 1957: v).

What is certain is that by the end of the nineteenth century Leucaena was widely distributed around the archipelago (Hitchcock, 1893:166). On Cat Island in 1970 it was locally common in recently-abandoned fields, pastures, and along roadsides.

Haematoxylum campechianium

Logwood is a thorny, leguminous tree with a rather shrubby habit. The heart-wood, which is deep reddish purple, is the source of the dye Haematoxylon. A native of Central America, logwood was widely introduced around the Caribbean during the late seventeenth and early eighteenth centuries (Wilson, 1936). Fortunately, there is a definite date for its introduction to the Bahamas. As was indicated earlier, Catesby reports that it was brought from the Bay of Honduras in 1722. As far as Cat Island is concerned, it seems likely that it was introduced by the loyalists at the end of the eighteenth century. Its present distribution is very localized in old plantation areas near Port Howe and Old Bight.

Manilkara zapota

The sapodilly is one of the most common fruit trees in the Bahamas. Supposedly Central American in origin, it was probably first introduced to the islands by the Arawaks. It is easily planted from seed in the Bahamas, and its fruits are characterized by a wide variability in size and shape (Morton and Morton, 1946: 88).

It was probably re-introduced to Cat Island in the late eighteenth century by the loyalist planters. In 1970 few families did not have at least one tree in their yard. In the woodland it is seen characteristically by the side of footpaths and only occasionally in the middle of a field. Presumably a large percentage of the woodland trees have grown from seeds, either intentionally planted or casually discarded. Both the fruit and seed are large and are probably not dispersed far by natural mechanisms.

Indigofera suffruticosa

Whether or not the New World indigo is native to the Bahamas is uncertain. It was cultivated in South America in pre-European times and may have been brought to the islands by the Arawaks (Harris, 1965). There are references to the cultivation of indigo around the turn of the seventeenth century, although what species was involved is not clear (Craton 1968: 89). The Asiatic indigo (Indigofera tinctoria) had probably been introduced by this time. Schoepf (1788) includes an Indigofera argentea in his list of common plants, and according to Britton and Millspaugh this is a synonym for the New World species (1920: 180).

In nineteenth century botanical literature, Indigofera suffruticosa (syn. I. anil) is recorded for several of the

Bahama Islands, although not for Cat (Hitchcock, 1893: 166).
It is certainly rare on the Island at present, and its alien
status is suggested by its localized distribution in
artificially-disturbed habitats.

Gossypium barbadense, G. hirsutum

Cotton is one of the few cultivated plants known to
have been introduced to the island by the Arawaks. However,
that it could have persisted the wild after the Arawaks left
seems doubtful. More than likely, the cotton seen in the
woodland today can be attributed to eighteenth-century or
even later introductions. At least four varieties were cul-
tivated in the nineteenth century: Anguilla, Flyaway, Bour-
bon, and Georgia (Johnston, 1867). The first three appear
to have been varieties of sea island cotton (G. bar-
badense), while the latter may have been a long-staple
variety of upland cotton (G. hirsutum). Both species are
listed in the Bahama Flora, although upland cotton is only
recorded for one island, Rum Cay (Britton and Millspaugh,
1920: 274). The species encountered on Cat Island in 1970
was sea island cotton. A weedy shrub, it was characteristi-
cally seen in disturbed habitats, such as roadsides or gar-
dens, and only occasionally in the woodland.

Heliotropium angiospermum

Unlike the five species discussed above, scorpion tail
has never been planted. A woody herb rather than a bush, it
is a widely-distributed tropical weed. Like many weeds its
origins are uncertain. However, its irregular distribution
in artificially-disturbed habitats strongly suggests that it
is not native to the Bahamas. It has been present on Cat
since at least the late nineteenth century (Hitchcock, 1893:
168), but was rarely seen in the woodland in 1970.

The Extent of the Invasion

One of the more important conclusions reached by Elton
in his The Ecology of Invasions (1958: 142) was that simple
communities are more prone to invasion than communities
which are rich in species. Harris reached much the same con-
clusion in his study of the Outer Leewards. He suggested
that the extent to which alien plants were able to become
established varied from place to place according to the his-
tory of disturbance and the floristic diversity of "ecologi-
cal resistance" of the native vegetation. Whether this was
also true of the Cat Island woodland was a basic question

considered in the analysis of the old field data. In the
discussion that follows, the three habitat-types types and
five age-classes are used as an organizing framework.

The Whiteland

As can be seen from Table 8, only 2 aliens were encoun-
tered in the whiteland samples, Leucaena and Gossypium, with
Leucaena being by far the most important. As was shown ear-
lier, Leucaena was in fact the third most important pioneer
on the whiteland only exceeded in the first two age-classes
by Gundlachia and Corchorus. In the third age-class it
replaces Corchorus to a certain extent, but it is still not
as important as Gundlachia. In the older woodland it
declines quickly (Figure 25).

The importance of Leucaena on the whiteland must in
part be attributed to planting. In the pre-automobile era a
great number of horses were grazed here, and it seems more
than likely that some of the Leucaena thickets owe their
origin to planting. Their persistence must in large part be
attributed to the species's ability to sprout. This method
of reproduction is especially effective in the loose sand
substrate. Clearing and burning have little impact on the
shrub, making it a troublesome weed (Figure 40). In
intermediate-aged fields, Leucaena usually forms dense
thickets 2 to 3 meters in height (Figure 41). The close
cover naturally prevents regeneration by other species.
However, as Table 8 shows, in fields over 30 years old it
accounts for only 2 percent of the average cover. What
appears to happen is that the taller, more deeply-rooted
shrubs, such as Coccoloba uvifera and Acacia buxifolia, gra-
dually extend their cover at the expense of Leucaena. If
clearing and burning were to cease and natural regeneration
allowed to take place, it seems unlikely that Leucaena would
be able tp persist.

Cotton (Gossypium barbadense) was the only other alien
encountered on the whiteland. It was seen only once and in
an area very close to the edge of the whiteland. Together
with Leucaena and Guilandina, it formed a dense thicket 3 to
4 meters high. According to the early historical accounts,
cotton never grew well on the whiteland, and there is no
evidence to suggest it was ever planted there in any quan-
tity. Although the data do not show it, cotton was more
frequently seen on the blackland and flatland than on the
whiteland. In either case, it accounts for a very small
part of the total cover.

Several other aliens were seen on the whiteland,

Figure 40. A whiteland corn field infested with <u>Leucaena</u>
<u>leucocephala</u>. This field, close to the edge of a
seasonally- flooded palmetto thicket, had been abandoned
because of the difficulty of eradicating <u>Leucaena</u> sprouts.

Figure 41. Here an older <u>Leucaena</u> thicket, probably 15-20
years old, is being replaced by native species. <u>Casasia</u>
<u>clusiafolia</u> is in the left foreground and <u>Coccoloba</u> <u>uvifera</u>
to the right and in the background.

TABLE 8

PERCENTAGE COVER ALIEN SPECIES

AGE IN YEARS	<5	5-14	15-29	30-50	>50
WHITELAND					
Leucaena.....	13.73	12.14	17.27	2.00	0.00
Gossypium....	0.00	0.00	0.80	0.00	0.00
Total	13.73	12.14	18.07	2.00	0.00
FLATLAND					
Leucaena.....	2.35	3.23	3.19	0.94	0.00
Haematoxylum.	0.00	1.30	7.25	0.67	0.00
Total	2.35	4.53	10.44	1.61	0.00
BLACKLAND					
Leucaena.....	3.62	2.08	3.40	0.36	0.08
Haematoxylum.	0.07	0.00	0.04	0.00	0.00
Manilkara....	0.00	0.00	0.00	0.19	0.95
Heliotropium.	0.03	0.13	0.00	0.00	0.00
Indigofera...	0.34	0.13	0.00	0.00	0.00
Total	4.06	2.34	3.44	0.55	1.03
ALL HABITATS					
Leucaena.....	5.05	3.46	5.87	0.75	0.04
Haematoxylum.	0.03	0.61	1.42	0.23	0.00
Gossypium....	0.00	0.00	0.14	0.00	0.00
Manilkara....	0.00	0.00	0.00	0.13	1.25
Heliotropium.	0.02	0.06	0.00	0.00	0.00
Indigofera...	0.17	0.00	0.00	0.00	0.00
Total	5.27	4.13	7.43	1.11	1.29

although they were not encountered in the sytematic sampling. The most important by far was <u>Casuarina equisetifolia</u>, the Australian Pine. Although usually restricted to a narrow zone just above the high tide mark, <u>Casuarina</u> has in certain areas escaped inland. It is occasionally seen along roadsides or in similar open habitats. Surprisingly, it has not been able to invade the recently-abandoned fields, although just what prevents it is not immediately obvious.

Also occasionally seen on the whiteland was sisal (<u>Agave sisalana</u>). Extensively cultivated in the latter part of the nineteenth century, it is still planted on a very small scale. Most of the sisal on the whiteland had the appearance of being planted, although some natural increase may have occurred. More conspicuous was its wild relative <u>Agave americana</u>, locally known as "the Bamboo". Its flowering stalk reaches a height of 10 meters or so, while its basal leaves are 2 meters tall.

Coconuts (<u>Cocos nucifera</u>) are often planted on the whiteland, usually as a means of satisfying government regulations, which require "improvement" of land grants. However,the coconut is definitely a cultigen here and no natural regeneration occurs.

Overall, very few woody aliens have been able to successfully establish themselves on the whiteland. <u>Leucaena</u>, which was formerly planted as a fodder crop, is the only alien to have become an important part of the wild vegetation.

The Flatland

Again, on the flatland only two aliens were encountered in the systematic sampling, <u>Leucaena</u> and Logwood. Taking the five age-classes as a whole, <u>Leucaena</u> was slightly more important than Logwood in both absolute and percentage terms (Table 8).

On the flatland the indurated rock surface makes the ability to reproduce from sprouts less advantageous than on the whiteland, and perhaps because of this, <u>Leucaena</u> is less important. Competition from the greater number of species adapted to this habitat has probably also been a factor. Whatever the reason, <u>Leucaena</u> covers a much smaller area of the woodland than it did on the whiteland. On the other hand, in terms of importance in different age-classes the pattern is much the same. It also seems likely that if clearing and burning were to cease, <u>Leucaena</u> would not be

able to persist for long.

The cover values for logwood cannot be properly inter-
preted without some further information. Logwood has a very
localized distribution on Cat Island. It was seen to be
especially common in the areas east of Old Bight and north-
east of Port Howe. It was never encountered in the northern
half of the island, where most of the sampling was carried
out. This localized distribution, undoubtedly the result of
its comparatively recent introduction, has meant that the
average values in Table 8 are somewhat misleading. In the
areas where it was encountered it was very common, but the
averages are low because over much of the island it has not
yet become established. Whether it will or not in the
future is another question.

The difference in the cover values for logwood in the
different age-classes is probably a reflection of the his-
tory of land use in the areas sampled. For example, in a
large flatland area east of Old Bight, logwood trees 3 to 4
meters tall were surrounded by a great variety of native
shrubs and small trees. Logwood regeneration was very poor,
although twenty to thirty years ago it had apparently been
good. This change in the woodland probably reflects a
decrease in the intensity of land use in the area. As over
the rest of the island, in the fifteen years between 1943
and 1956 the area under cultivation decreased significantly,
and since 1956 it has declined even further. In open condi-
tions thirty years ago, logwood was able to reproduce well,
but since then it has been less successful and the native
species have had a chance to recover. Furthermore, in the
continued absence of disturbance, it seems likely that log-
wood will not only have difficulty in reproducing but will
be outshaded by the taller native species such as poisonwood
(Metopium toxiferum) and pigeon plum (Coccoloba diversi-
folia). Both were actually seen to be growing up through
the laterally-branching arms of the logwoods. It is prob-
ably significant that logwood was not encountered in the
older woodland.

Although logwood was planted in the past, it seems
likely that most of the present growth is spontaneous. The
demand for the dyewood declined in the late nineteenth cen-
tury, and it probably has not been planted since. Even so,
it is still recognized locally as a valuable tree and is
spared because of this during clearing and burning.

Again, as on the whiteland, several aliens were seen
that were not encountered in the systematic sampling. Par-
ticularly common are the two fiber plants, sisal (Agave
sisalina) and bowstring hemp (Sansevieria sp.). Fruit trees

such as the sapodilly (Manilkara zapota), mango (Mangifera indica), tamarind (Tamarindus indica), and genip (Melicoccus bijugatus) were occasionally seen, although most of them had the appearance of being planted. The pawpaw (Carica papaya) was seen, both planted and wild, in cultivated or recently-abandoned fields. Overall, however, aliens have been less successful on the flatland than on the whiteland.

The Blackland

Five aliens were encountered on the blackland (Table 8). The higher number can probably be attributed to the greater area sampled here. Leucaena has similar cover values to those recorded on the flatland and was generally observed to have the same patchy distribution. Logwood was much less important. In part, this may be due to thin sampling in the area where logwood is ill-adapted to the more mesic blackland habitat. In its natural habitat in British Honduras, logwood grows on the low, seasonally-flooded areas of the coastal plain (Wilson, A.M., 1936). The sapodilly was the only alien encountered whose importance increased in the older age-classes. Unlike the others it is capable of reaching a size equal to most of the native species. According to Britton and Millspaugh it is "spontaneous after cultivation" in the Bahamas (1920: 324). However, as was indicated above, its ability to reproduce independent of man was not clearly established on Cat Island, and, as the old field data indicate, it has made little progress in the woodland.

The two doubtful aliens, Indigofera and Heliotropium, were each encountered only twice and therefore account for a very small fraction of the total cover. Furthermore, they were very rarely seen elsewhere in the woodland. Both are restricted to recently-abandoned fields and will be replaced when natural regeneration takes place.

All the aliens listed above as seen but not sampled on the whiteland and flatland, were also present on the blackland, as also were Acacia farnesiana and Euphorbia lactea. None, however, were of anything more than local importance or showed any indication of becoming permanently established. In total, aliens were even less important on the blackland than on the flatland.

The Woodland as a Whole

In general terms the conclusion reached by Elton and Harris, that success of aliens is determined by the

diversity of the native vegetation, is supported by the data
presented above. The progressive increase in the importance
of aliens from the blackland, to the flatland, to the white-
land is inversely proportional to the floristic diversity of
the native vegetation. Just why this should be so is not
immediately apparent. In part it appears to be determined
by the behavior of only two of the aliens, Leucaena and log-
wood; the former appears to be well-adapted to the white-
land, while the latter is well-adapted to the flatland.
Competition from native species is probably not as important
as the diversity hypothesis suggests. Leucaena, for exam-
ple, is more important on the blackland than the flatland in
three of the five age-classes.

The significant conclusion is that alien plants have
had limited success in the woodland. In spite of repeated
clearing, burning, and grazing, very few species have been
able to get established. Furthermore, the area they cover
is small and their presence promises to be ephemeral. This
situation contrasts sharply with that in the Outer Leewards,
where, according to Harris (1965: 59), aliens "exceed
natives in total mass of vegetation over extensive areas,"
or in Barbados, where Watts (1970: 100) has reported that
aliens are dominant in certain grassland areas, secondary
woodland, and thickets.

XII.   THE STABILITY OF THE WOODLAND

In view of the supposed vulnerability of island life, the most unexpected characteristic of the woodland to emerge from this study is its capacity to recover from disturbance by man.   In spite of almost a thousand years of clearing, burning, selective cutting, and, more recently, grazing and browsing, the woodland has survived. This is not to suggest that it has survived unchanged. Sensitive species have become rare, while species pre-adapted to disturbance have increased in importance. In fact, the present stability of the woodland may in large part be the result of man having given a selective advantage to weedy types.   Even so, the surprising fact remains that so many of the native species are inherently weedy. Furthermore, there is no concrete evi- dence that any one species has become extinct. This does not, of course, preclude the possibility of extinctions in the prehistoric period, but it does provide a marked con- trast with the Hawaiian Islands, where literallly dozens of species are known to have either become extinct or be seri- ously threatened with extinction (Fosberg, 1971: 6). The possible reasons for the unexpected resilience of the Cat Island woodland are the subject of the present chapter.

Adaptations to Clearing and Burning

In spite of a seasonally-dry climate and thin or non- existent soils, the woodland recovers very quickly after clearing and burning. The woodland is in fact inherently weedy.   This weediness can be considered in three different contexts: seed dispersal, seedling establishment, and regen- eration from sprouts.

Seed Dispersal

The discontinuous existence of an offshore archipelago such as the Bahamas, or indeed the West Indies as a whole, must have had an important influence on the evolution of plant-dispersal mechanisms. The Bahamas are not remote islands such as the Hawaiian Islands or the Galapagos; they are close to each other, and to Florida and the Greater Antilles. Ocean currents reach them after having passed through the whole of the Antilles. They are frequently crossed by hurricanes and other tropical storms. Further- more, many migrating birds spend their winters in the islands, or at least visit them on their way north or south. With all these means of dispersal regularly available, the

arrival of a viable seed in the Bahamas is not the rare, chance event it is in Hawaii.

A great many of the woodland species are prolific berry-producers, an obvious adaptation to dispersal by birds. The vast majority of woodland species are adapted to dispersal by birds, a small number are wind dispersed, and an even smaller number are adapted to dispersal by ocean currents. Unlike many plant species, which on reaching remote islands have had the efficiency of their dispersal mechanisms reduced (Carlquist, 1965: 241), the species in the Cat Island woodland have retained efficient dispersal mechanisms.

The relevance of all this to the present study is that a recently-cleared field is in fact an "island" in the ever-green woodland. The existence nearby of so many species pre-adapted to reach islands accelerates the rate of succession. If the intensity of the "seed rain" on abandoned fields on Cat Island could be measured, it would undoubtedly be high.

Seedling Establishment

Weediness involves more than prolific seed-production and efficient dispersal mechanisms. The ability to grow in droughty, disturbed habitats is also important. Recently-cleared fields in the woodland are certainly droughty and disturbed habitats. In fact, on first sight it is hard to imagine that any plant, wild or cultivated, could survive in such a difficult environment (Figure 42, 43). The existence of so many native species that can raises the question as to where they developed this ability. On Cat Island there are at least three possibilities: the savanna/evergreen woodland transition, the mangrove/evergreen woodland transition, and active sand dune situations.

The savanna/evergreen woodland transition. Around the upper margins of the seasonally- flooded savanna is a zone that is only flooded after exceptionally heavy rains, perhaps once every four or five years. Here woody growth is possible on a short-term basis only, and the only species able to survive are those capable of quick dispersal and establishment on what is virtually a bare limestone surface (Figure 44). Gundlachia corymbosa and Tabebuia bahamensis, both wind-dispersed species, are common in these areas, as also is Torrubia longifolia, a prolific berry-producer. All three are also important in the early stages of succession on the abandoned fields. Randia mitis, Byrsonima cuneata, and Evolvulus squamosus are also often encountered in this

Figure 42. A recently burned blackland field. The area
where the man is standing is the lowest part of the field
and therefore has the thickest accumulation of ash, probably
10 to 15 centimeters. On higher ground the surface is more
than 75 percent bare limestone.

Figure 43. A two year old blackland field. The rocky
nature of the blackland surface is well shown here. Most of
the regeneration is a result of sprouting. As the photo-
graph was taken in early June crops are not yet visible.
The banana in the background is the only exception.

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Figure 44.   Savanna/woodland   transition.   This indicates
something   of   the   naturally   open   aspect   of   the
savanna/woodland transition. Herbs on the lower ground give
way to palmettoes (Sabal palmetto) and hardwoods on the
well-drained sites. The two saplings that have become esta-
blished in the foreground are: Torrubia longifolia in the
center ad Tabebuia bahamensis to the right.

Figure 45. Mangrove/woodland transition. Along the   center
of this photograph is the normal high tide mark. On the
lower ground to the left is Rhizophora mangle. To the right
are plants adapted to brackish conditions, Gundlachia corym-
bosa in the foreground and Coccoloba uvifera in the back-
ground.

environment, although of these only <u>Randia</u> was commonly seen in the old fields.

The seasonally-flooded savannas cover only a small area of Cat Island at present (Figure 22), but they were probably more extensive in the past, particularly when the Bahama Banks were only slightly above sea level. Looking at the North American subtropics as a whole, it seems likely that the savanna/woodland transitional zone has been an important breeding ground for weedy types.

<u>The salt water/evergreen woodland transition</u>. Inland from the salt-tolerant vegetation of the coast and tidal flats, there is a transitional zone in which only the most drought-resistant of the woodland species can grow (Figure 45). Not only are these areas periodically washed with salt spray, but the fresh water lens is either thin or non-existent. During droughts, the only source of fresh water is condensation in the form of dew.

The floristic composition of this transitional zone appears to be largely determined by the nature of the sub-strate. On the loosely-consolidated dunes and beach ridges, several pioneer species are found, such as <u>Lantana involu-crata</u>, <u>Corchorus hirsutus</u>, <u>Croton linearis</u>, <u>Gundlachia corymbosa</u>,and <u>Salmea petrobioides</u>. On the harder Pleisto-cene surfaces, small trees are more common. Figure 46 shows the species present on a low Pleistocene beach ridge. In both environments, the salt water/evergreen woodland transi-tion is an important breeding ground for old field pioneers. The naturally droughty nature of the surface is basically similar to the surface of a recently abandoned-field.

<u>Active sand dunes</u>. There are no active sand dunes on Cat Island at present. A few small blow outs were observed on the Holocene dune ridges, but, in each case, in an area disturbed by man. The three dune ridges that comprise such a large part of the island are all fossil features. In spite of this, active sand dunes have probably played an important role in the development of weediness in Bahamian vegetation. Dune formation and erosion was a characteristic feature of the Bahamian environment even before the sea-level oscilla-tions of the Pleistocene. Furthermore, in several not very remote areas of the West Indies, there are dune systems still active today; for example, along the northern coast of Puerto Rico, where many of the Cat Island old field pioneers, or their congeners, are present in the sand dunes (Cook and Gleason, 1928).

Not all the old field pioneers have been accounted for in this brief survey, but the implication is clear.

KEY TO FIGURE 46

1. Rhizophora mangle
2. Laguncularia racemosa
3. Conocarpus erecta
4. Erithalis fruticosa
5. Gundlachia corymbosa
6. Rachicallis americana
7. Reynosia septentrionalis
8. Coccoloba diversifolia
9. Metopium toxiferum
10. Casasia clusiafolia
11. Pithecellobium keyense
12. Torrubia longifolia
13. Jaquinia keyensis
14. Coccothrinax argentea
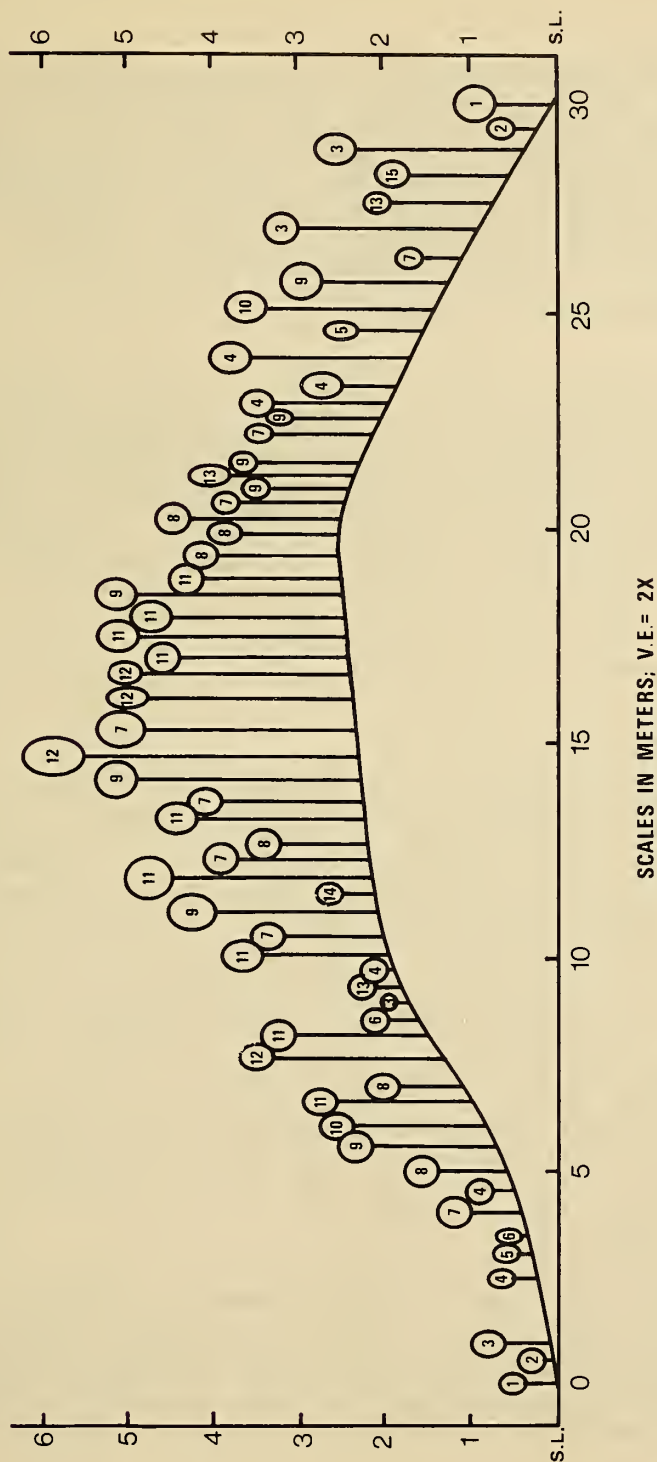15. Manilkara jaimiqui

SCALES IN METERS; V.E.= 2X

Figure 46. Diagram showing the Floristic Composition across a Low Limestone Ridge

Naturally open, droughty, or unstable habitats have always existed on Cat Island, and in similar environments throughout the North American subtropics. Certain plant species have adapted to these habitats, and when man created similar habitats they simply expanded their range. As has been shown elsewhere, the expansion of naturally weedy types into artificially-disturbed habitats is a widespread phenomenon (Sauer, J.D. 1950; Anderson, 1952).

Regeneration from Sprouts

Clearing is rarely complete. A great many native woodland species have the ability to sprout vigorously after cutting and burning. If a field is severely burned, all the pre-existing species may be killed. But this is rarely the case; most farmers are reluctant to burn too deeply because it results in lower yields. Consequently, sprout weeding occupies a large part of the farmer's time during the first year of cultivation. After a field is abandoned, any surviving sprouts have an obvious advantage over seedlings. Usually they can be identified by the way they project over the general level of the vegetation. The rapid recovery of the woodland after cultivation can in large part be attributed to the fact that so many species can reproduce from sprouts.

Sprouting ability is probably, in part at least, an adaptation that has developed as a response to breakage by hurricane-strength winds. Craighead (1962:17) has described how many of the tropical hardwoods in southern Florida recovered quickly after defoliation and breakage during hurricane Donna. Among the trees that responded most rapidly with new leaves were Lysiloma bahamensis, Bursera simaruba, Coccoloba diversifolia, Swietenia mahagoni, and Zanthoxylum fagara (syn. Fagara pterota). Significantly, all of these species are common in the old fields on Cat Island.

Lightning fires have also played a role in developing the ability to sprout. In southern Florida, it is now recognized that lightning fires have had an important influence on the development of the natural vegetation (Robertson, 1962). Furthermore, many of the tropical hardwoods have the ability to reproduce from sprouts. As Craighead has indicated:

> When fires destroy these hammocks..some roots usually survive. The regeneration from root suckers produces a new stand that is practically identical to the old. Repeated fires, however, destroy all of the hardwoods in time (Craighead, 1971: 157)

Even though lightning fires have not been common on Cat Island in the recent past, it seems unlikely that this has always been the case. Repeated clearing, burning, and grazing have prevented the accumulation of litter, and therefore reduced the chances of fire. In pre-human times, windfall and a deep litter accumulation would have provided ample fuel for lightning fires. Significantly, fires are especially severe in the southern Florida hardwood hammocks during the dry season after a hurricane. At such a time the accumulation of dead wood on the ground provides an ideal condition for fire.

Lightning fires and hurricanes have therefore both played a role in the development of sprouting ability. This background of natural disturbance has, in effect, preadapted the woodland to withstand many of the types of disturbance introduced by man. Because so many species have the ability to regenerate from sprouts, the impact of shifting agriculture has not been as drastic as it might have been otherwise.

Resistance to Grazing and Browsing

In view of the fact that no grazing or browsing mammals are native to the Bahamas, it was surprising to find that so many species were unpalatable to goats. The situation on Cat Island is very different to that on Three Kings Island, New Zealand, where goats have reduced a floristically diverse woodland to a woodland composed of only one species (Turbott, 1963) or on St. Helena, where goats brought about the complete removal of woody species (Darwin, 1839:486-487).

Just why so many species should be resistant to grazing and browsing pressures on Cat Island was not immediately obvious. The unpalatable species are unpalatable because of several reasons: some are poisonous, some are strongly aromatic, and some are armed with sharp spines or stinging hairs. More than likely, these characteristics developed in response to many pressures, of which grazing by mammals is only one.

Seasonal drought may have played a role in the development of essential oils, which assist in water conservation by reducing evaporation rates. Similarly, spiny leaves are also often regarded as an adaptation to droughty conditions. Insect larvae consume a considerable volume of plant material every year, and must have played a significant role in the evolution of the woodland species. Mammals may also have been important. Many of the trees and shrubs now found

in the evergreen woodland were formerly present in what is
now the south central United States. Presumably they could
have developed defensive mechanisms against grazing there.
Even today, deer browse in the floristically similar wood-
land on the Florida Keys (Craighead, 1971: 97).

The whole question is a complicated one and rather than
speculate further the point might simply be made that many
woodland species are pre-adapted to withstand grazing and
browsing by domesticated animals.

Resistance to Invasion by Alien Plants

In spite of repeated disturbance, very few alien plants
have been able to establish themselves in the woodland.
There are probably three basic reasons for this: the nature
of the woodland as an environment for plant life, the nature
of the aliens that have been introduced, and the lack of
efficient dispersal mechanisms.

Life in the evergreen woodland poses many problems that
each alien species must be able to cope with. As has been
repeatedly stressed, this low limestone island is in many
ways a difficult, environment for plant life. For the
native species it is not difficult because they have adapted
to it and similar environments over a geologically long
period of time. This is not the case with most aliens.
Drought, hurricanes, fire, an almost pure limestone surface,
and a diverse array of plant pathogens are all natural
hazards that any alien species must cope with if it is to
become permanently established. Superimposed upon all this
is the problem of competition with the native plant species,
with their prolific seed production and rapid growth rates.

The difficulties facing alien plants in the Bahamas are
well illustrated by the repeated failure of attempts to
establish commercial crops. Cotton, citrus, tobacco, and
sisal have all failed commercially, either because of an
insect pest or some other environmental problem (Mooney,
1905). Even with help from man, life in the Bahamas is too
difficult for a great many invaders. Perhaps significantly,
the only two successful aliens, Leucaena and Haematoxylum,
are native to environments not too different from the Baha-
mas.

On the other hand, the general failure of aliens to
invade the woodland must in large part be attributed to the
nature of the aliens themselves. Most of them have been
cultigens, incapable of spreading far without help from man.
The herbaceous weeds that have been introduced are largely

restricted to open habitats, such as roadsides and gardens. Yet, paradoxically, even though the woodland has been repeatedly disturbed by man, very few aliens have been able to get established. This raises the question of dispersal mechanisms.

Cattle have never been numerous on Cat Island. This has meant that an important plant-dispersal mechanism has been missing. Cattle have not played the role they have in parts of the West Indies, that of reducing the importance of native species and increasing the cover of aliens.

All of this does not necessarily mean that there are no species in existence which, given a chance could become permanently established in the woodland. For example, there are woodland species that grow on other Bahamian islands but not on Cat which presumably could become established if they were introduced. Looking further afield, it seems more than likely that there is a long list of potentially successful immigrants. Aliens can succeed without help from man, as Casuarina has shown along the coast.

The Significance of Diversity

Since Darwin's time, the assumption that diversity is synonymous with stability has been generally accepted. Darwin originally emphasized the importance of diversity because he was impressed by the success of continental species on oceanic islands. However, as has been shown more recently, the success of continental species on oceanic islands can largely be attributed to prior disturbance by man (Allen, 1936; Egler, 1942; Harris, 1962). In other words, most aliens do not have a competitive advantage because they evolved in floristically and faunistically more diverse environments; their advantage is due to the fact that they have evolved to withstand the types of disturbance associated with man.

In many parts of the world man has brought about a marked reduction in diversity. Natural vegetation that was floristically diverse has been replaced by secondary vegetation consisting of relatively few species. Surprisingly, on Cat Island this does not appear to have been the case. There are no significant differences in diversity between the remote, relatively undisturbed areas of the woodland and the areas close to the settlements. In fact, if the woodland is considered as a whole, man has actually increased its floristic diversity by the introduction of alien species. Although the number of aliens that have become established is not large, it probably exceeds the number that have

become extinct. The question whether the woodland is more stable now than it was in presettlement times is difficult to answer. Presumably it is more resistant to the types of disturbance introduced by man, but on the other hand it may be less resistant to natural forms of disturbance, such as hurricanes or disease outbreaks.

It is probably true to say that the importance of the relationship between diversity and stability has been over-emphasized in recent island studies. Diversity offers a collective advantage in the face of selective pressures such as insect pests, but means little where large-scale pressures such as clearing and burning are concerned. The resilience of Cat Island woodland is not due to floristic diversity, but to the fact that so many species are preadapted to withstand the types of disturbance introduced by man.

The Nature of Insularity

The anomalous resilience of the woodland can also be attributed to the imprecise meaning of the word island. Some islands are more insular than others. Before the arrival of man, remote islands such as the Galapagos or the Hawaiian islands were colonized by rare, chance migrations. The successful colonists evolved in isolation, and often diverged to form new species or even genera. These endemics are by their very nature vulnerable, and because of their limited numbers are likely candidates for extinction, regardless of their reproductive capacities or ecological tolerances.

On the other hand, islands such as Cat or indeed any island in the Bahamas or West Indies, are not characterized by endemic populations.[1] As far as plants are concerned, a constant interchange of seeds and pollen retards the evolution of new types.[2] Most of the species encountered in the Cat Island woodland are widely distributed around the North American subtropics. Each species consists of a large number of individuals, and the chances of extinction are therefore reduced.

1. On this point it is interesting to note that Taylor (1921) attributed the low rate of endemism in the Bahamian flora, less than 15 percent, to the geological youthfulness of the islands. As has been emphasized above, this has probably not been an important factor.
2. On several occasions, while at the northernmost point of Cat Island, a constant stream of butterflies, notably cloudless sulphurs (Phoebis spp.) and the Gulf fritillary (Agraulis vanillae), was seen being blown towards Eleuthera by the Trade Winds.

Insularity and, therefore, vulnerability depend not so much on distance, or the past presence or absence of land bridges, but on accessibility in terms of plant and animal dispersal capacities. Cat Island, like most islands, is much less accessible to animals than it is to plants. Its fauna is therefore impoverished, and the extinction of only a few species has a greater overall significance. The implication of all this is that the vulnerability of island life varies, not only from island to island, but from species to species. Vulnerability is a more variable factor than has generally been recognized.

Three recent studies in the Lesser Antilles have all emphasized the importance of limited accessibility as a basic reason for vulnerability (Harris, 1965; Watts, 1966; Merrill, 1958). While this may be true as far as animals are concerned, it seems unlikely that it is also true for plants. The Lesser Antilles are close to each other and to the continent of South America. Like the Bahamas, they are not inaccessible in the same way as Hawaiian Islands or the Galapagos. On the contrary, their accessibility has probably played an important role in decreasing their vulnerability to disturbance by man.

The Variable Intensity of Man's Impact

As a final point in this general discussion of the stability of the woodland, it should be emphasized that the human population density on Cat Island has always been low. As can be seen from Table 9, Cat is virtually uninhabited when compared to the islands of the Lesser Antilles. Barbados, for example, has 529 inhabitants per square kilometer, in contrast to only about 13 per square kilometer on Cat.

The significance of the low population pressure is that man's impact on wild vegetation has been less intense on Cat Island than it has been elsewhere. On Barbados, the woodland was almost completely cleared before the end of the seventeenth century (Watts, 1966: 45), and today some 50 percent of the cultivable land is permanently in sugar cane (Gourou, 1961: 211).

The high population densities that are characteristic of so many islands must be considered in any discussion of insular vulnerability. As Merrill (1958), Harris (1965), Watts (1966), and Kimber (1968) have indicated, the native plant and animal life of the Lesser Antilles has been drastically disturbed by man. The question arises, then, to what extent the degree of disturbance is due to an inherent vulnerability on the part of the plants and animals, and to

TABLE 9

AREA AND POPULATION OF SMALL WEST INDIAN ISLANDS, 1950-1958

(Gourou, 1961:208-209; *Sharer, 1955:92)

	Area in sq. km.	Population	Inhabitants per sq. km.
Barbados	431	235,000	529
Grenada	340	91,000	267
Martinique	988	239,000	240
Saint Vincent	340	81,000	238
Saint Thomas	68	14,000	205
Montserrat	80	14,000	177
Saint Christophe	175	30,000	169
Anguilla	85	14,000	164
Guadeloupe	1,503	229,000	150
Sainte Lucie	620	92,000	148
Tortula	30	7,000	140
Antigua	440	57,000	130
Saint Barthelemy	21	2,354	120
Saint Martin	52	5,377	103
Marie Galante	150	15,182	101
Nevis	140	11,300	88
Dominica	790	65,000	80
Sainte Croix	205	14,000	68
Desirade	27	1,654	46
CAT ISLAND*	240	3,000	13

what extent to the density of human population. In a sense it is misleading to compare the extent of change on a small, densely-populated island with that on comparatively uninhabited continental areas. Islands are vulnerable in the sense that they may become densely populated. This does not necessarily mean that island life is inherently more vulnerable to disturbance than that on the continents. The variable intensity of man's impact complicates any comparative analysis of insular vulnerability.

In conclusion, the stability of the woodland is the result of many factors. Basically, it reflects a long period of adaptation to natural disturbances: hurricanes, fires, sea-level change, erosion, and deposition. Because the woodland species are adapted to these various types of disturbance, man's impact has been less important than it would have been otherwise.

XIII. REVIEW AND CONCLUSIONS

The main purpose of this study was to determine the extent to which man has modified the vegetation of a small island in the Bahamas, Cat Island. In a broader sense, the question was considered whether or not the vegetation of Cat Island was vulnerable to culturally-induced disturbance in the same way as the vegetation of remote islands, such as the Hawaian Islands or the Galapagos.

The nature of man's impact on vegetation of Cat Island was determined by the use of both historical and ecological evidence. Particular attention was given to the mixed evergreen-deciduous woodland that covers most of the island.

The historical record for the Bahamas in general, and for Cat Island in particular, is frustratingly thin. Even so, the evidence recovered clearly shows that the Bahamas have not escaped the processes of change that have affected nearly all tropical islands during the period of human settlement. In the comparatively short period of a thousand years, the Cat Island woodland has been drastically disturbed by clearing, burning, selective cutting, grazing, and browsing. Unfortunately, the historical record is painfully qualitative and gives no clear indication as to what the consequences of this disturbance have been. In order to remedy this deficiency, a detailed analysis was made of the present woodland.

As no previous work of this kind had been attempted for this type of vegetation, it was necessary to develop what was basically a new methodology. With the aid of aerial photograph coverage for the years 1943 and 1958, 300 sampling sites were established, and at each site the percentage cover in 25 x 1 square meter quadrats was determined. These data were then analysed to determine the extent to which the floristic compostion of the woodland varied with respect to age and intensity of disturbance.

The most important conclusion to be drawn from the analysis was that the Cat Island woodland is remarkably well-adapted to withstand the types of disturbance introduced by man. This resilience is shown in three basic ways. First, a great number of native trees and shrubs are capable of quickly colonizing disturbed habitats as abandoned fields. Second, there is no evidence to suggest that any particular species has become extinct. And third, with few exceptions, alien plants have not been able to establish themselves in the woodland.

On the other hand, the woodland has not persisted unchanged since pre-settlement times. As a result of clearing, burning, selective cutting, grazing, and browsing, sensitive species have become rare, and have survived as important members of the woodland only in remote, relatively undisturbed areas. Conversely, weedy types have increased in importance; formerly restricted to naturally-disturbed or droughty habitats, they have expanded into the areas disturbed by man. This sequence of events is not a new one. The same changes have occurred wherever vegetation has been disturbed by man. What is unusual about the evergreen woodland is that such a large proportion of the species present are inherently weedy.

All of this does not mean that the hypothesis of insular vulnerability should be rejected. The high rate of extinctions on the Hawaiian islands and the Galapagos is indisputable evidence of vulnerability. The important point is that islands vary in their vulnerability as also do different species on any particular island.

The differences between the conclusions reached in this study and those reached in similar studies in the Lesser Antilles can probably be attributed to several factors. First, Cat Island has differed from many tropical islands in its persistently low population density. This has meant that man's impact on the vegetation has not been as severe as it has been elsewhere. Second, the Bahamas, because of their off-shore location, seasonal drought, and background of natural disturbance, are characterized by vegetation which is pre-adapted to withstand the kinds of disturbance introduced by man. And third, in view of the inadequacy of the historical record and the absence of any previous analysis of this type, it was necessary to develop a basically new methodology. This empirical approach prevented the easy acceptance of any theoretical interpretations.

Although small and insignificant in some respects, Cat Island has provided a useful setting for a study of man and vegetation change. In spite of a thousand years of discontinuous settlement, man's impact on the woodland has been surprisingly slight. What changes will occur in the future will depend largely on social and economic conditions in the colony. A decrease in the intensity of shifting agriculture will allow the woodland to continue its overall recovery. An increase will cause a reversion to conditions similar to those that existed in the late nineteenth century. Either way, the data gathered here will provide a useful base-line against which future change can be assessed.

ACKNOWLEDGMENTS

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APPENDIX I.

A systematic list of the plant species encountered on Cat
Island.   The numbers without parentheses following the name
are the collection numbers of voucher specimens deposited in
the herbaria of the Arnold Arboretum, Harvard University,
and the University of Wisconsin.   Species without numbers
are sight records. An asterisk indicates that the species
was encountered in the old field study.   The number in
parentheses following these species represents the code
number used to identify them during computer analyses.

ACANTHACEAE

*   Anthacanthus spinosus (Jacq.) Nees, 534, (75).
     Dicliptera assurgens (L.) Juss., 381.
     Ruellia tuberosa L., 238, 553.

AIZOACEAE

     Sesuvium portulacastrum L., 199.

ALISMATACEAE

     Echinodorus berteroi (Spreng.) Fawc., 568.

AMARANTHACEAE

     Achyranthes aspera (L.) Mill., 173.
     Alternanthera paronychioides St. Hil., 328.
     Amaranthus spinosus L., 547.
     Centrostachys indica (L.) Standley, 173.
     Gomphrena globosa L., 211.
     Iresine diffusa H. & B. ex Willd., 580.
     Philoxerus vermicularis (L.) P. Beauv., 456.

AMARYLLIDACEAE

     Agave americana L., "Bamboo".
*   A. sisalana Perrine, "Sisal", (104).
     Hymenocallis declinata (Jacq.) M.J. Roem., 92.

ANACARDIACEAE

     Mangifera indica L., "Mango".
*   Metopium toxiferum (L.) Krug. & Urban., "Poisonwood,"
     38, 474 (49).
     Spondias mombin L., "Hog plum".

ANNONACEAE

    Annona glabra L., "Pond apple."
    A. muricata L., "Soursop."
    A. squamosa L., "Sugar apple," 41.

APOCYNACEAE

    Anagadenia berterii (A. DC) Miers., "Lice root,"
    106,257, 476.
    Echites umbellata Jacq., 14.
    Catharanthus rosea (L.) G. Don., "Periwinkle."
    Nerium oleander L.
*   Plumiera obtusa L., "Milk bush," 249 (115).
*   Vallesia antillana Woods., "Man root", 126 (39).

ASCLEPIADACEAE

    Asclepias curassavica L., 398.
    Calotropis procera (Ait.) Ait. f., 56.
    Cryptostegia grandiflora R. Br., 469.
    Cynanchum eggersii (Schlt.) Alain, 435.
    C. northropiae (Schlecht.) Alain, 383.
    C. sp. 490.

BATIDACEAE

    Batis maritima L.

BIGNONIACEAE

    Crescentia cujete L., 350.
*   Jacaranda coerulea (L.), Griseb., "Clock bush" 252
    (22).
*   Neobracea bahamensis Britton, 422, 520 (110).
*   Tabebuia bahamensis (Northrop) Britton, "Five finger,"
    302, 479, 485 (21).

BOMBACACEAE

    Ceiba pentandra (L.) Gaertn.

BORAGINACEAE

*   Bourreria ovata Miers., "Strong bark," 36, 54, 80, 113
    (67).
*   Cordia bahamensis Urban, "Black granny bush", 213, 415,
    416 (11).
    C. britttonii (Millsp.) Macbr., 311.
    C. lucayana (Millsp.) Macbr., 455.

     C. sebestena L.
*   Heliotropium angiospermum Murr., "Scorpion tail", 1,
     187, 544, (90).
     H. curassavicum L., 59, 543.
     H. inaguense Britton, 378.
     Mallatonia gnaphalodes L., "Bay lavender", 20.
     Tournefortia volubilis L., "Soldier vine".

BROMELIACEAE

     Ananas comosus, "Pineapple".

BURSERACEAE

*   Bursera inaguensis Britton, "Beau Kamalamay", 251 (37).
*   B. simaruba Sarg., "Kamalamay", 52, 298 (36).

BUXACEAE

     Buxus bahamensis Baker, "Boxwood," 445, 531.

CACTACEAE

*   Opuntia dillenii, (Ker-Gawl), Haw., "Prickly pear"
     (94).

CANELLACEAE

     Canella winterana (L.) Gaertn., 161.

CARICACEAE

     Carica papaya L.

CASUARINACEAE

*   Casuarina equisetifolia Forst., 91, (83).

CELASTRACEAE

*   Crossopetalum rhacoma Crantz., 212, 439, (23).
*   Maytenus buxifolia (A. Rich.), Griseb., 76, 228, (41).

CHENOPODIACEAE

     Atriplex pentandra (Jacq.) Steud., 110.
     Chenopodium murale L., 510, 545.
     Salicornia perennis Mill., 108.

COMBRETACEAE

*   Conocarpus erecta L., "Buttonwood", 22, 299, 300, (89).
Laguncularia racemosa (L.) Gaertn., 89.
Terminalia catappa L., "Indian almond."

COMMELINACEAE

Rhoeo spathacea (Desv.) Stearn

COMPOSITAE

Ageratum conyzoides L. spp. latifolia (Cav.) Johnson, 9, 327, 504.
A. muticum Girseb., 112.
Ambrosia hispida Pursh., 104.
A. paniculata Michx., 496.
Aster bahamensi Britton., 117, 577.
Bidens pilosa L., 204.
Borrichia arborescens (L.) DC., 72.
Chaptalia dentata (L.) Cass., 574.
Eclipta prostrata (L.) L., 575.
Emilia sonchifolia (L.) DC., 569.
Erigeron canadensis L., 197, 563.
Eupatorium bahamense Northrop, 407.
E. capillifolium (Lam.) Small, 589.
E. lucayanum Britton, 70.
*   E. villosum Sw., "Bitter sage," 335, (2).
Flaveria linearis Jacq., 500.
F. trinervia (Spreng.) Mohr., 440.
Gaillardia pulchella Foug., 315.
Gochnatia bahamensis (Urb.) Howard & Dunbar, 256, 276.
G. ilicifolia Less., 312.
*   Gundlachia corymbosa (Urb.) Brit., "Horsebush," 304,(32).
Iva imbricata Walt., 77.
Lactuca intybacea Jacq., 484.
Melanthera deltoidea Michx., 116.
Parthenium hysterophorus L., 172.
Pectis linifolia L., 450.
Pluchea purpurascens (Sw.) DC., 4, 333, 337.
P. rosea Godfrey, 526.
Porophyllum ruderale (Jacq.) Cass., 557.
*   Salmea petrobioides Griseb., 406, (55).
Sonchus oleraceus L., 266, 540, 560.
Tridax procumbens L., 239.
Verbesina encelioides (Cav.) Benth. & Hook., 316.
Vernonia bahamensis Griseb., 419.
V. cinerea (L.) Less., 539.
*   Wedelia bahamensis (Britton) O.E. Schulz, 102, 310, (106).
W. Trilobata (L.) Hitch., 508.

CONVULVULACEAE

Evolvulus alsinoides L., 405.
E. sericeus Sw., 265.
* E. squamosus Britton, "Broom bush", 17, 290, (4).
Ipomoea acuminata (Vahl) R.&S., 307.
I. batatas (L.) Lam., 404, 409, 458.
I. microdactyla Griseb., 465.
I. triloba L., 61, 146.
I. macrantha R. & S. 354.
Jacquemontia cayensis Brit., 436.
J. jamaicensis (Jacq.) Hall. F., 271, 377.
Merremia dissecta (Jacq.) Hall., 549.

CRASSULACEAE

Bryophyllum pinnatum (Lam.) Kurz., 185.

CRUCIFERAE

Cakile lanceolata (Willd.) D.E. Schulz, 105.
Lepidum virginicum L., 158.

CYPERACEAE

Abilgaardia monostachya (L.) Vahl, 181.
Cyperus elegans L., 366.
C. filiformis Sw., 511.
C. fulgineus Chap., 347.
C. ligularis L., 363.
C. odoratus L., 565.
C. planifolius L.C. Rich., 551.
Dichromena colorata (L.) Hitchc., 121.
Eleocharis cellulosa Torr., 119. 576.
E. geniculata (L.) R.&S., 389, 512.
Fimbristylis cymosa R.Br., 460.
F. dichotoma (L.) Vahl, 516, 523.
F. ferruginea (L.) Vahl, 63.
Mariscus jamaicensis (Crantz) Britton, 90.
Rhynchospora cyperoides (Sw.) Mart., 578.
R. stellata (Lam.) Griseb., 121.
Scleria lithosperma (L.) Sw., 152.

DIOSCOREACEAE

Dioscorea Sp.

EBENACEAE

* Diospyros caribaea (A.DC) Standley, 273, 462, (29).

ERYTHROXYLACEAE

*   Erythroxylon areolatum L., 487, (18).
*   E. rotundifolium Lunan, 255, 444, (17).

EUPHORBIACEAE

    Acalypha alopecuroides Jacq., 593.
    Argythamnia candicans Sw., 453.
    A. lucayana Millsp., 515.
*   Bernardia dichotoma Muell. Arg., 360, (78).
*   Bonania cubana A. Rich., 486, (80).
    Breynia nivosus (W. Smith) Small, 498.
    Chamaesyce blodgetti (Engelm) Small, 69.
    C. hirta (L.) Millsp. 167, 246.
    C. hypericifolia (L.) Millsp., 167, 215, 247.
    C. lechioides (Millsp.) Millsp., 431, 530, (119).
    C. mesembrianthemifolia (Jacq.) Dugand, 10.
*   Croton bahamensis Millsp., "Pepper bush", 451, (43).
*   C. eluteria (L.) Sw., "Sweetwood bark", 35 214, 270, 483, (68).
*   C. linearis Jacq., "Granny bush", 16, 432, 471, (25).
*   C. lucidus L., 79, 95, (88).
    C. rosmarinoides Millsp., 254.
*   Drypetes diversifolia Krug & Urb., 382, 489, (15).
    Euphorbia heterophylla L. 3, 64.
    E. lactea Haw.
*   Grimmeodendrom eglandulosum (Rich.) Urb., 112, 533, (112).
*   Gymnanthes lucida Sw., "Crabwood", 424, 480, (12).
    Hippomane mancinella l., "Manchineel."
    Manihot esculenta Crantz.
    Pedilanthus tithymaloides Poit., 497.
    Phyllanthus acidus (L.) Skeels., "Otaheite gooseberry."
    P. carolinensis Walt. ssp. saxicola (Small) Webster, 461.
*   P. epiphyllanthus L., "Rockbush", 134, (53).
    P. niruri L., 170.
    Ricinus communis L., 160.
*   Savia bahamensis Brit., 365, 446, 454, (56).

FLACOURTIACEAE

*   Banara reticulata Griseb., 155, (116).
    Casearia bahamensis Urb., 275.
    Xylosma ilicifolia Northrop, 591.

GENTIANACEAE

    Eustoma exaltatum (L.) Griseb., 87.

Sabbatia stellaris Pursh., 525.

GOODENACEAE

*   Scaevola plumieri (L.) Vahl., 19, (108).

GRAMINEAE
Andropogon glomertus (Walt) B.S.P. "Bed grass", 297.
A. gracilis Spreng., 266, 522.
A. pertusus (L.) Willd., 371.
Aristida tenipes Cav., 359.
A. vilifolia Herit., 592.
Brachiaria subquadriparia (Trin.) Hitchc., 353, 538.
Cenchrus echinatus L., 26, 231.
C. tribuloides L., 208.
C. viridis Spreng., 13.
Chloris barbata (l.) Sw., 368.
C. gayana Kunth, "Rhodes grass", 342.
C. petraea (Sw.) Desv., 27.
C. sagraeana A. Rich., 536.
Cymbopogon citratus (D.C.) Stapf. f., "Lemon grass", 51.
Cynodon dactylon (L.) Pers., "Bermuda grass", 535.
Dactyloctenium aegyptium (L.) Wild., 459.
Digitaria ciliaris (Retz.) Koel. 174, 245.
D. decumbens Steut., "Pangola grass", 343.
D. diversiflora Swallen, 537.
Distichlis spicata (L.) Greene.
Eleusine indica (L.) Gaertn., 66.
Eragrostis ciliaris (L.) R.Br., 58, 144.
E. ciliaris (l.) R & Br. var. laxa Ktze., 388.
E. tenella (L.) Beauv. ex R. & S., 588.
Lasiacis divaricarta (L.) Hitch., 133, 227.
Leptochloa domingensis (Jacq.) Trin., 114.
L. plechtostachya K. Schum, 344.
Panicum dichotomiflorum Michx., 386.
P. maximum Jacq., "Guinea grass", 385.
P. muticum Forsk., "Para grass", 345.
Paspalum blodgettii Chapm., 25, 473, 558.
P. fimbriatum Kunth, 369.
P. laxum Lam., 267.
P. vaginatum Sw., 30, 296.
Pennisetum purpureum Schumach, "Elephant grass", 341.
Saccharum officinarum L. "Sugar cane".
Setaria geniculata (L.) Beauv., 85, 111. 283, 330.
S. setosa (Sw.) Beauv., 586.
Sorghum saccharatum (L.) Moench, "Guinea corn".
Sporobolus poiretii (R. & S.) Hitch., 387.
S. virginicus (L.) Kunth., 11, 65, 408.
Stenatophorum secundatum (Walt.) Kuntze, 561.

Trichachne insularis (L.) Nees, 505.
Uniola paniculata L., "Sea oats". 21.
U. virgata Griseb., 2.
Zea mays L.

GUTTIFERAE

Mammea americana L., 362.

HALORAGACEAE

Proseripinaca platycarpa Small, 581.

LABIATAE

Leonotis nepetaefolia (L.) R.Br., 495.
Salvia serotina L., "Catnip", 127, 145, 281.
Scutellaria havanensis Jacq., 503.
Teucrium cubense Jacq., 541.

LAURACEAE

*   Nectandra coriacea Griseb., 514, 518, (42).
Persea americana Mill., "Avocado", 48.

LEGUMINOSEAE

Abrus precatorius L., "Bead vine".
Acacia acuifera Benth., 356.
*   A. choriophylla Benth., "Cassina", 430, 478, (9).
*   A. farnesiana (L.) Willd., "Sail needle", 475, (97).
*   Ateleia gummifera (DC.) Dietr., 357, (77).
*   Caesalpinia bahamensis La., "Braziletto", 402, (81).
*   C. ovalifolia Urb., "Nickers", 268, (107).
Cajanus cajan (L.) Millsp., "Pigeon pea", 148.
*   Calliandra formosa (Dth.) Benth., 358, (114).
Canavalia rosea (Sw.) DC., "Sea Bean", 229, 338.
*   Cassia bahamensis Mill., "Stinking pea", 124, (64).
*   C. biflora L., (118).
C. diffusa DC., 392.
*   C. lineata, 159, 288, (8).
C. obutsifolia L., 391.
C. occidentalis L., 124, 463.
C. tora L., 322.
Centrosema virginianum (L.) Benth. 146, 269, 334, 502.
Crotalaria retusa L., 509.
Delonix regia (Bojer) Raf., "Poinciana".
Desmanthus virgatus (L.) Willd., 306, 448.
Desmodium canum (Gmel.) Schinz & Thellung, 329.
D. glabrum (Mill.) DC., 552.

Diplotaxis muralis (L.) DC., 393.
Galactia rudolphioides (Gmel.) B. & H., 96, 305.
G. spiciformis T. & G., 336.
G. striata (Jacq.) Urb., 195.
Guilandina bonduc L., "Nickers", 268.
* Haematoxylum campechianum L., "Logwood", (92).
* Indigofera suffruticosa Mill., 318, (103).
* Leucaena leucocephala de Wit.,= L. latisiliqua (L.)
Gillis., "Jumbay" 93, (35).
* Lysiloma bahamensis Benth., "Wild tamarind", 82, 284,
(74).
* L. latisiliqua (L.) Benth., "Horseflesh", 191, 253,
(33).
Macroptilium lathyroides (L.) Urb., 564.
Parkinsonia aculeata L., "Jerusalem thorn".
* Piscidia piscipula (L.) Sargent, "Dogwood", 34, (86).
* Pithecellobium keyense Britton "Ramshorn", 49, 81, 103,
200, 301, (52).
Rhynchosia Sp. 195.
Sophora tomentosa L., 287.
Stylosanthes hamata (L.) Taub., 82, 554.
Tamarindus indica L., 189, 233.
Tephrosia cinerea (L.) Pers., 321.

LILLIACEAE

Aloe barbadensis Mill
Sansevieria sp., "Bowstring hemp".
Smilax havanensis Jacq., 492.
Yucca aloifolia L., "Spanish bayonet".

LINACEAE

Linum bahamense North., 529.

LOGANIACEAE

Cynoctonium mitreola (L.) Brit., 528.
Spigelia anthelmia L., 293.

LYTHRACEAE

Ammania latifolia L., 562.

MALPIGHIACEAE

* Bunchosia glandulosa (Cav.) DC., 513, (82).
* Byrsonima lucida (Sw.) DC., 482, (7).
* Malpighia polytricha A. Juss., "Touch me not", 140,
587, (70).

Triopteris jamaicensis L., "Cough vine".

MALVACEAE

Abelmoschus esculenthus (L.) Moench "Okra".
Abutilon permolle (Willd.) Sweet, 144, 248, 494.
* _Gossypium barbadense_ L., 427, (120).
Herissantia crispa (L.) Briz., 282.
Malvastrum corchorifolium (Desr.) Brit., 464, 501.
Melochia tomentosa L., 449.
Phymosia abutiloides (L.) Desv., 590.
Sida acuta Burm., 182, 194, 390.
S. ciliaris L., 101, 573.
S. spinosa L., 396.
S. urens L., 559.
Thespesia populnea (L.) Soland.

MELIACEAE

Melia azedarach L., "Pride of India".
* _Swietenia mahagoni_ (L.) Jacq., 178, (38).

MORACEAE

Artocarpus altilis (Park.) Fosb., 570.
* _Ficus jacquinifolia_ A. Rich, 468, (111).

MORINGACEAE

Moringa oleifera Lam., 506.

MUSACEAE

Musa paradisiaca L.

MYRICACEAE

Myrica cerifera L.

MYRSINACEAE

* _Rapanea guyanensis_ Aubl., 452, (122).

MYRTACEAE

Eucalyptus tereticornis Sm., 517.
Eugenia axillaris (Sw.) Willd., 423.
* _E. buxifolia_ (Sw.) Willd., 262, 289, (65).
* _E. longipes_ Berg., "Sweet Margaret", 222, (85).
E. lucayana (Brit.) Alain, 250.

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*       E. monticola DC., 234, (66).
*       E. myrtoides Poir., 295.
        Psidium guajava L., 123, 169.
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NYCTAGINACEAE

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        Boerhaavea coccinea Mill., "Hogweed", 165, 243.
        Commicarpus scandens (L.) Standley "Rat ears", 216.
*       Torrubia longifolia Britton, "Beefwood", 83, (1).
*       T. obtusata (Jacq.) Brit., 519, (121).
        Pisonia rotundata Griseb., 571.
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NYMPHAEACEAE

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        Nymphaea  ampla  (Salisb.)  DC.  var.  pulchella  (DC.)
        Casp., 367.
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OLACACEAE

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        Schoepfia chrysophylloides (Rich.) Planch, 395.
        Ximenia americana L., 379.
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OLEACEAE

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        Forestiera segregata (Jacq.) Krug & Urb., 384,443.
        Jasminum fluminense Vell., 546.
        J. sambac Ait., 566.
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ONAGRACEAE

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        Jussiaea suffruticosa L., 567.
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ORCHIDACEAE

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*       Epidendrum sp., 29, 224.
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PALMAE

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*       Coccothrinax argentea Sarg., "Silver top", (60).
        Cocos nucifera L.
*       Pseudophoenix  vinifera  (Mart.)  Becc.,  "Hog  cabbage
        palm", (98).
*       Thrinax microcarpa Sarg., "Buffalo top", (5).
*       Sabal palmetto (Walt.) Lodd., "Pond top", (50).
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PAPAVERACEAE

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        Argemone mexicana L., 33.
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PASSIFLORACEAE

> Passiflora cuprae L., 320.
> P. pectinata Griseb., 18, 272.
> P. suberosa L., 132, 242, 319.

PHYTOLACCACEAE

> Rivina humilis L., 235, 241.

PLANTAGINACEAE

> Plantago major L., 550.

PLUMBAGINACEAE

> Plumbago scandens L., 399.

POLYGALACEAE

*   Polygala obovata Blake, "Strip me naked", 317, (100).

POLYGONACEAE

> Antigonon leptopus H. & A., 372.
* Coccoloba diversifolia Jacq., "Pigeon plum", 46, 448, 491, (46).
* C. krugii Lind., 351, (47).
* C. uvifera Jacq. "Sea grape", (59).

PORTULACEAE

> Portulaca oleracea L., 164.
> P. rubricaulis H.B.K., 348.
> Talinum triangulare (Jacq.) Willd., 244.

POTAMOGETONACEAE

> Potomogeton heterophyllus Schreb., 582.

PUNICACEAE

> Punica granatum L.,."Pomegranate".

RHAMNACEAE

> Auerodendron northropianum (Urb., 240.
> Colubrina elliptica (Sw.) Briz., & Stern, 373.
* C. ferruginosa (Mill.) Sarg., 260, (124).
> C. glandulosa Perkins, 418.

*   Krugiodendron ferreum (Vahl) Urban, "Ironwood", (34).
*   Reynosia septentrionalis Urb., "Dollen plum", 47, (14).
    Zizyphus taylori (Brit.) Johnston, 277.

RHIZOPHORACEAE

    Rhizophora mangle L., 332.

ROSACEAE

    Chrysobalanus icaco L., "Coco plum", 466.

RUBIACEAE

*   Antirrhea myrtifolia Urb., 7, 221, (123).
    Borreria laevis (Lam.) Griseb., 380.
*   Casasia clusiaefolia (Jacq.) Urban, "Sea bob", 6, (58).
    Catesbea parviflora Sw., 107, 292.
*   Chiococca alba (L.) Hitchc., "Piss the bed", 210, 313, 417, (48).
    C. pinetorum Brit., 524.
*   Erithalis fruticosa L., "Black torch", 15, 220, 421, (3).
*   Ernodea littoralis Sw., 3, 397, 555, 556, (87).
*   Exostema caribaeum (Jacq.) Roem & Schult., "Princewood", 223, (51).
*   Guettarda elliptica Sw., 232, 400, 401, (27).
*   G. scabra (L.) Lam., (26).
*   Hamelia patens Jacq., 467, (28).
*   Phialanthus myrtilloides Griseb., "Candlewood", 441, 532, (95).
*   Psychotria ligustrifolia (Northrop) Millsp., "Wild coffee", 209, (72).
    Rachicallis americana (Jacq.) O. Kuntze., 109.
*   Randia mitis L., "Fever bush", 122, 139, 278, 493, (20)/
    Spermacoce confusa Rendle, 331.
    S. tenuior L., 154.
    Strumpfia maritima Jacq., 1, 219.

RUTACEAE

*   Amyris elemifera L., "White torch", (57).
    Citrus aurantifolia (Christm.) "Swingle lime".
    C. aurantium L., "Bitter orange", 188.
    C. limon (L.) Burm. f. "Lemon".
    C. sinensis (L.) Osb. "Sweet orange".
    Fagara flava (Vahl.) Krug & Urban. "Satinwood".
*   F. pterota L., "Wild Lime". 477, (73).
*   Spathelia bahamensis Marie Victorin, 9, 225, 308, (99).

*   Zanthoxylum coriaceum Rich. "Hercules Club", 420, (105).

SAPINDACEAE

*   Exothea paniculata (Juss.) Radlk., 583, (19).
*   Hypelate trifoliata Sw., "Soapbush", 230, (96).
        Melicoccus bijugatus L. "Genip".
        Serjania diversifolia (Jacq.) Radlk., 130, 157, 291.
*   Thouinia discolor Griseb., "Three finger", 218, (69).

SAPOTACEAE

*   Bumelia retusa Sw., 303, 338, 340, (6).
*   Chrysophyllum oliviforme., "Wild saffron", 361, (102).
*   Dipholis salicifolia (L.) A.DC., "Cassadawood", 186, 481, (13).
*   Manilkara jaimiqui (Wright) Dubard, "Wild Dilly" 355, (101).
*   Manilkara zapota (L.) V. Royen, "Sapodilly" 42, (113).
*   Sideroxylon foetidissimum Jacq., "Mastic" 339, (40).

SCROPHULARIACEAE

        Bacopa monnieri (L.) Pennell, 579.
        Buchnera elongata Sw., 521.
        Capraria biflora L., "Goat weed", 7, 542.

SIMAROUBACEAE

*   Alvaradoa amorphioides Liebm., 376, (76).
*   Picramnia pentandra Sw., "Bitter bush", 584, (45).
        Picrodendrom macrocarpum (A.Rich) Britton, "Olive", 323, 364.

SOLANACEAE

        Capsicum annum L.
        Datura inoxia Mill, 594.
        D. stramonium L., 585.
        Nicotiana tabacum L., "Tobacco".
*   Solanum bahamense L., "Canker berry", 28, 236, (61).
*   S. erianthum D. Don., 81, 259, (62).
        S. nigrum L., 150.

STERCULIACEAE

*   Helicteres jamaicensis Jacq., 258, (30).
*   H. semitriloba Bert., 349, (31).
*   Melochia tomentosa L., 74, 285, (93).

Waltheria americana L., 68.
W. bahamensis Britton, 118, 374.
W. indica L., 375, 527.

SURIANACEAE

Suriana maritima L., 11.

THEOPHRASTACEAE

*   Jaquinia keyensis Mex., "Joewood", 5, 274, (109).

TILIACEAE

*   Corchorus hirsutus L., "Soapbush", 68, 226, (10).
    C. siliquosus L., 403.
    Triumfetta semitriloba L., 180.

TURNERACEAE

*   Turnera diffusa Willd., 237, (63).
*   T. ulmifolia L., 4, 8, 156, (117).

TYPHACEAE

Typha domingensis Pers.

ULMACEAE
    Trema lamarckiana (R. & S.) Blume, 286 (71).

UMBELLIFERAE

Anethum graveolens L., 449.
Centella erecta (L.) Fern., 548.

VERBENACEAE

Avicennia germinans (L.), "Black Mangrove", 179.
*   Callicarpa hitchcockii Millsp., "Boarhog bush", 125, 279, (79).
*   Citharexylum fruticosum L., 433, (84).
*   Duranta repens L., 346, 411, (16).
*   Lantana bahamensis Brit., "Goldenrod", 75, 263, 309, (24).
*   L. involucrata L., "Sweet sage", 12, 261, 470, (54).
    Lippia nodiflora (L.) Michx., 71, 572.
    L. stoechadifolia (L.) H.B.K., 264.
*   Petetia domingensis Jacq., "Banana wood", 125 (44).
    Priva lappulacea (L.) Pers., 280.
    Stachytarpheta fruticosa B.L. Robinson, 314.

S. jamaicensis (L.) Vahl., 190.

VITACEAE

Cissus intermedia A. Rich., 98, 324.
C. trifoliata L., 325.

ZYGOPHYLLACEAE

Guaiacum sanctum L., "Lignum vitae", 370, (91).

APPENDIX II.

Index to common names of plants mentioned in the text.

Australian pine	Casuarina equisetifolia
Avocado	Persea americana
Bamboo	Agave americana
Barbados pride	Poinciana pulcherrima
Bay cedar	Suriana maritima
Bay geranium	Ambrosia hispida
Bay lavender	Mallatonia gnaphaloides
Bay marigold	Borrichia arborescens
Beans, bonavist	Dolichos lablab
Beans, colored	Phaseolus vulgaris
Beans, lima	Phaseolus lunatus
Beefwood	Torrubia longifolia
Black mangrove	Avicennia germinans
Black torch	Erithalis fruticosa
Boarhog bush	Callicarpa hitchcockii
Bowstring hemp	Sansevieria sp.
Boxwood	Buxus bahamensis
Brasiletto	Caesalpinia vesicaria
Breadfruit	Arctocarpus communis
Broom bush	Evolvulus squamosus
Brown ebony	Dalbergia ecastophyllum
Buffalo top	Thrinax microcarpa
Burr Grass	Cenchrus spp.
Buttonwood	Conocarpus erecta
Caribbean pine	Pinus caribea
Cashew nut	Anacardium occidentale
Cassada	Dipholis salicifolia
Cassava	Manihot esculenta
Cassina	Acacia choriophylla
Cattail	Typha domingensis
Coconut	Cocos nucifera
Coco plum	Chrysobalanus icaco
Coral tree	Erythrina corallodendrum
Corn	Zea mays
Cotton	Gossypium barbadense
Cow peas	Vigna unguiculata
Custard apple	Annona reticulata
Dildo	Cephalocereus millspaughii
Dilly	Manilkara zapota
Divi-divi	Caesalpinia coriaria
Dollen plum	Reynosia septentrionalis
Elephant grass	Pennisetum purpureum
Fever bush	Randia mitis
Five finger	Tabebuia bahamensis
Frangipani	Plumiera rubra

Genip	Melicoccus bijugatus
Ginger	Zingiber officinale
Granny bush	Croton linearis
Green ebony	Brya ebenus
Grease bush	Corchorus hirsutus
Guava	Psdium guajava
Hog cabbage	Pseudophoenx vinifera
Hog plum	Spondias mombin
Horsebush	Gundlachia corymbosa
Horseflesh	Lysiloma latisiliqua
Horseradish tree	Moringa oleifera
Indian almond	Terminalia catappa
Indigo	Indigofera suffruticosa
Ironwood	Krugiodendron ferreum
Jerusalem thorn	Parkinsonia aculeata
Joewood	Jaquinia keyensis
Johnson grass	Sorghum halepense
Jumbay	Leucaena leucocephala
Kamalamay	Bursera simaruba
Lemons	Citrus limon
Lignum vitae	Guiacum sanctum, G. officinale
Lime	Citrus aurantifolia
Logwood	Haematoxylum campechianum
Love vine	Cassytha filiformis
Madeira	Dipholis salicifolia
Mahoe	Thespesia populanea
Mahogany	Swietenia mahogani
Mango	Mangifera indica
Manroot	Vallesia antillana
Mastic	Mastichodendron foetidissimum
Melon, musk	Cucumis melo
Melon, water	Colocynthis citrullus
Milkberry	Bumelia retusa
Milkweed	Chamaesyce mesembrianthemifolia
Morning glory	Ipomoea pes-caprae
Nickers	Guilandina bonduc
Onion	Allium cepa
Otaheite gooseberry	Phyllanthus distichus
Pangola grass	Digitaria decumbeus
Para grass	Panicum muticum
Paw paw	Carica papaya
Pigeon berry	Rhacoma crossapetalum
Pigeon peas	Cajanus cajan
Pigeon plum	Coccoloba diversifolia
Pineapple	Ananas comosus
Poinciana	Delonix regia
Poisonwood	Metopium toxiferum
Pomegranate	Punica granatum
Pond apple	Annona glabra
Pond top	Sabal palmetto
Pride of India	Melia azaderach

Princewood	Exostema caribaeum
Ramshorn	Pithecellobum keyense
Red mangrove	Rhizophora mangle
Rhodes grass	Chloris gayana
Sail needle	Acacia farnesiana
Salve bush	Pluchea rosea
Sandbox tree	Hura crepitans
Sawgrass	Mariscus jamaicensis
Sea bean	Canavalia maritima
Sea bob	Casasia clusiaefolia
Sea grape	Coccoloba uvifera
Sea lily	Hymenocallis declinata
Sea oats	Uniola paniculata
Sea pork	Sesuvium portulacastrum
Silver top	Coccothrinax argentea
Simon finger	Tabebuia bahamensis
Sisal	Agave sisalina
Soap bush	Corchorus hirsutus
Sorghum	Sorghum vulgare
Sours	Citrus aurantium
Spanish bayonet	Yucca aloifolia
Squash	Cucurbita sp.
Star grass	Leptochloa plechtostachya
Strong back	Bourreria ovata
Sugar apple	Annona squamosa
Sweet gale	Myrica cerifera
Sweet margaret	Eugenia longipes
Sweet orange	Citrus sinensis
Sweet potato	Ipomoea batatas
Sweet sage	Lantana involucrata
Sweetwood bark	Croton eluteria
Tamarind	Tamarindus indica
Tobacco	Nicotiana tabacum
Tomatoes	Lycopersicon esculentum
Wattle	Eugenia spp.
White mangrove	Laguncularia racemosa
White torch	Amyris elemifera
Wild cinnamon	Canella alba
Wild lime	Fagara pterota
Wild locust	Lysiloma bahamensis
Wild tamarind	Lysiloma bahamensis
Wild tobacco	Pluchea rosea
Yellow wood	Fagara flava

APPENDIX III

Data Sheet used during Analysis of Oldfields

CAT OLD FIELD DATA

Field Number_____
Photo Reference_____
Age Class_____
Habitat-Type_____
Height Class_____
Soil-Type_____
Moisture Class_____
Grazing Class_____

Species No.	Area	Species No.	Area	Species No.	Area	Species No.	Area	Species No.	Area
001		026		051		076		101	
002		027		052		077		102	
003		028		053		078		103	
004		029		054		079		104	
005		030		055		080		105	
006		031		056		081		106	
007		032		057		082		107	
008		033		058		083		108	
009		034		059		084		109	
010		035		060		085		110	
011		036		061		086		111	
012		037		062		087		112	
013		038		063		088		113	
014		039		064		089		114	
015		040		065		090		115	
016		041		066		091		116	
017		042		067		092		117	
018		043		068		093		118	
019		044		069		094		119	
020		045		070		095		120	
021		046		071		096		121	
022		047		072		097		122	
023		048		073		098		123	
024		049		074		099		124	
025		050		075		100		125	

APPENDIX IV.

A list of the minor species encountered in each habitat-type and each age-class. Species are listed in order of importance.

WHITELAND

Maximum cover value in age-class 1 (less than 5 years).

    1. Croton linearis
    2. Turnera ulmifolia
    3. Wedelia trilobata
    4. Croton eluteria

Maximum cover value in age-class 2 (5-14 years).

    1. Salmia petrobiodes
    2. Cassia lineata
    3. Cordia bahamensis
    4. Chamaesyce lechiodes
    5. Ernodia littoralis
    6. Melochia tomentosa
    7. Amyris elemifera
    8. Phyllanthus epiphyllanthus

Maximum cover value in age-class 3 (15-29 years).

    1. Piscidia piscipula
    2. Caesalpinia ovalifolia
    3. Calliandra formosa
    4. Bursera simaruba
    5. Gossypium barbadense
    6. Bursera inaguensis
    7. Bunchosia glandulosa
    8. Solanum bahamense
    9. Agave americana
    10. Helicteres semitriloba
    11. Scaevola plumierii
    12. Cassia bahamensis
    13. Fagara pterota

Maximum cover value in age-class 4 (30-50 years).

    1. Sabal palmetto

Maximum cover value in age-class 5 (more than 50 years).

    1. Jaquinia keyensis
    2. Antirrhoea myrtifolia

FLATLAND

Maximum cover value in age-class 1 (less than 5 years).

1. Guettarda scabra
2. Lantana involucrata
3. Corchorus hirsutus
4. Cassia lineata
5. Wedelia trilobata
6. Cordia bahamensis
7. Guettarda elliptica
8. Trema lamarckiana
9. Psychotria ligustrifolia
10. Solanum eriathum
11. Croton eluteria
12. Thrinax microcarpa
13. Chrysophyllum oliviforme
14. Helicteres semitriloa
15. Duranta repens
16. Anthacanthus spinosus
17. Petitia domingensis
18. Solanum bahamense
19. Hamelia patens
20. Caesalpinia ovalifolia
21. Colubrina ferruginosa
22. Banara reticulata
23. Ficus jacquinifolia

Maximum cover value in age-class 2 (5-14 years).

1. Coccoloba krugii
2. Tabebuia bahamensis
3. Leucaena leucocephala
4. Eugenia monticola
5. Randia mitis
6. Erithalis fruticosa
7. Eugenia buxifolia
8. Malphigia polytricha
9. Eupatorium villosum
10. Phyllanthus epiphyllanthus
11. Turnera ulmifolia
12. Calliandra formosa
13. Torrubia obtusata
14. Croton lucidus
15. Croton bahamensis
16. Neobracea bahamensis
17. Picramnia pentandra
18. Callicarpa hitchcockii
19. Opuntia dillenii

Maximum cover value in age-class 3 (15-29 years).

1. Reynosia septentrionalis
2. Maytenus buxifolia
3. Diospyros caribaea
4. Fagara pterota
5. Exostema caribaeum
6. Ernodea littoralis
7. Gymnanthes lucida
8. Lantana bahamensis
9. Cassia bahamensis
10. Turnera diffusa
11. Agave americana
12. Nectandra coriacea
13. Crossopetalum rhacoma
14. Melochia tomentosa
15. Casasia clusiaefolia
16. Bernardia dichotoma
17. Evolvulus squamosus
18. Helicteres jamaicensis

Maximum cover value in age-class 4 (30-50 years).

1. Bourreria ovata
2. Dipholis salicifolia
3. Thouinea discolor
4. Piscidia piscipula
5. Conocarpus erecta
6. Cassia biflora
7. Coccoloba uvifera
8. Erythroxylon rotundifolium
9. Grimmeodendron eglandulosum
10. Coccothrinax argentea
11. Sabal palmetto
12. Manilkara emarginata
13. Spathelia bahamensis
14. Jaquinia keyensis
15. Erythroxylon areolatum

Maximum cover value in age-class 5 (more than 50 years).

1. Byrsonima lucida
2. Swietenia mahagoni
3. Amyris elemifera
4. Chiococca alba
5. Savia bahamensis
6. Plumiera obtusa
7. Pseudophoenix vinifera
8. Drypetes diversifolia
9. Jacaranda coerulea
10. Exothea paniculata
11. Krugiodendron ferreum
12. Brumelia retusa

13. <u>Ateleia gummifera</u>

BLACKLAND

Maximum cover value in age-class 1 (less than 5 years).
1. <u>Leucaena leucocephala</u>
2. <u>Fagara pterota</u>
3. <u>Corchorus hirstus</u>
4. <u>Eugenia monticola</u>
5. <u>Lantana bahamensis</u>
6. <u>Cassia bahamensis</u>
7. <u>Randia mitis</u>
8. <u>Cordia bahamensis</u>
9. <u>Wedelia trilobata</u>
10. <u>Phyllanthus epiphyllanthus</u>
11. <u>Melochia tomentosa</u>
12. <u>Psychotria ligustrifolia</u>
13. <u>Cassia biflora</u>
14. <u>Anthacanthus spinosus</u>
15. <u>Exothea paniculata</u>
16. <u>Trema lamarckiana</u>
17. <u>Malphighia polytricha</u>
18. <u>Jacaranda coerulea</u>
19. <u>Indigofera suffruticosa</u>
20. <u>Calliandra formosa</u>
21. <u>Solanum bahamense</u>
22. <u>Turnera ulmifolia</u>
23. <u>Croton eluteria</u>
24. <u>Evolvulus squamosus</u>
25. <u>Croton bahamensis</u>
26. <u>Vallesia antillana</u>
27. <u>Haematoxylum campechianum</u>
28. <u>Banara reticulata</u>
29. <u>Coccothrinax argentea</u>
30. <u>Neobracea bahamensis</u>

Maximum cover value in age-class 2 (5-14 years).
1. <u>Lantana involucrata</u>
2. <u>Croton linearis</u>
3. <u>Maytenus buxifolia</u>
4. <u>Exostema caribeum</u>
5. <u>Eupatorium villosum</u>
6. <u>Chiococca alba</u>
7. <u>Croton lucidus</u>
8. <u>Guettarda elliptica</u>
9. <u>Agave americana</u>
10. <u>Sabal palmetto</u>
11. <u>Atelia gummifera</u>
12. <u>Nectandra coriacea</u>

13. Cassia lineata
14. Heliotropium parviflorum
15. Bunchosia glandulosa

Maximum cover value in age-class 3 (15-29 years).
1. Tabebuia bahamensis
2. Piscida piscipula
3. Erithalis fruticosa
4. Diospyros caribaea
5. Thrinax microcarpa
6. Crossopetalum rhacoma
7. Petitia domingensis
8. Citharexylum fruticosum
9. Turnera diffusa
10. Eugenia longipes
11. Caesalpinia bahamensis
12. Bumelia retusa
13. Helicteres jamaicensis
14. Helicteres semitriloba
15. Spathelia bahamensis

Maximum cover value in age-class 4 (30-50 years).
1. Dipholis salicifolia
2. Thouinea discolor
3. Gymnanthes lucida
4. Eugenia buxifolia
5. Bursera inaguensis
6. Lysiloma latisiliqua
7. Savia bahamensis
8. Solanum erianthum
9. Casasia clusiaefolia
10. Conocarpus erecta
11. Erythroxylon areolatum
12. Polygala obovata
13. Plumiera obtusa

Maximum cover value in age-class 5 (more than 50 years).
1. Amyris elemifera
2. Coccoloba kruggii
3. Sideroxylon foetidissimum
4. Manilkara zapota
5. Torrubia obtusata
6. Guettarda scabra
7. Pseudophoenix vinifera
8. Ficus jaquinifolia
9. Coccoloba uvifera
10. Erythroxylon rotundifolium
11. Chrysophyllum oliviforme
12. Rapanea guyanensis
13. Krugiodendron ferreum
14. Picramnia pentandra

15. Zanthoxylum coriaceum
16. Guaiacum sanctum
17. Byrsonima lucida