ATOLL RESEARCH BULLETIN

NOS. 397-398

THE NATURAL HISTORY OF CAROLINE ATOLL, SOUTHERN LINE ISLANDS

EDITED BY

ANGELA K. KEPLER AND CAMERON B. KEPLER

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
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NO. 397. PART I. HISTORY, PHYSIOGRAPHY, BOTANY, AND ISLET DESCRIPTIONS
BY ANGELA K. KEPLER AND CAMERON B. KEPLER

NO. 398. PART II. SEABIRDS, OTHER TERRESTRIAL ANIMALS, AND CONSERVATION
BY CAMERON B. KEPLER, ANGELA K. KEPLER, AND DAVID H. ELLIS

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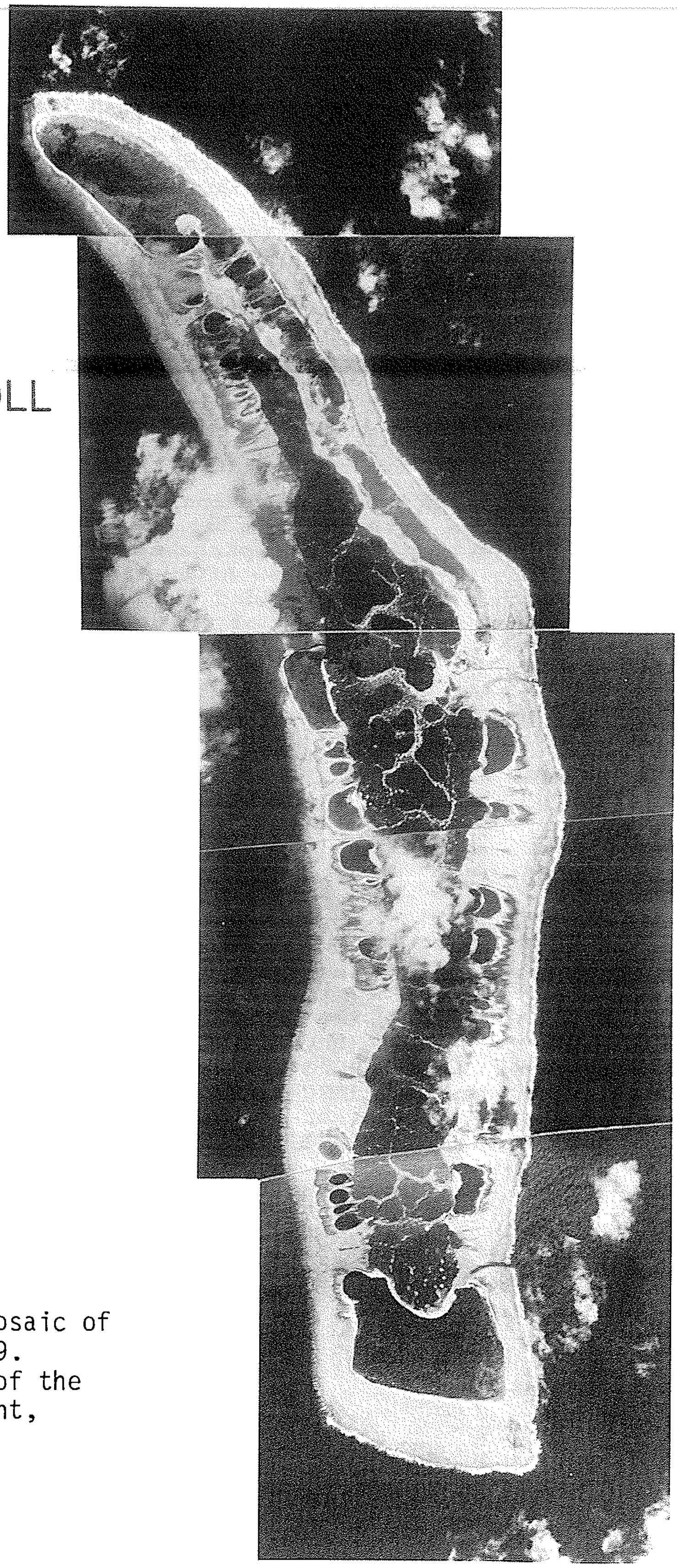
CAROLINE ATOLL



Frontispiece. Airphoto mosaic of Caroline Atoll, RNZAF 6569. Reproduced by permission of the Lands and Survey Department, New Zealand.

Preface

This study is primarily a result of the research efforts of the First Joint US-USSR Central Pacific Expedition (Line and Phoenix Groups, Gilbert Islands, Micronesia, inland Philippine seas, and South China Sea). In turn, it was part of the second phase of a longer expedition from Vladivostok, USSR, via Dutch Harbor, Unalaska, Aleutian Islands to Singapore (26 July to 31 October 1988), which included oceanographic and seabird investigations in arctic, temperate and tropical waters.

The authors boarded the Soviet Research Vessel (R/V) *Akademik Korolev* (7,000 tons, 124 m in length) in Hilo, Hawaii, bound for Christmas Island (02°N, 157°W), where we picked up Katino Teeb'aki, a conservation officer for the Republic of Kiribati, who represented his government and helped our land-based research efforts. The next stop was at little-known Caroline Atoll (10°S, 150°W), on the southeastern edge of the Line Group. After landing on Caroline on 22 September, we camped in 2 locations for 7 nights, surveying the terrestrial plants and animals on all 39 islets.

A small amount of data was also added from 2 visits of the ICBP (International Council for Bird Preservation) 1990 Line and Phoenix Islands Expedition (2 March to 31 May 1990) aboard the New Zealand cutter, R/V *Te Manu* (7.5 tons, 10.5 m).

Caroline is a relatively untouched atoll with its native plant communities nearly intact on all but 3 islets, and teeming seabird communities that, collectively, are second in the Line Group only to Christmas Island (Kiribati) in diversity. For several historical reasons, the natural values of this spectacular blend of marine and terrestrial resources have been overlooked.

These papers attempt to synthesize what is known about the atoll. We have analyzed our own data in the light of several important historical accounts from the "gray literature," including records from early navigators, guano and copra enterprises, incidental travellers, and a solar eclipse expedition, some of which were critical to understanding the present situation. We include a new map of the atoll (the first for over 100 years, with additional islets and shoals), the first descriptions of physiography, plant communities and floristics, and individual islets, the first published climatic records and the first photograph and measurements of its intact, ancient Tuamotuan *marae* (religious site). We also report 14 new species records (5 plants, 2 seabirds, 1 shorebird, 1 land bird, 3 lizards, 1 possible turtle, 1 marine mammal).

In Part I we have attempted to reconstruct and describe Caroline's botanical history, including ecological succession, species-area relationships, and the remarkable recovery of its indigenous forests (*Pisonia grandis, Cordia subcordata, Tournefortia argentea*). In Part II, discussions of seabirds and coconut crabs are rounded off by bringing to light current threats to the atoll's well-being, and ongoing conservation efforts.

An expedition of this magnitude entailed the help of many people, and it gives us great pleasure to thank them. We are indebted to Hal O'Connor and Randy Perry, Patuxent Wildlife Research Center, for making possible our participation. Steve Kohl, FWS Office of International Affairs, and Terry Whitledge aided immensely by handling innumerable details with their Soviet colleagues. Members of the Fish and Wildlife Service Mauna Loa Field Station, especially Jim Jacobi, Julie Williams, Jack Jeffrey, and Martha Moore, provided welcomed logistical support in Hilo, and Paul Sykes willingly shouldered additional responsibility that freed CBK to join the expedition.

On the Soviet side, we thank Professor Alla V. Tsyban, Chief Scientist of the expedition, for extensive help and friendship during the voyage, Capt. Oleg Rostovtsev, Yevgeniy Nelepov, Yuri Volodkovich, and the crew for ship-to-shore transport, and Svetlana Petrovskaya and Valeriya Vronskaya for translation. We thank Greg Smith and Chuck Stafford for Zodiac transport at Caroline.

Katino Teeb'aki shared the transect work; his skills at obtaining and opening coconuts often energized us. Abureti Takaio, former Minister for the Line and Phoenix Groups, permitted us to work on Caroline and, with the residents of Christmas Island, arranged a memorable evening of dancing and food, despite the fact that their last supply ship was 10 months previous.

Financial assistance for the 1988 expedition and for writing the manuscript was provided by the U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, and the Natural Environment and Climate Monitoring Laboratory, Goskomgidromet USSR.

Grateful thanks are extended to Derral Herbst for identifying and preparing plant specimens (deposited in the B. P. Bishop Museum, Honolulu, Hawaii) and George Zug for identifying lizards (deposited in the U.S. National Museum). The Royal New Zealand Air Force supplied the aerial photos. Roger Clapp, Ray Fosberg, Gene Helfman, Ernst Reese, and David Stoddart shared unpublished manuscripts and other information. We are grateful to Lynda Garrett and Wanda Manning (Patuxent Wildlife Research Center Library, Laurel, Maryland) for digging out obscure historical references. Harry Maude of the Australian National University supplied plantation records and other literature indispensable in understanding Caroline's past and present ecology. The libraries and herbarium at the University of Georgia were also helpful. Thanks to Dorothy Schaumberg, Mary Lea Shane Archives of the Lick Observatory, University of California, Santa Cruz, for the letter from W. W. Campbell (1908) and extracts from E. B. Campbell's unpublished diary (1908). We especially thank Bonnie Fancher for her efficiency, enthusiasm, and hard work, often late at night and on weekends, on the computer and in other clerical matters in preparing the monograph. The manuscript has benefitted from reviews by Roger Clapp, Ron and Anne Falconer, Ray Fosberg, Ian Macintyre, Mark Merlin, Pat Roscigno, Betty Ann Schreiber, Fred Sibley, Thomas Spencer, Terry Whitledge, and Stephen Zeeman.

AKK, as co-leader of the ICBP 1990 expedition, expresses much gratitude to Christoff Imboden, International Council for Bird Preservation, Cambridge, U.K., and co-leader/expedition initiator Martin Garnett, for sharing finances. Thanks also to Annie Garnett, John Phillips, and Mark Linsley for help with field work, and to Alve Henricson for his sailing skills. The expedition would not have been successful without the dedication of Capt. Graham Wragg, skipper/owner of *Te Manu*, who transported us 7,585 km in the central Pacific (including 2 visits to Caroline), helped with field work, shared finances, and whose competence and consideration in many areas eased the varied hardships associated with 3 months at sea in a 10.5-m ketch. Thanks also to Sandy Bartle, National Museum, Wellington, New Zealand, for support, and to Scott Miller for providing insect vials, and David Preston for preparing and depositing insect specimens in the Bishop Museum, Hawaii.

On remote Caroline, the Falconers were exceptionally hospitable hosts, helping us with field work during, and after, the expedition. Special thanks go to 7-year old Alexandre, who discovered the first Blue-gray Noddy nest for the island and 3 new plant records. French Polynesian residents who assisted in various ways include Jacques Florence, Les and Gloria Whiteley, Rick Steger, Michael Poole, Jean Roudeix, and friends who supplied us with fresh provisions.

We particularly thank those who have aided us in follow-up conservation efforts: Kelvin Taketa, Jim Maragos and staff of The Nature Conservancy-Hawaii, Christoff Imboden and staff at ICBP, Alex du Prel, Jean-Michael Chazine, Philippe Siu, George Monet, Graham Wragg, Papeete Customs, George Ariyoshi, Kaiarake Taburuea of the Ministry of the Line and Phoenix Islands, John Claasen, New Zealand High Commission, Tarawa, and Peter Timeon, Ministry of Foreign Affairs, Tarawa.

AKK, CBK, DHE

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PART I. HISTORY, PHYSIOGRAPHY, BOTANY, AND ISLET DESCRIPTIONS

BY

ANGELA K. KEPLER[1] AND CAMERON B. KEPLER[2]

ABSTRACT

Caroline Atoll (Frontispiece) is situated at 10°00'S latitude and 150°13'W longitude in the south-central Pacific Ocean. Caroline is the southeasternmost of the Southern Line Islands, a group of 3 islands which also includes Vostok and Flint, lying 230 km to its west and southwest, respectively. Although archaeologically and geographically within Polynesia, Caroline is owned by the Republic of Kiribati (formerly Gilbert Islands).

Caroline, 9.7 km long, 2.3 km wide at its widest point, and 26.9 km in circumference, is a crescentic coral ring with 39 islets (motus) centered on a continuous reef enclosing a relatively shallow lagoon. Its total land area above high water is 399 ha., with motus ranging in size from 0.02 to 107.5 ha. Motus extend along 55% of the reef perimeter. The closed lagoon, rich in marine life, contains a maze of patch reefs and impeccably clear water.

The atoll, uninhabited, was "discovered" by de Quiros in 1606. Although traces of an ancient Tuamotuan culture still exist, the atoll apparently never supported a long-term permanent population and has been less affected by man than most Pacific islands. Its European history includes guano export, a multinational expedition to observe a solar eclipse, and copra production. It has been uninhabited since the early 1930s (a factor contributing to its relatively undisturbed ecology), except for the presence of one family from 1987 to 1991. The primary factors responsible for its lack of permanent settlement are remoteness, apparent absence of usable ground water, repeated failure of its coconut plantations (diseases, destruction by coconut crabs, rats and seabirds, smothering by vines), absence of a passage into the lagoon, and a paucity of safe boat anchorages.

Until the 1988 USSR/USA expedition, only an 1883 chart was available, which named 7 islets. We drafted an accurate map based on field work and recent aerial photographs, naming 32 previously unnamed islets, 4 islet groups and an inlet. During 8 days' intensive field work, we surveyed 38 islets, walking 33 km in systematic cross-islet transects and around islet perimeters. This paper presents much new data on Caroline from 3 visits in 1988 and 1990, and attempts to summarize, expand and synthesize previous information in the light of new findings.

1 400 Snapfinger Drive, Athens, Georgia, 30605, USA
2 National Biological Survey, School of Forest Resources
The University of Georgia, Athens, Georgia, 30602, USA

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Soils, principally of coral, mollusc, and algal origin, are categorized into 5 types, from barren coral rubble to rubble mixed with humus and guano. Caroline provides an excellent example of soil development through different age and size classes of motus.

Preliminary descriptions of the atoll's reef, motu and lagoon morphology are given, including the background geological setting of the Line Islands. Physiographic features include inland upraised reefs (*feo*) and deep sand deposits, coalesced islets, exposed older reefs, lithified beachrock, a conglomerate platform, a "perched lagoon," a nonfunctional *hoa*, and changes in motu size and shape during the past century.

Caroline's lush vegetation supports 26 species of plants organized into 7 plant communities, 6 natural and one anthropogenic. The atoll-wide distribution of each plant species is mapped. Plant species (including 5 new island records) and communities are detailed, emphasizing the atoll's past history. The atoll's insular flora, although impoverished due to its geographical location, is *89% indigenous* (possibly 92%), an extremely high figure for anywhere in the world. Although Caroline's motus are covered with extensive tracts of indigenous plant communities, the *Pisonia grandis* forests, up to 21 m high and covering 22% of the woodlands, are particularly notable as they constitute some of the best groves left in the Pacific. *Pisonia* is treated in detail, including data on rapid recovery and growth rates during the past 70-odd years. *Tournefortia argentea* (43% of the woodlands) is abundant, and *Cordia subcordata*, becoming quite rare elsewhere, occurs on 21 motus (54%). *Cocos* is present, but only dominates one islet; 22 islets harbor wholly indigenous vegetation.

Motus of varied age and size classes provide excellent examples of substrate and vegetation development, accompanied by an increasing diversity of bird life. On account of its relatively low human disturbance and rapid forest recovery to a more natural state, especially since 1920, Caroline is one of the few Pacific islands that is truly an "outdoor ecological laboratory": many motus have recovered so remarkably they are almost indistinguishable from those that have remained pristine, while others are in different stages of recovery resulting from varied management (or non-management) practices. Exotic plant species are very few: ancient Polynesian-introduced (*Cocos*, possibly *Pandanus*), recent Polynesian-introduced (*Hibiscus tiliaceus*, *Thespesia populnea*, *Tacca leontopetaloides*, *Ximenia americana*), 20th century exotics (*Phyllanthus amarus*, in one small area). Some garden species, cultivated from 1987-1990 have an uncertain future and are not treated as part of the atoll's viable flora.

An analysis of ecological succession on motus of increasing size reveals that by the time a motu reaches 0.8 ha in size, all the natural plant communities, most plant species, and most species of seabirds are present. This is in striking contrast to species-area relationships on inhabited atolls with more introduced plant species, for example Kapingamarangi.

Each motu is individually mapped and the main physiographic features, known history, vegetation patterns (including species-area relationships), seabirds, and miscellaneous biota (coconut crabs, rats, lizards) are detailed. Appendices provide weather data and describe the practicalities of anchoring boats, landing, and moving small boats around the reefs and lagoon.

Permanent protection of Caroline is currently underway as The Nature Conservancy of Hawaii negotiates with the government of Kiribati for a Southern Line Islands Wildlife Preserve, which includes Caroline, Vostok and Flint.

A. INTRODUCTION

Caroline Atoll[1] (Frontispiece; Figs. 1, 2) is a small, low coral island situated at 10°00'S latitude, 150°13'W longitude in the south-central Pacific Ocean. Its maximum height is less than 3 m above MSL. It lies 2,800 km south of Hawaii, 830 km north of Tahiti, and 1,030 km west of the Marquesas Islands. Its nearest neighbors are Vostok and Flint, 230 km to the west and southwest, respectively.

Recent measurements by the ICBP 1990 Line and Phoenix Islands Expedition, using a compact satellite navigation computer "Magellan" NAV 1000, indicate that the atoll lies one nautical mile east of its previously charted longitude position, 150°14'W. Its range of coordinates are: 09°54' to 10°01'S latitude, 150°12' to 150°14' W longitude. The given coordinates, 10°00'S and 150°13'W, intersect in the lower lagoon just west of the "blind passage."

Although archaeologically and geographically within Polynesia, the Line Group was uninhabited when discovered by Europeans; its islands were variously claimed by the United States and England. With the exception of U.S.-owned Jarvis, Palmyra, Johnston and Kingman Reef, all are now governed by the Republic of Kiribati (formerly Gilbert Islands).

Caroline, 9.7 km long by 2.3 km wide at its widest point, is a crescentic coral ring 26.9 km in circumference. Composed of 39 islets (Fig. 2, Table 9) and three incipient islets, it is centered on a continuous reef flat, submerged at high tide, that encloses a relatively shallow lagoon. Most are well-wooded, but 4 tiny ones, less than 0.1 ha in size, are scarcely more than coral rubble piled on the reef, supporting sparse patches of *Tournefortia* and *Heliotropium*. One islet, Noddy Rock (Pl. 18), is a vestige of a former reef segment. The total land area above high water is 399 ha. One of the oceanic islands contributing to Darwin's theory of atoll formation (Darwin 1842), its

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[1]Caroline Atoll is neither physically, geographically, nor politically associated with the Caroline Islands, now part of the Federated States of Micronesia, more than 6,000 km to the northwest. Because of this confusion, we use the name "Caroline Atoll" instead of "Caroline Island."

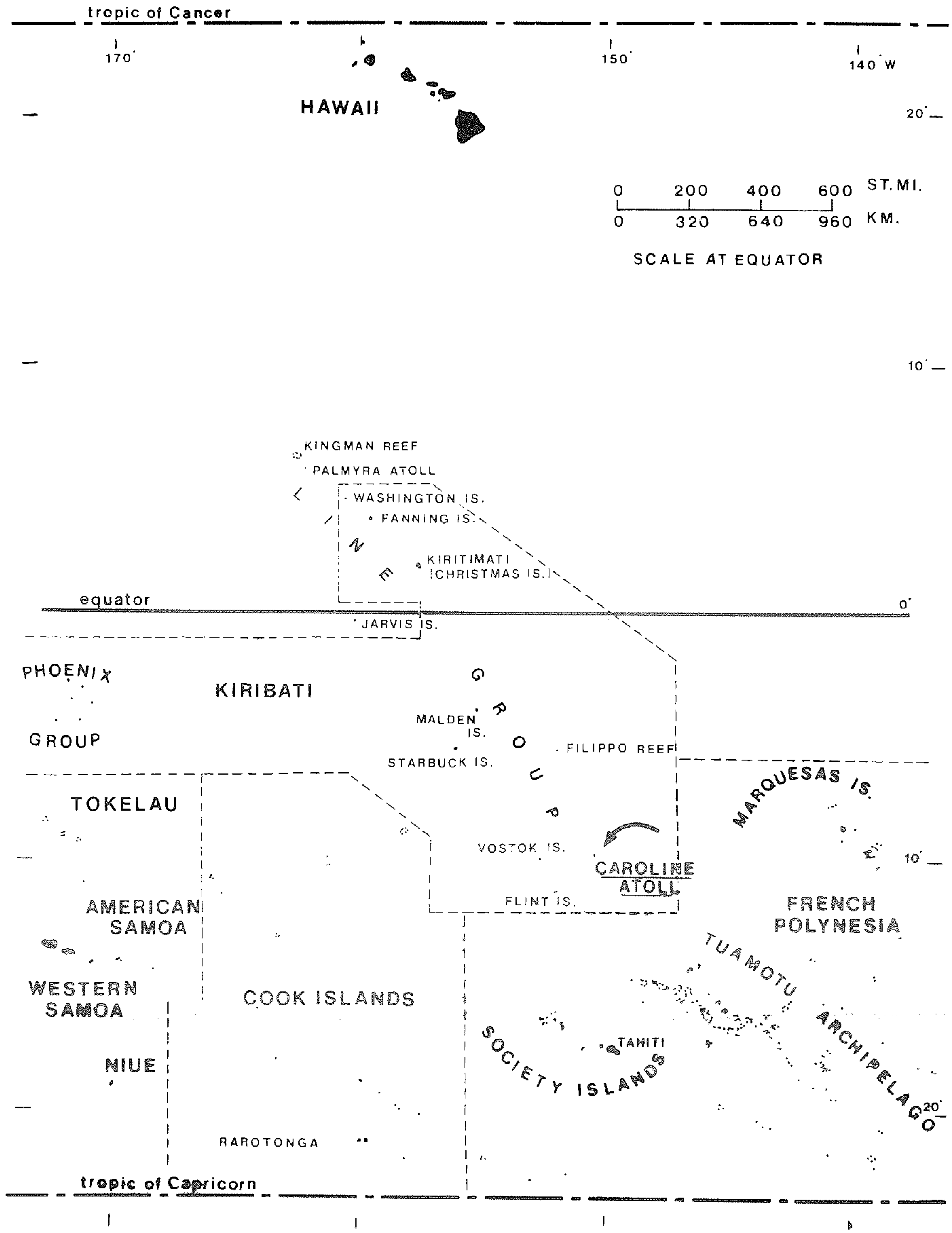

Figure 1. Line Islands: geographic location in the Pacific Ocean. After map by the Hawaii Geographic Society (1981).

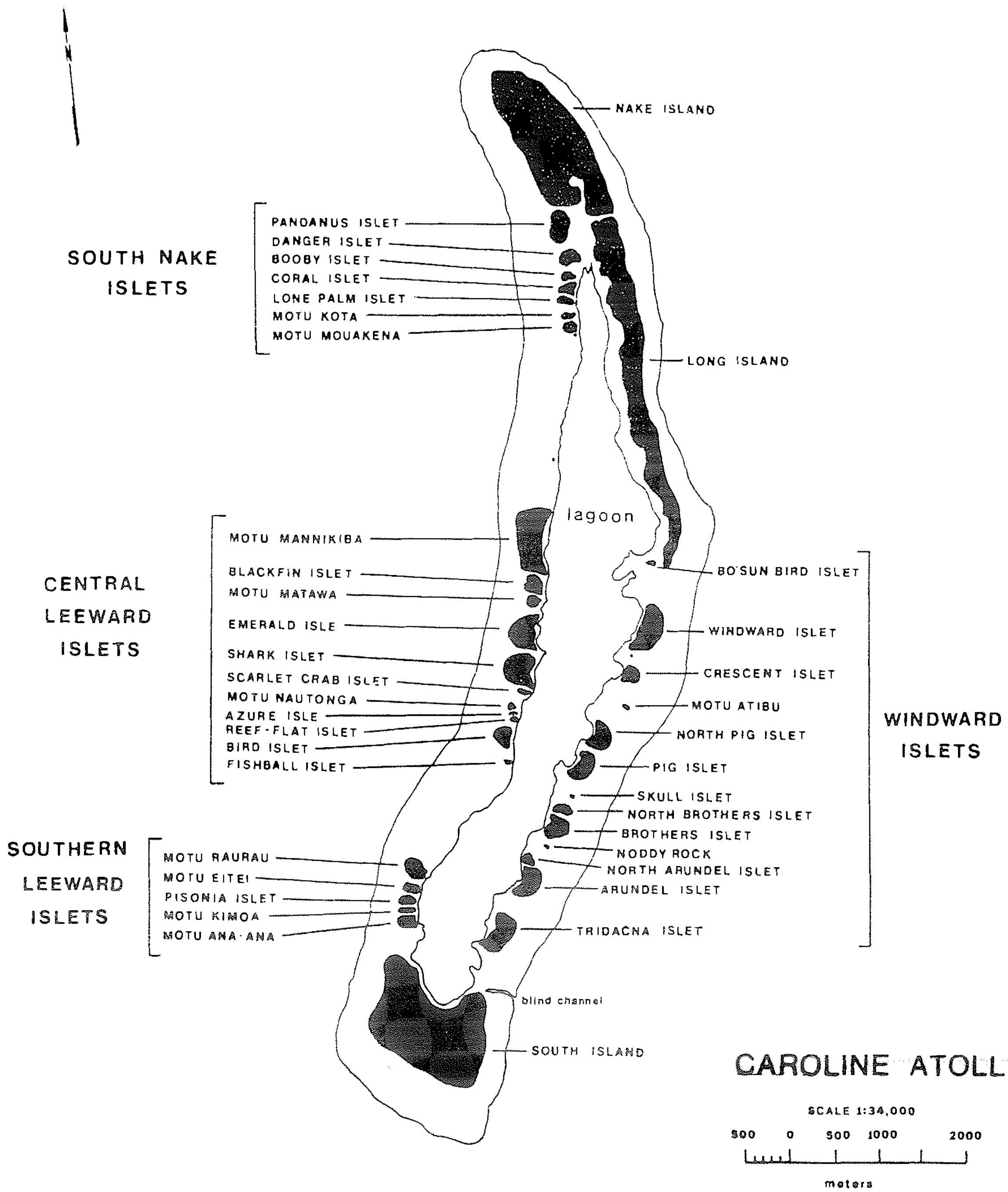

Figure 2. Caroline Atoll, Republic of Kiribati, with newly-named islets. Based on photos by the Royal New Zealand Air Force (RNZAF 1986).

geology, soils, climate, and vegetation are typical of low latitude atolls and are relatively unmodified by man.

This paper presents much new data on Caroline from 3 visits in 1988 (September) and 1990 (March, May) and attempts to summarize, expand and synthesize widely scattered information in the light of new findings. The only significant previous biological information on Caroline was from the Smithsonian's Pacific Island Biological Survey Program's 2-day visit in 1965 (Clapp & Sibley 1971).

B. HISTORY OF CAROLINE ATOLL

Pre-European History: Tuamotuan Period

Centuries before Europeans encountered Caroline, the atoll was inhabited by Polynesians. No oral traditions of this occupation are known, but evidence of former habitation was evident when de Quiros found the atoll in 1606. He noted "an old canoe, lying on her side," and a small grove of coconuts planted on South Island (Bennett 1840, Markham 1904).

No further clues were unearthed until Messrs. Brown, Brothers, and Arundel exposed about 50 ancient Polynesian sites in the 1870s while digging for guano (Holden 1884, Arundel 1890). Polynesian inhabitants at that time called them "marai" (*marae*). Arundel photographed and drew plans of them (Fig. 3): depicted are a platform of coral and conglomerate rock, surrounded by 10 smaller slabs resembling gravestones, all arranged in a rectangular plan. Although the largest 2 were marked as "graves" on Arundel's 1883 map (Fig. 4), no bones, ashes or human remains were found. Their findings were later identified as Tuamotuan *marae* (Emory 1947). *Marae*, according to ancient belief, "bound the ancestral spirits and gods of the kindred to the land, putting it under their eternal guardianship" (Emory 1947). The largest *marae* was on northwest Nake Island, and a smaller one was found near the southern tip of Long Island. Both locations conform to such prerequisites for building *marae* as nearby shorelines and birds (see Sect. H.1), which Tuamotuans believed housed divine spirits (Emory 1947, p. 123). Although AKK, G. Wragg and R. Falconer located, photographed (Pl. 36), and measured these in 1990 (A. Kepler 1990d), no field work by archaeologists has been conducted. Our data and numerous photographs have been sent to Dr. Jeff Irwin, Auckland University, New Zealand.

Post-European History: 17th to 19th Centuries

On 21 February 1606, the Portuguese explorer Pedro Fernandez de Quiros, employed by Spain, "discovered" Caroline Atoll (Markham 1904, Stevens & Barwick 1930), naming it San Bernardo. Despite its remoteness, Caroline was encountered early in Pacific history, long before Tahiti, Rarotonga, and Hawaii. This is possibly due to its location, for early navigators tended to sail due west from South

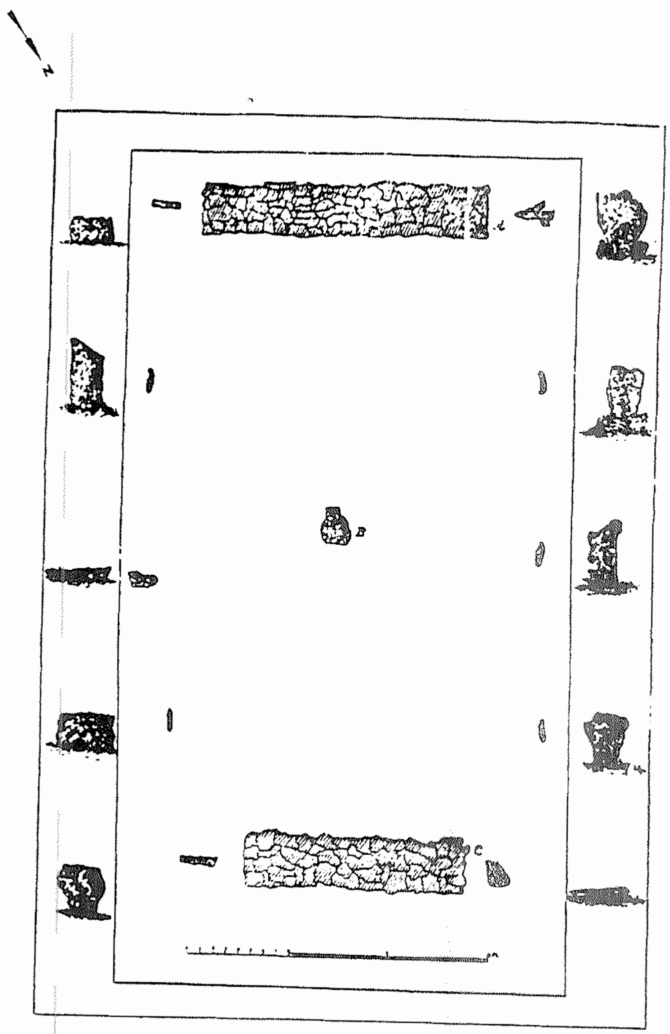

Figure 3. Main *marae* on Nake Island, Caroline Atoll, based on a plan published by the Solar Eclipse Expedition (Holden & Qualtrough 1884). Figures in the margins show side views of the peripheral blocks shown in the plan. The 2 end walls are represented in ground plan.

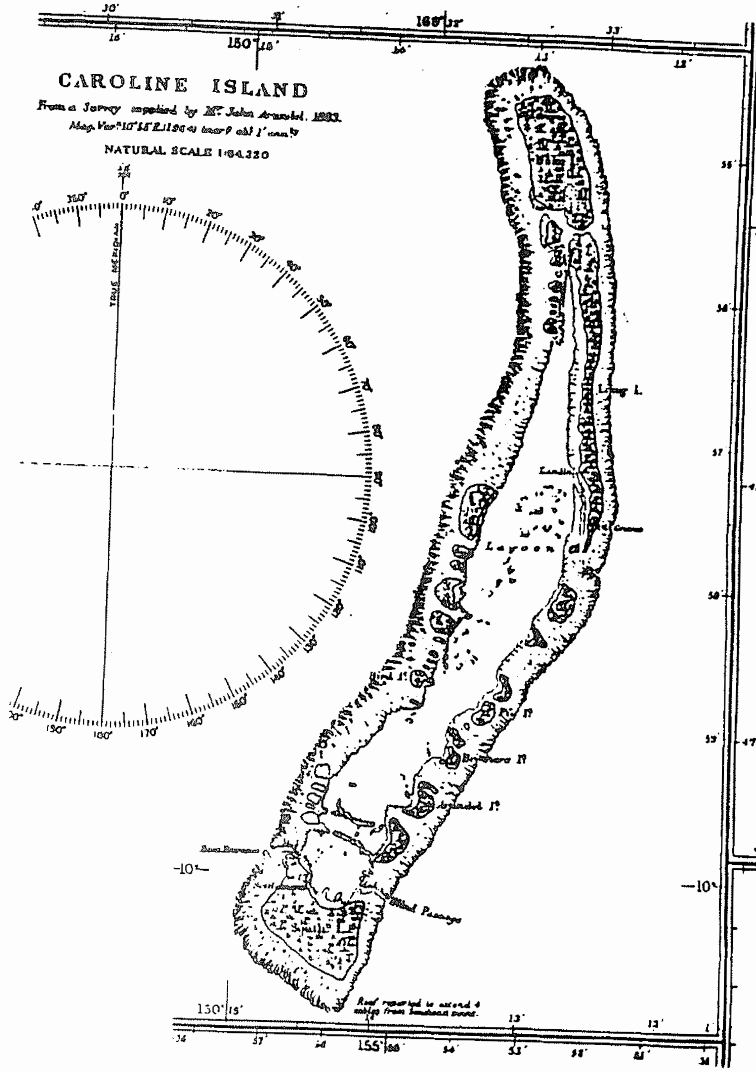

Figure 4. Caroline Atoll, as surveyed by John Arundel, 1883. This is still the standard hydrological chart for the atoll (Admiralty Chart No. 979). Though quite accurate, it has never been used in scientific publications.

America along lines of latitude, and 10°S was an obvious choice. De Quiros, the last adventurer in the Spanish age of discovery, was leading his second major trans-Pacific expedition with 3 ships and 150 men obsessed with finding the fabled "Terra Australis Incognito." The descriptions of Caroline by his crew, although at variance with one another, still apply today (Pl. 1). Their first at-sea impression was that it was "divided into four or five hummocks, and all the rest submerged. Its circumference appeared to be ten leagues" (Markham 1904). After landing, they found that

> "There was a great number of fish inshore, and, owing to the water being very shallow, they were killed with swords and poles. There were great numbers of lobster and crawfish, and other kinds of marine animals. They found a great quantity of cocoa-nuts in a heap at the foot of the palm trees, many large, and of different sizes. There were a great quantity of sea birds of several kinds, and so importunate that they seemed to want to attack the men. We took plenty of all these things...It seemed to the Captain that on an island where there are so many trees there could not fail to be water" (Markham 1904).

Fresh water was crucial to de Quiros and his crew, who were suffering from lack of food and water. Despite their efforts, however, they failed to obtain water. Disappointed and lacking energy, they continued their voyage the following morning. Their demoralized state may explain one statement that Caroline "consisted of twenty-two islets, uninhabited and without water, trees or scrub for wood."

In 1795, Capt. W. R. Broughton, on the British sloop *Providence*, rediscovered and named the atoll while voyaging from Tahiti to Hawaii (Broughton 1804):

> "The southern extremity was the highest part, covered with trees, most probably cocoa-nut from their appearance, as they stood in detached clumps along the shore. The island... appeared to be low, and covered with trees, and if I am right in its estimated distance, its length will be about five miles in a north and south direction. I named it Carolina Island in compliment to the daughter of Sir P. Stephens of the Admiralty."

Because early navigation techniques and communication were far less sophisticated than today, especially with regards to longitude, Caroline was sighted or "discovered" by several more explorers who were unsure of its identity. By 1821 the atoll had amassed a collection of coordinates and names: San Bernardo, Island of Fish, Thornton, Hurst's, Clark's, Independence, and Carolina (which later became Caroline). Some navigators equated Caroline with an island named "San Bernardo" by the Spanish explorer Mendaña in 1595. "San Bernardo" has recently been verified as Puka-Puka, northern Cook Islands (Maude 1968).

The best early description of the atoll comes from an 1835 visit by F. D. Bennett, who was reasonably well versed in natural history (Bennett 1840). He noted that the islets then, as now, were "covered with verdure...surprisingly luxuriant, when compared to the arid soil it covers." Although Bennett had visited many atolls, he was particularly impressed with the quality of Caroline's coral reefs. His party observed "rats of a red-brown color" and various birds but no reptiles (Pt. II). Although he discusses "land lobsters (*Coenobita* species)," no mention is made of coconut crabs (*Birgus latro*): perhaps the latter were lumped with the former.

First Occupation: The existence of 2 small coconut groves on Caroline prompted 2 British entrepreneurs, representing the Tahitian firm Collie and Lucett, to establish a stock raising venture there in 1846. This first known settlement was located adjacent to the main coconut grove on the northwest peninsula of South Island; a smaller grove evidently existed "on the south-south-west side" of the same island (Lucett 1851). Tahitian laborers tended pigs, hens, turkeys, and grew many food plants, including pumpkins and melons. They dried and salted fish, planted coconuts, and extracted coconut oil (Maude 1942, Garnett 1983), and were evidently still there in May 1852 (Ellsworth 1990).

Political Annexation: Though inhabited in prehistory by Tuamotuans, officially "discovered" by the Spanish, and visited by British, French, and American ships, it took centuries for Caroline to acquire a political identity. It was formally annexed to Britain by Captain Nares, R. N., who arrived in the H.M.S. *Reindeer* in 1868, finding 27 residents.

Caroline was under the control of various merchants in the late 19th century: Lionel Brown, Captain Brothers, and later John Arundel, a well-known businessman, trader, and guano merchant in the Pacific. Arundel's 1883 map (Fig. 4) of Caroline is the only reasonably correct chart published prior to this paper.

The Guano Era

Though bonded under the American Guano Act in 1860, no phosphate was dug on Caroline until Arundel was granted a 7-year license in 1874. A few months earlier, a set of moorings were laid off the lee side of South Island, allowing ships of up to 1,000 tons to lie safely during trade wind weather. Guano was the only successful business venture at Caroline: approximately 10,000 tons were shipped to California and Australia between 1873 and 1895, when supplies became exhausted (Young ca. 1922). We have no direct information on which islands were mined except South and Nake. We strongly suspect that Tridacna, Arundel, Mannikiba, and perhaps others also yielded guano. The tonnage extracted from Caroline was small compared to that from dry, barren, more northerly islands with little vegetation, where populations of Sooty Terns, an important guano species (Hague 1862), number in the millions.

Solar Eclipse Expedition

In 1883 Caroline received international publicity when astronomers calculated that it lay directly under the path of a pending solar eclipse. Three parties of astronomers (American, British, French) arrived in the U.S.S. *Hartford* and set up camp on South Island, making detailed observations of this celestial event (Pl. 2). At that time Caroline was more famous, and housed more people, than before or since: 7 "natives," scientists and crewmen totalled 51 occupants. Legacies from former inhabitants included 3 houses (Pl. 3), 2 sheds, 3 huts on smaller motus, nautical flotsam and jetsam, and 2 shallow wells. To this they added tents, observatory frames, a marble slab, flagpole, and brick "piers" for their telescopes, most of which remained temporarily as technological litter.

This expedition (Dixon 1884, Holden 1884, Holden & Qualtrough 1884, Trelease 1884, Young 1884) also marked the first attempt to describe the topography, climate, flora, and fauna of the atoll. Drawings included an artist's rendering of Caroline, "settlement" map (Pl. 5) and views along South Island's lagoon shore (Pls. 6, 7). An atoll map was drafted but is highly inaccurate. Their biological observations were sketchy (Dixon 1884, Butler & Strecker 1884). For example, Dixon, the zoologist, listed such organisms as "shrimp," "hermit crabs," "gnat." As with Bennett, there was no mention of coconut crabs, even though they were evidently abundant on South Island in 1910 (Young ca. 1922).

The Late 19th and 20th Centuries

In 1875, C. D. Voy, a naturalist from California, visited Caroline, collecting molluscs (Pilsbry & Vanatta 1905a, b) and fish (Fowler 1901).

In 1885, Arundel began to clear land and plant coconuts, but his planned copra industry was unsuccessful. In 1897 he sold his business to the Pacific Islands Company, Ltd., which also failed. The plantations suffered from disease and poor vitality, coconut crabs chewed on seedlings, seabirds destroyed the developing nuts, *Ipomoea* vines strangled young trees, and populations of Polynesian rats apparently exploded, causing further damage to both intact nuts and drying copra (Young ca. 1922, Maude ca. 1938, 1942). By 1904, when the H.M.S. *Icarus* visited Caroline, only 6 Polynesians lived there. A few months later they were repatriated to Niue, and Caroline remained uninhabited until 1916, when a new effort was made to develop the coconut plantation by Messrs. S. R. Maxwell and Co., Ltd.

During the uninhabited years, South Island's vegetation and wildlife began to recover from the earlier forest felling (Pls. 2-6). When Mr. J. L. Young, then managing director for S. R. Maxwell and Co., Ltd. (Young ca. 1922), visited the atoll in July 1910, he described it as a wilderness, teeming with Sooty Terns, fish and coconut crabs:

"The ground was covered with nests of seabirds which latter rose like a cloud when disturbed: the noise of their shrieking was so great that one had to shout to enable oneself to be heard by his companions. Hundreds of great Coconut Crabs were seen: 40 large ones were caught by the crew of the schooner in an hour. The reef and the lagoon swarmed with fish and small sharks."

From 1916 to 1929, Caroline was altered more than before or since. All the available land on South was deforested to make room for thousands of palms, and laborers demolished huge numbers of coconut crabs and seabirds (Young ca. 1922). In addition, coconuts were planted on all of the main windward islets, southern Nake, and on Mannikiba. (The windward islets recovered their forests remarkably quickly, see Sect. G). Plantation workers in great part lived off the land, feasting on fresh fish, seabirds, seabird eggs, turtles, and coconut crabs. Most of the leeward islets escaped alteration for plantations.

Copra exports averaged around 14 tons per year from 1929 to 1934, after which the company ran into debt. Concurrently, the French government forbade further recruitment from Tahiti; by 1936 only a few families were left (N.I.D. 1943). In 1941 the atoll carried a price tag of 600 English pounds (Maude, pers. comm.), but was never purchased.

Occupation leases for Caroline were cancelled in 1943, after which the British Western Pacific High Commission repossessed it (Maude 1953). However, new "queen's leases" were granted to M. P. A. Bainbridge of Papeete, Tahiti, 1951-1964 (Nicholson & Douglas 1969), then to Capt. Omer Darr of Moorea, French Polynesia, from 1964 to 1989. When the British granted independence to the Gilbert and Ellice Islands in 1979, a new country, the Republic of Kiribati, assumed ownership of Caroline, along with most of the Line and Phoenix Islands.

Apart from occasional parties of Tahitians cutting copra and a shipwrecked sailor in the early 1980s, the atoll remained uninhabited for over 50 years. During this time Caroline's vegetation and wildlife recovered to such an extent that, were it not for unpublished manuscripts (Maude ca. 1938, ca. 1942, and no date, Young ca. 1922) and comparisons with Flint and Vostok (St. John & Fosberg 1937, A. Kepler 1990b-d, and Kepler, in prep.), we would have been unaware of the extent of previous human interference or of the rapidity of forest recovery (the fact that 60% of Caroline's motus harbored wholly indigenous vegetation, and the presence of one small patch of one exotic plant aside from a few standard Polynesian-introduced plants, seemed to indicate a relatively pristine atoll).

In 1987, the Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM, a French scientific research agency) was requested by the Kiribati government to conduct a short study at Caroline on the feasibility of pearl-shell culture (G. Monet, pers. comm.). Their results concluded that the atoll would be inappropriate for this type of development.

Also from 1987 to 1991, a Scotsman, Ron Falconer, his French wife Anne, and 2 small children settled on Caroline. From October 1989 to November 1990 a new lease was under negotiation by Felix Urima, a French businessman, who planned to blast a channel through the reef, construct an airstrip, build a small hotel, cut timber, and engage in various commercial ventures including fishing, a turtle farm and pearl-shell culture. In April 1990, Urima's workers began commercial fishing, killing turtles and coconut crabs, and clearing land (A. Kepler 1990a). This was a major new insult to the atoll which, in spite of its long history of intermittent human occupation, remains to this day "possibly one of the least spoiled of true atolls in the Pacific" (Stoddart 1976). Reports from our expeditions to Caroline (Kepler & Kepler 1989, A. Kepler 1990a and d) resulted in the short-lived cancellation of Urima's tentative lease in November 1990 by the government of Kiribati. As of this writing, Urima has returned to unlimited fishing of Caroline's reefs. Since 1988, conservation efforts have been underway for Caroline to become part of a triple-island wildlife preserve with Vostok and Flint (Pt. II, Sect. G).

20th Century Scientific Studies

In June 1965, a field party from the Smithsonian Institution's Pacific Ocean Biological Survey Program (POBSP) visited Caroline for 2 days (Clapp & Sibley 1971a). Their survey and specimens added much to the previous botanical and ornithological knowledge of the island. Other quick visits were made by Gilbert and Ellice Island officials and Drs. H. & H. Grossman, ornithologists from Germany, and Mr. W. Cooke, a graduate student in corals from the University of Hawaii, comprising the Line Islands Expedition on 9-10 September 1974, and by Roger Perry, then Wildlife Warden of the Line and Phoenix Islands, on 12-13 November 1977, from which no reports can be found other than a short popular account of the Southern Line Islands (Perry 1978).

In 1990, AKK also visited Caroline twice with the ICBP 1990 Line and Phoenix Islands Expedition (A. Kepler 1990d). These visits were primarily to discuss conservation matters with the Falconers; introduce Caroline to Dr. and Mrs. M. Garnett, representatives from ICBP; confirm the illegal taking of fish, turtles, and coconut crabs; collect invertebrates; and fill in gaps from the 1988 expedition.

C. METHODS

Field Techniques

From 22-29 September 1988, Drs. A. K. Kepler, C. B. Kepler, D. H. Ellis (U.S.A.) and Mr. Katino Teeb'aki (Republic of Kiribati) surveyed all 39 motus at Caroline Atoll (Fig. 2), gathering detailed information on plants, seabirds, land birds, mammals, reptiles, coconut crabs, and human disturbance. Some incidental data have been added from the 2 visits in 1990 (10-13 March, 18-28 May) by Dr. A. K. Kepler, Capt. G. Wragg, A. Garnett, M. Linsley, J. Phillips (March), and Dr. M. Garnett (May).

Prior to the first expedition, a series of transects and known botanical information were mapped to ensure that 5% of each motu was sampled, and to maximize our chances of encountering all known plant species. Transects on the 3 larger motus were spaced approximately 400 m apart and, with one exception, were perpendicular to the long axes of each islet (Tr. 3 on Nake extended first from east to west, then ran south parallel to the west coast). On motus longer than 400 m, we used 2 transects. Transects on the smaller motus passed through their widest points. Their lengths ranged from 77 m (Azure) to 2,000 m (Tr. 3, Nake).

Considerable modifications were required when we realized that all previous maps (Figs. 4-7) were incorrect. We redrew the transects on Arundel's 1883 map (Figs. 4, 8), secured just prior to the expedition. On South Island, due to impenetrable draperies of *Ipomoea* vines, Transect 3 was omitted, Transect 5 ran only from the lagoon south to the *Ipomoea* curtain (75 m), and Transects 4 and 6 ran north and south until we reached an impasse (Pl. 8).

Compass headings were determined by the configuration of each island. Beginning at high water mark, all distances (islet dimensions, widths of reef flats and substrates, and plant communities) were measured using hip chains with biodegradable cotton thread. These parameters were later checked against aerial photographs in stereoscopic pairs (RNZAF 1986), which provided 3-dimensional overviews of most islets. Vegetation maps, reef and islet areas, and areas of plant communities were derived by outlining on graph paper, enlarging, then counting dots.

Data were collected in a 30 m swath along each transect (15 m to each side) and recorded on field forms. Within each plant community we took photographs, assessed the relative abundance of each plant species (see Sect. E), measured notable trees, and recorded plant community width, plants collected, and substrate type. We also estimated the maximum height of the dominant vegetation and percentage of ground area covered by each species. Data on seabirds, land birds, reptiles, mammals and coconut crabs is reported in Part II.

In addition to the linear transects, an additional 19,300 m of perimeter surveys were conducted on 21 islets (Fig. 9). The combined distance for linear and perimeter transects was 32.6 km. Seven tiny islets (Noddy Rock, Skull, Atibu, Bo'sun Bird, Coral, Reef-flat, Fishball) were surveyed completely.

In 1988 we camped on the atoll for 7 nights, establishing base camps (Fig. 8; Pl. 9) on the northwest point of South (22-24 September) and southwest Long (25-28 September). We relocated camps using a Zodiac with outboard motor, and an inflatable Sevylor canoe. All transects were surveyed during daylight hours, beginning at dawn. Walking the interislet channels was relatively easy at low tide, but became

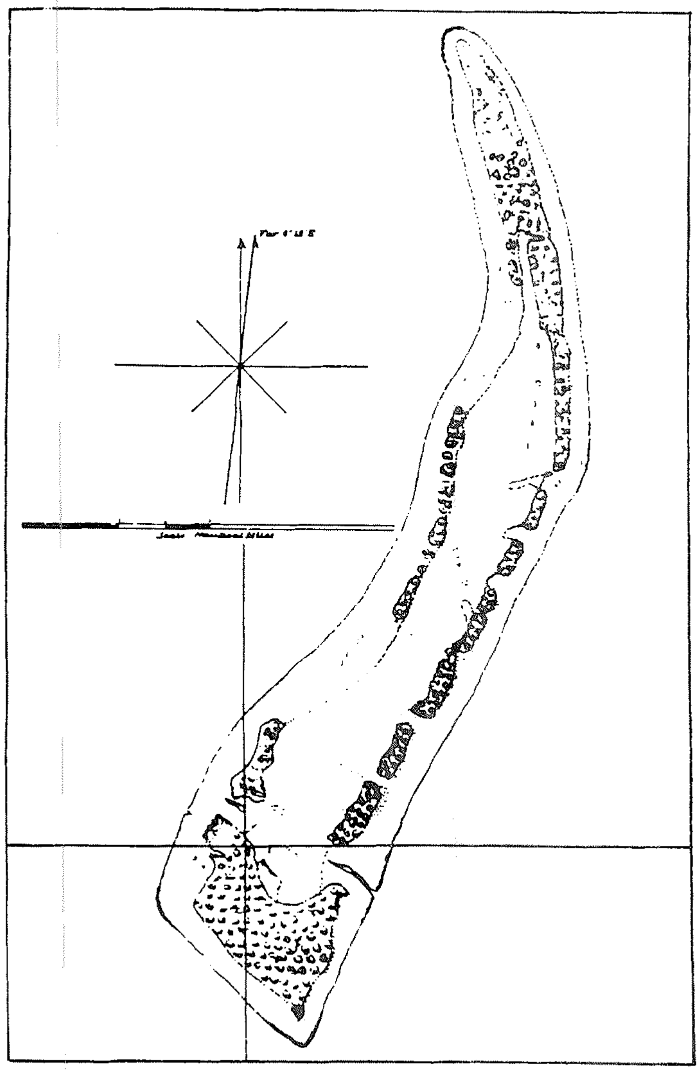

Figure 5. Caroline Atoll, as charted by the Solar Eclipse Party, also in 1883 (Holden & Qualtrough 1884).

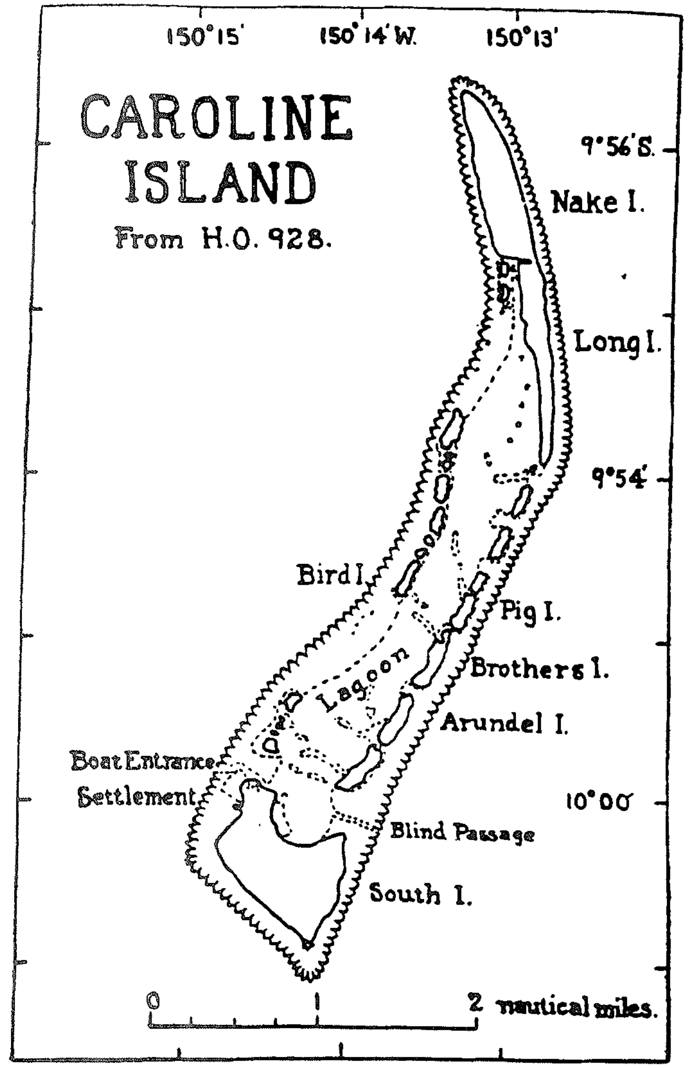

Figure 6. Caroline Atoll, a modified version of the Solar Eclipse Party's map (1883) as portrayed by Bryan (1942). Though highly inaccurate, modifications of this map have been used in all publications since Bryan (1942).

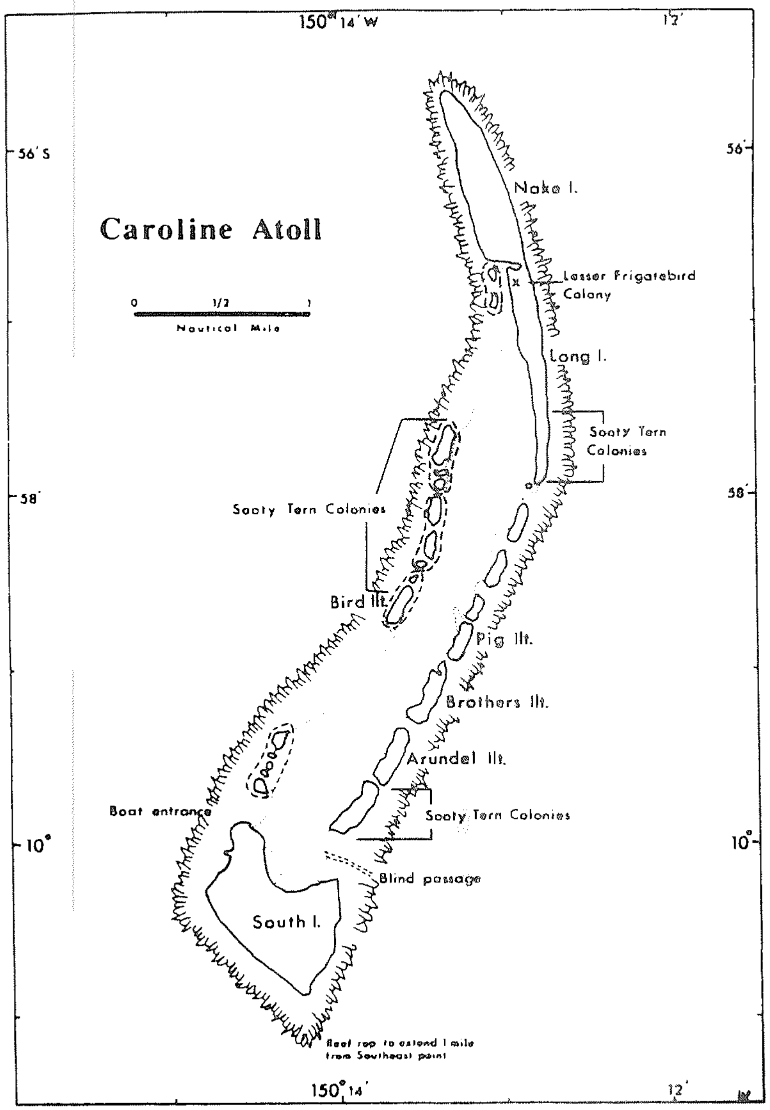

Figure 7. This map, by Clapp & Sibley (1971a), was based on Figure 6.

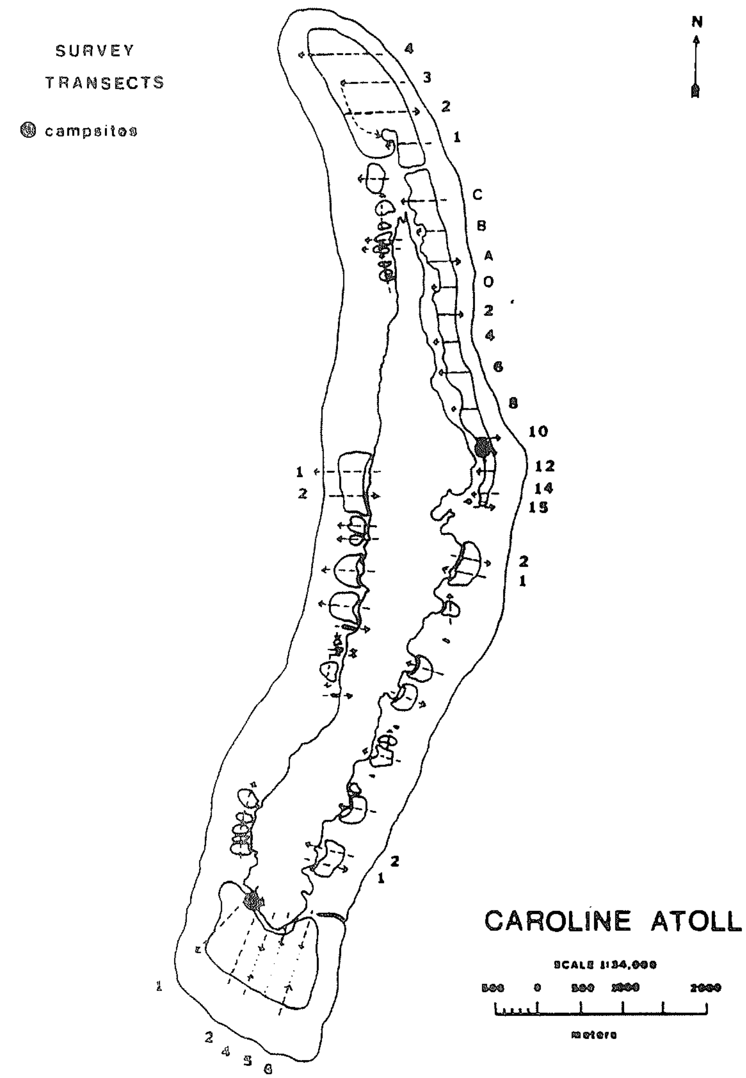

Figure 8. Caroline Atoll: survey transects. The distance covered was 13.3 km.

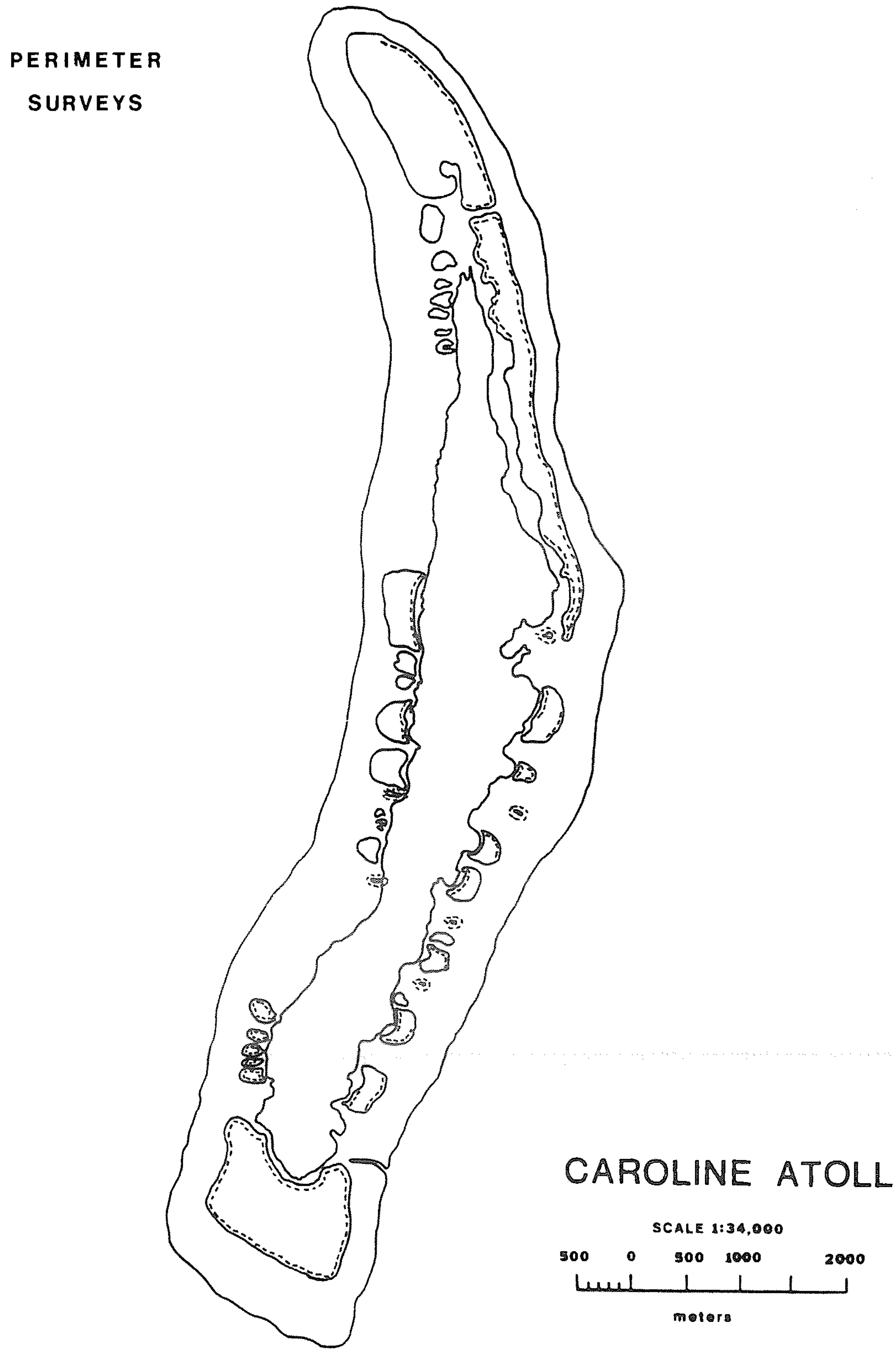

Figure 9. Caroline Atoll: perimeter surveys. The distance covered was 19.3 km.

hazardous at incoming or high tide on account of numerous aggressive black-tipped reef sharks, *Carcharhinus melanopterus* (Pl. 10).

During the 1990 visits, we stayed on Motu Ana-Ana with the Falconers. Work was not intensive, as in 1988. We walked or motored an inflatable Lancer, visiting 20 motus gathering incidental data, locating the *marae*, etc.: Ana-Ana, Kimoa, Pisonia, Eitei, South, North Arundel, Noddy Rock, Brothers, North Brothers, Skull, Pig, North Pig, Bo'sun Bird, Long, Nake, Mouakena, Shark, Scarlet Crab, Bird, and Fishball. Insects were preserved in ethyl alcohol. We used a "Magellan" NAV 1000 to obtain accurate geographical coordinates of Caroline.

Naming Caroline's Motus

Previous literature has provided vague or incomplete data on Caroline's constituent motus (Bennett 1840, Markham 1904, Stevens & Barwick 1930, Holden & Qualtrough 1884, Bryan 1942, Clapp & Sibley 1971a, Garnett 1983). This confusion resulted because most previous visits had been brief. The only charts available were a quite accurate survey by Arundel, a guano merchant who mapped the atoll in 1883 (Fig. 4, Admiralty Chart, No. 979, 1965), and a map, greatly in error, drafted by an international Solar Eclipse Party, also in 1883 (Fig. 5). There are no hydrological navigation charts. Unfortunately, the astronomers' map has been used in all subsequent scientific, historical, military and sociological publications [N.I.D. 1941, Bryan 1942 (Fig. 6), Maude 1968, Clapp & Sibley 1971a (Fig. 7), Garnett 1983]. It shows only 25 of the 39 motus and many shapes are distorted. The 38 motus on Arundel's map are similar to those in the RNZAF (1986) aerial photographs. Only a few appear to have changed in minor ways since 1883: major discrepancies in Arundel's map, we believe, are due to difficulties involved in the accurate rendition of small land areas (i.e. the South Nake Islets). Maude (ca. 1938) counted 36 islets, but never published his information.

To aid our survey we named 32 islets and 4 islet groups (Fig. 2). Our names reflect appropriate aspects of islet biology. Etymology is provided in Section H. Gilbertese names are prefixed with *motu* (see next section). Any name not appearing on Arundel's map (Fig. 4) was given to the islets by us. They have been sent to the British Admiralty and U.S. Hydrographic Office (along with corrections to the Pacific Pilot) for official recognition.

D. PRELIMINARY STRUCTURE AND TOPOGRAPHY

Our geological terminology is based on Tracey et al. (1955) as cited by Wiens (1962), to which we add *motu* (Polynesian for "islet"), now a technical term for detrital reef islands (Danielsson 1954, Stoddart & Steers 1977). In this paper the terms *motu* and islet are used interchangeably.

Background Geological Setting

Caroline is the southeasternmost of the Line Group (Fig. 1), a major volcanic lineament in the Pacific, comparable in size to the Hawaiian-Emperor chain to the north and the Marshall-Gilbert-Ellice chain to the west. This quasi-linear chain, 4200 km long, is composed of dozens of simple and complex seamounts and linear ridges, 6 atolls, 5 islands, and 2 submerged reefs. The Line Islands are now considered to include Johnston Atoll (Duncan 1983, Schlanger et al. 1984), and thus lie between 17°N and 12°S latitude, and 169° and 150°W longitude. The name, Line Group, reflects its equator-straddling location.

The geological complexities of the East Pacific in general and Line Islands in particular were poorly understood until a few years ago. However, recent remote-sensing technologies, deep-drilling techniques, improved sea-floor mapping and multidisciplinary studies of sea-level changes have clarified much previous speculation (Jarrard & Clague 1977, Orwig & Kroenke 1980, Montaggioni & Pirazzoli 1984, Schlanger et al. 1984, Pirazzoli & Montaggioni 1988, Spencer 1989).

The Line Islands are now known to exhibit changing geomorphology from north to south: elongated submarine ridges and coalesced seamounts merge into a broad central high plateau, then progress to scattered isolated seamounts in the south (Duncan 1983, Schlanger et al. 1984).

This long chain of geologically related and unrelated islands exhibits a complex history of volcanism involving activity from multiple "hotspots" and overprinting events dating as far back as 93 million years (Jarrard & Clague 1977, Orwig & Kroenke 1980, Crough & Jarrard 1981, Haggerty 1982, Duncan 1983, Schlanger et al. 1984). Furthermore, although numerous studies, using high technology, have been conducted from oceanographic vessels, very little data has been gathered from the islands themselves (M. O. Garcia & J. A. Haggerty, pers. comm.), and a clear understanding of the myriad interacting processes which formed the Line Islands has not yet emerged. This is particularly true of the central and southern Line Islands.

However, recent palaeoecological research in the Tuamotu Archipelago includes generalities which are applicable to the Line Islands (Montaggioni & Pirazzoli 1984, Pirazzoli & Montaggioni 1988).

The known geological history of the Line Islands can be summarized as follows:

1) During the Cretaceous period (140-65 m.y. B.P.), ridge-building volcanic events occurred, giving rise to scattered volcanoes, older in the north. This period of mountain-building was a worldwide phenomenon, in the eastern Pacific supported by hotspot activity in the vicinity of Easter Island.

2) A second eruptive phase during the Palaeocene-Eocene period (65-38 m.y. B.P.), and age-progressive from north to south, overprinted

earlier volcanoes. This was either a result of "hotspot" activity along the Line-Marquesan Swell or part of Pacific-wide volcanism.

3) The history of reef growth and subsidence is complex and has not been studied in detail. The Line chain was in latitudes amenable to reef growth throughout its history from the Late Cretaceous (100 m.y. B.P.) to the present (Schlanger et al. 1984). A general pattern for the northwest Tuamotus, close to the southern Line Islands, shows primarily Holocene reefs 6000-3000 years old (Pirazzoli & Montaggioni 1988). However, a few older reefs do exist, and dredge hauls near Caroline (Schlanger et al. 1984) recovered reef limestones of Eocene through Pleistocene age (54 m.y. to 10,000 years B.P.).

We found no visible fragments of Caroline's volcanic heritage, summarized above.

Sea Level Changes

Data on the history of sea levels for the Southern Line Islands is lacking. However, studies in French Polynesia (Pirazzoli & Montaggioni 1988), and which appear to have been a general phenomenon in the South Pacific, indicate that:

1) A stable sea level occurred, slightly less than 1 m above its present level, from 5000-1500 B.P. This peaked at approximately +1.0 m between 2000 and 1500 years ago.

2) Since then the level has been dropping gradually to its present position, reached only recently (Pirazzoli & Montaggioni 1988).

General Account

No geomorphological or geophysical studies have been carried out at Caroline. However, 2 deep undersea dredge hauls near the atoll uncovered reef limestones dated at Eocene through Plio-Pleistocene (Schlanger et al. 1984), and recent studies in the northwestern Tuamotus date the exposed coral reefs in the Holocene around 6000 to 3000 years B.P. (Pirazzoli & Montaggioni 1988). There is much scope for research within Caroline's reef matrix, varied shorelines and upraised reefs.

Caroline's overall shape resembles a flattened crescent, 9.7 km long on its north-south axis (Fig. 2), with outer perimeter 26.9 km and greatest breadth 2.3 km. The longest islet, Long, extends 4.23 km north-south, while South Island, extending 1.2 km east-west, claims the widest stretch of land.

The motus, lying upon a wide, continuous reef flat which encloses an elongated, relatively shallow lagoon, fall naturally into groupings of 3 large islands (South, Nake, Long) and 4 groups of smaller islets (13 Windwards, 5 Southern Leewards, 11 Central Leewards, 7 South Nakes).

There are 4 basic motu shapes, molded by the prevailing easterly winds and currents, periodic storms, overall atoll shape, etc:

1) long, linear, and parallel to the reef axis, e.g. Long Island.

2) small, linear or oval, and perpendicular to the reef axis, e.g. Southern Leeward Islets.

3) triangular or crescentic, with the apex facing the seaward reef, e.g. most of the Windward Islets.

4) large and quadrangular, occupying the ends of the atoll, e.g. South, Nake.

Caroline's motus have similar length-width ratios as those elsewhere (Stoddart & Steers 1977) and are similarly situated on the inner half of the reef flat, having their lagoon beaches close to the lagoon reef slope. Individual motus are discussed in detail in Section H.

It is hoped that the following preliminary observations of Caroline Atoll will inspire further research. As well as exhibiting features similar to many atolls, its 39 islets also present individual details that pose interesting questions which may help in deciphering sea-level changes in the Eastern Pacific and in unraveling the somewhat speculative geological history of the Line Islands (Jarrard & Clague 1977, Schlanger et al. 1984). Examples include the presence of an inland, vegetated reef substrate on Long; deep inland sand on Nake; conglomerate rock on South; hardpan on Mannikiba, Nake and Long; an emergent reef platform (Noddy Rock); and exposed older reefs of uniform height (Nake). Aerial photographs have indicated that Long Islet has been formed most recently from the coalescence of 5 former islets, which show even older subdivisions. Nake, previously at least 2 islets, has changed shape on both its north and south ends by the addition of gravel ridges and silt, respectively, in the past 100 years. Brothers Islet has incorporated a small motu within its confines since 1883; several other motus have also added bars and spits, and the lagoon has filled in further during that short time period. The questions of phosphatic hardpan beneath *Pisonia* forest and the extent of ground water lenses need attention.

Reef Flats

Caroline's peripheral reefs, which completely surround the lagoon, and upon which the motus rest, are consistently wide (average 562 m, range 396-759 m, N = 100). The windward and leeward reefs differ in structure and dimensions. Neither are entirely dry, even at the lowest tides. They consist primarily of barren calcareous rock, frequently smooth, which on other atolls generally represents the erosional surface of an older reef. Jagged "mushrooms" of exposed newer (but dead) reef framework dot the leeward reefs, forming an open platform off southwestern Nake (Pl. 11). Their structure and uniform height (~0.3 m) are similar to those on Hikueru Atoll, Tuamotus, which have been dated as 2565 ± 55 years B.P. (Pirazzoli & Montaggioni 1988). There are no passes from ocean to lagoon, a typical feature of central Pacific atolls (Wiens 1962). In the Southern Hemisphere, reef flats tend to be widest in the southwest sector and narrowest in the northeast (Wiens 1962), a generality which Caroline fits (Pls. 12, 13).

The reef rim, irregularly dentate and 26.9 km in circumference, is surmounted by motus for 55% of its length. On 72% of all Pacific atolls, less than half the reef circumference is occupied by land (Wiens 1962); Caroline lies within a 28% minority in which one-half to two-thirds of the reef rim contains land. Corresponding values for 2 Tuamotuan atolls, Rangiroa and Raroia, are 33% and 35% (Stoddart & Sachet 1969). Where motus exist, the reef flat is divided into the seaward reef flat (Pl. 12), motu, and lagoon reef flat (Pl. 14).

At low tide all reef flats can be waded. Black-tipped reef sharks were highly aggressive in 1988 but by 1990 dozens had been killed. The South Nake and Central Leeward channels were particularly hazardous, reflected in motu names such as Blackfin, Shark, and Danger.

<u>Windward Reef Flats</u>: Constantly pounded by surf, the windward reefs are typically narrower than those to leeward, averaging 519 m (range 396-759 m), though this is less evident from a map than in the field.

The windward reef is 13.5 km long, surmounted by 16 motus that total 63% of its length. This fits a recurrent pattern on central Pacific and Tuamotuan atolls where motus are more frequent along windward reef rims (Thomas 1961, Wiens 1962), due to active movement of debris associated with the prevailing easterly winds, waves and storms. The longest islets are Nake (1,980 m) and Long (4,226 m), both formed from the coalescence of 2 or more smaller islets. The rest vary from 18 m to 858 m in length.

The character of these reef flats differs, depending on the presence or absence of land, interisland distances, lagoon depth, and recent weather conditions. In February 1990, severe cyclonic weather rearranged tons of sediments, especially to windward, uprooting *Tournefortia* scrub, obliterating extensive sections of herb mats, exposing beachrock, depositing storm blocks, and altering the shape and slope of the beach crests. Since Caroline has been essentially uninhabited for 60 years, no data exists on the frequency of such storms, although it is well-known that windward beaches worldwide are undergoing erosion and retreat, and are thus characterized by beachrock outcrops and other lithified sediments (Stoddart & Steers 1977).

<u>Reef Rim with Motu</u>: The width of the seaward flats is quite uniform, averaging 307 m (range 193-396 m), occupying 57% of the rim width. It consists of a slightly raised algal ridge bearing the brunt of incessant wave action, and a rubbly reef flat, partly drying at low water, which sweeps up to the motu's beach (Pl. 13).

The motus differ considerably in width, ranging from the narrow tip of Long, merely 30 m wide, to Windward, 290 m wide. Nake and South Islands, forming "caps" to the atoll at its upper and lower ends, respectively, exhibit characteristics more typical of windward than leeward motus. Whenever atoll reefs turn sharply, debris-loaded waves become deflected around the points, thus depositing more gravel than on a straight shoreline. Hence, these 2 motus are the widest on the atoll (Pl. 16). A comparison of maps a century apart (Figs. 2, 4) indicates that several layered ridges of coral debris have accumulated on northern Nake since 1883.

Reef Rim without Motu: Zonation within the reef flat is less marked where there is no land. Within these interislet reef flats, however, areas of high water transport have carved surge channels and erosional grooves, and tidal fans extend into the lagoon, especially at its northern end where sedimentation is most active. Caroline has no deep pass or navigable channels into the lagoon, nor a ship anchorage beyond the reef, though small boats may anchor within the close lee of South Island during normal trade winds and low seas. Landing in an inflatable is best made across the reef slightly north of the "boat entrance," marked by an upright anchor (App. I).

The reef flat between Tridacna and South Island, serrated with 6 erosional grooves, one labelled "blind passage," is of particular importance to navigators (App. I). The blind passage, the most southerly channel, is a narrow diverticulum 380 m long within a reef 430 m wide. On all previously published maps this passage is drawn as though it completely connects ocean and lagoon (Figs. 4-7). However, it is a nonfunctional *hoa* or *tairua*, an erosional channel cut only partly across a continuous atoll rim. Its lagoon end (Fig. 50, Pl. 72) serves as a sheltered anchorage for motored yachts, but it can only be entered or exited during high winds or moderate-to-high surf. Chevalier (in Stoddart & Steers 1977, p. 77) has suggested that *hoa* features are partly a result of sea-level changes altering the balance of sedimentation and erosion.

Leeward Reef Flats: These are wider, flatter, gentler, more consolidated, and less filled with rubble than the windward reefs (Pl. 11). An orange, semi-transparent alga, blanketing the coralheads, chunks of upraised coral (Pl. 11), carbonate rock, and giant clams, is abundant. This alga is found on many atolls, for example Enewetak and Rangiroa (U.S. Department of Energy 1987, Stoddart & Sachet 1969). Living coral is sparse.

Surge Channels: These occur in a variety of shapes and sizes, depending on the distances between motus, the extent and buildup of reef flats adjacent to land, and lagoon depth. Surge channels and reef grooves are deeper on the windward side. The vigorous currents washing daily into Caroline's lagoon have created larger debris fans between windward motus than between those to leeward (Frontispiece).

Beaches

Caroline's beaches--the zones lying between low water mark and the inland limit of wave-deposited debris--are entirely of reef origin. There is, however, considerable variation in their composition. The windward beaches and surge channels, in a constant state of erosion or deposition, support the greatest variety of sediments: well sorted sands (indicated by grain-size distribution); gravels of coralline, algal (including *Halimeda*) and molluscan origin; and a wide assortment of coral fragments. The atoll's prime stretch of sand (Shark Islet) is thickly overlain with pink granules, possibly Foraminifera tests, which are abundant in the Tuamotus (Stoddart & Steers 1977).

Almost all exposed rubble on Caroline is colored gray, a consequence of penetration by cyanobacteria. Typically the oldest rubbles, highest up the beach and extending into the interior, are darkest. A marked beach crest rises, gently or abruptly, from the windward beaches, at the crest of which is deposited an assortment of flotsam and jetsam: bottles, plastic, wood, coconuts, etc. (Pl. 19). No storm blocks were found in 1988, but in 1990 many littered the windward reefs and shores, the result of recent cyclonic weather. Similarly, in 1990, thick deposits of coarse sand had overlain the rubbly windward beaches and interislet channels of 1988 (Pl. 33).

Alterations to Caroline's beaches provide the major changes in motu shape. Aggradation occurs principally on the lagoonward points of the larger windward islets, for example, Brothers (which is now joined with a separate islet mapped by Arundel), and Windward and Tridacna (which have added more sediments to their southwest points during the last century).

Beachrock: These elongated strata of eroded reef, brown consolidated sands and reef detritus, from one to a few meters wide, are not abundant on Caroline. Occurring as seaward dipping strips at the low water mark, they flank the windward beaches of Nake, Long and South (Figs. 37, 38, 50; Pl. 54) and a few of the leeward islets. Beachrock results from lithification of tropical intertidal sediments by calcium carbonates, in part due to seawater evaporation during low tide (Scoffin & Stoddart 1983). Beachrock outcrops become more exposed after storms, indicating that some cementation may occur beneath a shallow sediment cover. A coarser conglomerate platform (Pl. 20), possibly a relic of a former, high sea level, occurs on the northwest point of South Island, creating the "landing" (Pl. 20). This appears to be of similar age to the remnant reefs of southwest Nake, which are less consolidated (Pl. 11). Although the platform's upper surface rests slightly above high water level, we do not know if it represents a former reef exposed by a recent fall in sea level. The origins of such platforms are controversial (Stoddart & Steers 1977).

Upraised Reef: In a few areas, jagged, eroded upraised reef (*feo*) comprises some of the islet's interior--for example, the lower quarter of Long. A thin soil cover supports a forest of lower stature than would otherwise be expected. The rocky substrate is pitted with cavities and undermined with subterranean tunnels in which at least 2 species of land crabs (*Birgus latro*, *Cardisoma* spp.) shelter (Pl. 21). Noddy Rock (Pl. 18), the smallest motu (0.02 ha), and many jagged coralline "mushrooms" found on the reef flats (Pl. 11) are probably remnants of former reef flats formed when sea levels were several feet higher than present. It is hoped that further investigation will determine whether these older limestones are from the Holocene or Pleistocene.

Lagoon

Caroline's lagoon, 8.9 km long, is closed; its total area is less than that of the combined reef flats. The lagoon is relatively shallow, tapering in shape and depth at each end, containing both reticulate and patch reefs of living coral. Its bathymetry is unknown.

In the north the lagoon is more sheltered, as the presence of continuous vegetated land buffers the easterly trades, and silty sediments increase. At its northern extremity, merging reef flats squeeze the lagoon until it disappears east of Pandanus Islet. A filled-in portion of the former lagoon penetrates Nake for 300 m as a fishhook-shaped mudflat, Sandy Inlet (Fig. 37, Pl. 22), before succumbing to encircling vegetation. At the lagoon's southern end, where winds whip through the "blind channel," it is choppy, having more sediment and slightly less visibility. However, within the lee of South Island's north-central curve the lagoon is frequently quiet and reflective (Pl. 23).

Lagoon Hydrology

Although Caroline's hydrology has not been studied, the south end of the lagoon and "blind passage" (Fig. 50, Pl. 72) were closely observed for 2 years by Ron Falconer. He noticed that the lagoon is typically "perched" at a level above that of all but the daily high tides. High tide water flows rapidly over the reef flats into the lagoon, but is held back by the reefs as the tide lowers. Lagoon water at low tide is about 0.3 m higher than water in the "blind passage." Water moves out of the lagoon through a few channels that, although deep in places, form broad, shallow troughs over the reef flats. A major channel with a current flowing west at several knots passes along the northwest point of South Island, although water passage is impeded by the reef flats west of South Island. If a channel were to be blasted through the reef flats, as has been proposed, this delicate hydrology would be disrupted. For example, the high tide water is never more than 20 cm above the coral heads and reefs in the lagoon. A man-made reef channel for vessels could lower water levels 30-40 cm, thereby exposing and killing the extensive *Acropora-Tridacna* reefs within the lagoon.

The "blind passage" is sustained by a powerful northward flow of water along the east coast of South Island and a strong southward flow of water along the seaward reefs of Tridacna Islet. The South Island flow is augmented by water draining from a large shallow basin on its windward reef flats. Water spills into the "blind passage" and drains east at about 4 knots against the prevailing trade winds and surf. There is minimal current at the west (inner) end of the passage, where less water is collected, and throughout the passage at low tide when there is essentially no water flow out of the lagoon.

Patch Reefs

Darwin (1842) recognized 3 basic reef types (fringing and barrier reefs, atolls). A fourth type, patch reef, is now widely accepted. Patch reefs are smaller than the other 3 reef types, lack a lagoon but are located within lagoons, are submerged up to low tide level, and, unlike other oceanic reefs, have foundations of sediments or sedimentary rocks. They are subcircular to irregular in shape when viewed from above, and in their smaller sizes merge with coral knolls, coral thickets, or coral heads (Ladd 1977, Fagerstrom 1987).

A complex series of patch reefs and coral knolls (primarily *Acropora* spp.), circular and elongated, flank the smaller motus and crisscross much of Caroline's lagoon (see Frontispiece). They are particularly evident in the southern two-thirds of the lagoon. Coral limestone bedrock, surmounted by abundant living coral, molluscs, and other invertebrates, provides their basic structure (Sirenko & Koltun, in press). The atoll's perimeter reefs provide shelter from storms, surf, and excessive erosion. In shallow areas they tend to be curvilinear (Central Leeward Islets), while in deeper water, coral knolls and pinnacles are more characteristic (Pl. 63).

Caroline's lagoon is gradually filling in with ever-expanding patch reefs and debris washed in from the fringing reefs. Since Arundel's time, the effects of detrital deposition can be discerned as changes in the shapes of islets such as Nake, Danger, and Arundel (compare Figs. 2 and 4).

Such change is typical of atoll evolution. Geologically, Caroline is a few steps behind one of its "neighbor" Line Islands, Christmas, where sediments and coral growth have converted the original lagoon into a maze of supersaline, mini-lagoons and tiny islets, mostly cut off from the sea. Further steps in evolution are exemplified by completely filled-in atolls such as Jarvis and Vostok, where not even salty pools remain.

Tridacna-Acropora Reefs

Though the giant clam (*Tridacna maxima*) is an abundant component of Caroline's lagoonside reefs, exceptional aggregations flank the most southerly windward motus (Brothers through Tridacna, Figs. 44 to 48). Two especially outstanding reefs extend across the lagoon from Tridacna to Ana-Ana (Fig. 10, Pl. 25) and Tridacna to Kimoa (Fig. 48), where *Tridacna* attach to *Acropora* spp. corals, a favored substrate (Braley

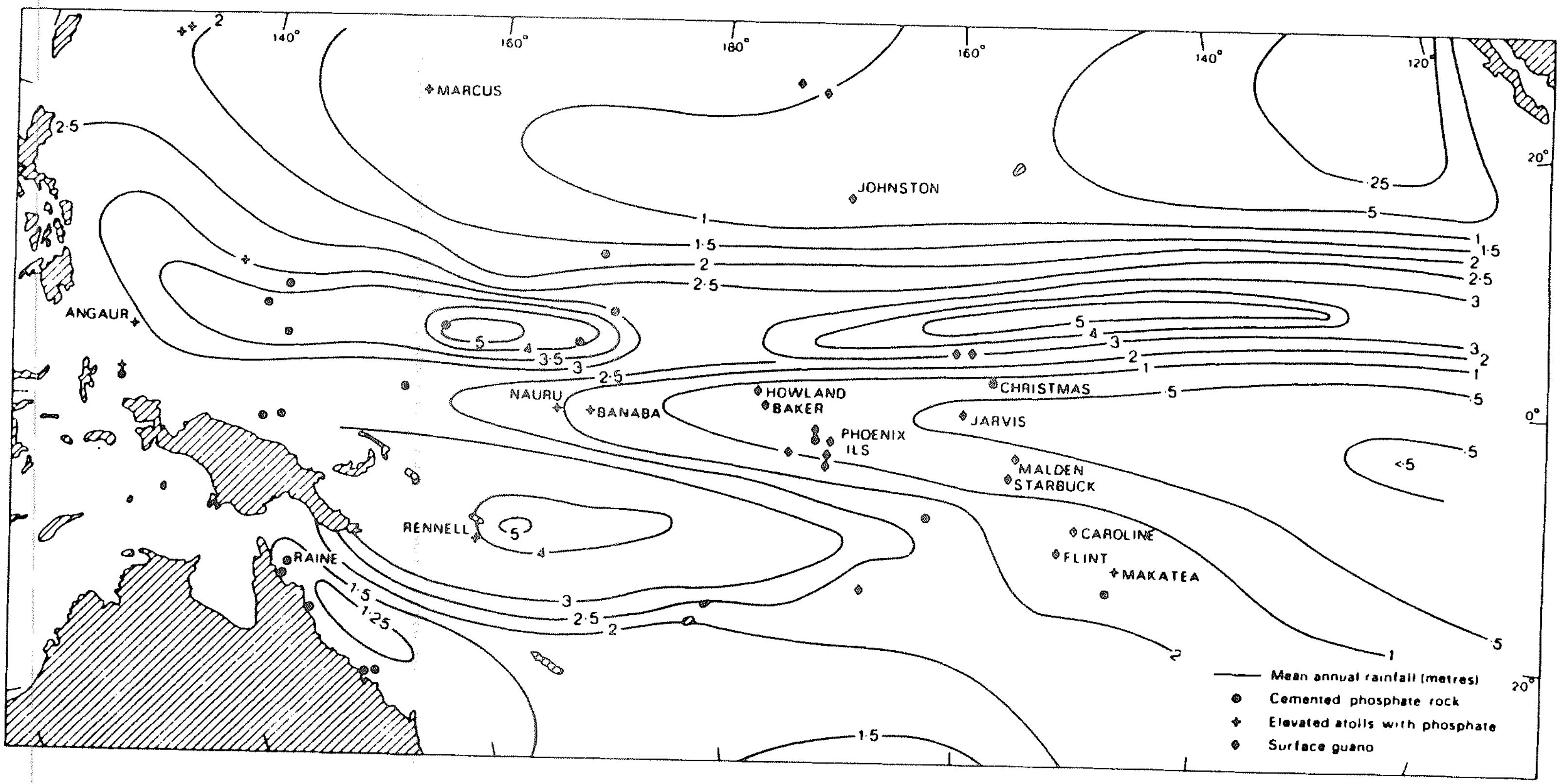

Figure 10. Relationship between mean annual rainfall and distribution of phosphate islands in the tropical Pacific (Fig. 13.1, Stoddart & Scoffin 1983).

1987). Abundant inshore *Tridacna* on all these islets suggest that their density is similar to that on the main reef: up to 20/.25 m^2 (i.e. 80/m^2), averaging 35/m^2 for the entire area surveyed (Sirenko & Koltun, in press). This density exceeds the highest known aggregations of *Tridacna*: up to 60/m^2 at Reao Atoll, Tuamotu Archipelago (Richard 1985). Densities of 6-20 clams per square meter, as found at Takapoto Atoll (Tuamotus), are considered high. Throughout Caroline, the clams averaged 18 x 10 cm in size. Several species of Indo-Pacific *Tridacna* have suffered greatly from poaching and overharvesting, leaving few undisturbed populations (Braley 1987). Caroline is thus a special refuge for *T. maxima*.

Lagoon Reef Flats

These vary considerably but are narrower and more gently sloping than the seaward reef flats. They are typically covered with fine coral gravel and coarse sand. In sheltered areas (lower Long, Windward, Crescent, South, upper end of lagoon) lush shrubbery--*Cordia*, *Tournefortia*, *Pisonia*, *Cocos*--overhangs the lagoon. Here fine silt, sand and/or an algal slime are common (Pl. 27). In 1988, narrow, sandy beaches were limited to northern South (Pl. 23) and eastern Shark (Pl. 28), but in 1990, sand occurred throughout Caroline.

Where the lagoon shorelines are less sheltered and vegetation does not overhang the lagoon, unvegetated rubble and sparse herb mats are typical. Here, lagoonside rubble averages less than 2 m wide (Pl. 30). This contrasts with their seaward reef flats, which average 21 m wide (Pl. 11).

Lagoon Reef Fauna: A Brief Summary

Caroline's marine environment is rich yet essentially undocumented: knowledge is limited to preliminary lists of fish, invertebrates and lagoon plankton (Dixon 1884; Fowler 1901; Pilsbry & Vanatta 1905a, b; Tsyban & Smith 1988, Sirenko & Koltun, in press). All early travelers remarked on the beauty, abundance and variety of Caroline's reefs (Markham 1904, Bennett 1840); today they are still relatively untouched.

The usual assemblage of reef invertebrates--echinoderms, molluscs (*Turbo*, *Nerita*, *Cypraea*), crustaceans, porifera, tunicates, etc.--are present. Corals include several important Holocene reef-constructors: *Acropora*, *Pocillopora*, *Porites*, and *Montipora*. Calcareous algae include *Halimeda*, *Porolithon* and *Lithothamnion* (Sirenko & Koltun, in press). Large numbers of black sea cucumbers (*Ludwigothuria* sp.), about 20 cm long, are particularly abundant lagoonward of the southern windward islands (Pl. 10). Conspicuous fish families include parrot fish (Scaridae), butterfly fish (Chaetodontidae), surgeonfish (Acanthuridae), damselfish (Pomacentridae), pufferfish (Tetraodontidae), and wrasses (Labridae).

Substrata

Throughout the atoll, substrates reflect a reef origin. There is little "soil" in the accepted sense. Various grades of jagged, eroded coral and molluscan rubble (from fist-sized to tiny pebbles), together with sand, coralline algae, and relatively small proportions of organic litter, humus and guano, are present. Such accumulations of reef and terrestrial debris are similar to those of other low, coral atolls (Fosberg 1953, Stone 1953, Wiens 1962, Niering 1963, Stoddart & Sachet 1969, Garnett 1983, Reese 1987, Gessel & Walker 1992).

Generally speaking, atoll soils are calcareous and extremely immature, a consequence of their limited age and frequent disturbance by storms. Barely modified beyond the reef that spawned their presence, they are rich in calcium and magnesium carbonates. Water retention, if any, is due to accumulated organic matter and its associated chemical changes. Accumulations of guano react with the calcium carbonate of reef sands and elevated limestones to form nitrogen-rich "soils" and phosphatic hardpan (Hutchinson 1950, Fosberg 1953, Stoddart & Scoffin 1983).

Reese (1987) categorizes atoll "soils" into 5 types, all of which occur, in different proportions, at Caroline. The degree of organic matter, decomposition, amount of humus, and the depth of the "soil" strata are directly correlated with age and size of Caroline's motus.

1) *Accumulations of coral rubble, mainly of stone size*. These youngest of "soils" are most evident around the edges of the motus, acting as a substrate for natural herb mats. Often extending well inland, they can support surprisingly lush *Tournefortia* scrub.

2) *Unaltered coral sand and gravel*. Although exposed sand was uncommon at Caroline in 1988, this substrate occurred intertidally where the lagoon was filling in and on actively growing sandbars, primarily in the upper lagoon (Pls. 22, 27), northeast and northwest South (Pls. 23, 31), and the lagoonward edge of Shark (Pl. 28). In 1990, a single storm deposited tons of sand on Caroline.

3) *Soils with a weakly developed A-horizon, with color only slightly darker than the unaltered sand below, but with no evidence of structural development*. Especially evident in 1988 within the ancient interislet channels that compose Long Island (Pl. 32), much of this substrate is now storm-eroded and overlain by fresh sand (Pl. 33).

4) *Soils with a more developed A-horizon, deeper and darker than above, with some structural development*. This stage defines areas where the rubbly/sandy substrate approaches a true, but poor, "soil." As such, it represents older, more stable parts of each island. It is common within the islet interiors where *Pisonia* is (or was) present. Its composition may be likened to a coarse mixture of gravel, sand, bones, humus, eroded coral and shells, all mixed with sparse amounts

of partly-decomposed litter. Land crabs are particularly numerous, further breaking down organic matter into finer particles.

5) *Soils with an accumulation of raw humus on the surface and with a relatively deep A-horizon. During this stage phosphatic hardpan may develop.* These true soils, though somewhat depleted by guano diggers, cover significant areas on South and Nake. *Cocos* and/or *Pisonia* debris heightens their dark coloration and moisture content. This earthy substrate is composed primarily of rotting *Cocos* fronds and nut fibers shredded by coconut crabs. Patches of blackish muck on South Island support local patches of *Tacca leontopetaloides*.

On Caroline, we noticed a type of hardpan (Pl. 67) in several areas (primarily South, Nake, Long, Emerald, and Mannikiba). In each case it resembled a flat sheet of old asphalt road, present within, or adjacent to, herb mats and peripheral *Tournefortia* scrub. Since hardpan forms when phosphatic derivatives from guano interact with permeable, reef-derived carbonate sediments (Stoddart & Scoffin 1983), it is possible that these barren clearings represent areas of high guano concentration. Worldwide, the major guano-producing seabirds are boobies, terns and frigatebirds (Hutchinson 1950). Adjacent to, or nesting on, these areas of hardpan which we observed were Red-footed Boobies (all motus), Great Frigatebirds (all except South), Lesser Frigatebirds (Nake), Masked Boobies (Long), and Sooty Terns (only 1990 on Long, but recorded from open areas of Emerald and Mannikiba, June 1965 and July 1990, see Pt. II, Fig. 11).

We did not take soil profiles within *Pisonia* forests to ascertain the presence of subsurface phosphatic hardpan. However, AKK and John Phillips found both surface and subsurface phosphatic hardpan on nearby Vostok, having the typical "pepper-and-salt," coloration and crumbly texture characterized by the Jemo soils found in the Marshall Islands (Fosberg, 1954 and pers. comm.).

Caroline provides an excellent example of the progression of soil development through islets of different age and size classes (see Sect. F). From a wave-washed mound of coral rubble, barely above sea level (Fig. 5), the substrate gradually improves in texture and fertility as the emerging islet ages and organic matter accumulates. Pioneer plants are hardy, salt-tolerant, low-lying mats consisting primarily of *Heliotropium*, and later, *Tournefortia*. Increasing numbers of shrubs provide shade and branches for nesting seabirds. Larger trees (*Pisonia, Cordia, Morinda*) add more shade and thereby increase humidity, as well as provide opportunities for additional organic "fallout": leaves and bird remains (nests, eggs, chicks, droppings, regurgitated food, dead adults).

Each stage of substrate development accelerates the accumulation of organic material and helps to define an emerging, deeper A-horizon. Soil maturity is indicated by more organic matter, improved soil texture, and a lowered volume of coralline and molluscan debris. Caroline's soils barely exceed several centimeters in depth and are always intermingled with coral fragments. As a result, they are unsuitable for burrowing seabirds such as petrels and shearwaters.

Hydrology

Hydrological information is essentially lacking. No standing fresh water exists. The quality, extent, and salinity of the freshwater lenses, as well as their variability according to tide, season, and rainfall, are unknown. At the time of Caroline's "discovery" (1606), de Quiros and his party were desperate for fresh water. After noting how lush and green Caroline was, they expected to find good water supplies, but there was "nothing but salt water in the holes they dug" (Markham 1904). Maude (1968) suggested, in hindsight, that had they waited longer the salt water in their shallow wells might have run fresh, as has been his experience on some other atolls. During the 19th century, 3 wells were used--one on Nake and 2 on South (Holden & Qualtrough 1884). One South Island well contained fresh water at 1.5 m depth in 1974 (Garnett 1983). We saw no wells, but located 2 concrete cisterns, one built in 1937 near the "landing" and rebuilt by the Falconers in 1989, and another uncovered one (dating from 1938) within a *Cocos-Pisonia* grove along Transect 2, about 200 m east of the southwest corner of Nake.

Caroline's paucity of fresh water may be partly responsible for the lack of a permanent population. The annual rainfall in 1989 (App. II) was 1,242 mm (48.9"). However, like the similarly lush Nikumaroro and Orona (Phoenix Islands), Caroline's rainfall may vary greatly from year to year, resulting in undependable water supplies. Residents always relied on rainfall catchment for fresh water (Maude ca. 1938; R. Falconer, pers. comm.).

The relationships between fresh water and *Pisonia* forests are uncertain (see Wiens 1962 and Sect. F).

Climate

Meteorological records for Caroline were sparse until 1989, when Ron Falconer began daily records of rainfall and wind direction (App. II). Some data is available from the plantation years 1916-1920 (Young ca. 1922) and during the 1883 Solar Eclipse Expedition (20 April - 8 May) (Upton 1884), when 203.2 mm (8") fell. Generalizations on regional weather conditions are found in N.I.D. (1943), Seelye (1950), Fosberg (1956), Newell (1956), Wiens (1962), Taylor (1973), Stoddart & Scoffin (1983), and various papers on the Tuamotus (Stoddart & Sachet 1969, Sachet 1983). Islands in the Line Group experience a wide range of climates. In general, those near the equator are dry, with rainfall increasing with increasing latitude north or south (Fig. 10).

Caroline experiences a tropical oceanic climate with little annual variation. Temperatures are uniformly warm to hot, normally tempered by trade winds from the southeast to northeast. Falconer (pers. comm.) did not record daily temperatures but estimated an annual average of 29° C (range 26°-31° C). Mean annual temperatures for the Central Equatorial Islands lie between 24° and 29° C. Surface temperatures increase rapidly in early morning and remain hot throughout the day. Forest interiors are humid. The daily range of temperatures exceeds the annual fluctuation in the daily mean.

Atmospheric pressure, sunshine, and cloud cover are probably similar to the northern Tuamotus, uniform except during storms.

Wind and Rainfall

Caroline is dominated by trade winds. As on all low atolls, land topography has very little appreciable effect on weather. Although it lies within an area primarily influenced by southeast trades, there is a small annual oscillatory movement northward and southward. Appendix II indicates that, at least for 1989 and 1990, winds blow primarily from the north and northeast, and rarely from the southeast (April - August).

The atoll lies within a belt of variable rainfall, along with Vostok, Flint, and the Northern Tuamotus. Young (ca. 1922) measured rainfall for 1919 (2,172 mm) and 1920 (1,854 mm), noting that Caroline's rainfall is "certainly less than that of Flint." He estimated "probably not more than 50" (1270 mm)" during 1916, 1917 and 1918, figures extrapolated from Flint (1,600, 1,346, 1,295 mm, respectively). Falconer measured 1,242.1 mm (48.9") in 1989 and 2,209.8 mm (87") in 1990. An unusually wet February in 1990 brought 640 mm (25.2") of rain, due to cyclones "Peni" (centered near Vostok) and "Ofu" (centered further west). Rainfall distribution isohyets (Taylor 1973, Stoddart & Scoffin 1983) assign Caroline an approximate annual precipitation of 1,500 mm (60"), a perfect average of the above 6 years ($\bar{x}$ = 1,513 mm). In general, "winter" (May - October) corresponds roughly to a dry season, and "summer" (November - April) to a wet season.

Cyclonic Storms

Atoll motus are active structures, undergoing repeated death and rebirth. Violent storms contribute to ongoing erosional and rebuilding processes. Storms deposit debris along windward shores (Pls. 17, 19), into the lagoon and often far inland.

Although the south-central Pacific is relatively free of cyclonic storms (cyclones, typhoons, hurricanes), they occur with enough frequency and devastating force that any discussion on climate should include them. Although detailed records of hurricanes and tropical storms exist for the inhabited Tuamotus since European discovery, we know little of those that have affected Caroline. The following evidence suggests that Caroline experienced 3 major hurricanes since the 1820s and that periodic violent storms modify the atoll substantially:

1) Between 1822 and 1825. When de Quiros visited Caroline in 1606, the northwesterly *Cocos* plantation on South Island was healthy. When Bennett arrived in 1834, he noted that all the palms were "of dwarf stature," and that "amidst the original groves, the number of vigorous seedlings fully confirmed Captain Stavers' statement [who had visited the atoll in 1828] that these palms had increased greatly since his last visit to the spot" (Bennett 1840).

A few years before 1828, therefore, something had affected the palms. By 1834 they were all of an even height and quite short, yet bore nuts. French records indicate that 2 devastating storms whipped through the Tuamotus during this time--in 1822 and 1825 (Sachet 1983). At least one of these could have affected Caroline.

2) The 1878 cyclone. The first unambiguous record of major devastation at Caroline comes from the letter of a certain J. M. Salmon, dated 1883 and reproduced in Holden (1884). Speaking of the time when Messrs. Brown and Brothers took possession of Caroline (somewhere between 1865 and 1872), he stated that "it seemed as if there had been a storm or hurricane at some short period previous, which had desolated the place." Arundel (1890) attributed this to a tidal wave that swept across the Pacific from South America to New Zealand and Australia in 1868 (Arundel 1890), but atolls do not generally suffer greatly from tsunamis because they lack focusing relief. The Hydrographer of the Navy (1931, Vol. III, p. 154), however, referring to Caroline, clearly states that in "1878 a cyclone passed over the islands, destroying most of the coconut trees."

The Great Britain Naval Intelligence Division (N.I.D. 1943, p. 490), in reference to Caroline, also states that "in 1878 a hurricane wrought great destruction." This was possibly the violent storm of 6-7 February 1878, which killed 117 persons on Kaukura Atoll, 750 km southeast of Caroline in the Tuamotus (Sachet 1983).

3) The 1906 hurricane. Serious storms occurred in the Tuamotus during 1903 and 1906 (T. Spencer, pers. comm.). There is no record of the effects of the latter storm on Caroline. However, it affected Flint Island (Campbell 1908, p. 2), hence must have passed over Caroline as it passed westward from the Tuamotus. Campbell, leader of the Solar Eclipse Expedition to Flint (1907-1908) states that "the great hurricane of 1906 February or March drove water to (the manager's residence, native huts and copra warehouses, all located 22 feet ASL and slightly inland) and the water threw the warehouses off their post foundations."

Ten or more coconut palms on Flint were struck by lightning in March of 1917 and 1918 (Young ca. 1922).

4) The 1990 storms. Our second visit to Caroline was 2 weeks after cyclone "Peni," centered near Vostok (February 1990), affected the atoll. Violent winds, torrential rain, and high seas had defoliated and uprooted vegetation in some windward areas (Pl. 33) and greatly altered Caroline's shorelines, interislet channels, tidal fans, and incipient islets from our 1988 visit. Tons of sand and rubble were rearranged on

both windward and leeward islets, Motu Atibu virtually disappeared, and the main interislet channel that divides Long Island lost its herb mats and many *Tournefortia* shrubs, becoming smothered with fresh sand.

We note here that nothing is known of the effects of the 1982-83 El Niño Southern Oscillation at Caroline. This phenomenon is characterized by the appearance and persistence, for 6 to 18 months, of anomalously warm water in the equatorial waters of Peru and Ecuador. Its biological consequences are dramatic and large-scale, extending far into the central Pacific Ocean: diminished plankton production, reduced fish stocks, starvation and mass breeding failure of seabirds, heavy rainfall, growth of vegetation and disappearance of nest sites (Barber & Chavez 1983, Cane 1983, Stoddart & Scoffin 1983, Schreiber & Schreiber 1984). Our only comments are that our seabird population figures were either similar to or greater than those in 1965 (Pt. II) and that the only dead birds we saw were in March 1990, victims of the cyclonic weather described above.

Because islets on coral atolls rarely exceed 5 m in elevation, the tidal surges associated with Class IV or Class V hurricanes, often exceeding 5 m in depth, can overwhelm them, not only altering or destroying the vegetation, but in extreme cases completely removing them from the coral rim (Frisbie 1944). It is essential to consider the ephemeral nature of Caroline's motus in the discussions that follow.

Sea Conditions

Because the most extensive coral rubble deposits occur around northern Nake and southern South Island, and because the *Cocos* plantation of northwest South was so badly hit by storms last century, the following Tuamotuan generalities (Newell 1956) probably also apply to Caroline:

1) Prevailing trade winds from the east give heavy seas on the northeast or windward side;

2) Southern ocean swells generated in the sub-Antarctic break heavily on the south or seaward side; and

3) Occasional hurricanes or tropical storms strike in the northwest or stormward quarter.

Tides

Only scanty data are available. In May 1883 (Holden & Qualtrough 1884), the greatest daily variation ranged from 475 mm (1'7") to 125 mm (5"), i.e. 350 mm (1'2"). The standard hydrological chart (Fig. 4) states 1.5 feet (0.5 m), which we use in the schematic profiles (Figs. 32, 35, 36) as the difference between low and high spring tidal levels. For Flint, W. Campbell (1908) guesses "about two feet" (0.6 m), while Ward (1974) estimates 1.5 feet (0.5 m). Tidal fluctuations are similar to those occurring in the Tuamotus, around 0.7 m (2′) (Newell 1956, Stoddart & Sachet 1969).

E. FLORA: VASCULAR PLANTS AND FLORISTICS

Botanical History

All early visitors to Caroline described a well-wooded atoll with numerous islets whose vegetation extended to the shoreline. It has changed little in the 384 years since its Western discovery. The first botanical collection and notes were those of Bennett in 1835 (Bennett 1840), who recorded 10 flowering plants and a fern, and planted Tahitian chestnut, sweet potato, and Polynesian arrowroot. He noted that "some of the loftier trees" on South Island and the Southern Leewards, were 20 feet high, perhaps a consequence of cyclonic weather in the 1820s. The location of his plant collection, if it still exists, is unknown (Clapp & Sibley 1971a).

The only indication of tall, native forests is given by Arundel (who mined guano and later cleared land for coconuts) in an unpublished manuscript to shipowners, where he states that "the trees on the extreme northern and southern islets (i.e. Nake, South) are about 80 to 100 feet high" (Arundel 1875). Beginning in 1885, coconuts were planted on about half of the motus, but the copra industry failed twice, and from 1929 to 1987 the atoll was essentially uninhabited.

Dixon made the first true botanical collection in 1883 during the Solar Eclipse Expedition (in Trelease 1884). All specimens were from South Island except *Laportea ruderalis*. His collection included several ornamentals and vegetables grown by early settlers (Lucett 1851) but not reported since, an important point as these temporary introductions have since been cited in the literature as part of Caroline's 35 plant species. Many were not found by the POBSP party, yet because no scientific investigations had been conducted for 80 years, they were counted as part of the atoll flora (Clapp & Sibley 1971a). Two more visits to Caroline, plus periodic searching by the Falconers, have also failed to uncover most of these ornamentals.

Vascular Plants of Caroline Atoll

Plant Collections

To avoid duplicating Long's plant collection (Clapp & Sibley 1971a), we collected only 5 specimens in 1988 and 33 in 1990. Dr. D. Herbst assisted with identification, prepared and deposited the specimens with Long's in the Bernice P. Bishop Museum, Honolulu, Hawaii. Collection numbers preceded by 'K' were collected by A. Kay Kepler; those preceded by 'L' are those of the late C. R. Long. Earlier collections of Bennett in 1835 (Bennett 1840) and Dixon in 1883 (in Trelease 1884) are noted by date only.

Working with Long's location records for some species has proven difficult. He was working with an incorrect map (Fig. 7), which showed only 25 islets instead of thirty-nine. Much of his work was done at night, which in some places would have made it hard for him to determine his exact location. His references to South, Long, and Nake are undoubtedly correct, and presumably the following: "second islet south of Long" = Crescent; "islet northeast of South Island" = Tridacna; and "fourth islet north of Bird Islet" = Emerald. Long records *Pandanus* on the "second islet south of Nake Island," which lacked *Pandanus* when we surveyed the island. Moreover, the first islet south of Nake supports an extensive grove of large *Pandanus* trees on its eastern (lagoon) shore, and we feel confident in ascribing Long's specimen to this island, which we had named "Pandanus" because of this grove. To be consistent, we have ascribed all his other "second islet" specimens to Pandanus Islet as well, and assume he made no collections on the actual second islet (Danger). However, Sibley (pers. comm.), the ornithologist, told us that the party visited every islet.

Species Lists, Annotated Checklist and Maps of Terrestrial Vascular Plants

Following recent authors (Lamberson 1987, Sachet & Fosberg 1983), we do not consider Caroline's transient or extinct vascular species (Table 1) or the vegetables and ornamentals in the Falconer's garden as part of Caroline's viable flora. Table 2 summarizes the current flora, detailing the relative abundance of each species within each plant community. These tables are based on sight records supplemented by all collections, past and present. No beach drift seeds are known from Caroline apart from those species already represented. English and Gilbertese names in Tables 1 and 2 are from Thaman (1987), St. John (1973), and Perry & Garnett (n.d.). If no common name is available, the Hawaiian name, familiar to many students of Pacific botany, is used.

Table 3 lists the distribution and abundance of plant species (with subdivisions into tree, shrub and herb components) on all motus. Figs. 11-25 map the entire atoll distribution of each species according to data from transects and aerial maps.

Families are arranged phylogenetically, according to Fosberg & Sachet (1987), with species arranged alphabetically within each family. The taxonomy of vascular plants follows W. Wagner et al. (1990), and ferns H. Wagner (pers. comm.). "% cover" means the percentage of the ground area covered by a particular plant species. In all text and tables the following symbols apply:

° New record for Caroline

* Indigenous--plants native but also occurring elsewhere (I)

Table 1. Plants reported from Caroline Atoll, but considered to be transient or extinct members of the flora.[1]

Scientific Name	English and Gilbertese Names	Date Last Reported	Comments
CLASS ANGIOSPERMAE			
Family Graminae			
Eleusine indica (L.) Gaertn.	goosegrass, te uteute	1884	Introduced weed
Eragrostis amabilis (L.) H. & A.	lovegrass, te uteute	1884	Introduced weed
Family Cyperaceae			
*Kyllinga brevifolia Rottb.	kyllinga		One clump by cistern, South Is., on recently disturbed ground
Family Bromeliaceae			
Ananas comosa L.	pineapple, te bainaboro	1884	Introduced for cultivated fruit
Family Liliaceae			
Crinum sp.	lily, te kiebu	1884 Presently cultivated	Introduced ornamental. One small specimen found on South Is. by Anne Falconer, 1990. Collection no. K-90-14
Family Moraceae			
*Artocarpus altilis (Park.) Fosb.	breadfruit, te mai	Presently cultivated	Not yet established, 2 trees on South and Ana-Ana
Ficus carica L.	common fig, te biku	1884	Introduced for cultivated fruit
Family Basellaceae			
Boussingaultia gracilis Miers	Madeira vine	1884	Introduced "vine climbing over portico" (Trelease 1884)
Family Leguminosae			
Inocarpus fagifer (Parkins. ex Z) Fosb. (= I. fagiferus)	Tahitian or Pacific chestnut, mape (Tahiti), te ibi	1840	Unsuccessful introduction in 1834. Food plant
Vigna marina (?)	beach pea		"Vigna luteola in clearings on South Island" (Line Island Expedition Report 1974). Not noted or collected otherwise. Perhaps a misidentification of Ipomoea macrantha?
Family Euphorbiaceae			
Euphorbia hirta (= E. pilulifera)	garden spurge, sleeping plant, te kaimatu	1884	Introduced weed, unsuccessful
Family Guttiferae			
Calophyllum inophyllum L.	Alexandrian laurel, tamanu (Tahiti), te itai	1884	In the 1940s, a "few taller Calophyllum and Pisonia" (N.I.D. 1943). No other reference; did observer confuse Calophyllum with Cordia?
Family Caricaceae			
Carica papaya	Papaya, pawpaw, te babaia, te mwemwera	Presently cultivated	Cultivated for fruit in 1884, not seen in 1965. In garden on Ana-Ana, one on South Is. by cistern
Family Cucurbitaceae			
Cucurbita pepo L.	Pumpkin, te baukin, te bamakin	Presently cultivated	Cultivated in 1884, not found in 1965
Family Convolvulaceae			
Ipomoea batatas L.	Sweet potato, te kumara	Presently cultivated	Introduced in 1840, not reported again until this expedition (tubers brought in 1988). Collection nos. K-159, -160
I. pes-caprae brasiliensis (L.) v. Ooststr.	beach morning glory, pohuehue (Hawaii), te ruku		Found in 1965 by copra shed; extensive searching on 3 expeditions in 1988 and 1990 failed to find it
Family Scrophulariaceae			
Russelia equisetiformis Schlecht.	Coral plant, te kaibaun ("golden plant")	1884	Unsuccessful introduction in 19th century

[1]Since 1988, the Falconers have added more vegetables and ornamentals to their ever-expanding garden: green beans, lemon grass, peppermint, okra, banana, Tahitian gardenia (tiare), tomato, breadfruit, red hibiscus, etc.

*Not previously reported from Caroline Atoll.

Table 2. Vascular flora of Caroline Atoll: relative abundance of each species within the major ecosystems, with data on seabird utilization.[1]

Scientific Name	Common & Gilbertese Names	Seabird Utilization: Breeding	Seabird Utilization: Roosting	Natural Ecosystems, Coastal: Natural Herb Mat	Natural Ecosystems, Coastal: Beach Scrub With Suriana	Natural Ecosystems, Coastal: Tournefortia Scrub	Natural Ecosystems, Inland: Tournefortia Forest	Natural Ecosystems, Inland: Pisonia Forest	Anthropogenic Ecosystem, Coconut Woodlands: Cocos Plantation	Anthropogenic Ecosystem, Coconut Woodlands: Dying Cocos/Ipomoea Plantation	Anthropogenic Ecosystem, Coconut Woodlands: Mixed Forest With Cocos
TREES											
Pisonia grandis	pisonia, puka tree, te buka	X	X		R	UC	C	A	L,UC	L,UC	R-C
Morinda citrifolia	Indian mulberry, te non			O	C	R-C	R-VC	R-A	R-C	C	O
Cocos nucifera	coconut, te ni	X	X			R-O	UC	O	A	A	C-A
Cordia subcordata	sea trumpet, kou (Hawaii), te kanawa	X	X			UC	UC-C	R-VC		L,UC	R
Pandanus tectorius	pandanus, screwpine, te aroka, te kaina	X	X		O	C	C	O	O		A
Hibiscus tiliaceus	beach hibiscus, hau (Hawaii) te rau								L,R		
Thespesia populnea	milo (Hawaii), te bingibing								L,R		
SHRUBS											
Tournefortia argentea	tree heliotrope, te ren	X	X	O-UC	VC	A	A	UC-A	UC		C
Suriana maritima	bay cedar, te aroa, te marou			O	VC-A	O					
Ximenia americana	monkeyplum					S			LA		
*Scaevola taccada	scaevola, saltbush, half-flower, te mao			R							
HERBS											
Heliotropium anomalum	"sand rose," hinahina (Hawaii)	X	X	A	UC	VC					
Boerhavia repens	pigvine, te wao			R-UC	R-C	R-A	R-A	R-A	UC-A	UC	C-A
Portulaca lutea	yellow portulaca, seaside purslane, te bointari, te boi			O-A	R-UC	UC-C	O	L,O		R-C	R
Laportea ruderalis	"nettle," te ukeuke, te nekeneke			R-VC	UC	C-A	C	LC	LC	R-UC	UC-C
Achyranthes canescens						R-C	C	C	O		A
Phymatosorus scolopendria	maile-scented fern, laua'e or lawai fern, te raukota, te keang				R	LC	LC	C-A,L	R-A	R-UC	C-A
Lepturus repens	bunchgrass, te uteute			R-UC	UC-A	L,R-A			R		
Ipomoea macrantha	morning glory, wild moon-flower, te ruku					R	R	R-UC	UC	A	
Tacca leontopetaloides	Polynesian or island arrowroot, pia (Hawaii & Tahiti), te makemake								LA		
Lepidium bidentatum	peppergrass			LR		LR					
Psilotum nudum	upright psilotum, "reed fern," te kimarawa								LR		
Phyllanthus amarus									LR		
Sida fallax	'ilima (Hawaii), te kaura								LR		
+Digitaria sp.	crabgrass, te uteute								(S)		
Tribulus cistoides	puncture vine, te kiebu			R							

[1]Excludes transient and extinct species (Table 1). Species arranged according to their overall abundance on the atoll.
*New records for Caroline.
+Not seen on this expedition, last seen 1965 (Clapp and Sibley 1971a).

** Aboriginal introduction--useful plants brought by Polynesians in pre-historical times (AI)

Recent introduction--plants of accidental or deliberate introduction after Western discovery of the atoll (RI)

A Abundant--the major or dominant species in a given area

VC Very common--often seen but not quite as abundantly as above

C Common--generally distributed in large numbers

UC Uncommon--observed uncommonly but >10 times in a given area

O Occasional--here and there, often widely scattered but not forming a major component of the vegetation

R Rare--observed 2-10 times in a given area

S Single--only one specimen observed

L Local--found only or principally in one or more restricted areas

D Drift seedling--plant derived from a water-borne seed

+ Not seen 1988-1990 but probably still present

PSILOTACEAE

* *Psilotum nudum* (L.) Beauv Fig. 11

Formerly Known Distribution: L-3233 from Nake.

Present Distribution: Cosmopolitan, common on remote islands, rare on Caroline. K-90-15 from South. In 1965 common on wet base of *Cocos* only on Nake. In 1988 and 1990 a few clumps found similarly on South in shady, damp locations, close to lagoon, under 18 m canopy, northwest sector.

POLYPODIACEAE

* *Phymatosorus scolopendria* (Burm. *f*) Pichi-Sermolli Fig. 12, Pl. 34
Phymatodes scolopendria (Burm. *f.*) Ching
Polypodium phymatodes L.
Polypodium scolopendria Burm. *f.*
Microsorium scolopendria (Burm.) Pichi-Sermolli

Formerly Known Distribution: Recorded 1840, collected 1884; L-3244, L-3250, L-3287 from Nake, Long and South Islands.

Table 3. Distribution and abundance of plant species on Caroline Atoll.[1] Motus are arranged geographically from north to south (windward), then similarly on the leeward side.

			Windward Motus														South Nake Motus						
	Nake	Long	Bo'sun Bird	Windward	Crescent	Atibu	North Pig	Pig	Skull	North Brothers	Brothers	Noddy Rock	North Arundel	Arundel	Tridacna	South	Pandanus	Danger	Booby	Coral	Lone Palm	Kota	Moukakena
TREES (7 spp.)																							
Pisonia grandis	A	VC		A	A		A	A		A	A		VC	A	R	R	VC	A	VC	UC	R	R	R
Morinda citrifolia	UC	UC		UC	O		R	UC		R	O		O	UC	VC	C	R	R	R	R	R	R	
Cocos nucifera	LA	LA						LR			LO		R			A					LR	LR	
Cordia subcordata	UC	UC		C	LA		C	VC		C	VC		C	UC		R		LA					
Pandanus tectorius	LA															LO	LA						
•Hibiscus tiliaceus																LR							
•Thespesia populnea																LR							
SHRUBS (4 spp.)																							
Tournefortia argentea	A	A	VC	A	A	O	A	A	O	A	A	O	A	A	A	C	A	A	A	A	A	C	A
Suriana maritima		LR									LR				LC	UC,LC							
•Scaevola taccada				S																			
•Ximenia americana								S								LA							
HERBS (15 spp.)																							
Heliotropium anomalum	C	VC	UC	C	C	UC	UC	UC	R	UC	C		O	UC	VC	C	C	O	UC	UC	UC	UC	R
Boerhavia repens	C	LC		C	C		C	C		UC	C		A	UC	C	VC	C	O	O	R	R	R	R
Portulaca lutea	C	C	C	C	C	UC	UC	C	C	A	A	A	A	C	C	C	C	UC	O	O	O	O	R
Laportea ruderalis	C	VC		C	UC		UC				C			C	UC	UC	C	O	O	R	R	R	R
•Achyranthes canescens	LC	O			O		C	O		LC			VC	VC	LC	R	O	O	R	R	R	R	R
Lepturus repens	R	R	R	R			R			R	R	C		C	C	O	R	R	R	R	R	R	R
Phymatosorus scolopendria	VC	LA,UC			UC		UC	UC						O	C	LA,UC					R	R	
Ipomoea macrantha	LC	O		UC				O								A							
Tacca leontopetaloides	+LC															LR							
Psilotum nudum	+LR															LR							
Phyllanthus amarus																LC							
Tribulus cistoides		S																					
Sida fallax																LR							
Lepidium bidentatum																S							
+Digitaria sp.																S							

Table 3. Continued.

	Central Leeward Motus											Southern Leeward Motus							
	Mannikiba	Blackfin	Matawa	Emerald	Shark	Scarlet Crab	Nautonga	Azure	Reef-flat	Bird	Fishball	Raurau	Eitei	Pisonia	Kimoa	Ana-Ana	Total	% Frequency On Each Motu[2]	Origin
TREES (7 spp.)																			
Pisonia grandis	C	VC	UC	C	A		O	R		A		A	C	A	VC	A	32	82	I
Morinda citrifolia	R		R	R	R		R			R	D	UC	R	R	R	C	30	77	I,AI?
Cocos nucifera	LR	LR		LO	LR					LR		LR		LO		LC	17	44	AI,RI
Cordia subcordata	O	UC	C	O	LO		O			UC		C	C	C	C	C	23	59	I
Pandanus tectorius			R	C	C							LR		LR		LR	9	23	I,AI?
•Hibiscus tiliaceus																	1	3	RI?
•Thespesia populnea																	1	3	RI?
SHRUBS (4 spp.)																			
Tournefortia argentea	A	A	A	A	A	R	C	C	R	A	UC	A	A	A	A	A	39	100	I
Suriana maritima			R							UC			LR	LR	LR	O	10	19	I
•Scaevola taccada																	1	3	I
•Ximenia americana	S																2	5	RI
HERBS (15 spp.)																			
Heliotropium anomalum	C	C	C	C	C	R	C	C	R	R	UC	UC	C	C	C	UC	38	98	I
Boerhavia repens	C	UC	UC	C	UC	R	R	R		UC	R	UC	UC	UC	O	C	34	88	I
Portulaca lutea	C			C	UC	R	R	R	R	UC	R	UC	C	UC	C	LC	37	95	I
Laportea ruderalis	UC	UC	O	C	UC	R	R	R		R	R	UC	VC	UC	O	C	32	82	I
•Achyranthes canescens	UC	O	R	UC	LA		R	R		UC	R			O	C	O	29	72	I
Lepturus repens	R	R		R		R				UC	R			R	R	UC	27	69	I
Phymatosorus scolopendria	O				R											UC	14	36	I
Ipomoea macrantha														O		R	7	18	I
Tacca leontopetaloides																	1	3	RI,AI?
Psilotum nudum																	1	3	I
Phyllanthus amarus																	1	3	X
Tribulus cistoides																	1	3	I
Sida fallax																	1	3	I
Lepidium bidentatum														S			2	5	I
+Digitaria sp.																	1	3	?

[1]Species arranged according to frequency of occurrence. List excludes transient and extinct members of the flora (Table 1).
[2]No. motus having a particular species, divided by total no. motus x 100%.
•New records for Caroline.
+Not seen on 3 visits but possibly still present.

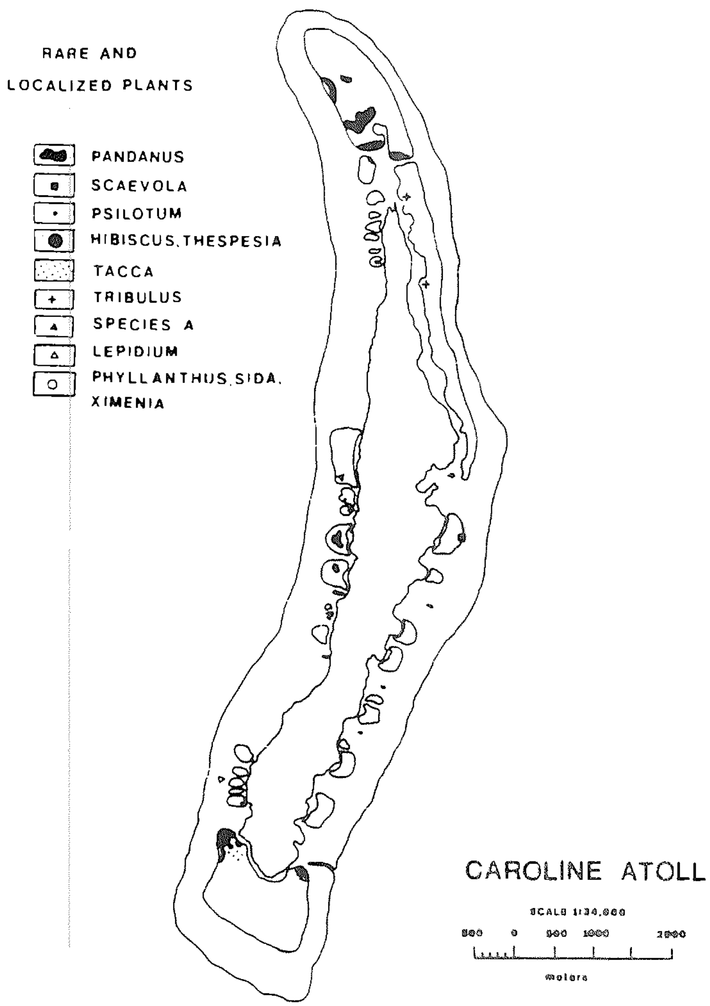

Figure 11. Entire distribution map of rare and/or localized plants on Caroline Atoll: *Hibiscus tiliaceus*, *Lepidium bidentatum*, *Pandanus tectorius*, *Phyllanthus amarus*, *Psilotum nudum*, *Scaevola taccada*, *Sida fallax*, *Tacca leontopetaloides*, *Thespesia populnea*, *Tribulus cistoides*, *Ximenia americana*, and Species A. *Psilotum* may still exist on Nake.

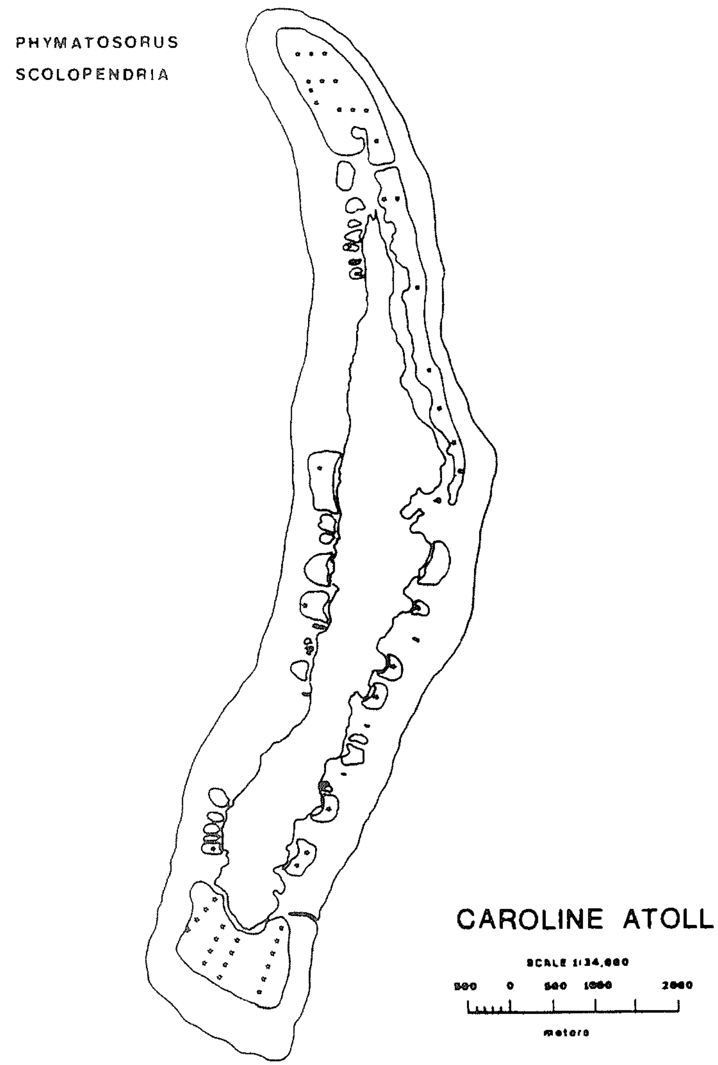

Figure 12. Transect distribution map of the fern *Phymatosorus scolopendria* on Caroline Atoll.

Present Distribution: Range extension from 3 to 11 motus. Rarely a continuous ground cover, locally rare to abundant. Commonest on Nake, 10-80% cover. Well represented on South, especially in open areas of the interior, where soils are moister. On other motus local distribution varied from less than 1 to 80%; accurate mapping is difficult. Absent from motus less than 0.6 ha in size, where habitats cannot provide appropriate cover, moisture, and substrate.

Ecology: Hardy. Leaves burn in sun but can withstand very dry conditions. Primarily in *Tournefortia* scrub, mixed forests with *Pisonia* and *Pandanus*, or *Cocos* plantations. Associated with *Cordia*, *Morinda*, *Suriana*. In open clearings within dying *Cocos* forests occurs in dense mats intermingled with *Boerhavia*, *Ipomoea*, and *Portulaca*. Sometimes gathers in thick bands at the interface of *Tournefortia* and *Pisonia* forests. Prefers shelter from winds, high humidity, "soil," and relative lack of wind, but absent from deeply shaded forests. Rhizomes never exposed on ground surface or epiphytic on trunks, as in wetter islands such as Hawaii or Samoa (pers. obs.) or in the moister Line Islands (Wester 1985), indicating that Caroline's habitats are suboptimal. Although most ferns are not halophytic, this species grew (rather stunted) in 1988 amongst sparse herb mats (1% cover) on older beach sands of an ancient reef channel on Long Island (Tr. C), where rainfall provides the sole fresh water, but was (temporarily ?) obliterated in February 1990. Rare to uncommon in outer beach strand, and beach scrub with *Suriana* (South, Arundel, Shark).

Substrata: Dry coral rubble, sand and gravel, rubble with sparse humus, lagoon mud, relatively fertile humus, older beach sands.

PANDANACEAE

* **? *Pandanus tectorius* Park. Fig. 11; Pls. 35-38

Formerly Known Distribution: Recorded 1840, unidentified *Pandanus*; L-3227, Pandanus Islet, seen on Nake by Long.

Present Distribution: A minor plant community (Sect. G), *Pandanus* is primarily associated with *Tournefortia* or *Pisonia* on the leeward motus. Most common on Nake. Range extension from 2 to 7 motus.

Phenology: Flowers and fruit in October, March, and May.

Substrata: Variable. Prefers lagoon mud, pure sand and rubble-humus, but survives in almost pure rubble.

GRAMINAE

* +? *Digitaria* species

Collected 1883 and recorded as ?*Panicum* (*Digitaria*) *marginata*. Examined by Long, who believes it a *Digitaria* identical to his L-3235. Not found by the authors.

* *Lepturus repens* (Forst. f.) R. Br. Fig. 13, Pl. 2

Formerly Known Distribution: Collected 1883; L-3211, 3221, 3236, 3238, 3247, 3259, 3286 from Windward, Tridacna, Nake, Long, Emerald, Crab and South Island, respectively.

Present Distribution: Many Pacific atolls. K-88-4, 5; 90-1, 2, 19 to 21, 25 from South, Tridacna, and Ana-Ana. On Caroline, range extension from 6 to 26 motus.

Ecology: Patchy, rare to locally common. Usually in exposed herb mats with *Heliotropium*, *Laportea*, *Portulaca*, and low *Tournefortia* scrub. Abundance 1-5% cover where not in thick patches. Occasionally inland under *Tournefortia*, *Cordia* or *Cocos*, persisting as forest undergrowth. Tufts tiny (few centimeters), dry and scrappy in exposed areas, but to 3 dm where shaded. Never in tall, upright clumps, as turf, or in the same abundance as on the drier, filled-in equatorial atolls or islands with sandier habitats (Christopherson 1927, Fosberg 1953, pers. obs.).

Substrata: Able to survive in coral rubble of varying coarseness, down to high water mark, but preferred habitat is part sand. L-3286 was from "numerous clumps under *Suriana* scrub on South Island," perhaps the low, sandy portion of the northwest point (Pl. 45), our best *Lepturus* site. Comparison of Arundel's chart (1883), recent aerial surveys, and earlier photographs indicate that several motus have altered shape since 1883. The amount of open area on South Island has also decreased markedly since 1883. The distribution of *Lepturus* parallels these changes; there is clearly much less on South Island, and more in newly-created islet fringes.

Since 1965 the lagoon shore of South Island has become overgrown by *Cocos*, so much that both *Suriana* and *Lepturus* are much less common than previously (Pls. 39, 40). However, sand and debris will always be shifting, so that *Lepturus* will move from place to place, establishing wherever conditions permit. In the second situation, a comparison of Plates 2 and 23 from 1883 and 1988, respectively, shows that a century ago the lagoon-facing shores of South Island were far more open than the dense *Cocos* plantations of today. The clumped grass in the foreground of Plate 2 is undoubtedly *Lepturus*, probably mixed with introduced grasses not seen since that time (*Eleusine indica*, *Eragrostis plumosa*), and the dubious *Digitaria* sp.

PALMAE

** # *Cocos nucifera* L. Figs. 14, 36, 51; Pls. 2, 3, 17, 23, 34, 37, 44

Formerly Known Distribution: Recorded 1840, 1884; L-3285 from South Island, extensive groves on South and Nake, scattered on north portion of Long.

Present Distribution: Range extension from 3 to 15 motus. Planted groves on South, Nake, and Long; the rest derived from drift.

Phenology: Flowers and fruit year-round.

Ecology: Forms a major vegetation type (Sect. F). Primarily South and Nake, where closed canopy forests average 21 m high.

TACCACEAE

**? *Tacca leontopetaloides* (L.) O. Kuntze Fig. 11
Tacca pinnatifida Forster

Formerly Known Distribution: Normally an aboriginal introduction on Pacific islands, but on Caroline is first mentioned as planted in 1834 (Bennett 1840); L-3213, 3219, and K-90-7, 16 from moist muck, South Island. L-3234, common under *Cocos* and numerous patches found in muck, south end, Nake.

Present Distribution: Common in northwest South. None in flower; each plant had 2-3 leaves, possibly dying back. None found on Nake, despite searching the south end. Has large underground tubers, dies back, and though cultivated, still occurs spontaneously in *Cocos* groves on many atolls. Harvested by the Falconers.

Ecology: Needs fine, moist soil and shade. Though its seeds float for months (Guppy 1906), it has not established itself on other motus in 150 years, probably due to the prevalence of rubbly substrates.

Phenology: Flowers and fruit in March and May, dies back in October.

URTICACEAE

* *Laportea ruderalis* (Forst. f.) Chew Fig. 15
Fleurya ruderalis (Forst. f.) Gaud. ex Wedd

Formerly Known Distribution: Reported 1840, collected 1884. L-3215 common in shady areas South Island; L-3229 scattered on exposed coral and sand, west side Crescent Islet. L-3253 under shade of *Cocos* and *Pisonia* on north side of Long Island.

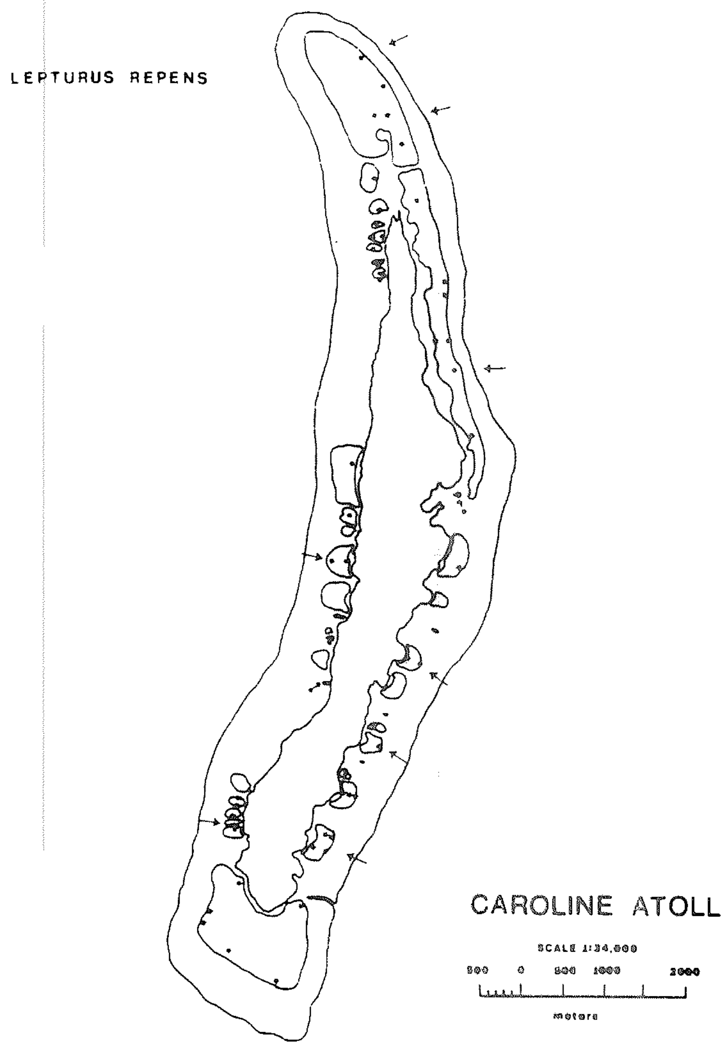

Figure 13. Transect distribution map of the grass *Lepturus repens* on Caroline Atoll. Arrows indicate areas of highest density.

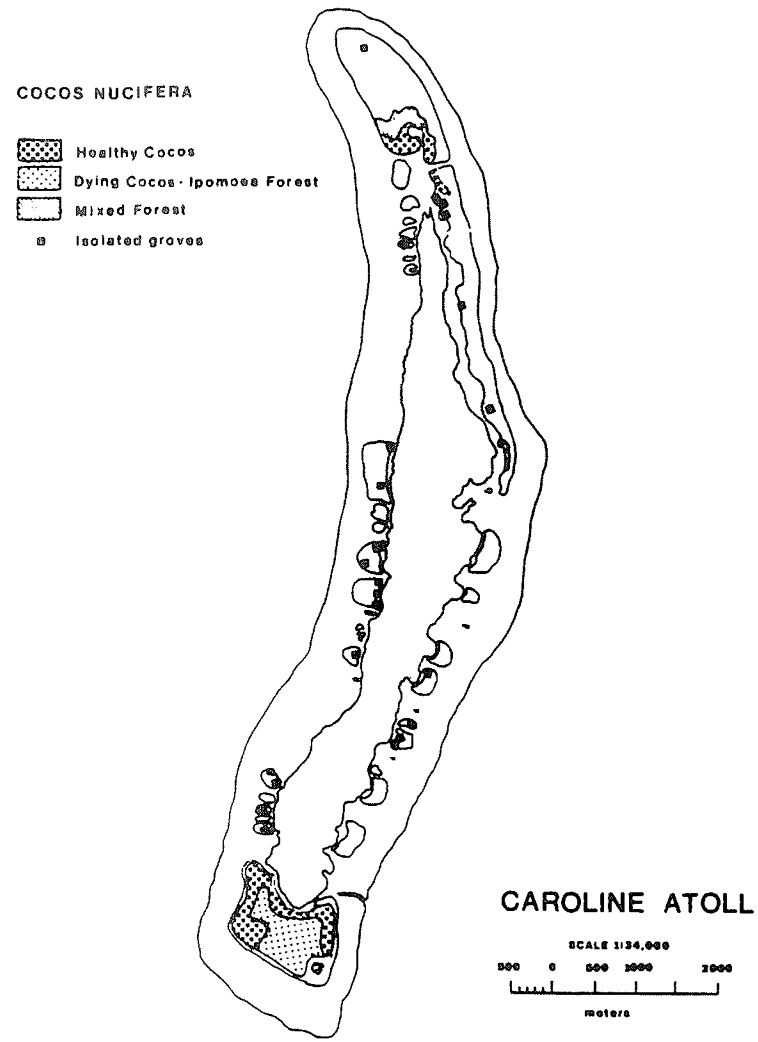

Figure 14. Entire distribution map of the coconut *Cocos nucifera* on Caroline Atoll. Note that the dying *Cocos-Ipomoea* forest covers approximately two-thirds of the original plantation.

Distribution and Abundance: K-88-3 South Island, Transect 1, elevation 0.3 m, under old *Cocos* plantation, in humus and rubble. Range extension from 3 to 32 islets (Table 3). Commonest and most widespread ground cover, patchily distributed. Rare to locally abundant, percentage cover from less than 1% in herb mats of tiny motus to 60% in tall *Pisonia* forest. Best represented on Nake, Long, Brothers, South, Pisonia, Eitei and Mannikiba, where coverage exceeded 50% in appropriate habitats. To 1.1 m tall on Kimoa.

Ecology: Largest (to 0.5 m) specimens found under *Tournefortia, Pisonia, Cocos*, or *Pandanus*. Tiny (1-2 cm) and tougher in sunny, exposed sites. Halophytic, pioneering in herb mats on islets less than 0.75 ha in size (e.g. Fishball). Optimum habitat is *Tournefortia* scrub, in sunny clearings or belts behind beach scrub. Uncommon in *Pisonia* forest. Occurs in both windward and leeward sites, but in greater density leeward. Will persist through several stages of plant succession if given adequate shade.

Phenology: Flowers and fruit in October, March, and May.

Substrata: Primarily beach gravel or coarse rubble. Also rubble-sand mixtures; not lagoon silt.

OLACACEAE

° * (#?) *Ximenia americana* L. Fig. 11

Never previously collected. K-90-170 South Island, 50-100 m north of cistern, elevation 0.3 m, 10-20 m from coastal *Tournefortia* fringe, within *Cocos* plantation. Collected by crew of the yacht *Amanita* and posted by Anne Falconer to AKK. K-90-23 and 24, single sterile shrub 2.5 m tall, southwest Motu Mannikiba, leathery leaves, arching stems 4-5 m long. Found by John Phillips, collected by JP and AKK, identified by D. Herbst and R. Fosberg.

Distribution and Abundance: Locally abundant in one location, about 50 bushes (3-4 m high, 2-3 m wide) spread over about 100 m. Adjacent to indigenous scrub, on edge of *Cocos* plantation near old settlement.

Phenology: Flowering in July 1990.

Substrata: Moist soil (South), coarse strand rubble (Mannikiba).

AMARANTHACEAE

° * *Achyranthes canescens* R. Br. Fig. 16, Pl. 41

Never previously collected. K-88-1 South Island, Transect 5, to 0.7 m, elevation 0.3 m, in *Tournefortia* fringe, coral rubble.

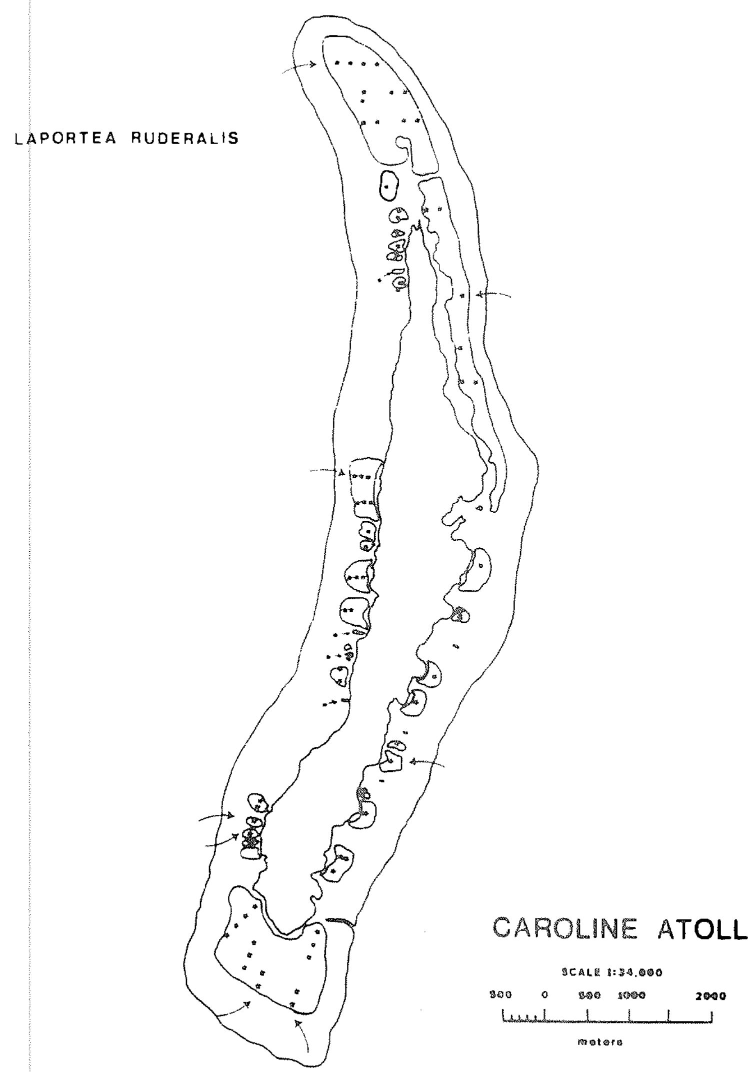

Figure 15. Transect distribution map of *Laportea ruderalis* on Caroline Atoll. Arrows indicate areas of highest density.

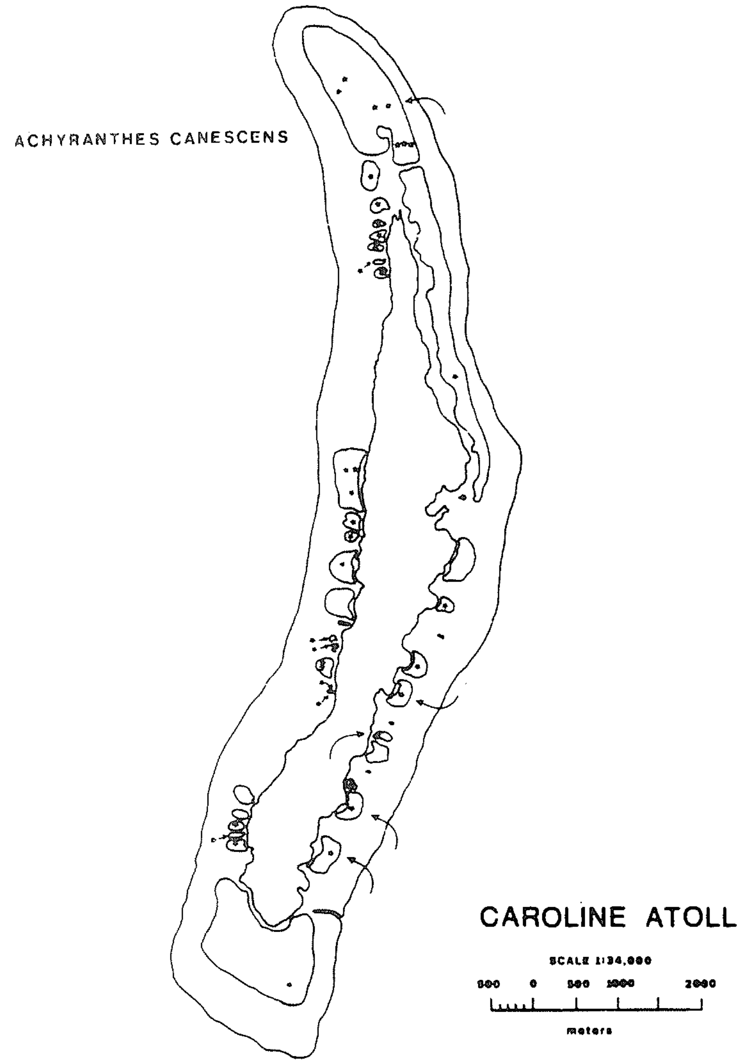

Figure 16. Transect distribution map of *Achyranthes canescens*. Arrows indicate areas of highest density.

Distribution and Abundance: Quite widespread, primarily in interior scrub and forest of 19 motus (Table 3), from tiny, barely vegetated Fishball (0.73 ha) to the largest, South (106 ha). Density variable: from less than 1% in *Tournefortia* scrub to 50% local ground cover in mixed *Pandanus* forest. Primarily associated with *Tournefortia*. May be locally abundant in clearings in *Pisonia* forests, pure or mixed. Often in a zone dividing *Tournefortia* and *Pisonia* trees, especially on Pig, Brothers, and Nake.

Ecology: Never in natural herb mats. Needs shade but requires some direct sun; rare in pure stands of *Cocos* and *Pisonia*. Prefers small, sunny openings in forest or scrub. Drought-resistent and probably partly halophytic. Dies back annually in the dry season and reappears with winter rains (Anne Falconer, pers. comm.). To 1.5 m tall. Little or no capacity for dispersal by sea. On other islands, seeds carried by birds, especially fruit pigeons (Guppy 1906), but pigeons are absent from the Line Islands. Perhaps dispersed by the Long-tailed Cuckoo (Ellis et al. 1990).

Phenology: Flowers and fruit present in October, March, and May.

Substrata: Lushest growth in humus soils of forest interiors. Often grows in pure rubble.

NYCTAGINACEAE

* *Boerhavia repens* L. — Fig. 17, Pl. 34

Boerhavia diffusa L.
Boerhavia hirsuta: sensu Bennett 1840
Boerhaavia species: Dixon 1884

Formerly Known Distribution: Reported 1840, collected 1884; L-3210, 3324, 3239, 3225, 3252, 3262, 3289, 3291 from Windward, Tridacna, Nake, Long, Emerald, and South, respectively.

Present Distribution: Cosmopolitan, widespread in the Pacific. K-90-164 and 165 from Ana-Ana. Range extension on Caroline from 6 to 33 motus (Table 3).

Abundance: Present in every habitat, leeward and windward, ranging from less than 1 to 80% cover. Often in large patches. Best locations (>50% cover) on Nake, Long, Windward, Pig, Brothers, Arundel, Tridacna, South, Ana-Ana, Pisonia, and Pandanus Islets.

Ecology: Mostly found beneath *Tournefortia*, either in pure scrub or mixed with *Pisonia*, *Cordia*, *Morinda*, *Suriana*, or *Cocos*. Not in deep *Pisonia* shade; rarely in herb mats. Thick ground cover in indigenous scrub (Shark) or within clearings in old *Cocos-Ipomoea* forest (South), where it mingles with *Phymatosorus*, reaching a high density (Pl. 34) and large size (rooting at nodes, vines exceeded 1 m long).

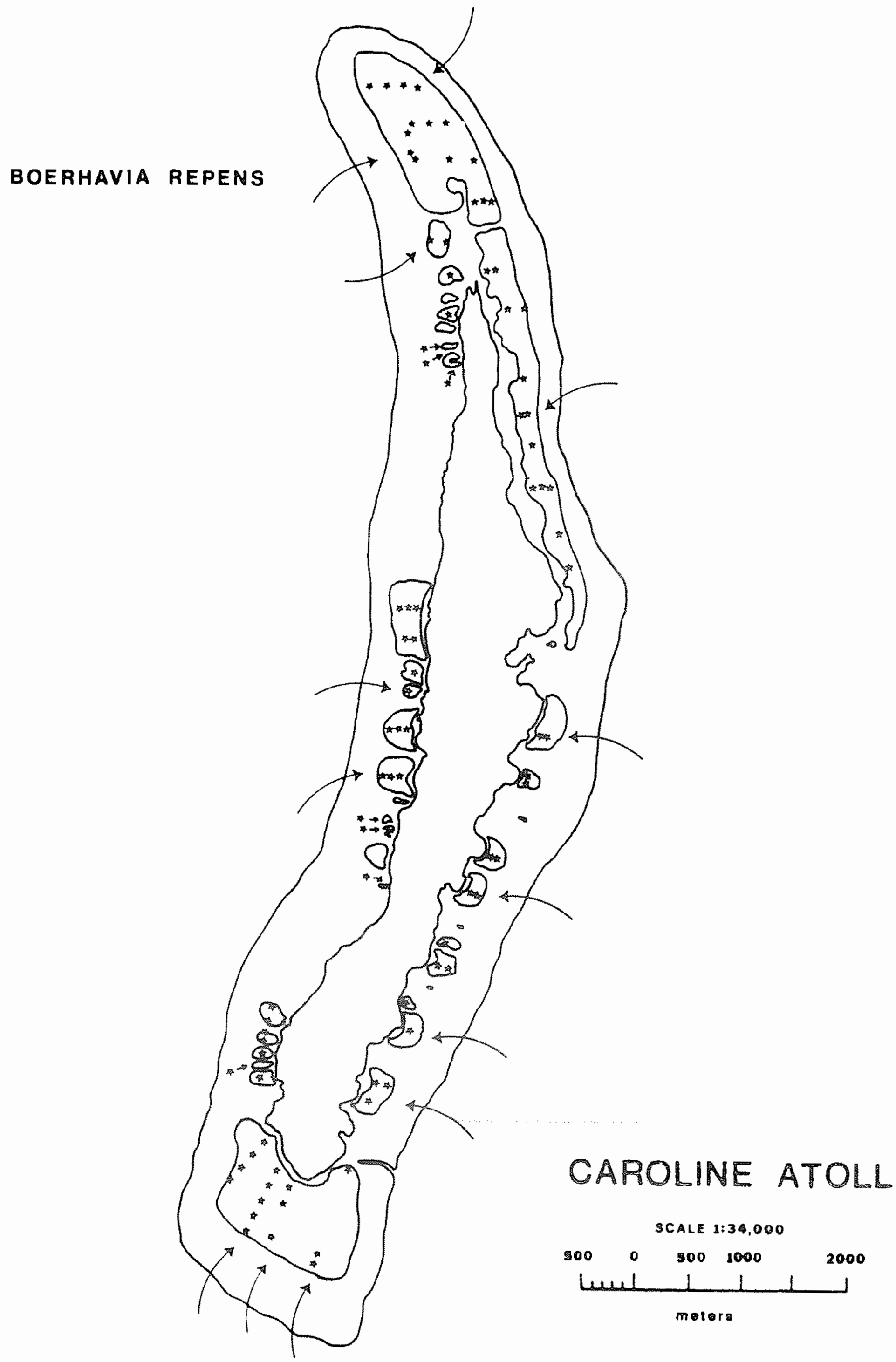

Figure 17. Transect distribution map of *Boerhavia repens*, Caroline Atoll. Arrows indicate areas of highest density.

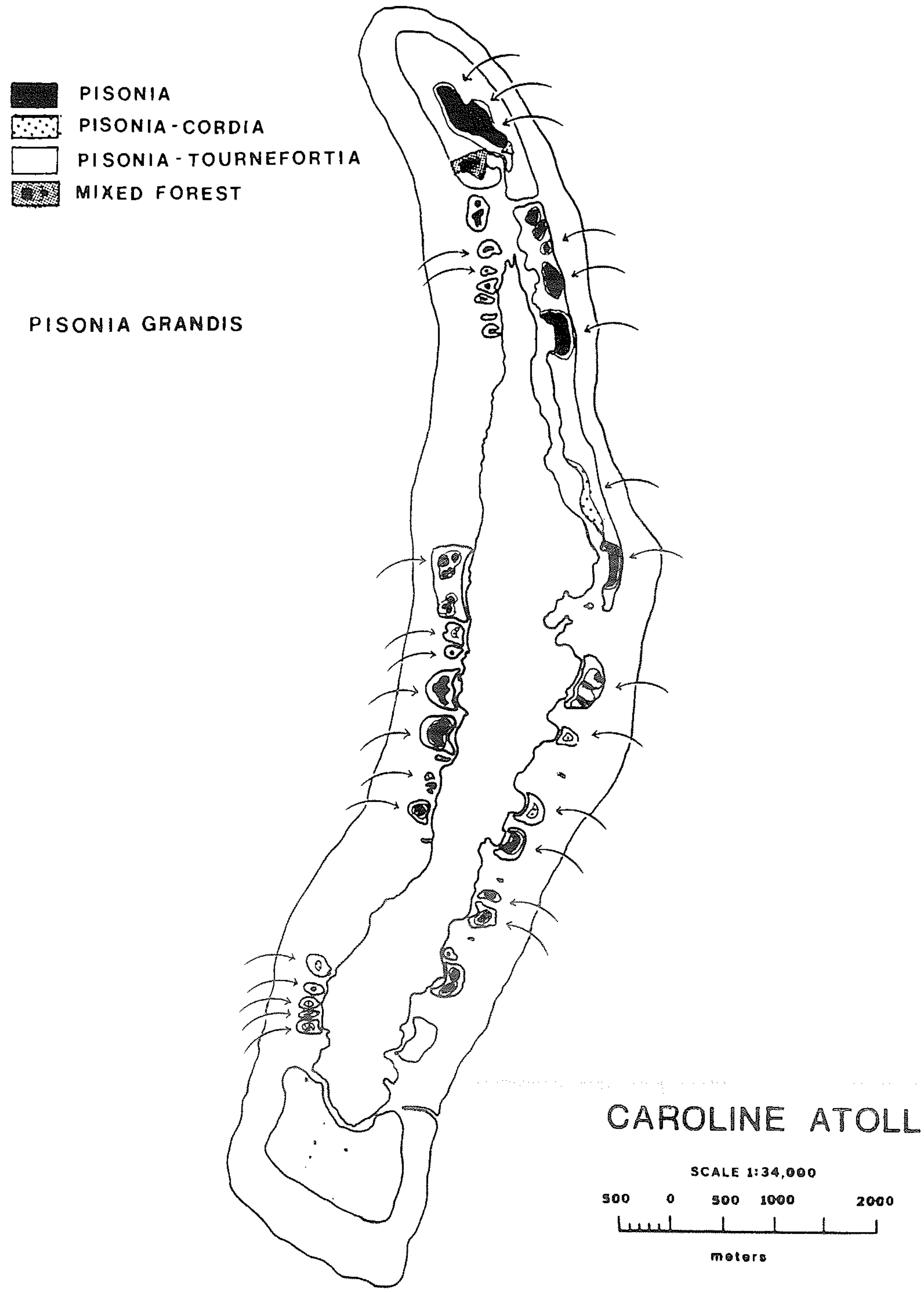

Figure 18. Entire distribution map of *Pisonia grandis*, Caroline Atoll. Arrows indicate forests from 10 to 21 m tall.

BIRDS: Bristle-thighed Curlews fed within the *Boerhavia* mat in old *Cocos* forests, South. Sticky fruits (3 mm long) found entangled in preened down and adhering to contour feathers of a juvenile Great Frigatebird (Pl. 42). Species is customarily dispersed around large oceanic areas and within atolls by tree-nesting seabirds (Guppy 1906, Ridley 1930).

Phenology: Small mauve flowers and seeds present in October, March, and May.

Substrata: Coral rubble with sand or humus, rarely pure beach rubble. Lushest growth in humus-and-guano-laden rubble clearings where *Pisonia* forest once grew.

* *Pisonia grandis* R. Br. Fig. 18, Pl. 43

Formerly Known Distribution: Collected 1884; L-3280 4 m tree, north shore, South. Small grove, north end, Long.

Present Distribution: Indo-Pacific. Caroline range extension from 2 to 29 motus (Table 3).

Abundance: A major plant community (Sect. G), of special conservation value.

Substrata: Occupies, and contributes to, best soils on atoll: mixture of rubble, humus, and guano.

PORTULACACEAE

* *Portulaca lutea* Solander ex Forster F. Fig. 19; Pls. 34, 38

Formerly Known Distribution: Reported 1840 and 1884; L-3233 and 3292, 3231, 3237, 3255, 3257, from South, Pandanus, Nake, Long, and Emerald, respectively, in open coral, rubble, gravel and exposed areas, to 1.5 dm high.

Present Distribution: Range extension from 5 to 33 islets (Table 3).

Abundance: Along with *Heliotropium anomalum* is a component of the plant community, Natural Herb Mat (Sect. G). Widespread, predictable on coast and former reef channels but local inland. Covered from one to 60% of land area on almost every transect, windward and leeward, especially facing lagoon. Best areas are Long, Transect 4 (36 m wide meadow); South, north end of Transect 6 (50 m wide); Brothers, lee, almost pure mat covering 20% ground (6 m wide); Kimoa, north side (8 m wide), 10 cm high; Eitei, north side, 5 cm high.

Ecology: Primarily occurs along edges of motus in rubble mat and open *Tournefortia* scrub, averages 12 cm high. Prominent in sparsely vegetated areas, extending seaward to high tide level. Halophytic; highly tolerant of sun. A flat mat in exposed areas but lusher inland, rising to 2 dm tall. Generally found with *Heliotropium, Lepturus, Boerhavia*, or *Laportea*, but may form pure mats. Uncommon in *Tournefortia* scrub, patchy in clearings within *Pisonia* forests up to 13 m high. Exceptionally common in old *Cocos* groves with *Boerhavia*, etc. (Pl. 34); otherwise rare or absent from closed canopy *Cocos* plantations. Pinker stems found in sunny sites. BIRDS: Provides nesting cushion for Masked Booby, Sooty Tern, Brown Noddy. On Noddy Rock, Brown Noddies nest on a thick mat of pure *Portulaca*. Feeding location for shorebirds.

Phenology: Flowers and fruit October, March, and May.

Substrata: Coral rubble and gravel, fine to very coarse. Healthier on older sands and coral-humus.

ZYGOPHYLLACEAE

* *Tribulus cistoides* L. Fig. 11

Formerly Known Distribution: Collected 1884. L-3245 in open sandy area among *Tournefortia* shrubs, Long Island. Not seen elsewhere on atoll.

Present Distribution: Not seen on our surveys, but present in 2 sites on west-central Long Island. K-90-161 (collected by Anne Falconer), probably from one of same sites as 1965 collection. Flowers in March.

SURIANACEAE

* *Suriana maritima* L. Fig. 20; Pls. 20, 39, 40, 44

Formerly Known Distribution: Collected 1884. L-3220, shrub to 1.8 m, east edge of Tridacna Islet.

Present Distribution: K-90-5, 6 from South Island. Range expansion from one to 9 motus (Table 3).

Abundance: Occasional. Forms a vegetation unit, Beach Scrub with *Suriana* (Sect. G).

Phenology: Flowers in March and May.

Substrata: Best sites in sand but also on coral rubble.

EUPHORBIACEAE

Phyllanthus amarus Schum. and Thonn. Fig. 11

Formerly Known Distribution: Collected 1884. L-3283, herb *Phyllanthus niruri* L. (Trelease 1884) to 4 dm, common on north side of South Island.

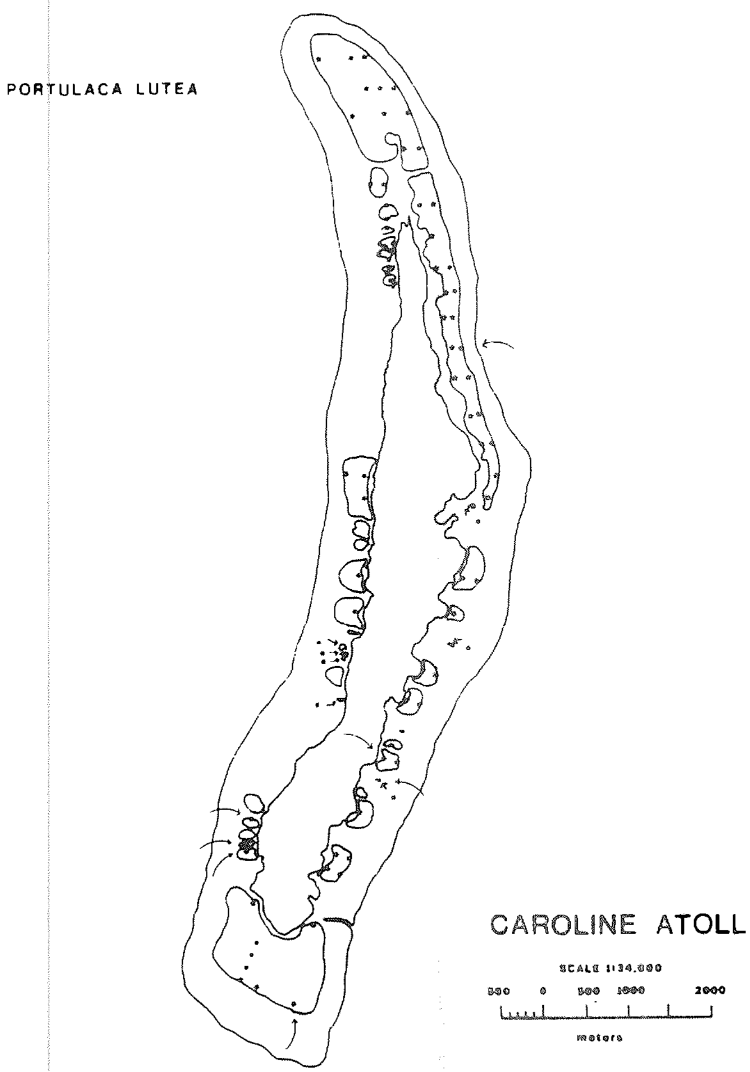

Figure 19. Transect distribution map of *Portulaca lutea*, Caroline Atoll. Arrows indicate pure *Portulaca* flats.

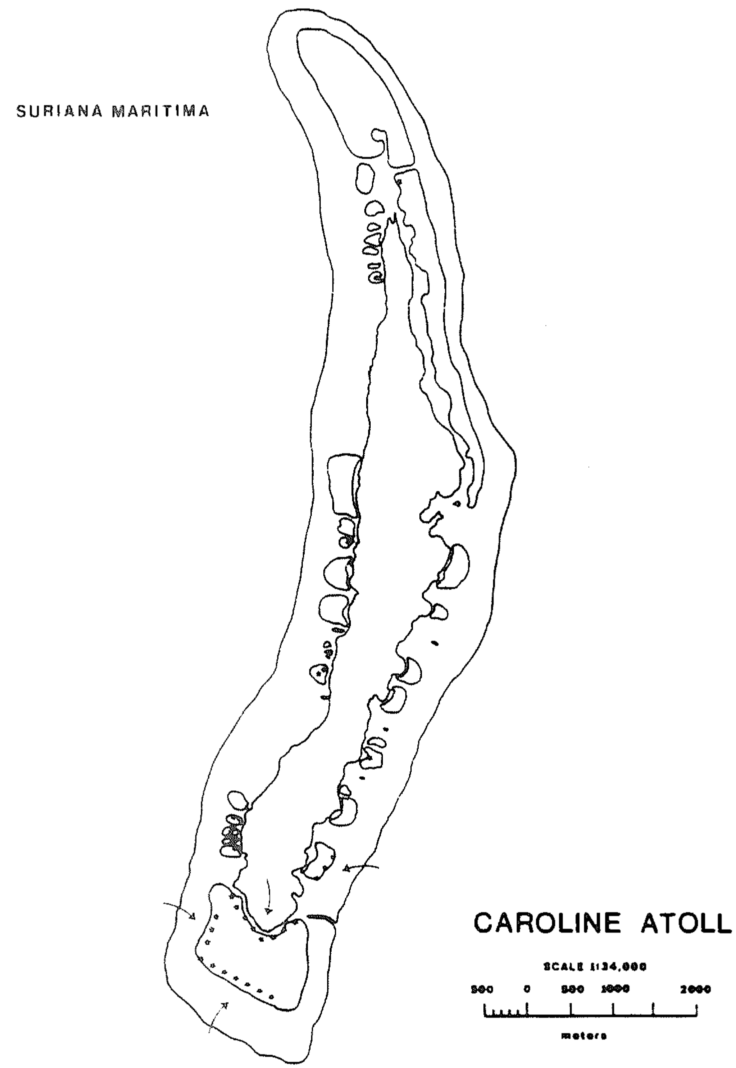

Figure 20. Transect and perimeter survey distribution map of *Suriana maritima*. Arrows indicate areas of highest density.

Present Distribution: K-90-10-13, herb, 2 small patches, South Island. Limited to a few square meters in the atoll's only weedy area, less than 10 m^2 in 2 small clearings by the recently-renovated cistern, South. A fairly common weed in the Society and Tuamotu Islands, probably arriving with 20th century copra-cutters and perhaps again within the last 2 years. Caroline's only established "weed" (excluding Polynesian introductions such as *Cocos*).

MALVACEAE

° * (**?) (#?) *Hibiscus tiliaceus* L. Fig. 11

Never previously collected. K-90-8, 9 from South Island, northwest peninsula, in *Cocos* plantation near old settlement and "landing," in coral rubble and humus, 0.6 m in elevation.

Present Distribution: Two or 3 large spreading trees in heavy *Cocos* shade, 10 m tall, with recumbent branches forming an impenetrable thicket, similar in size and form to specimens in Flint's settlement. Since Flint was evidently first settled in 1872 (i.e. no aboriginal population was present, see Kepler, in prep.), Caroline's trees, restricted to the old settlement area, are most likely recent Polynesian introductions.

° * (**?) (#?) *Thespesia populnea* (L.) Soland. ex Correa Fig. 11

Never previously collected. K-90-22, 154, 155 from South Island, in *Cocos* plantation and in lagoon strand, northwest peninsula, near "landing."

Present Distribution: Two trees (10 m tall), one near the cistern, the other in a fringe of native vegetation bordering the lagoon. The history of this species is probably the same as *Hibiscus tiliaceus*.

* *Sida fallax* Walp. Fig. 11

Formerly Known Distribution: Collected by Dixon, 1884, who found one specimen.

Present Distribution: Not seen for 106 years. K-90-156, 157, 158 from South Island, at edge of cistern, north side. One clump located in a sunny clearing, recently enlarged by the Falconers.

CONVOLVULACEAE

* *Ipomoea macrantha* R & S Fig. 21; Pls. 34, 37
Ipomoea tuba (Schlecht.) G. Don

Formerly Known Distribution: L-3228 and 3293, 3242, 3251 on South, Nake, and Long, respectively. Trailing vines, white flowers, stems to 25 m long climbing over *Tournefortia*, *Morinda*, and *Cocos*.

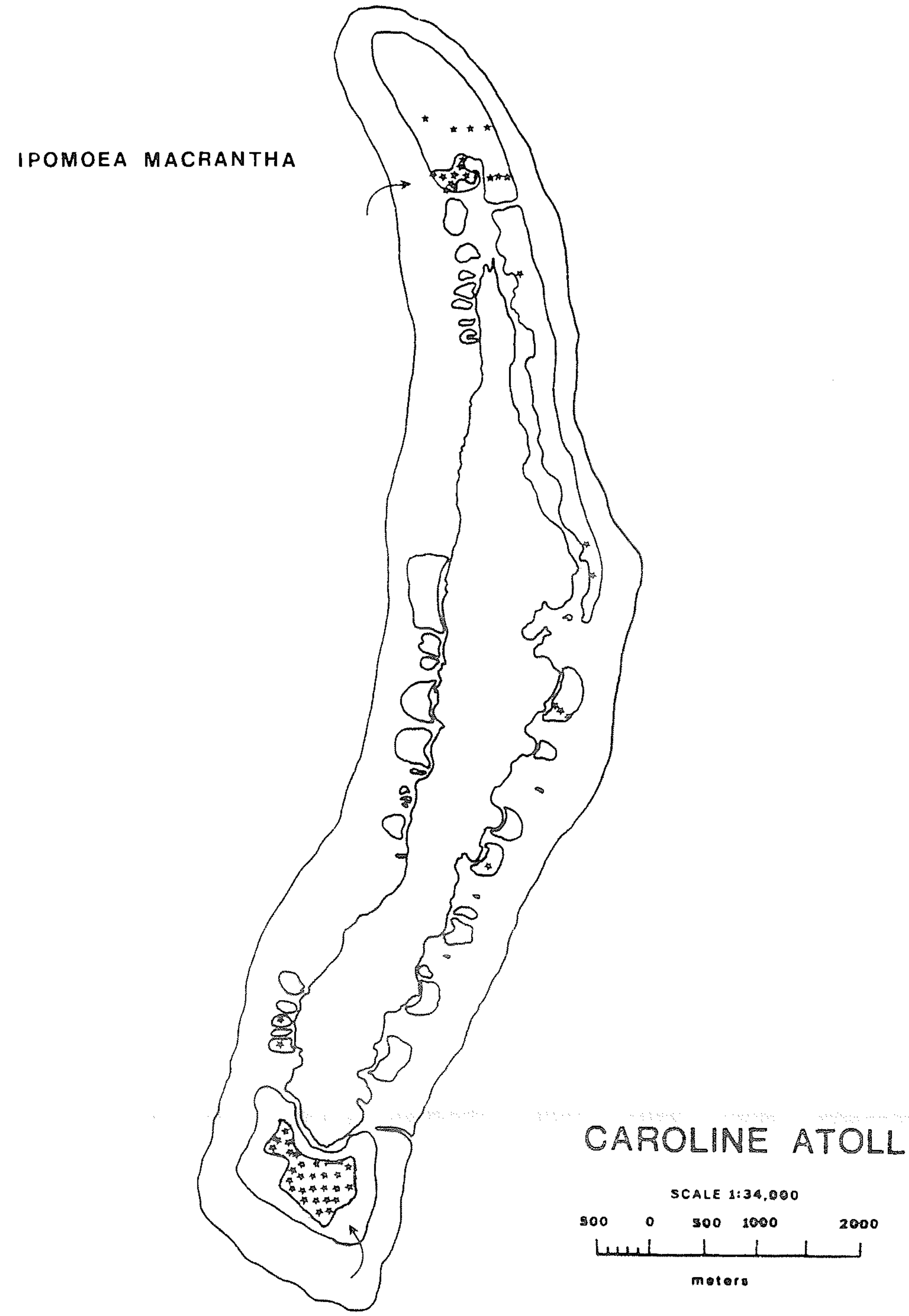

Figure 21. Transect distribution map of *Ipomoea macrantha*. Entire distribution is shown for South Island. Arrows indicate areas having significant amounts of this vine.

History: Not collected last century, though plantation records indicate that it was a major reason for the abandonments of the coconut plantations: "The Pohue Vine[2], which is the worst pest on the island, was reported in 1921 to be under control" (Young ca. 1922). Today it strangles about 54 ha, two-thirds of South Island's plantation.

Present Distribution: Range extension from 3 to 7 motus, 5 Windward and 2 Southern Leeward Islets (Table 3).

Abundance: Forms part of a vegetation subunit, Dying *Cocos-Ipomoea* Forest (Pl. 34, Sect. F). An indigenous, nonparasitic vine, abundant in disturbed areas. Rampant growth over most of the interior of South Island, where it forms dense tangles up to 25 m high. Less dense thickets on southern Nake drape *Pandanus, Tournefortia, Morinda*, and *Cocos* to 10 m. Coverage 2-5% elsewhere, except in 2 *Pisonia* sites, where its coverage was 20% (Long Island, Tr. B; Windward Islet, Tr. 1).

Ecology: Lush in dying *Cocos* forests and mixed forest with *Pandanus*, aided by relatively fertile soils, moisture, humidity, and partly sunny clearings. Strangles all but the tallest *Pisonia* and *Cordia*. Typically sea-dispersed to atolls (seeds germinate after floating up to 1 year in seawater), crawls inland, progressively dropping seeds, to attain full size in interior forests (Guppy 1906, Ridley 1930). Seeds of *I. pes-caprae* are known to be ingested by White Terns in the Marshall Islands, perhaps as gizzard stones (Fosberg 1953). Possibly these same terns, abundant at Caroline, once aided the seed dispersal of *I. macrantha*. Also characteristic of *Cocos* plantations elsewhere in the Pacific (Lamberson 1987, Stoddart & Sachet 1969, Fosberg 1965).

Substrata: Prefers humus-laden rubble, but can grow in coarse rubble and sand, especially in leeward areas.

BORAGINACEAE

* *Cordia subcordata* Lam. Fig. 22, Pl. 26

Formerly Known Distribution: Collected in 1884. L-3213 and 3261a, 3228, 3246, and 3261b on South, Pandanus, Long, and Emerald, respectively; flowering trees to 4.5 m high in leeward coral rubble or along lagoon.

Present Distribution: Africa to Polynesia. K-90-3 from South Island, lagoon edge. Range expansion on Caroline from 5 to 23 motus (Table 3).

Phenology: Peak flowering November through April, fruits collected in March and May.

[2] misidentified as *Tuumfetta* [= *Triumfetta*] *procumbens*.

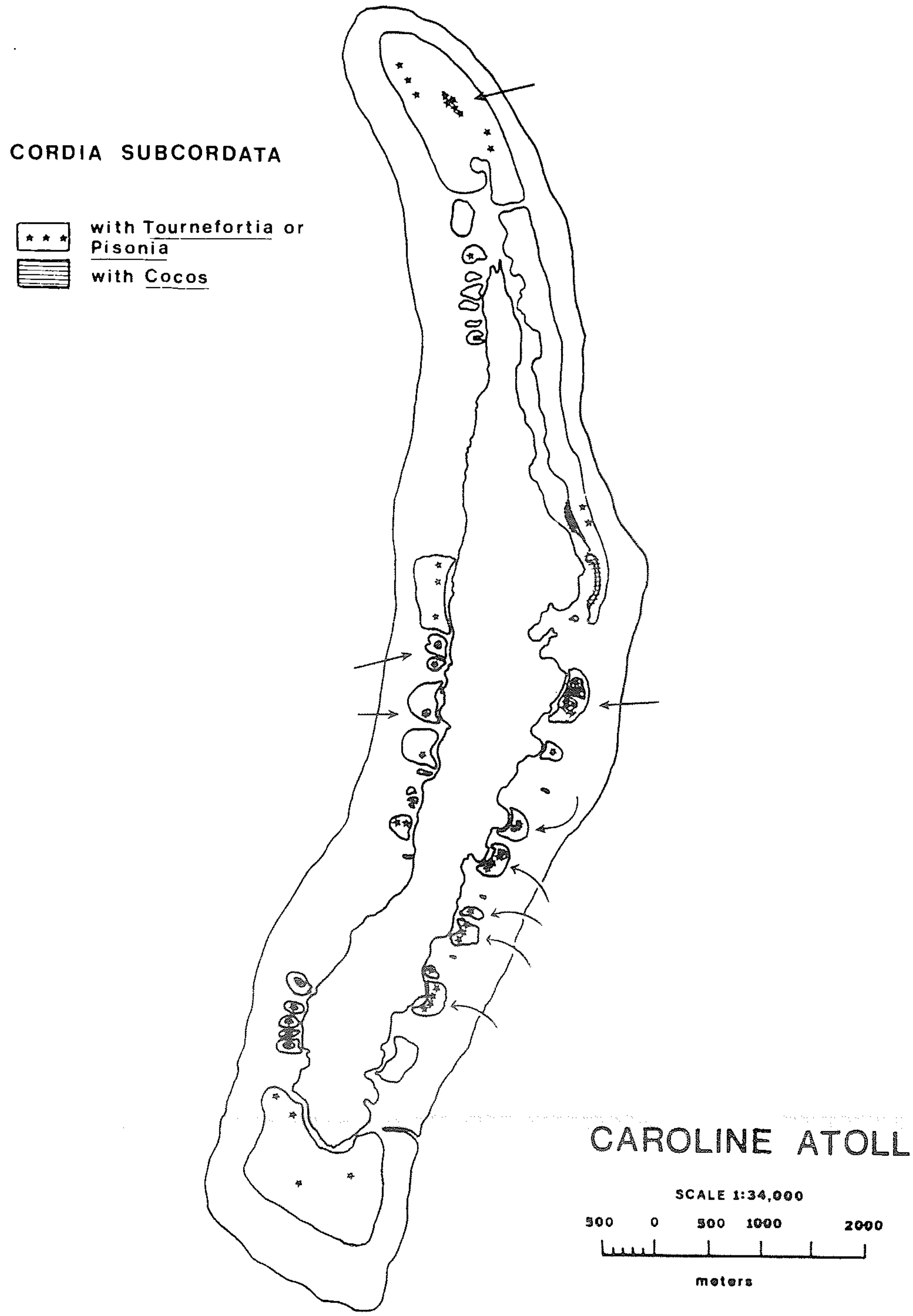

Figure 22. Entire distribution map of *Cordia subcordata*. Arrows indicate small, but monotypic, stands.

Abundance: A separate, though minor, plant community (Sect. F). Although groves are small and mixed with other emergents, individual trees attain 13 m tall. *Cordia* has special conservation value.

* *Heliotropium anomalum* H. & A. Fig. 23; Pls. 16, 32, 45-47

Formerly Known Distribution: Recorded (mistakenly as *H. curassavicum*) in 1840, collected in 1884. L-3222 and 3288, 3240, 3248, 3256, 3288 on South, Danger, Long, and Emerald, respectively.

Present Distribution: Central and Eastern Pacific. K-90-17 from Ana-Ana. In coral gravel, leeward and windward shores. Range extension on Caroline from 4 to 34 motus (Table 3).

Abundance: Forms part of a major vegetation unit, Natural Herb Mat (Sect. G), often associated with *Laportea, Lepturus*, or *Boerhavia*. Area coverage ranges from less than 1% to 50%. Widespread, predictable on wind- and salt-blown, low flats where vegetation does not overhang edge of motu. Also in ancient reef channels and newly evolving land connecting islets. Covers major areas of islets, that is those less than 1.0 ha (e.g. Fishball, Skull, and Bo'sun Bird). Best developed on Skull, Tridacna, South, Emerald, and Mannikiba (50% coverage, western seaward rim).

Ecology: Halophytic pioneer. Heights to 22 cm, averaging 7 cm. Thrives in heat and exposure.

Phenology: Flowers and fruits year-round.

Substrata: Primarily coral rubble and rubbly sand. Marginal habitats extend down to high tide line in areas of coarse coral chunks, where it is tiny and leathery.

* *Tournefortia argentea* L. Fig. 24; Pls. 9, 37, 47, 48
Messerschmidia argentea (L.f.) Johnston

Formerly Known Distribution: Collected 1884. L-3216, 3226, 3241, 3249, 3258 from South, Tridacna, Nake, Long, and Emerald Isle; shrub to 3 m high, edge of lagoon and above high tide, with white flowers.

Present Distribution: Range extension from 5 to 38 motus (Table 3). Widespread in the Pacific, especially on small islets, but rarely inland. Reaches Ducie Atoll, the most southeasterly island in Polynesia. Caroline's large tracts are excellent examples of relatively undisturbed, pure *Tournefortia* scrub and forest.

Abundance: Dominates the atoll woodlands, forming the major vegetation type (Sect. G). On almost every motu ranging from a spattering of exposed shrubs within herb mats, through scrublands and taller forests to 14 m high.

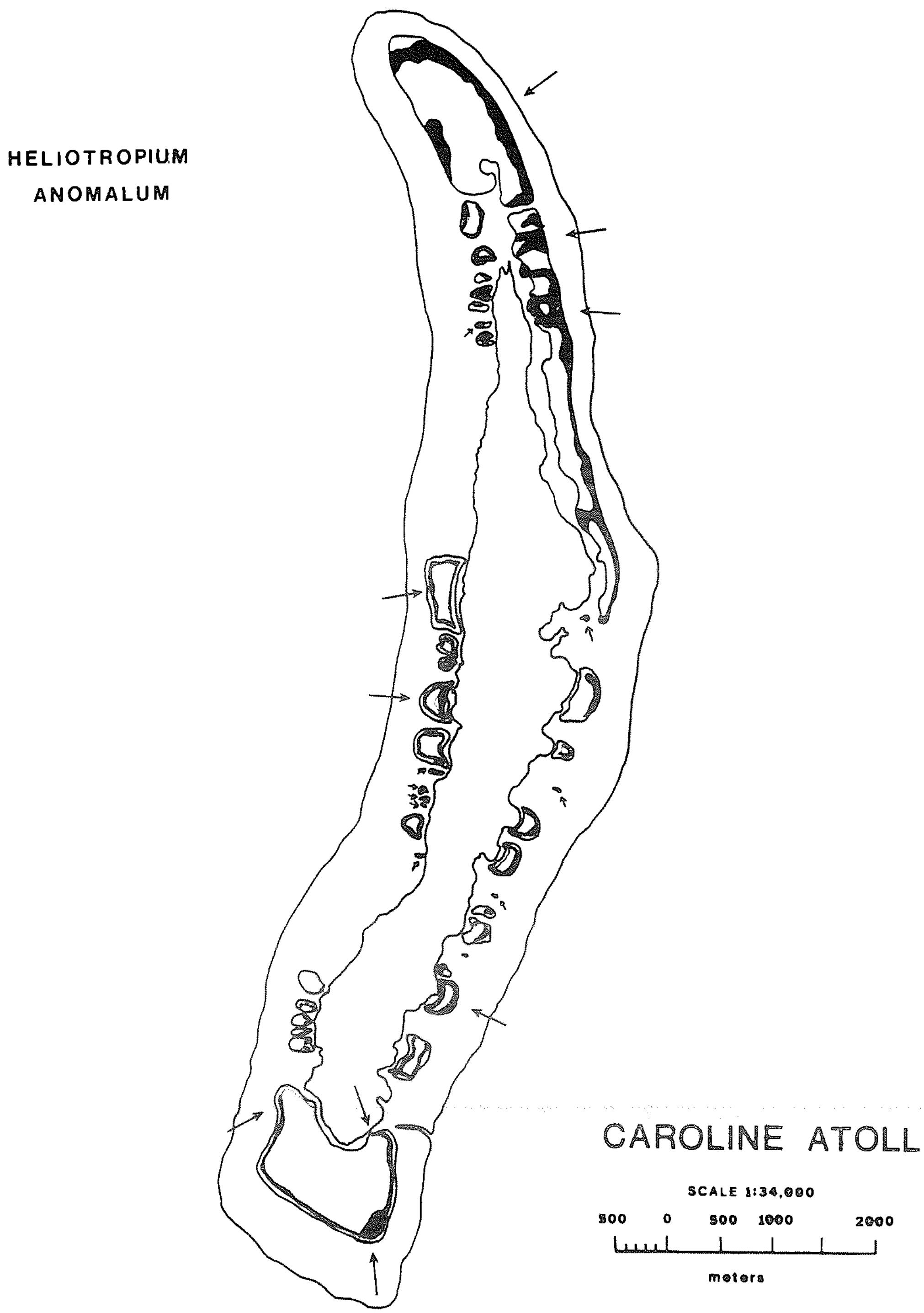

Figure 23. Entire distribution map of *Heliotropium anomalum*. Arrows indicate areas of highest density.

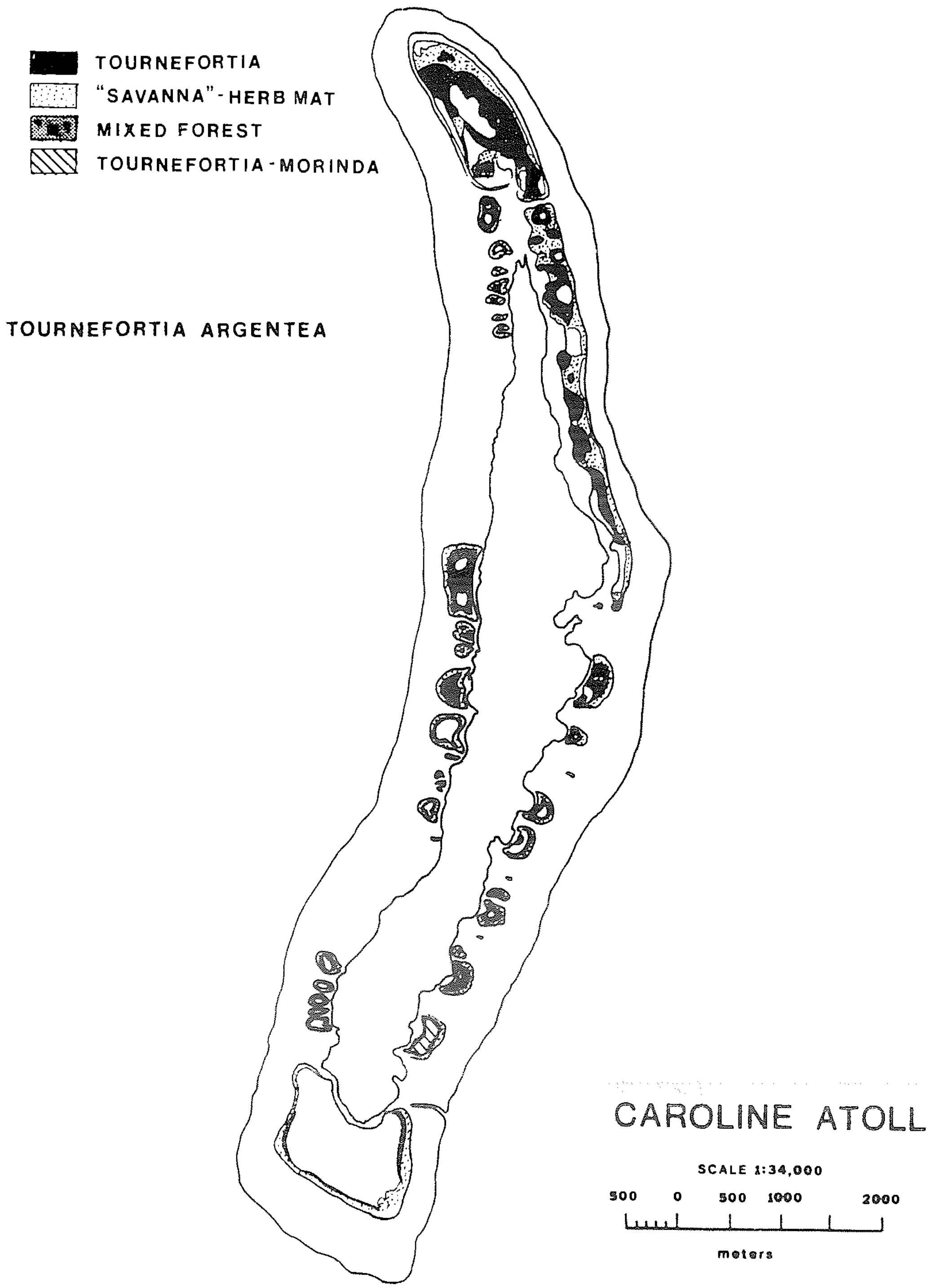

Figure 24. Entire distribution map of *Tournefortia argentea*. Because this shrub dominates Caroline's woodlands, there are no individual arrows to indicate areas of high density.

Ecology: Supports 7 species of breeding seabirds; provides feeding habitats for Reef Herons (*Egretta sacra*), shorebirds, land crabs, and rats.

Phenology: Flowers and fruits year-round.

Substrata: Pure coral clinker; mixtures of rubble, gravel, sand, and humus.

BRASSICACEAE

* *Lepidium bidentatum* Montin Fig. 11

Formerly Known Distribution: Reported in 1825: "a boat load of pepper-grass and pursley" (Paulding 1831) and in 1835, "a *Lepidium* of luxuriant growth" (Bennett 1840). Collected by Dixon as *L. piscidium* Forst in 1883.

Present Distribution: Widely distributed throughout the North and South Pacific. K-90-169 and 171 (collected by Alexandre Falconer), on Tridacna and Pisonia, most probably in coastal *Tournefortia* scrub. Entire and serrated leaf forms present, which have also been collected on Flint (St. John & Fosberg 1937).

RUBIACEAE

* *Morinda citrifolia* L. Fig. 25, Pl. 48

Formerly Known Distribution: Reported 1840, collected 1884. L-3214, 3217 and 3282; 3232; 3254 on South, Nake, and Long, respectively.

Present Distribution: K-90-4, 18 from South's lagoon edge and Ana-Ana, respectively. Range extension on Caroline from 3 to 30 motus (Table 3).

Abundance: Coverage 2% to 50%. Basically an inland species, widespread and predictable in scrub and forest understory. Rarely a canopy component, except on Raurau, where 12 m tall in a 13 m *Pisonia* forest. Associated with established *Tournefortia* woodlands on motus greater than one hectare in size. Quite common on South despite major disturbance, occurring within beach strand, *Cocos*, and dying *Cocos-Ipomoea* interior. Best locations (40-60% coverage): Nake, Transect 3; Tridacna, both transects; Long, Transect 8; Raurau and Ana-Ana.

Ecology: Appears early in plant succession: in *Tournefortia* scrub as an early pioneer (Stage I), then from Stages II to IV, progressively becoming more common and robust. Not in pure *Pisonia* forest (Stage V). Much less common in *Pandanus* stands. Thrives in light to heavy shade, preferably growing in moist substrata.

Biogeographical Note: *Morinda* is generally considered a naturalized aboriginal introduction in the Pacific. Although possibly introduced to

Fig. 25. Transect distribution map of *Morinda citrifolia*. The outlined area on Tridacna Islet (northeast of South Island) encloses *Tournefortia-Morinda* forest. Arrows indicate areas of highest density.

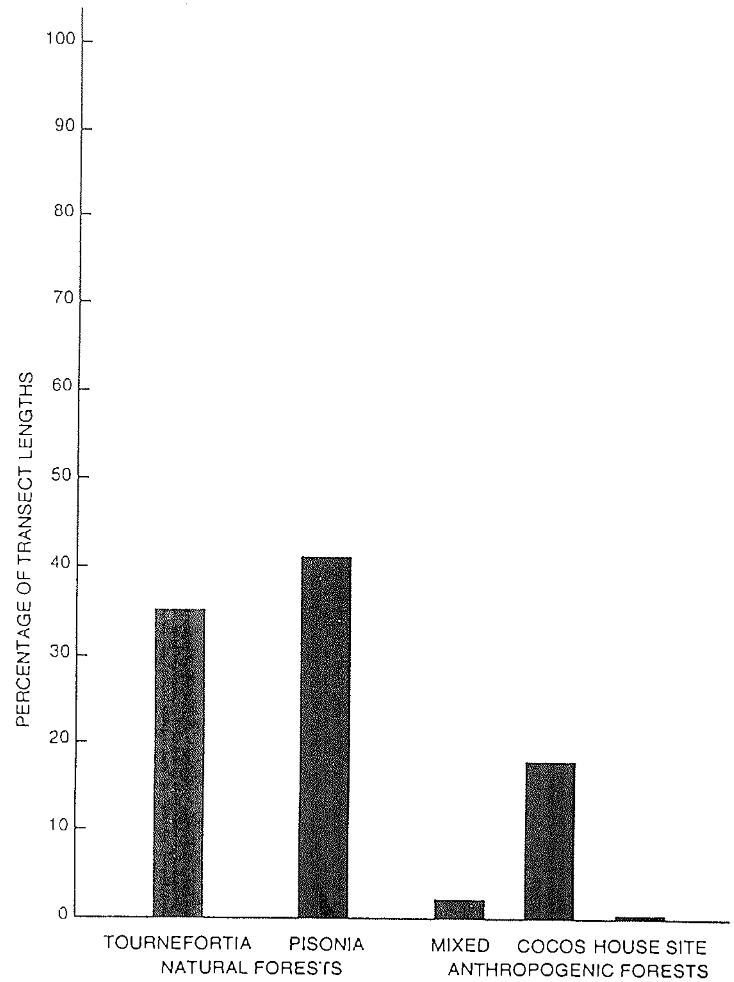

Fig. 26. Evidence for the indigenous status of *Morinda citrifolia* on Caroline Atoll: percentage cover on transects within natural and anthropogenic forests. *Morinda* occurs on 30 (77%) motus, never in a "planted" situation.

Caroline by early Tuamotuan settlers, its present distribution strongly suggests that it is indigenous, as theorized for the northern Line Islands (Wester 1985). *Throughout the atoll* Morinda *occurs in the greatest densities on motus with no anthropogenic forests or in areas distant from historical settlements* (Fig. 26). Furthermore, it is present on (30) 77% of the motus, virtually all those larger than 0.4 ha in size, and many of which are presumed virgin. On Nake, *Morinda* occurs frequently--in places abundantly--within the interior indigenous forests, yet its coverage is only 5-10% in the mixed *Cocos* forests of the southern sector. It also appears to be part of natural biological succession (Table 6). However, on nearby Flint, which was probably never settled in prehistoric times and where our 1990 surveys found *Morinda* in all habitats (mixed woodland, native coastal scrub, *Cocos* plantations, and abandoned settlement), the largest tree and highest abundance was close to the old settlement (Kepler, in prep.).

Originating in southeast Asia, *Morinda* has been widely dispersed by man, but has spread, unaided by man "widely by sea in the Malayan and Polynesian Islands" (Ridley 1930). Fosberg (1974) notes that it is always difficult to determine its true status. Its air-filled, buoyant pyrenes can float for at least 53 days and "its seeds are almost certainly disseminated by birds and bats" (Guppy 1906). It could also be disseminated by *Coenobita* crabs and rats within and between motus, as has been found elsewhere by Ridley.

Phenology: Flowers and fruits year-round.

Substrata: Coral rubble, gravel, sand, and humus. Rarely found in coarse clinker. On larger motus, prefers moist soils under tall forests.

GOODENIACEAE

° * *Scaevola taccada* var. *sericea* (Vahl) St. John — Fig. 11
Scaevola sericea var. *sericea* Vahl

Never previously collected. K-88-2, Windward Islet, central-windward side, elevation 0.3 m.

Distribution and Abundance: One wind- and salt-sheared "hedge," found by K. Teeb'aki on Windward Islet, was growing on a coarse rubble beach. "The saltbush..., being recorded for the first time too from the island...covered approximately 3% of the islet's land area,[3] occupying the mid-windward side. The patch grew very low--only up to 2' high with its foliage forming an extended raised mat canopy all along the area it occupied" (Teeb'aki 1988). We have been unable to return to this spot to observe and photograph it directly.

[3] This probably translates as "3% of the area covered at that location on the transect," as we understood from Teeb'aki's description that it was small.

Because *Scaevola* is hardy, halophytic, and widespread in the Pacific, it is surprising that it is so rare on Caroline. However, none occur on Vostok, and only one clump is known from Flint (St. John & Fosberg 1937). Fosberg (1953) noted that *Scaevola* seeds are transported by Bristle-thighed Curlews (*Numenius taitensis*) in the Marshall Islands: curlews are common on Caroline (Pt. II) and could have brought seeds from elsewhere.

Substrata: Coarse rubble, windward beach.

° * *Scaevola taccada tuamotensis* St. John — Fig. 11
Scaevola sericea var. *tuamotensis* (St. John) Fosb.

Never previously collected. K-90-168 (collected by Alexandre Falconer), northeast peninsula, South Island, in coral rubble.

Present **Distribution:** One individual, of unknown size, with *Suriana* and *Heliotropium*, northeast peninsula, South Island, facing the inner side of the "blind passage."

Floristics and Ecology of the Motus

Size of the Flora

Atoll floras characteristically lack diversity. Numbers of species range from 1 (Ducie Atoll) to around 150 in the Pacific and 284 in the Indian Ocean. Tiny gravel banks such as Kingman Reef (Line Islands) and Motu-One (Marquesas) have no vascular flora at all (Fosberg 1974). The flora of the Southern Line Islands is particularly impoverished because of 1) their easterly location (far from the major source areas of Australasia), 2) low profiles (most only rise a few meters above sea level), 3) lack of topographic diversity (most have a very limited range of habitats), 4) low to medium rainfall (approximately 1,500 mm p.a.), and 5) edaphic factors such as salinity, highly calcareous soils, etc. Long-distance dispersal and hardiness are important factors in establishing a flora, especially since the closest high island, Tahiti, is 830 km away, and the ultimate source of its flora, the Malayan-Melanesian region, is over 8,000 km away. South America, the closest continent, is approximately 9,000 km distant. The motus of Aitutaki, for example, at a similar latitude but further west and wetter, are considered depleted with 45 species. Fanning, at a similar longitude but wetter, has 123 species. Tarawa, 3,900 km to the northwest, receives a similar rainfall but supports 109 species.

Where an atoll's potential flora is larger, the increased shade and greater protection from wind, salt spray, and storms result in a greater number of natural plant species on its larger motus. However, such atolls are generally inhabited and alterations by both aboriginal and modern man have modified their original flora. Caroline's isolation, variety of motu areas, and minimal human disturbance all contribute to its excellence for the study of atoll evolution.

The number of species presently established on Caroline's 39 motus is 26 (Tbs. 2, 3). The previous expedition in 1965 (Clapp & Sibley 1971a) collected 20 species, of which 4 were new to the atoll. Their total of 35 species, however, incorporating reports and collections from the 1800s, is misleading. Our total, 5 of which were new records, would have brought the atoll total to 43 (plus about 15 more unestablished, mostly garden, plants). However, following recent custom (see Sect. E), we have listed transient or extinct members of the flora separately (Table 1).

The 1883 drawings of the South Island settlement, inhabited when most of Caroline's species were catalogued, shows that the island was vastly different then (compare Pls. 2, 3 and 23). A century ago homes were set amidst large grassy clearings; now the site is completely obliterated beneath shady 21-m-tall coconut palms. Nine exotic species have not been seen for over a century (Table 1). Evidently most ornamentals and domestic vegetables perished during uninhabited periods. The Falconers struggled to keep garden plants alive because of poor soils, irregular rainfall, and foraging land crabs. This situation has been noted for other atolls (Fosberg 1949). A few native species might also have been eliminated during the guano and copra-harvesting years.

Numbers of Indigenous Plants

A comparison of the percentage of indigenous species between different island groups (Table 4) shows that Caroline, with 85% (N = 23)[4] indigenous, is unusually high. Only 12 of 45 Pacific islands reviewed have more than 75% of their species indigenous. Of these, 9 (including Caroline) are remote and lack permanent human occupation. Vostok, Caroline's nearest neighbor (243 km west), is one of only 2 islands in the world which have less than 4 species (Fosberg, pers. comm.).

The Tuamotu Islands (149° to 134°W) lie east and south of Caroline, yet they harbor considerably larger floras. Rainfall is similar. Three of them average 121 species (Table 4), averaging 42 indigenous species. When the variables rainfall and distance from a colonization source to the west are considered, the proximity of the Tuamotus to the diverse high islands of the Societies seems to play a major part in determining their indigenous flora. A similar situation exists in the southern Cook Islands. Caroline and other remote Line and Phoenix Islands are sufficiently isolated from high volcanic and raised reef (*makatea*) islands that they exhibit a much simpler flora. Tahiti, the closest high island (830 km south), is in the wrong direction for prevailing currents, winds, or vagrant birds to bring seeds to Caroline.

[4]Perhaps as high as 92%; the *Digitaria* sp., if still extant, is of unknown identity and origin.

Table 4. Sizes of Pacific atoll floras, with emphasis on the percentages of indigenous plants.[1] Islands in bold have more than 75% of plant species indigenous.

Island Group	Atoll	Total[2] No. Species	No. Species Indigenous	% Indigenous	Source
Caroline Is. (Fed. States of Micronesia)	Kapingamarangi	98	38	39	Niering 1962
Cook Is. (New Zealand)	Aitutaki (motus)	45		50	Stoddart & Gibbs 1975
	Rarotonga (motus)	49		≈60	Stoddart & Fosberg 1972
Gilbert Is. (Rep. of Kiribati)	**Onotoa**	60	50	83	Moul 1957
	Tarawa	109	28	26	Catala 1957
Northwest Hawaiian Is. (U.S.A.)	Kure	42	23	55	Lamoureux 1961, Clay 1961
	Laysan	38	27	71	Ely & Clapp 1973
Line Is. (Kiribati)	**Caroline**	26	23(24?)	89(92?)	This paper
	Christmas (Kiritimati)	69	19	28	Garnett 1983
	Fanning	123	23	19	Wester 1985
	Flint	43	18	42	Kepler (in prep.)
	Malden	9	9	100	Garnett 1983
	Palmyra	58	21	36	Wester 1985
	Starbuck	7	4	57	Garnett 1983 (incomplete, little known)
	Vostok	3	3	100	Kepler 1990c
	Washington	91	25	27	Wester 1985
Marshall Is. (Fed. States of Micronesia)	Ailuk	56	26	46	Fosberg 1955
	Arno	125	40	32	Hatheway 1953
	Enewetak	128	55	43	Lamberson 1987
	Jaluit	288	55	21	Fosberg & Sachet n.d.
	Jemo	34	17	50	Fosberg 1955
	Kwajalein	89	25	28	Fosberg 1955, 1959
	Lae	61	35	57	"
	Likiep	91	31	34	"

Table 4. Continued.

Island Group	Atoll	Total[2] No. Species	No. Species Indigenous	% Indigenous	Source
Marshall Is. (cont.)	Taka	23	18	78	Fosberg 1955
	Ujae	61	32	52	Fosberg 1955, 1959
	Ujelang	50	29	58	"
	Utirik	55	26	47	"
	Wotho	40	28	70	"
Phoenix Is. (Kiribati)	Kanton (Abariringa)	164	14	9	Degener & Gillaspy 1955,
		129	18	14	Garnett 1983
	Birnie	3	3	100	Fosberg & Sachet (n.d.)
	Enderbury	23	18	78	"
	Nikumaroro	35	17	49	"
	Orona	≈29	19	≈66	"
	McKean	7	7	100	"
	Phoenix	6	6	100	"
	Manra	≈18	14	≈77	"
Society Is.	Tetiaroa	95	47	49	Sachet & Fosberg 1983
Solomon Is.	Ontong Java	150	58	39	Bayliss-Smith 1973
Tokelau Is. (N.Z.)	Nukunono	55	35	64	Parham 1971
Tuamotu Is. (France)	Rangiroa	121	39	32	Stoddart & Sachet 1969
	Raroia	135	54	40	Doty 1954
	Takapoto	106	33	31	Sachet 1983
Outlyers	Clipperton (U.K.)	31	14	45	Sachet 1962
	Ducie	1	1	100	Rehder & Randall 1975
	Oeno	17	14	82	St. John & Philipson 1960
	Wake	94	20	21	Fosberg & Sachet 1969

[1]An updated version of Table 11, p. 105, Stoddart and Gibbs (1975).
[2]Number of species of those indigenous are not always comparable. Ferns are usually included, but certain ornamentals may not be. *Artocarpus*, *Morinda*, and *Pandanus* may be indigenous, aboriginal introductions, or both. Without its full scientific name, a species has an unknown biogeographical status.

Composition of the Flora (Tbs. 2, 3)

Caroline's botanical affinities lie with other Southern Line Islands and the Tuamotus. Although the strand and inland floras consist of pan-Pacific or pan-tropical species, there are several widespread species and communities that are notably absent (see below). Those that survive have withstood the atoll tests of time--poor soils, scarcity of fresh water, periodic inundation by salt water, intermittent cyclonic storms and hurricanes, harsh climate, high seedling mortality, and human impacts. Caroline provides an excellent ecological laboratory in which floristic correlations with variations in habitat, motu size, vegetational zonation, and leeward/windward aspect may be studied. Fosberg (1985) and Sachet (1967) have noted the importance of such details in understanding the biogeography and taxonomy of Pacific plants.

Caroline's present established flora includes very few introduced species: ancient Polynesian introductions (*Cocos*, possibly *Pandanus* and *Morinda*), recent Polynesian introductions (*Hibiscus tiliaceus*, *Thespesia populnea*, *Tacca leontopetaloides*, *Ximenia americana*), and 20th century exotics (*Phyllanthus amarus*). This latter is restricted to one tiny patch <2 sq m in area.

The number of indigenous plants is complicated by the fact that 3 species most likely introduced by recent Polynesians (*Hibiscus*, *Thespesia*, *Ximenia*) could also be indigenous, as is the case with *Pandanus* and *Morinda*. In Table 4 we have counted these 5 as indigenous until later research proves otherwise. The unknown *Digitaria* sp. accounts for the query in Table 4.

Trees: Seven species present. Only 3--Pacific-wide natives--are widespread: *Pisonia grandis*, *Morinda citrifolia*, and *Cordia subcordata*. *Cocos nucifera* and *Pandanus tectorius* are locally abundant, while *Thespesia populnea* and *Hibiscus tiliaceus* are rare and limited to the old settlement site. The absence of typical Pacific species such as *Calophyllum inophyllum* and *Guettarda speciosa* is notable, as they are both present on nearby Flint (with a similar plantation history to Caroline) and occur naturally on more easterly atolls such as Rangiroa (Stoddart & Sachet 1969).

Shrubs: Four species present, at least 4 indigenous. Only *Tournefortia argentea* is abundant; its most abundant size class is under 4 m. *Scaevola* and *Suriana*, tough and widespread elsewhere, are poorly represented on Caroline. It is noteworthy that 2 varieties of *Scaevola taccada* are present. *Ximenia americana* is represented by a single, large patch and one individual on South and Mannikiba, respectively. *Pemphis acidula*, though common on atolls of similar latitude and climate, is typically absent from most of the Line and Phoenix Groups (Stoddart & Gibbs 1975, Fosberg & Sachet n.d.). This may be due to the paucity of its preferred habitats: low rocky substrates (reef or conglomerate rock) and sand-gravel ridges.

Herbs: Fifteen species present, at least 12 indigenous. Of these only 7 are common: *Heliotropium anomalum, Boerhavia repens, Portulaca lutea, Laportea ruderalis, Achyranthes canescens, Lepturus repens*, and *Phymatosorus scolopendria*. *Ipomoea macrantha* and *Tacca leontopetaloides* are locally abundant, while *Phyllanthus amarus, Tribulus cistoides, Lepidium bidentatum*, and *Psilotum nudum* are rare and localized. *Digitaria* sp. may be extinct. The fact that *Sida fallax* has only been recorded twice in 106 years is curious.

F. ECOLOGICAL SUCCESSION

We have attempted to trace the development of Caroline's flora from the smallest to largest motus, using field data and aerial photos, which reveal past geological processes of unknown dates or duration. The general processes involved in motu formation are treated in Stoddart & Steers (1977, p. 95).

Three tables provide our analysis of ecological succession: Table 5 presents Caroline's motus in order of ascending size, together with the numbers of plant species and major plant communities. Since the atoll's total land area is small, our data provides relatively complete floristic lists for each islet and detailed maps of their plant communities (Figs. 37-57). The number of species varied from 3 growing on 4 tiny islets (0.02 ha each) to 23 on South (104.41 ha). Because the total number of species for the entire atoll (27) is also small, the addition of one or 2 rare species contributes significantly to the total flora. Such additions must be kept in perspective when evaluating plant succession.

Table 3 provides a summary of plant species distribution by islet, and Table 6 is a summary of plant species distribution and relative abundance with respect to islet area and the primary mode of seed dispersal.

Basic Seral Stages

Islets appear, grow, mature ecologically or vanish in violent storms. Many interacting factors, including geographical (islet area, atoll shape, distance from high islands and continents), geological (changes in sea level, reef growth and destruction), chemical (nitrates from bird droppings, leaf fall, etc.), climatological (wind, droughts, storms, microclimates), and biological (seabirds, rats, land crabs, reef bioerosion, and man, both aboriginal and modern) constantly interact to change conditions. The relative influence of some of these factors is evident when comparing the floras on motus of different sizes.

Seed-dispersal mechanisms (Table 6) and the presence of underground fresh water are also vital. Unfortunately, the relationships between groundwater salinity, species distribution, and vegetation patterns on atolls are poorly understood (Fosberg 1985). The presence and relative salinity of permanent water depends on

Table 5. The distribution of plant subcommunities, together with the numbers of plant species on the motus of Caroline Atoll. Motus are arranged according to increasing area, illustrating seral stages in plant succession.

Motu	Area Category / ha	Motu Area / ha	Number of Plant Species[1]: Trees	Shrubs	Herbs	Total	Natural – Coastal: Natural Herb Mat	Beach Scrub with Suriana	Pandanus Forest	Tournefortia Scrub <5 m tall	Natural – Inland: Tournefortia Forest >5 m tall	Cordia Forest	Tournefortia/Pisonia Forest	Pisonia Forest	Anthropogenic Plant Subcommunities: Cocos Plantation	Dying Cocos/Ipomoea Forest	Mixed Forest with Cocos
Noddy Rock	<0.2	0.02	0	1	2	3	X										
Skull Islet		0.02	0	1	2	3	X										
Motu Atibu		0.02	0	1	2	3	X										
Reef-flat Islet		0.09	0	1	2	3	X										
Azure Isle	0.2 - 0.7	0.20	1	1	5	7	X			X							
Motu Nautonga		0.34	3	1	5	9	X			X	X						
Scarlet Crab		0.46	0	1	5	6	X			X							
Fishball Islet		0.57	1	1	6	8	X			X							
Motu Kota		0.64	3	1	7	11	X			X	X						
Booby Islet	0.8 - 25.0	0.84	2	1	6	9	X			X	X		X	X			
Bo'sun Bird Islet		0.86	0	1	3	4	X			X							
North Arundel Islet		0.91	4	1	6	11	X			X	X		X	X			
Motu Mouakena		1.00	1	1	6	8	X			X	X		X				
Motu Eitei		1.41	3	1	5	9	X	X	X	X	X	X	X	X			
Coral Islet		1.70	2	1	6	9	X			X	X		X				
Motu Matawa		1.71	4	2	4	10	X			X	X	X	X	X			
North Brothers Islet		1.71	3	1	5	10	X			X	X		X	X			
Motu Kimoa		1.80	3	2	6	11	X	X		X	X	X	X	X			
Lone Palm Islet		1.99	3	1	7	11	X			X	X		X				
Motu Ana-Ana		2.16	5	2	8	15	X		X	X	X	X	X	X			
Pisonia Islet		2.45	5	2	8	15	X	X	X	X	X	X	X	X			
Blackfin Islet		2.62	3	1	5	9	X			X	X	X	X	X			
Danger Islet		2.71	2	1	7	10	X		X	X	X	X	X	X			
Crescent Islet		3.10	3	1	6	10	X			X	X	X	X	X			
Motu Raurau		3.48	5	1	4	10	X		X	X	X	X	X	X			
Bird Islet		4.05	4	2	6	12	X			X	X		X	X			
Brothers Islet		4.31	3	2	5	10	X			X	X		X	X			
North Pig Islet		5.44	3	1	7	11	X			X	X	X	X	X			
Pandanus Islet		7.20	3	1	6	10	X		X	X	X		X	X			
Pig Islet		7.25	4	1	6	11	X			X	X	X	X	X			
Arundel Islet		7.34	3	1	7	11	X			X	X		X	X			
Shark Islet		7.98	5	1	6	12	X		X	X	X	X	X	X			
Emerald Isle		8.34	5	1	6	12	X		X	X	X	X	X	X			
Tridacna Islet		9.08	2	2	9	13	X	X		X	X						
Windward Islet		11.42	3	1	7	11	X			X	X	X	X	X			
Motu Mannikiba		21.49	4	2	7	13	X			X	X		X	X			
Long Island	>25.0	75.98	4	2	9	15	X	X		X	X	X	X	X	X		
South Island		104.41	7	3	13	23	X	X	X	X	X		felled		X	X	
Nake Island		107.46	5	1	10	16	X		X	X	X	X	X	X	X		X

[1]Excludes transient and extinct species.

Table 6. Distribution and abundance of plant species in relation to motu size.[1] Species are arranged according to their dispersal mechanisms: sea, bird, wind, man (aboriginal and "recent"[2]). Within these categories, species are further subdivided in order of decreasing frequency on the motus.

	Size of Motu (ha)																						
	< 0.2		0.2 - 0.7					0.8 - 25.0												> 25.0		
	0.02 (3)*	0.09 (1)	0.2 (1)	0.3 (1)	0.4 (1)	0.5 (1)	0.6 (1)	0.8 (2)	0.9 (1)	1.0 (1)	1.1-2.0 (6)	2.1-3.0 (4)	3.1-4.0 (2)	4.1-5.0 (2)	5.1-6.0 (1)	7.0-8.0 (4)	8.1-9.0 (1)	9.1-10.0 (1)	11.0-12.0 (1)	21.0-22.0 (1)	75.0-76.0 (1)	104.0-105.0 (1)	107.0-108.0 (1)
INDIGENOUS SPECIES																							
SEA-DISPERSED																							
Tournefortia argentea	R-O		C	C	R	UC	C	VC-A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A
Heliotropium anomalum	R	R	C	C	R	UC	UC	UC	UC	R	O-C	R-C	UC	R-C	UC	UC-C	C	C	C	C	VC	C	C
Portulaca lutea	UC-A	R	R	R		R	O	O-C	C	R	O-A	R-UC	C	A	UC	UC-C	C	C	C	C	C	C	C
Laportea ruderalis			R	R	R	R	R	O	UC	R	R-VC	O-UC	UC	R-C	UC	UC-C	C	C	C	UC	VC	UC	C
Achyranthes canescens				R		R	R	R	UC	R	R-C	O		UC	C	O-LA	UC	LC	O	UC	O	R	LC
Lepturus repens	R-C					R	R	R	R	R	R	R		R	R	R-C	R	C	R	R	R	O	R
Cordia subcordata				R-O							O-C	UC-LA	LA	VC	UC	UC	O		C	O	UC	R	UC
Suriana maritima											RL	O		O							LR	LC	
Pandanus tectorius[3]												LR	LR			LR-LC	C					LO	LA
Ipomoea macrantha												LR-O				O			O		O	A	LC
Scaevola taccada																					R,S		
Morinda citrifolia[3]				R		O	R	R	R		R	R-UC	UC-O	R-O	R	R-UC	R	VC	UC	R	UC	C	UC
Hibiscus tiliaceus[3]																						LR	
Thespesia populnea[3]																						LR	
Sida fallax																							R
Lepidium bidentatum[4]												S					S						
Ximenia americana[4]																				R,S			LA
+Digitaria sp.[4]																						+LR	
BIRD-DISPERSED																							
Boerhavia repens			R	R		R	R	O	O		R-UC	O-UC	UC-C	UC-C	C	UC-C	C	C	C	C	LC	VC	C
Pisonia grandis			R	O			R	VC	VC		R-A	VC-A	A	A	A	VC-A	C	R	A	C	VC	R	A
Tribulus cistoides																					LR		
WIND-DISPERSED																							
Phymatosorus scolopendria							R		R		R	UC	UC		UC	R-UC		C		O	LA	LA	VC
Psilotum nudum																						LR	+LR
INTRODUCED SPECIES																							
MAN-DISPERSED																							
Aboriginal Introductions																							
Cocos nucifera				LR			LR				LR	LR-LC	LR	LR		LR	LR			LR	LA	A	LA
"Recent" Introductions																							
Tacca leontopetaloides																						LR	+LC
Phyllanthus amarus																						LC	

[1] List excludes transient and extinct members of the flora (Table 1).
[2] "Recent" covers the time period 1834 to an unknown date in the 20th century.
[3] Possibly also an aboriginal introduction.
[4] Dispersal method unknown.
* Number in parentheses refers to the number of motus in this area category.
\+ Not seen but possibly still present.

Ghyben-Herzberg lenses of varying thickness on different islets, and this in turn depends upon island dimensions (especially width), soil porosity, rainfall, tidal fluctuation, and other hydrological factors. Though groundwater supplies have been studied on many atolls (Wiens 1962, Maude 1953), each island group is so unique that it is unwise to extrapolate information from one to the other.

Caroline's 39 motus fall naturally into 4 size classes: motus with areas of: a) <0.2 ha, b) 0.2 to 0.7 ha, c) 0.8 to 25.0 ha, and d) >25.0 ha. These size groupings harbor all 5 of the seral stages identified on Enewetak Atoll (Lamberson 1987), tailored to reflect Caroline's particular geography, geology, and impoverished flora. Each stage may be the sole example of ecological succession on an islet or may occur as one of several stages. Typically the early stages cover the peripheral rubble and scrubby outer zones, while the later ones appear as a series of roughly concentric bands progressing inland.

Stage I — Early pioneers on sandbars, spits or small rubbly islets subject to storm damage and washover. Harsh conditions, intense sun, drying winds, salt spray. High salt concentration in the substrate. Lack of fresh water and nutrients. Plant genera present include *Heliotropium*, *Portulaca*, *Lepturus*, *Boerhavia*, and seedling or open *Tournefortia* scrub. No *Cocos*. This stage covers many small motus (Noddy Rock, Fishball) and former interislet channels (e.g. Long Island) or occurs peripherally on larger motus.

Stage II — Thick scrub of mixed genera, often impenetrable. Its protective barrier allows for the development of vegetation on the larger islets. Seabirds begin to contribute to the soil (guano, eggs, regurgitated fish, decaying nesting material). Plant genera include *Tournefortia*, *Suriana*, *Cordia*, and *Laportea*. If *Cocos* present, accompanied by coconut crabs. Very common around the periphery of most motus just inland of the natural herb mats or flanking sheltered shores adjacent to the lagoon (South, Kota).

Stage III — Trees larger, seabirds add further to soil fertility. Open grassland may develop in sunny clearings (Tridacna Islet). Added plant communities are *Cordia-Tournefortia*, *Tournefortia-Morinda*, and *Pisonia-Tournefortia* forests. Occurs in the next inner concentric zone of vegetation to Stage II on larger motus (Nake, Long) or, more commonly, the entire interior of smaller ones (Pandanus, Southern Leeward Islets).

Stage IV — *Pisonia* dominates the older mixed forest. *Morinda* and *Tournefortia* mature. Forests are more open. Undergrowth mostly a ground cover of *Laportea*, *Boerhavia*, *Lepturus* and *Portulaca*. Covers the main portion of larger islets. If *Cocos* and *Pandanus* present, forms a mixed forest with vines (southern Nake, Shark). Coconut crabs common. A widespread stage in the center of most motus (Central Leeward, Windward Islets).

Stage V *Pisonia* takes over. Other trees are confined to the forest edges. Always in the deep interior of the larger islets. Little or no ground cover. Abundant nesting Black Noddies (*Anous minutus*). A more restricted stage (Brothers, Raurau, central Nake, Pig).

Ecological Succession on Motus of Different Size Classes

To assist discussions of succession on Caroline's motus, see individual vegetation maps and graphs (Figs. 27-57) and photographs (Pls. 13-70). Figures 27-30 summarize the amounts of each islet's surface covered by each major plant community and provide the numbers and percentages of indigenous species for each islet.

1) Motus with Areas <0.2 ha Figs. 27, 31; Pl. 49; Tbs. 5, 6

Caroline has 4 motus in this category, 3 windward and one leeward, whose combined area totals 0.15 ha. There are also 3 incipient islets which, because of their temporary character, have not been counted in Caroline's overall total (Fig. 2, Pl. 15). With the exception of Noddy Rock, a jagged, upraised limestone plateau, all consist predominantly of coarse coral rubble (75-98% coverage). These tiny motus are the simplest ecosystems on the atoll, representing early Stage I in plant succession. The number of plant species per motu averages 3, all hardy, sea-dispersed and salt-tolerant pioneers (*Heliotropium*, *Portulaca*, *Lepturus*, *Tournefortia*). The sole plant community is a natural herb mat of varying thickness and extent. *Tournefortia*, though stunted and scattered, is not sufficiently common to form a separate scrub habitat. Indigenous vegetation covers 2 to 25% of the islet areas. Seabirds, especially Brown Noddies and Red-tailed Tropicbirds, may attempt to nest.

2) Motus with Areas 0.2 to 0.7 ha Figs. 28, 31; Tbs. 5, 6

There are 5 leeward motus in this category, whose combined areas total 2.21 ha. Their vegetative cover is more extensive and diverse than in size class a, with herb mats and *Tournefortia* scrub and forest, but open rubble is still abundant (30-55% cover). Plant succession corresponds to late Stage I and Stage II. The average number of species is 8.2 (range 6-11), one-third of Caroline's total. All vegetation is indigenous except for a few *Cocos* palms. Seeds are dispersed by sea, wind and birds.

With the appearance of shrubs, the number of species increases markedly, and woodlands, primarily of *Tournefortia*, form and expand to create dense thickets averaging 5 m tall and covering 25% of the land area. Canopies of 10 m occur on Motus Nautonga and Kota. Seabird colonies of up to 6 species (Brown and Red-footed Boobies, Great Frigatebirds, Black and Brown Noddies, White Terns) are present.

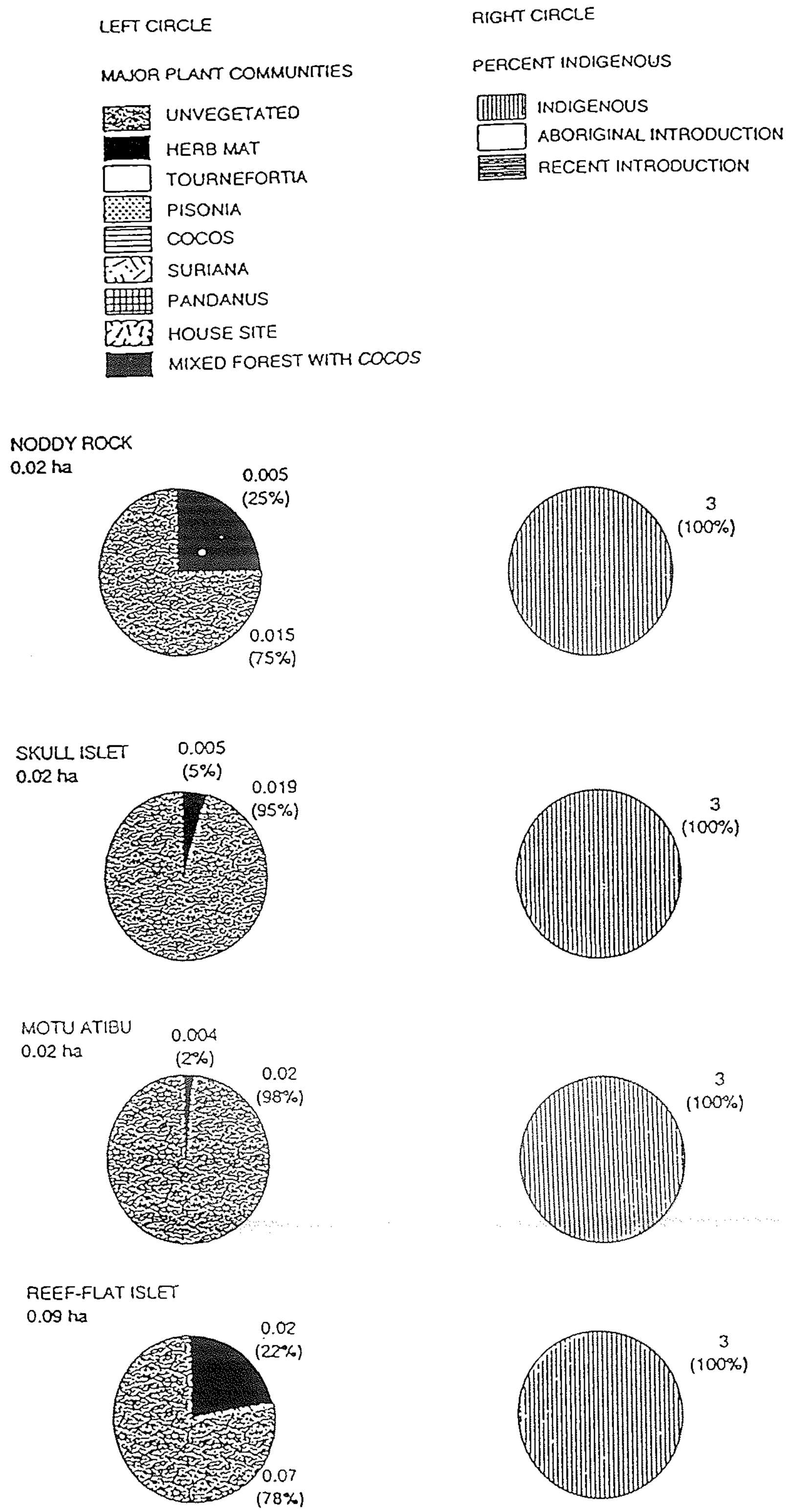

Fig. 27. Plant communities and amount of indigenous vegetation on motus less than 0.1 ha, Caroline Atoll. The left "pie" depicts the relative amount of a motu's total surface area covered by each plant community; numbers indicate actual area in hectares. The right "pie" depicts the numbers and percentages of indigenous and anthropogenic species per motu. Data is based on the vegetation maps for each motu (Figs. 37-57) and Tables 2 and 9.

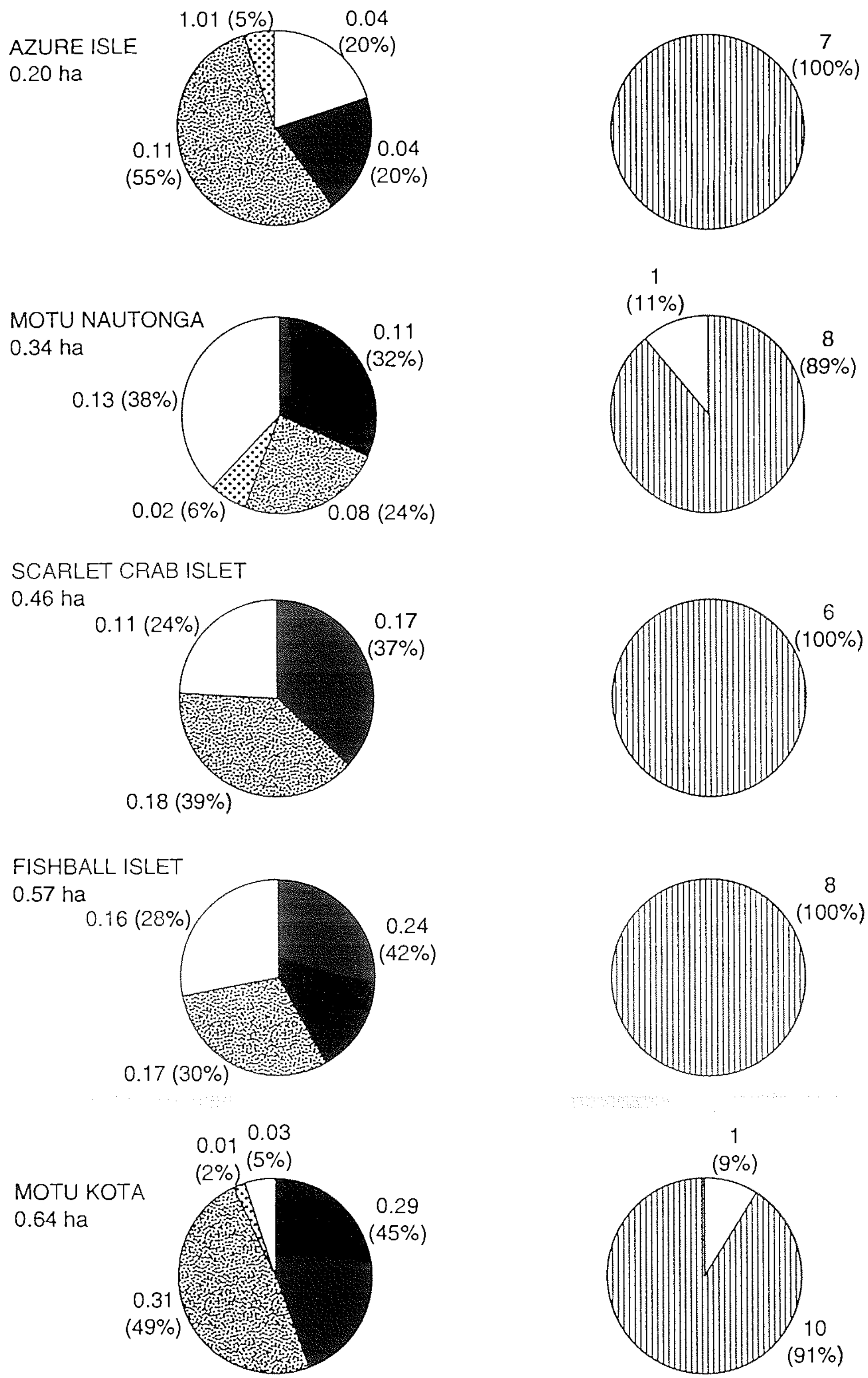

Fig. 28. Plant communities and amount of indigenous vegetation on motus 0.2 to 0.7 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

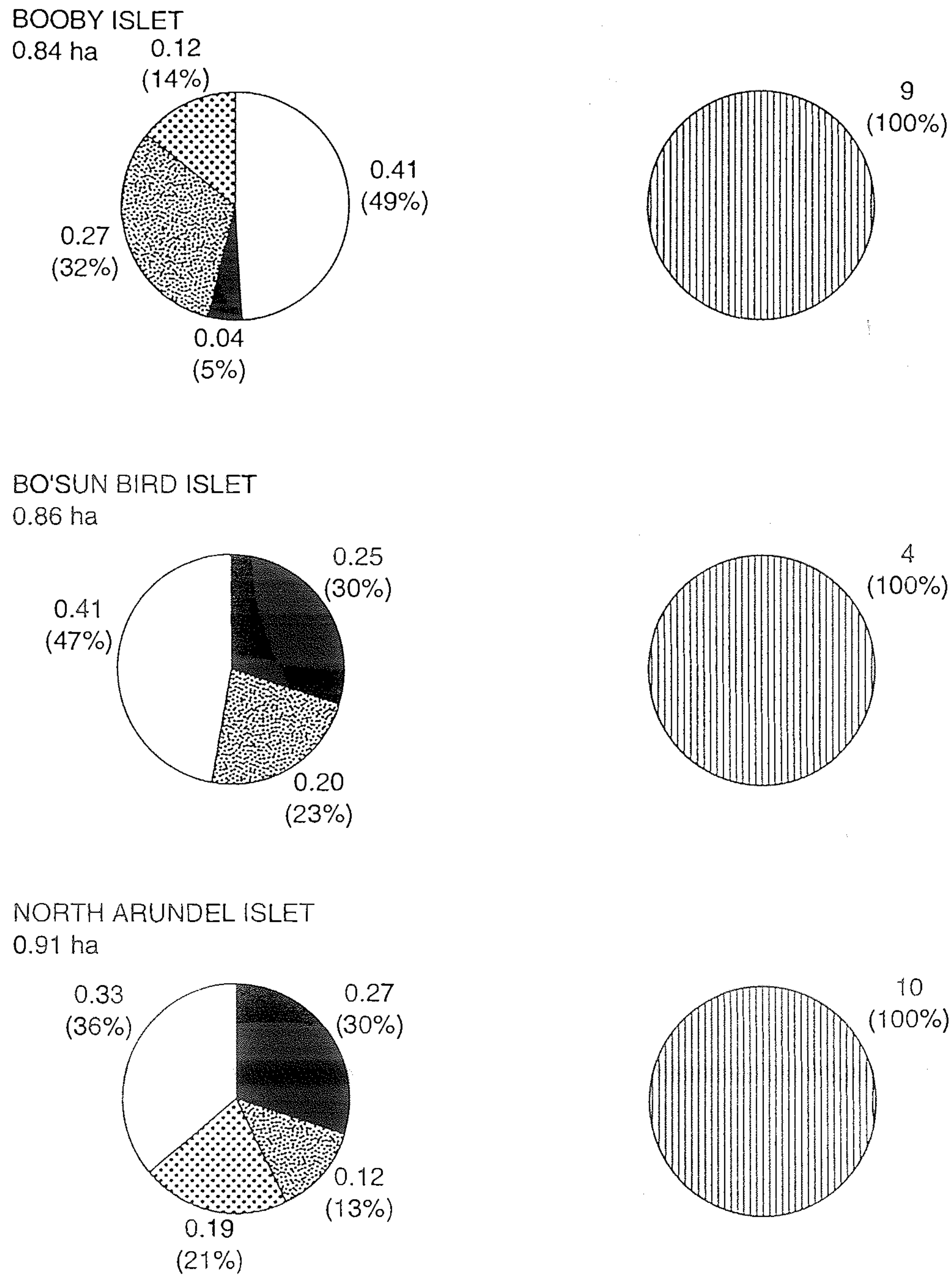

Fig. 29a. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

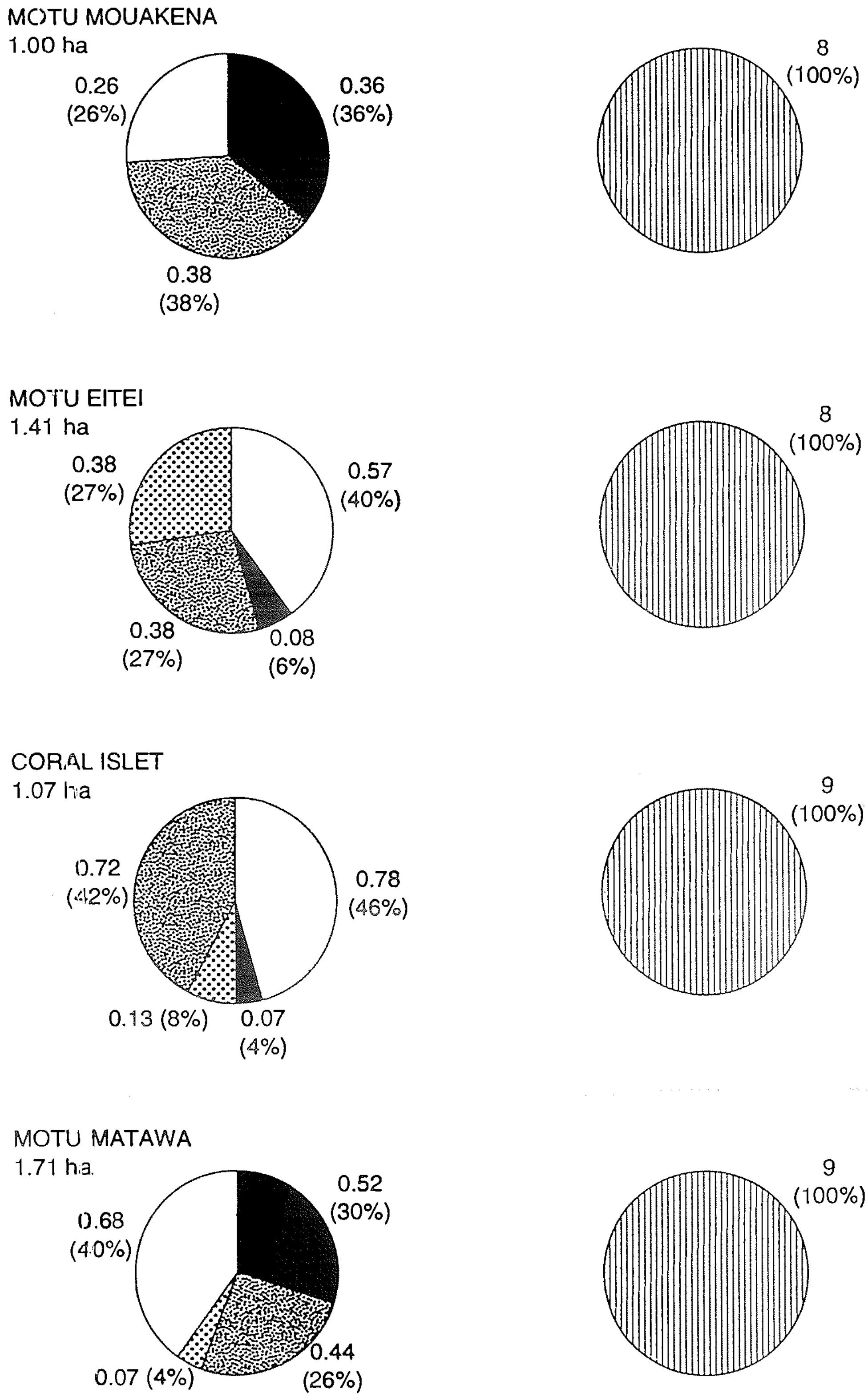

Fig. 29b. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

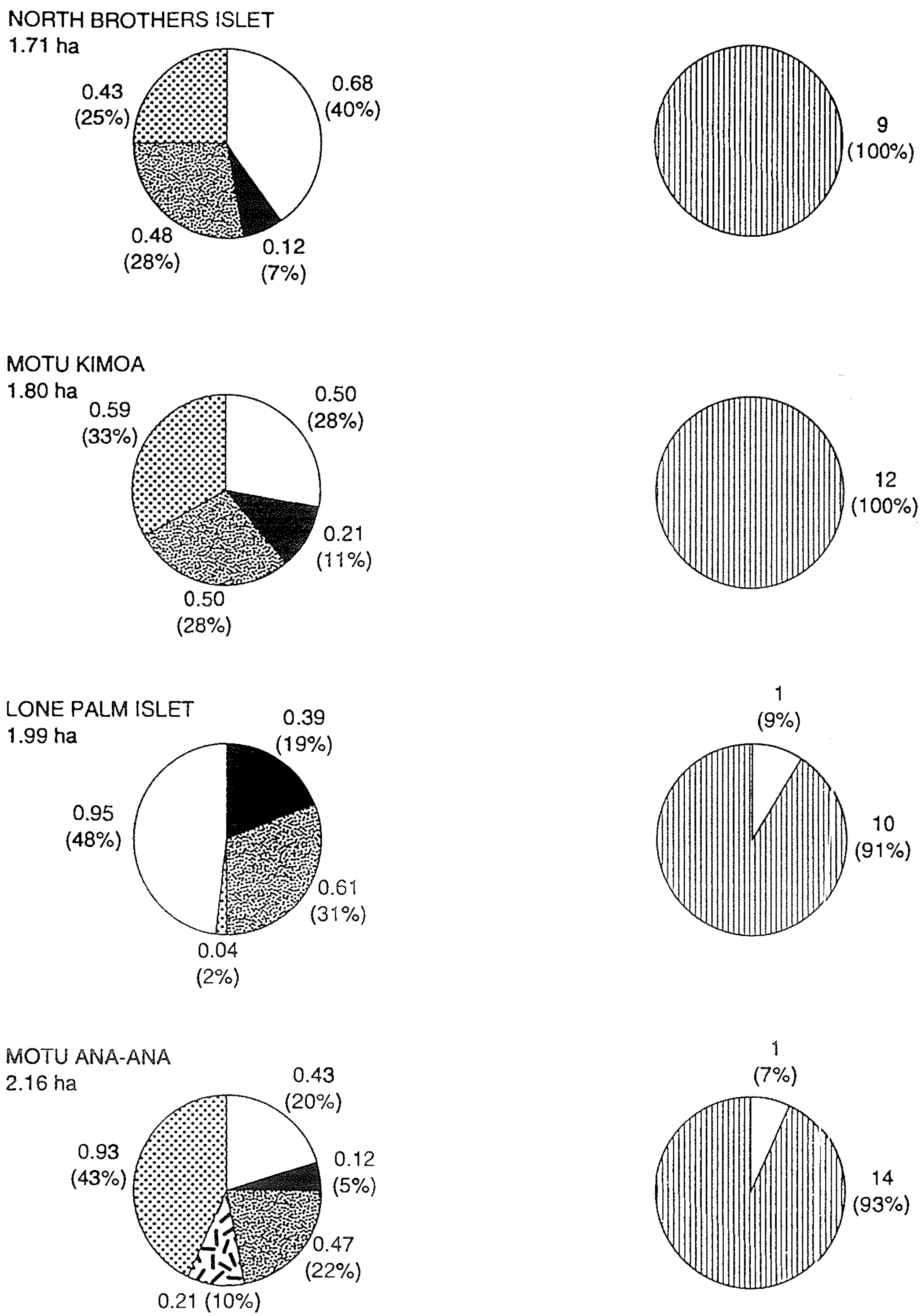

Fig. 29c. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

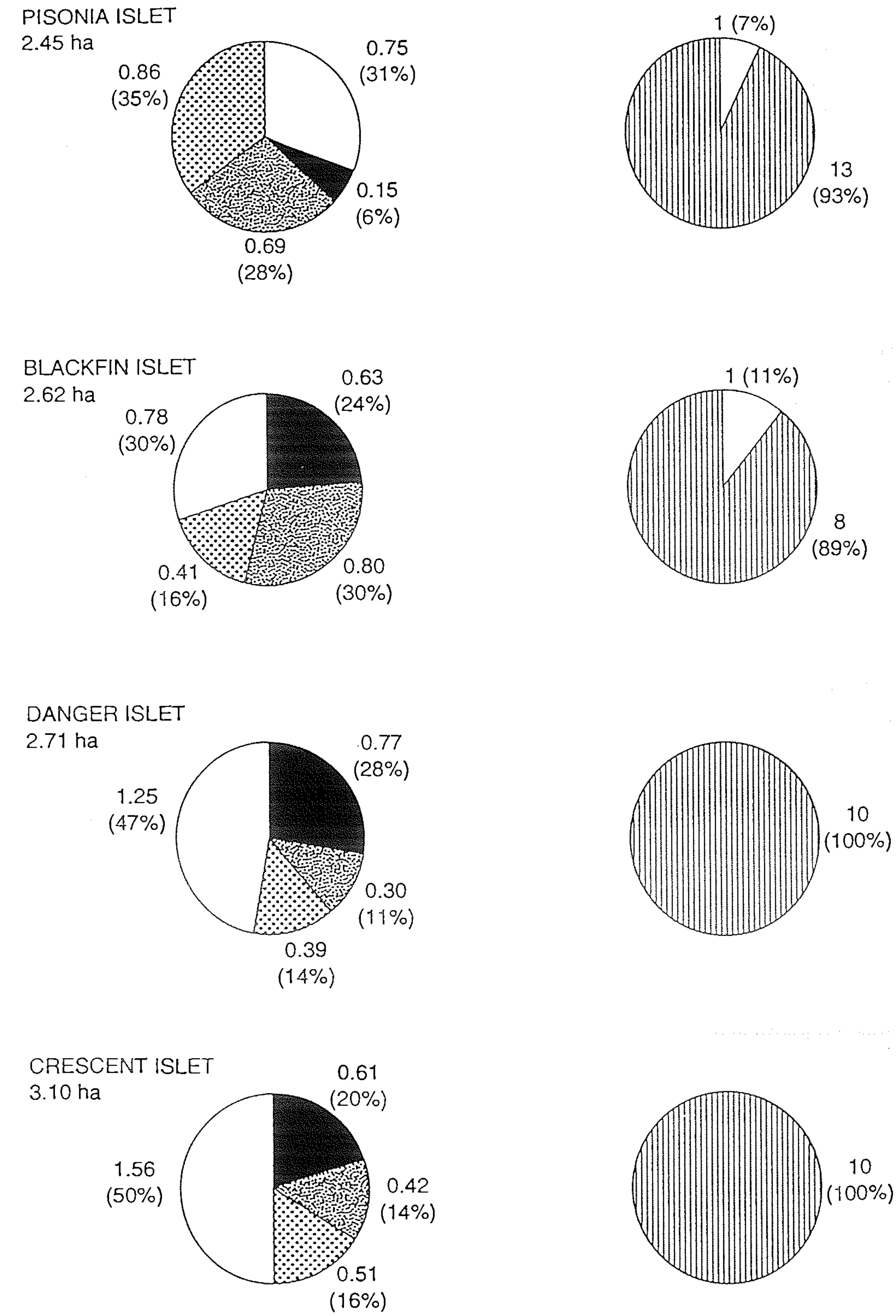

Fig. 29d. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

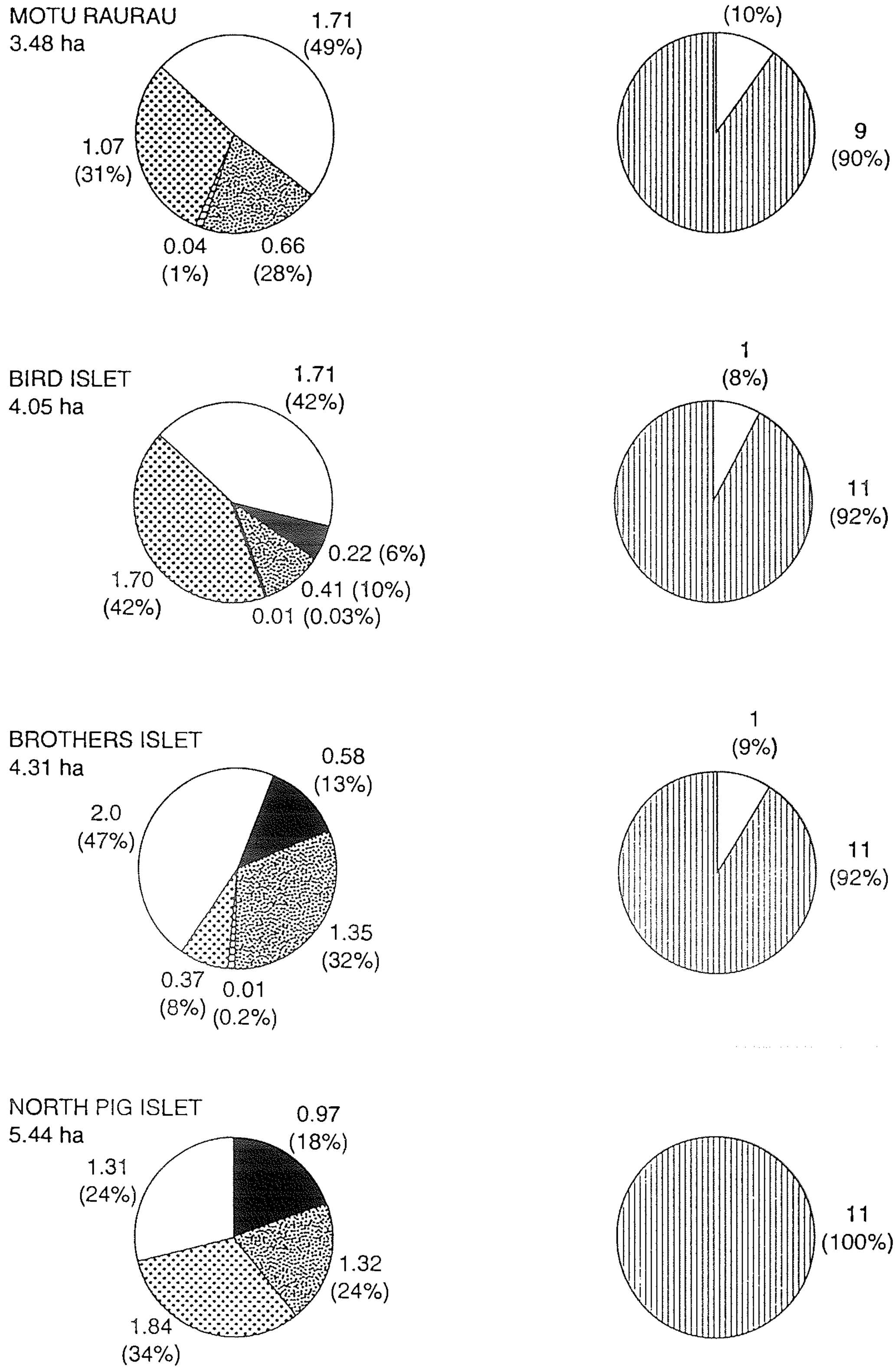

Fig. 29c. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

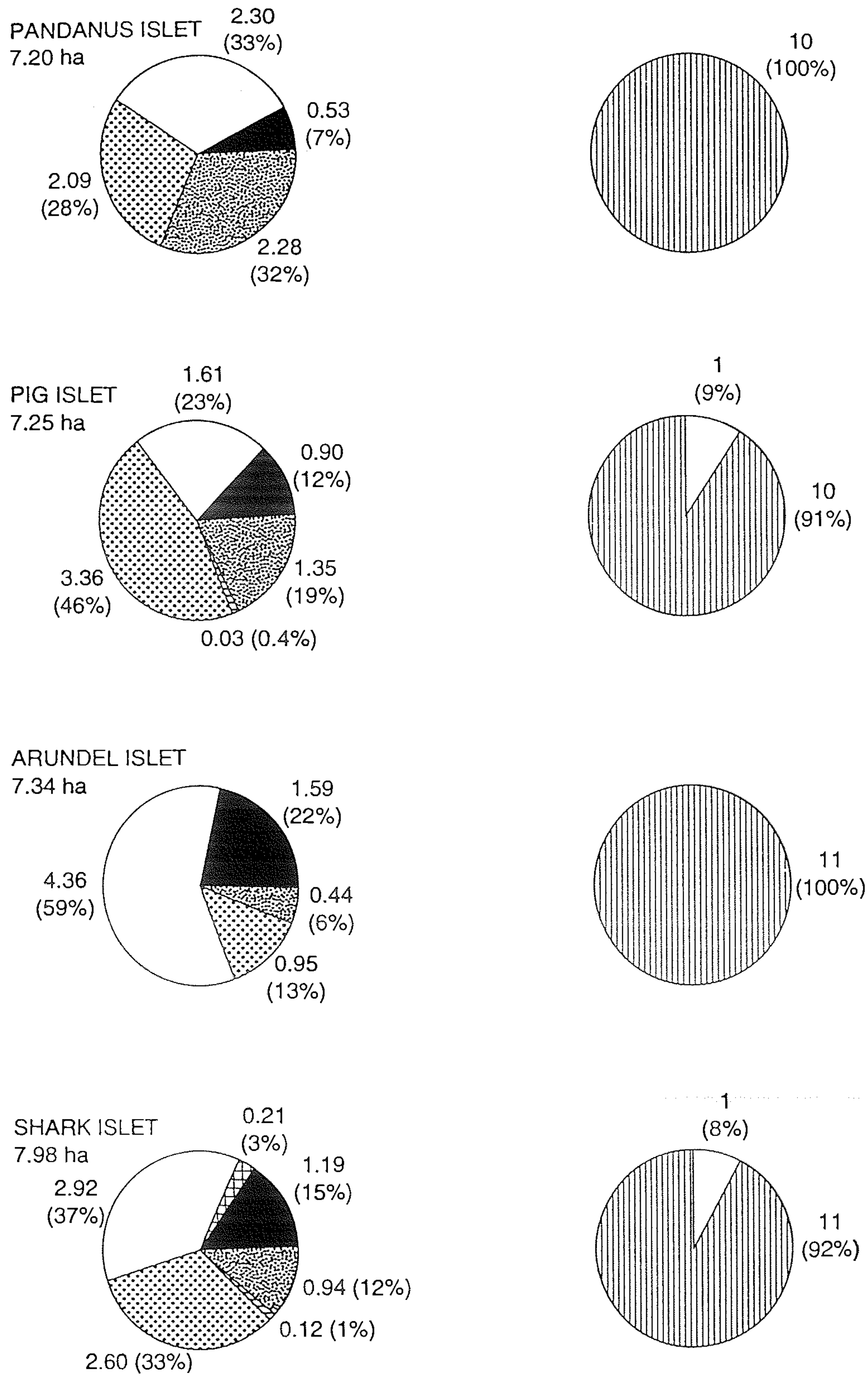

Fig. 29f. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

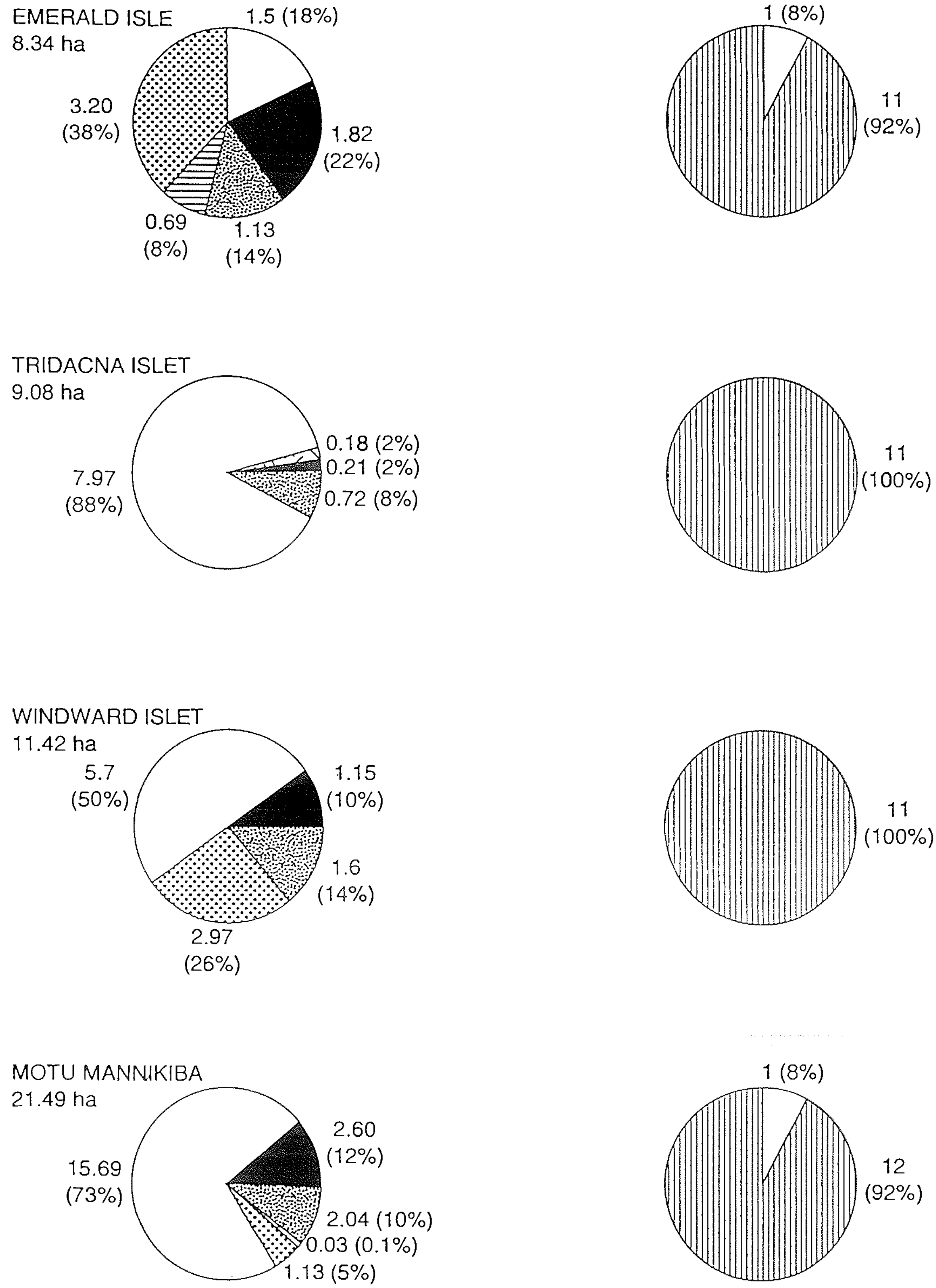

Fig. 29g. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

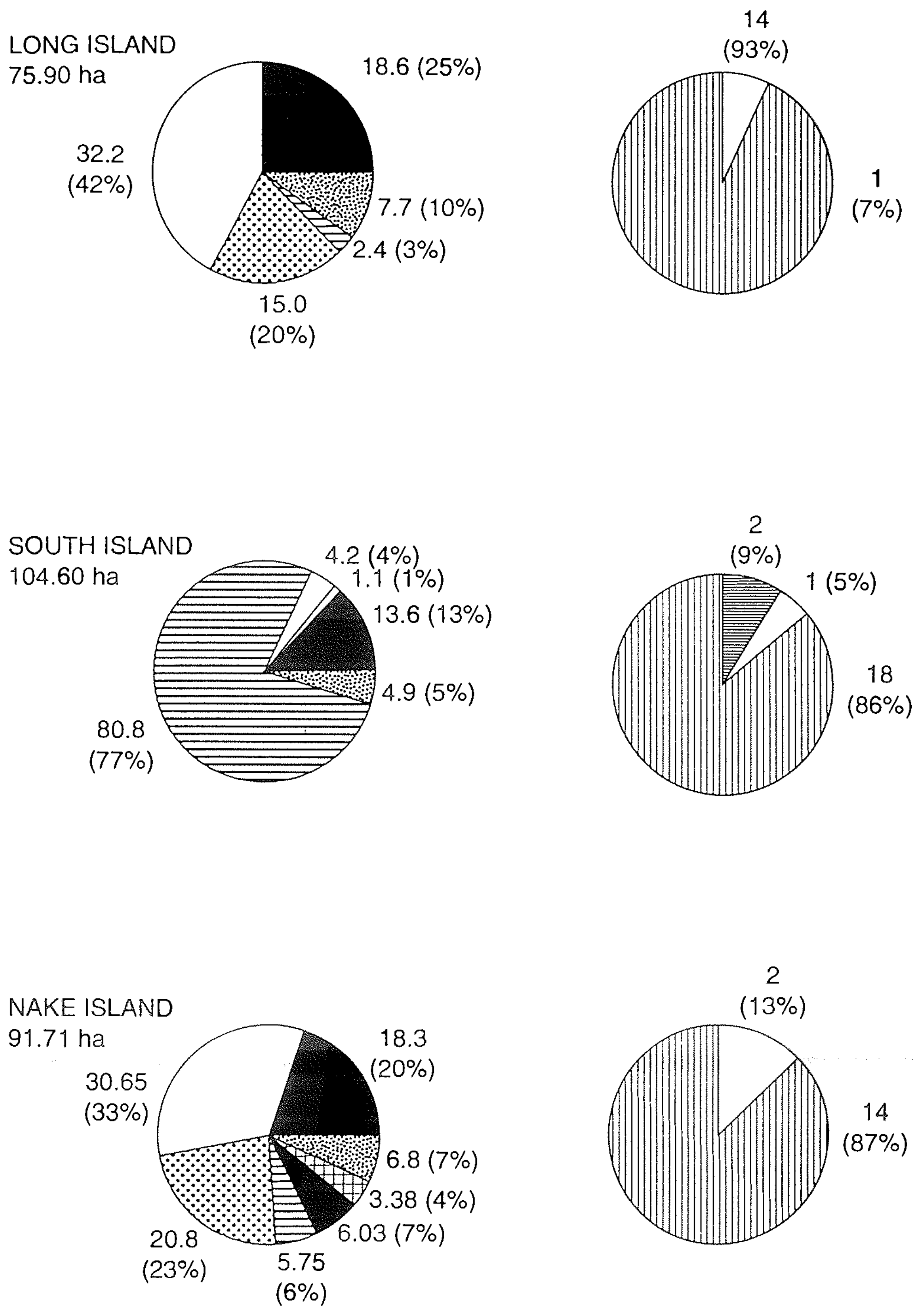

Fig. 30. Plant communities and amount of indigenous vegetation on motus over 25.0 ha. See Fig. 27 for explanation of the figure.

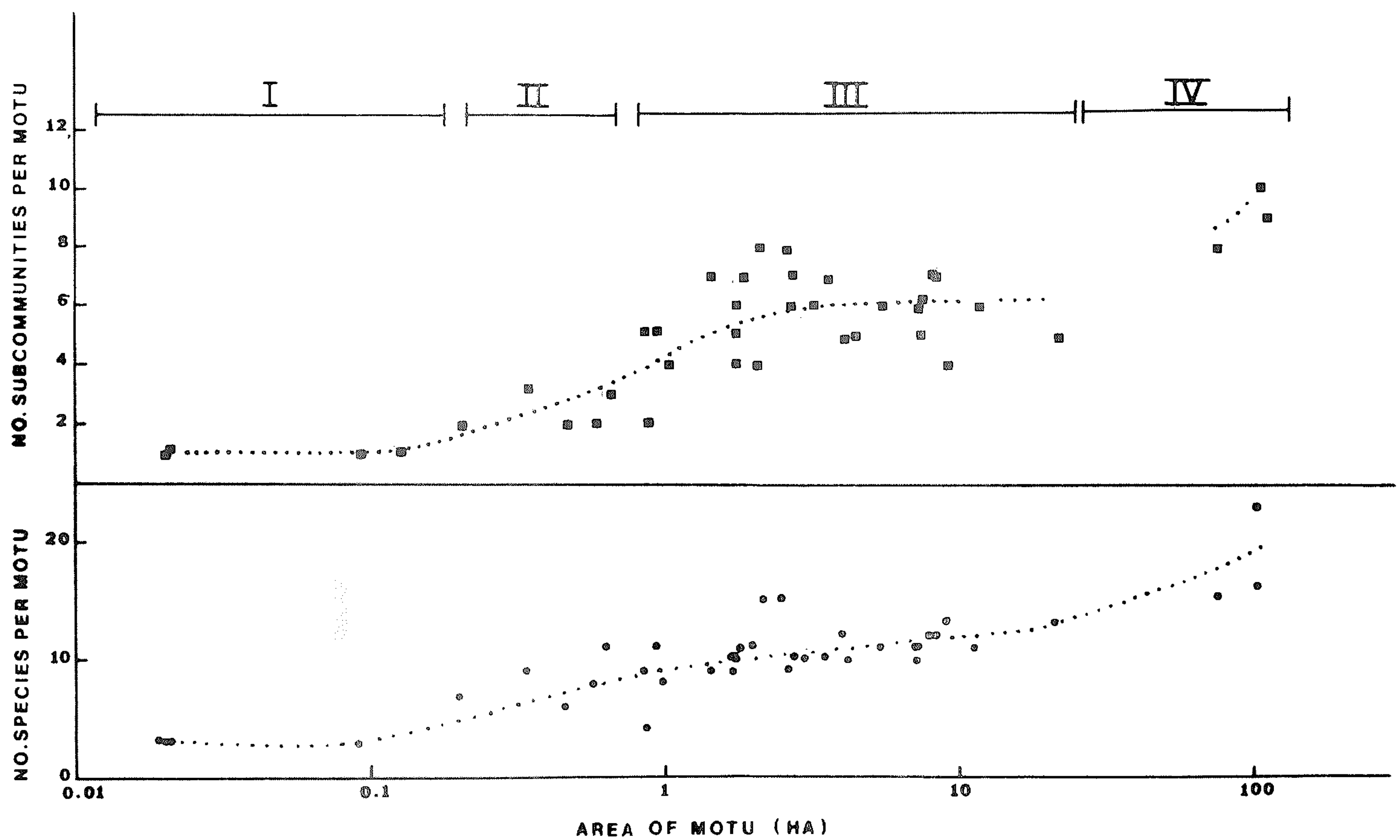

Figure 31. Total numbers of plant communities (upper graph) and species (lower graph) in relation to motu area, demonstrating plant succession on the different sized motus encircling Caroline's lagoon. Roman numerals refer to size classes of the motus: I = < 0.2 ha, II = 0.2 to 0.7 ha, III = 0.8 to 25.0 ha, IV = > 25.0 ha. The break between II and III marks a substantial increase in the diversity, area coverage, and height of the forest ecosystems. Data is based on Table 5.

A low herb mat, dominated by *Heliotropium, Portulaca, Boerhavia*, and, more rarely, *Lepturus*, develops first, after which *Tournefortia* quickly becomes established. Shade, producing locally humid conditions, and better "soils" derived from guano, decomposing leaves, and the activities of land crabs and rats, provides appropriate habitat for *Laportea* and occasional *Phymatosorus* and *Achyranthes*. The major tree species--*Pisonia, Morinda, Cordia*, and *Cocos*--subsequently appear, but are relatively rare. *Pisonia*, typically an inland species assumed to need underground water (Spicer & Newbery 1979, Wiens 1962), could well be salt tolerant as it occurs on motus as small as 0.2 ha (Tbs. 5, 6). In this size class *Pisonia* occupies only 2-6% of the total islet areas.

3) <u>Motus with Areas from 0.8 to 25.0 ha</u> Figs. 29, 31; Tbs. 5, 6

All 27 motus in this category share a similar complement of species and plant communities (Tbs. 5, 6). Their combined area totals 124.35 ha. They are well-wooded (Fig. 29), although the leeward motus have a higher proportion of rubble and herb mats, and forests are higher to windward. Unvegetated rubble covers less land area (21%) than in size classes a and b (87% and 39%, respectively). Within the woodlands of these motus, substrates mature from basic rubble to primitive "soils" with small, but significant, structural development. Their flora shows increasing diversity with size, and almost the full complement of seabirds may nest.

All natural ecosystems are firmly established; canopy heights range from 4 to 21 m. On small Booby Islet (0.84 ha), *Pisonia* is very common, and the *Pisonia* forests on North Brothers (1.71 ha) and Pig (7.25 ha), at 21 m, are the tallest on Caroline. As rich guano and dead foliage accumulate, a layer of phosphate-rich humus enables those species already present but poorly represented on the small motus (*Pisonia, Morinda, Boerhavia, Laportea, Achyranthes*) to increase in abundance and stature (Table 6). Additional species are *Suriana, Pandanus, Ipomoea, Lepidium*, and *Ximenia*.

Plant succession, ranging from Stage III to Stage V in the interior, primarily involves forest maturity rather than the addition of large numbers of species. On the larger islets, the number of plant species increases by relatively small increments, filling out the sub-canopy layers and, in the cases of *Cordia* and *Pandanus*, adding variety to the canopy.

The average number of plant species is 11.0, ranging from 4 to 15. If we divide the motus into smaller size classes, we find that their species numbers show a slight overall increase with increasing size: 8.0 species for areas 0.8-1.0 ha, 9.8 species for areas 1.1-2.0 ha, 11.5 species for areas 2.1-4.0 ha, 11.3 species for areas 4.1-10.0 ha, and 12.0 for areas 10.1-22 ha. An increase in herbs (range 3-9) is primarily responsible for these higher averages (Table 5).

Despite the large range of motu sizes in this category, plant communities are essentially natural (Table 5). Their overall species composition is 96% indigenous. Seventeen of the motus lack *Cocos*, the only introduced species in this area category, which is represented by small, isolated clumps or individual palms.

On the larger motus, and within the taller forests, more species of birds, especially Red-footed Boobies, Great Frigatebirds, White Terns, and Black Noddies, nest in increasingly large colonies, furnishing more minerals to the developing soils, especially where *Pisonia* covers large areas.

In summary, by the time a motu on Caroline has reached 0.8 ha in size, all the natural plant communities, most species of trees, shrubs and herbs, and most species of seabirds are present, assuming no major intervening disturbances (for example, hurricanes) have occurred. In Caroline's depauperate flora there are few species left to increase floral diversity on the larger islets, regardless of their size. This is very different from the inhabited atolls such as Kapingamarangi (see next section).

Although we do not know when true freshwater lenses develop, they may occur in motus of this size class. If we assume that *Pisonia* is not specially salt-tolerant, limited fresh water must be available on motus as small as 0.2 ha, and actual freshwater lenses may begin forming at ca. 0.7 ha, as indicated by the sudden proliferation of *Pisonia* forest (Tbs. 5, 6). However, the Falconers were unsuccessful in locating underground fresh water on Motu Ana-Ana (2.16 ha), which suggests that *Pisonia* may be somewhat salt-tolerant.

4) Motus with Areas >25.0 ha — Figs. 30, 31; Tbs. 5, 6

On Caroline no motus fall between 22 and 75 ha in size. Thus the 3 motus in this category (Nake, South, Long) cover a limited range: 75.98 to 107.50 ha. They average 18.0 plant species. The floral components and forest heights of these larger motus (Figs. 33, 34; Table 5) are essentially the same as for class c. There are no additional natural ecosystems (mangrove swamps, salt flats, grasslands, etc.) or understory layers. One additional plant community (3 subcommunities) exists, dominated by the introduced coconut palm. Ten species, all rare or uncommon, are present only on the larger motus (Table 3): *Scaevola*, *Tribulus*, *Hibiscus*, *Thespesia*, *Ximenia*, *Psilotum*, *Tacca* (introduced in 1834), *Phyllanthus*, *Sida*, and the dubious *Digitaria*. Four, possibly as many as 8, are indigenous. In 1965, one vine of the indigenous *Ipomoea pes-caprae* was also found, but 3 subsequent surveys failed to locate it.

Species-Area Relationships

The relationship between the numbers of plant species and island size has long attracted interest (Fosberg 1949, Wiens 1962, MacArthur & Wilson 1967, Whitehead & Jones 1969), yet data from uninhabited islands is scant. The studies from Kapingamarangi (Niering 1956, Wiens 1956) and Aitutaki (Stoddart & Gibbs 1975) treat atolls with long histories of human occupancy. Some of the villages on Kapingamarangi's 23 motus date to 1200 A.D. Aitutaki's 16 uninhabited motus lie adjacent to a westernized volcanic island in an "almost-atoll." People on both these atolls have profoundly influenced their flora.

Caroline provides an opportunity to compare the numbers of species on motus of different sizes in an uninhabited atoll, then to compare the results with Kapingamarangi, Aitutaki, and uninhabited islands in the Line and Phoenix Groups that have no introduced species and have experienced minimal human contact (Table 8). Comparison of Caroline with remote, uninhabited Oeno and Ducie Islands, also having entirely indigenous flora (Fosberg et al. 1989) would also be beneficial (T. Spencer, pers. comm.).

Comparisons of Species-Area Relationships with Other Atolls

Studies of Kapingamarangi (Niering 1956) contributed greatly to theories of island biogeography (MacArthur & Wilson 1967). Because its motus cover the same range of sizes as Caroline, the 2 atolls might be expected to exhibit similar patterns. However, their species-area relationships are completely different. On Kapingamarangi, islets less than 1.4 ha showed a constant, small number of species, after which islets up to 100 ha showed a direct correlation of area with numbers of species. On Caroline, a motu of 1.4 ha supports almost two-thirds of the total number of species, and plant diversity on islets up to 107 ha shows only a slight, but not necessarily steady, increase (Table 5).

Species-area relationships on the motus of Aitutaki (Stoddart & Gibbs 1975, Figs. 33 and 34 of that paper) conformed to the Caroline model: the number of species increased only slightly on motus from 4 to 71 ha. Unfortunately, Aitutaki had only one motu less than 1.4 ha, so comparisons for smaller islets cannot be made. The floras of all 3 atolls have been impacted by man, but Caroline far less so than the others. Much of the floral diversity on larger islets at Kapingamarangi is derived from plants introduced by man and cannot be considered natural.

Six islands in the Line and Phoenix Groups (Malden, Starbuck, McKean, Phoenix, Vostok, Birnie) are uninhabited, *with entirely native flora*. All are Caroline's "neighbors" in an oceanic sense, and all except Vostok are dry, receiving about 750 mm (30") of rain p.a. They are old, essentially filled-in atolls, containing hypersaline central lagoons or no lagoon at all. Although the largest island (Malden) has the greatest diversity, there is only a very small linear increase in plant species with increasing area (Table 7). Plant diversity is more a function of climate (hot and dry) and distance from source areas, than size, similar to the situation on Caroline.

The Question of Fresh Water

The Kapingamarangi data were analyzed with availability of fresh water in mind (Wiens 1962, Whitehead & Jones 1969). These authors

Table 7. Species-area relationships of six Pacific islands with entirely indigenous flora.

Island	Area	No. Species
Malden	39.3 sq km	9
Starbuck	16.2 sq km	6
McKean	57 ha	7
Phoenix	49 ha	6
Vostok	24 ha	3
Birnie	20 ha	4

Islands are arranged according to decreasing area. Data is from Garnett (1983), Fosberg and Sachet (n.d.), Clapp and Sibley (1971b), and pers. obs.

suggested that 1.4 ha is the threshhold at which a freshwater lens can develop. Below this size only halophytes can survive. They argue that as there are only a limited number of salt-tolerant species, the floral composition on islets below 1.4 ha is relatively constant. On larger islets, species numbers increase in direct proportion to land area, because permanent groundwater promotes the survival of an increasing variety of nonhalophytic plants.

The groundwater vs. plant model does not apply to depauperate Caroline for a number of reasons: first, the number of plant species is not constant on islets below 1.4 ha: in fact, species are added *faster* on motus from 0.02 to 1.4 ha than between any other size range.

Second, on Kapingamarangi, the number of species increased in direct relation to islet size from 1.4 ha to 100 ha. On Caroline, species numbers increased only slightly from 1.4 to 22 ha and exhibited another minor increase from 70 to 108 ha (see Fig. 31; Tbs. 5, 6; and Sect. F, Ecological Succession). Thus, Caroline's data do not support the area-diversity theory.

Third, Whitehead and Jones (1969) argue that the flora on "small" motus lacking a freshwater lens (i.e. <1.4 ha) consists *only* of salt-tolerant strand species. This is not true on Caroline (Table 6). In addition to harboring the usual strand species (*Tournefortia, Portulaca, Laportea, Heliotropium, Boerhavia, Lepturus*), Caroline's "small" motus also support inland species that are generally considered non-halophytic (*Pisonia, Morinda, Achyranthes, Cordia, Phymatosorus*). Either these latter 5 species are moderately salt tolerant, or on Caroline the minimum islet size with a freshwater lens is much less than 1.4 ha, or both.

Fourth, Whitehead and Jones (1969) postulate that the non-halophytic species are those that control overall species-area associations. This may be a good generalization for less remote islands, but does not hold up for atolls with depauperate floras (Table 6). For example, on Caroline the halophytic *Ipomoea macrantha, I. pes-caprae, Scaevola taccada, Sida fallax, Lepidium bidentatum, Hibiscus tiliaceus, Thespesia populnea*, and *Tribulus cistoides*, which theoretically should only occur as strand species on the smaller islets, occur *only* on larger islets.

Fifth, the authors do not mention bird-dispersal of seeds, which is probably a factor that needs to be taken into account on remote islands: at Caroline, *Pisonia* and *Boerhavia* occur on islets from 0.2 ha to 108 ha. In addition, the numbers and diversity of seabirds and migrant shorebirds are much greater on unoccupied islets/atolls than on inhabited ones, strongly affecting the distribution of certain plant species.

Sixth, Caroline does not have an assemblage of nonstrand plants that *only* occur on larger motus; the only naturally occurring, nonstrand plant is *Psilotum*.

Seventh, the greatest factor complicating our understanding of Kapingamarangi's natural evolutionary processes is the presence of numerous exotics: of its 98 vascular plants, only 38 (39%) are indigenous. Its exotics include numerous weedy herbs and food plants which occupy gardens, abandoned house sites, taro patches, and plantations (*Cocos, Pandanus, Artocarpus*). These man-made habitats are particularly prevalent on larger islands. Such an abundance of exotics, both in species and area covered, renders a discussion of natural processes on Kapingamarangi almost impossible. Relatively undisturbed habitats such as those on most of Caroline's motus, and on other uninhabited Pacific islands such as Ducie and Oeno, whose quota of indigenous plants exceeds 75%, provide far better data on species-area relationships.

Motu Size in Relation to the Distribution of Trees, Shrubs and Herbs

As one progresses from small to large islets (Table 5), the number of tree species rises from zero to 7, the number of shrubs from one to 4, and the number of herbs from 2 to 12. Caroline's trends are similar to those at Aitutaki (Stoddart & Gibbs 1975), where the numbers of trees and shrubs are relatively constant over a wide range of motu sizes (3.8-71 ha), while the number of herbs shows a slight increase. There are too many recent exotics on Kapingamarangi for comparisons to be valid. We believe that if Niering's data were reanalyzed, using *only* indigenous species, similar generalizations would be found, viz: most species on atolls establish rapidly on small motus, after which a few additions occur on motus of increasing size until the maximum number of potentially available species is reached. Cursory examination of Niering's Figure 31, detailing the breakdown of total species numbers into indigenous and non-indigenous components, bears out this hypothesis.

G. PLANT COMMUNITIES

General Account

The total area covered by vegetation on Caroline is 357.55 ha, 90% of the combined areas of all the motus. Of this, two-thirds (289.82 ha) is woodland. Substantial areas of Caroline's native woodlands and herb mats are relatively pristine, and 89% (possibly 92%) of its plant species are indigenous. Twenty-three (60%) of its 39 motus harbor wholly indigenous vegetation (Figs. 27-30). Atolls supporting substantial areas of native forest are typically remote and uninhabited. Where people are present, native vegetation is usually confined to the smallest motus or the extremities of larger ones--areas with marginal human usefulness.

Overall vegetation patterns strongly support the theory that the original vegetation of many atolls is arranged in concentric or parallel belts according to salinity and ground water gradients, drainage, and exposure to salt spray (Fosberg 1976). Because of its impoverished flora, Caroline has no mixed broadleaf forest *per se* but is rich in pure stands or simple combinations of 2 or 3 species (Figs. 17, 21, 23, 26-29). Monotypic stands of shrubs and trees are common on atolls, but unusual for the continental tropics, where species diversity is considerably larger.

The present vascular flora of Caroline, 26 species, is organized into 7 plant communities (11 subcommunities) defined principally by dominant species (Fosberg 1953, 1976), whose areas are given in Table 8. Eight subcommunities are natural, 3 are anthropogenic (Table 5). The subcommunities include a mix of dominant species, which are discussed in the major community sections below.

NATURAL COMMUNITIES:
Natural Herb Mat
Beach Scrub with *Suriana*
Pandanus Forest
Tournefortia Scrub and Forest
Cordia Forest
Pisonia Forest

ANTHROPOGENIC COMMUNITY:
Coconut Woodlands

Natural Herb Mat (67.73 ha)

Figs. 19, 23; Pls. 19, 32, 34, 45, 46, 47

Widespread and predictable on wind- and salt-blown coastal coral rubble and incipient motus, these mats are composed primarily of *Heliotropium* and *Portulaca*. They are pioneers on newly emergent motus, cover most of the ground area of small motus, extend inland along ancient reef channels, and typify newly evolving land which connects or augments established islets. Natural herb mats may persist through all

Table 8. Areas of plant communities on the islets of Caroline Atoll.

	Area (ha)	% of Total Land Area	Total Area (ha)	%
Unvegetated Habitats			41.39	10.37
Coral Rubble and Sand	41.39	10.37		
Natural Plant Communities			261.41	65.53
Natural Herb Mats	67.73	16.98		
Beach Scrub with *Suriana*	1.49	0.37		
Pandanus Forest[1]	3.38	0.85		
Tournefortia Scrub and Forest	25.25	31.40		
Cordia Forest[2]	1.39	0.35		
Pisonia Forest	62.17	15.58		
Anthropogenic Community			96.14	24.10
Coconut Woodlands	96.14	24.10		
Total Area Above High Water			398.94	

[1] Pure *Pandanus* only. Also mixed with *Pisonia*, *Tournefortia*, and *Cocos*.
[2] *Cordia*, where mixed with *Pisonia* and *Tournefortia*, is included in totals for those forest communities.

5 stages of plant succession as long as sunny openings occur. Caroline's motus illustrate 2 general principles: 1) the smaller the area the more extreme is the strand character of its vegetation, and its corollary, 2) as areas enlarge, strand flora becomes less important (Fosberg 1949).

The following species are present (see Table 2 for abundance indices):

Trees: *Morinda citrifolia* (1 drift seedling on 1 motu);

Shrubs: *Tournefortia argentea*, *Suriana maritima*, *Scaevola taccada*; and

Herbs: *Heliotropium anomalum*, *Portulaca lutea*, *Boerhavia repens*, *Lepturus repens*, *Laportea ruderalis*, *Lepidium bidentatum*, *Ipomoea macrantha*.

Near the high water mark, the herbs are recumbent, leathery, and somewhat desiccated. As environmental conditions improve further inland, they spread more laterally and average up to 7 cm tall. Their rubbly habitat, often sprinkled with *Tournefortia*, resembles a low savannah. Although these prostrate herbs can tolerate intense sunlight, they grow optimally in slight shade, sandy soils, and higher relative humidity, when they may reach 22 cm tall, forming a fairly thick mat (Pl. 45). With too much shade the mats disappear or their species proportions and abundance changes according to the presence or absence of sunny clearings. Thus, natural herb mats may be found in patchy clearings within forests up to 13 m tall. They are common in the abandoned *Cocos* plantations of South Island, where *Boerhavia* proliferates into thick mats which completely cover the substrate, vying with *Phymatosorus* and *Ipomoea* for "lebensraum" (Pl. 34). A thick, exposed mat of succulent herbs, primarily *Portulaca*, is found on Noddy Rock.

Herb mats occurred on almost every transect, windward and leeward, ranging from 1% to 60% coverage (Figs. 19, 23), predominating in sparsely vegetated areas. The most extensive areas (coverage 35-50%) were on Skull, Tridacna, interior South, Emerald, and Mannikiba. Their widths varied according to the age, shape, exposure, and geographic position of the motu but were widest on seaward-facing shores. Wide bands of herb mats may encircle an entire motu; to windward they average 36 m (Table 9), while, bordering the relatively placid and intermittently shaded lagoon, they shrink to a mere 0.9 m. On leeward motus, the corresponding figures are 18.5 m and 4.2 m.

Table 9. Widths of natural herb mats on seaward- and lagoon-facing shores, Caroline Atoll.

	Average Width of Herb Mat (m)	
	Seaward	Lagoonward
Leeward Motus	18.5 (3-81)	4.2 (0-28)
Windward Motus	36.0 (24-69)	0.9 (0-3)

Although reef flats widen where islets turn sharply, it is not unexpected that these perimeter bands are the most extensive on the extremely exposed shores of northern Nake (Pl. 16) and southern South Island. On the latter, they are up to 59 m wide. Similarly, on small exposed motus (e.g. Skull, Noddy Rock), they carpet most of the area (Fig. 27). Under such conditions, *Portulaca* and *Boerhavia* develop much redder stems, possibly due to the presence of a chemical "sunscreen" or introgression with *P. oleracea* (Fosberg, pers. comm.).

Seabird Use

Whether bordering the edges of established islands or composing the entire ground cover of tiny motus and ancient reef channels, herb mats are nesting sites for Red-tailed Tropicbirds, Masked and Brown Boobies, Sooty Terns, and Brown Noddies. They provide sites for the development of phosphatic hardpan (Sect. D, Substrata). Herb mats also provide foraging grounds for shorebirds.

Beach Scrub with *Suriana* (1.49 ha) — Fig. 20; Pls. 23, 39, 44

Uncommon on Caroline, Beach Scrub with *Suriana* is typically found on sand or sandy rubble bordering *Tournefortia* or *Cocos*. On Caroline, it is evidently limited by the paucity of low-lying sand and gravel sheets, with which it is normally associated elsewhere (Fosberg 1953, Wiens 1962, Stoddart & Gibbs 1975).

The following species are present (see Table 2 for abundance indices):

Shrubs: *Tournefortia argentea*, *Suriana maritima*; and

Herbs: *Heliotropium anomalum*, *Boerhavia repens*, *Portulaca lutea*, *Laportea ruderalis*, *Phymatosorus scolopendria*, *Lepturus repens*.

This plant community was found on 9 motus (Fig. 20), either in thick bands or as scattered shrubs. *Suriana* is most robust on sandy substrates, especially fringing the lower lagoon on South Island (Fig. 36; Pls. 23, 39) and on windward Tridacna. The fringe, repeatedly interrupted by other species, grows to 12 m wide and 1.8 m high. Here the shrubs are closely appressed and slightly entangled, forming dense shade which supports a sparse understory. On South, where its roots are submerged at high tide, it is being shaded out by overhanging *Cocos* (compare Pls. 39 and 40), having retreated since 1965. *Suriana* also occurs as scattered individuals or in open bands in coarse rubble. Beach strand up to 60 m wide, containing herb mats, *Tournefortia*, and scattered *Suriana*, were found on South (Tr. 1, Pl. 20), Long (Tr. C), Brothers, Matawa, Long, and the Southern Leeward Islets.

Pandanus Forest (3.38 ha[5]) — Fig. 11; Pls. 17, 35-38

Although several species of *Pandanus* are native to the Line Islands, and their seeds are common components of Pacific sea-drift (Ridley 1930, Stone 1968), it is possible that the groves of *P. tectorius* on Caroline represent both natural forests and cultivars transported by early Polynesians. However, we have no data to verify

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[5]This figure is pure *Pandanus* forest. Mixed forests containing *Pandanus* account for a further 14.96 ha.

this, except that its present and past distribution on Flint Island suggests that it is indigenous there (Kepler, in prep.). Its largest acreages are on 2 islands that contained historical settlements (Nake, South). However, its presence within the interior forests of a few motus lead us to conclude that it may have experienced a dual introduction. On Emerald, 3.20 ha (38% of the islet) supports a mixed forest of *Tournefortia*, *Pisonia*, and *Pandanus*. Similarly, Shark's interior woodlands of *Tournefortia*, *Pisonia*, and *Cordia* (5.52 ha, 70% of the islet's area) also contain a substantial amount of *Pandanus*, but there was possibly a hut on Shark last century. The occurrence of *Pandanus* groves or lone trees on other islets (Fig. 11) is easily attributable to drift seedlings. Dried *Pandanus* phalanges are the most conspicuous litter along Caroline's lagoon beaches (Pl. 38); its seeds last for months in seawater (Guppy 1906) and are probably distributed locally by rats and land crabs, as noted elsewhere (Ridley 1930). Phalanges from Nake's southern mixed woodlands undoubtedly established the grove on Pandanus Islet.

The mixed forest with *Pandanus* on south Nake (with *Cocos*, *Cordia*, *Pisonia*, and *Tournefortia*) contains up to 50% *Pandanus* attaining heights of 12 m (Fig. 37).

Many *Pandanus* trees were felled on South Island during the coconut planting era (ca. 1873-1925), as we know that they were "somewhat numerous" in 1834 (Bennett 1840), but only "one or more of the screw pines were found growing in various parts of the island" in 1883 (Trelease 1884). A drawing in this latter paper depicts a grove from South, where today *Pandanus* is uncommon in the beach scrub bordering the *Cocos* plantation.

Trees were fruiting abundantly in September 1988. The green phalanges, 17.5-20 cm in diameter, ripen to yellow and orange when they fall, to be eaten by hermit crabs, *Coenobita perlatus* (Pl. 38).

<u>*Tournefortia* Scrub and Forest</u> (125.25 ha) Figs. 24, 32; Pls. 7, 9, 19, 29, 47

General Distribution

Characteristic of many Pacific islands, *Tournefortia*, a broadleafed evergreen, dominates the wooded motus of Caroline, forming 40% of its vegetative cover and 31% of the total land area (Fig. 24, Table 8). Its pale foliage and hemispherical canopies (to 14 m tall) typically surround the taller, darker canopies of *Pisonia* and *Cordia*.

A hardy halophyte, *Tournefortia* occurs on every motu and in every habitat except pure *Pisonia* forest. It is tallest, widest and lushest on the windward motus, particularly on those where *Pisonia* is also best developed. Without direct sun though, as under dense *Pisonia* or *Cocos*, it withers (Pl. 23).

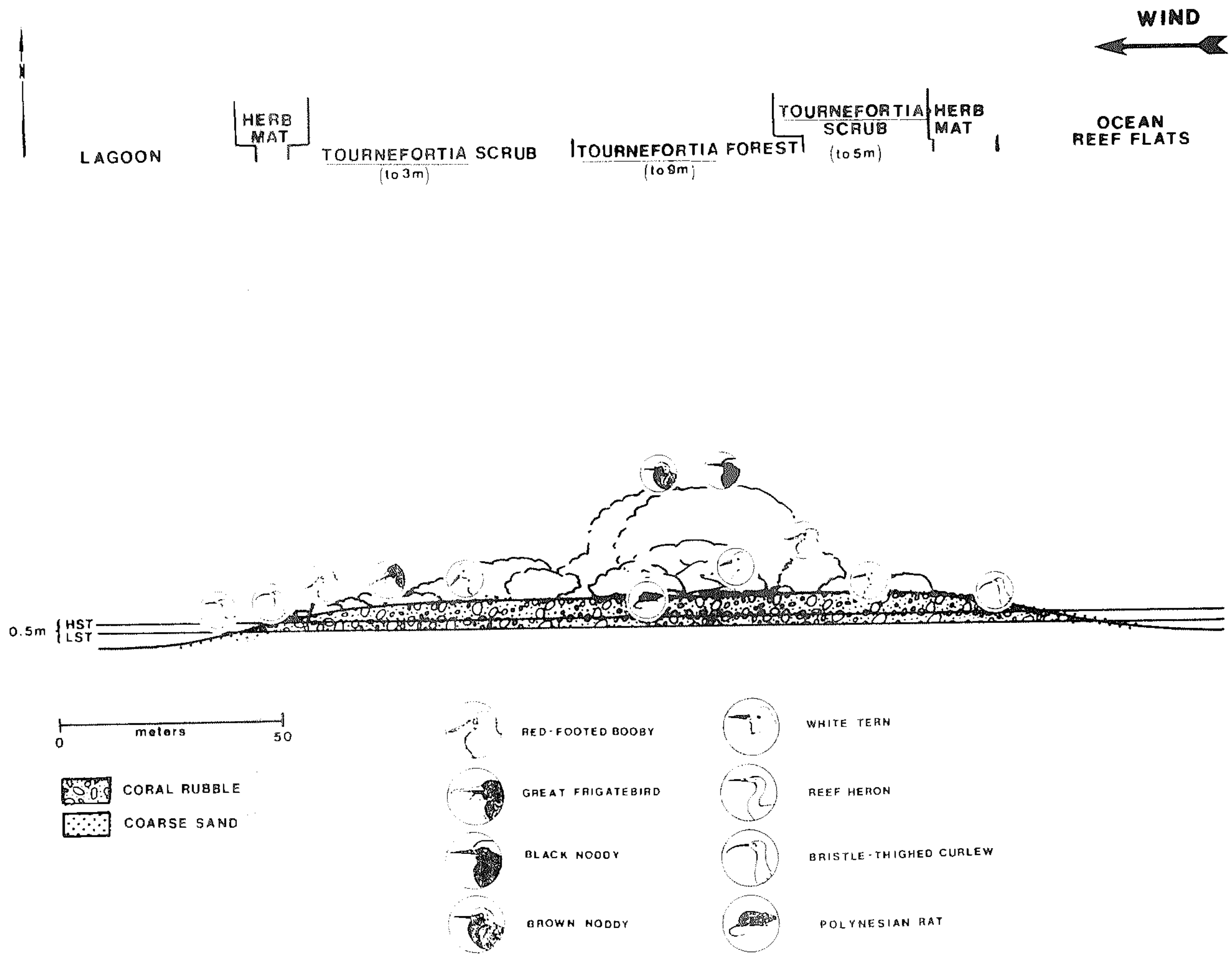

Figure 32. Schematic profile through Arundel Islet, recovering from disturbance over 60 years ago, showing natural herb mats, *Tournefortia* scrub and forest, and 5 species of breeding seabirds. Vertical height is exaggerated.

On other atolls *Tournefortia* forms a narrow or interrupted belt inland of the beach, or is a component of mixed scrub (Fosberg 1953). However, given the floristic poverty on Caroline, especially of shrubs and trees, *Tournefortia* not only has expanded into niches which might elsewhere be occupied by combinations of *Scaevola*, *Pemphis*, *Suriana*, *Terminalia*, *Hernandia*, *Thespesia*, *Hibiscus*, etc., but frequently occurs in pure stands (113.03 ha) that extend well inland. It thus occupies a much higher percentage of the islet areas on Caroline than on atolls with greater biodiversity. For example, Nake, the largest islet, has the greatest amount of *Tournefortia* (79.68 ha): 28.9 ha of pure scrub and forest, 18.28 ha of "savannah," 17.48 ha with *Cordia*, 8.99 ha with *Pisonia*, and 6.03 ha mixed with *Cocos*, *Pandanus*, and *Pisonia*.

Overall, we classify *Tournefortia* as a shrub (Stoddart & Gibbs 1975). However, following Mueller-Dombois et al. (1981, p. 58), we also distinguish between its shrub (scrub) and tree communities. Because they intergrade, we may lump them together (vegetation maps and schematic profiles of the motus), or treat them separately (Tbs. 2, 5, 10 and ecological discussions):

1) *Tournefortia* Scrub: ≤5 m high ($\bar{x}$ = 2 m), <60% canopy coverage (Pls. 19, 29, 32, 47). This open scrub growth is typically confined to islet perimeters or emergent reef channels and covers much of the vegetated rubble on smaller islets. Its species composition is similar to that of the taller forest, except that herbs are more prominent.

2) *Tournefortia* Forest: >5 m high ($\bar{x}$ = 8 m), >60% canopy coverage (Pl. 48). This taller, closed forest, with maximum height 15 m, develops as a second belt of woody vegetation approaching the interior of the larger islets. Figure 32 depicts a schematic profile through pure *Tournefortia* scrub and forest, while Figure 35 diagrams a profile of a larger islet where *Tournefortia* is represented only on its periphery.

Species Diversity in *Tournefortia* Woodlands

The following species occur in both scrub and forest. Those marked "*" occur primarily in the scrubland (Table 2).

Trees: *Pisonia grandis*, *Morinda citrifolia*, *Pandanus tectorius*, *Cocos nucifera*, *Cordia subcordata*;

Shrubs: *Suriana maritima*, *Tournefortia argentea*, *Scaevola taccada*, *Ximenia americana*; and

Herbs: **Heliotropium anomalum*, **Boerhavia repens*, **Portulaca lutea*, **Lepturus repens*, **Laportea ruderalis*, **Achyranthes canescens*, *Phymatosorus scolopendria*, *Ipomoea macrantha*.

Caroline's tallest *Tournefortia* stands (12-15 m) occur on Nake. On all other windward motus, the *Tournefortia* canopies vary between 6 and 9 m tall, shorter than expected if their forests were virgin. This has historical significance: we do not know the extent of forest felling (if any) on the Windward Islets (Crescent through Tridacna) during the guano era, but we do know that 4,587 coconut palms were planted during 1919-20, and that "misses" (dead seedlings) were fastidiously replaced over the following 2 years (Young ca. 1922). Thus, their forests, though weed-free today, comprise secondary growth around 60 years old. It is not surprising that *Achyranthes canescens* and *Lepturus repens*, both weedy (though indigenous), are particularly common inland on some windward motus (Figs. 13, 16). *Tournefortia*'s rapid recovery illustrates that ecosystems in the pioneer stage generally recover their original condition rapidly when left alone (Fosberg 1983).

Stature and Area Coverage

Forming an umbrella-like canopy, a typical *Tournefortia* forest is very simple. Its twisted branches and gnarled trunks stretch untidily over an open understory. The lower branches die off as the trees increase in stature. Sometimes a scant herbaceous cover develops in localized pockets of better soil, such as a clearing where a dead tree fell or a semishaded spot beneath a colony of seabirds.

Tournefortia is abundant throughout the atoll. Areas with 90%-100% canopy cover were found on Nake (Tr. 4), Long (Trs. B, C, 4, 6, 10, 12), North Pig, Pig, North Brothers, Brothers, Crescent, Arundel (Fig. 32), Tridacna (Trs. 1, 2), South (Trs. 1, 4), all 5 Southern Leeward Islets, all Central Leewards over 0.5 ha, and Pandanus Islet. *Tournefortia* is present across the entire width of some small motus, e.g. Fishball (144 m wide). Even on larger motus such as Mannikiba (280 m wide), *Tournefortia* blankets nearly all the land (Pl. 63). Long (75.98 ha) is a composite motu: long, narrow, and derived from the coalescence of at least 5 former islets. Because *Tournefortia* encircled the perimeters of these ancient islets, it is now present in 5 sets of concentric circles, connected by herb mats, down the length of the island (Fig. 39).

In the herb mats, *Tournefortia* is small ($\bar{x}$ = 1.4 m) and widely scattered (Table 10). It may be of typical hemispherical shape or irregularly windshorn (Pls. 13, 45). On windward coasts they typically form a tight wind barrier, one or 2 trees thick. Moving inshore from the seaward fringe, the trees become progressively taller ($\bar{x}$ = 6 m) with a more open understory. *Cordia* often mixes with *Tournefortia*, either as scattered individuals in the understory or canopy, or as small groves. On the Southern Leeward Islets such belts border the seaward scrublands.

Although still widespread in the Pacific, *Tournefortia* is far less abundant than formerly. On inhabited islands it exists primarily in relict patches or as edging around anthropogenic forests. It rarely covers most of the land area of islets; exceptions are Taongi and Bikini (Marshall Islands), Gaferut (Caroline Islands), and Ducie Atoll (Pitcairn Islands) (Fosberg 1956, Wiens 1962). The finest quality

Table 10. Stature and percentage cover of Tournefortia in the major habitats of Caroline Atoll.

	Av. Hgt. (m)	Av. Width (m)	% Tournefortia Cover	No. Motus	No. Transects
Natural Herb Mat	1.4 (0.3 - 1.8)	49 (3 - 198)	25 (5 - 95)	14	20
Tournefortia Scrub & Forest	6 (0.3 - 15)	55 (2 - 287)	81 (5 - 100)	38	71
Tournefortia-Pisonia Forest	9.5 (5 - 15)	98 (8 - 284)	47 (5 - 90)	18	27

Tournefortia on Caroline (15 m tall, 80% cover) occupy central and northern Nake (Fig. 37), but even this islet was completely felled for *Cocos* (Table 13). These 15-m *Tournefortia* compare favorably with 18 m specimens found at Jemo Island by Fosberg (1956). Perhaps Jemo's trees are at the upper size limit for the species, as *Tournefortia* is generally recorded as 3 to 6 m tall (Wiens 1962).

Ecology

Tournefortia is an integral part of the atoll's evolution and ecology. Bearing seeds capable of floating for at least 4 months in the sea (Guppy 1906), it is the first woody plant to establish on Caroline's tiny motus (<0.1 ha), appearing immediately after the native herbs have begun to germinate in the coarse coral rubble. It is the only plant species on tiny Ducie Atoll (Fosberg et al., 1989). Requiring little or no soil and adequate rainfall, it can grow up to 2 m a year (Fosberg 1959). *Tournefortia*'s leaves contribute to soil development, paving the way for plant succession from Stages I through IV, for it only persists in soils that are conducive to the growth of its mesophytic competitors (Fosberg 1953). The most mature trees ($\bar{x}$ = 9.5 m) occur at the *Tournefortia-Pisonia* interface, but die off as *Pisonia* expands. When *Tournefortia* has reached its maximum height, most of its lower branches have fallen, leafage is reduced, and flowers and fruits are few. *Tournefortia* usually drops out after one generation. Seedlings are rarely seen in heavy shade, and fallen trees are fairly common on the edge of the interior forests where *Pisonia* replaces it.

An example of complete replacement of *Tournefortia* by *Pisonia* is illustrated by nearby Vostok. It has heretofore been assumed that Vostok's sole tree species was *Pisonia grandis* (Fosberg 1936, Bryan

1942, Clapp & Sibley 1971b, Garnett 1983). However, Young (ca. 1922) stated that when Capt. J. Larsen, of the schooner *Papeete*, planted 100 coconuts there on 31 May 1922, he found "*Pukatea* and *Tauhinu* trees, etc. 60 to 80 feet high," that is, *Pisonia grandis* and *Tournefortia argentea*, but no "Tou" trees (*Cordia subcordata*). By 1935 only *Pisonia* remained (Fosberg 1936); hence, the last *Tournefortia* must have been eliminated naturally by *Pisonia*.

Along some coasts (Long, Nake, South), *Tournefortia* overhangs the water, its roots immersed at high tide. We found floated debris up to 20 m inland within dense *Tournefortia* forest, indicating that this hardy shrub can withstand periodic storms and high tides. If a rosette of *Tournefortia* leaves is placed in fresh water, it droops within an hour, indicating that its tissues require a high salt concentration in order to maintain turgidity (pers. obs.). Perhaps decreased salinity in the ground water, coupled with reduced light intensity in advanced seral stages, contribute to the eventual disappearance of *Tournefortia* in the center of coral islands.

Seabird Use

Tournefortia is a favored roosting and breeding site for most of Caroline's seabirds. The taller the trees, the greater the bird diversity they harbor: scrub contained 4 species (36%) and forest, 9 (82%). Sooty Terns nest in tight colonies in its shade, its canopies support large populations of Red-footed Boobies and Great Frigatebirds (Pt. II), and its branches are favored by White Terns (Figs. 32, 35, 36). *Tournefortia* leaves provide nesting material for noddies.

Cordia Forest (1.39 ha) — Fig. 22, Pl. 26

General Distribution

Cordia does not form "the main native woodland" on Caroline Atoll, as implied by Clapp & Sibley (1971a) and stated by Stoddart & Gibbs (1975, p. 104). It occupies far less area than *Tournefortia* or *Pisonia* (Table 9). *Cordia* is generally mixed with other emergents: monotypic *Cordia* forest covers only 1.39 ha, while *Tournefortia* or *Pisonia* containing substantial amounts of *Cordia* total 25.89 ha. *En toto*, this is less than 10% of Caroline's woodlands, and *Cordia* is usually subdominant. These "mixed" forests of *Cordia* mixed with *Pisonia* or *Tournefortia* (rarely all 3), occasionally with a *Morinda* understory, are the closest equivalent to Mixed Broadleaf Forests of other coral islands. This widespread Pacific plant community (Fosberg 1953, 1976; Wiens 1962) is conspicuous by its absence on Caroline. We treat *Cordia* forest as a separate plant community because of its increasing rarity on Pacific atolls, which makes Caroline's groves an increasingly important resource in need of conservation. *Cordia* forest occurs primarily on Nake, Windward, Crescent, North Pig, Pig, Danger, Shark, and the Southern Leeward Islets.

History

Bennett (1840) recorded "two species of *Tournefortia*" on Caroline, possibly referring to *Tournefortia* and *Cordia*. There are no other 19th-century records. From *Cordia*'s present distribution we can infer that it was formerly more extensive on South and Nake. Scattered trees within and bordering the *Cocos* plantations suggest that its history is similar to the species on Flint, which was "in 1872...covered with a forest of 'Tou' trees *Cordia subcordata*)" (Maude ca. 1942). Both Flint and Caroline were worked simultaneously by the same companies for guano (1872-1890) and copra (into the 1930s). *Pisonia* and *Cordia* forests were felled to make room for coconuts. From Flint, several hundred *Cordia* logs were exported to San Francisco for furniture and panelling. The last logs were exported in 1896, 6 years after the guano supplies were depleted, but coconuts were still being planted (Young ca. 1922), and some large *Cordia* trees were still present in the southern 20% of the island still covered with virgin forest (E. Campbell 1908, Kepler, in prep.). Today, Flint's recovering forests contain much *Cordia* (A. Kepler 1990b), unlike Caroline, where *Cordia* is rare in similar habitats. Some of Flint's present windward *Cordia* trees may be those "few tiny, struggling...trees...recently planted" (St. John & Fosberg 1937).

Abundance and Distribution

Cordia seeds are dispersed by ocean currents and can germinate after 40 days in sea water (Guppy 1906). On Caroline this species develops both as an understory shrub and forest emergent (to 15 m high). It typically occupies the woodland periphery, occurring in small circular or linear groves, or mixing with *Tournefortia* and/or *Pisonia* (Table 5). *Cordia* may form tall, straight-trunked trees (Pl. 26) or sprawl like *Hibiscus tiliaceus*. In dry rubble sites it may become chlorotic or semideciduous. The tallest groves are on Pig (Pl. 26), where 6 trees averaged 12.6 m tall, 116 cm circumference at 1.5 m (cbh), and 99.8 cm base circumference. Lush *Cordia* groves occur in sheltered parts of the upper lagoon on Long Island (Tr. 10).

Flowering times are unpredictable. Two flowers were seen in September 1988. In November 1989, flowers were abundant, extending through March, yet in November 1990 not one flower was observed (pers. obs., Anne Falconer and AKK).

Seabird Use

Black and Brown Noddies, frigatebirds, and White Terns nest in *Cordia* wherever it is a forest component. Great Frigatebirds and Red-footed Boobies favor roosting in the lush, lagoonside forest of *Cordia* and *Pisonia* near the south end of Long Island.

Pisonia **Forest** (62.17 ha)

Figs. 18, 33, 34, 35, 39, 41; Pls. 43, 50, 51; Tbs. 11-14

General Distribution

Although *Pisonia grandis* was previously recorded as "present" (Trelease 1884, Clapp & Sibley 1971a), the quality and extent of its forests has not been recognized. Some stands are prime representatives of a major ecosystem that was formerly far more widespread in the Pacific.

Common throughout the atoll, *Pisonia* occurs on 29 motus, covering 22% of the woodlands. Well developed groves, 10-21 m tall and up to 359 cm circumference at 1.5 m, are present on 23 of these (Table 11). Although present on motus less than one hectare in size (Table 5), it typically occupies interior forests (schematic profile, Fig. 35), with individual trees or groves contributing from 5% to 100% of the canopy. In general, Caroline's windward motus support the lushest forests: the maximum height of windward *Pisonia* forests is 21 m, of leeward forests, 15 m.

Mature *Pisonia* forests are monocultures of grandeur. The trees bear one to several stout boles of irregular shape, whose rotting cavities often harbor large coconut crabs or miniponds alive with mosquito larvae. Their scraggly branches occasionally bend over and reroot. It is dark and humid, but open except for exposed roots and scattered broken branches. Few seedlings occur. Polynesian rats scurry underfoot.

In September 1988 we saw no flowers or fruit. Anne Falconer reported flowers on Motu Ana-Ana in August 1990. *Pisonia* was beginning to bloom on Vostok in March 1990 (A. Kepler, in prep.).

An Historical Perspective

Some of Caroline's most mature *Pisonia* groves (to 21 m tall, 660 cm circumference at 1.5 m, multiple trunks) appear to be virgin, (Pl. 43) but are most likely only 60-70 years old. Overall dimensions of the trees, the low species diversity, and general character of the plant community compare favorably to virgin groves on Vostok (Table 12; A. Kepler 1990c, d).

Despite the maturity of many groves, especially those to windward, planting records from 1916-22 indicate that *Cocos* was planted throughout not only South, but also on Nake, Long, and all the major Windward Islets (Young ca. 1922). Given the standard planting density of 73 m^2/palm (Young ca. 1922), we calculated the approximate area on each islet given over to *Cocos* plantations, based on the number of coconuts planted times the area required for each tree. We then compared this to the usable areas based on today's forest cover (Table 13). On the 9 Windward Islets, collectively, 36.36 ha were planted in *Cocos*, fully 92%

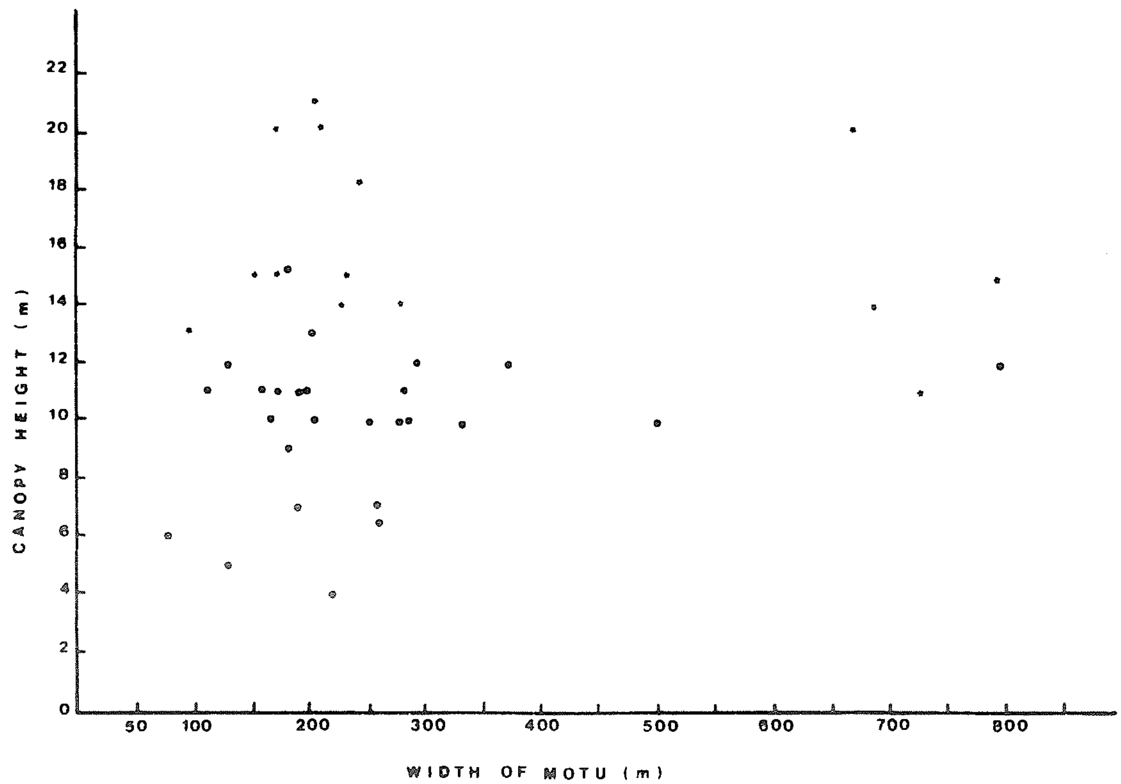

Figure 33. Maximum heights of *Pisonia* forests in relation to width of the motus. Stars represent forests with 90-100% canopy cover; dots represent forest or scrub with less than 90% cover.

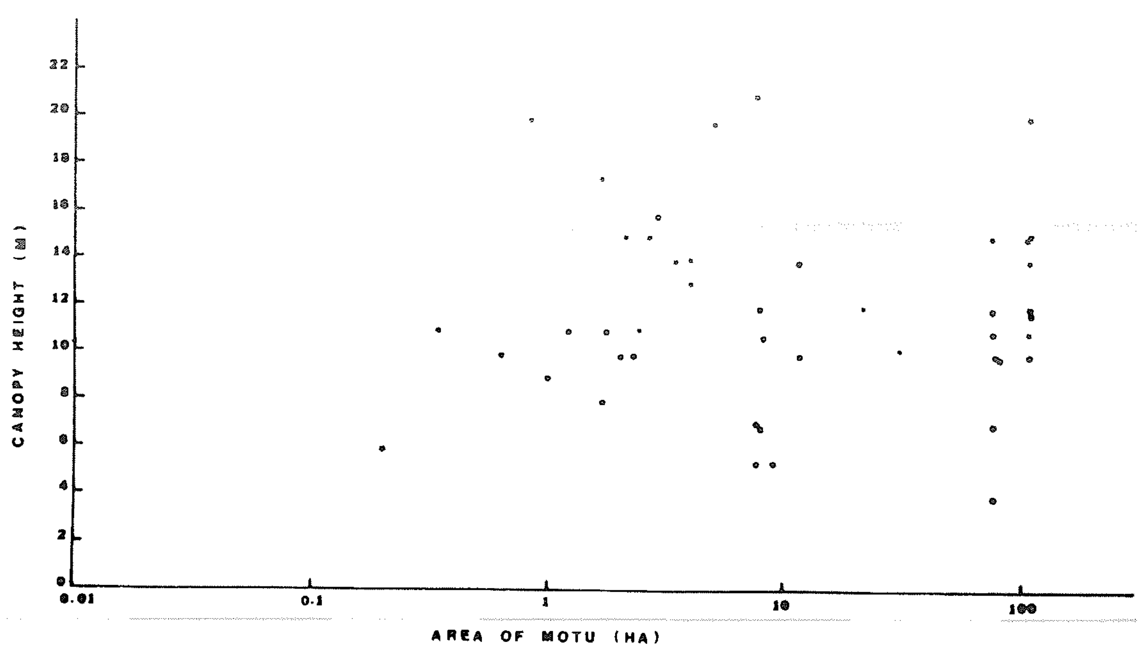

Figure 34. Maximum canopy heights of *Pisonia* forests in relation to motu area. Stars represent forests with 90-100% canopy cover; dots represent forest or scrub with less than 90% cover.

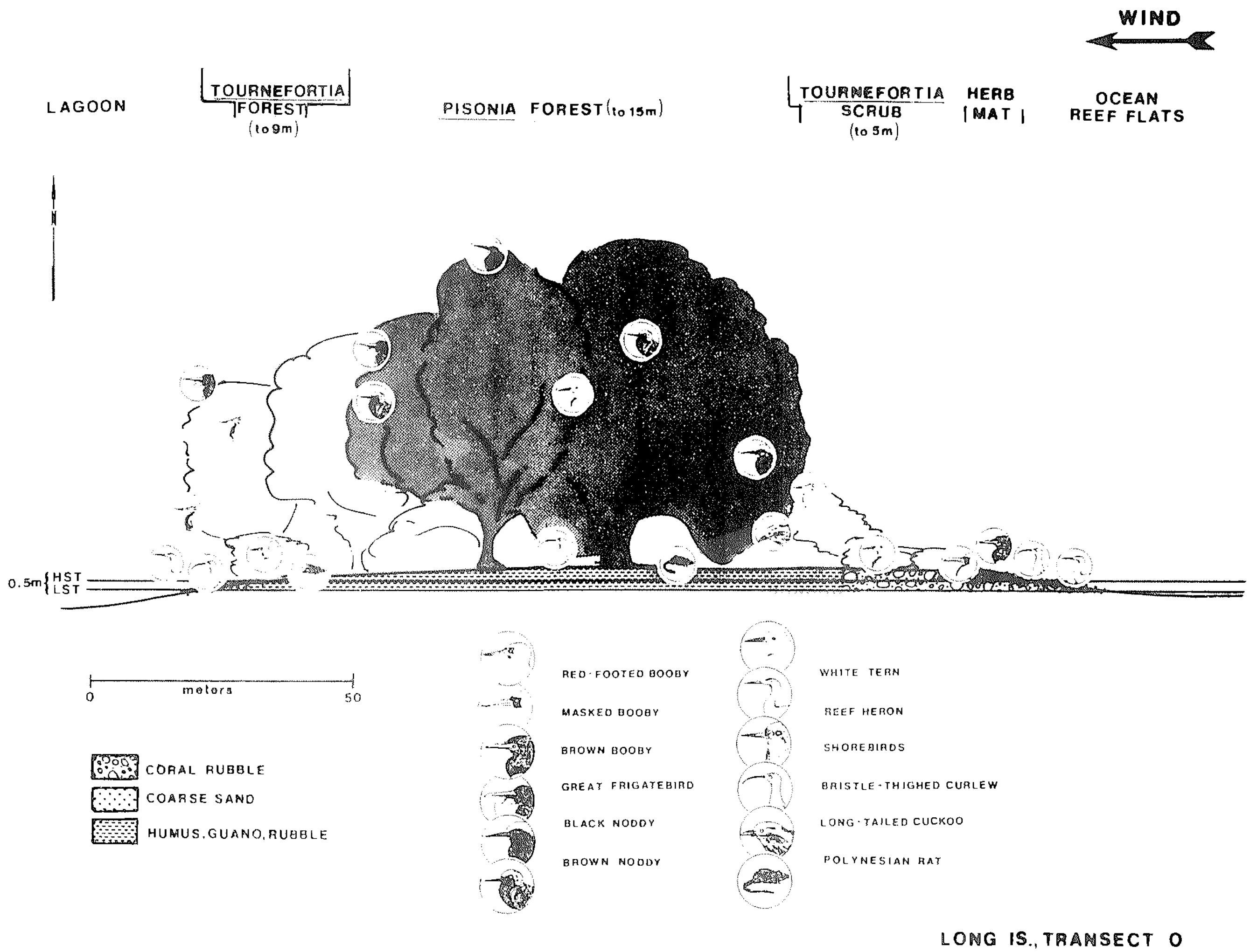

Figure 35. Schematic profile through Long Island, Transect O. Although Long Island has been formed in the recent past by a merger of 5 smaller islets, this section of the islet is very mature, containing natural herb mats, *Tournefortia* scrub and forest, and tall *Pisonia* forest. Seven species of seabirds breed. Vertical height is exaggerated.

Table 11. Distribution of well-developed (≥10 m height) _Pisonia_ forests on the motus of Caroline Atoll.[1] Motus and transects are arranged according to the decreasing height of their _Pisonia_ groves. Capitals indicate those motus whose forests were felled for _Cocos_ plantations from 1916-20.

Motu & Transect	_Pisonia_ Height (m)	Area of _Pisonia_ (ha)	Motu Area (ha)
PIG	21*	3.36	7.21
NAKE, Transect 4	20*	20.79	107.46
Booby	20*	0.12	0.84
NORTH PIG	20*	1.83	5.44
NORTH BROTHERS	18*	0.43	1.71
NAKE, Transect 3 (central)	15*	20.79	107.46
LONG, Transect 0	15*	15.00	75.98
BROTHERS	15*	0.37	4.31
Ana-Ana	15*	0.93	2.16
Danger	15*	0.39	2.71
NAKE, Transect 2	14*	20.79	107.46
Bird	14*	1.70	4.05
WINDWARD, Transect 2	14°	2.97	11.42
Raurau	14*	1.07	3.48
CRESCENT	13°	0.51	3.10
Mannikiba, Transect 1	12*	1.13	21.49
Shark	12°	2.60	7.98
NAKE, Transect 3 (west)	12°	20.79	107.46
LONG, Transect 12	12°	15.00	75.98
Pisonia	11*	0.86	2.45
Matawa	11	0.07	1.71
Nautonga	11°	0.02	0.34
NAKE, Transect 3 (southwest)	11°	20.79	107.46
Kimoa	11°	0.59	1.80
Emerald	11°	3.20	8.34
Eitei	11°	0.38	1.42
LONG, Transect B	10°	15.00	75.98
LONG, Transect 8	10	15.00	75.98
NAKE, Transect 1	10°	20.79	107.46
WINDWARD, Transect 1	10	2.97	11.42
Blackfin	10°	0.41	2.62
NORTH ARUNDEL	10°	0.18	0.91

[1] _Tournefortia_ or _Cordia_ may be present, but sub-dominant to _Pisonia_.
*90-100% canopy cover.
°50-80% canopy cover.

Table 12. Area and Dimensions of Pisonia grandis on Vostok, Flint, and 5 islets of Caroline Atoll. Comparative data are from A. Kepler (1990b,c,d).

Island/Islet	Area of Pisonia (ha)	No. trees or main trunks	Mean Height (m)	Range of Heights (m)	Mean cbh[1] (m)	Range of cbh (m)	Mean base[2] (m)	Range of base circumferences (m)
CAROLINE	62.17							
North Pig	1.83	25	19	11-21	221	110-359	261	205-470
Brothers	0.37	10	15	15	140	50-219	243	154-340
Pig	3.36	5	16	12-17	338	290-660	282	230-333
North Brothers	0.43	3	18	18			314	293-332
Long	15.00	3	15	15			414	282-500
Total for above islets at Caroline	20.99	46	18	11-21	213	50-660	293	154-500
VOSTOK	13.5	58	18	10-25	218	67-510		
FLINT	approx. 4 (fragmented)	20	17	8-30	160	60-200	598	100-1000

[1]cbh = circumference at 1.5 m.
[2]base = base circumference at 0.3 m.

Table 13. Number of trees and areas planted in *Cocos* on Caroline's islets during the major planting era (1916-1920), also showing remnant *Cocos* data for 1990. Note the remarkable recovery of indigenous forests on all islets except South.

Islet	Islet Area (ha)	Area Forest or Scrub Usable for *Cocos* in 1990[1] (ha)					1916-20		% *Cocos* 1990	Approx. % 1990 Forest Planted in *Cocos* 70 Yrs Ago
		Tournefortia	*Pisonia*	Other	*Cocos*	Total	No. *Cocos* Planted	Approx. Area *Cocos*[2] (ha)		
South	104.41	4.20	0	1.1	80.00	86.10	13,006	94.94	77	100%
Nake	107.46	30.65	20.8	9.41	5.75	66.61	10,544	76.97	6	100%
Long	75.98	32.20	15.0	-	2.40	49.60	1,343	9.80	3	20%
Tridacna (A1)[3]	9.08	7.97	0	0.18		8.15	910	6.64	0	82%
Arundel	7.34	4.36	0.95	-	0	5.31	646	4.71	0	89%
N. Arundel (A2)	0.91	0.33	0.19	-	few trees	0.52	69	0.50	0	100%
Brothers	4.31	2.00	0.37	-	0.01	2.38	315	2.30	0.2	97%
N. Brothers (A3)	1.71	0.68	0.43	-	few trees	1.11	180	1.31	0	100%
Pig	7.25	1.61	3.36	-	0.03	5.00	538	3.93	0.4	79%
N. Pig (A4)	5.44	1.31	1.84	-	0	3.15	402	2.93	0	93%
Crescent (A5)	3.10	1.56	0.51	-	0	2.07	228	1.66	0	80%
Windward (A6)	11.42	5.70	2.97	-	0	8.67	1,299	9.48	0	100%
						238.49		215.10		

[1] "Usable area" does not include unvegetated rubble or natural herb mats.
[2] Based on Caroline's planting densities of 28 x 28 sq ft (Young ca. 1922).
[3] The "A" series of islet names are from Young (ca. 1922).

of all usable ground; in several cases the amount calculated for *Cocos* by Young exceeded our estimates of potentially usable ground. Thus, *Cocos* was planted so intensively on the Windward Islets that virtually all *Pisonia* and most *Tournefortia* woodlands were felled.

Two remarkable points emerge from Table 13: 1) scarcely any *Cocos* remains today on the 9 Windward Islets; not one palm exists on 7 motus (Figs. 43, 44, 47, 48), and 2) the recovery of indigenous plant communities, Stages I through V (Sect. F) on the windward side has been rapid and, at least on Brothers Islet (Fig. 46), reasonably complete with regard to ecological succession and species diversity of plants and seabirds. Today the Windward Islets have the lushest and tallest plant communities, with a higher species diversity than the leeward islets (Table 3), which have evidently experienced far less human disturbance.

This differential disturbance on the windward and leeward sides of the atoll explains enigmas such as 20 m tall *Pisonia* forest on the leeward Booby Islet (0.84 ha), taller than most of the windward forests; the absence of *Pisonia* on windward Tridacna Islet (9.08 ha), which, being close to South Island, probably supported *Cocos* which was managed longer than the more distant windward islets; and the patchy distribution of *Pisonia* in the interior of several islets (e.g. Windward, Arundel). This last point also applies to Mannikiba (21.49 ha), the largest leeward islet. According to Young (ca. 1922), 6,000 seed sets were brought from Flint to Caroline in 1920 and kept on Mannikiba. This "nursery stock" was used to replant "misses" on other islets, due mostly to destruction by coconut crabs and poor planting. Today, Mannikiba's total acreage of *Pisonia* (Fig. 53) is very small and fragmented relative to the islet's size: 1.13 ha, 5% of the total land area. Compare this with Bird Islet (Fig. 55) which, as far as we know, has never been disturbed: 1.70 ha *Pisonia*, 42% of the islet's land area.

On both Caroline and Flint there is much variation in the quality of the regenerated *Pisonia* forests (Table 12). Some trees bear enormous, partly rotting boles, black algae smothering the bark, multiple trunks, and few or no understory herbs. Other trees are tall, straight-trunked, with characteristic whitish bark, and bear no rotting holes in their bases. These observations suggest that when their indigenous forests were felled, only minimal cutting was done, and many *Pisonias* were able to regenerate quickly by sprouting from rooted stumps and fallen branches. This speculation is supported by the fact that some of Vostok's *Pisonia* trees regenerated similarly. Maude (1953, p. 96) states that "there is room for 8,000 palms on Vostok, but only 100 have been planted and most of these have been choked in the luxuriant 'buka' (*Pisonia grandis*) forest: no attempt having been made to exploit the island since the initial planting."

Pisonia, a soft, pulpy wood, has a well-known ability to sprout or send up suckers from dismembered branches or fallen trunks (Fosberg 1953), and it has been noted that older trees are virtually indestructible, fire being the only effective means of clearing forests

(Wiens 1962, p. 397). The senior author has photographed leaf sprouts from partly burned twigs as small as 1 m long and 5 to 6 cm in diameter.

Since the existing *Cocos* plantations on South and southwest Nake contain few *Pisonia*s, it seems that forest clearing was more thorough on the atoll's larger islets than on the smaller ones, which today manifest scant traces of their former history. Fortunately for Caroline, its coconut plantations were plagued by a number of problems, which resulted in their double abandonment: coconut crabs, seabirds, rats, *Ipomoea* vines, and an unknown disease (see under Coconut Woodlands, this section).

A footnote in Young (ca. 1922, p. 15) states that "the larger portion of the 30,000 trees planted were either badly planted or smitten with some disease as in 1927 it was reported by Mr. Bunckley that most of them had perished." In 1929 only 13,215 trees were left, and more were being planted. Considering the distribution of both palms and natural forests today, it appears that plantations continued on South and Nake and were abandoned on the smaller islets, allowing for a better recovery than might be expected had the *Cocos* grown to maturity. Tridacna (close to South) and Mannikiba (a nursery) were likely the most intensely managed of the smaller islets, as their *Pisonia* today is meagre compared to their overall areas.

Once a *Cocos* plantation has been well established and subsequently abandoned, *Pisonia* regrowth is more difficult. This is characteristic of many tropical islands. For example, on Cousin Island (Seychelles Islands, Indian Ocean), an ICBP wildlife perserve since 1968, *Pisonia* is currently reestablishing within a deteriorating *Cocos* plantation. Phillips & Phillips (1990, p. 37) envisioned "centuries rather than decades before something like a natural ecosystem develops." We predict a similar time frame for Caroline's South Island, sooner for Flint. Forest recovery on islands elsewhere has evidently not been studied in detail (Fosberg, pers. comm.).

Annual Growth Rates

Data on *Pisonia grandis* growth rates is very limited. A 7-year study on Kabelle Island, Rongelap Atoll, Marshall Islands, disclosed mean diameter growth rates of 1.32 and 0.39 cm/yr at 2 sites (Gessel & Walker 1992). On Cousin Island, vegetation changes, including *Pisonia* and *Cocos*, have been monitored since 1974, but no growth rates are yet available (Phillips 1984, Phillips & Phillips 1990).

Because of this paucity of data on *Pisonia*, and because its forests have diminished significantly this century, we present the following data in the hopes that it might inspire more research.

One point is clear: on all 3 of the Southern Line Islands *Pisonia grandis* has recovered fast from disturbance (except for total forest elimination), reaching close to its maximum height and ecological maturity in 70 years or less. Mature *Pisonia*, under optimal conditions of soil, temperature and rainfall, may attain 35 m, as on Fanning and Washington (Garnett 1983 and pers. comm.). However, in the Southern Line Islands, canopies of similarly virgin *Pisonia* on Vostok rarely exceed 25-30 m tall (A. Kepler 1990c), and only 16-18 m on the Great Barrier Reef (Walker 1991).

Caroline's prime groves, 21 m tall, with circumferences to 660 cm, and bearing multiple trunks and root suckers, we now know date back only to the 1920s. The largest trees, 21 m high and 660 cm cbh, appear to have averaged annual growth rates of 0.32 m in height and 3.4 cm in diameter.

Further evidence of fast growth rates is provided from Flint. In 1934 only one small *Pisonia* and a few tiny, struggling *Cordia*, recently planted, were recorded (St. John & Fosberg 1937). Virtually the entire island (324 ha) was a *Cocos* plantation. In 1990 *Pisonia*, quite common on the windward side, attained maximum heights of 30 m, with base circumferences and at 1.5 m (cbh) of 1,000 cm and 200 cm, respectively (Table 12). These compare favorably with 2 trees of similar heights and cbh to 510 cm on Vostok and a large *Pisonia*, presumably virgin, measured on Atafu Island (Tokelaus) by the U.S. Exploring Expedition in 1840, which was more than 600 cm in base circumference and about 12 m tall (Wilkes 1845, Vol. V, p. 9). Furthermore, pure indigenous mixed broadleaf forests (*Pisonia, Cordia, Guettarda*), to 25 m tall, covered 57 ha, 23% of Flint's vegetated area (Kepler, in prep.), with a further 65 ha (26% of the woodlands) in mixed forests containing less than 50% *Cocos*. Thus, *Pisonia*s have established themselves since the plantation was abandoned in the late 1930s. The largest trees, 30 m high and 200 cm cbh, now indicate a mean annual increment of 0.6 m height and 1.32 cm diameter over the past 50 years. A faster growth in height than on Caroline is likely due to Flint's higher rainfall and greater relative humidity due to the presence of a more successful coconut plantation inland: Caroline's annual output of copra was 15 tons, compared to 230 tons for Flint (Young ca. 1922, Maude 1953).

Species Diversity in *Pisonia* Forests

Caroline's motus harbor every stage in the development of a *Pisonia* forest, from stately monotypic groves to a single tree. The plant communities between these extremes harbor the greatest species diversity and most luxuriant growth on the atoll. The following species are present (Table 2):

Trees: *Morinda citrifolia, Cordia subcordata, Cocos nucifera, Pandanus tectorius, Pisonia grandis*;

Shrubs: *Tournefortia argentea*; and

Herbs: *Boerhavia repens, Portulaca lutea, Laportea ruderalis, Lepturus repens, Achyranthes canescens, Phymatosorus scolopendria, Ipomoea macrantha.*

The number of species within *Pisonia* forests ranges from one to 14 (Table 14). As *Pisonia* becomes more dominant, their trees are taller (21 m), and species diversity is less (Table 14). Here the average number of species is 3.4. Species diversity is also very low at the other extreme of *Pisonia* development: in one young motu (Azure), only a single 6-m-tall *Pisonia* tree is present ($\bar{x}$ = 4.0 species). The smallest islet on which we found *Pisonia*, Azure is only 0.20 ha in area and 77 m wide (Fig. 55, Pl. 51); more than half of it is rubble. The width of its scrub is only 38 meters. Along a transect within the majestic *Pisonia* grove (100% canopy cover) on Brothers (Fig. 46), we found no other plant species, an extreme case of the barrenness of *Pisonia* understory. This grove, 13 m tall and extending 42 m from east to west, was sharply delineated from the 6-m-high *Tournefortia* forests on both sides and provides a striking example of complete ecological succession since its *Cocos* plantation days of the 1920s.

The highest species diversity occurred with mixed co-dominants (*Tournefortia*, *Cordia*) and *Pisonia* coverage 25-50% (Fig. 34, Table 14). Here, the average number of species was 6.2 (range 3-10). Regardless of the area or width of the motu on which they occurred, these mixed stands ($\bar{x}$ = 7 m tall) were always shorter than pure *Pisonia* forest.

Ecology

On Caroline, most plant species establish early in the evolution of individual motus, increasing in abundance and stature while the land area is quite small. *Pisonia* typifies this pattern: single trees occur on 2 motus whose areas are only 0.2 ha (Table 6), suggesting that *Pisonia* is partly salt-tolerant, at least in its early growth stages. In general, however, motus less than 0.7 ha on Caroline have little *Pisonia* (Table 6). It is difficult to imagine a freshwater lens on Motu Nautonga (1 ha), where an 11-m-tall *Pisonia* forest is found (Table 11). Further evidence for the salt-tolerant nature of *Pisonia* comes from Vostok, where a *Pisonia* forest, the sole woodland, extends to the edge of the shoreline rubble and herb mat. The trees, tightly pruned by wind and salt, have no buffer of coastal scrub. During storms, seawater reaches Vostok's interior forest, yet this 24-ha island supports one of the largest and tallest (25-m-high) groves in the Pacific (Clapp & Sibley 1971b, Fosberg 1977 and pers. obs.).

Many *Pisonia* trees were heavily infested with scale insects (Coccidae) and Neuropteran larvae (*Chrysopa* sp.), identified by Dr. Scott Miller (Bishop Museum, Honolulu, Hawaii). This appears to be a natural phenomenon, as they were also abundant on the virgin *Pisonia* forests on Vostok and also on secondary *Pisonia*s at Flint.

Relationships Between *Pisonia* Forest Height and Motu Dimensions

Contrary to expectations, the tallest, most mature forests did not all occur on the largest motus (Table 11). The 3 prime forests (90-100% canopy cover) were on Nake (total land area 107.46 ha), Pig (7.21 ha),

Table 14. Species diversity in _Pisonia_ forests of decreasing maturity, Caroline Atoll. Groves are arranged according to the degree of coverage of their constituent _Pisonia_ trees. Where _Pisonia_ is present, even in low percentages, it is always the tallest tree. Note that there is an inverse relationship between the purity of the _Pisonia_ forest and its species diversity.

Canopy Cover	Av. Canopy Hgt. (m)	Numbers of Species/Transect					No. Transects
		Av. No. Spp.	Trees (incl. _Pisonia_)	Shrubs	Herbs	Total	
100% (_Pisonia_ only)	13	1	1	0	0	1	1
100% (codominant present)	15	3.4	2	0	5	7	9
90 - 95%	10	5.2	5	1	7	12	9
50 - 90%	10	6.2	5	2	7	14	15
25 - 50%	7	6.2	4	1	6	11	5
<25%[1]	9	5.6	3	2	9	14	6
Single _Pisonia_ tree only	6	4.0	3	1	3	7	2

[1]South Island not included, as its _Pisonia_ is too rare.

and Booby (0.84 ha). Trees on Booby measure less in girth than those on Nake and Pig, but their height (20 m) is impressive. Evidently, Booby was never exploited for guano or planted in *Cocos*. Fine forests occur on other small, undisturbed motus; for example, *Pisonia* grew to 14 m on Raurau (3.48 ha) and to 11 m on Kimoa (1.80 ha).

A positive correlation exists between *Pisonia* height and island width (Fig. 33). Motus appear to reach a minimum width of 90 m before closed canopies of 13 m develop, and canopy height increases to 21 m as motu width enlarges to 200 m (Pig, topmost star in Fig. 33). Further increases in motu width did not result in taller trees. However, even on motus with sufficient width, *Pisonia* did not develop unless other environmental conditions were suitable. For example, on Long, *Pisonia* only occurred in the centers of its former islets, not in the scrubby areas where coalescence is more recent. Tridacna and Mannikiba, both ideal for *Pisonia*, have not yet recovered fully from their *Cocos* plantations.

Pisonia-Seabird Relationships

Seabirds are an integral part of *Pisonia* ecology. Its sticky fruits adhere to the feathers of, and are thus dispersed by, seabirds such as terns, boobies, and frigatebirds; thus, its early appearance on small motus is not surprising.

On Caroline, 6 species of seabirds nest in its branches, dropping considerable amounts of guano to the ground below. Black Noddies, amassing in dense colonies, nest almost exclusively in *Pisonia*, along with Brown Noddies, White Terns, Great and Lesser Frigatebirds, and Red-footed Boobies. Pig Islet, with 7.25 ha of excellent *Pisonia* forest, supported a dense colony of nearly 2,000 pairs of Black Noddies (Pt. II). Bristle-thighed Curlews feed on the ground beneath its open understory, and the Long-tailed Cuckoo forages within its canopy.

Seabirds may be so much a part of *Pisonia* ecology that a debate exists as to whether *Pisonia* actually *requires* guano for successful germination and establishment of seedlings (Shaw 1952, Fosberg 1953, Wiens 1962). Very high phosphate and nitrogen levels are associated with mature *Pisonia*, and concurrently the development of *Pisonia* forest results in greatly modified soils that perpetuate its existence (Wiens 1962, Spicer & Newbery 1979). The formation of a highly acid raw humus on the surface of the ground, sometimes in association with phosphatic hardpan, has also been documented on several atolls by Fosberg (1953, 1956, no date; Stoddart & Scoffin 1983), including Vostok (AKK and John Phillips, pers. obs.). We have no information on phosphatic hardpan in Caroline's *Pisonia* forests. For further discussion, see Section D, Substrata.

Remnant *Pisonia* Forests in the Pacific

Though naturally and widely distributed throughout Indo-Pacific islands (excluding Hawaii), *Pisonia grandis* forests have been subjected to great destruction and are now rare. Pure *Pisonia* forest was formerly the most widespread indigenous forest on Pacific atolls, and may have formerly covered the greatest area of any tree species in the Pacific (Wiens 1962, Fosberg 1976). Shaw (1952), summarizing its distribution, stated that it only occurs on remote, generally uninhabited islands ranging from the western Indian Ocean to the eastern Pacific, including Malaysia. However, more recent studies, particularly by Fosberg, indicate that because its habitat occupies, and is in part responsible for, the most fertile areas of inhabited islands, its formerly extensive forests have been largely replaced by coconuts. Though *Pisonia*'s soft wood is of little use to either atoll inhabitants or to the timber industry, its soils were rich sources of phosphate fertilizer and were thus greatly disturbed during the guano mining era. *Pisonia* is highly adapted for growth on coralline substrates, also having developed unique morphological and physiological characteristics associated with seabird colonies and mycorrhizal fungi (Walker 1991). Caroline, with 62.73 ha in *Pisonia* forest (36.94 ha in monotypic groves) holds some of the finest representatives of this ecosystem in the Pacific, even though much of it is not virgin.

One of the prime Pacific *Pisonia* stands (13.5 ha on Vostok) was partly burned in 1977 (Fosberg 1977). The Royal New Zealand Air Force found it smoldering 3 months later (Fosberg 1977, pers. comm.). In a March 1990 visit to Vostok, we found that approximately 1.5 ha were completely cleared (A. Kepler 1990c) and a further unknown amount of land was affected. Cays of the southern Great Barrier Reef have recently been found to harbor ca. 160 ha of uncut *Pisonia* forest. The largest stand (94 ha) is on Northwest Island (Walker 1991). Other fine groves exist on Palmyra and Washington (Northern Line Group), Rose Atoll (American Samoa), Bikar, Taongi, and Jabwelo (Marshall Islands), and Fanna (Southwest Palau Islands). Flint (Southern Line Group); Christmas (Northern Line Group); Nikumaroro (Phoenix Group); Jemo and Ujae (Marshall Islands); and Aitutaki, Penrhyn, Suwarrow, and Manihiki (Cook Islands) have relatively small stands. Not all are healthy. For example, groves on Bikar, Jabwelo, and Palmyra were recently devastated by typhoons (Flint et al. 1992, IUCN 1992) and that on Taongi is unhealthy (Thomas et al. 1989).

<u>Coconut Woodlands</u> (96.14 ha) — Figs. 14, 36; Pls. 17, 22, 23, 27-29, 32, 34, 37, 39, 40, 44

General Distribution

Cocos, although present on 15 motus and known to be planted intensively on at least 13, covers significant areas only on the 2 largest islets, South and Nake (Table 13). Individual trees and small

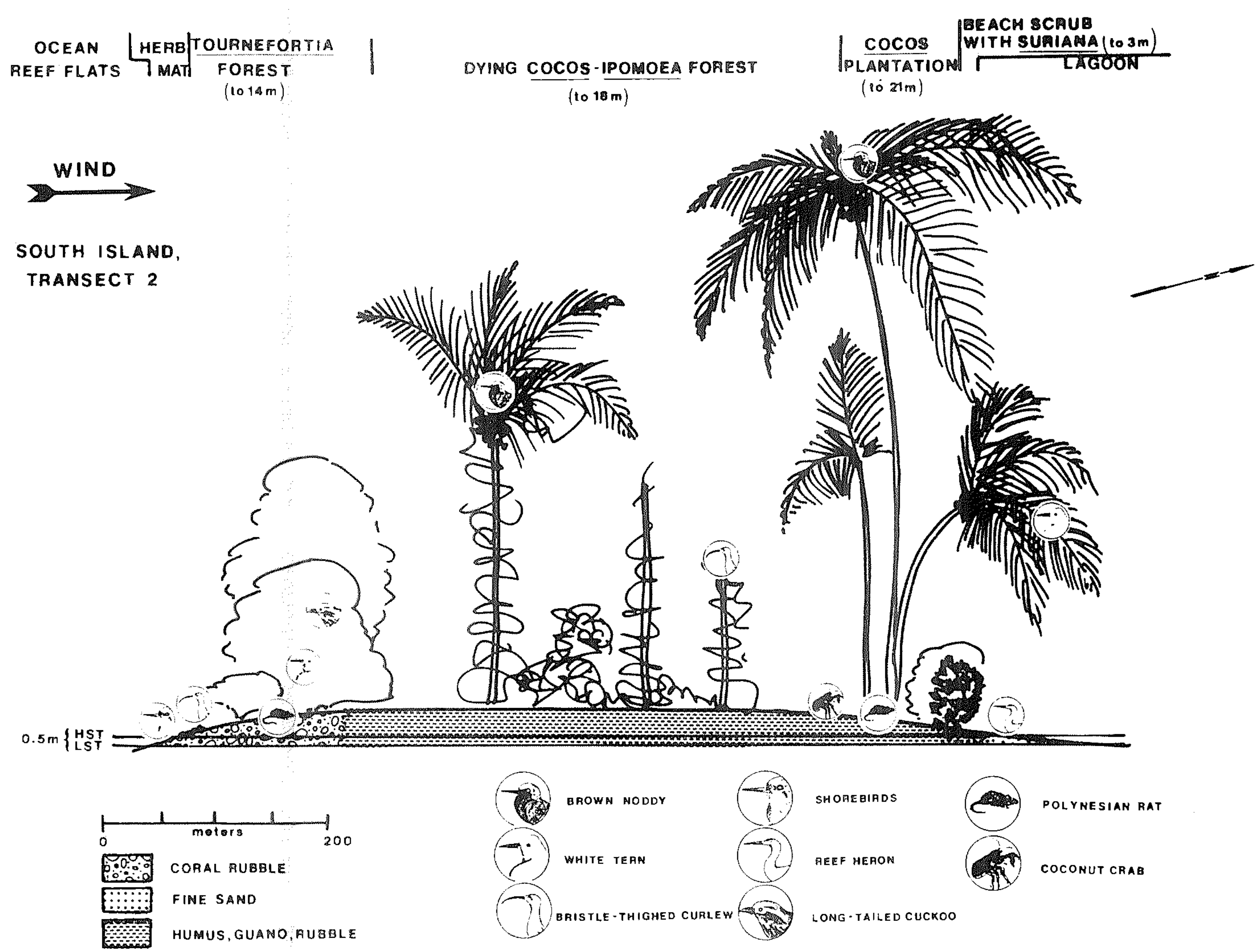

Figure 36. Schematic profile through South Island, where 77% of the land surface is covered with *Cocos* forests, primarily in a dying state. Vertical height is exaggerated.

groves elsewhere are drift-derived or remnants of plantings made from 1916 to 1920.

The following species occur in habitats containing *Cocos* (Table 2):

Trees: *Pisonia grandis*, *Morinda citrifolia*, *Pandanus tectorius*, *Cordia subcordata*, *Cocos nucifera*, *Thespesia populnea*, *Hibiscus tiliaceus*;

Shrubs: *Tournefortia argentea*, *Ximenia americana*; and

Herbs: *Boerhavia repens*, *Portulaca lutea*, *Laportea ruderalis*, *Achyranthes canescens*, *Phymatosorus scolopendria*, *Ipomoea macrantha*, *Lepturus repens*, *Tacca leontopetaloides*, *Psilotum nudum*, *Phyllanthus amarus*, *Sida fallax*.

The distribution of *Cocos* (Fig. 14) in order of decreasing abundance is as follows: SOUTH: Forests old and neglected. Living palms line the lagoon, currently shading out strip of native scrub. NAKE: Southern forests (50-80% *Cocos*) healthier, younger, with more native trees and *Pandanus* than on South; grove of about 50 palms on northeast. LONG: Range from <1% cover (Tr. C) to dense fringe adjacent to lagoon. EMERALD: Northeast and west-central patches. MANNIKIBA: Main grove, northeast: 40 palms, 20 m high, another patch in south center. ANA-ANA: House site, northeast point. BIRD, BLACKFIN, BROTHERS, NAUTONGA, NORTH BROTHERS, PIG, PISONIA, RAURAU, SHARK: Few trees each, primarily in *Tournefortia*. LONE PALM: One tree, central forests.

History

A relatively small coconut grove was planted on South Island prior to the 16th century by Tuamotuan settlers (Emory 1947, Maude 1968). In 1606 de Quiros noted "plenty of palms" and "many cocoa-nuts" (Markham 1904). Since then, every visitor has recorded them since they grew, and still grow, adjacent to the boat "landing." A smaller grove evidently also existed in the south-southwest portion of South Island (Lucett 1851). Palms were also periodically planted--and destroyed--"by whalers and other chance visitors to the island" (Maude ca. 1938).

Until Arundel's arrival in 1885, *Cocos* was basically confined to this single grove in the northwest sector of South (Maude ca. 1942). In 1885, land clearing began, and from then till 1929 nearly 38,000 palms were planted, 29,480 between 1916 and 1920 and another 7,000 young trees after 1927 to replace thousands that had perished (Young ca. 1922). Arundel's initial license gave him the exclusive rights to occupy Caroline and Flint, planting coconuts and other trees for 21 years, in return for an annual rental of 50 pounds sterling (Maude ca. 1942). In 1929 13,215 trees remained, after which no one has counted them. Our field work and scrutiny of aerial photographs indicate that far fewer exist today.

Caroline's plantations produced copra periodically from 1873 to 1934, but never profitably. They suffered greatly from the atoll's abandonment from 1901-1916. Dying and poorly planted palms presented continual setbacks (Young ca. 1922); in 1878 a hurricane wrought great destruction (N.I.D. 1943), and although no record exists of the effects of the 1906 hurricane on Caroline, waters reaching well inland on Flint threw warehouses off their foundations and flooded all buildings within the settlement (Campbell 1908). In addition, plantation managers lamented their poor productivity due to choking "by undergrowth and Pohue Vine,[6] destruction of inflorescences by great numbers of seabirds which roosted in the tops and broke off the flowers as they appeared," disease, and ruination of nuts by Polynesian rats and coconut crabs. As a result of this, the laborers slaughtered many crabs, and "greatly reduced the numbers of sea birds, who migrated to unoccupied islets." The rat problem was never resolved and appears to be the major reason for the eventual abandonment of plantations on both Caroline and Flint. Their enormous numbers and voracious eating habits greatly reduced both the crops of potentially healthy nuts as well as the volume of dried copra. In 1920, 4,600 were trapped on South Island, and hundreds more were killed by small terriers introduced specifically to control them (Young ca. 1922). Maude (pers. comm.) recalls that one terrier still survived in the 1940s. Rats still abound, especially within coconut groves and *Pisonia* forests. Another serious problem was due to coconut crabs digging up recently planted nuts and pinching off young shoots. After the palms had attained one year's growth this was no longer a problem (Young ca. 1922).

Before abandonment (1902 to 1916, and after 1934), Caroline's plantations were owned by several companies whose average annual copra output was approximately 14 tons. From 1934 to the 70s copra was harvested sporadically by small parties from Tahiti (Garnett 1983), but within the last 2 decades it stopped altogether.

Despite the relatively fertile soils of South Island, the problems in the plantations hampered the establishment of permanent settlements on Caroline. In the 1930s Maude estimated that the atoll could support 400 Gilbertese, increasing to over 1000 "when the island has been fully planted" (Maude ca. 1938). Colonists were never established though, since the failure of the plantations was never cured (Maude 1953), leaving Caroline "one of the least spoiled islands in the Pacific" (Stoddart 1976). However, as plantation information in Young's (ca. 1922) unpublished "Memoranda" indicates, Caroline is not as pristine as it appears, but the rapid recovery of most of its windward forests is remarkable (see *Pisonia* Forests, this section).

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[6]Said to be *Tuumfetta* (= *Triumfetta*) *procumbens*, most likely a misidentification of *Ipomoea macrantha*.

Distribution and Abundance

We recognize 4 subdivisions of the coconut woodlands: *Cocos* Plantations, Dying *Cocos-Ipomoea* Plantation, Scattered Groves on Small Motus, and Mixed Forest with *Cocos*.

1) *Cocos* Plantations (34.07 ha)

Superannuated palm forests dominate South Island and southwestern Nake. Although the planting of *Cocos* on South eliminated most of its original habitats, Nake escaped with less damage: *Cocos* covers 77% of the area on South but only 6% of Nake (11% including mixed forests). The 60 to 100-year-old trees form tall, closed canopy woodlands (Pl. 23) 21-25 m high, the customary maximum height recorded for old plantations (Fosberg 1953). Figure 51 shows the distribution and abundance of plant species along a transect running centrally through the island, while Figure 36 depicts a schematic profile of the same swath.

Pure coconut plantations harbor relatively few species: up to 7 trees, zero to 2 shrubs, and 5-11 herbs. The understory layers are almost exclusively indigenous, an unusual feature. However, skirting the edge of the lagoon, tall palms overhang the water, crowding native plants; *Suriana* and *Tournefortia* were less abundant in 1988 (Pl. 28) than in 1965 (Pl. 40).

2) Dying *Cocos-Ipomoea* Plantation (53.92 ha)

Mature plantations characteristically become overgrown with shrubs and vines (Fosberg 1953, 1956). *Ipomoea macrantha*, the sole vine on Caroline, forms tangled, impenetrable thickets. Indigenous, nonparasitic, and widely dispersed by ocean currents, it forms a very minor component of Caroline's natural habitats, but grows rampantly in disturbed areas. Vine-covered coconut woodlands cover two-thirds of South Island's interior (Fig. 50). This moribund forest is bordered by a belt of living palms, which in turn are sheltered by a narrow rim of indigenous vegetation (Figs. 36, 51).

While traversing the South Island transects, the authors stomped over intertwining thickets up to 3 m high (Pl. 8) and crawled through tightly-knit masses of vines descending from the crowns of old palms, *Pisonia*, and *Morinda* bushes, until this too, proved impenetrable. In sunny clearings dotted with dead or disintegrating palms, *Ipomoea*, *Boerhavia*, and *Phymatosorus* proliferated luxuriantly. Choking of the palms by *Ipomoea*, one of the prime reasons for the twice-abandonment of the copra enterprises, continues to destroy the coconuts, encouraging natural ecological succession to begin anew.

3) Scattered Groves on Small Motus (0.82 ha)

Drift-derived palms were observed as long ago as 1834 (Bennett 1840). In 1916, when planting operations were commenced after a break of 14 years, about 40 trees grew beyond the plantations (Maude ca. 1942). Today, small *Cocos* groves, up to 50 palms, drift-derived and plantation remnants, generally close to the shoreline (Pls. 28, 29), occur on 11 motus.

4) <u>Mixed Forest with *Cocos*</u> (6.24 ha)

This forest type is a simplified version of more complex and varied mixed forests that occur on most inhabited atolls. Composed of anthropogenic and indigenous elements, it contains a high proportion of *Cocos* (50-80%) mingled with variable proportions of *Tournefortia*, *Pisonia* and *Pandanus*. This forest type occurs primarily in southern Nake (Fig. 14), but also on Emerald, Shark, and southwest Long, where it mixes with *Cordia* and *Tournefortia*.

House Site: A clearing on Motu Ana-Ana, approximately 40 m x 70 m, contains a few *Cocos*, a vegetable garden and thatched former living quarters (Pl. 51).

Seabird Use

Cocos-dominated habitats were ornithologically the most depauperate on Caroline: only Brown Noddies and White Terns breed. The noddies nested high within the frond and inflorescence bases, whereas the White Terns preferred lower sites, occasionally atop an arching frond. The absence of other species suggests that anthropogenic *Cocos* forests seriously inhibit seabird use and may continue to do so for decades until they are replaced by native vegetation.

<u>Absent Plant Communities</u>

Caroline's impoverished flora and relatively simple physiography and geology has resulted in a limited variety of ecosystems. The atoll is thus notable not only for its *Pisonia* forests, extensive monotypic stands of *Tournefortia*, and *Cordia* groves, but also for the absence of several ecosystems that are generally considered typical of Pacific atolls:

1) *Sesuvium* Flats;

2) *Pemphis*, *Scaevola*, and *Sida* Scrub (2 *Scaevola* plants are present, and the only 2 *Sida* records are from 1884 and 1990); and

3) Mixed broadleaf forests including *Barringtonia*, *Calophyllum*, *Guettarda*, *Hernandia*, and *Neisosperma*.

4) Plant associations (except *Cocos*) typical of native cultures on atolls: breadfruit groves (*Artocarpus altilis*), taro pits (*Cyrtosperma chamissonis*, *Colocasia esculenta*, *Xanthosoma sagittifolia*), cultivated ornamentals (*Hibiscus rosa-sinensis*, *Plumeria* spp., etc.), or weedy grasslands/wastelands (*Paspalum*, *Sporobolus*, *Wedelia*, *Vigna*, etc.). Even widespread introduced strand

species such as *Terminalia catappa* and *Casuarina equisetifolia* are absent.

In addition, there are no mangroves, peat bogs, marshes, ponds, salt flats, or other habitats associated with fresh or brackish water. Poorly represented are:

1) *Lepturus* Grassland. Although *Lepturus* is present in coastal herb mats, and occasionally in patches within the forest understory, it does not form a separate plant community. However, it may once have covered the extensive clearings on South Island (Pl. 2, 3).

2) Mixed Forest. Though 6.24 ha of Mixed Forest (with *Cocos*) occurs (primarily on Nake), it is of such minor importance to Caroline's overall vegetation that it is treated as a subsection of Coconut Woodlands.

H. DESCRIPTION AND ECOLOGY OF THE MOTUS

These islet accounts synthesize the history, physiography, vegetation patterns, ecology, seabird colonies, miscellaneous biota, and the effects of human activity (if any) on Caroline's 39 motus (Fig. 2). Mapping is based on the coast-to-coast transects, perimeter surveys, complete surveys (smaller motus), color transparencies, and aerial photographs.

All motus are detrital reef islets representing many evolutionary stages from barely emerged coral rubble to large islets with relatively fertile "soils" supporting lush vegetation. There is one tiny old reef platform in its final stages of erosion.

We discuss and map them in geographic order beginning in the north with Nake and progressing down the windward reef through Long and the 13 Windward Islets to South Island. Beginning anew in the north, we move south through 7 South Nake Islets, 11 Central Leeward Islets, and finally the 5 Southern Leeward Islets.

Because of the variety of islet shapes, "long" or "length" refers to the longest dimension lying parallel to the outer reef edge (normally north-south) and "wide" or "width" to the longest dimension perpendicular to the outer reef edge (normally east-west). South Island, the only exception, is considered to lie adjacent to the southern reef edge, so its "length" is measured east-west. Seabird numbers are from Part II, Table 1. For convenience in locating particular islets, the order is as follows:

1) NAKE (Fig. 37)	2) LONG (Fig. 38)
WINDWARD ISLETS	
3) Bo'sun Bird (Fig. 42)	4) Windward (Fig. 43)
5) Crescent (Fig.43)	6) Atibu (Fig. 43)
7) North Pig (Fig. 44)	8) Pig (Fig. 44)
9) Skull (Fig. 44)	10) North Brothers (Fig. 46)
11) Brothers (Fig. 46)	12) Noddy Rock (Fig. 47)
13) North Arundel (Fig. 47)	14) Arundel (Fig. 47)
15) Tridacna (Fig. 48)	16) SOUTH (Fig. 50)
SOUTH NAKE ISLETS	
17) Pandanus (Fig. 52)	18) Danger (Fig. 52)
19) Booby (Fig. 52)	20) Coral (Fig. 52)
21) Lone Palm (Fig. 52)	22) Kota (Fig. 52)
23) Mouakena (Fig. 52)	
CENTRAL LEEWARD ISLETS	
24) Mannikiba (Fig. 53)	25) Blackfin (Fig. 54)
26) Matawa (Fig. 54)	27) Emerald (Fig. 54)
28) Shark (Fig. 55)	29) Scarlet Crab (Fig. 55)
30) Nautonga (Fig. 55)	31) Azure (Fig. 55)
32) Reef-flat (Fig. 55)	33) Bird (Fig. 55)
34) Fishball (Fig. 55)	
SOUTHERN LEEWARD ISLETS	
35) Raurau (Fig. 57)	36) Eitei (Fig. 57)
37) Pisonia (Fig. 57)	38) Kimoa (Fig. 57)
39) Ana-Ana (Fig. 57)	

1) <u>NAKE ISLAND</u> (91.72 ha) Figs. 30, 37; Pls. 17, 22, 35-37, 43

History: Nake's large size and underground water lens, coupled with topography and soils more varied than elsewhere on Caroline, attracted Polynesian settlers. Because early European visitors stayed primarily on South Island, there is only a single reference to *Cocos* prior to the late 19th century (1 tree seen in 1825 by Paulding 1831).

The far northwest of Nake (also North Island in Young ca. 1922) houses the only true archaeological site on Caroline--a large *marae* (Figs. 3, 37; Pl. 36). Discovered during the guano era, the site is marked as "graves" on Arundel's map. Arundel, who was living on the atoll when the *marae* was discovered, describes it thus: "On the north-west end of Caroline are some curious old native remains, whether places of burial or of sacrifice I cannot determine. I opened one of these, but could find no indication whatever to guide me in a decision" (Arundel 1890). AKK, R. Falconer, and G. Wragg located, measured, and photographed this *marae* in 1990. The entire courtyard was approximately 18 m long by 14 m wide. All 10 peripheral stones and the central one were easily identifiable from the 1883 plan (Fig. 3), although a few had fallen over or broken due to encroaching vegetation. The lower wall, partly destroyed by Arundel, had not been reconstructed. It is probable

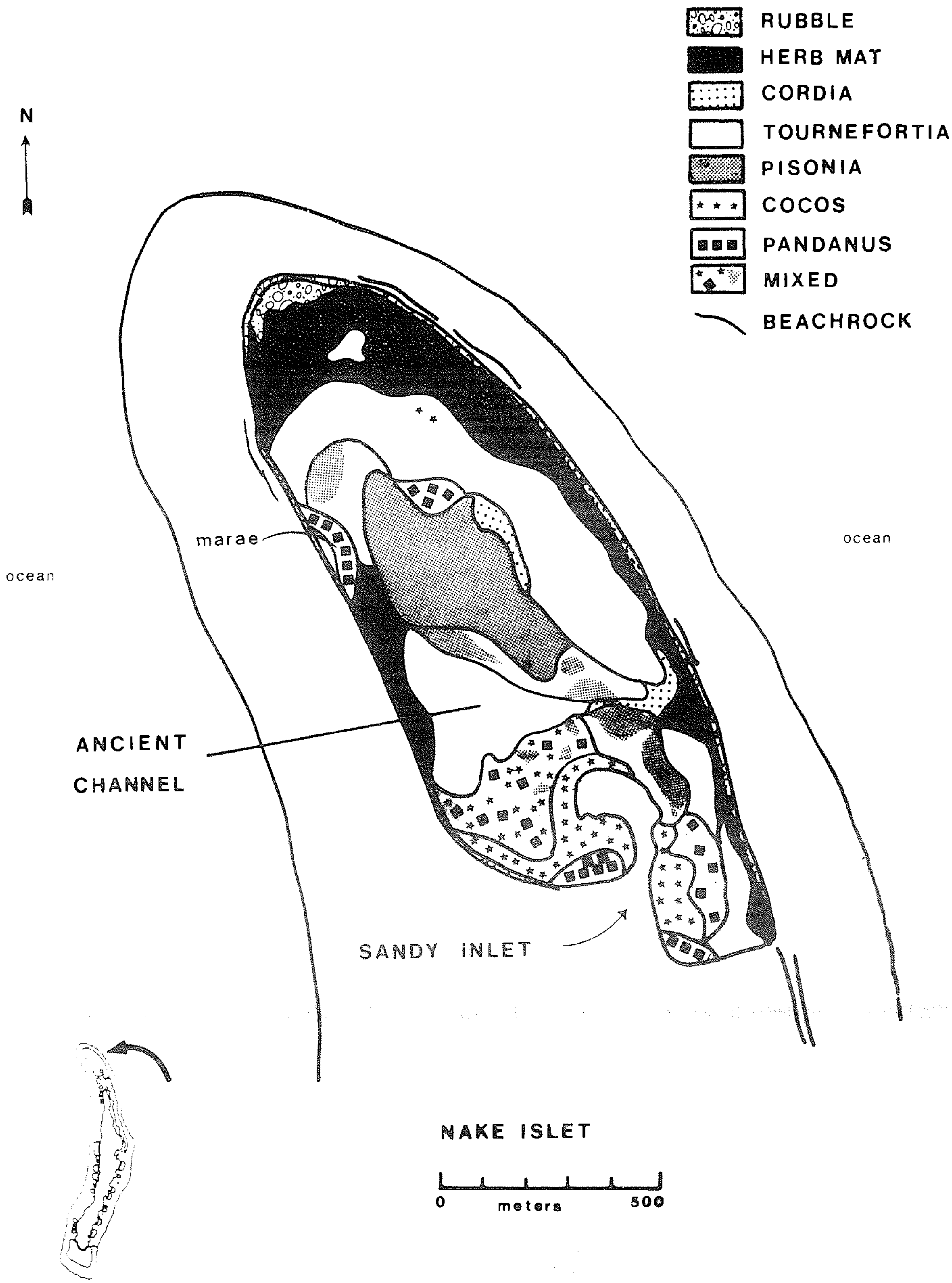

Figure 37. Nake Island: vegetation and physiography.

that this *marae* had not been seen since the 1880s; though discussed by Emory (1947), he never visited Caroline personally.

Northwest Nake is particularly suitable for a place of worship and sacrifice: it fits most of the environmental criteria indispensable to ancient Tuamotuan religious ritual (Emory 1947). First, flat ground was necessary, preferably lying at right angles to, or parallel to, the lagoon. Second, it was important to have the wind blowing across the *marae* to waft away the smells of sacrificed animals. Third, ceremonial items included branches of the *Pisonia* tree, leaves of *Cocos* (for leaf charms/"rosaries"), and the aerial roots of *Pandanus*. Fourth, feathers from "black terns" (Black Noddy), frigatebirds, and Red-tailed Tropicbirds were also necessary for rituals. Rather than a smooth substrate, the early Polynesians would have had to be content with leveled coral rubble and distance from the lagoon. The only organism not living near the *marae* today is the tropicbird; however, their elongated tail feathers could have been plucked from adults nesting on nearby motus.

Since *marae* are sacred places, there is possibly a significance to the location of the main "courtyard" close to the atoll's northern tip. It is well known that the northern extremities of islands were auspicious places for all Polynesians; in such places, they believed, disembodied spirits were whisked to the netherworld.

In 1938 a cistern was built in southwest Nake, which is still visible (see Sect. D, Hydrology). We failed to find evidence of occupation, but in September 1974 there was "a small, barely-furnished thatched hut," a stack of approximately 3 tons of copra on a raised platform, and a "three fathom canoe of Polynesian construction" (Ward 1974).

Physiography: Largest in area, Nake is the northernmost motu, separated from Long by a 40-m channel (Pl. 17). With maximum dimensions 2,000 m long and 685 m wide, it is basically rectangular with rounded corners and a peninsula-like extension in the southeast.

Nake lies north of the lagoon, having a southern, dry "bay" (Sandy Inlet), in which silt, sand, and fine coral debris are being actively deposited (Pl. 22). This hard, flat expanse of silty and sandy sediments is 145 m wide at its mouth, extending 200 m north into the main islet. Its 3.50 ha provide a favorite feeding location for shorebirds, especially Bristle-thighed Curlews. If Arundel's chart (Fig. 4) is correct, Sandy Inlet has increased its land area during the last century.

On the reef flats off the west side are extensive remnants of jagged upraised reef of unknown age (Pl. 11) and occasional beachrock. The exposed beaches and reef flats at Nake's north point are especially broad, characteristic of reef flats at the exposed corners of islands. Comparisons of the northern sweep of rubble on recent aerial photos with Arundel's map indicate that much coral debris, curved shingle ridges (Pl. 16), has been added since 1883. This area, the northernmost tip of the atoll, is subjected to heavy wind, wave and swell action. It is possible that particular ridges can be attributed to individual storms as has been documented for some other atolls (Stoddart & Steers 1977). In 1990, the deep, fine coral rubble mixed with sand east of the *marae* yielded 3 old turtle nests. Overall, only 6% of the land area was unvegetated. However, sparsely vegetated expanses of hardpan occupied the south-central sector (immediately inland of the coast within a belt of *Tournefortia* forest), and pure sand at least to 0.5 m deep bordered Sandy Inlet.

Nake's windward coast, complete with a peaked beach crest and discontinuous beachrock, is 30 m wide in the north, narrowing to 3 m in the south. Offshore, submerged reef flats form a sandy moat.

In the distant past, Nake consisted of 2 separate motus: aerial photos (Frontispiece) reveal an oblique, ancient channel about two-thirds of the way down the isletwhich is now well vegetated centrally but scrubby peripherally.

Vegetation: Before the major clearing for coconut plantations, Nake's native forests were "80 to 100 feet high" (Arundel 1875). Today there are 16 plant species (5 trees, 1 shrub, 10 herbs), 62% of Caroline's flora. It is the lushest motu, with woodlands (82.39 ha) about 80% native and 20% *Cocos* (Pl. 37). Although in 1916 there were about 260 palms, and the entire island was evidently planted with 10,544 palms in 1918-1919 (Young ca. 1922, Table 13), substantial tracts of each major vegetation type occur today. Its interior is rich in *Pisonia*, with the largest acreage (20.79 ha) and some of the tallest trees (20 m high) and largest trunks on the atoll (Pl. 43, Table 11). In addition, *Cordia* is well-represented: 2 major groves of *Cordia-Tournefortia* forest occupy 11.8 ha, 2% of Nake's area. Extensive pioneer herb mats, flanked on their inner sides by *Tournefortia* scrub, occur in the north and east. The remaining *Cocos*, essentially in the southern quarter, comprise Caroline's second largest coconut grove.

Birds: Nake, with 80% of Caroline's breeding seabird species, shows a direct correlation between islet size and bird species diversity. Nine species of seabirds breed, all with larger populations (pairs) than previously reported (Clapp & Sibley 1971a): Masked Booby (105), Brown Booby (1), Red-footed Booby (496), Great Frigatebird (522), Lesser Frigatebird (56), Brown Noddy (390), Black Noddy (814), Sooty Tern (nesting in 1989; Anne Falconer, pers. comm.), and White Tern (1,094).

2) <u>LONG ISLAND</u> (75.98 ha) — Figs. 30, 35, 38-41; Pls. 9, 17, 19, 27, 32, 47, 54

Third largest in area, this longest of motus covers nearly one-third of the atoll's windward side. In the north it is separated from Nake by a narrow channel; from its southern tip a chain of smaller motus extends south along the windward reef.

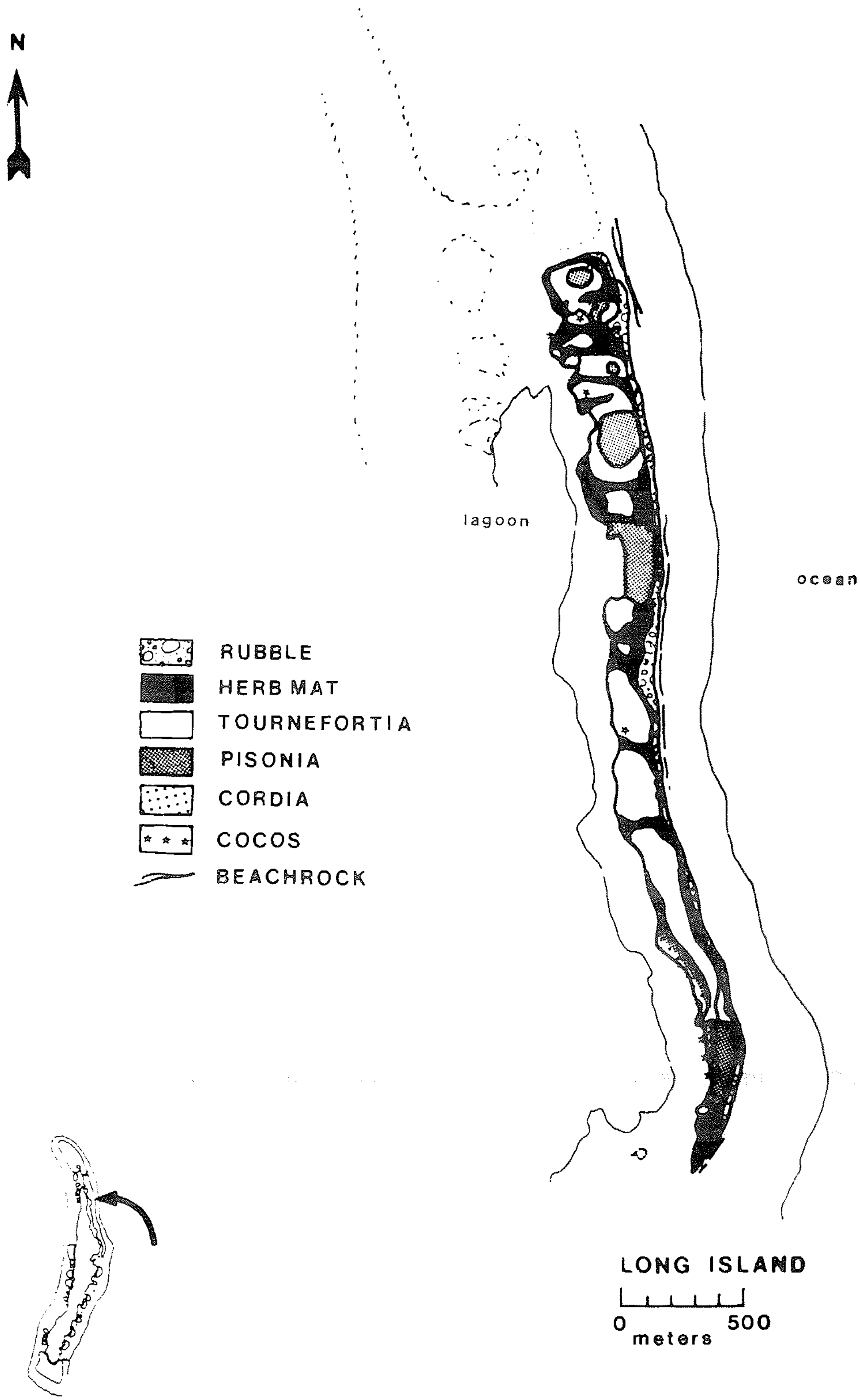

Figure 38. Long Island: vegetation and physiography.

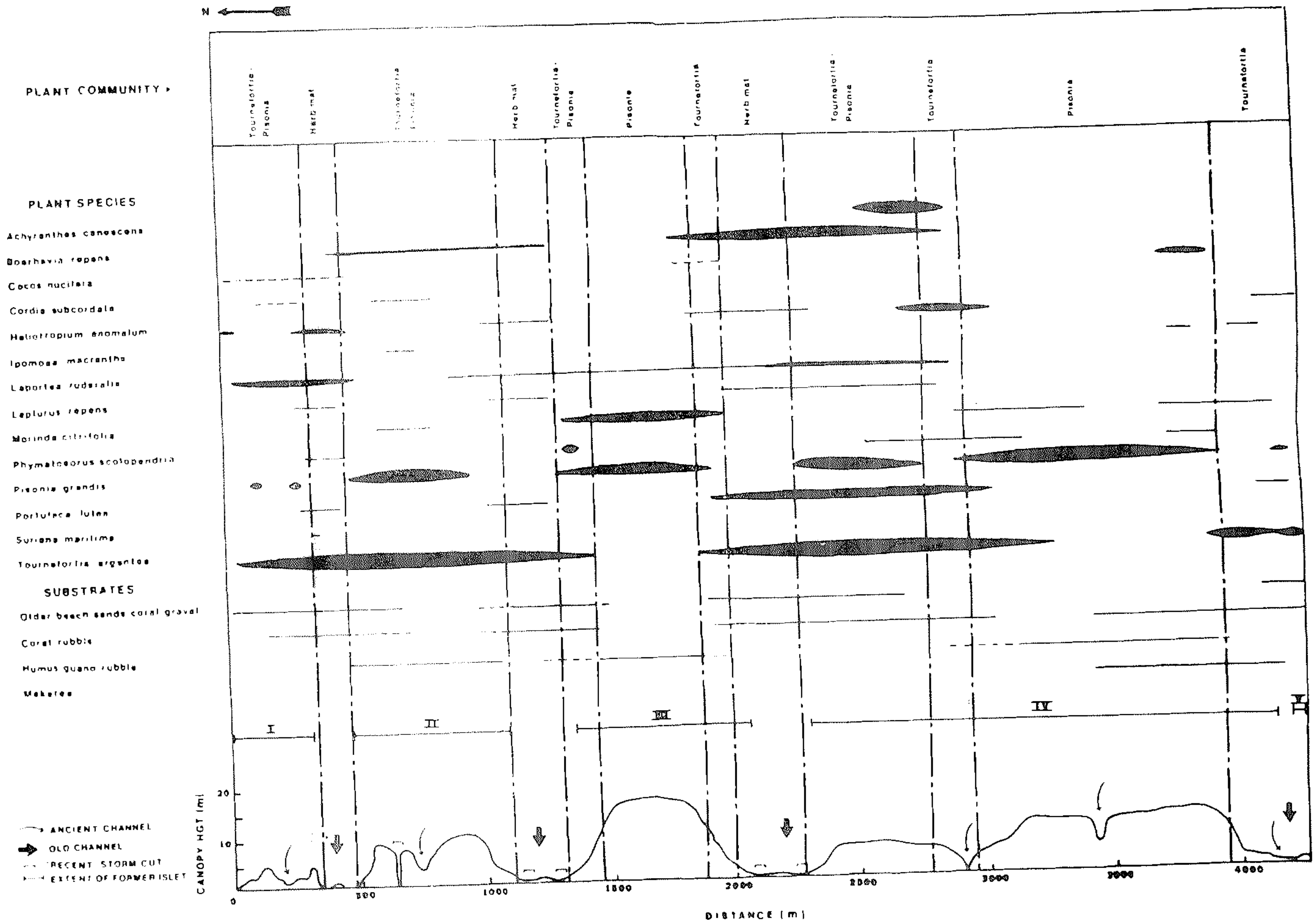

Figure 39. Long Island: north-south transect showing division into former islets, floristic composition, relative abundance of plant species, degree of species overlap, and canopy heights. Vertical height is exaggerated. The exact locations of the formerly more extensive *Cocos* plantations are unknown.

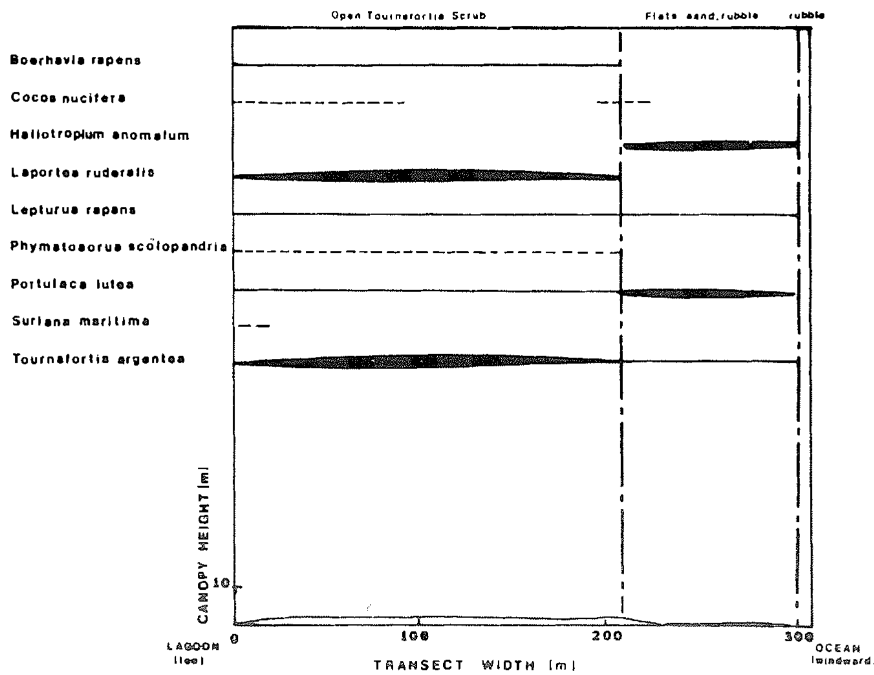

Figure 40. Long Island: east-west cross-section through Transect C, a former inter-islet channel, showing floristic composition, relative abundance of plant species, degree of species overlap, and canopy heights. Vertical height is exaggerated.

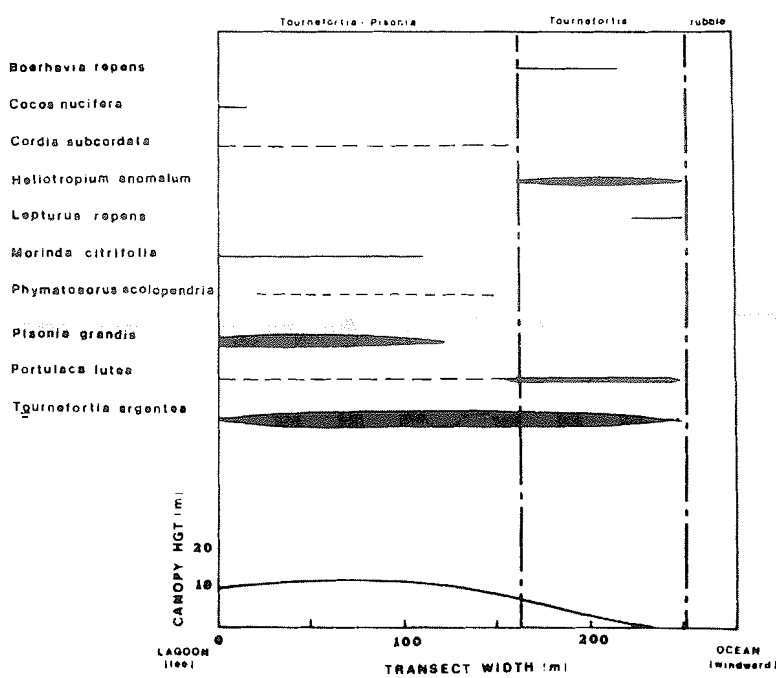

Figure 41. Long Island: east-west cross-section through Transect B, which passes through mature interior *Pisonia* forest of largest of Long's coalesced motus. Data includes floristic composition, relative abundance of plant species, degree of species overlap, and canopy heights. Vertical height is exaggerated. Note the absence of low vegetation on the leeward shore.

Physiography and History: Long, 4,226 m long and 330 m wide, is somewhat snake-shaped, with an enlarged northern "head" and attenuated "tail." From a distance its vegetation appears as a series of humps. Long has experienced a fairly complex geological history, noted by the Solar Eclipse Party: "On some of the islands there are spaces void of vegetation, extending from lagoon to beach, which indicate the existence at a former time of a water separation" (Holden & Qualtrough 1884).

At present, Long is composed of 5 distinct former motus separated by sparsely vegetated channels of coarse sand and coral gravel. Aerial photographs also reveal further, older subdivisions (see below). Coalescence and fracturing of the original motus probably occurred repeatedly. Since erosion proceeds faster on an atoll's windward reefs, providing coral fragments, coralline algae, and pulverized molluscs, it is no surprise that the first series of Caroline's motus to fuse were those facing this rich source of parent material.

Long's coarse rubble beaches (Pl. 19) are a mirror image of those on Nake: they widen progressively southward. The swath of unvegetated rubble above high tide line in the upper two-thirds of Long averages 8 m wide, while in the lower third it is 40 m wide. Unvegetated coral debris accounts for 10% of the island's area (Fig. 30). Beachrock, flanking the windward shoreline for most of its length, is more abundant than elsewhere (Pl. 54).

Long's lagoon flank is edged with submerged sand and silt, and is one of the most sheltered parts of Caroline. Sand and rubble deposition off the south point has formed a lagoon islet (Bo'sun Bird), which could, in the future, coalesce with Long's south point to form a hook.

An uncommon substrate on Caroline, upraised reef forms a low rampart (generally <1 m high) paralleling the ridge crest inside the vegetation for much of the lower quarter of Long. Although we camped in this area and conducted 4 transects through this upraised reef, we found no plant species that indicated the presence of *feo*, such as can be found in the Tuamotus (Fosberg, pers. comm.).

In 1990 G. Wragg found some scattered large stones, similar to those of the Nake *marae*, located centrally 100 m north of the southern tip of Long, confirming the report of the remains of a smaller *marae* on Long Island (Holden & Qualtrough 1884). Wragg noted that the *marae* was small, measuring approximately 3 m wide by 8-10 m long. Its orientation appeared to be northeast-southwest. The wall on one end was evidently smashed by storm waves. Only 2 of the peripheral upright stones were standing, of similar size to those on Nake. The platform was in reasonable condition, with a huge *Pisonia* tree growing through it. Some rock slabs were large (2 x 2 m). The entire *marae* was situated within a *Pisonia* grove, with nearby *Cocos*. We do not know if this coconut grove (1.6 ha) was present before 1,343 palms (20% of the islet's area) were planted in 1918-19 (Young ca. 1922). The sheltered location and a *Pisonia-Cocos* forest, which suggests an old clearing, further indicate prior occupation.

In 1990, Wragg also uncovered an RNZAF survey marker just inland of Long's southernmost tip.

Vegetation: There are 15 plant species (4 trees, 2 shrubs, 9 herbs), on Long, 58% of the total flora. Long's variety of habitats, vegetation heights, substrata, and birds make it the most diverse islet on Caroline. Only 3% of its area remains in *Cocos*. All the atoll's seabirds have bred here. Its ecology is best understood with reference to Figures 35 and 39-41.

Within the basic pattern of 5 coalesced motus, it may be seen that:

1) From north to south (measured from the midpoint of each former channel) the motus, of divergent size and shape, are approximately 320, 620, 700, 1,840, and 100 m long.

2) Each former motu, crowned by *Pisonia* forest, contains concentric rings of decreasing fertility around its core and is morphologically similar to motus surrounded by water, except that the coarse coral gravel along the former perimeter is less marked. More specifically, beach sands and gravel extend for 200-300 m north and south of the old channels, after which they increasingly accumulate coral rubble, humus, and guano.

3) *Tournefortia* dominates, interspersed with 4 patches of taller *Pisonia* forest and scattered clumps of *Cocos* and *Cordia*. Interrupted herb mats parallel the windward coast and often extend across the island along former interislet channels (Pl. 32). Vegetation height varies from 2 cm to 15 m.

4) Plant species diversity is highest in *Tournefortia-Pisonia* and lowest in *Pisonia* forests.

5) Long's tallest, most mature *Pisonia* groves (up to 100% *Pisonia*) occur on the largest of the former islets. The *Pisonia* forest near the south end (Tr. 10), although healthy, is only 12 m tall. This may be due to its impoverished upraised pitted reef substrate barely covered with "soil." Since it lies adjacent to Long's most luxuriant *Cocos* grove, its land could well have been cleared in 1918-19, with the *Pisonia* forest taking longer than elsewhere to recuperate. Because tern guano increases soil fertility, contributing to *Pisonia* growth, it is of interest that neither Black nor Brown Noddies nested here.

6) Deep dips in Figure 39 (lower graph) correspond to east-west corridors formed from old channels. Vegetation in these relatively infertile, sandy flats is low, similar to that on small developing motus (i.e. native herbs with scattered *Tournefortia* <2 m high). One sandy channel (Tr. C, Pl. 32) supported sparse *Suriana*. During the February 1990 cyclone, all vegetation was either uprooted, washed away, or smothered with fresh sand and coral gravel along Transects A and C (Pl. 33). Storm erosion was particularly marked within the channel that almost bisects the island (Tr. A).

7) Secondary dips mark even older interislet channels ("ancient channels"), visible on aerial photographs (Frontispiece) but barely recognizable in the field. They are overgrown with *Tournefortia* and/or *Pisonia*.

8) Sharp dips within established forests or herb mats denote relatively recent channels gouged out by storms ("recent storm cuts"). These were also altered during the winter 1990 storm.

Figures 40 and 41 illustrate some differences between the windward and leeward coasts. Transect C (Fig. 40) crosses the north end of Long through an old interislet channel now filled with sand and rubble. Its low profile reflects the simple habitat harboring halophytic herbs and *Tournefortia* shrubs less than 2 m high. Although the shrubs are scattered, the lagoon half of the transect passes through slightly higher ground, which encourages denser *Tournefortia*. This transverse section is similar to that of a formative motu such as Fishball (Fig. 56). This exposed, scrubby swath, 300 m wide, harbors Red-footed Boobies, Great Frigatebirds, and a discrete population of Masked Boobies. Approximately 127,000 pairs of Sooty Terns nested in a similar sandy channel 740 m to the south (Tr. A) in 1988.

Transect 8 (Fig. 41) crossed the islet nearer the southern tip (Fig. 8). This profile departs significantly from the usual parabolic cross-section seen on most of the small motus and which exists further north on Long Island. From east (windward) to west, there is first a wide expanse of coarse, unvegetated rubble, followed by rubble dotted with herbs, then *Tournefortia* scrub increasing to 9 m high. Further inland, a forest of 10-m-high *Tournefortia*, *Pisonia* and *Cordia* continues westward to the lagoon. This leeward margin of Long, extending southward nearly to its tip, is the only location on Caroline where tall, indigenous vegetation overhangs and shelters the lagoon. No herb mat is present.

In summary, Long contains examples of all major plant communities, as well as 2 minor ecosystems, *Pisonia-Cordia* (3.2 ha) and *Cocos-Cordia* (0.82 ha). Its woodlands total 49.60 ha. Coconut crabs inhabit all areas containing *Cocos* and *Pisonia*; our rough population estimate is 200.

Birds: In 1988 Long supported 9 (10 in 1965) species of breeding seabirds, as follows (pairs): Red-tailed Tropicbird (5), Masked Booby (69), Brown Booby (12), Red-footed Booby (659), Great Frigatebird (808), Sooty Tern (179,800), Brown Noddy (207), Black Noddy (986), and White Tern (751). From 1988 through 1990, Sooty Terns occupied 19 large colony sites (Fig. 11, Pt. II).

Comments: Polynesian rats were abundant, especially in *Cocos* and *Pisonia* habitats. It was often possible to see 3 or 4 simultaneously while conducting daily surveys, and 20 or more around camp. At night, their numbers increased substantially. Azure-tailed skinks (*Emoia cyanura*) were noted.

WINDWARD ISLETS

This chain of 13 islets occupies the southern half of Caroline's east coast. All rest on the same reef flat, separated by channels varying in width and depth. They can be waded with care at low tides, but most harbor black-tipped reef sharks: up to 4 were visible in the shallows within 50 m of an observer. Several motus have altered shape since 1883, including Brothers, which has incorporated a small cay into its present confines.

The motus range in size from Noddy Rock (0.02 ha) to Windward (11.42 ha). They support every major vegetation type from simple herb mats to *Pisonia* forests, 21 m tall. Because of their constant exposure to trade winds, the seaward vegetation is wind- and salt-shorn. Though appearing primarily untouched, all of the Windward Islets were planted with *Cocos* (Table 13) from 1916-20 (Young ca. 1922). However, these incipient plantations experienced difficulty and appear to have been abandoned within a few years, and their vegetation recovered remarkably (see Sect. G).

Flanking the lagoon of the southern motus (Brothers through Tridacna), and extending westward, are reefs densely studded with *Tridacna* clams, which add to Caroline's outstanding natural assets (Pl. 25; Pt. II, Sect. G).

3) BO'SUN BIRD ISLET (0.86 ha) Figs. 29, 42

We named this motu for its Red-tailed Tropicbirds, commonly called Bo'sun birds. The sizeable population is the largest on Caroline. In addition, our 1988 records constituted the first known breeding of this species on the atoll.

Physiography: Bo'sun Bird Islet, 165 m west of Long's southern tip, is the only motu lying within Caroline's lagoon. It shares the same reef as Long, however, and is not a true "lagoon motu."

Amoeboid in shape, Bo'sun Bird is greatly affected by the tidal waters that spread across the shallow reef flats and gush through the channels separating Long and Windward. Because it sits near the inner edge of a wide windward reef flat, the layering of sediments around it is complex and transitory; our observations indicate that more rubble was deposited on the islet's western edge since the aerial photos were taken in 1985. Its western shoreline rises gradually to a high water mark, and slight changes in water level greatly change its overall size and shape. At high tide its perimeter is ovoid with a long westerly extension. The "head" is approximately 70 m wide and 115 m long, while the "nose" is 45 m long and 15 m wide.

Vegetation and Birds: Bo'sun Bird Islet, composed of coral rubble and sand, supports only natural herb mats (*Heliotropium, Portulaca, Lepturus*) and *Tournefortia* scrub (to 4 m tall). These 2 simple plant communities cover 35% and 55% of the land area, respectively. For its

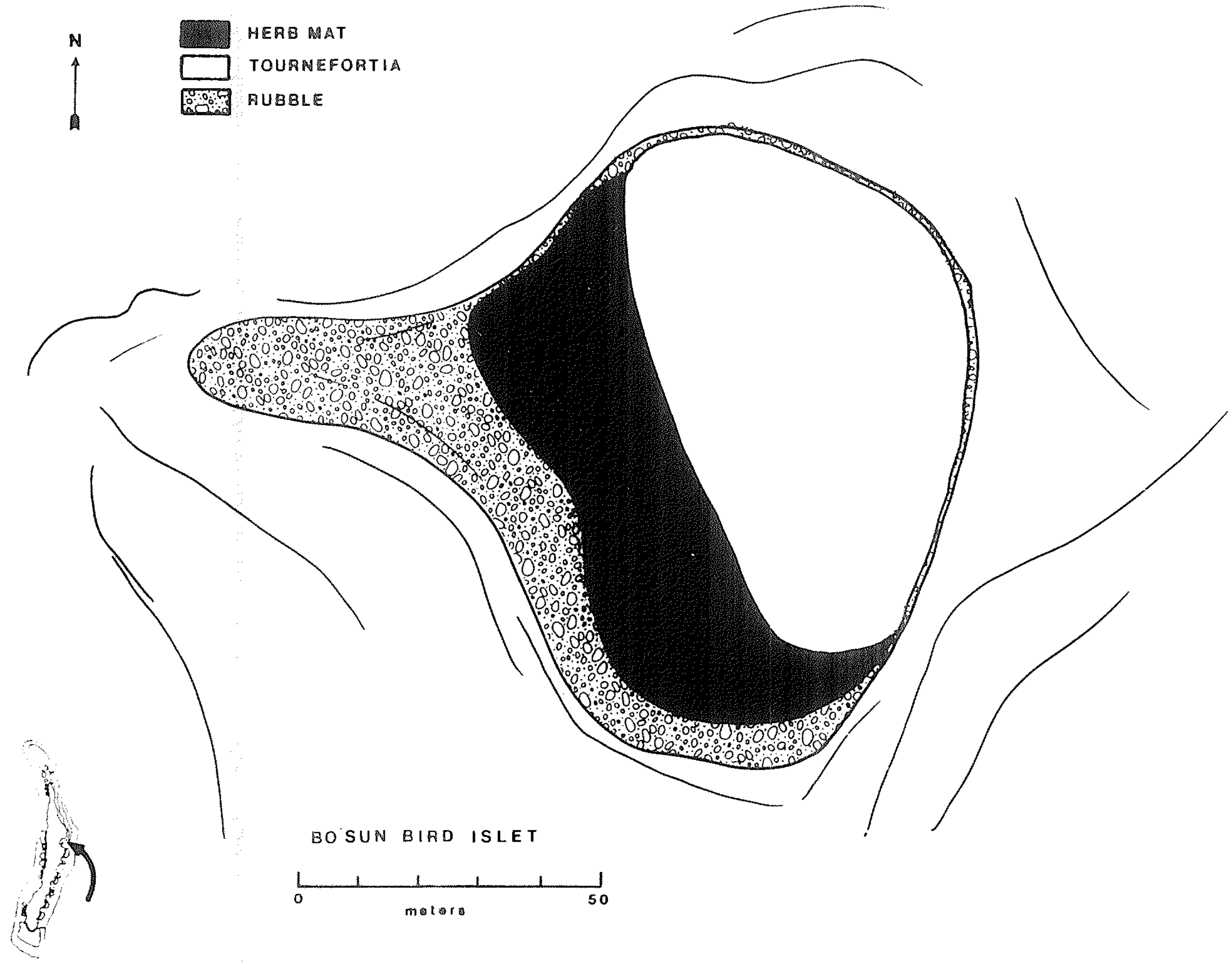

Figure 42. Vegetation and physiography of Windward Islet no. 1: Bo'sun Bird Islet. Scale is larger than on the vegetation maps of other islets.

size, the motu is sparsely vegetated, with only 4 plant species (1 shrub, 3 herbs), 15% of Caroline's total flora. There are no introductions.

Bo'sun Bird's most notable attributes are its 4 species of breeding seabirds: Red-tailed Tropicbird (47 pairs in 1988, 130 pairs in 1990), Sooty Tern (8,400 pairs), Brown Noddy (10 pairs), and White Tern (6 pairs).

4) **WINDWARD ISLET** (11.42 ha) Figs. 29, 43

We named this "Windward" because it is the first major, and largest, Windward Islet.

Physiography: Broadly crescentic in shape, 508 m long by 287 m wide, it parallels the reef's longitudinal axis and is set close to the lagoon. Its seaward beach is quite narrow (3 m wide); there is no lagoon beach.

Vegetation: Windward has 11 species of plants (3 trees, 1 shrub, 7 herbs), 42% of the total flora. A windward crescent of halophytic herbs borders a zone of *Tournefortia* scrub, which mixes quite densely with *Pisonia* and *Cordia* over most of the interior in a bilobed pattern. These latter forests, reaching 14 m high in the south and 9 m in the north, total 8.67 ha. This unusual distribution of central forests undoubtedly reflects *Pisonia*'s recovery from 100% land clearing for *Cocos*--1,299 palms--in 1920 (Young ca. 1922, Table 13). It is remarkable that not one *Cocos* remains as a legacy of this disturbance.

The east-west profile of Windward, similar to that of Transect 8, Long Island (Fig. 41), is typical of most motus, except that lagoon-facing herb flats are almost nonexistent. *Scaevola taccada* var. *taccada*, a new plant record for the atoll, was only found on this motu, although *S. t.* var. *tuamotensis* was found on South Island in 1990.

Birds: Five species of breeding birds were present, all in appreciable numbers (pairs): Red-footed Booby (163), Great Frigatebird (207), Brown Noddy (20), Black Noddy (28), and White Tern (134).

Comments: In May 1990, AKK noted a possible motu midway between Windward and Crescent Islets during midtide. It appeared an upraised reef platform like Noddy Rock, but because of extensive shallow reticulate reefs in this area, its presence at high tide has not yet been confirmed.

5) **CRESCENT ISLET** (3.10 ha) Figs. 29, 43

We named this islet for its cupped shape.

Physiography: Crescent Islet is 190 m long by 225 m wide. It is almost entirely composed of coral rubble, with a little humus in the interior. The seaward beach is variable (up to 50 m wide), the lagoon beach, insignificant.

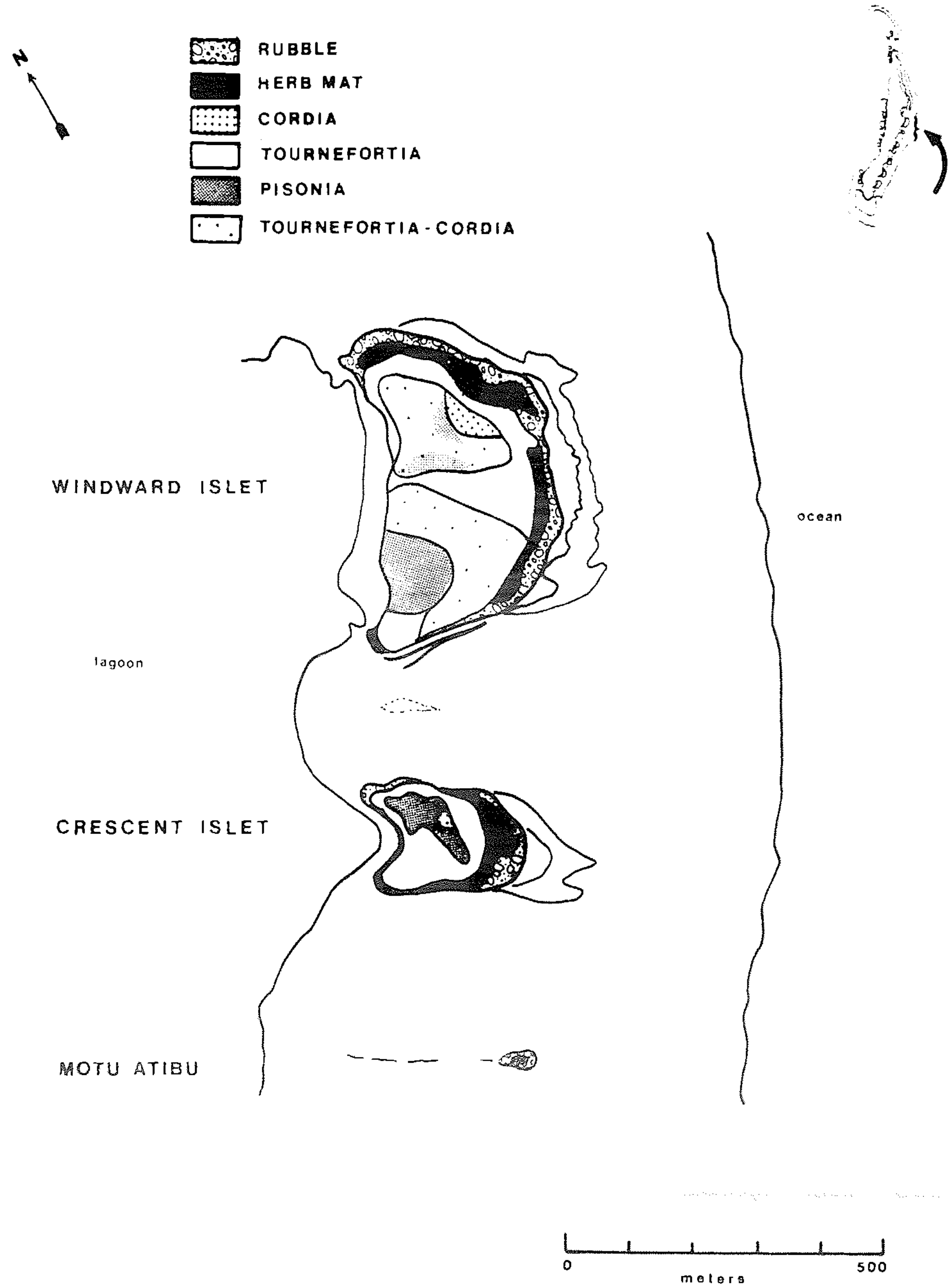

Figure 43. Vegetation and physiography of Windward Islets nos. 2, 3 and 4: Windward and Crescent Islets, and Motu Atibu ("Coral Rubble Islet"). Atibu appears to have been severely damaged during the February 1990 storm.

Vegetation: There are 10 species (3 trees, 1 shrub, 6 herbs), 39% of Caroline's flora. No introduced plants occur. Plant diversity is poorer than on Windward, a reflection of small size, poor soils, and scant herb mats. However, woodlands cover two-thirds of its area, and the central stand of *Pisonia* and *Cordia* is 87 m wide and up to 13 m high. Crescent was heavily planted (80% of total area, 228 palms) in *Cocos* in 1920 (Table 13), but today none remain.

Birds: Crescent Islet was used by the following numbers of breeding pairs: Red-footed Booby (28), Great Frigatebird (5), Brown Noddy (36), Black Noddy (60), and White Tern (8).

6) <u>MOTU ATIBU</u> (**"Coral Rubble Islet"**) (0.02 ha) Figs. 27, 43

Motu Atibu was Caroline's smallest and least vegetated islet. Third in the windward chain, it measured 13 x 18 m. We named it for its basic rubble character. Vegetation covered only 2% of the land surface and consisted of a few *Tournefortia* shrubs (<1 m high) encircled by narrow swaths of low herbs and rubble. Its 3 plant species (1 shrub, 2 herbs)--12% of Caroline's flora--were among the most meager on the atoll. Atibu's profile was similar to that of Fishball (Fig. 56). There were no breeding birds.

Comments: Since a February 1990 storm, Atibu has apparently disappeared, having been reduced to a thin strip of coral gravel below high tide level.

7) <u>NORTH PIG ISLET</u> (5.44 ha) Figs. 29, 44; Pls. 55

We named the fourth windward islet "North Pig" for its location immediately north of Pig Islet.

Physiography: Classically crescentic, North Pig is 350 m long and 230 m wide. Though approximately half of Pig's area and less wooded overall, North Pig has a similar distribution of sediments (including sand on the lee side), vegetation, and breeding birds. Profiles of the 2 motus are nearly identical (Fig. 45).

Vegetation: There are 11 plant species (3 trees, 1 shrub, 7 herbs), 42% of Caroline's flora. No introduced plants are present. Proceeding south along the windward islets, lagoon-side herb mats develop and islet cross-sections assume a more perfect symmetry--low at the edges and forming a hump in the middle.

North Pig's 3 vegetation zones are predictably symmetrical: a peripheral band of herbs (more extensive on the "horns"), curved belts of *Tournefortia*, and a spacious central forest of mixed *Pisonia*, *Cordia*, and *Tournefortia*. The latter (to 20 m tall) covers more than one-half the islet's width and one-third its area, and includes fine *Cordia* groves (Fig. 44). This excellent forest is surprising because 402 *Cocos* palms were planted on 93% of North Pig's usable land in 1920 (Young ca.

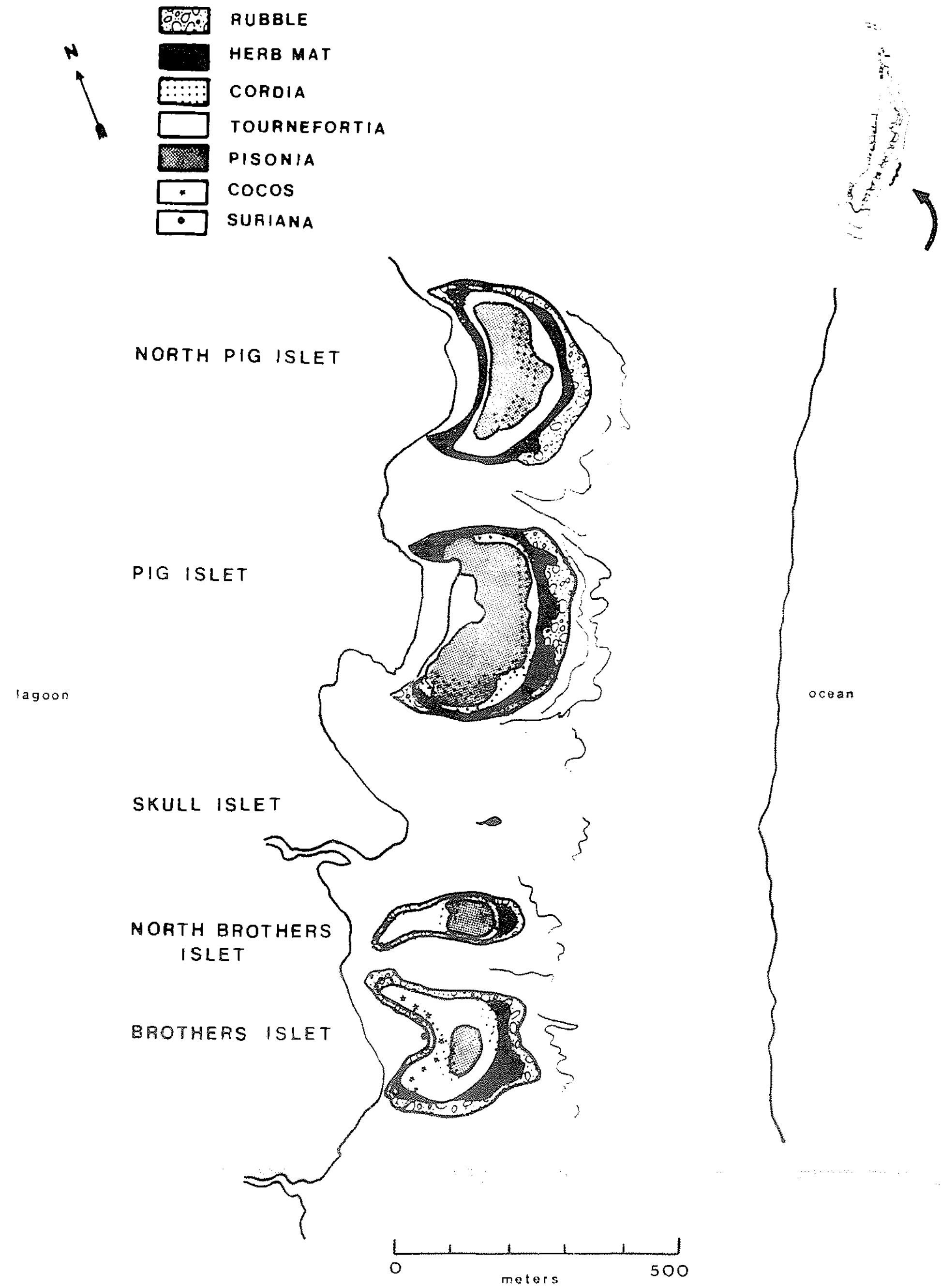

Figure 44. Vegetation and physiography of Windward Islets nos. 5 through 9: North Pig, Pig, Skull, North Brothers, and Brothers Islets. Note the reefs extending westward into the lagoon.

1922, Table 13). Measurements from 25 *Pisonia* trees (main trunks) averaged 19 m in height, 221 cm cbh and 261 cm in base circumference (Table 12).

Birds: Five species of seabirds bred: Red-footed Booby (31 pairs), Great Frigatebird (17 pairs), Brown Noddy (76 pairs), Black Noddy (3,199 pairs), and White Tern (110 pairs). The largest colony of Black Noddies on Caroline nested in the tall *Pisonia*s.

Comments: Rats and coconut crabs were common.

8) <u>PIG ISLET</u> (7.21 ha) Figs. 29, 44; Pls. 26, 41, 50, 55

Number 5 down the chain, Pig was named prior to 1883. Domestic pigs were introduced to Caroline in 1828 by Captain Stavers but evidently died out before 1834. Reintroduced in 1848 with the first recorded settlers, it is not known how long they lasted. One would expect that they were only on South Island, but the statement that "about one-third the distance up the lagoon a canvas hut exists on one of the smaller islets on the eastern side of the lagoon" (Holden & Qualtrough 1884) suggests that perhaps domestic animals also inhabited Pig. Though this is weak evidence, there must have been some reason for this curious name. Today no pig devastation is evident anywhere on the atoll.

Physiography: Bean-shaped, Pig is 330 m long and 255 m across. It is separated from North Pig by a channel 60 m wide.

Vegetation: The islet has 11 plant species (4 trees, 1 shrub, 6 herbs), 42% of Caroline's flora. *Cocos*, the only introduction, is rare (0.03 ha). In 1920, 538 palms were planted (Young ca. 1922), which covered approximately 79% of Pig's usable area (Table 13).

Pig's vegetation profile (Fig. 45) is classic: a wide, windward herb mat, bordered by *Tournefortia* and *Cordia*, which, in turn, grades rapidly into an outstanding *Pisonia* forest (to 21 m tall, 3.36 ha), one of Caroline's best groves. Measurements from 5 trees, mostly multiple-trunked, averaged 16 m in height, 338 cm in circumference (at 1.5 m), and 282 cm in base circumference (Table 12). This *Pisonia* also occupies the largest proportion (46%) of any islet area. It is striking that such quality forests could regenerate in about 65 years (see Sect. G). In the *Cordia* forest (Pl. 26), also the finest on Caroline, 6 trees averaged 12.6 m in height, 116 cm in circumference (at 1.5 m), and 99.8 cm base circumference. On the lee side of Pig, *Tournefortia* extends directly to the lagoon shore.

Birds: Five species of seabirds bred: Red-footed Booby (14 pairs), Great Frigatebird (118 pairs), Brown Noddy (82 pairs), Black Noddy (1,928 pairs), and White Tern (164 pairs).

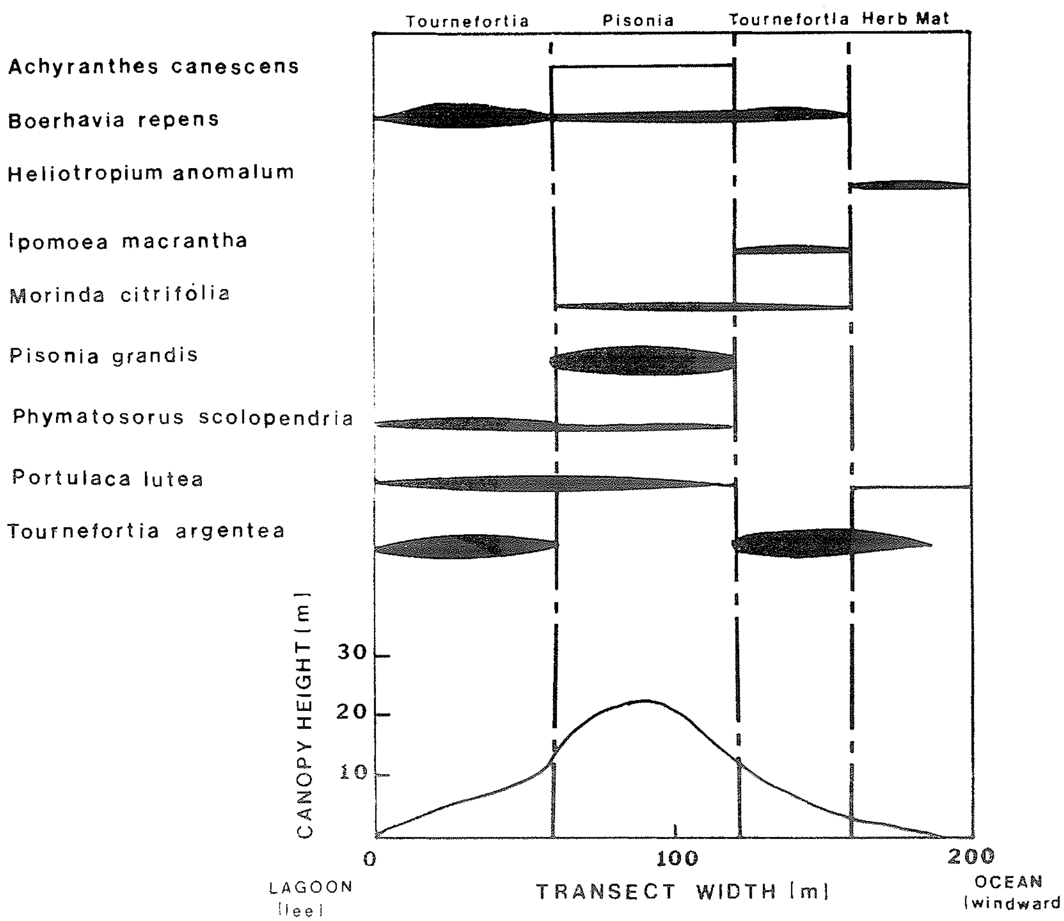

Figure 45. Pig Islet: east-west cross-section through center of islet. Data includes floristic composition, relative abundance of plant species, degree of species overlap and canopy heights. Vertical height is exaggerated. Pig's profile is especially symmetrical. It is remarkable that this islet was totally felled for coconuts in 1920.

Comments: Rats and coconut crabs were common. In 1990 a grayish gecko (possibly mourning gecko, *Lepidodactylus lugubris*) was seen by A. Garnett.

9) SKULL ISLET (0.02 ha) Figs. 27, 44; Pls. 46, 49

Sixth in the windward chain, we named Skull Islet after finding the skull, tail feather, and eggshell of a Red-tailed Tropicbird, the first evidence that this species bred on the atoll. A low shelf of coral rubble and sand, barely above high tide mark, this motu is barren except for a small herb mat under 5 *Tournefortia* bushes (1 m high) on the lagoon side. Only 2% of the surface area is vegetated. There are 3 plant species (1 shrub, 2 herbs), 11% of the atoll's flora. Although appearing young, the motu is marked on Arundel's chart (Fig. 4). After February 1990, several large storm blocks rested in the channel close to Skull Islet.

In 1988 there were no birds. However, in March 1990, a colony of 150 Brown Noddies was in a prelaying phase, accompanied by 6 Sooty Terns, a Brown Booby and a Wandering Tattler.

10) NORTH BROTHERS ISLET (1.71 ha) Figs. 29, 44; Pl. 55

The seventh windward motu, we named this islet North Brothers because of its location directly north of the named motu, Brothers.

Physiography: North Brothers is shaped like an oval that curves lagoonward toward Brothers, 40 m away. The concave shorelines and lack of herb mats on the opposite shorelines of these 2 islets suggest that they might have been formerly connected. Composed primarily of rubbly substrates, with slightly better soils centrally, it is 95 m long and 250 m wide.

Vegetation: Plant species number 10 (3 trees, 1 shrub, 6 herbs), 39% of Caroline's flora. A few *Cocos* trees are present, remains of the 180 planted in 1920 (Young ca. 1922), which covered 100% of all available land on the islet (Table 13). Plant communities on North Brothers are simple: *Tournefortia* (more open in the west) rises to an excellent *Pisonia* forest, 80 m wide and 18 m tall, on the east end. Average measurements from 3 *Pisonia* trees were: height 18 m, base circumference 314 cm, and number of trunks, 2.3 (Table 12).

Birds: Five species of seabirds bred on the islet in 1988 (pairs): Red-footed Booby (25), Great Frigatebird (9), Brown Noddy (23), Black Noddy (40, plus hundreds of old nests), and White Tern (69). In September 1989, Sooty Terns nested on the windward beach (Anne Falconer, pers. comm.), and in May 1990, a prebreeding swirl of thousands of Sooty Terns swarmed above Brothers and North Brothers.

Comments: Gecko eggs were seen on *Pisonia* trunks in 1990.

11) **BROTHERS ISLET** (4.31 ha) Figs. 29, 44, 46; Pls. 29, 55

The eighth windward motu, Brothers Islet was named last century after Captain Brothers, who managed a stock-raising venture on Caroline. In 1873 his rights to the atoll passed into the hands of John Arundel.

Physiography: Crescentic in shape, with longish horns extending toward the lagoon, Brothers Islet lies about two-thirds of the way down Caroline's windward reef. It is 198 m long x 178 m wide through the center. A *Tridacna* reef extends westward almost completely across the lagoon.

An interesting aspect of Brothers' structure is that Arundel's chart (Fig. 4) indicates a tiny, separate motu off the southwest point. Our survey and the 1986 aerial photos show that this motu is now joined to Brothers Islet. Its former identity is marked by a small patch of *Tournefortia*, around which the recently deposited sand and rubble is sparsely dotted with native herbs.

Vegetation: There are 11 plant species (4 trees, 2 shrubs, 5 herbs), 42% of Caroline's flora. *Cocos*, along the leeward shore, is the only introduced plant. Three distinct plant communities are present: peripheral herb mats (including leeward *Portulaca* with *Suriana*), *Tournefortia* scrub and forest (to 6 m high) bordered with *Cordia*, and a central *Pisonia* forest. Larger trees had up to 15 trunks and multiple root suckers. Measurements of 10 trees (main trunks) averaged 15 m in height, 140 cm in circumference (at 1.5 m), and 243 cm base circumference. Distances to nearest neighbor for 10 trees averaged 4.2 meters. As on its neighbor islets, the *Pisonia* forest on Brothers is striking, especially since it has matured to a closed-canopy monotypic stand devoid of any subcanopy species (Fig. 46), evidently in about 65 years. In 1920, Brothers Islet was planted with 315 *Cocos* palms, which covered approximately 97% of the usable land area (Table 13).

Birds: Four species of seabirds bred: Red-footed Booby (25 pairs), Brown Noddy (8 pairs), Black Noddy (15 pairs), and White Tern (50 pairs). In May 1990, large numbers of Sooty Terns swirled over Brothers and North Brothers.

Comments: Many mature *Pisonia* trees contained capacious cavities in their boles that housed large coconut crabs. In March 1990, several of these holes had feathered skeleta of Sooty Terns (and possibly also Brown Noddies) outside their entrances, along with freshly-snipped *Pisonia* branches (see Pt. II, Sect. F).

12) **NODDY ROCK** (0.02 ha) Figs. 27, 47; Pl. 18

We named this ninth motu in the Windward Islets for its only known breeding seabird, the Brown Noddy. In September 1988, at least 80 pairs were incubating their eggs on the *Portulaca* mat that covers its central lee section.

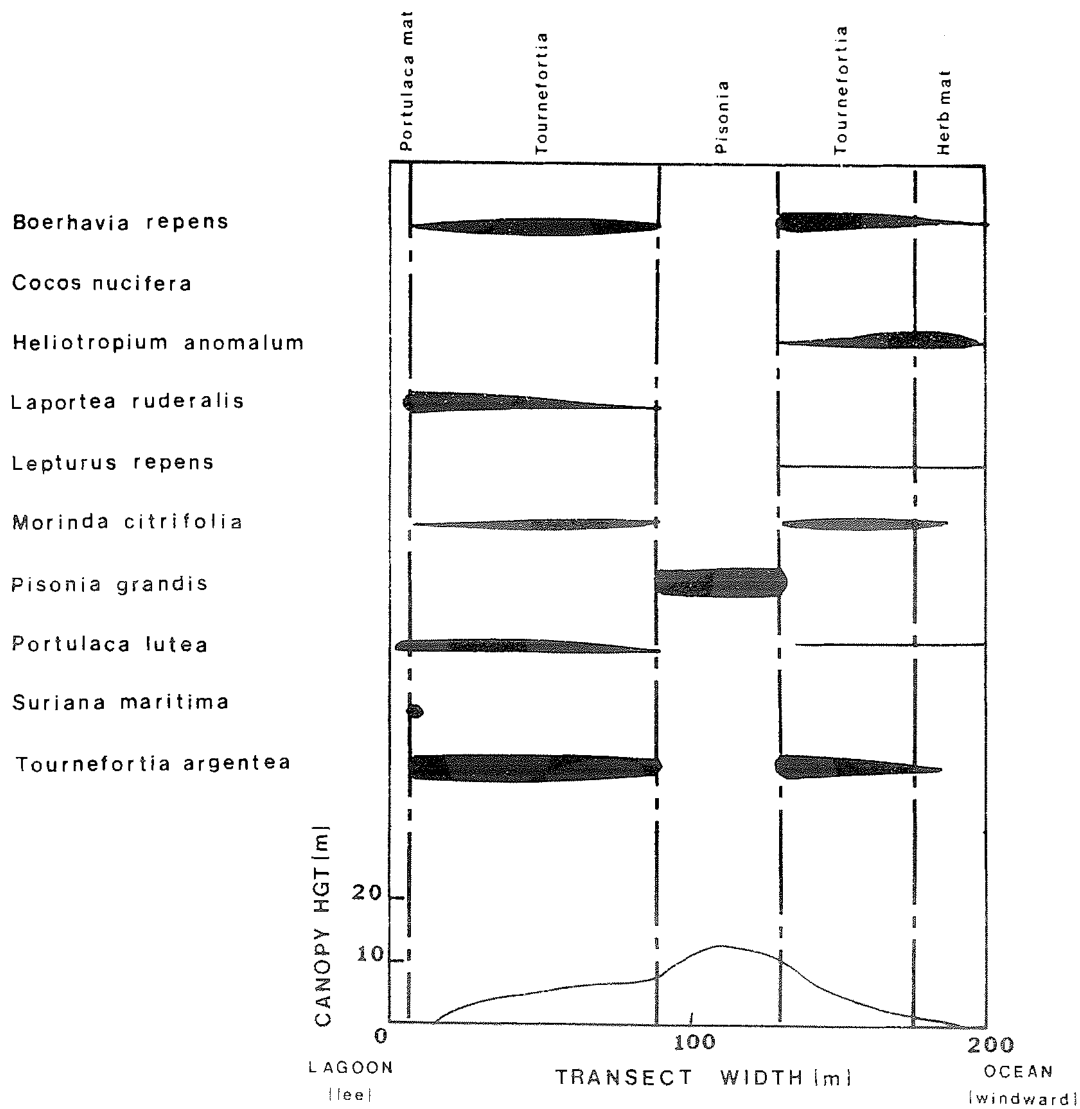

Figure 46. Brothers Islet: east-west cross-section through center of islet. Data includes floristic composition, relative abundance of plant species, degree of species overlap and canopy heights. Vertical height is exaggerated. Note the central monotypic stand of *Pisonia* forest. This islet's forests were totally felled in 1920.

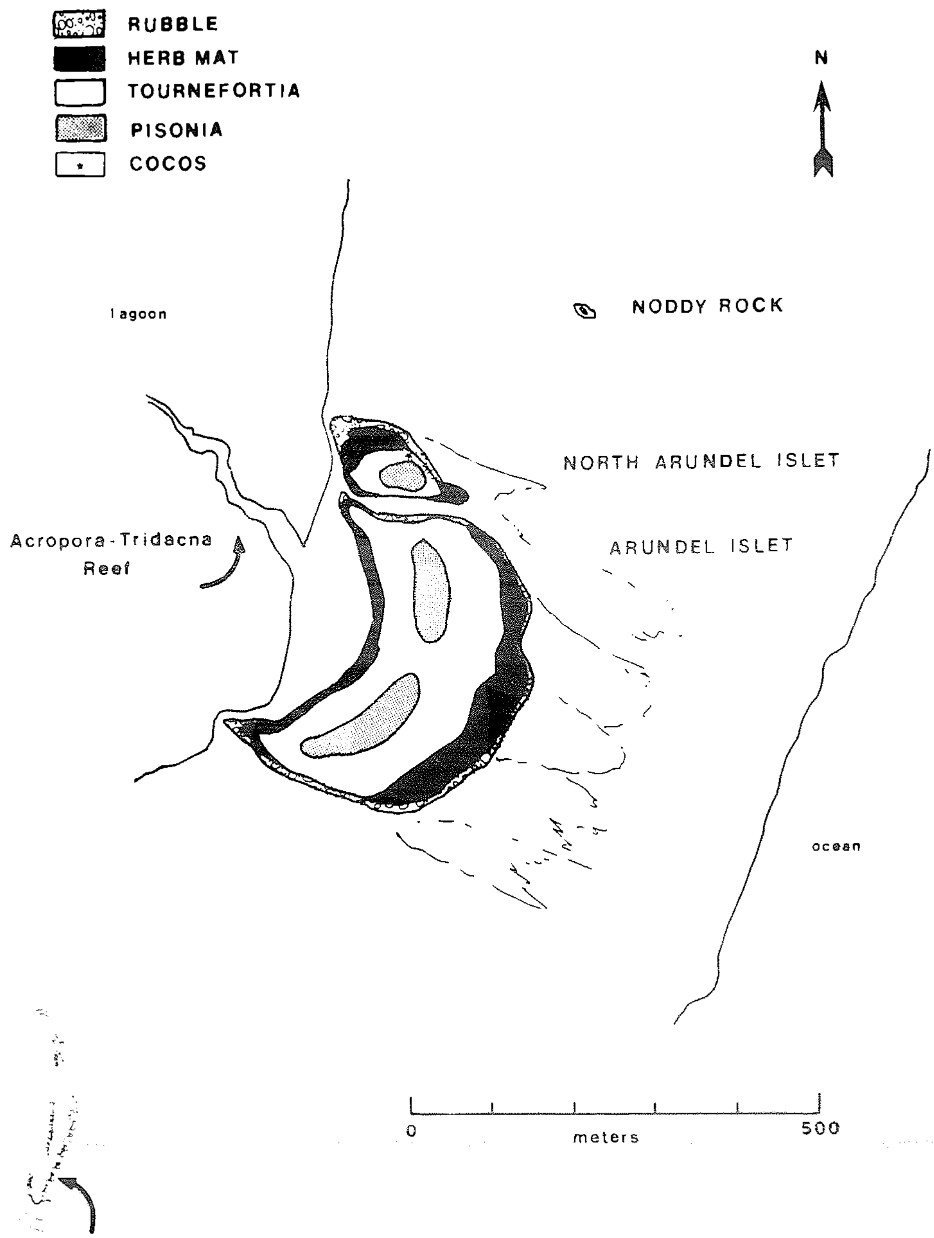

Figure 47. Vegetation and physiography of Windward Islets nos. 10 through 12: Noddy Rock, North Arundel, and Arundel. See text for explanation of the relatively small amount of *Pisonia* cover (Sect. H).

Noddy Rock, an eroded limestone plateau of unknown age, is 26 m wide by 9 m long and 0.5 m above high water. It is windswept and salty, with waves generally splashing over its eastern edge. During storms it is completely awash (Anne Falconer, pers. comm.). Only 3 species of plants (11% of Caroline's flora) grow here, thinly covering the western (leeward) third of the island in the following proportion: 75% *Portulaca*, 20% *Lepturus*, and 5% *Tournefortia*.

13) **NORTH ARUNDEL** (0.91 ha) Discussed below
14) **ARUNDEL** (7.34 ha) Figs. 29, 32, 47; Pls. 14, 56

Arundel Islet was named last century in honor of John T. Arundel. A British trader and guano digger, Arundel was one of the leading figures in the Pacific phosphate industry, directing guano and coconut planting operations on Caroline and other islands from 1873 to 1897. His most valuable contributions, however, were his excellent surveys and maps of several central Pacific islands, including Caroline (Fig. 4). The islet immediately to its north, Arundel's "cap," we named North Arundel.

Physiography: Arundel is crescentic, with wedge-shaped North Arundel lying across a short channel immediately to its north. North Arundel is 80 m long x 130 m wide, while Arundel is 375 m long x 210 m wide. They are composed almost exclusively of coarse coral rubble, flanked on their inner edges by *Acropora-Tridacna* reefs. Arundel's lagoonward "horns" have evidently added more sand and rubble since 1883 (Figs. 4, 47).

Vegetation: There are 11 plant species (3 trees, 1 shrub, 7 herbs) on Arundel, 42% of Caroline's total. There are no introductions. North Arundel also has 11 (4 trees, 1 shrub, 6 herbs), 42% of Caroline's flora, including one introduction, *Cocos*.

The vegetation on the motus, along with Tridacna to the south, consists of extensive herb mats, low scrub and small interior forests (Fig. 32), slightly less lush than the more northerly windward motus. Their woodlands are primarily *Tournefortia*, with thin belts of *Cordia* and central *Pisonia* groves (a bilobed pattern on Arundel). *Morinda* is unusually common on Arundel, and *Achyranthes* abundant on North Arundel. *Pisonia* occupies only 13% of the land area on Arundel, compared to 46% on Pig. Their poor soils are a possible legacy of the guano era.

Both motus were heavily planted with *Cocos* in 1919-20 (69 and 646 palms, respectively). All usable land was cleared (Table 13). Despite today's paucity of *Cocos*, the relatively scant *Pisonia*, compared to motus further north, suggests that their plantations were more successful and maintained more frequently.

Birds: Five species of seabirds bred on Arundel: Red-footed Booby (37 pairs), Great Frigatebird (on territory, September 1988; breeding confirmed, early 1989 by Anne Falconer), Brown Noddy (11 pairs), Black Noddy (249 pairs), and White Tern (227 pairs). In May 1990, thousands of Sooty Terns swarmed both motus.

15) <u>TRIDACNA ISLET</u> (9.08 ha) Figs. 29, 48, 49; Pls. 1, 25, 48, 56, 57

The 13th and southernmost motu in the windward chain was named by the present authors and Boris Sirenko for its outstanding coral reef densely studded with giant clams (*Tridacna maxima*).

Physiography: Somewhat crescentic, measuring 446 m long and 250 m wide, Tridacna is one of the largest motus on Caroline. Its terrain is heavily littered with coral rubble, having a sandy strip above the beach crest on the windward edge.

Vegetation: There are 13 plant species (2 trees, 2 shrubs, 9 herbs), 50% of the atoll's flora. For its size, Tridacna's vegetation is surprisingly lacking in tall forests, a legacy of the 910 *Cocos* palms planted on 82% of its available land area (Table 13). Vegetation patterns follow the usual concentric zonation: peripheral herb mats border a discontinuous belt of *Suriana* (windward side), while the large central mass is dominated by scrubby *Tournefortia-Morinda* woodlands, which cover 88% of the islet's area, yet only attain 7 m in height. In cross-section (Fig. 49), the short woodlands are particularly noticeable. Compare the present lack of *Cordia*, paucity of *Pisonia*, and richness of herbs, both in species numbers and abundance, with Pig (Fig. 45) and Brothers (Fig. 46). Although there are no introduced plants, thick patches of *Lepturus* also reflect past forest clearing.

Birds: Four species of seabirds were nesting in 1988: Red-footed Booby (111 pairs), Brown Noddy (11 pairs), Black Noddy (249 pairs), and White Tern (227 pairs). Tridacna is periodically a major breeding area for Sooty Terns. Clapp & Sibley (1971a) found 4 main colonies totalling 250,000 birds, and large numbers nested along the windward beach in August 1989 (Anne Falconer, pers. comm.). Nests were located under shrubs, or in open areas bordering them, and were evidently preyed upon by coconut crabs.

16) <u>SOUTH ISLAND</u> (104.41 ha) Figs. 30, 36, 50; Pls. 1-8, 12, 23, 34, 39, 40, 44, 45, 56

History: The history of South Island (called Rimapoto in Young ca. 1922) is essentially the history of Caroline, for most information about the atoll prior to 1965 is from here. It is the second largest islet, and the staging area for trips up-lagoon as it lies adjacent to both the "boat landing" and "blind passage."

South Island was inhabited in prehistory by Tuamotuans, who planted the first small coconut grove on its northwest point. The first Europeans to land, in 1606, found coconuts, fish, lobsters, and seabirds in abundance. They dug for fresh water in vain. Two hundred years later, in the decade after a cyclone in 1825, pigs, sweet potatoes, arrowroot, and South Sea chestnut were introduced. However, "the unfriendly character of the soil, and the number of land crabs that infest it, gave us but little hope of the experiment succeeding"

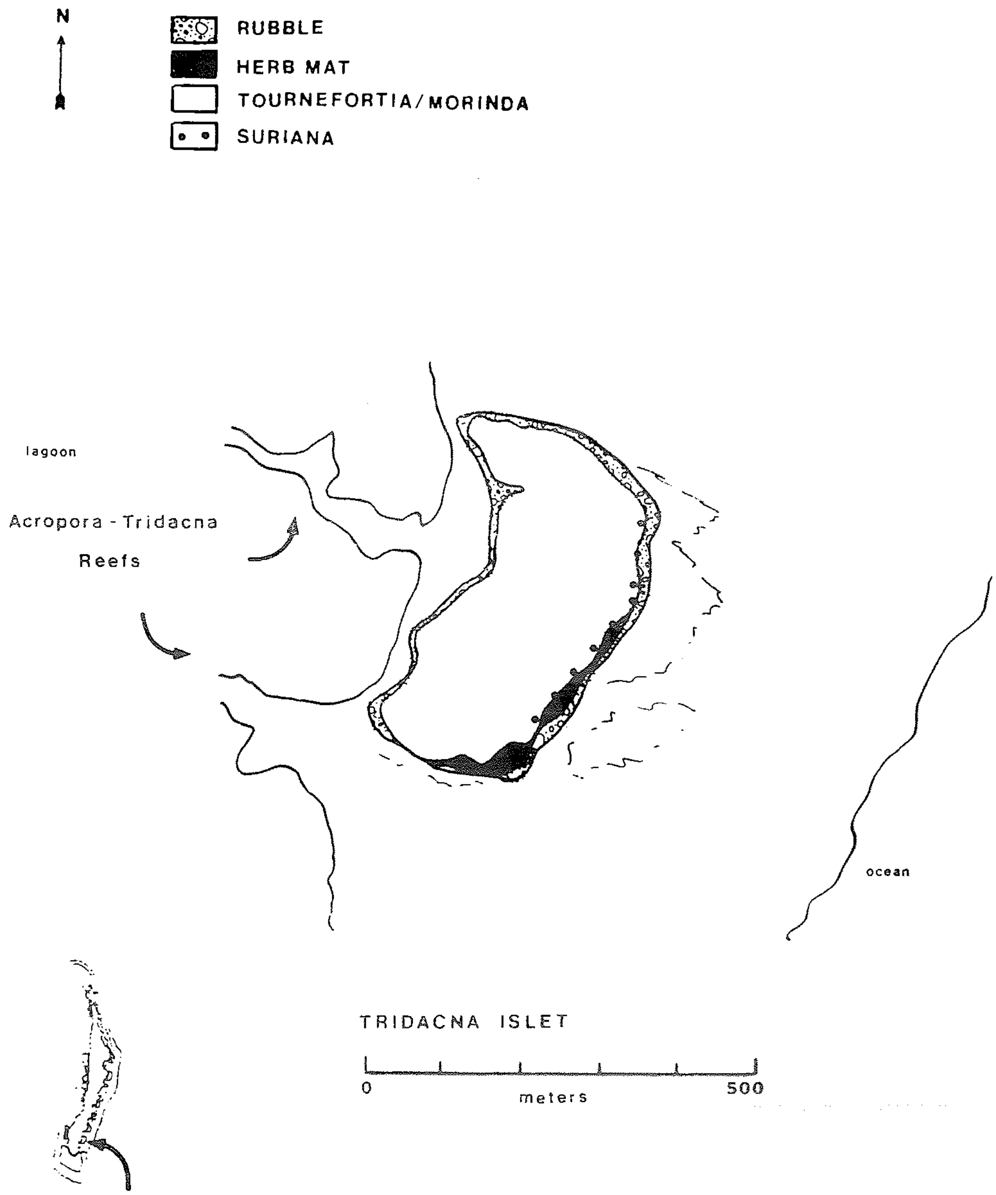

Figure 48. Vegetation and physiography of Windward Islet no. 13: Tridacna Islet. The best quality *Acropora-Tridacna* reefs extend clear across the lagoon from this motu. See Section H for explanation of unusual forest cover.

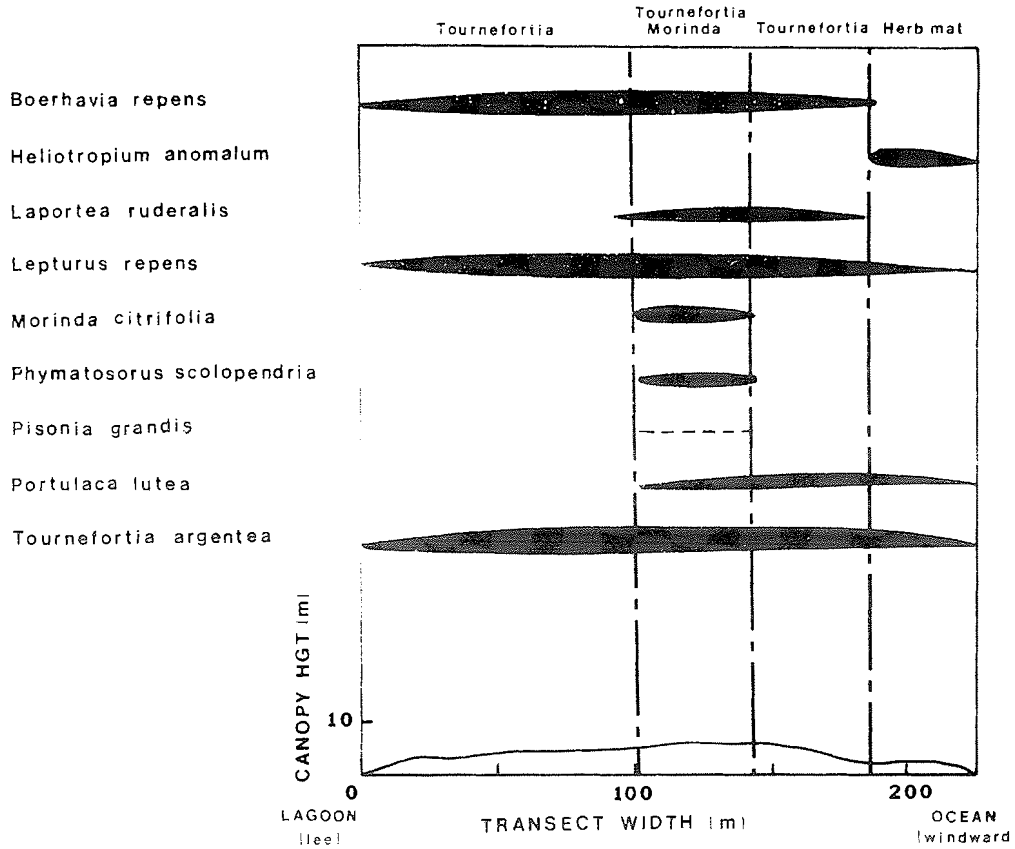

Figure 49. Tridacna Islet: east-west cross-section through lower center of motu. Data includes floristic composition, relative abundance of plant species, degree of species overlap and canopy heights. Vertical height is exaggerated. Note the absence of well-developed interior forests, unusual for a motu of this size (see Sect. H).

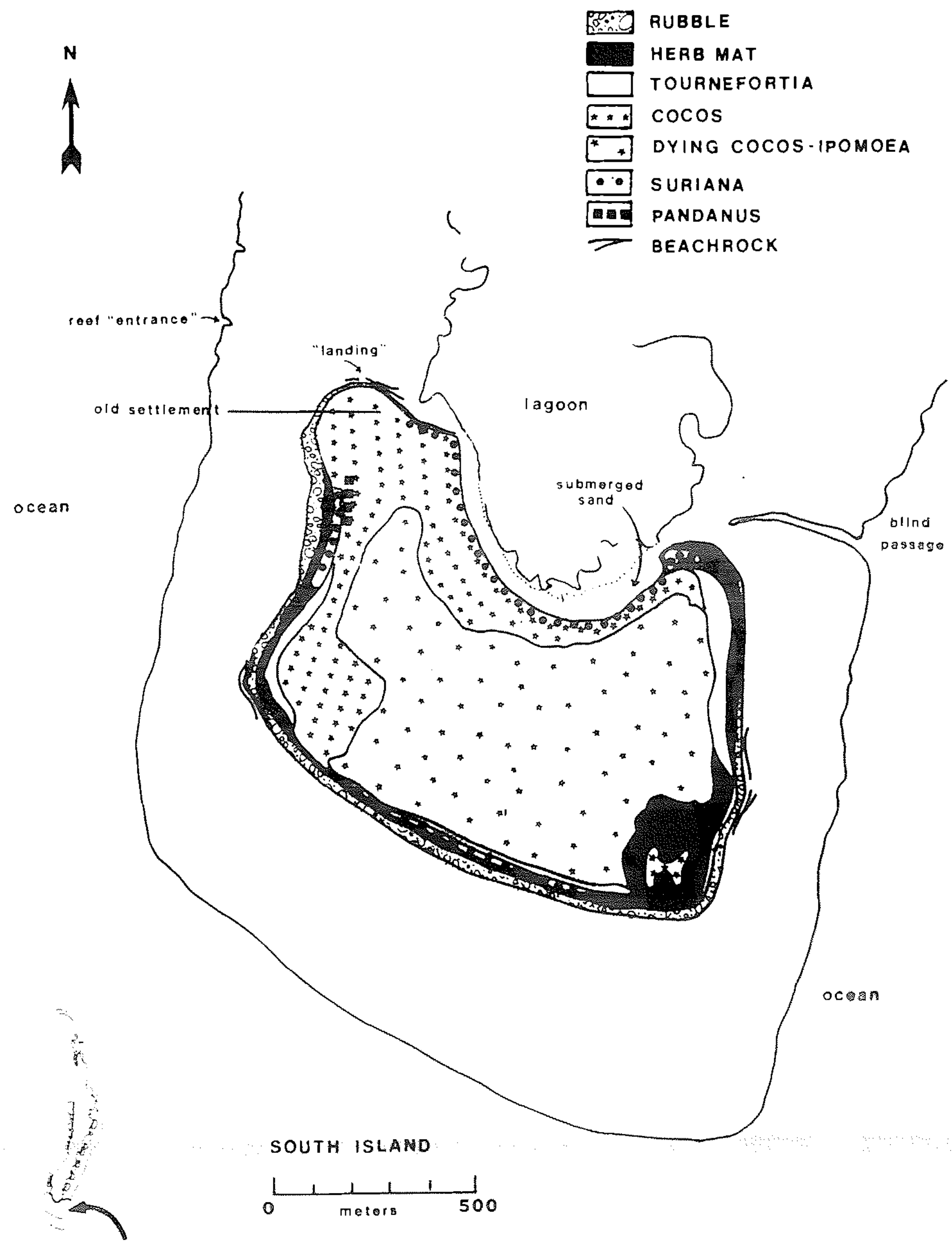

Figure 50. South Island: vegetation and physiography. Note the accepted landing route across its leeward reef flats.

(Bennett 1840). The pigs soon expired. The arrowroot, tenacious and adapted to island environments, still exists today (unless later immigrants brought it). Of the others, plus many other later food plants and ornamentals, no traces exist (Table 1). Tropical heat, droughts, storms, excessive shade from *Cocos*, poor germination, poor soils, terrestrial crabs, and lack of care all undoubtedly contributed to their demise.

The first recorded settlement on Caroline, and first for the Line Islands was in 1846, on the northwest point. These settlers, as well as subsequent ones, eked out a spartan living by raising stock, drying fish and copra, and digging for guano. Their managers built "proper" dwellings, so when U.S., British, and French astronomers arrived to observe the solar eclipse in May 1883, South Island was quite "civilized," far more than it is today. Three houses and 2 sheds "were in good repair," and a variety of "anchors, chains, spars, and pieces of the woodwork of vessels" littered its reefs (Holden & Qualtrough 1884). Large grassy clearings adjacent to the lagoon accommodated several European-style houses (Pls. 2-6). The astronomers' account of South, illustrated with pen-and-ink drawings (Pls. 2-7), is the only record of buildings on Caroline, apart from mention of the manager's house, reported in 1936 by the "H.M.S." *Wellington* to be "in excellent condition and spotlessly clean" (Maude ca. 1938), and a copra shed (Clapp & Sibley 1971a). Arundel took photographs, including the *marae* on Nake, which we have not examined.[7]

Today, the houses, sheds, brick piers (constructed in 1883 for telescopes and observatory frames), signboard, flagpole, marble slab with inscription "U.S. Eclipse Party, 1883, May 6," and all but one of the introduced plants have disappeared. In 3 trips we found no traces of the copra shed, nor have the Falconers, after repeated visits over 2 years. All that remains of the formerly extensive open areas are 2 small palm-shaded clearings, in 1988 used by the U.S. and Soviet scientists for a base camp and work area. In 1987, the Falconers lived in one clearing, and in 1990, fishermen expanded the other by burning an area 35 x 22 m, then erecting a tin shack, cookhouse, and fishtrap, all destroyed in a summer 1990 storm.

Our "civilization list" probably covered all that could be seen on South Island without digging: a 26-foot wrecked sloop (AK 6691 J.), complete with trail to a "Robinson Crusoe-type" campsite strewn with remnants of radio and navigational equipment, sail, cans, clothing, etc. (southeast coast); assorted flotsam and jetsam (whisky bottles, Japanese fishballs, plastic debris, etc.); a large rubber ship fender; a bench mark from the 1985 RNZAF survey team; a recently renovated concrete cistern (by the landing); and an old wooden canoe lying on its side just like de Quiros found in 1606.

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[7] Arundel's memorabilia (photos, letters, diaries, a microfilm, etc.) are in the Rare Book Collection, National Library and Pacific Manuscripts Bureau, Research School of Pacific Studies, Australian National University, Canberra, A.C.T., Australia.

We assume that all the Polynesians, ancient and recent (Tuamotuans, Tahitians, Niueans as far as is known), lived in native thatched huts similar to the ones on Ana-Ana today. Fashioned from coconut palms and pandanus trees, they disappear quickly when abandoned. The largest number of inhabitants recorded for Caroline (probably all on South Island) was "two managers and 52 laborers" in 1873 (The Commercial Advertiser 1873).

The history of South Island's coconut plantations from 1885-1901, and from 1916-1929, is discussed under Coconut Woodlands (Sect. G).

Physiography: South Island forms the base of the thinly crescentic isosceles triangle whose limits define the atoll. Its own shape is that of an irregular parallelogram 858 m wide x 1,254 m long at its longest points (Fig. 50). The north coast, a curved bay, forms the lower boundary of the lagoon. This palm-lined shore, along with the adjacent northwest peninsula, has been the most trodden by man, one of the most picturesque spots on the atoll (Pls. 23, 39).

The reef flats surrounding the outer 3 sides of South are the widest on the atoll, averaging 231 m, 578 m, and 363 m on the east, south and west, respectively. The windward and leeward reefs immediately to its north are 530 m wide. To leeward is the small boat "landing," on a conglomerate platform (Pl. 20), and to windward, the "blind passage," a non-functional *hoa* (Pl. 72).

Vegetation: There are 23 plant species (7 trees, 3 shrubs, 13 herbs), 89% of the atoll's flora. *Cocos* dominates South Island, occupying 77% of its area. The superannuated closed-canopy plantations (21 m tall) that border its coastlines give no indication of the vast overgrown, dying groves that occupy 80 ha, two-thirds of its interior (Fig. 50; Pls. 8, 34). Here, 3 species of herbs (*Boerhavia repens, Portulaca lutea, Phymatosorus scolopendria*) have proliferated unnaturally to form dense carpets, and the vine (*Ipomoea macrantha*) climbs in tangled, strangling masses to the tops of the highest palms.

The natural communities that prevail on other motus are only minor components on South (Fig. 50): herb mats (13% of the total area), Coastal Scrub with *Suriana* (1%), and *Tournefortia* Scrub (4%). Conspicuously absent are prime scrublands and forests of *Tournefortia, Pisonia*, and *Cordia*, which undoubtedly once swept in a lush expanse from shore to shore, stratified and zoned as on other motus, and which were "80 to 100 feet high" before extensive cleaning began (Arundel 1875). Canopy heights of the plantations are uniform (21 m), and the outer fringe of indigenous scrub (*Tournefortia, Cordia, Suriana*) and herbs (*Heliotropium, Portulaca*) occupy a small proportion of the island's width (Figs. 36, 51). Note the abrupt transition of canopy heights as they drop to the level of coastal scrub on both sides of the plantation. *Pandanus*, too, is less extensive than formerly: Bennett (1840) called it "somewhat numerous." During our survey, we observed only one small *Pandanus* grove and a few scattered trees. Bennett also noted that the island was "covered with verdure," with "trees attaining the height of twenty feet." However, 9 or 10 years previous to Bennett's visit a

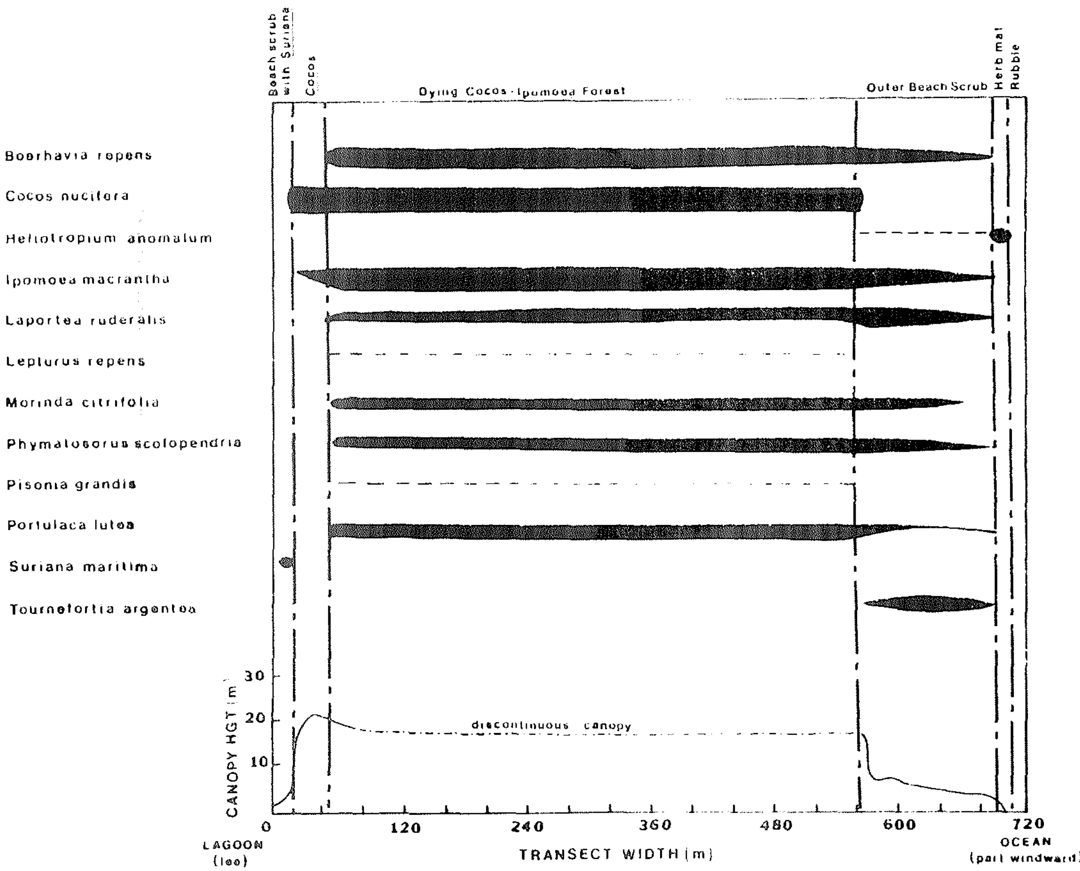

Figure 51. South Island: distribution and abundance of plant species along Transect 2, which runs at an angle of 60° from the lagoon to the south shore through the western center of the islet. Data includes floristic composition, relative abundance of plant species, degree of species overlap and canopy heights. Vertical height is exaggerated. Horizontal scale is half that of the profiles from smaller motus.

violent storm had whipped over the atoll. By the early 1870s, trees were approximately 30 m high again (Arundel 1875). Remnant *Tournefortia* and *Pisonia* are illustrated in drawings of South Island's lagoon shore in 1883 (Pls. 4, 5).

Apart from the coastal buffer zone, little native forest remains. Other sizable trees (*Pisonia, Cordia*), up to 17 m tall, are rare, but *Morinda*, tolerant to both sun and shade, is still quite common. Though we have not been able to trace any records to Caroline, it is possible that shiploads of *Cordia* logs were exported to San Francisco on guano ships, as was the case on Flint, worked simultaneously by Arundel's company (Young ca. 1922).

A final noteworthy aspect of South Island is that, despite its history of sporadic occupation and extensive forest felling for coconut plantations, *only one exotic* (a tiny patch of *Phyllanthus amarus*) *and no vegetable or garden ornamentals* (excluding Polynesian introductions) *have survived.*[8] The 19th century gardens, once drenched in sunshine, have long been buried beneath the deep shade of palm groves (compare Pls. 2, 3 and 23). In addition, rare hurricanes, periodic storms, droughts, irregular rainfall, nutrient-poor soils, rats, land crabs, and the harsh salty environment must have contributed to the eradication of alien species except traditional native food and medicinal plants, which are specifically adapted for atoll environments. Studies on other atolls, even those near high islands (Stoddart & Gibbs 1975, Stoddart & Fosberg 1972), have demonstrated also that many exotics do not survive, despite the proximity to source areas containing garden ornamentals and weed plants. On our last 2 visits (March, May 1990), however, we discovered a weed not previously reported (*Kyllinga brevifolia*) near the *Phyllanthus*, a consequence of recent clearing around the cistern. This area was an extension of the Falconers' vegetable garden on Motu Ana-Ana. *Kyllinga* is listed as a temporary species (Table 1).

Birds: Only 2 species of birds bred on South in September 1988, a reflection of its paucity of natural habitats: Brown Noddy (163 pairs) and White Tern (381 pairs). Bristle-thighed Curlews are very common, gathering in small flocks on the rubbly shores (Pt. II). They also forage in the open *Ipomoea-Cocos* forest, perching on dead coconut stumps 6-10 m high, then flying down to feed in the thick herb mats.

Terrestrial Crabs: Caroline's highest population of coconut crabs, having many huge individuals decades old, occupies the open *Cocos* forests (Pls. 21, 53). A crude minimum estimate for South Island is 500 mature individuals.[9] We also found a fist-sized blue hermit crab within

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[8]We are unsure of the status of *Hibiscus tiliaceus, Thespesia populnea* or *Ximenia americana*. Although indigenous to the area, a recent analysis of the vegetation of Flint Island (Kepler, in prep.) indicates that these species were most likely introduced to both islands in the late 19th century.

[9]Since March 1990, these have become much reduced due to killing and preserving in formalin for curios.

a ***Turbo argyrostomus*** shell, possibly ***Coenobita brevimanus*** (Yaldwyn & Wodzicki 1979; E. Reese, pers. comm.). As elsewhere on the atoll, land crabs such as the reddish-purple ***Cardisoma*** sp. and scarlet hermit crabs, ***Coenobita perlatus*** (in *T. argyrostomus* shells) were abundant (Pl. 38). *Geograpsus* sp., closer to the shore, was less common.

Rats: Polynesian rats were abundant, constantly afoot in broad daylight, and at night flashlight beams often revealed a half dozen at a time.

SOUTH NAKE ISLETS

Fig. 52

This chain of 7 islets extends 1,500 m south from Nake on the west side. They range in size from 0.64 ha (Kota) to 7.36 ha (Pandanus). All are well-wooded and support every natural plant community. Proceeding south, the overall plant cover thins somewhat, but not to the dryness and openness of the Central Leeward Islets. The herb mats are more extensive than on the windward islets, especially to seaward. Aboriginal introductions (*Cocos*, *Pandanus*) are sparse. We have found no historical records indicating human disturbance to these islets, thus their vegetation, with the possible exception of Pandanus Islet, is evidently natural. The 2 scrawny *Cocos* are probably drift-derived.

On the Solar Eclipse Party's map of Caroline (Fig. 5), only the top 2 islets of this group are drawn. The South Nake Islets constitute the only cluster of motus that show appreciable differences between Arundel's chart (Fig. 4) and the 1985 aerial photos: most were shown as smaller, and with slightly different shapes, by Arundel. The interior vegetation on these motus includes mature forests of *Tournefortia*, *Pisonia*, and *Pandanus*, so it is unlikely that these differences reflect changes to the center of the motus. However, since the islets now appear larger, accretions of coral rubble and sand that may have occurred in the past 105 years, and are now barren or covered only with herb mats, could account for most of the differences (see Coral Islet discussion).

Although we have no actual records of Sooty Tern colonies on this chain of islets, in May 1990 AKK observed pre-breeding swirls over Lone Palm, Kota, and Mouakena (Pt. II, Fig. 11).

17) PANDANUS ISLET (7.36 ha)

Figs. 29, 52; Pl. 58

This motu was named by the present authors for its coastal *Pandanus* grove, probably a drift-derived offshoot from a parent colony on Nake.

Physiography: Pandanus Islet, first in the chain, is irregularly oval, 400 m long and 258 m across. It is nearly twice the size shown on Arundel's map (ca. 3.4 ha). It occupies a sheltered spot at the apex of the lagoon. Sand, actively filling in the adjacent lagoon, is an important substrate component on Pandanus, extending one-third of the

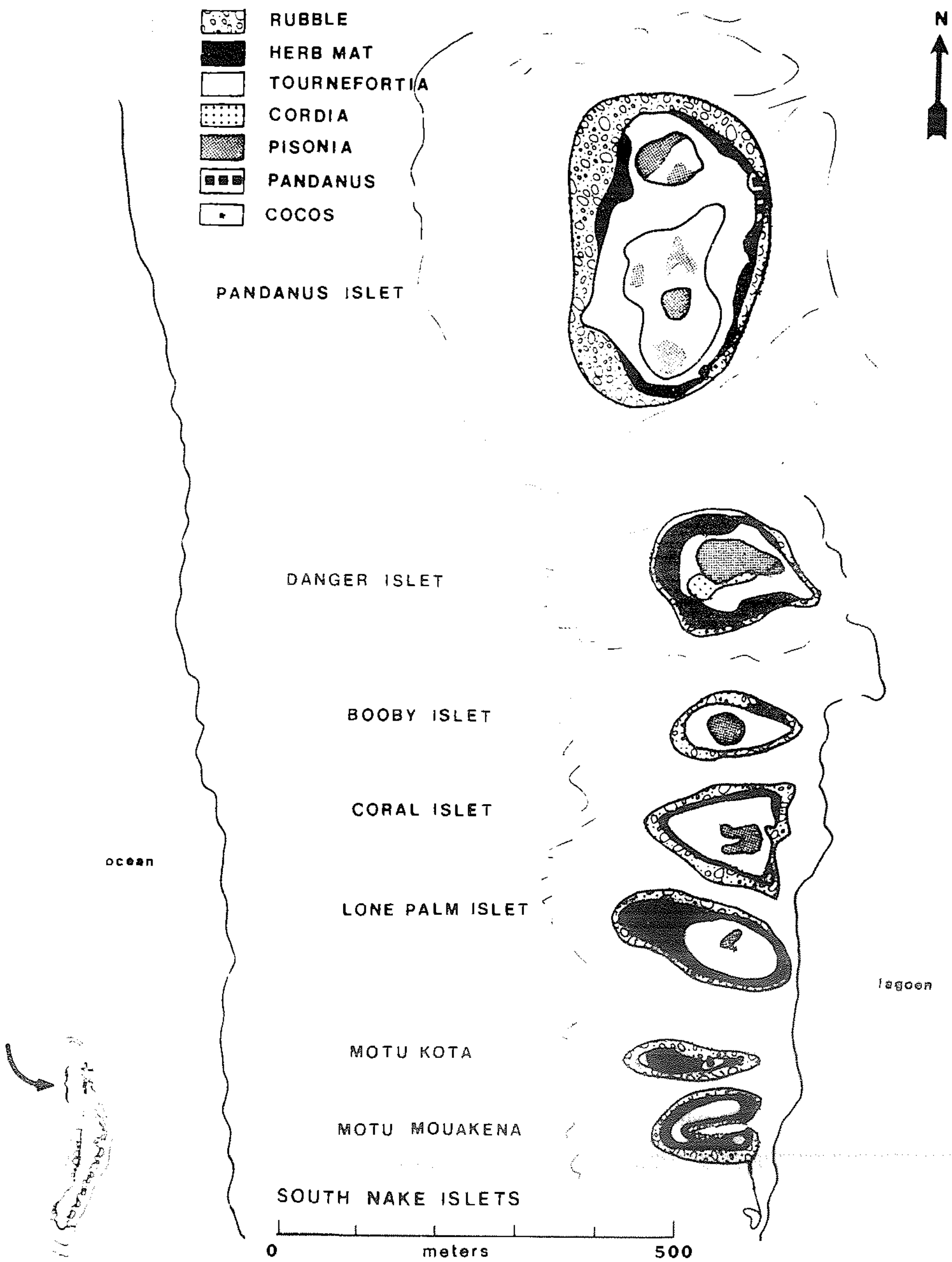

Figure 52. Vegetation and physiography of the 7 South Nake Islets: Pandanus, Danger, Booby, Coral, and Lone Palm Islets, Motu Kota ("Red-footed Booby Islet"), and Motu Mouakena ("Masked Booby Islet").

way across the islet. Although tidal reef flats are absent on the lagoon edge, they average 75 m wide on the seaward side, producing a fairly high proportion of rubble compared to the total land surface (32%).

Vegetation: Plant species total 10 (3 trees, 1 shrub, 6 herbs), 39% of Caroline's flora. *Cocos* is absent, despite the motu's close proximity to Nake. Pandanus Islet has 4 basic vegetation zones: natural herb mats, *Tournefortia* Scrub (with *Pandanus*), *Tournefortia-Pisonia* Forest, and pure *Pisonia*. Woodlands cover 62% of its area. The widest pioneer mats (13 m) of any leeward motu occupy its east edge and though sparsely vegetated (20% *Heliotropium*, 5% *Lepturus*, 5% *Portulaca*) reflect active growth toward the lagoon. Proceeding west across the island, *Tournefortia* scrub (2 m high), with pockets of pure *Pandanus* (10 m high), merges into *Tournefortia-Pisonia* Forest (to 14 m high), whose bimodal distribution suggests that the islet was once divided. The seaward coast supports open *Tournefortia* (5 m high), beneath which herbs eventually thin out onto the extensive reef flats.

Birds: Five species of seabirds breed: Masked Booby (2 pairs), Red-footed Booby (32 pairs), Great Frigatebird (26 pairs), Brown Noddy (26 pairs), and White Tern (52 pairs).

Comments: Skinks and rats were observed, along with the ubiquitous *Coenobita* and *Cardisoma* land crabs.

18) <u>DANGER ISLET</u> (2.71 ha) Figs. 29, 52; Pl. 59

We named Danger Islet to commemorate the deep, shark-infested channel to its north, a barrier that aborted our first attempt to survey the South Nake Islets.

Physiography: Danger, of rounded shape, is approximately 150 m long and 215 m wide. It is composed almost entirely of coral rubble; interior humus is scant. Its reef-channel flats are 21 m (north) and 14 m (south) wide. The east and west beaches, narrow and wide respectively, are typical of all the leeward motus.

Vegetation: Danger has 10 plant species (3 trees, 1 shrub, 6 herbs), 39% of the total flora. There are no introductions. The vegetation is concentrically zoned: herb mats, *Tournefortia* scrub and forest, central *Pisonia*, and *Cordia* in the southwest. The herb mats are wide, extending 22 m and 15 m on the north and south shores, respectively.

Birds: Four species of nesting seabirds were present in 1988: Red-footed Booby (139 pairs), Great Frigatebird (26 pairs), Brown Noddy (26 pairs), and White Tern (52 pairs).

19) BOOBY ISLET (0.84 ha) Figs. 29, 52; Pl. 60

We named this motu, third in the chain, for its 2 species of boobies, the common Red-footed and rarer Masked Booby.

Physiography: Booby, shaped like a teardrop, is 70 m long and 125 m wide. Its coral rubble flats extend 10 m and 30 m on the north and south sides, respectively.

Vegetation: Despite its small size, the most notable feature of Booby is its *Pisonia* forest, 20 m tall and undoubtedly virgin. It occupies the exact center of the islet in a circle about 40 m in diameter. Surrounding this is *Tournefortia* scrub (to 8 m tall), thinning out to peripheral bands of coral rubble. Although less than one hectare in size, Booby Islet's woodlands occupy two-thirds of this area. Booby Islet has 9 species of plants (2 trees, 1 shrub, 6 herbs), 35% of Caroline's flora, and no introductions.

Birds: Five species of seabirds breed: Masked Booby (7 pairs), Red-footed Booby (52 pairs), Brown Noddy (2 pairs), Black Noddy (1 pair), and White Tern (6 pairs).

20) CORAL ISLET (1.70 ha) Figs. 29, 52; Pl. 60

Fourth from the north, Coral Islet was named for its reef-derived coralline substrate.

Physiography: Arrowhead-shaped, Coral is approximately 130 m long by 200 m wide, more than 3 times the size mapped by Arundel (Fig. 4). Most of its area is barely higher than the surrounding inter-islet channels. The shallow reef flats between Coral and its 2 southern motus are only several centimeters deep at low tide; all 3 may be destined to unite. Unless closely inspected, they appear to have already merged, a fact which, together with Bryan's incorrect map (Fig. 6), helps account for the widely differing number of motus attributed to Caroline.

Vegetation: There are 9 species of plants (2 trees, 1 shrub, 6 herbs), 35% of Caroline's flora, and no introductions are present. Plant communities comprise a small *Pisonia* forest (0.13 ha), which is surrounded by the predominant *Tournefortia*, in turn fringed with a narrow band of native herbs. "Soils" are extremely coarse.

Birds: Five species of seabirds bred in 1988: Masked Booby (1 pair), Red-footed Booby (28 pairs), Great Frigatebird (2 pairs), Brown Noddy (6 pairs), and White Tern (15 pairs).

21) LONE PALM ISLET (1.99 ha) Figs. 29, 52; Pls. 60-61

We named Lone Palm, fifth in the chain, for its single coconut palm which towers, flag-like, above a dense mound of *Tournefortia*.

Physiography: Similar to Kota (to its south), Lone Palm is sausage-shaped, 97 m long and 240 m wide, and 4 times the size mapped by Arundel. Although composed almost entirely of coral rubble, some sand borders the lagoon. Following a pattern prevalent on all leeward motus, its lagoon beach is 2 m wide, while the seaward beach is 17 meters.

Vegetation: Eleven species of plants are present (3 trees, 1 shrub, 7 herbs), 42% of Caroline's flora. Plant communities are simple: a wide band of herb mats and open *Tournefortia* flanks an oval of *Tournefortia* forest (to 10 m tall). A line of *Pisonia* trees, with a lone *Cocos* surmounting the scrub, identifies this islet from lagoon or ocean.

Birds: Three species of seabirds bred in 1988: Masked Booby (2 pairs), Red-footed Booby (48 pairs), and White Tern (9 pairs). In May 1990, we saw a large pre-breeding swarm of Sooty Terns.

22) MOTU KOTA "Red-footed Booby Islet" (0.64 ha) Figs. 28, 52; Pls. 60

We named this motu for its high density of Red-footed Boobies (*kota* in Gilbertese).

Physiography: Sixth in line south of Nake, sausage-shaped Motu Kota is 50 m long and 175 m wide. At low tide it is almost connected to Motu Mouakena. Both surveys indicate that coral rubble, the islet's predominant substrate, had further accumulated on its south side since the 1985 aerial photos, and also since 1988.

Vegetation: Though barely wooded, Kota has 11 species of plants (3 trees, 1 shrub, 7 herbs), 42% of Caroline's flora. One introduced species is present, one tattered *Cocos*. Plant communities include: peripheral herb mats and a central *Tournefortia* scrub (to 10 m tall), with a few *Pisonias*.

Birds: Three species of seabirds bred in 1988: Brown Booby (1 pair), Red-footed Booby (12 pairs), and White Tern (3 pairs). In May 1990, a single Masked Booby was on territory, and Sooty Terns swirled overhead.

23) MOTU MOUAKENA "Masked Booby Islet" (1.00 ha) Figs. 29, 52; Pls. 15, 62

This islet was named for its nesting Masked Boobies, a relatively uncommon seabird on Caroline.

Physiography: Somewhat U-shaped, Motu Mouakena is seventh, and southernmost, in the South Nake chain of islets. Both sides of the "U" were, in the recent past, separate islets. By joining on the west, a narrow, V-shaped inlet was created on the lagoon side. Motu Mouakena, 100 m long and 160 m wide, is extremely rubbly and infertile; much rubble was reorganized during the February 1990 storm. Seventeen meters to its south lies a newly emerging shoal of sand and gravel (Pl. 15), perhaps destined to be Caroline's fortieth motu. Since the above storm, rubble has further accumulated on this shoal, its adjacent reef flats, and in the channel separating it from Mouakena. It already supports one *Tournefortia* shrub, 2 dozen *Heliotropium* plants, and scant *Lepturus* and *Portulaca*.

Vegetation: Mouakena has 8 species (1 tree, 1 shrub, 6 herbs), 31% of Caroline's flora, with no introductions. It is thinly vegetated with open *Tournefortia* scrub (to 9 m tall, 26% cover), a few small *Pisonia*, and sparse herb mats.

Birds: This motu supports less vegetation and fewer birds than its overall area implies, since 38% of the land consists of unshaded, coarse coral rubble (Fig. 29b). Although unproductive botanically, this provides ideal nesting grounds for Masked Boobies, one of its 2 species of 1988 breeding seabirds: Masked Booby (3 pairs) and Red-footed Booby (8 pairs). In May 1990, we also saw one Great Frigatebird nest with eggs and a swirl of Sooty Terns.

CENTRAL LEEWARD ISLETS

This chain of 11 motus occupies the central west side of Caroline. All are separated by channels, wadable only at low tide but prowled by belligerent sharks. Approximately 1,600 m south of Motu Mouakena lies a sandy shoal (0.5 m high, 7 m wide, 4 m long), close to the lagoon edge of the reef flats and connected only by a thin thread of rubble to Motu Mannikiba to its south.

The islets range in size from Mannikiba (28.50 ha), the most northerly, to Fishball (0.46 ha), the most southerly. All support good seabird populations. Although most are well-wooded, they are nonetheless the least lush motus on Caroline. Historical records are meagre: much of Mannikiba's forest was felled to make room for a *Cocos* seedling "nursery" (Young ca. 1922). The bulk of "40 trees on other islets," in Young's plantation totals, were most likely from Shark and Emerald. The rest of this group is evidently pristine; Bird Islet is particularly notable.

In common with all western motus on Caroline, the lagoonside beaches are narrow and leeward reef flats wide. The latter exhibit a greater variety of substrata than the former, including older raised reefs and beachrock. Periodically, thousands of nesting Sooty Terns occupy their open spaces (Clapp & Sibley 1971a; AKK, pers. obs.; Anne Falconer, pers. comm.).

24) MOTU MANNIKIBA "Seabird Islet" (21.49 ha) — Figs. 29, 53; Pls. 63-65

We named this motu for its teeming seabirds, *mannikiba* in Gilbertese.

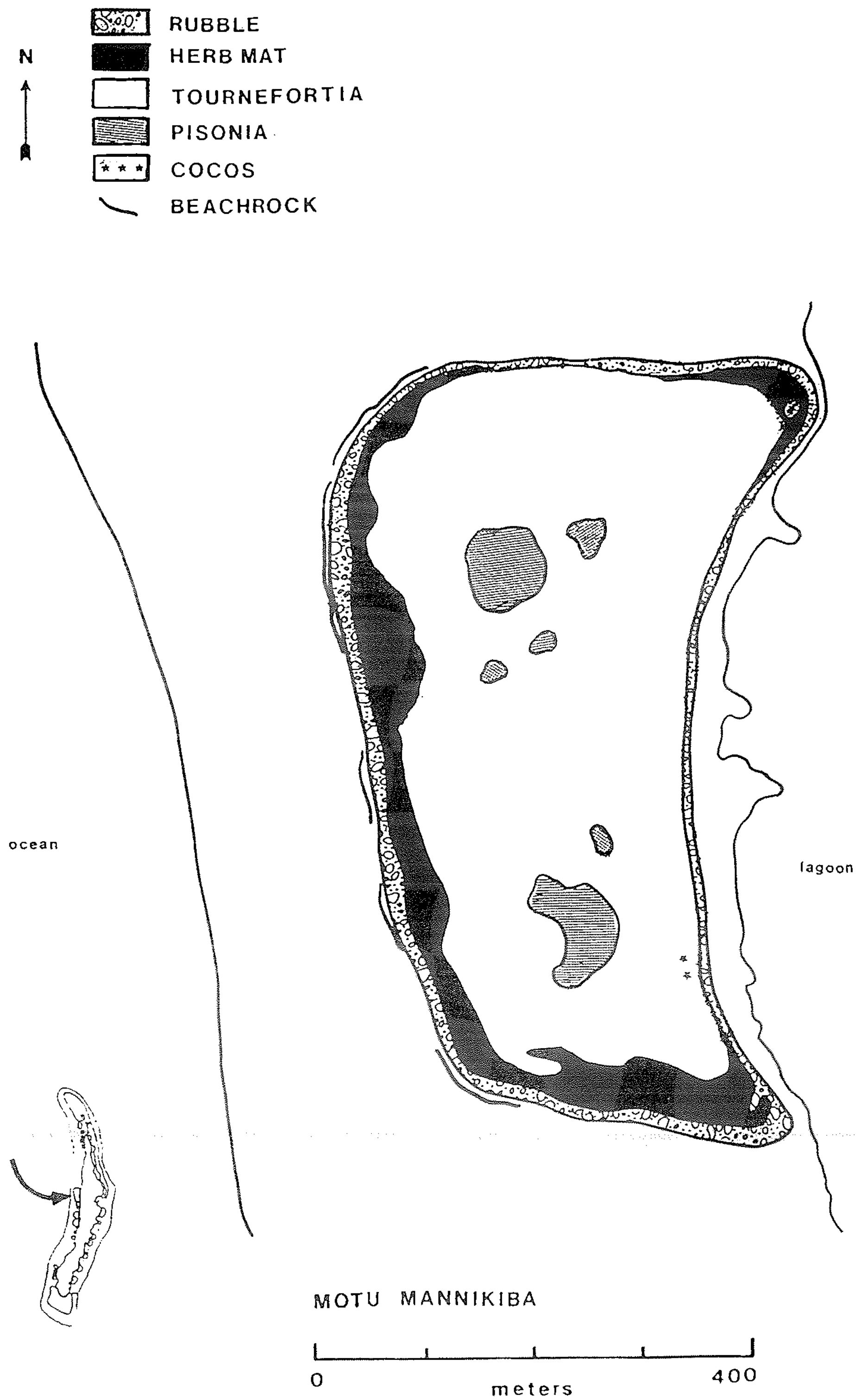

Figure 53. Vegetation and physiography of Central Leeward Islet no. 1: Motu Mannikiba ("Seabird Islet").

Physiography: Largest and most northerly of the Central Leeward Islets, Mannikiba is somewhat rectangular with rounded corners. Its reef flats, supporting an incipient islet, stretch 2.0 km north to the South Nake Islets.

Mannikiba's maximum dimensions are 700 m long and 375 m wide. On the lagoon side, the scrub skirts high water, but when the tide drops, a strip of blinding white sandy coral lines the lagoon. To seaward, upraised reef, beachrock, and successive layers of rubble stretch in a wide swath (40 m) toward the outer reef, 130 m distant. The primary inland substratum is coral rubble with hardpan in the northeast.

Vegetation: Mannikiba, the fourth largest motu, harbors 13 plant species: (4 trees, 2 shrubs, 7 herbs), 50% of Caroline's flora. The only introduction is *Cocos*, occupying 0.1% of the land area. The single, sterile *Ximenia americana* is indigenous, but may have grown from a seed derived from the other patch of this species on South.

Mannikiba's vegetation, denser toward the north end, is clearly zoned: herb mats, *Tournefortia* scrub and forest, and scattered *Pisonia* groves. The few clumps of peripheral *Cocos* are probably not drift-derived, but the remnants of 6,000 "seed sets" brought from Flint Island in June 1920. These were stored on Mannikiba and "used to replant misses on other islets" (Young ca. 1922).

Pisonia, though present, occupies only 5% of the land area, a small percentage for such a large islet. This suggests that large areas of the interior forests were felled to accommodate the coconut "sets." This is also confirmed by the presence of several old cut stumps (*Cordia*?) in the interior, undoubtedly a legacy of S. R. Maxwell and Co., Ltd., who erected huts around 1920 (Young ca. 1922). Although nothing more is known of Mannikiba's history, collection of guano from its numerous seabirds may account for further past disturbance.

Transect 1 (north-central sector, Pl. 64) passed through the heart of a fine interior forest, while Transect 2 (south-central sector) passed through scrub and herb mats which may represent part of the former *Cocos* "nursery." Profiles through these 2 cross-island transects resemble those from Brothers (Fig. 46) and an old interisland channel on Long (Fig. 40), respectively.

The low, peripheral herb mats (absent from the lagoon side) are composed of 30% *Heliotropium*, 20% *Boerhavia*, 15% *Tournefortia*, and less than 1% of *Portulaca* and *Laportea*. They are best represented in the southern sector. The *Tournefortia* forest, 6 m high on both sides, is thick, having 95% canopy coverage. The *Pisonia* forests, though fragmented (12 m high, 100% canopy cover), contain *Morinda*, *Boerhavia*, *Achyranthes*, *Laportea*, and *Phymatosorus*, but none cover more than 10% of the ground area.

Seabirds: Six species are known to breed: Red-footed Booby (184 pairs), Great Frigatebird (287 pairs), Brown Noddy (161 pairs), Black Noddy (176 pairs), and White Tern (195 pairs). No Sooty Terns nested on this islet in 1988, but Clapp & Sibley (1971a) estimated 2,500 pairs in 1965, and the Falconers reported large colonies on Mannikiba, Blackfin and Matawa in July - August 1990.

Comments: Coconut crabs live in the *Cocos* grove. Azure-tailed and snake-eyed skinks (*Cryptoblepharus poecilopleurus*), as well as a gecko, were noted in 1990 (DHE, G. Wragg, pers. obs.).

25) <u>BLACKFIN ISLET</u> (2.62 ha) Figs. 29, 54; Pls. 29

We named this motu, second in the Central Leeward chain, for 2 shark attacks (near misses) within its northern channel.

Physiography: Blackfin, shaped like conjoined ovals, is 140 m long and 190 m across. Coral rubble covers 30% of its surface; all beaches and upper reef flats are of variable widths, due in part to the fact that it has recently incorporated a smaller, circular motu into its northern confines.

Vegetation: Blackfin Islet has 9 species of plants (3 trees, 1 shrub, 5 herbs), 35% of Caroline's flora. The only introduction, *Cocos*, is rare. Four plant communities were present. Herb mats are well represented, especially around the newly incorporated islet. The *Tournefortia* scrub, 21 m wide in the east, is short (to 2 m), but approaches the stature of a forest (to 6 m) in the west. The central forests of *Cordia* and *Pisonia* (0.41 ha) are 9 m high.

Birds: Three species of seabirds bred in 1988: Great Frigatebird (4 pairs), Brown Noddy (37 pairs), and White Tern (11 pairs). In May 1990, one Red-footed Booby sat tight on a nest, while 2 months later large numbers of Sooty Terns began laying.

26) <u>MOTU MATAWA</u> "White Tern Islet" (1.71 ha) Figs. 29, 54; Pl. 3 (Pt. II)

On arriving at this motu, the authors were greeted by 15 White Terns, *matawa* in Gilbertese.

Physiography: Of oval shape, Motu Matawa is third from the north in the Central Leeward chain. It is 105 m long and 190 m wide. The entire motu is composed of coral rubble of varying grades, whose unvegetated portion comprises one-fourth or more of the land area. Its lagoon beach is 2.5 m wide, while the seaward beach (sparsely vegetated) is 6 m wide.

Vegetation: Matawa has 10 species of plants (4 trees, 2 shrubs, 4 herbs), 39% of Caroline's flora. There are no introductions. Vegetation is less lush and more open as one progresses south on the leeward side. *Tournefortia* (to 7 m) covers half the islet, surrounding an east-central *Pisonia-Cordia* forest (to 8 m).

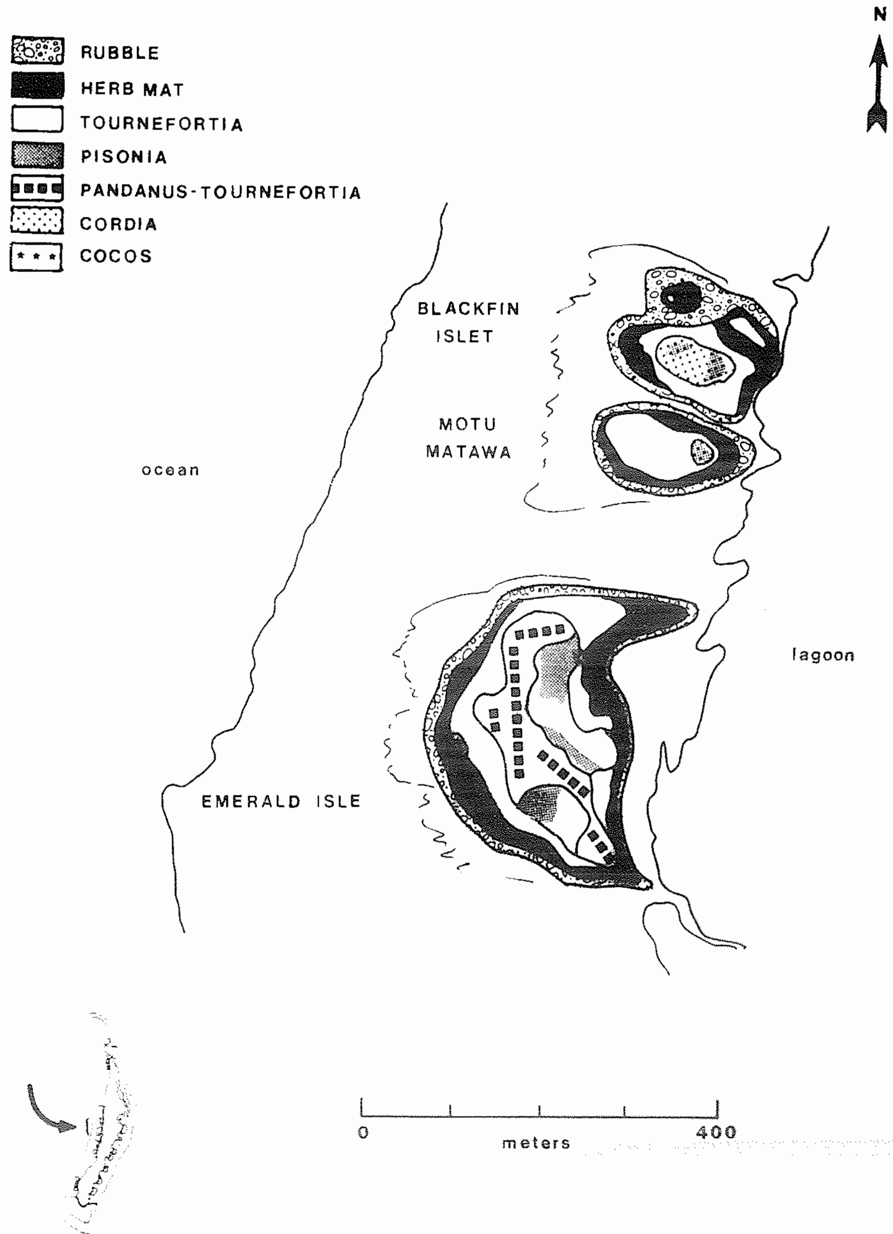

Figure 54. Vegetation and physiography of the Central Leeward Islets nos. 2 through 4: Blackfin Islet, Motu Matawa ("Fairy Tern Islet"), and Emerald Isle.

Birds: In 1988 four species of seabirds bred: Red-footed Booby (5 pairs), Great Frigatebird (1 pair), Brown Noddy (3 pairs), and White Tern (13 pairs). Most conspicuous were White Terns, with 9 pairs breeding on the 30-m-wide transect swath. One dark morph Reef Heron fished in the shallows. In summer 1990, Sooty Terns also bred.

27) <u>EMERALD ISLE</u> (8.34 ha) Figs. 29, 54; Pls. 24, 66, 67

Fifth down the chain, we named Emerald for the richly colored, translucent lagoon waters that fringe its shorelines.

Physiography: Crescentic Emerald, 330 m long and 240 m wide has lagoonside reefs, patch reefs, and coral knolls irregularly patterned with sandy channels.

Vegetation: Emerald Isle has 12 species of plants (5 trees, 1 shrub, 6 herbs), 46% of Caroline's flora. The only introduction is *Cocos*. Four plant communities, with a fairly high species diversity, are present: the herb mats, covering one-fourth of its land area, are composed almost exclusively of *Heliotropium* (35% cover) with scattered low *Tournefortia* (30% cover). The *Tournefortia* attains a maximum height of 8 m and, for variety, is mixed about equally with *Pandanus* over most of its seaward width (144 m).

The interior forest (to 11 m tall) is also mixed, with *Pandanus*, *Tournefortia*, *Pisonia*, and a little *Cordia* (Pl. 66). This 3.20 ha mixed forest, as on Shark, suggests that *Pandanus* may be both native and Polynesian-introduced, although we do not have specimens to verify this. *Cocos* is present as 2 small groves, complete with coconut crab sign (mounds of shredded fibers, Pl. 53), beside the east and midwest shores. We have been unable to trace the history of Emerald's forests; the *Cocos* and fragmented *Pisonia* suggest past disturbance.

Birds: Six species of breeding seabirds were present: Red-tailed Tropicbird (1 pair), Red-footed Booby (3 pairs), Great Frigatebird (230 pairs), Brown Noddy (7 pairs), Black Noddy (150 pairs), and White Tern (83 pairs).

Although we did not locate any Red-tailed Tropicbird nests, 2 adults circled steadily overhead. Two Reef Herons (1 dark morph, 1 light) foraged in the inshore reef shallows.

28) <u>SHARK ISLET</u> (7.98 ha) Figs. 29, 55; Pls. 28, 68

We named this islet to commemorate a particularly pugnacious shark charged shoreward and leaped to the beach toward our feet.

Physiography: Stoutly crescentic, Shark Islet is 280 m long and 310 m wide in the center. The sandy lagoon beach and rubbly seaward beach are each 3 m wide. The former is Caroline's prime stretch of sand, overlain by numerous pink granules, possibly due to Foraminifera tests, as in

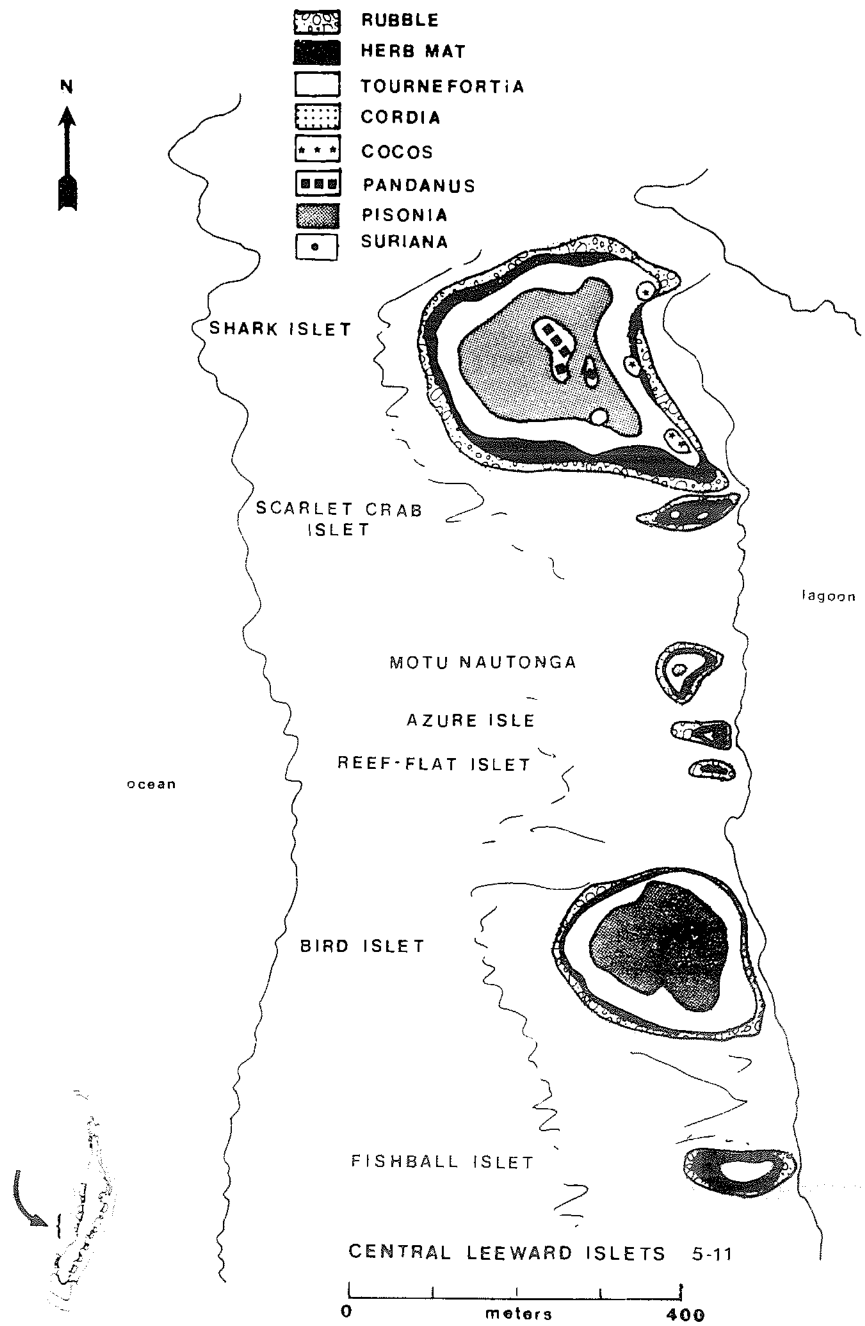

Figure 55. Vegetation and physiography of the Central Leeward Islets nos. 5 through 11: Shark and Scarlet Crab Islets, Motu Nautonga ("Sea Cucumber Islet"), Azure Isle, Reef-flat, Bird and Fishball Islets.

common in the Tuamotus (Stoddart & Steers 1977). Beyond high water the seaward reef flats extend for 280 m.

Vegetation: There are 12 species of plants (5 trees, 1 shrub, 6 herbs), 46% of the atoll's flora. One introduction, *Cocos*, forms 3 clumps along the lagoon beach (1% of the islet's area). Shark's rings of vegetation approximate the islet's outline. Herb mats dot the fine sand lagoonward, while to seaward they grow in coarse rubble. The *Tournefortia* (to 7 m tall) eventually gives way to a 12-m-high *Pisonia* forest studded with *Cordia* and *Pandanus*. Centrally this mixed forest is unnaturally open, suggesting past disturbance.

Birds: Four species of seabirds bred in 1988: Great Frigatebird (118 pairs), Brown Noddy (37 pairs), Black Noddy (125 pairs), and White Tern (44 pairs). Red-footed Boobies were nesting in 1990. The notable colonies of Great Frigatebirds and Black Noddies are due in part to the extensive *Pisonia* forest, covering one-half of the islet.

29) <u>SCARLET CRAB ISLET</u> (0.46 ha) Figs. 28, 55

This motu was named by the authors in honor of *Coenobita perlatus*, the scarlet, fist-sized hermit crab that is abundant both here and on the entire atoll.

Physiography: Scarlet Crab, sixth in the chain and only 40 m long by 125 m wide, is a young oval motu. It skirts the southern shore of Shark, from which it is separated by a channel 16 m wide. Because its eastern end points into the lagoon, there is no true lagoon beach. Together with the next 3 islets, Scarlet Crab's seaward reef flats (480 m) are the most extensive on Caroline's lee side.

Vegetation: Vegetative cover is slight: less than 1% area coverage of *Heliotropium* and *Laportea*, interspersed with 10 small *Tournefortia* (to 1.5 m). Its species count is 6 (1 shrub, 5 herbs), 23% of Caroline's flora. There are no introductions.

Birds: Although during storms this motu is undoubtedly awash, 2 species of seabirds were breeding in 1988: Brown Noddy (1 pair, on ground) and White Tern (2 pairs, in low scrub).

30) <u>MOTU NAUTONGA</u> "Sea Cucumber Islet" (0.34 ha) Figs. 28, 55

We named this motu for the Gilbertese word for the black sea cucumbers or "beche-de-mer" (*Ludwigothuria* sp.) that are strewn ubiquitously within the lagoon shallows (Pl. 10).

Physiography: Semicircular in shape, Nautonga is seventh in the Central Leeward chain, measuring 70 m long and 80 m wide. Situated close to the lagoon, it is one of 3 small motus that barely protrude above the reef flats. Nautonga's perimeter beaches are all narrow (2 m), while its seaward reef flats are wide (495 m).

Vegetation: There are 9 indigenous species (3 trees, 1 shrub, 5 herbs), 35% of the atoll's flora. Though small, Nautonga's vegetation is concentrically zoned, comprising herb mats (10-14 m wide) and a central forest of *Tournefortia* and *Pisonia* (84 m wide), to 10 m tall.

Birds: Five species of seabirds bred in 1988: Red-footed Booby (11 pairs), Great Frigatebird (2 pairs), Brown Noddy (7 pairs), Black Noddy (32 pairs), and White Tern (10 pairs). Lesser Frigatebirds appeared to be preparing to nest in May 1990. One pair of Blue-gray Noddies, flying south, was seen in May 1990.

31) AZURE ISLE (0.20 ha) — Figs. 28, 55; Pl. 51

We named this small, wedge-shaped motu for the striking colors of its nearby lagoon.

Physiography: Eighth from the north, this small, elongated triangle of land is 30 m long and 66 m wide. Its seaward reef flats are wide (512 m), while the adjacent channels are narrow and shallow.

Vegetation: Azure has only 7 species (1 tree, 1 shrub, 5 herbs), 27% of Caroline's flora. A young motu, Azure is a superb example of an early stage of biological succession. Its plant cover consists of a single mound of *Tournefortia* scrub crowned by a single *Pisonia* tree (6 m tall), growing only one meter above sea level. Only 45% of the motu is vegetated; the rest, primarily to seaward, is coarse rubble. Azure Isle illustrates the minimum width of vegetation (38 m) in which *Pisonia* develops on Caroline.

Birds: This motu illustrates the speed at which seabirds will utilize newly available habitats. Within its dozen or so *Tournefortia* shrubs (to 4 m tall), 3 species of seabirds nest: Red-footed Booby (7 pairs), Great Frigatebird (2 pairs), and White Tern (2 pairs). A pair of Blue-gray Noddies were seen in May 1990.

32) REEF-FLAT ISLET (0.09 ha) — Figs. 27, 55

We named this young motu for its primary characteristic: reef flats. Ninth in the Central Leeward chain, this curved strip of coarse rubble lies parallel to the channels that surround and spawned it. It measures about 20 m long and 60 m wide. Three species of plants (1 shrub, 2 herbs), 12% of Caroline's flora, cover less than one-fourth of its area and are distributed so sparsely that not one bird was present.

33) BIRD ISLET (4.05 ha) — Figs. 29, 55

This is one of the motus named on Arundel's chart (Fig. 4), probably because of numerous Black Noddies and/or Sooty Terns.

Physiography: Bird is ovoid, measuring 230 m long by 200 m wide. It sits close to the inner edge of the lagoon reef, whereas 400 m of seaward reef flats stretch westward.

Vegetation: There are 12 species of plants (4 trees, 2 shrubs, 6 herbs), 46% of Caroline's flora. A small *Cocos* grove is the only introduction. It is well-wooded, with very narrow herb mats (6% of total area). *Tournefortia* (to 8 m) and *Pisonia* (to 14 m) each cover 42% of its surface; the rest is rubble. The *Pisonia* forest is of good quality (90-95% canopy cover), having scattered *Morinda*, *Boerhavia*, and *Achyranthes* as an understory. One large clump of *Suriana* (14 x 14 m, 2.5 m high) grows centrally (A. Garnett, pers. comm.). Bird Islet shows very few signs of past disturbance, having prime plant communities, rich in breeding seabirds.

Birds: Five species of seabirds nested in 1988: Red-footed Booby (29 pairs), Great Frigatebird (6 pairs), Brown Noddy (42 pairs), Black Noddy (329 pairs), and White Tern (48 pairs). In June 1990, many thousands of Sooty Terns laid on Bird and adjacent Fishball.

34) <u>FISHBALL ISLET</u> (0.57 ha) Figs. 28, 55, 56

Eleventh and southernmost in the Central Leeward chain, we named Fishball after finding a large glass fishing float with a broken bottom, decorously placed in the islet's center amidst coral slabs.

Physiography: *Paramecium*-shaped, Fishball lies close to the lagoon and is separated from Bird by a shallow, rubble strewn channel 100 m wide. The motu is 45 m long by 144 m wide, with seaward reef flats 595 m in extent. South of the islet, the reef flats--wadable at very low tide--stretch 1.4 km to the Southern Leeward Islets.

Vegetation: The number of plant species is 8 (1 seedling "tree," 1 shrub, 6 herbs), 31% of Caroline's flora. Figure 56 depicts an east-west cross-section of Fishball, showing a vertical profile and the relative abundance and distribution of each species. Fishball exemplifies a young motu. All plants are low and halophytic; most are herbs. The motu is half-covered with a sparse herb mat of *Heliotropium* (10% cover), with scattered *Laportea*, *Lepturus*, and *Portulaca* (each <1% cover). Small *Tournefortia* shrubs (to 2 m tall) are scattered in the central sector, while a tiny drift seedling of *Morinda*, 7 cm high, struggled to gain a foothold in the exposed, salty rubble.

This motu is a fine example of the initial stages of islet formation and colonization, demonstrating that sea-dispersed, halophytic herbs first appear later becoming shaded out by *Tournefortia*, enabling a greater plant species diversity to establish. It is very unlikely that a ground water lens is present.

Birds: Two species of seabirds bred in 1988: Red-tailed Tropicbird (3 pairs) and Brown Noddy (5 pairs). In May 1990, many thousands of Sooty Terns covered the ground and swirled in the air, day and night. We

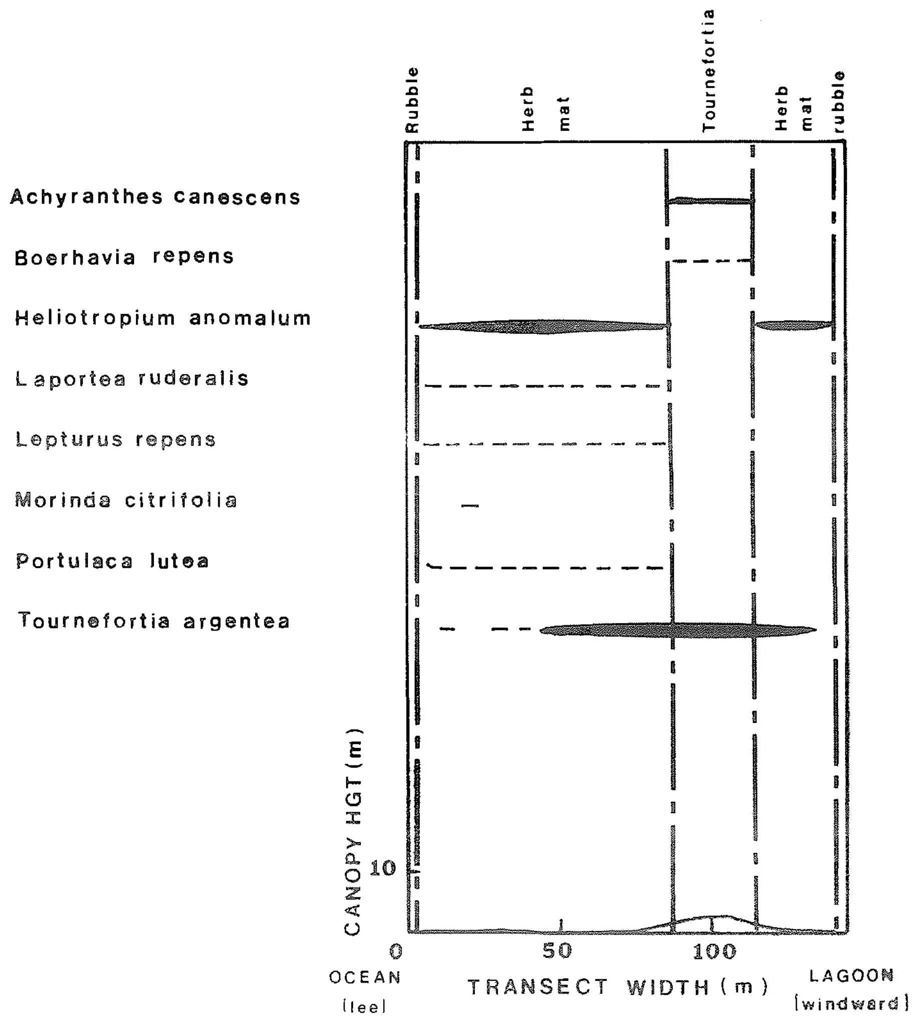

Figure 56. Fishball Islet (no. 11, Central Leewards): east-west cross-section through the center of this young motu, which exhibits early stages of geological and biological evolution. Data includes floristic composition, relative abundance of plant species, degree of species overlap and canopy heights. Vertical height is exaggerated.

found no eggs, but laying occurred in June here and on adjacent Bird Islet (Anne Falconer, pers. comm.).

SOUTHERN LEEWARD ISLETS Pls. 14, 69

This chain of 5 small motus lies along the southwestern edge of the lagoon. All are built upon piles of rubble about 3 m high, oriented east-west, and separated by shallow, narrow channels. From 1.51 to 3.67 ha in size, their topography, vegetation, and breeding seabirds are similar. Although situated on the leeward side of the atoll, the Southern Leeward Islets exhibit some windward characteristics; they lie opposite and slightly north of a wide break in the windward reef which allows trade winds to sweep, uninterrupted, across the lagoon. This promotes their 60-80% cover of scrub or forest. Ana-Ana, the southernmost, was periodically occupied from 1987-1991 by the Falconer family.

Of particular botanical interest are the interior forests, composed of *Pisonia* mixed with more *Cordia* than elsewhere on the atoll. Pure *Cordia* groves (mostly too small to map accurately) typically occupy the forest peripheries.

Their history (previous to 1987) is unknown; all appear to harbor virgin plant communities mingled with occasional drift-derived *Cocos* or *Pandanus*.

35) **MOTU RAURAU "Blue-Gray Noddy Islet"** (3.48 ha) Figs. 29, 57; Pls. 14, 69

Northernmost of the Southern Leeward Islets, we named this motu for the Blue-gray Noddies (*raurau* in Gilbertese) observed there.

Physiography: Raurau is ovoid, with a small lagoonside bay, and maximum dimensions of 180 m long and 231 m wide. It has the most expansive rubble of all the Southern Leeward Islets. This coarse coral clinker extends, apron-like, around the islet, widest (40 m) closest to the lagoon, and narrower (10 m) to seaward. The seaward reef flats extend 446 m to the ocean.

Vegetation: The number of plant species is 10 (5 trees, 1 shrub, 4 herbs), 39% of the atoll's flora. Raurau's 2 plant communities are simple: a very scant herb mat is sprinkled with *Tournefortia*, which rises to 6-m-high scrub all around the islet. *Laportea* forms a narrow band at the interface between coral rubble and scrub. Centrally a *Pisonia* forest (to 13 m), dotted with *Cordia* on the periphery, harbors much *Morinda* in the understory, including the tallest *Morinda* (13 m) seen on the atoll. A handful of drift-derived *Cocos* and *Pandanus*, the only introductions, dot the scrub.

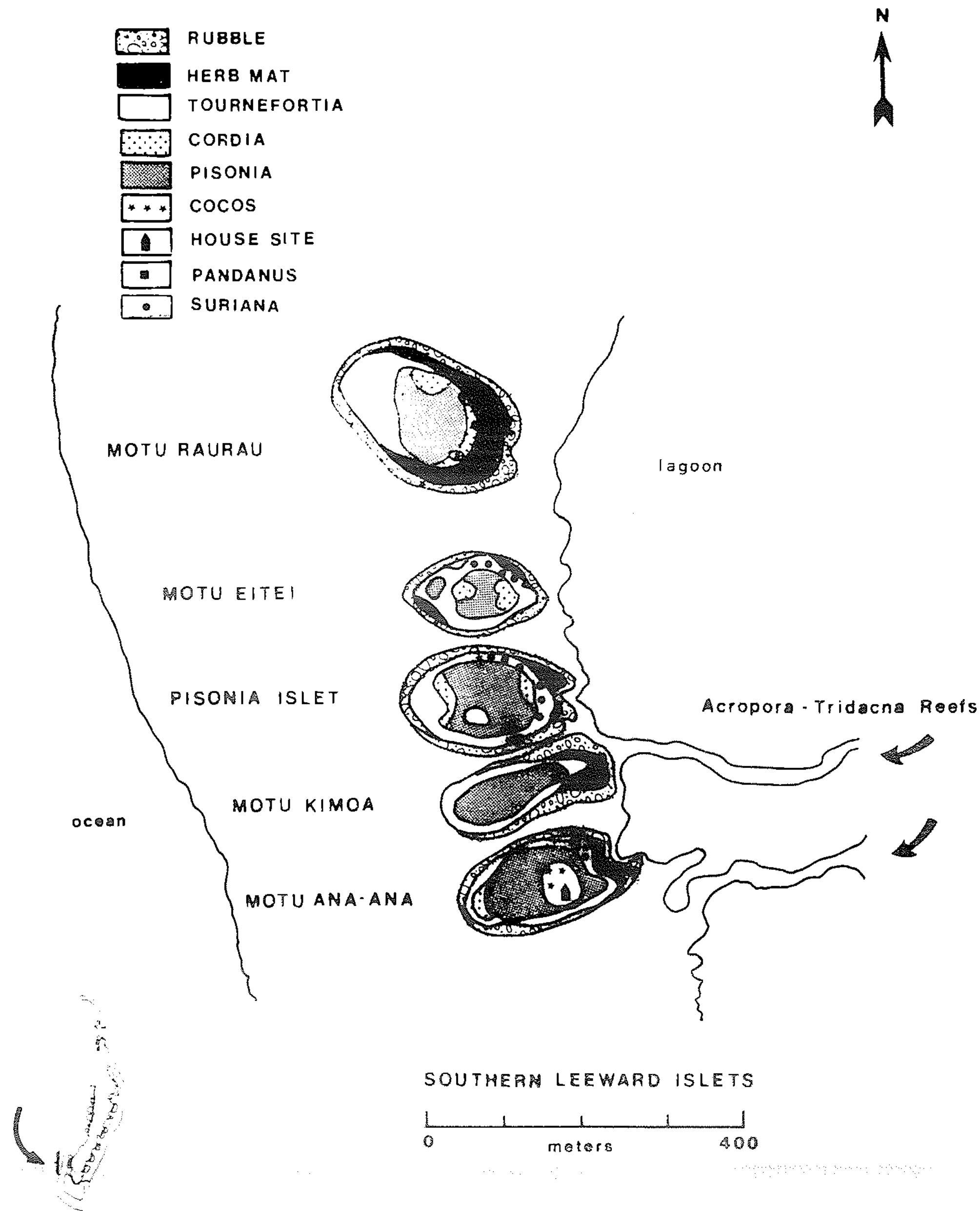

Figure 57. Vegetation and physiography of the 5 Southern Leeward Islets: Motus Raurau ("Blue-gray Noddy Islet"), Eitei ("Frigatebird Islet"), Pisonia Islet, Kimoa ("Rat Islet"), and Ana-Ana ("Anne's Islet").

Birds: No seabirds were found on transect, but a perimeter walk in 1988 revealed 4 species breeding in the leeward *Tournefortia*: Red-footed Booby (10 pairs), Great Frigatebird (31 pairs), Brown Noddy (1 pair), and White Tern (2 pairs). This islet, for its size, is particularly rich in frigatebirds.

Comments: Polynesian rats are present.

36) <u>MOTU EITEI</u> "Frigatebird Islet" (1.41 ha)

Figs. 29, 57; Pls. 14, 69

Second in line from the north, we named this motu for its nesting Great Frigatebirds, *eitei* in Gilbertese.

Physiography: Motu Eitei is rounded, 105 m long and 280 m wide. Lying perpendicular to the reef axis, it touches the lagoon edge on its inner side. To seaward, the reef flats are 644 m wide.

Vegetation: There are 8 species of plants (3 trees, 1 shrub, 4 herbs), 31% of the atoll's flora, with no introductions. Eitei is carpeted with 3 plant communities in the usual concentric arrangement. However, there is a slight difference in the species composition of the herb mats: on transect, the southern mat (2 m wide) consisted solely of *Portulaca*, while the north side contained a 3-m swath of *Heliotropium*, *Laportea*, and scattered *Suriana*. Inside the mat is a ring of *Tournefortia* scrub (to 5 m) and a central *Pisonia-Cordia* forest (to 11 m). *Laportea* is particularly abundant, while *Portulaca*, normally confined to the edges, abounds in small openings within the interior woodlands.

Birds: Four species of seabirds bred on Motu Eitei in 1988: Red-footed Booby (17 pairs), Great Frigatebird (14 pairs), Brown Noddy (6 pairs), and White Tern (18 pairs). The atoll's first Blue-gray Noddy nest was found in 1990 (Pt. II).

37) <u>PISONIA ISLET</u> (2.45 ha)

Figs. 29, 57; Pls. 14, 69

We named this motu for its fine *Pisonia* forest.

Physiography: Pisonia, third in the chain from the north, is almost circular, and lies closely appressed to its neighbor islets. Its maximum dimensions are 140 m long and 220 m wide. Like Raurau, it possesses a wide "apron" of coral rubble and sparse herbs on the lagoon side. Its seaward reef flats are 300 m wide.

Vegetation: The number of plant species is 15 (5 trees, 2 shrubs, 8 herbs), 58% of the atoll's flora. The only introduction is *Cocos* (few, scattered, north and south shores). Well-wooded, Pisonia harbors the customary 3 plant communities: the herb mat is almost pure *Heliotropium*, dotted with *Suriana*. One specimen of *Lepidium bidentatum* was found in 1990. The *Tournefortia* scrub and forest, covering half of the motu's length and width, grows to 9 m, while the *Pisonia-Cordia* forest, covering 0.86 ha (35% of the islet's area), reached 10 meters.

Birds: Despite the fine *Pisonia* forest, no Black or Brown Noddies nested. Only 3 species of seabirds bred in 1988: Red-footed Booby (26 pairs), Great Frigatebird (14 pairs), and White Tern (10 pairs). Best represented were Red-footed Boobies; a perimeter count yielded 18 tended nests, all in *Tournefortia* scrub. A Long-tailed Cuckoo was heard in the interior.

Comments: Rats were common: 6 were noted on a mid-morning transect survey.

38) MOTU KIMOA "Rat Islet" (1.80 ha)

Figs. 29, 57; Pls. 14, 69, 70

Fourth from the north, we named this motu for Caroline's single mammalian inhabitant, the Polynesian rat, *kimoa* in Gilbertese.

Physiography: Kimoa, smallest of the Southern Leeward Islets and shaped like a flared teardrop, is squeezed between its neighbor motus. Its maximum dimensions are 92 m long and 218 m wide, almost 4 times the size mapped by Arundel (Fig. 4). The southeast rubble and herb mats are wide. The distance to the outer reef edge is 307 meters. Of special note is the emergent *Tridacna-Acropora* reef which stretches completely across the lagoon to Tridacna Islet. This reef is 15-20 m wide (Fig. 48; Pls. 25, 57) and 1,023 m long, which, together with an equal length in blind diverticulae, totals over 2 kilometers. The *Tridacna* clams aggregate in densities up to 80/sq m (Sirenko & Koltun, in press).

Vegetation: Kimoa has 11 species of plants (3 trees, 2 shrubs, 6 herbs), 42% of Caroline's flora. There are no introductions. Though small and narrow, Kimoa is well-vegetated. Its herb mats are composed of *Heliotropium* on the south side and *Portulaca* (plus *Suriana*) on the north. The interior *Tournefortia-Pisonia-Cordia* forests (to 11 m) cover nearly half the islet's area.

Birds: Four species of seabirds bred in 1988: Red-footed Booby (21 pairs), Great Frigatebird (3 pairs), Black Noddy (2 pairs), and White Tern (7 pairs). Red-footed Booby nests occupied perimeter sites.

39) MOTU ANA-ANA "Anne's Islet" (2.16 ha)

Figs. 29, 57; Pls. 7a, 14, 52, 69, 71

This motu includes a small settlement with 3 thatched huts (cooking, eating, sleeping), a water tank, chicken coop, and garden. It was occupied from 1987-1991 by Anne and Ron Falconer, 2 small children, chickens, Muscovy ducks, and a dog. A wooden sign marked "Ana-Ana" indicated that the islet had been named.

It is interesting to compare Plates 7a and 71, identical profiles of Ana-Ana 105 years apart.

Physiography: Ana-Ana is the southernmost motu in the Southern Leeward Islets, 120 m long by 222 m wide at its widest point. Approximately 3 m high, it is roughly oval, with a hooked point and curved bay facing the lagoon. This point is actively growing as more and more rubble is deposited by the large flow of water passing through the channel (430 m wide) that separates Ana-Ana and South Island. This channel contains abundant clams that amass into an extensive *Acropora-Tridacna* reef stretching approximately 900 m across the lagoon to Tridacna Islet. The outer reef flats measured 281 meters.

Vegetation: Ana-Ana has 15 species of plants (5 trees, 2 shrubs, 8 herbs), 58% of Caroline's flora. Introductions include *Cocos*, vegetables, a few ornamentals and, as yet, no weedy exotics. Ana-Ana's vegetation is typical of the other Southern Leeward Islets except for the settlement. Narrow trails from the southern channel lead to a neat clearing, approximately 40 m x 70 m, the only inhabited portion of the atoll. We advised the Falconers against introducing alien plants with spreading seeds and requested them to destroy all introductions when vacating the island permanently.

Ana-Ana has sparse herbaceous mats: *Suriana, Heliotropium, Portulaca, Laportea*, and *Lepturus*. The *Tournefortia* strand includes *Cocos, Cordia*, and *Pandanus*. Quality *Pisonia* forest, 15 m high, covers 43% of the islet's area.

Birds: No breeding seabirds were found on any of the 3 visits to Caroline. However, the Falconers found a few White Terns and one Great Frigatebird nesting in the perimeter scrub, as well as groups of Brown Noddies sitting on the beach. Long-tailed Cuckoos were seen around the huts in March, April, and May 1990. It is to be hoped that seabirds return now that the motu is again uninhabited.

Comments: Rats and large cockroaches are abundant. Despite the tidy site, 12 rats occupied a pile of coconut debris, while others scurried amongst the forest litter. The Falconers trapped over 1,300 rats one 2-year period. Several pale geckos with a few spots and largish heads were seen in and around the huts (probably mourning geckos).

I. CONCLUSION

Lushly wooded Caroline Atoll, with the majority of its 39 islets (399 ha of land) either in near-pristine condition or having recovered remarkably from past disturbance, is one of the least spoiled atolls in the Pacific. Uninhabited, it harbors plant ecosystems and breeding seabirds (Pt. II) of national and international importance. Its marine and terrestrial ecosystems are prime outdoor ecological laboratories for research on geological processes including ground water, sea level changes, the dynamics of motu formation, fish poisoning, and numerous facets of ecology including plant succession and *Pisonia* growth rates.

Caroline boasts prime coral reefs thickly studded with *Tridacna* clams, substantial numbers of coconut crabs, breeding sites for green turtles, wintering grounds for shorebirds including the rare Bristle-thighed Curlew, ancient Tuamotuan *marae*, and a crystalline, unpolluted lagoon. The variety, abundance, and quality of its flora and fauna qualify it for status as an officially recognized international preserve (Pt. II, Sect. G). Efforts toward its conservation have thus far been unsuccessful: in 1992 it was leased to a private French businessman who is currently fishing the reefs for commercial profit, as well as disturbing seabird, turtle and coconut crab populations.

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APPENDIX I

Reef Information for Navigators

We include this section because no accurate hydrological chart exists, and the *Pacific Islands Pilot* (Hydrographer of the Navy 1982) section for Caroline is incomplete. Arundel's 1883 map (Admiralty Chart No. 979, Fig. 4) is still used today.

Caroline is visible "from aloft" at about 23 km (Ward 1974). It has neither a deep pass, nor navigable channels into the lagoon, nor a ship anchorage beyond the reef. In 1873 a set of moorings was placed off the west coast of South Island for the convenience of guano ships, approximately "a mile north of the south-west point, in about 60 fathoms of water and some distance from the shore" (Arundel 1875). These are long gone, although small boats can still anchor within the close lee of South Island during normal trade winds. Today's ships, however, must drift well offshore after approaching the atoll from the west (Pl. 12).

Of special note is a possible extension of the perimeter reef south and southwest of Caroline. Arundel's map notes: "Reef reported to extend four cables from southeast point." This information probably originated in Findlay's South Pacific Directory, quoted by Holden (1884). Evidently the windward reef of South Island extends approximately 1.7 km from its southeast point. From here "this reef sends out two branches to a distance of 2.5 km, one toward the southeast, the other toward the southwest and is consequently dangerous to approach at night." Arundel's map does not include this bifurcation which, according to Findlay (1884), extends at least across the width of South Island. He also states that "a landing (not always safe) may be effected on the north side of the southwest bifurcation, described above." No trace of these submerged reefs is evident on the RNZAF aerial photos.

The "boat entrance" (Figs. 4, 50), a narrow nick in the outer leeward reef, marked by the stock and ring of an anchor and immediately to the west of South Island's northwest point, is not necessarily the easiest route to the lagoon. Landing is possible across the steep-to reef at many locations along the leeward reef; opposite the southern end of Ana-Ana is good.

Landing adjacent to the anchor is fairly straightforward in calm seas, especially when one becomes familiar with the crooked notch which narrowly pierces the outer reef. After negotiating a powerful backwash, one's boat is swept onto the shallow reef flats--liberally laced with chunks of jagged reef--which is exposed at low tide and barely covered at high tide. A swift current passes west out of the lagoon between South Island and Ana-Ana, sweeping over the reef at the notch. Only small craft with virtually no draft can effect the 500-m journey to South Island. Because the shallows are unchanneled and not navigable even at high tide, skiffs must be carefully hauled through the water to a sheltered landing spot adjacent to South's northwest point (Pl. 12).

An alternative landing method used by yachts in calm weather is via the "blind passage" (Sect. D, Fig. 50), between northeast South and Tridacna Islet. Despite the fact that the inner one-third of this narrow diverticulum is calm, the outer two-thirds are rough most of the time. Its channel leading to and from the open sea is particularly turbulent and should not be attempted without land-based assistance, and only at first light.

Landing is also possible across the reef flats off leeward Nake, but there is no boat passage into the lagoon. Ward (1974) states that at high water, light draught boats can land over the reef opposite the middle of the western side of South Island. This would be the only cross-reef landing which does not involve walking a boat across the uneven reef flats.

APPENDIX II

Weather Data, Caroline Atoll, 1989-1990

A. Wind Direction and Speed (mph), 1989

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	NNE 15	NW 18	E 25	E 12	E 20	E 15	E 25	E 20	-	NE 10	N 20	NE 8
2	NE 10	W 5 Variable	E 15	E 16	E 20	NE 18	SE 20	E 12	-	NE 12	N 15-17	NE 10
3	NE 10	NE 20	E 12	SE 14	S 15-20	E 18	E 20	SE 25	-	NE 15	NE 15	NW 20
4	NE 15	NE 15	E 12	SE 15	E 15	E 15	E 20	SE 20	-	NE 15	NE 12	NW 20
5	NE 20	NE 15	NE 15	E 12	NE 8	E 15	E 18	E 18	-	NE 12	E 12 big swells	NW 18
6	NE 20	NE 20		SE 10	NE 8	E 15	E 10	E 18	-	NE 12	E 10	N 10
7	NE 12	SE 18	E 12	E 14	NE 10	NE 25 E 10	-	E 12	-	NE 15	NE 12	NW 18
8	NE 12	E 15	calm	SE 10	E 10	NE 20	SE 12 squalls	NE 18	-	NE 15	calm	NW 18
9	NE 12	E 18	SE 10	E 20	E 15	NE 18	SE 20	E 12	-	NE 12	N 10	NE 10
10	NE 15	E 16	NW 10	E 20	E 15	E 15	SE 16	E 12	-	NE 10	NE 12	NE 10
11	NE 10	NE 16	calm	SE 25-E 10 squalls	E 15	NE 15 E 15	E 15	calm	-	NE 10	E 18	NE 5
12	NE 20	SE 14	E 10	W 14	E 15	E 15	E 12	E 12	-	NE 16	E 17	NE 12
13	NE 15	E 12	E 12	E 16	NE 16	NE 16	E 12	-	-	NE 11	E 14	NE 12
14	NE 15	E 10	NE 10-18	E 20	NE 16	NE 8	E 12	calm	-	ENE 10	E 10	NE 14
15	NE 15	NE 8	E 8	E 18	E 15	E 10	E 10	-	-	NE 10	calm	NE 14
16	NE 15	SE 8	E 12	E 18	E 22 squalls	E 10	NE 10	-	-	NE 12	calm	NE 15
17	NE 18	E 20	NE 15	E 18	E 25	E 15	E 10	-	-	NE 14	calm	NE 12
18	NE 12	E 12	E 8	E 18	NE 18	E 15 big swells	E 15	-	-	NE 15	N	NE 14
19	NE 12	E 12	E 10	E 18	NE 14	E 10	E 16	-	-	NE 13	NW 10	E 12
20	NE 18	E 12	E 10	E 18	NE 14	E 15	E 18	-	-	E 15	NW 15	E 10
21	NE 15	NE 10	SE 8	E 14	E 12	NE 20	E 20 squalls	-	-	E 16	N 16	E 10 big swells
22	NE 20	E 15	calm	E 14	E 12	E 10	E 15	-	-	NE 14	NE 14	E 12-NE 10
23	NE 18	thunder squalls	N 18 thunder	SE 14	SE 10	E 10	E 15	-	NE 20-30	E 20	NE 16	calm
24	NE 15	E 25	N 12	SE 14	SE 10-25	E 10	E 12	-	E 20-30	NE 15	NE 12	NE 15
25	NE 12	E 15	N 12	E 12	E 18	SE 17	E 10	-	E 20	NE 15	NE 12	NE 16
26	NE 12	E 15	N 10	E 10	NE 14	E 10	calm	-	E 20	NE 15	N 10	NE 15
27	NE 12	E 25	SE 10	NE 10	E 18	E 10	calm	-	NE 17	E 9	E 9	NE 15
28	NE 12	E 14	E 12	E 13	E 18	E 10	E 15-35	-	E 15	NE 10	E 8	NE 15
29	NE 15		E 14	E 18 big swells	E 15	E 18	E 15	-	N 10	NE 8	E 7	NE 12
30	NE 12		E 12	E 13	-	E 18	E 15	-	calm	calm	-	E 10
31	calm		E 18				SE 18	-		N 20		E 16

B. Rainfall, 1989-1990

Month/Year	Mean Monthly Rainfall (mm)	Mean Number of Rain Days
Jan '89	71.1	7
'90	177.8	22
Feb '89	160.0	14
'90	640.1	10
Mar '89	259.1	20
'90	215.9	14
Apr '89	190.5	16
'90	48.3	6
May '89	66.0	10
'90	325.1	8
Jun '89	48.3	11
'90	78.7	11
Jul '89	45.7	12
'90	68.6	8
Aug '89	35.6	12[a]
'90	109.2	14
Sep '89	50.8	3[b]
'90	81.3	6
Oct '89	73.7	11
'90	175.3	9[c]
Nov '89	78.7	7
'90	134.6	14
Dec '89	162.6	11
'90	154.9	9
Annual '89	1,242.1	134
'90	2,209.8	131

Source: Ron Falconer, Caroline Atoll (pers. comm.).
[a]Based on 16 days' data.
[b]Based on 9 days' data.
[c]Based on 18 days' data.

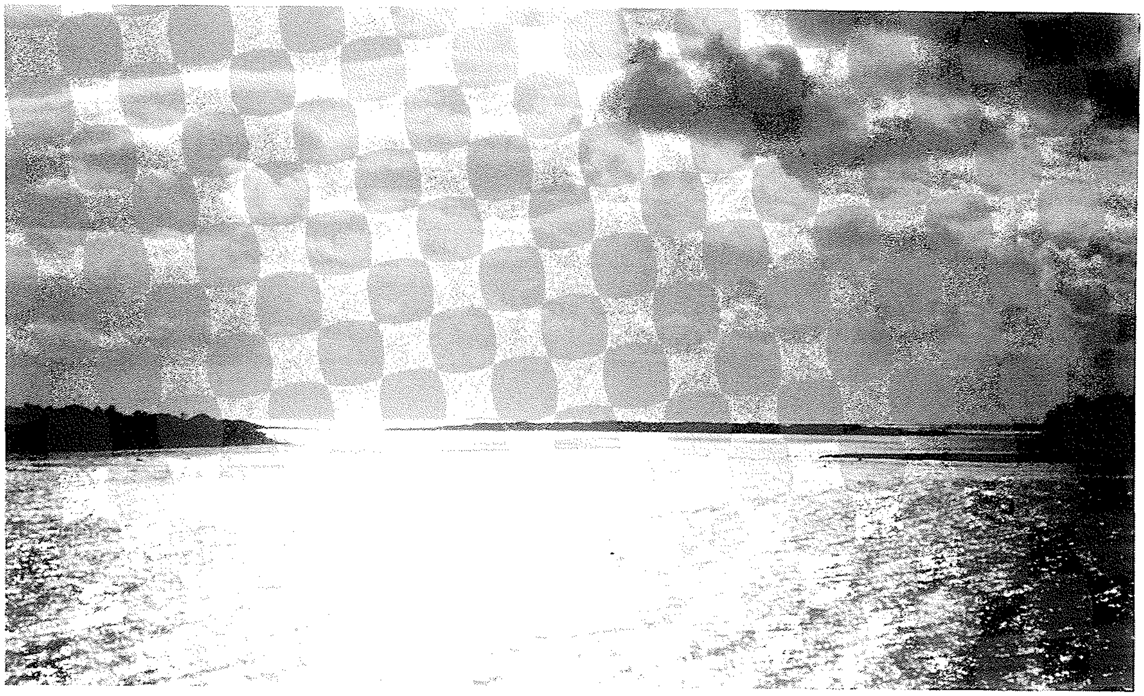

Plate 1. A 1988 dawn view of Caroline as seen from its leeward seas, very similar to that seen by the atoll's Western "discoverer," de Quiros, in 1606. Left to right: Motu Ana-Ana, Tridacna Islet, South Island. Open reef area in the foreground is the 1883 chart's "boat entrance."

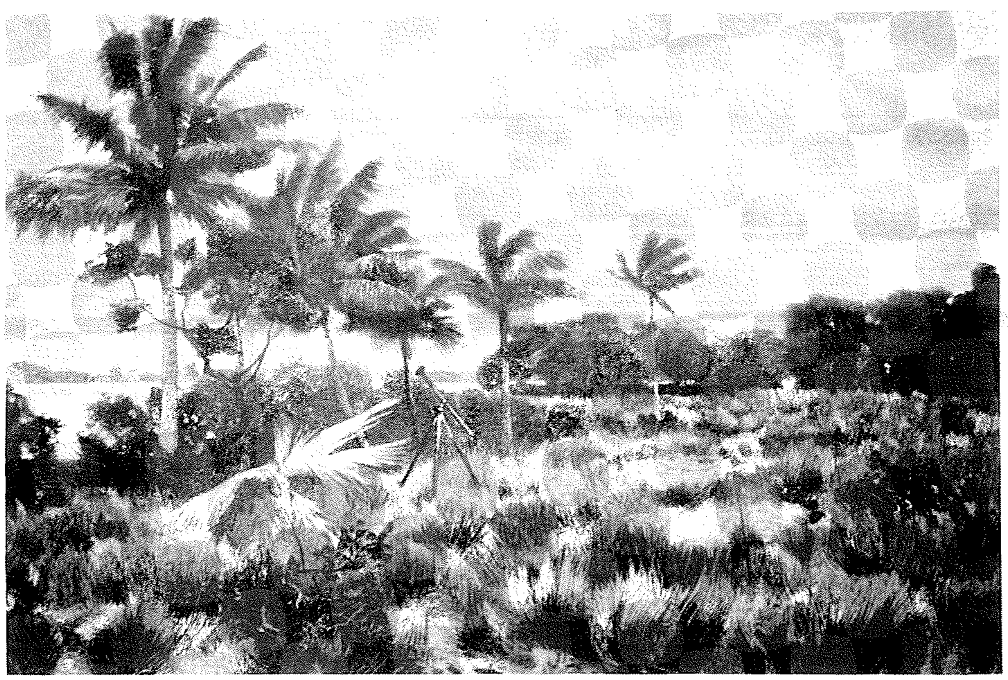

Plate 2. A clearing on South Island from which the Solar Eclipse Party made their observations in 1883. Today the area is covered with dense *Cocos* forest (from Holden & Qualtrough 1884).

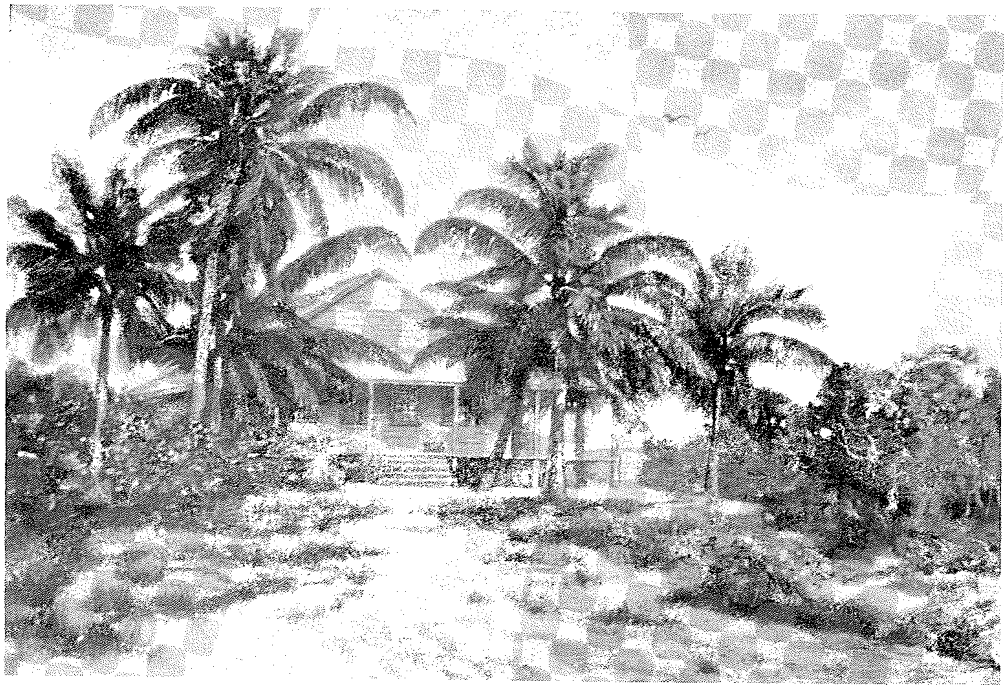

Plate 3. One of the 3 European-style houses that have ever been built on Caroline, drawn in 1883 (ibid.).

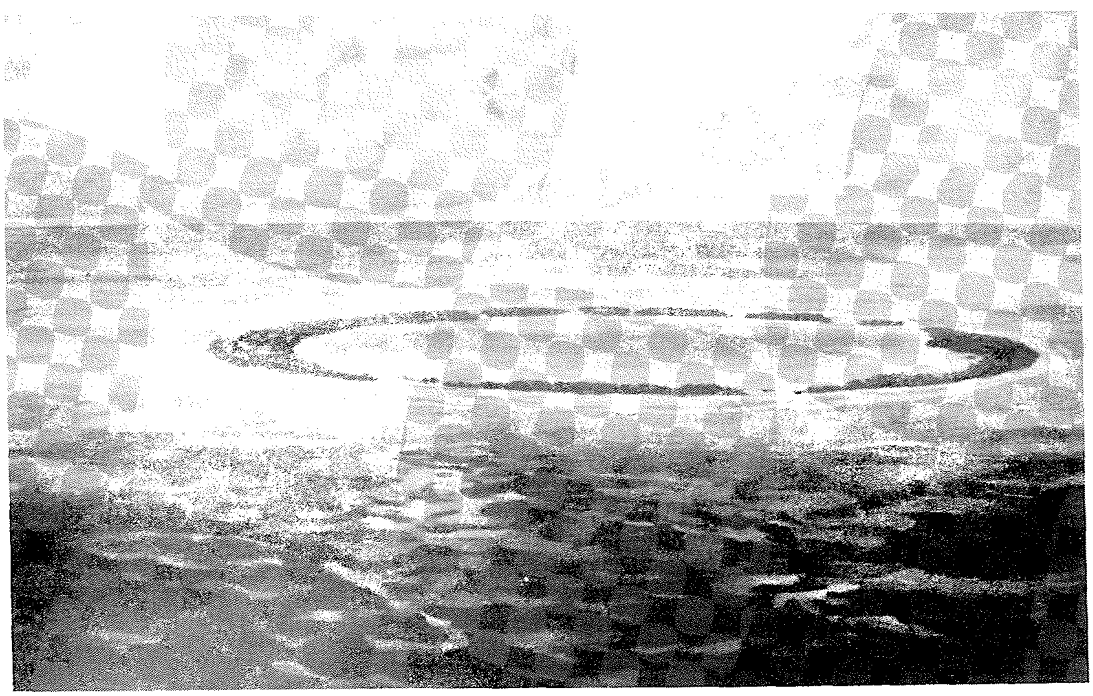

Plate 4. An artist's very free rendering of Caroline in 1883 (from Holden & Qualtrough 1884).

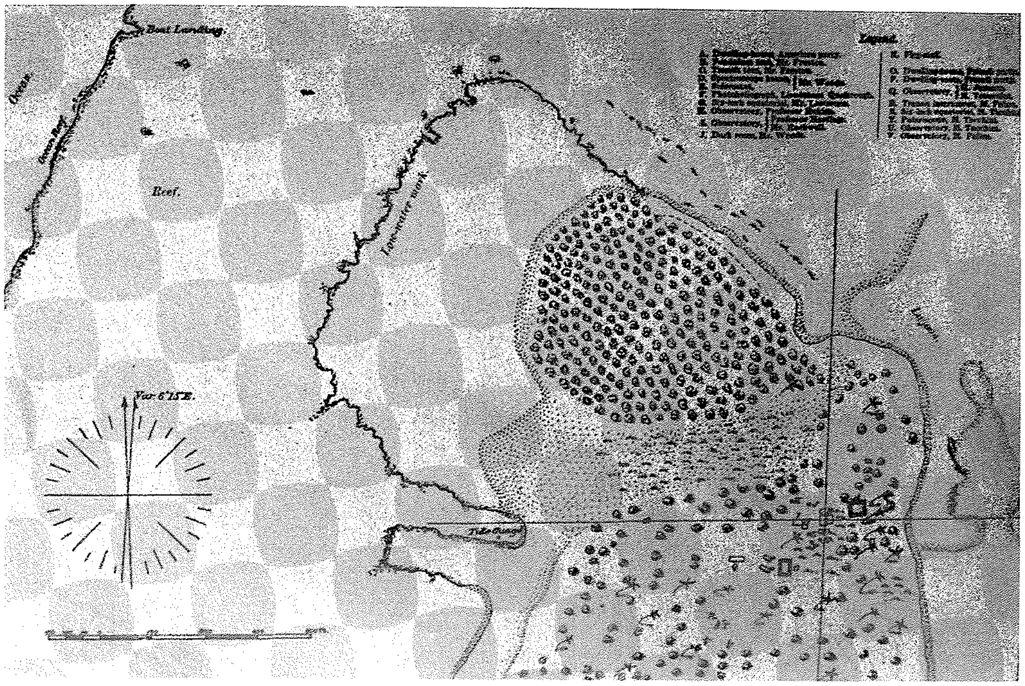

Plate 5. Map of the "settlement" on South Island, as drawn by the Solar Eclipse Party (ibid.).

Plate 6. Two lagoon views a century ago along the north coast of South Island (from Holden & Qualtrough 1884). Compare these drawings with Plate 23.

Pl. 6a

Pl. 6b

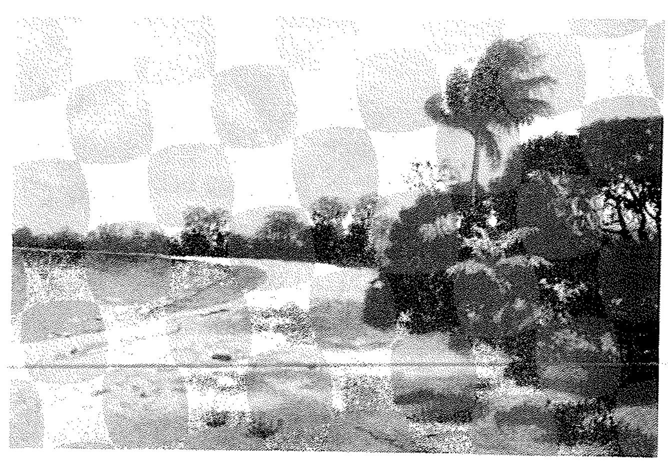

Plate 7a. Motu Ana-Ana, unnamed in 1883 (Holden & Qualtrough 1884) but appearing virtually identical then, as to today (Pl. 71).

Plate 7b. A large Tournefortia tree along South Island's lagoon edge, 1883.

Plate 8. CBK in Ipomoea macrantha thicket, dying Cocos-Ipomoea forest, South Island.

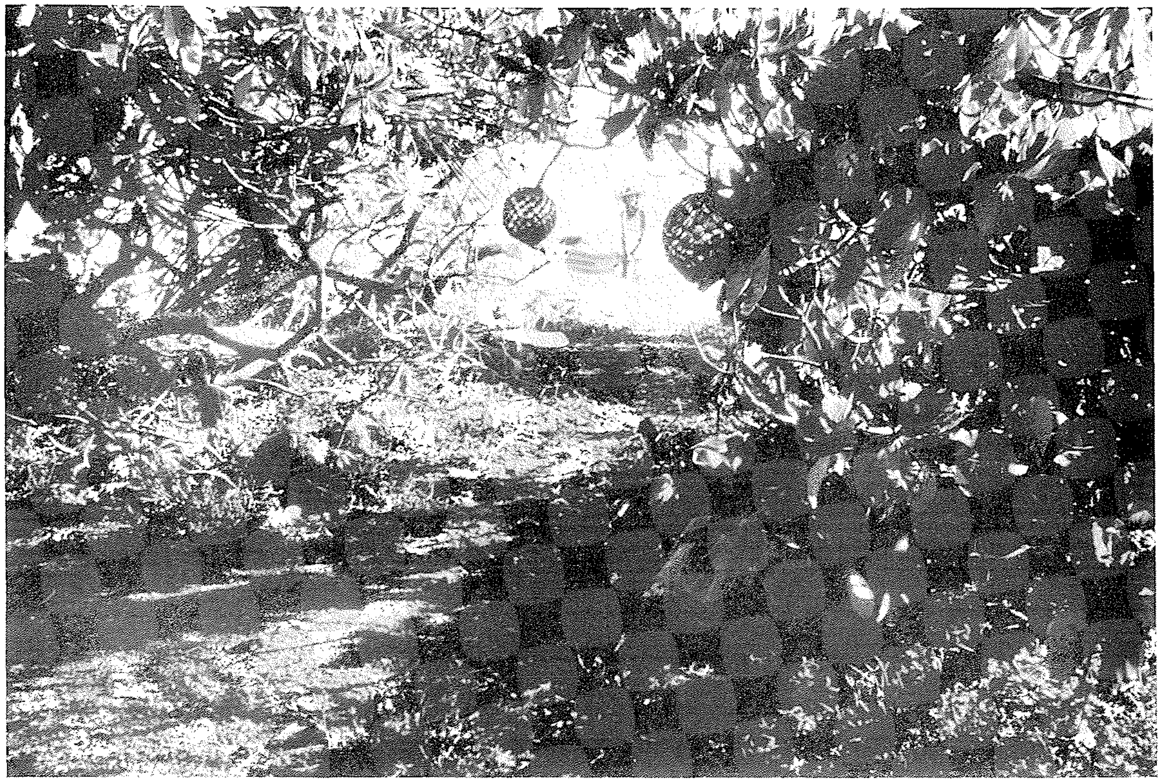

Plate 9. "Rat City" base camp, southwest Long Island.

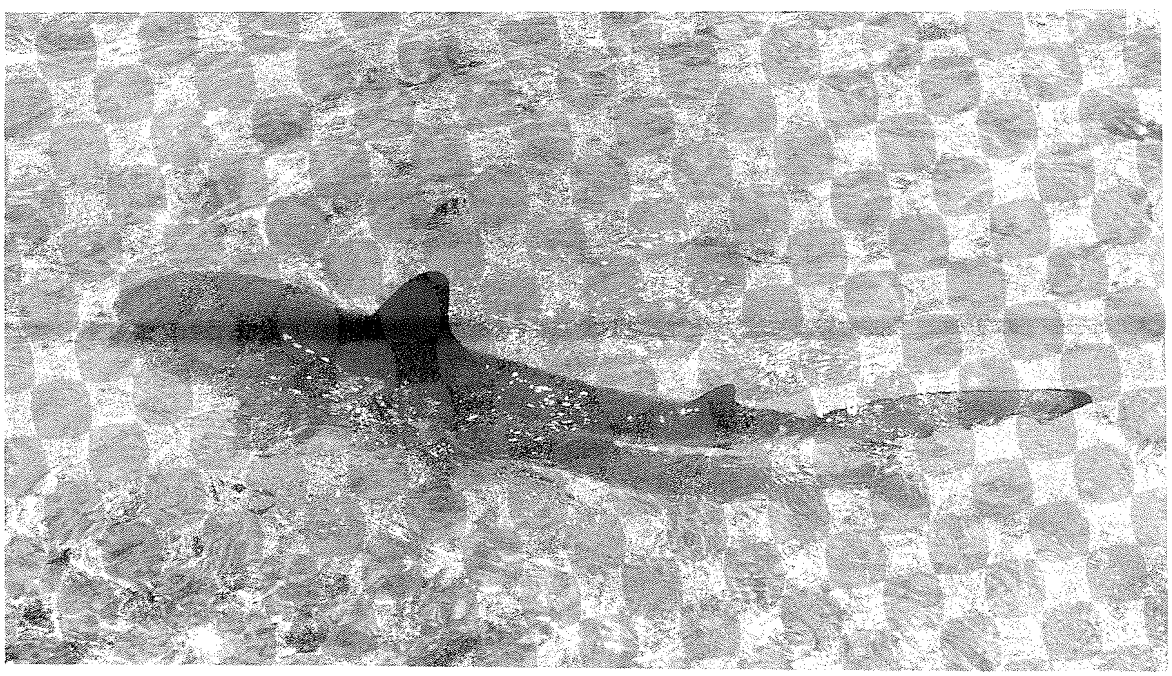

Plate 10. Black-tipped reef shark (*Carcharhinus melanopterus*), numerous and aggressive in Caroline's lagoon. Note the abundant sea cucumbers (*Ludwigothuria* sp.).

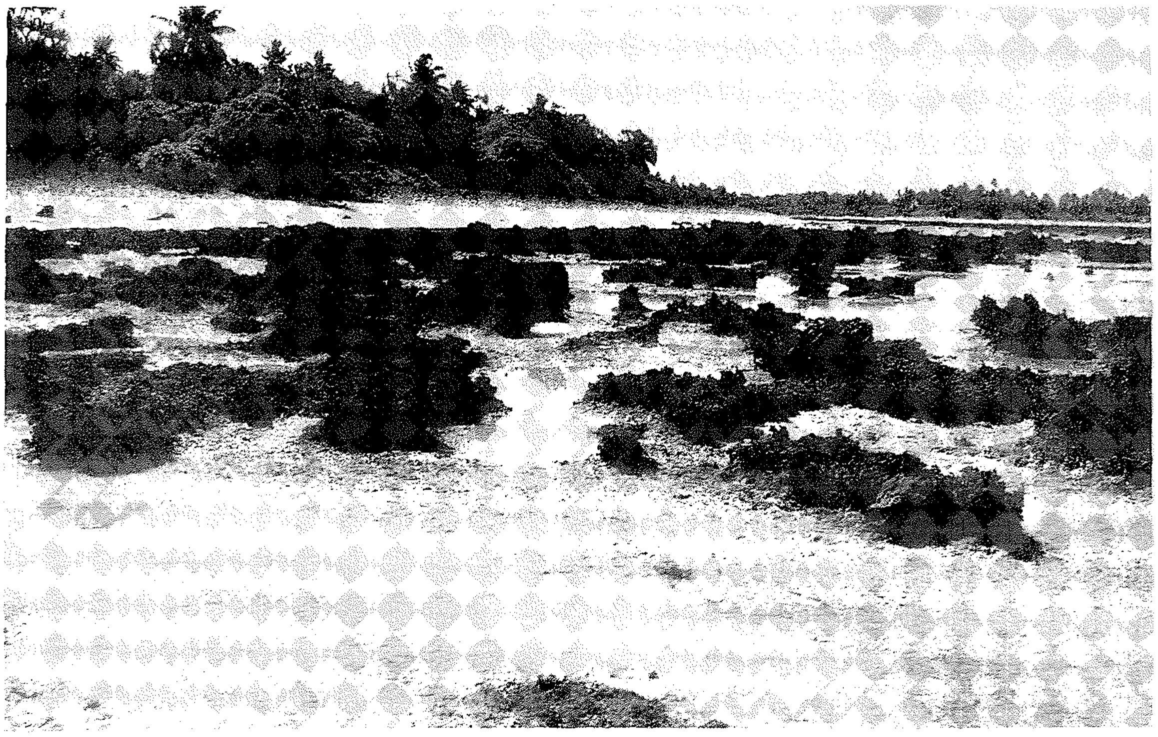

Plate 11. Laterally continuous, upraised older reefs of unknown age, southwest Nake. Note the wide reef flats.

Plate 12. Floating a small boat across the southwest reef flats in calm weather from the "boat entrance" to the "landing" on South Island. Note the wide reef flats. The *Akademik Korolev* drifts offshore.

Plate 13. Beach crest, sandy rubble, seaward moat and narrow reef flats off southeast Nake Island.

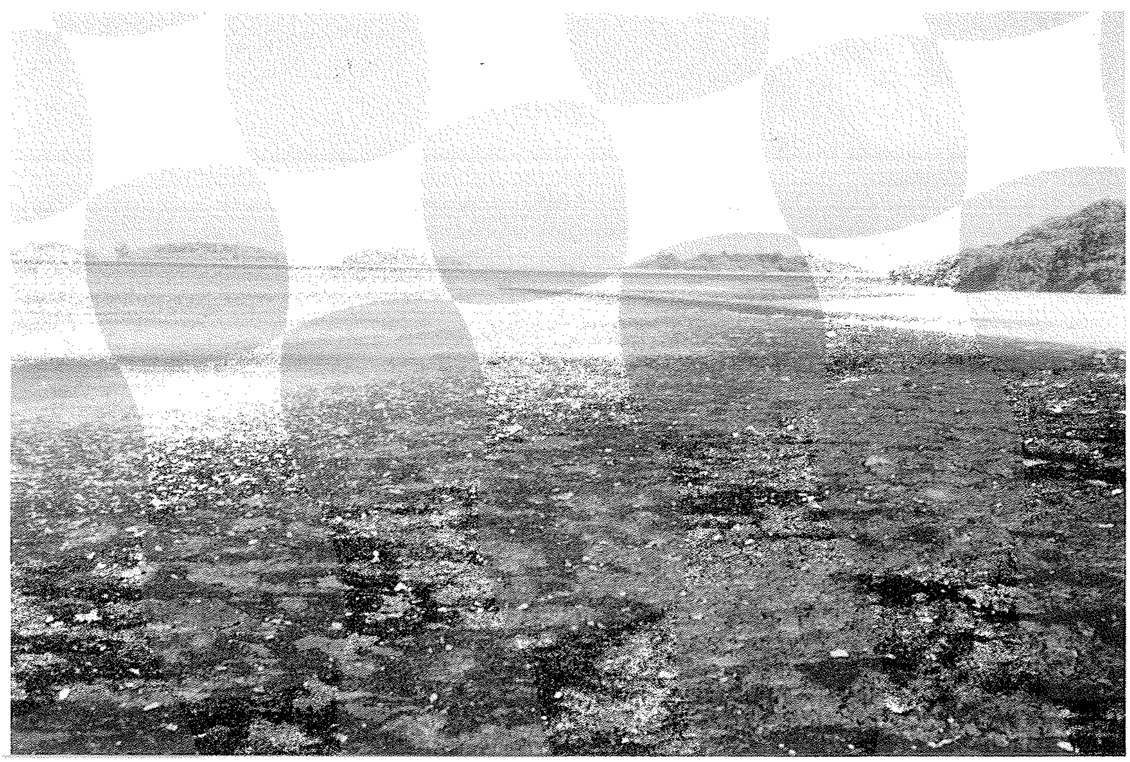

Plate 14. Extensive lagoon reef flats south of Arundel Islet on the windward side. Note the 5 Southern Leeward Islets in the distance.

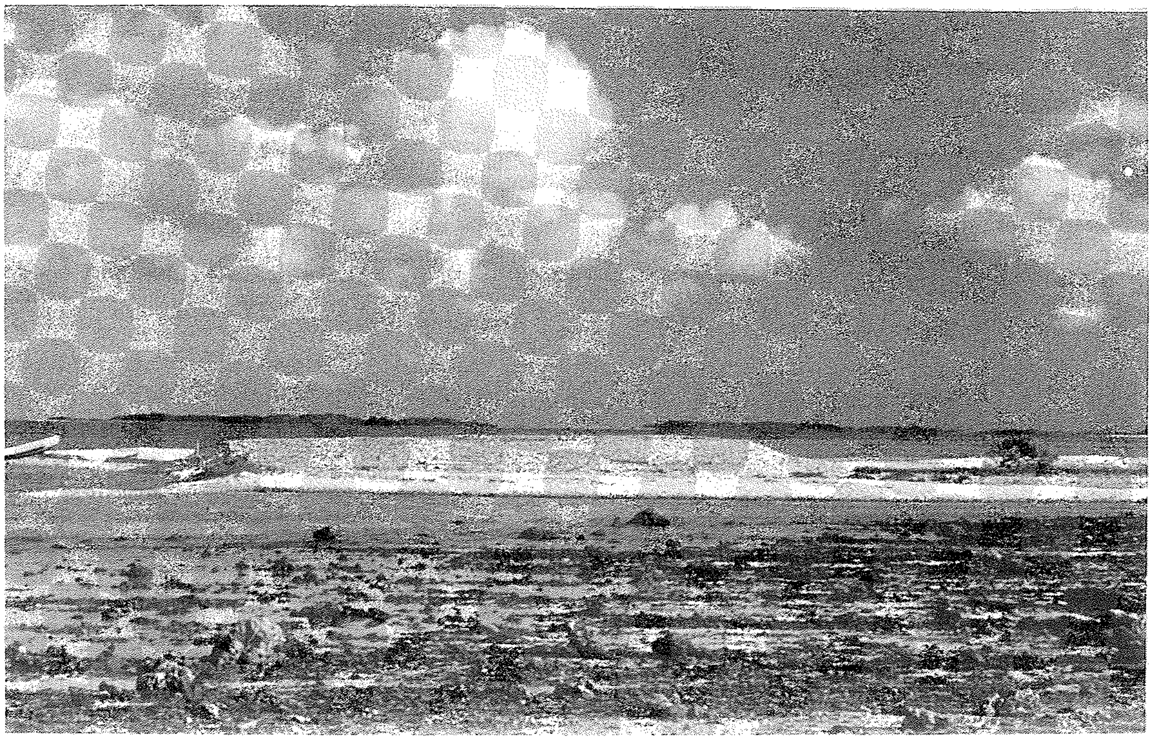

Plate 15. An incipient motu, barely connected to Motu Mouakena's southern shore. See also Plate 62.

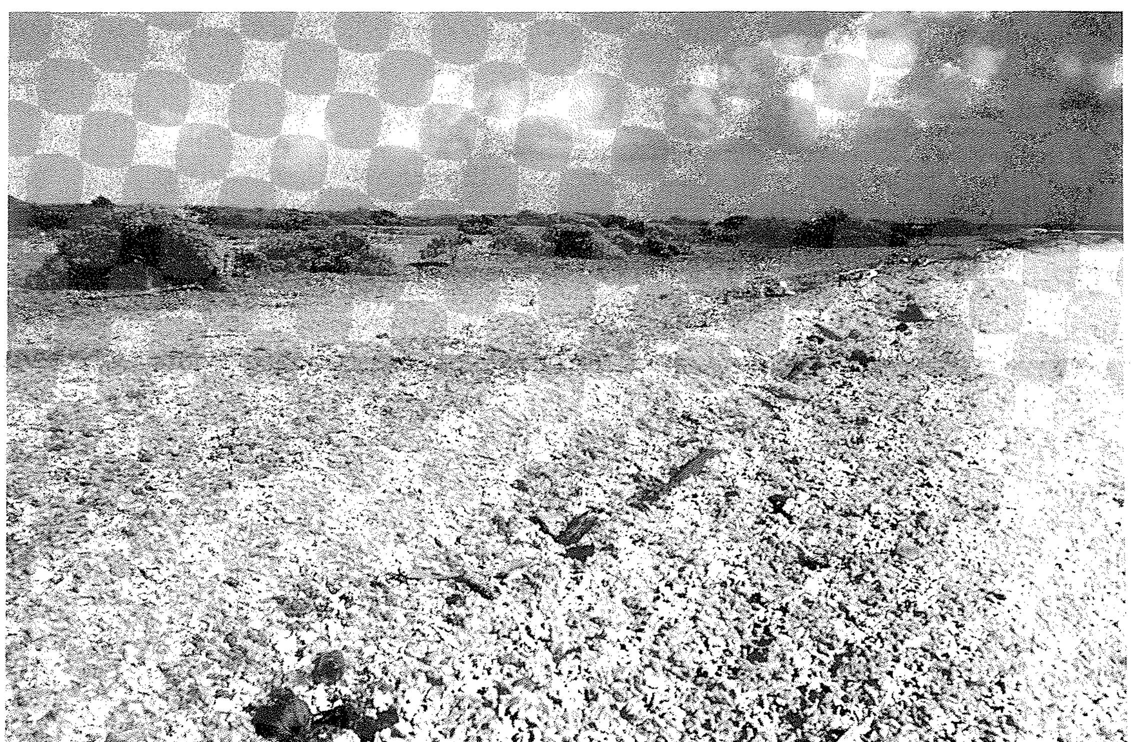

Plate 16. Successive ridges of coral rubble deposited by past storms, northeast Nake Island.

Plate 17. Channel between the 2 northern islets, Long and Nake. Note the mixed forest with *Cocos* and *Pandanus*, and filled-in upper lagoon.

Plate 18. Noddy Rock (0.02 ha), an emergent reef platform of unknown age along the windward reef flats. A northward view. Islet is completely awash during storms.

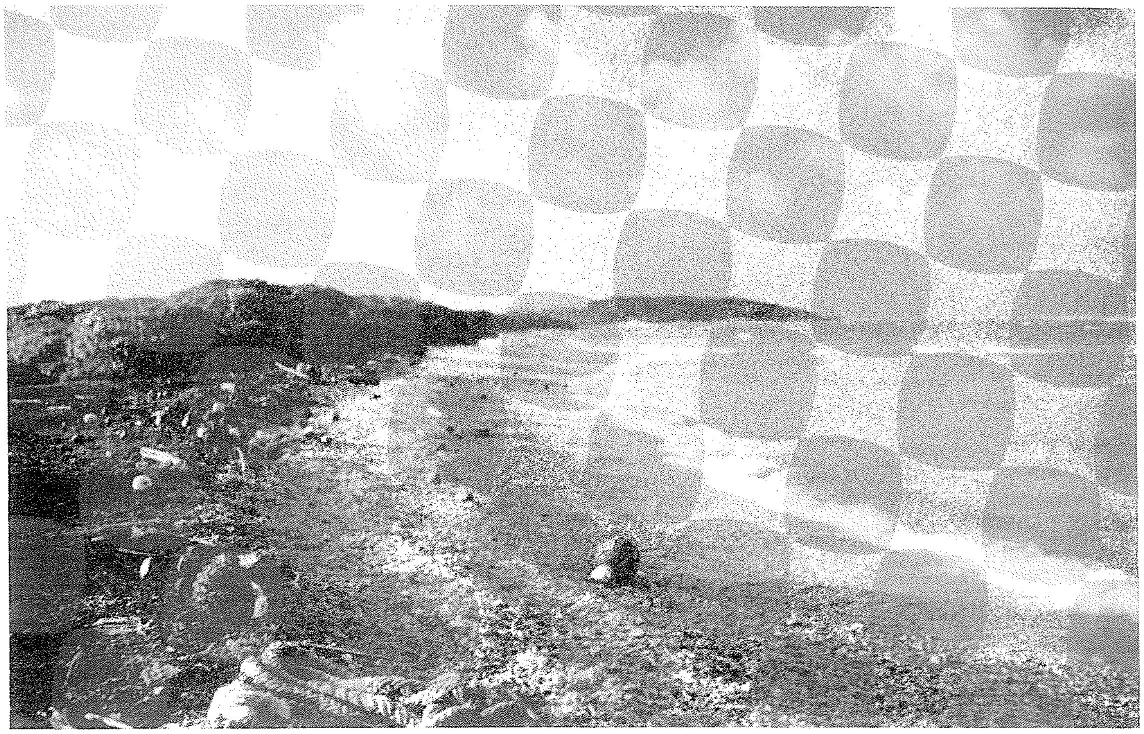

Plate 19. Windward beach, Long Island, showing wide rubble flats inland of the beach crest, rimmed by oceanic flotsam and jetsam.

Plate 20. Conglomerate platform, northwest point, South Island. Russian vessel *Akademik Korolev* drifts offshore and a lone *Suriana maritima* dots the blinding coral beach.

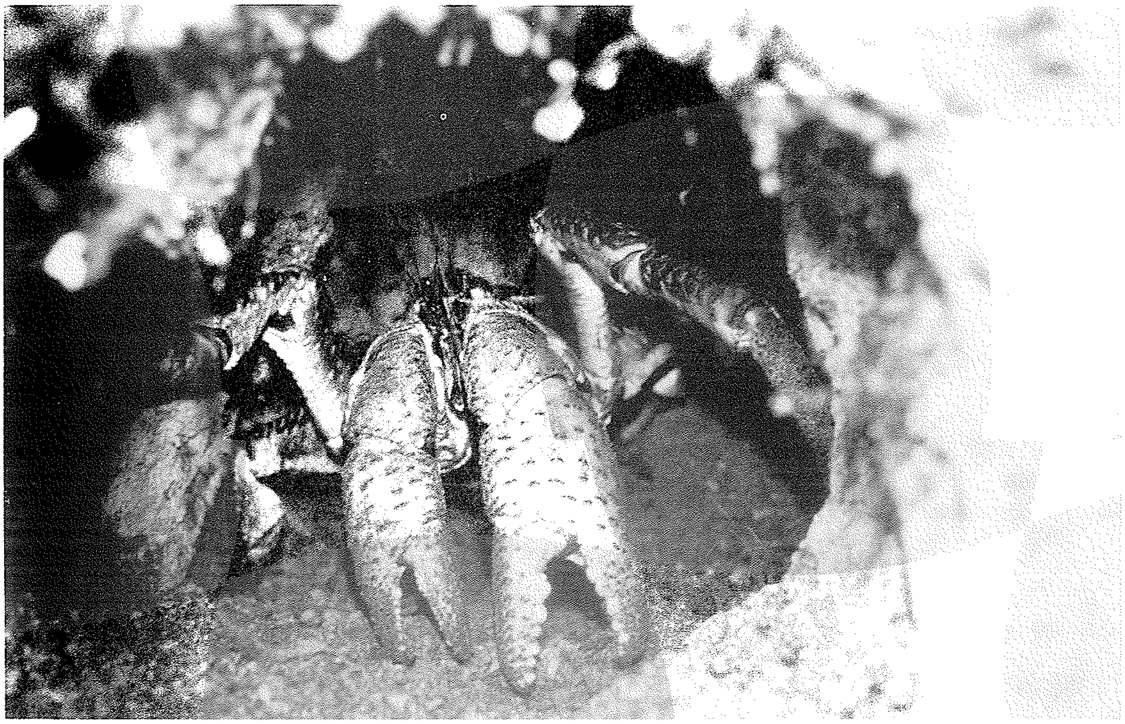

Plate 21. A large coconut crab (*Birgus latro*) shelters in a subterranean cavity in the *feo*. Some males were among the largest ever measured.

Plate 22. Sandy Inlet, a filled-in portion of the lagoon, extends its fishhook-shaped mudflat 300 m northward into Nake's landmass. Here grow the healthiest and most productive *Cocos* on Caroline. Note the Bristle-thighed Curlews in the foreground.

Plate 23. South Island's pure *Cocos* plantation, looking west along the lagoon. This extensive grove has now obliterated all traces of the former "settlement" (Pls. 2-6). Note the dead *Tournefortia* bush, killed by excessive shade.

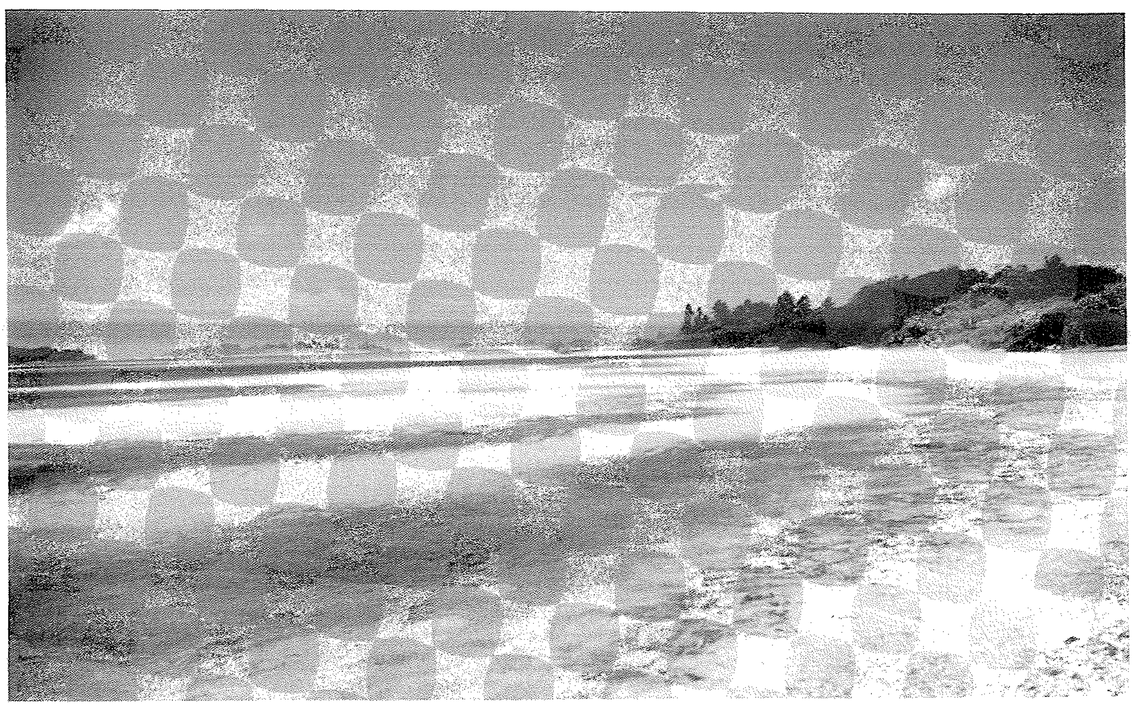

Plate 24. Crystalline lagoon waters adjacent to Emerald Isle (Central Leeward Islets) are studded with submerged reefs and sandy channels.

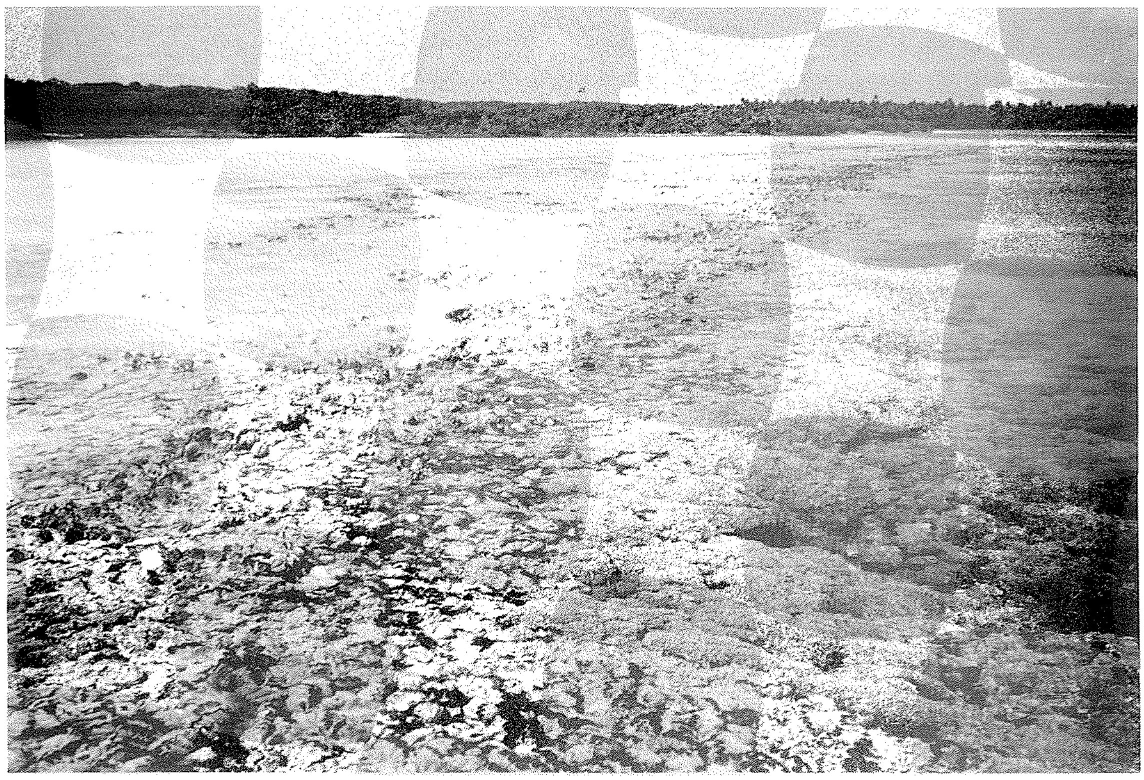

Plate 25. A highly productive cross-lagoon reef of *Acropora* spp. corals and *Tridacna maxima* clam shells joins Tridacna Islet with Motu Kimoa. Sirenko & Koltun (in press) estimate 300,000 living *Tridacna*/km.

Plate 26. *Cordia* Forest (to 12.6 m tall), Pig Islet.

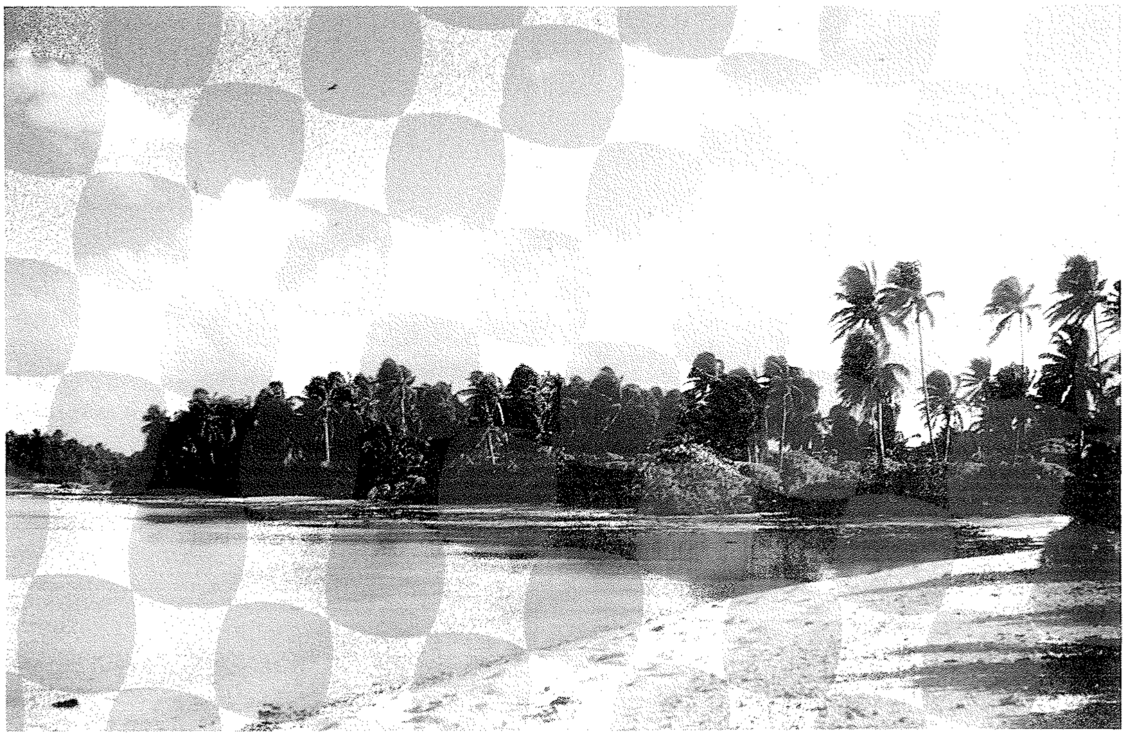

Plate 27. Sand, silt, rubble and hardpan mingle on the upper reaches of Long Island adjacent to the lagoon.

Plate 28. Caroline's sandiest beach flanks the lagoon shore of Shark Islet.

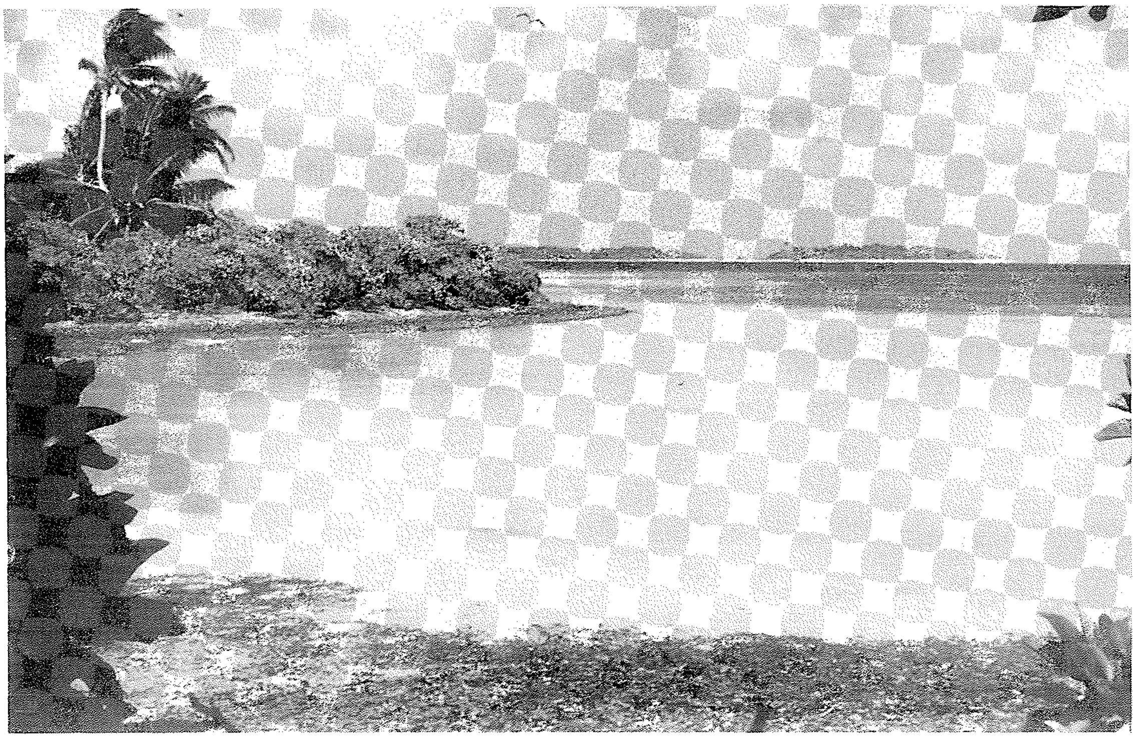

Plate 29. Sheltered bay, Brothers Islet. Raurau Islet lies across the lagoon. Note the sparse herb mat and silty shallow waters.

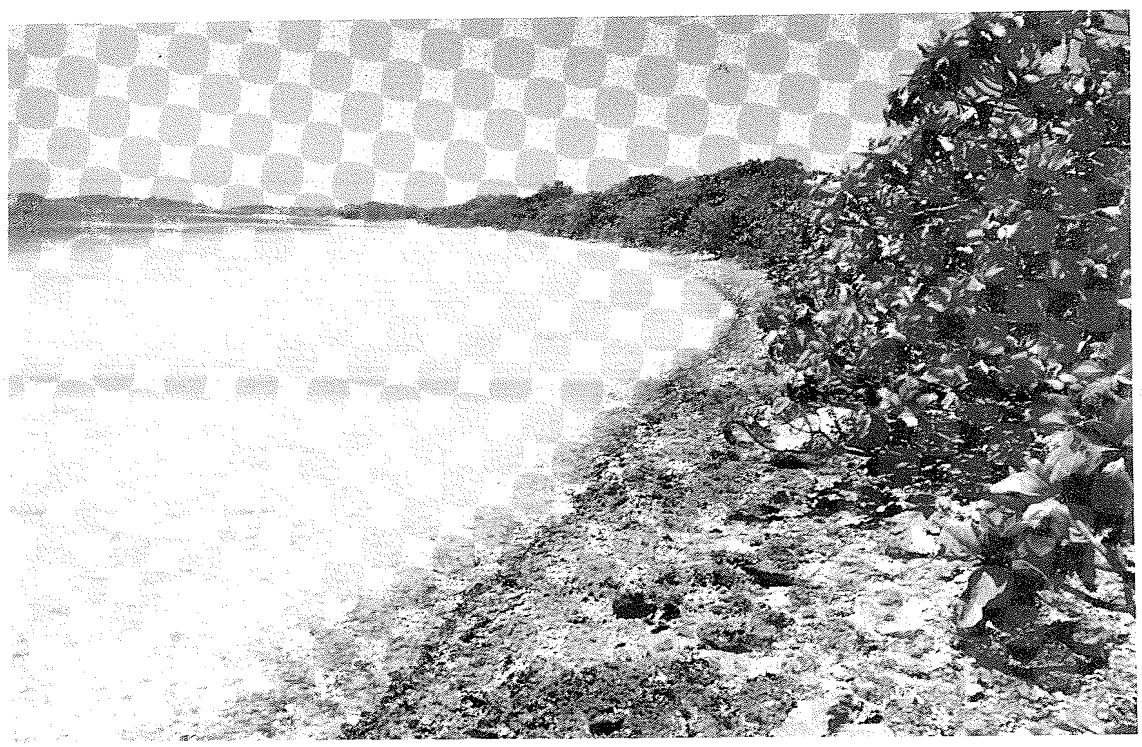

Plate 30. Narrow lagoon beach lined with *Tournefortia* scrub, Blackfin Islet (Central Leewards).

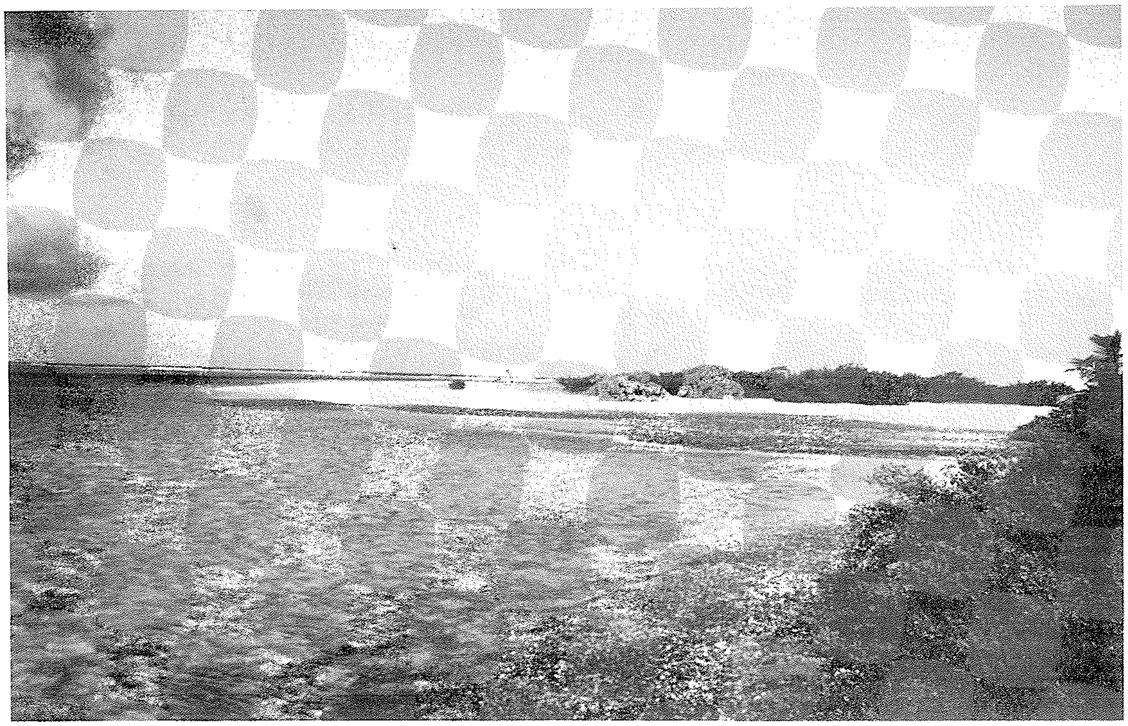

Plate 31. Recent sand additions to South Island's northeast point, partly covered with excellent natural herb mats and healthy *Suriana* scrub (right).

Plate 32. An old inter-islet channel (Tr. C, Long Island) filling in with herbs, *Tournefortia* scrub and *Cocos* in 1988, but smothered with fresh sand during the February storm of 1990 (see Pl. 33). Note the nesting Masked Boobies in middle right. A westerly view toward the lagoon.

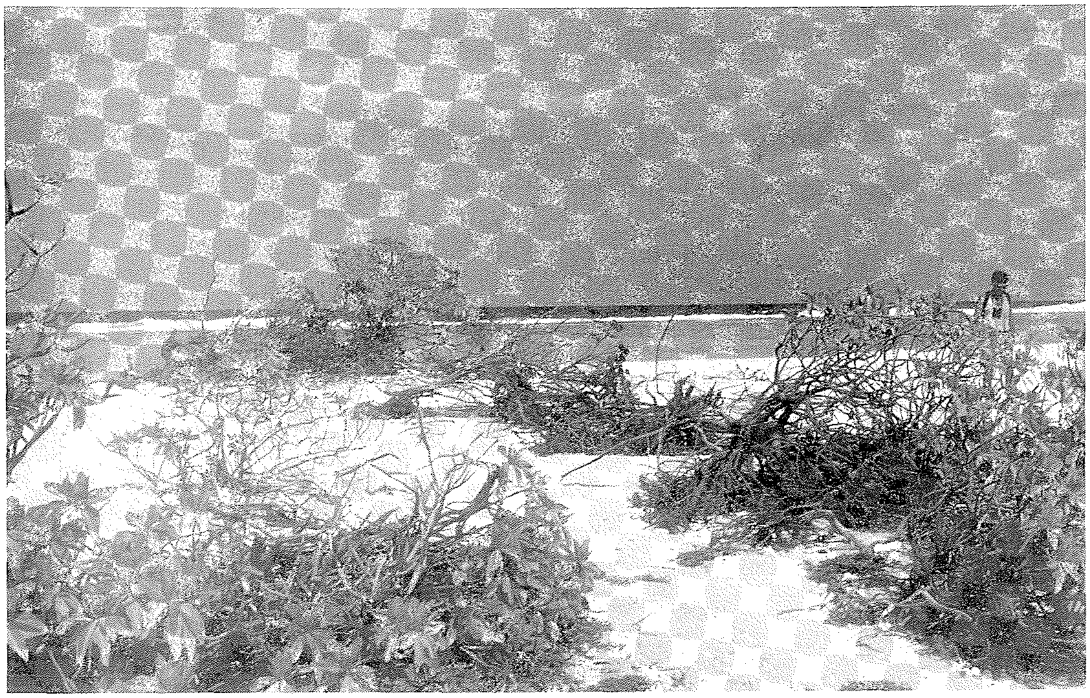

Plate 33. The same area as Pl. 32, March 1990, 2 weeks after the severe cyclonic weather. The herb mats had been smothered with sand, and a large percentage of *Tournefortia*s were partly uprooted and defoliated. An easterly view, toward the windward ocean.

Plate 34. A clearing within the dying *Cocos-Ipomoea* forest, interior South Island. Note the prolific mats of *Boerhavia*, *Phymatosorus* and *Ipomoea*.

Plate 35. *Pandanus* forest, south Nake.

Plate 36. The north end wall of the ancient Tuamotuan *marae*, northwest Nake.

Plate 37. Mixed forest with *Cocos*, southwest Nake Island.

Plate 38. Orange, scarlet and green phalanges of *Pandanus* rest on a clump of *Portulaca*. The ubiquitous *Coenobita perlatus* forage on their stringy flesh.

Plate 39. Inner edge of lagoon, South Island, 1988. *Cocos* is progressively shading out the beach scrub with *Suriana maritima*.

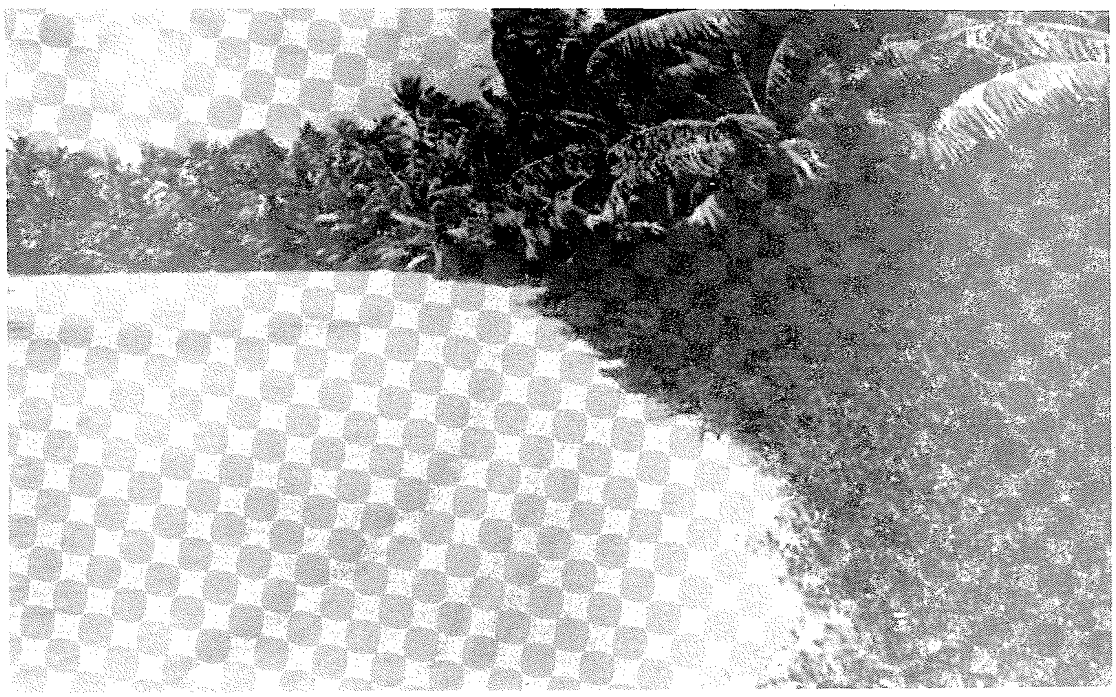

Plate 40. Inner edge of lagoon, South Island, 1965, taken from approximately the same location as Plate 39. Note the greater extent of sand and *Suriana* coverage above high water than today, due to less encroachment and shading by the palms.

Plate 41. Heavy understory of *Achyranthes canescens*, *Boerhavia repens* and *Phymatosorus scolopendria* in a clearing adjacent to *Pisonia* forest, Pig Islet.

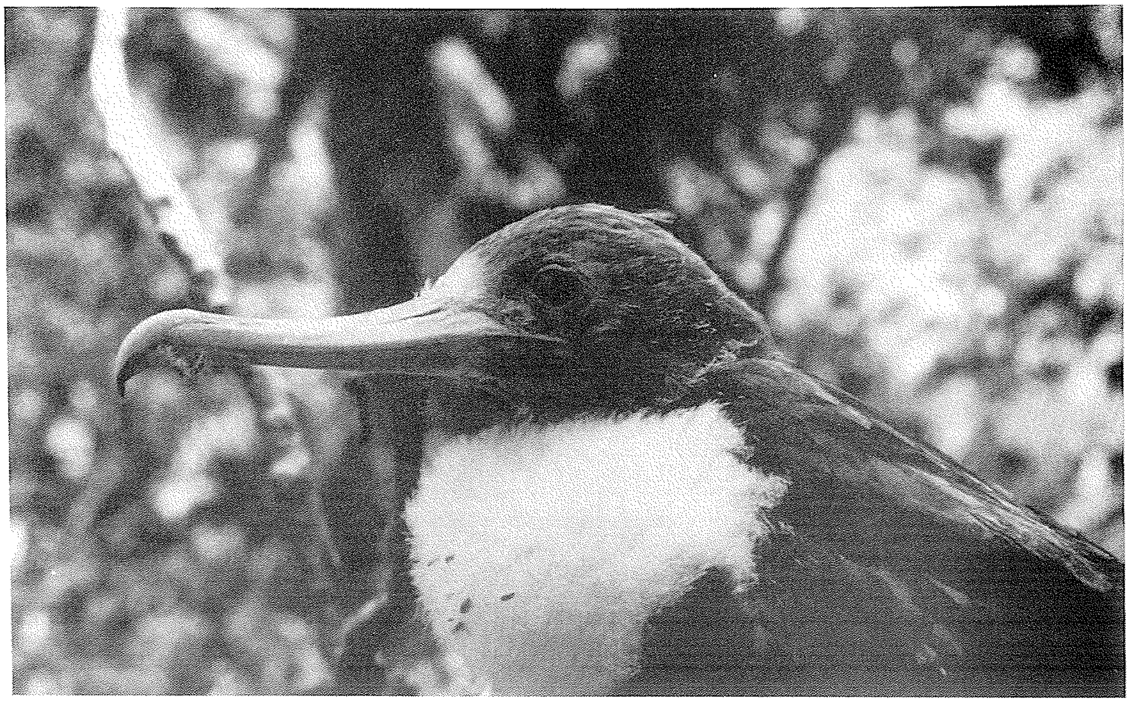

Plate 42. *Boerhavia* fruits on feathers and bill of a Great Frigatebird.

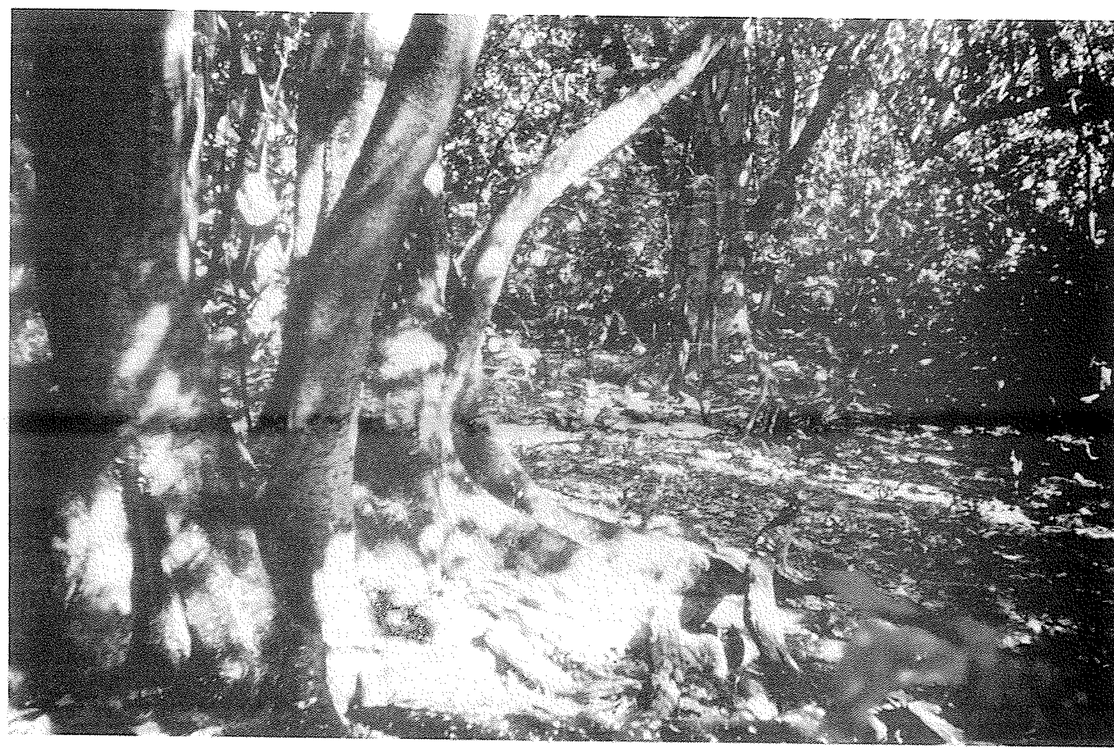

Plate 43. Inside a mature *Pisonia grandis* forest, interior Nake Island. Note the barren, dark aspect, virtually devoid of undergrowth except root suckers. Appearing virgin, this quality stand is possibly only 60-70 years old.

Plate 44. Fringe of *Suriana*, northeast point, South Island.

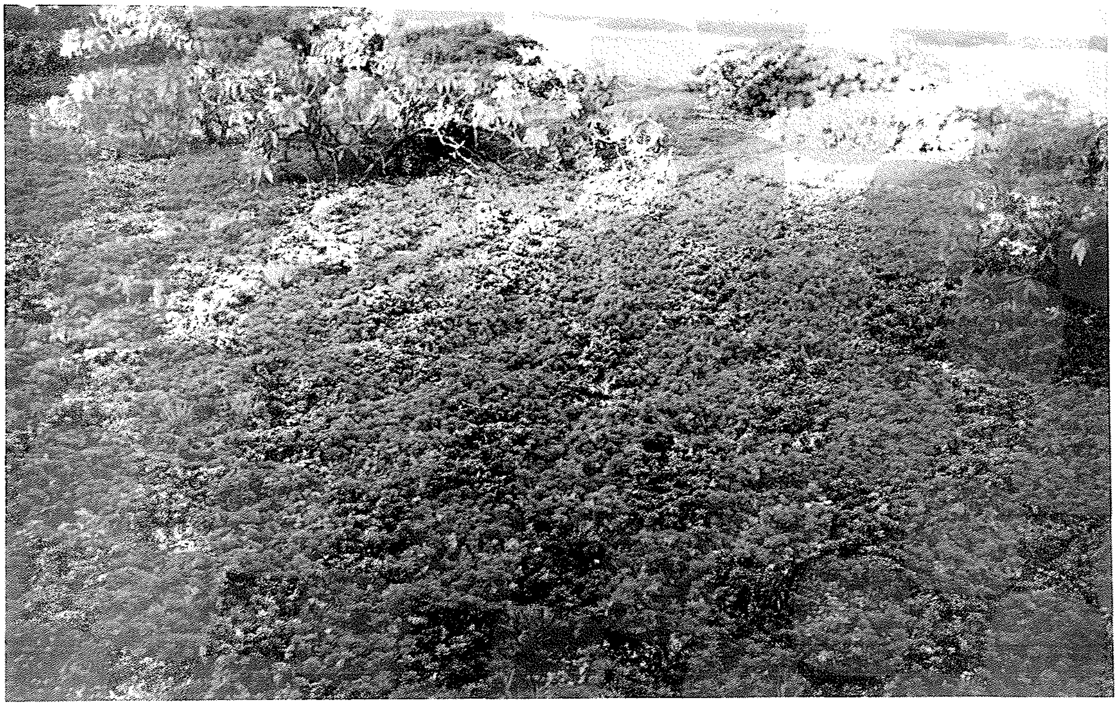

Plate 45. Well-developed natural herb mat, primarily *Heliotropium anomalum* and *Lepturus repens*. Scattered *Tournefortia* forms a "savannah." Here sandy soils support a lush *Heliotropium* cover, northeast point, South Island.

Plate 46. Detail of *Heliotropium anomalum*, Skull Islet, with remains of the first evidence of tropicbirds on Caroline.

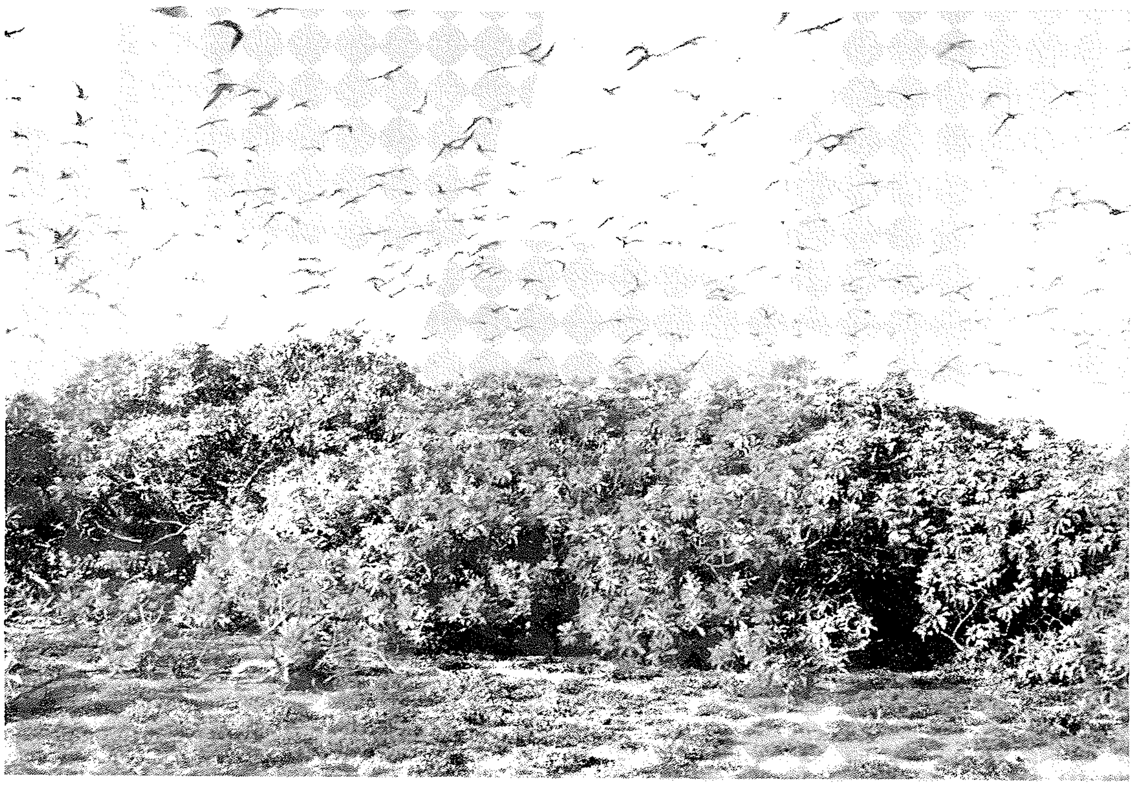

Plate 47. *Tournefortia* scrub, fringed by a natural herb mat, and occupied by a colony of Sooty Terns. An old inter-islet channel, northern Long Island. Note the nesting Red-footed Boobies.

Plate 48. *Tournefortia-Morinda* forest, with nesting Brown Noddies, interior Tridacna Islet. This is secondary growth, as this motu was heavily planted with coconuts in the 1920s.

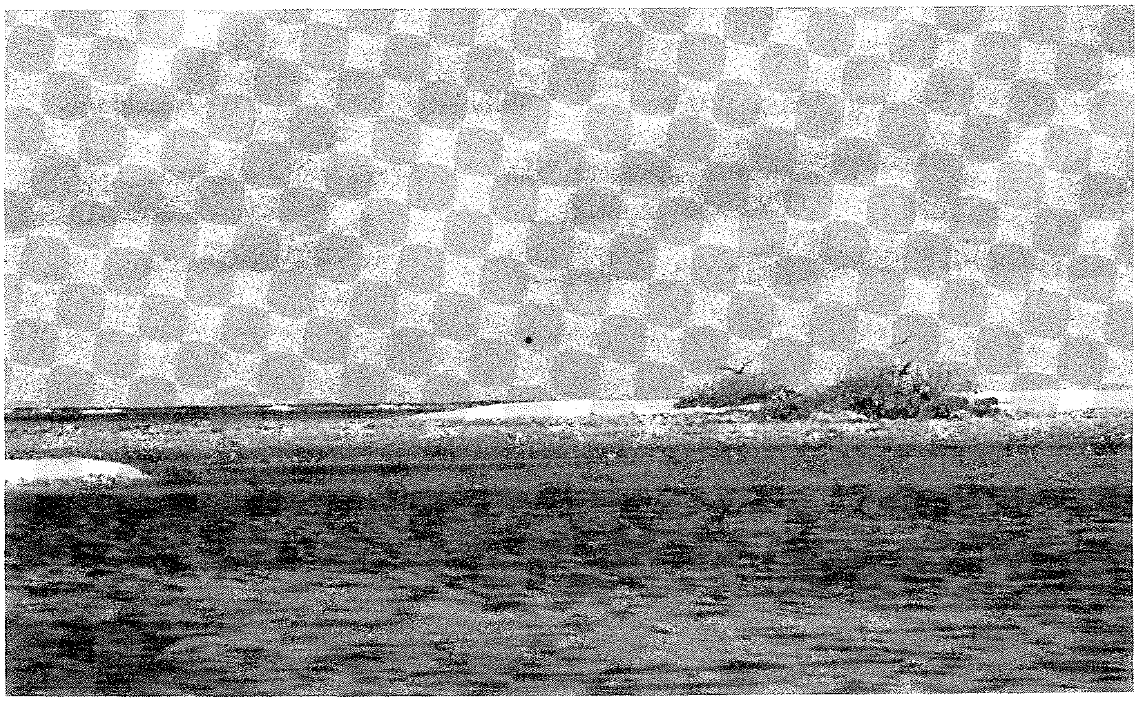

Plate 49. Skull Islet (0.02 ha), with Brown Noddy terns, looking east to the windward reef.

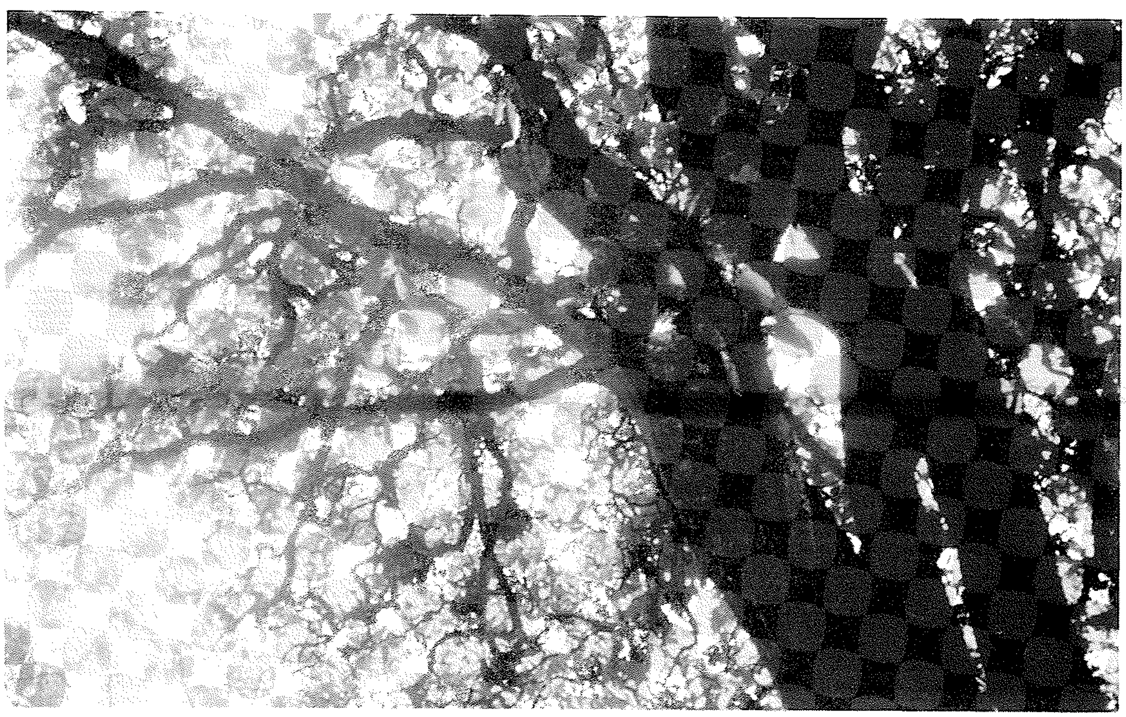

Plate 50. Mature *Pisonia grandis* canopy with incubating Black Noddies and a White Tern, Pig Islet. With a canopy height of 21 m, this was one of the most majestic interior forests on the atoll, although it is only approximately 65 years old.

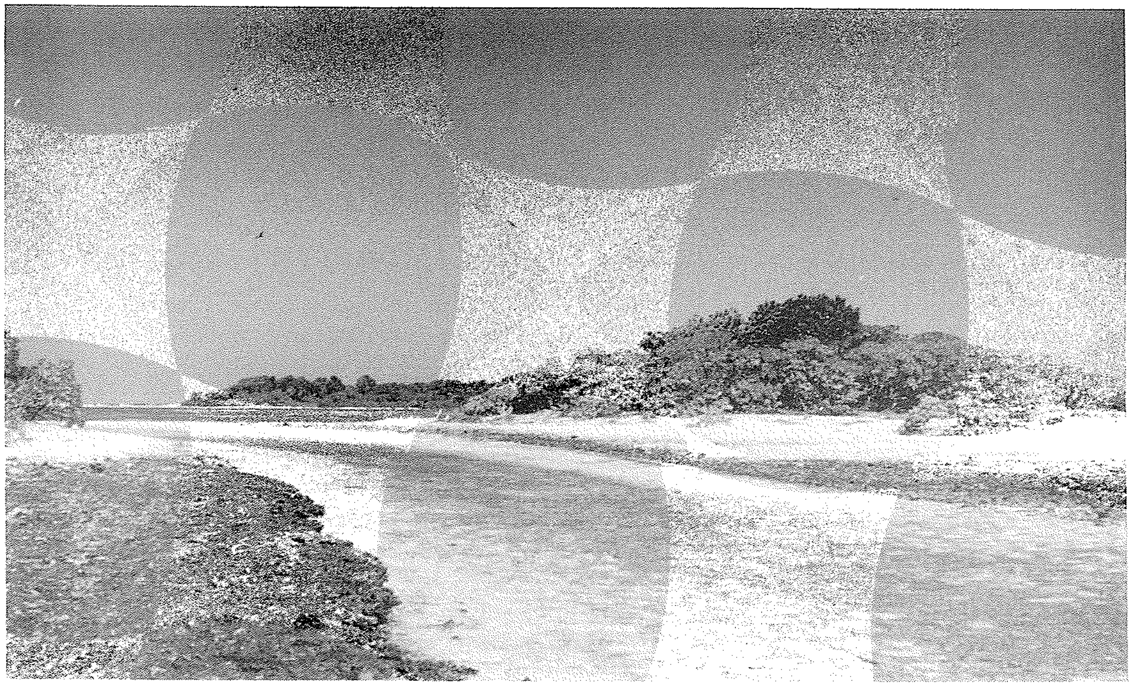

Plate 51. Azure Isle (Central Leewards)--an example of a motu containing a single *Pisonia* tree. Note the narrow, but still shark-patrolled, inter-islet channel. View east from Motu Nautonga, with Brothers Islet in the distance.

Plate 52. Caroline's sole clearing, with now-abandoned Tahitian-style huts, Motu Ana-Ana.

Plate 53. Piles of fibrous shavings--coconut crab sign.

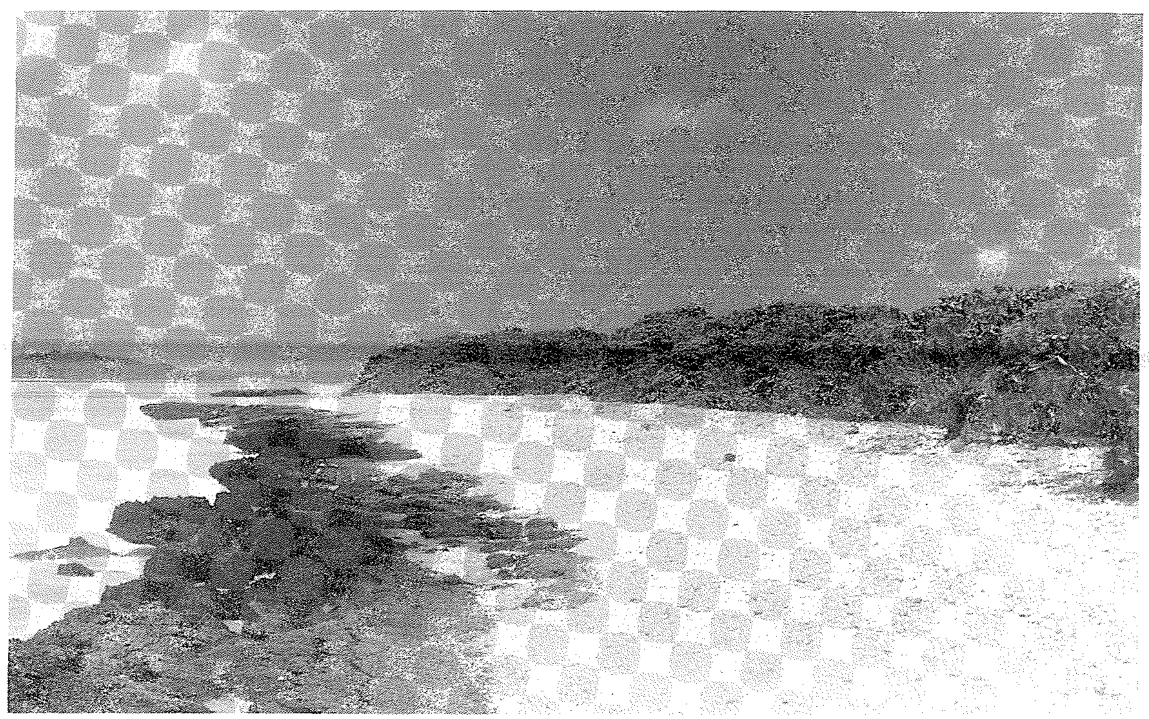

Plate 54. Beachrock at the lower, windward tip of Long Island, typically found at low water.

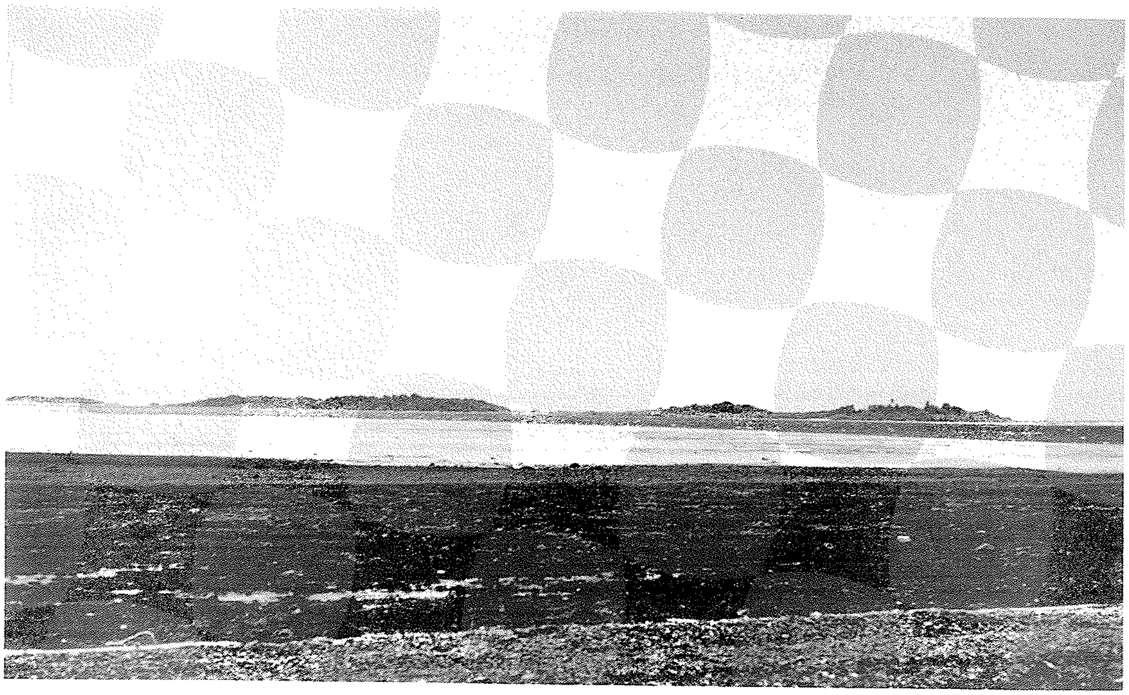

Plate 55. Windward Islets nos. 5-9 (left to right): North Pig, Pig, Skull (not visible), North Brothers and Brothers.

Plate 56. Arundel Islet (foreground), looking south-southwest across Tridacna Islet to South Island. Distant Motu Ana-Ana lies on the right.

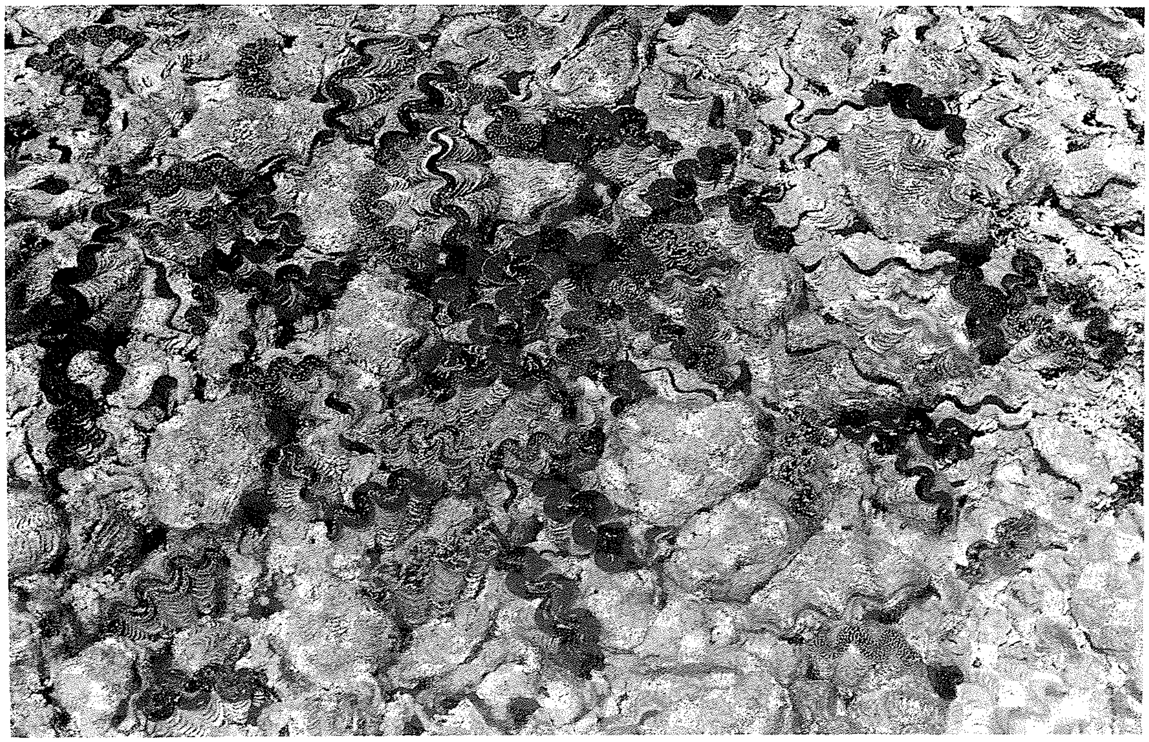

Plate 57. Detail, *Tridacna maxima* reefs, lagoonside of Tridacna Islet. This dense aggregation of giant clams amassed up to 80 per square meter.

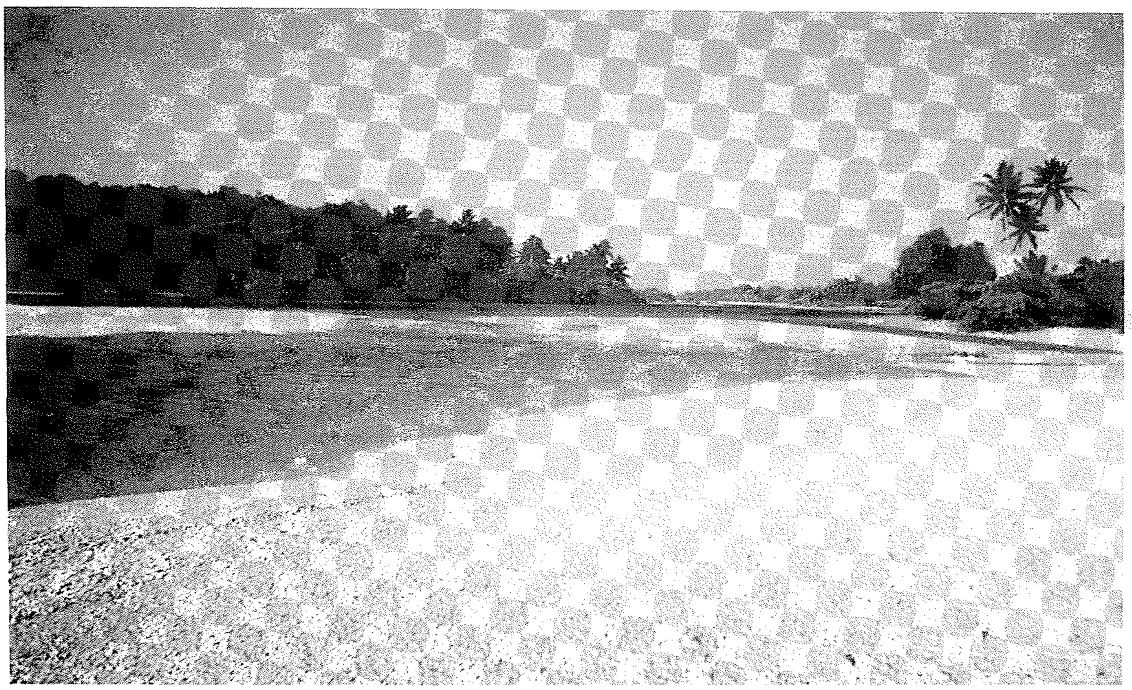

Plate 58. View of Pandanus Islet (center) west down the channel separating Nake (right) and Long (left) Islands.

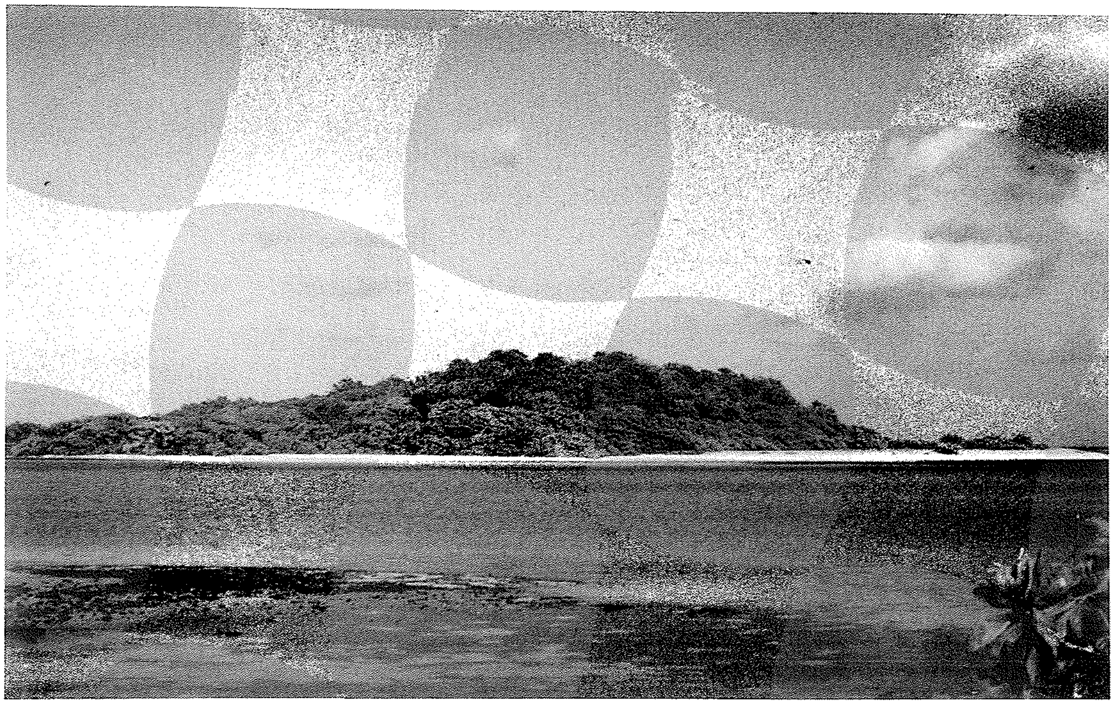

Plate 59. Danger Islet (South Nake no. 2), looking due west across the shallow upper lagoon from Long Island.

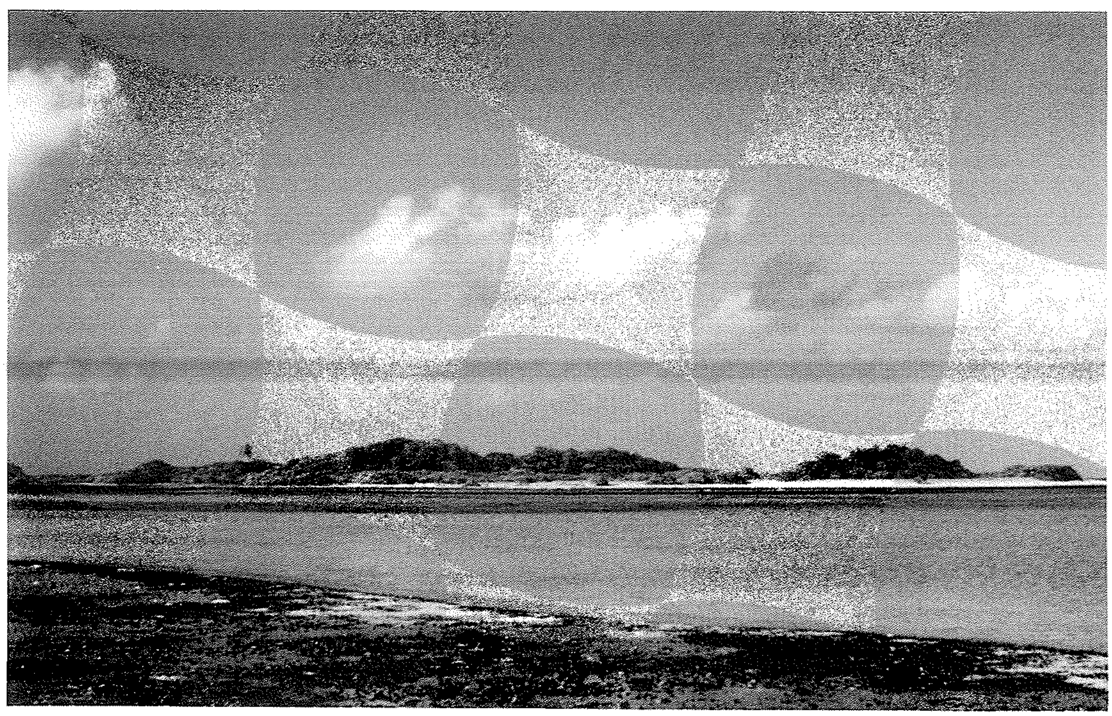

Plate 60. South Nake Islets nos. 3-6 (right to left): Booby, Coral, Lone Palm, and Kota. Westerly view across the shallow upper lagoon from Long Island.

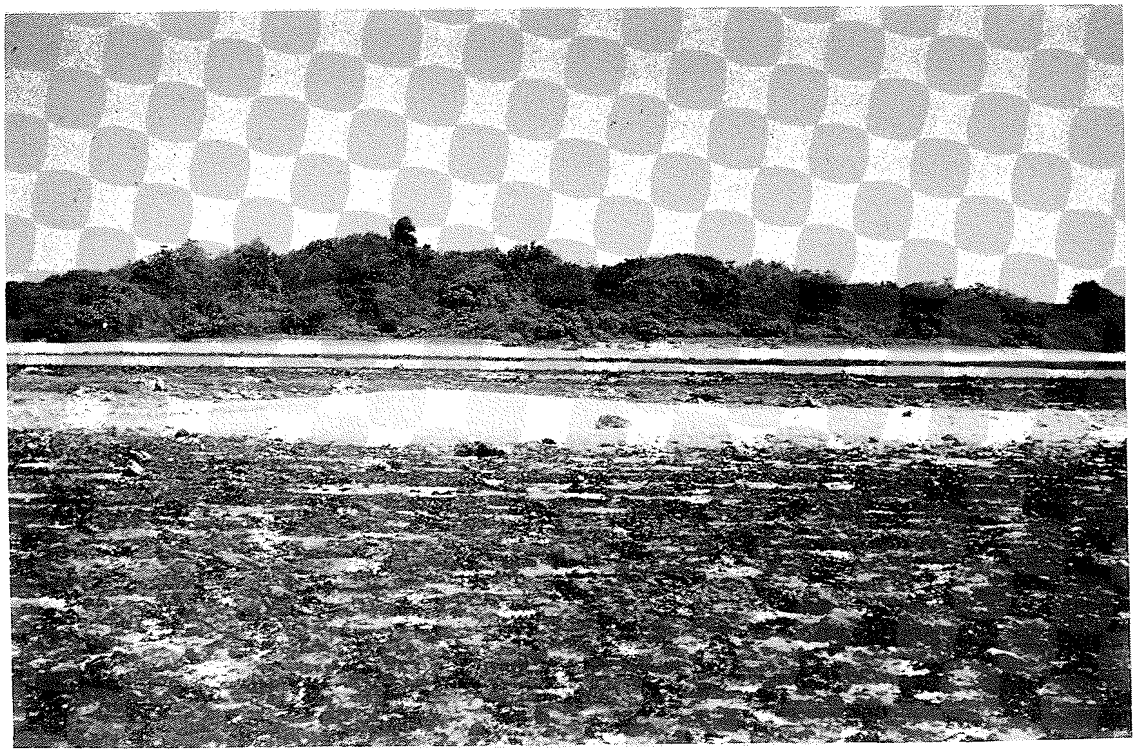

Plate 61. Lone Palm Islet (South Nake no. 5): a southerly view from the shallow tidal flats of Coral Islet.

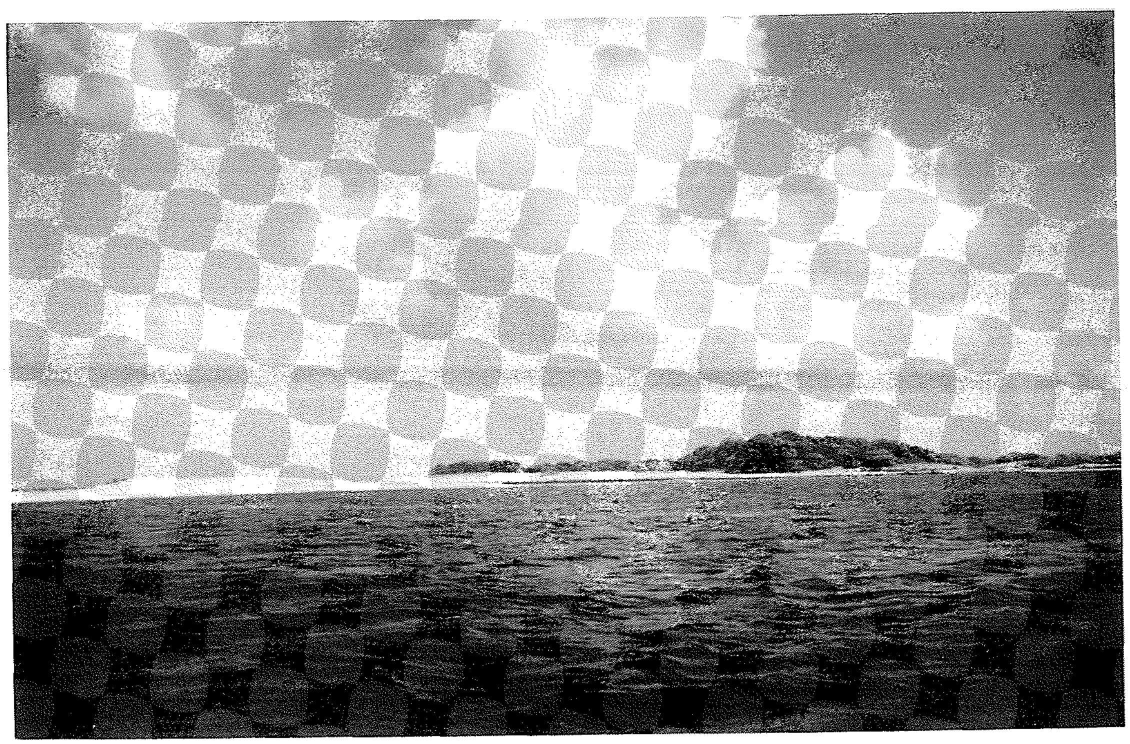

Plate 62. Motu Mouakena (South Nake no. 7), with connected cay. A westerly view from the upper lagoon. Compare with Plate 15.

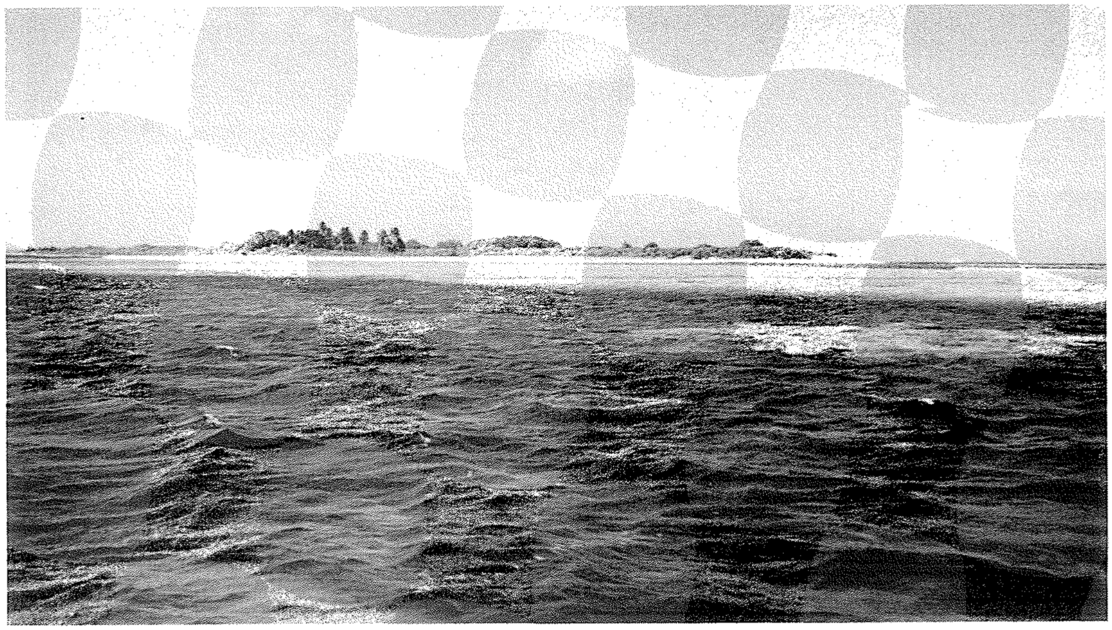

Plate 63. North end, Motu Mannikiba "Seabird Islet" (Central Leewards no. 1) showing mounds of *Pisonia* and a closer *Cocos* grove. Note the circular patch reef at right.

Plate 64. Motu Mannikiba, looking east along Transect 1. Natural herb mats on coral rubble give way to *Tournefortia*, then a distant patch of *Pisonia*. The extensive interior forests of this motu were felled 70 years ago to support a well-maintained coconut nursery. Forest recovery has been much slower than on islets where the *Cocos* was not managed as intensively.

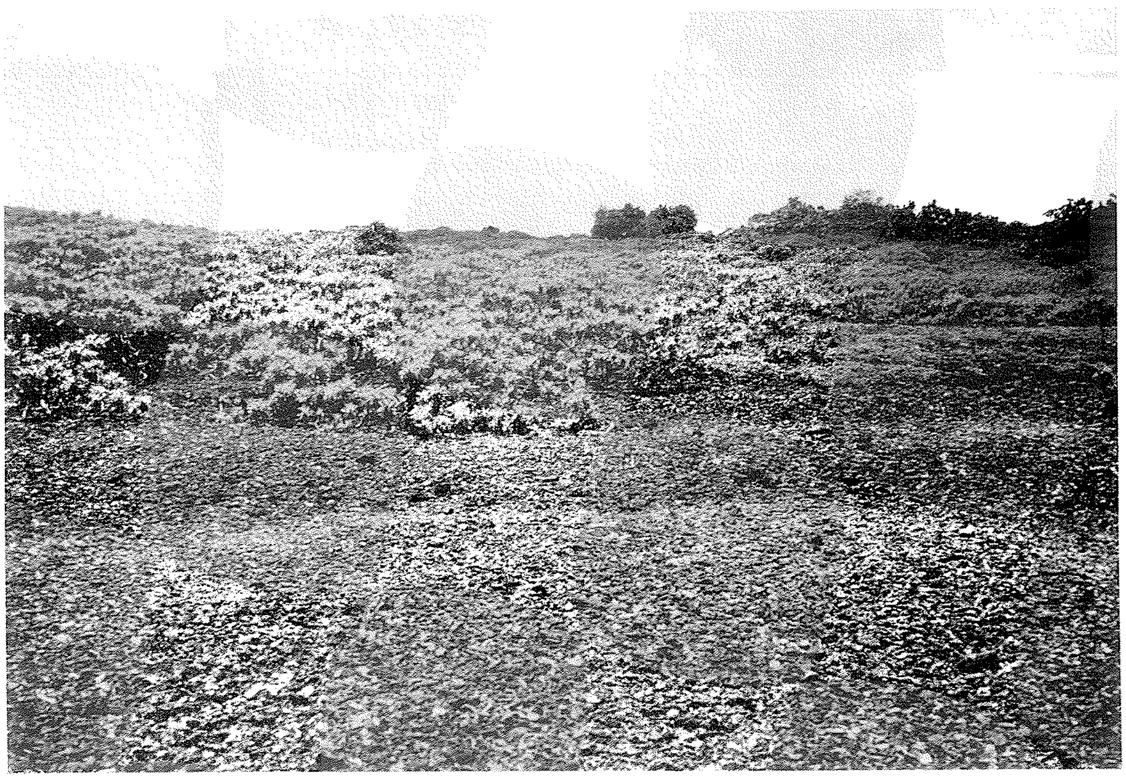

Plate 65. Motu Mannikiba, looking east along Transect 2. Low *Tournefortia* scrub covers a coarse rubbly substrate, probably a former inter-islet channel.

Plate 66. Mixed *Pandanus-Tournefortia* forest, interior Emerald Isle.

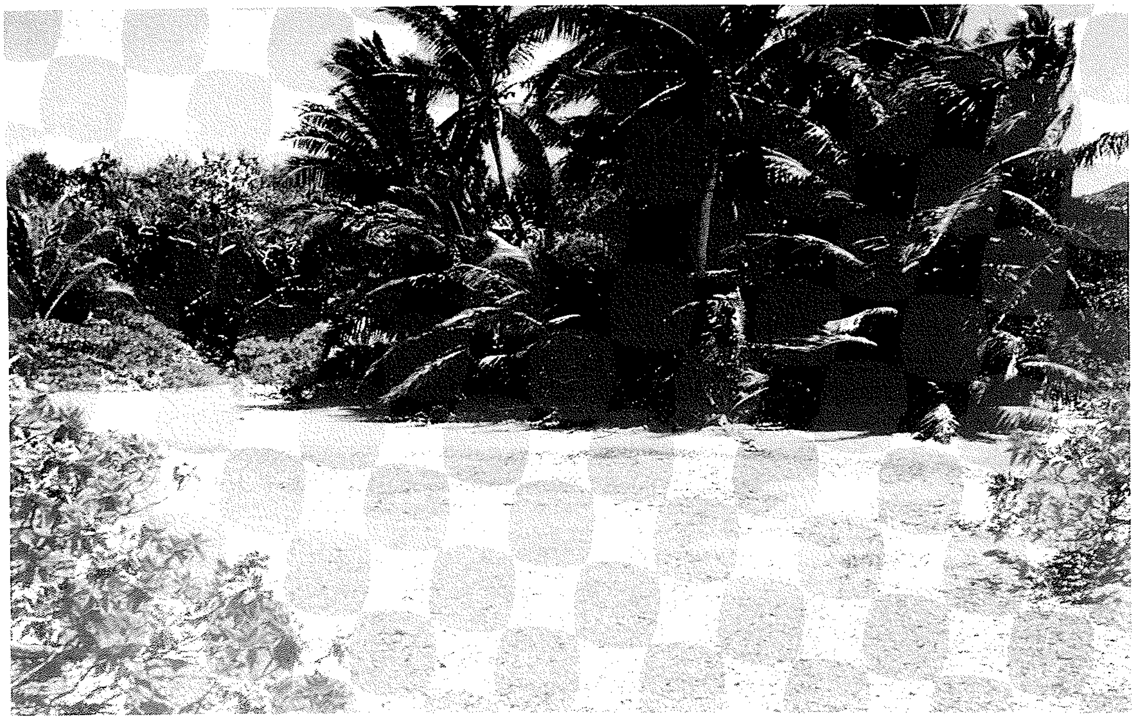

Plate 67. Emerald Isle, looking west across the open lagoonside scrub and hardpan to a densely vegetated interior.

Plate 68. Shark Islet (Central Leewards no. 5): view across patch reefs to a sandy beach.

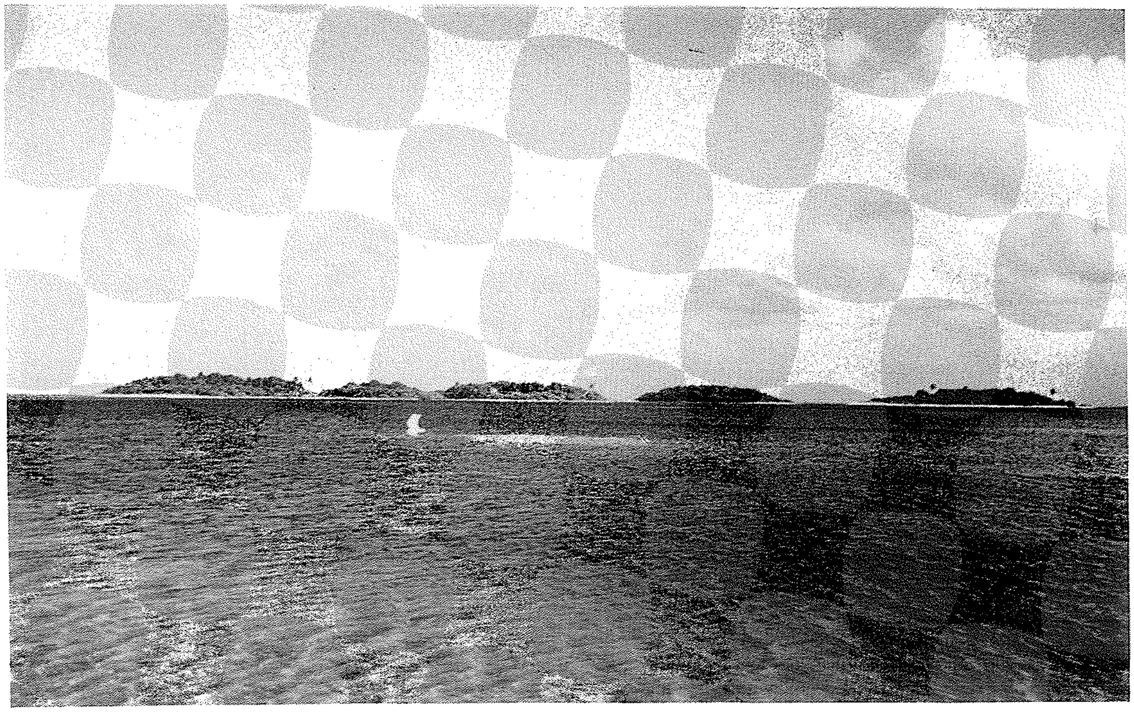

Plate 69. Southern Leeward Islets nos. 1-5 (right to left): Motus Raurau and Eitei, Pisonia Islet, Motus Kimoa and Ana-Ana. View northwest from Tridacna Islet.

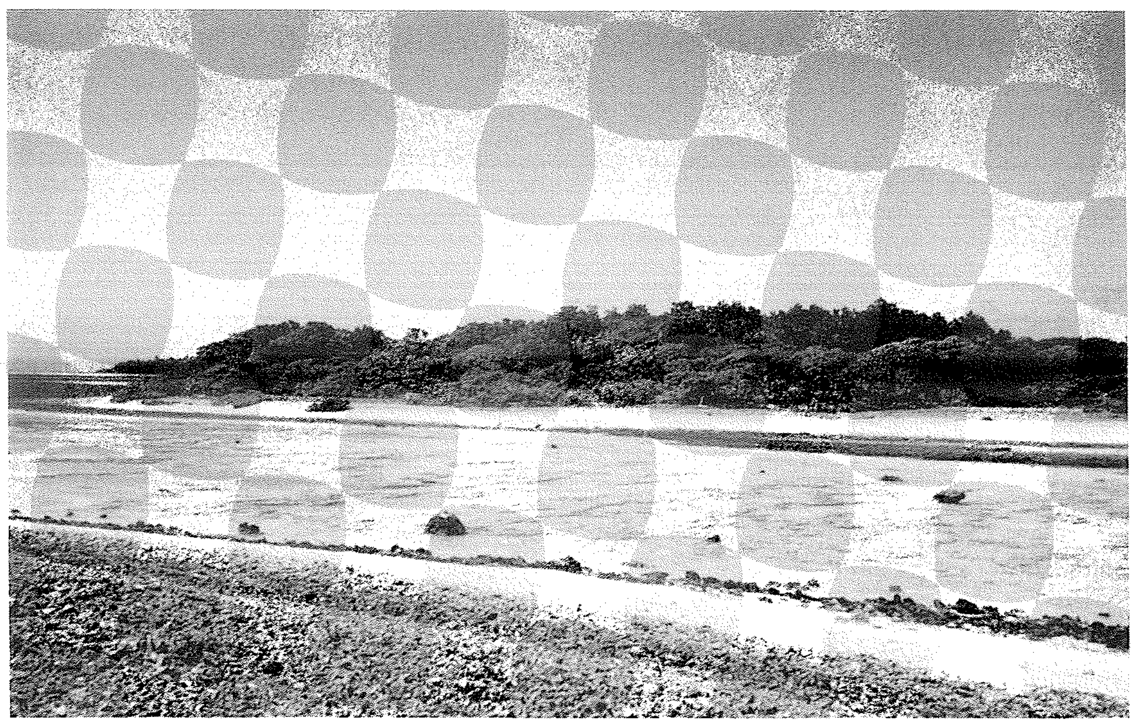

Plate 70. View of Motu Kimoa ("Rat Islet") from Pisonia Islet. Its central forest, typical of the Southern Leewards, is a mixture of *Pisonia* and *Cordia*.

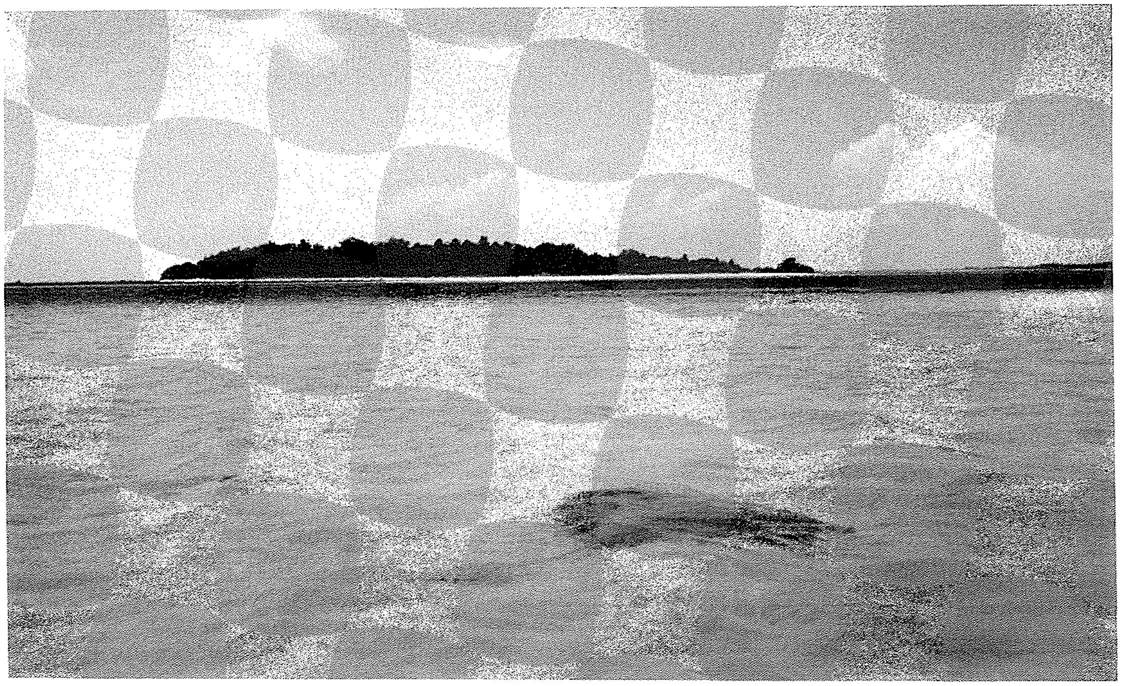

Plate 71. Motu Ana-Ana ("Anne's Islet"): a view with giant ray, from the shallows of the lagoon's southern end adjacent to South Island. Note the similarity to Plate 7, dating from 1883.

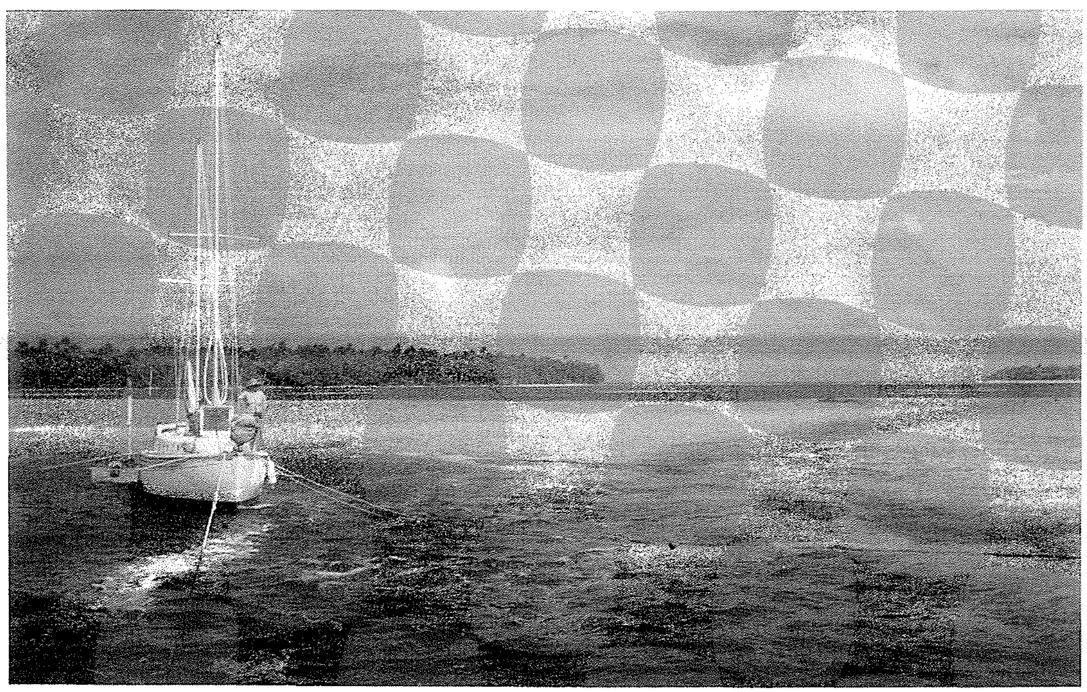

Plate 72. The "blind passage" (non-functional *hoa*), looking west from its inner end across the shallow reef flats to the lower lagoon.

ATOLL RESEARCH BULLETIN

NO. 398

PART II. SEABIRDS, OTHER TERRESTRIAL ANIMALS, AND CONSERVATION

BY

CAMERON B. KEPLER, ANGELA K. KEPLER, AND DAVID H. ELLIS

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PART II. SEABIRDS, OTHER TERRESTRIAL ANIMALS, AND CONSERVATION

BY

CAMERON B. KEPLER[1], ANGELA K. KEPLER[2], AND DAVID H. ELLIS[3]

ABSTRACT

Approximately 1,000,000 seabirds of 11 species bred on Caroline Atoll between September 1988 and June 1990. The most abundant species, with over 900,000 birds, was the Sooty Tern. Two species (Red-tailed Tropicbird, Blue-gray Noddy) are reported breeding for the first time. The known seabird fauna now includes one tropicbird, 3 boobies, 2 frigatebirds, and 5 terns.

Seabird distribution on Caroline is determined by the distribution of plant communities and nonvegetated substrates, the prevailing trade winds, and to a lesser extent, rats and coconut crabs. Red-tailed Tropicbirds and ground-nesting Brown Noddies nested on small islets relatively free of rats and coconut crabs. Masked and Brown Boobies preferred exposed windward beaches, primarily on Long and Nake. The tree-nesting Red-footed Booby and frigatebirds attained their highest nest densities in areas with reduced wind speed. Black Noddies were found in dense colonies, generally high in pisonia trees, while the uncommon Blue-gray Noddies nested solitarily on open coral rubble. Sooty Terns nested in large colonies, generally near or under relatively open *Tournefortia* scrub, but also in open areas under *Tournefortia* and closed-canopy *Pisonia* forests. Not all sites were utilized annually. Tree-nesting Brown Noddies and White Terns, found throughout the native forests, were the only species utilizing anthropogenic forests. The lowest seabird population densities were found in the disturbed forests on South and southwest Nake, and no seabirds nested on inhabited Motu Ana-Ana.

About 300 Bristle-thighed Curlews overwinter on Caroline, foraging in all terrestrial habitats, including *Pisonia* and disintegrating *Cocos-Ipomoea* forests. We extended the known winter range of the Long-tailed Cuckoo by discovering a small population on the atoll, the first record for the Southern Line Islands.

The known lizard fauna was increased from 3 to 6 species. Approximately 2,200 coconut crabs inhabited 12 islets on Caroline. Although primarily associated with *Cocos*, we also found them in *Pisonia* and *Tournefortia*. Pacific green turtles breed in small numbers; we found the first known nests (old) in 1990. Polynesian rats are abundant, and Pacific bottlenose dolphins were seen close to the windward side in 1990.

1 National Biological Survey, School of Forest Resources, The University of Georgia, Athens, Georgia, 30602, USA

2 400 Snapfinger Drive, Athens, Georgia, 30605, USA

3 National Biological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, 20708, USA

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The populations of seabirds and coconut crabs on Caroline Atoll are of national and international importance. The Black Noddy (17,000 birds) and White Tern (8,000 birds) populations are the largest in the Republic of Kiribati, while the Red-footed Booby population (7,000 birds) is one of the largest in the world.

Caroline's conservation attributes are numerous: large, varied seabird populations, wintering grounds for several species of migratory shorebirds and the Long-tailed Cuckoo, plant ecosystems of national and international importance (lushly wooded motus with significant groves of *Pisonia grandis, Cordia subcordata, Tournefortia argentea*), virtually pristine coral reef ecosystems exceedingly rich in giant clams (*Tridacna maxima*), a coconut crab population of Pacific-wide importance, ancient Tuamotuan *marae* (religious sites), and a breeding site for green turtles. The marine ecosystems, terrestrial biota, and geology of its 39 motus of varied size, 22 of which are pristine or near-pristine, provide prime outdoor ecological laboratories for numerous areas of research. These qualities, plus its exceptionally clear, essentially unpolluted lagoon, and its relative lack of disturbance, render it worthy of permanent protection.

A. HISTORY OF ORNITHOLOGICAL STUDIES

"There were a great quantity of sea birds of several kinds, and so importunate that they seemed to want to attack the men" (Markham 1904). So wrote the Portuguese explorer de Quiros on 21 February 1601, the first European to see Caroline Atoll.

Precisely which seabirds were present remained a mystery until the island was surveyed 364 years later by the Pacific Ocean Biological Survey Program (POBSP) (Clapp & Sibley 1971a). Prior to that visit, accounts of the avifauna had been incomplete. Bennett (1840) described Red-footed Boobies, a frigatebird (species ?), White Terns, Bristle-thighed Curlews, tattlers, and "a great number of small pigeons" with white heads (certainly noddy terns, perhaps both *A. minutus* and *A. stolidus*). The "shoal birds" that greeted him were probably Sooty Terns. His most unusual contribution was mention of a possible flightless rail: "The other birds of the coast were a kind resembling a coot..." (p. 372).

The 1883 Solar Eclipse Party (Pt. I, Sect. B) published a few sketchy notes, adding Lesser Golden-Plover, Reef Heron, and Masked Booby ("gannet") to the bird list. Of dubious identity were 2 species of "seagull" and a "snipe" (Dixon 1884). Holden, one of the astronomers, heard "the notes of a singing bird," which prompted us to add mist nets to our equipment in the hopes of capturing an *Acrocephalus* warbler. This resulted in our discovery of the Long-tailed Cuckoo (Ellis et al. 1990) and piqued our curiosity about what Holden might really have heard.

The POBSP expedition spent 3 days on Caroline in June 1965. They found 10 species of seabirds (9 breeders), 4 migrant shorebirds, and a Reef Heron (Clapp & Sibley 1971a), providing rough population estimates for each species. This work laid the foundation for later expeditions. Brief visits to Caroline by the Kiribati government in 1974 (Gilbert & Ellice Islands Government 1974, Vickers 1974) and Roger Perry in 1977 (Perry 1974, Garnett 1983) added no further information.

The 1988 expedition to Caroline was longer and more extensive than all former visits. We found 3 new island records: a breeding seabird (Red-tailed Tropicbird), a shorebird (Sanderling), and a migratory land bird (Long-tailed Cuckoo), and mapped islet-by-islet distributions for each species. Our population estimates, calculated from numerous transect surveys, aerial photographs, and detailed vegetation analysis, indicate that Caroline's avifauna is far more important than had previously been suspected (King 1973, Garnett 1983). In March and May 1990, the ICBP 1990 Line and Phoenix Islands Expedition (Pt. I, Sect. C), of which AKK was co-leader, filled in minor gaps in our knowledge. Seven-year-old Alexandre Falconer, then living on Caroline, added another breeding seabird, the Blue-gray Noddy, in summer 1990.

B. METHODS

From 22-29 September 1988, C. B. Kepler, A. K. Kepler, D. H. Ellis, and K. Teeb'aki surveyed all of Caroline's 39 islets except North Arundel Islet, naming most of them (Fig. 1; see also Pt. I, Sect. C). We established 50 linear transects, extending 13,300 m x 30 m, laid out to ensure that at least 5% of each islet was sampled for birds and plants (see Pt. I, Sect. C and Fig. 9). Sampling was increased with 19,300 m of perimeter surveys along the windward and leeward coasts of 21 islets (Pt. I, Fig. 9). On Noddy Rock, Skull, Atibu, Bo'sun Bird, Coral, Reef-flat, and Fishball (Fig. 1) we made total counts of the breeding seabirds. All surveys were conducted during daylight hours. Some incidental data have been added from the 1990 ICBP expedition.

Distribution and habitat preference: We described 7 major plant communities on Caroline Atoll (Pt. I). With the use of aerial photos and the transect data, we mapped the communities found on each islet. Bird distribution was determined and plotted using these islet vegetation maps. If a species nested within a particular plant community, it was plotted on the distribution maps as occurring throughout that community unless determined otherwise.

Population sizes and breeding phenology: We measured transect distances for each islet using a hip-chain and biodegradable cotton thread. We recorded all birds seen within the 30-m-wide strips; transect width was estimated visually. We assigned birds to one of several mutually exclusive categories: adults present, adults on territory, adults on nests (contents unknown), eggs, naked chicks, downy chicks, chicks with remiges erupting, chicks with scapular feathers, or chicks in juvenile plumage. We created a range of possible laying dates for each egg and

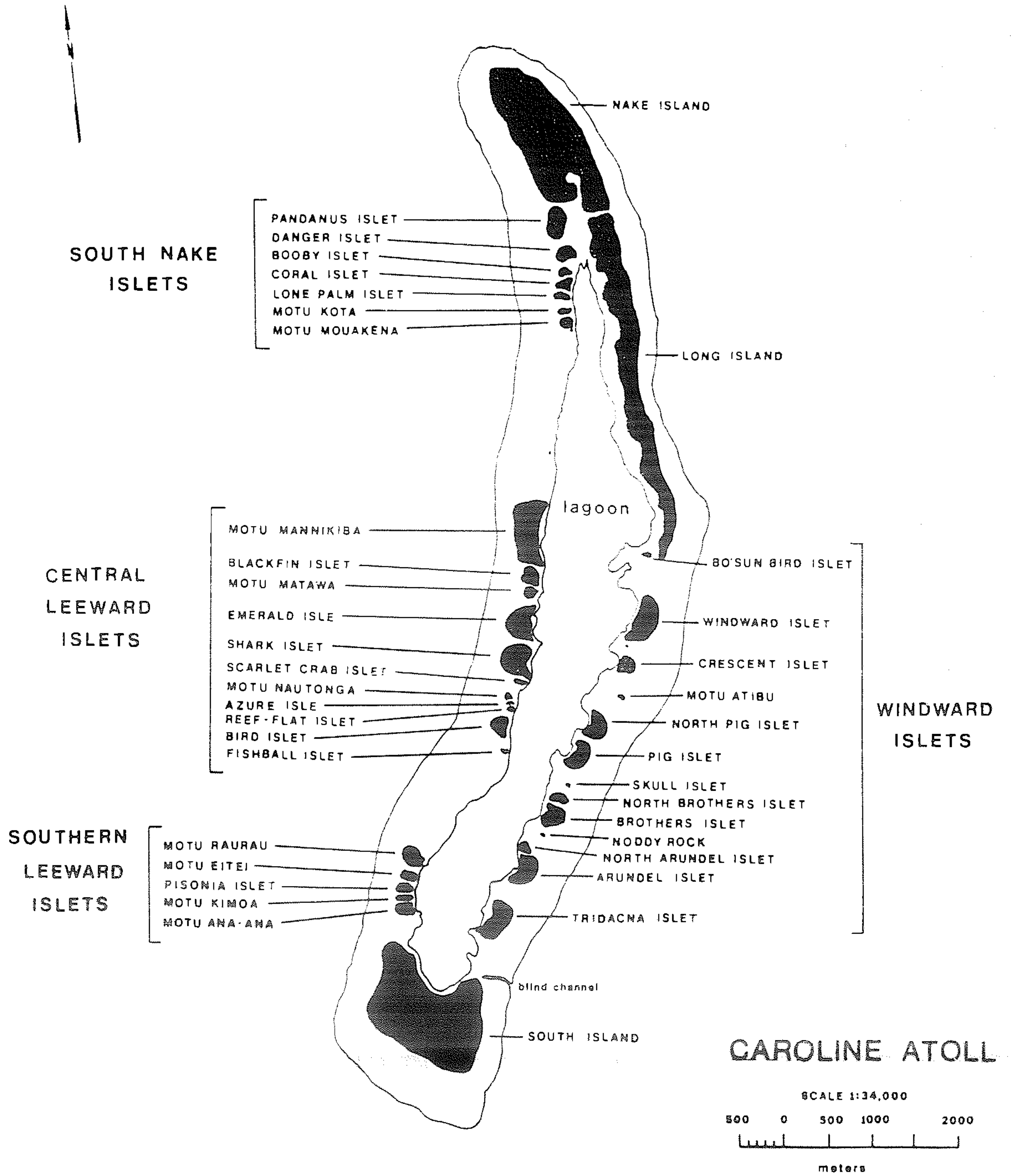

Figure 1. Caroline Atoll, Republic of Kiribati, with newly-named islets.

chick using known growth parameters for each species (C. Kepler 1978, Kepler & Kepler 1978). This enabled us not only to estimate seabird populations, but also to determine and plot a rough breeding phenology for each species (Figs. 3, 5, 7, 9, 10, 12). In these figures, the height of the bar for each category ("downy," "scapulars," etc.) represents the number of nests found or estimated with that development stage in September 1988. The bar width represents the approximate time span over which eggs could have been laid to produce that stage, while the "no. days" is a count back from the survey dates to accommodate growth and development that had occurred. Thus, while each figure shows what breeding stages we found, we extend those nests back in time to show roughly when they would have begun. The number of clutches begun per day is determined by dividing the number of nests per stage by the time span in days over which those eggs were laid.

Sooty Terns nested in dense colonies. Each colony was mapped, and its total size (m^2) was calculated. A minimum of 10 plots (3 m x 3 m or 3 m x 6 m), within which all eggs and chicks were counted, were randomly located along a compass line in each colony. The population size of each colony was estimated from these plot densities.

Mist nets: We operated 4 ATX 4-shelf 36 mm mesh mist nets (2.6 x 12 m) for 43.5 net hours, according to the following schedule: 14.5 net hours (daylight) beneath a 10-15 m *Cocos* canopy on South, 27.5 net hours (day and night) in *Pisonia-Cocos* interface (12 m tall) near Transect 10 on Long, and 1.5 net hours in *Pisonia-Tournefortia* within a 4-6 m canopy on Transect 4, Long. One cuckoo was collected (USNM 607191).

Collecting other vertebrates: Lizards that were active and conspicuous were collected at base camps on South and Long, either by hand or with a blowgun firing steel darts. No attempt was made to search for reptiles under coral, litter, or in other concealed locations. Rats were collected with a blowgun or snap traps baited with coconut, the former proving far more effective because most traps were sprung by hermit crabs. We preserved all specimens in formalin and sent them to the U.S. National Museum.

C. SEABIRD SPECIES ACCOUNTS

Eleven species of seabirds occur at Caroline, most of which breed in large numbers. They include one tropicbird, 3 boobies, 2 frigatebirds, and 5 terns.

RED-TAILED TROPICBIRD (*Phaethon rubricauda*) Figs. 2, 3; Pl. 1

Red-tailed Tropicbirds breed at widely scattered locations throughout the tropical Pacific and Indian Oceans. In the Line Group, they nest from Palmyra south to Starbuck (Perry 1980), with a large population (8,500 birds) on Christmas Island (Clapp 1967). Prior to our expedition it was unrecorded from Caroline, Vostok, or Flint.

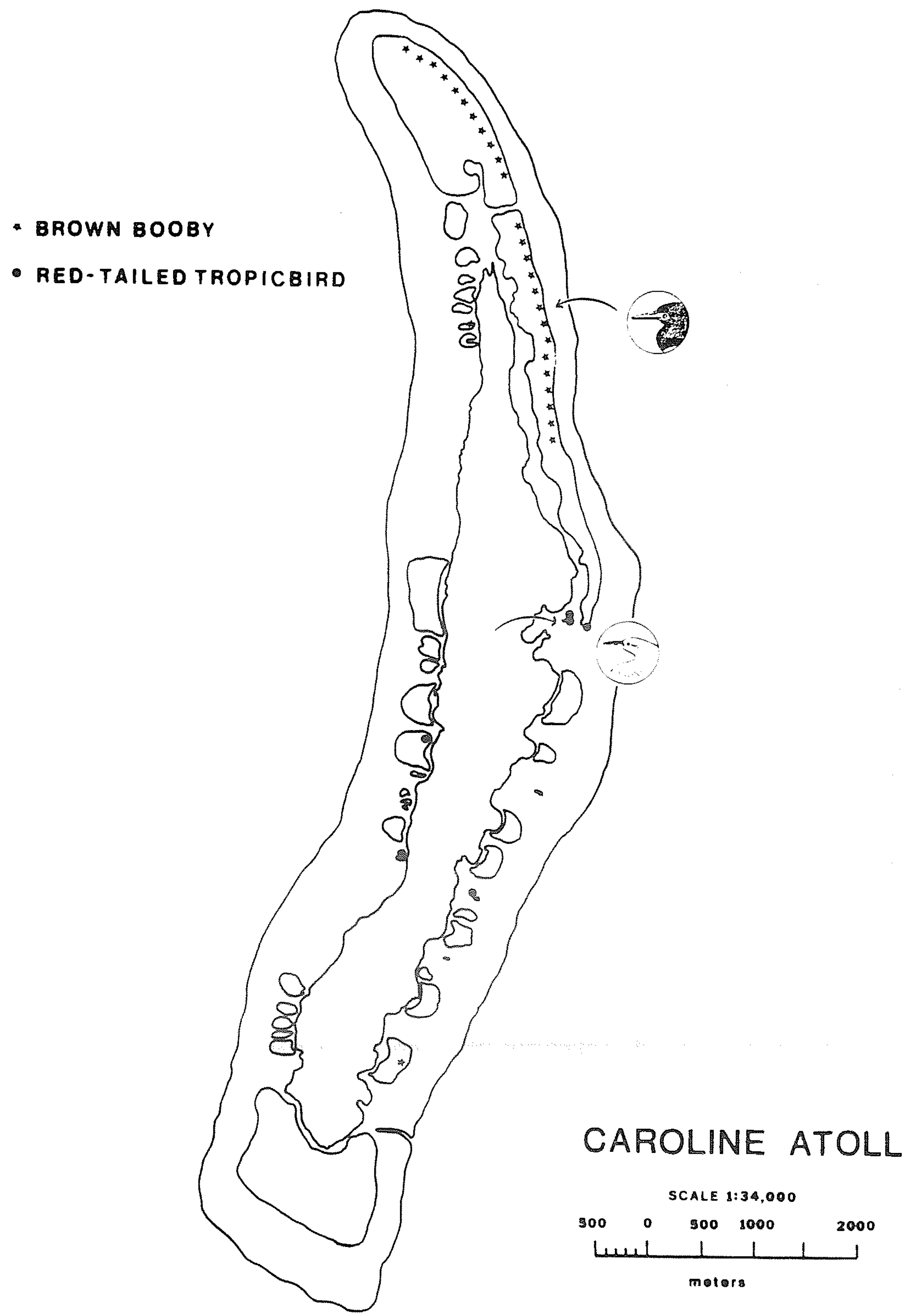

Figure 2. Distribution map of breeding Red-tailed Tropicbirds and Brown Boobies on Caroline Atoll, September 1988. In this and the following distribution maps, arrows indicate concentrations of breeding birds.

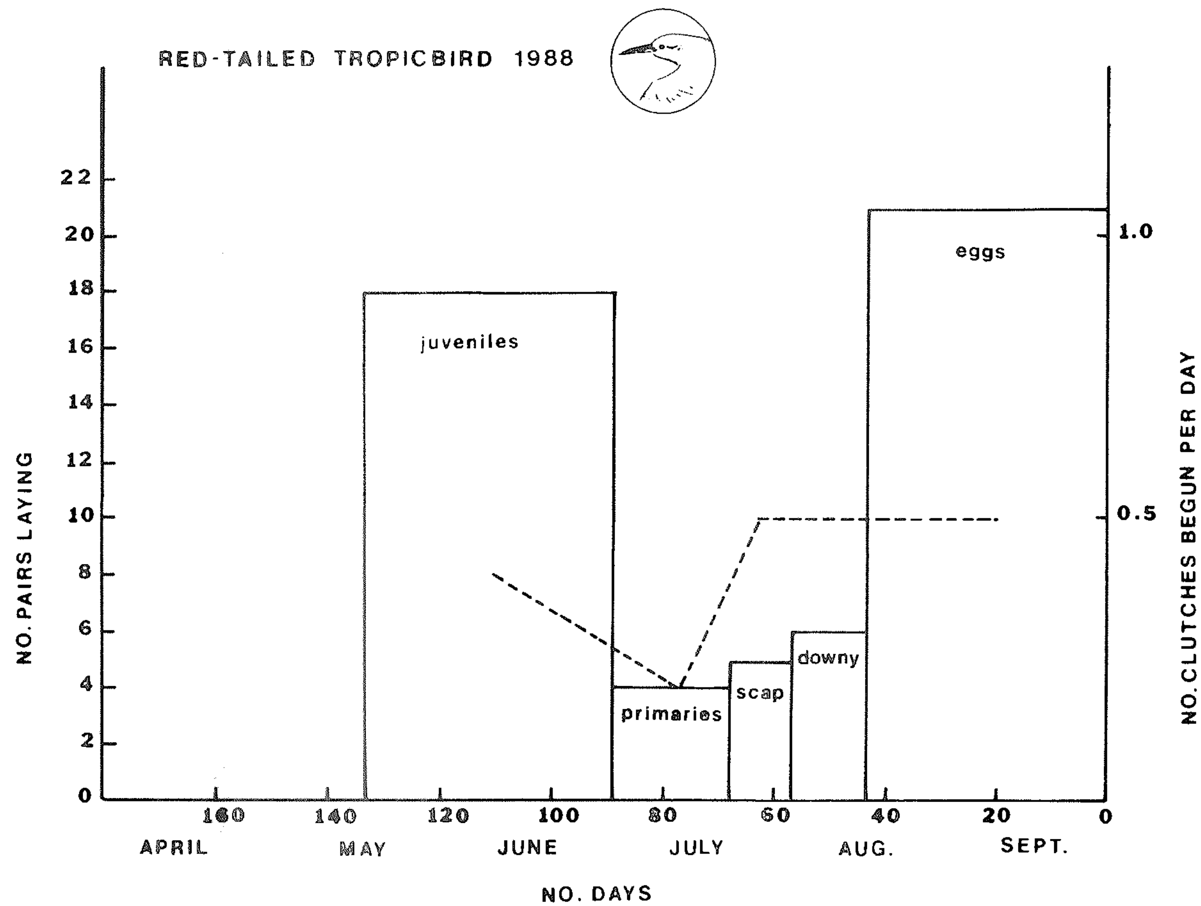

Figure 3. Approximate laying dates for Red-tailed Tropicbird nests found on Caroline Atoll in September 1988. In this and the following similar figures the numbers of nests begun during a given time period (bars) were determined by tallying each nest into one of several age classes (bar labels): bar widths indicate length in days for each class. The dotted line connects mean number of surviving clutches begun per day for each class. For example, a juvenile found in September began its egg stage in the previous May or June. The number of days are counted backwards from field observations.

Distribution and habitat preference: Our first indication that Red-tailed Tropicbirds nested on Caroline was the discovery of a skull, tail feather, and broken egg (Pt. I, Pl. 46) under a small *Tournefortia* bush on a previously unnamed islet between Pig and North Brothers Islets. We named this sparsely vegetated collection of rubble "Skull Islet" (Pt. I, Pls. 46, 49). We later found 47 nests on another islet, naming it Bo'sun Bird (Fig. 1) after the species' common name.

All nests were located under relatively open *Tournefortia* scrub less than 3 m tall in open, windy locations, with the majority (91%) on small islets (0.24-0.86 ha). All nests were under shrubs with few stems within a 0.5 m^2 nest space, and most had peripheral cover on the sides of the shrubs, both important factors in nest-site selection (Clark, Ricklefs, & Schreiber 1983). All nests were in areas relatively free of Polynesian rats (*Rattus exulans*) and coconut crabs (*Birgus latro*): five nests on Long were within 50 m of the island's south point.

There are large populations of Polynesian rats and coconut crabs on Caroline's bigger, more wooded islets. This rat, though basically vegetarian, is an effective seabird predator (C. Kepler 1967, Norman 1975) that in some years has taken 65% of the Red-tailed Tropicbird eggs and 100% of the chicks on Kure Atoll (Fleet 1972). Coconut crabs are also known bird predators (Helfman 1979, Reese 1987): on Caroline in 1965 they preyed upon Sooty Terns (Clapp & Sibley 1971a), and in 1990 AKK photographed the aftermath of predation or scavenging on at least one species of tern on Brothers Islet. It may be no accident that tropicbirds on Caroline occur only on small, relatively open islets that harbor few, if any, rats and crabs, and the southern tip of Long Island, where predator densities are low. We saw no rats on Bo'sun Bird Islet. Although rats could swim the 165 m to the islet, the nearly continuous presence of black-tipped reef sharks (Pt. I, Pl. 10) in the channels surrounding the islet provides protection to its nesting tropicbirds.

Numbers: In September 1988, we found 56 active nests on 5 islets (Fig. 2, Table 1) and estimated a minimum population of 60 pairs. The May 1990 expedition found 130 nests on Bo'sun Bird; our revised estimate for Caroline is approximately 300 birds. Bo'sun Bird Islet was surveyed by POBSP in June 1965, and no tropicbirds were located on the ground or in the air (F. Sibley, pers. comm.). It is unlikely that Red-tailed Tropicbirds were present but overlooked at that time, suggesting that they have colonized the atoll only recently. The Caroline population is now the second largest colony known from the Line Group, and Caroline is only one of 5 islands in the archipelago where Red-tailed Tropicbirds are known to breed.

Phenology: Of the 56 nests found in 1988, 54 contained eggs or chicks (Table 2). The 33 chicks were divided into 4 age classes (Fleet 1974, Diamond 1975a) which, together with the 21 eggs, provided an indication of laying phenology for 140 days prior to our arrival (Fig. 3). Eggs in surviving nests had been laid at a fairly even rate from early May (possibly starting earlier) through September. The finding of only 2 additional pairs on territory, and only one courtship flight, indicated

Table 1. Estimated number of breeding seabird pairs on Caroline Atoll, September 1988.

Location	Red-tailed Tropicbird	Masked Booby	Brown Booby	Red-footed Booby	Great Frigatebird	Lesser Frigatebird	Sooty Tern	Brown Noddy	Black Noddy	Blue-gray Noddy	White Tern
Nake	-	105	1	496	522	56	-	390	814	-	1,094
Long	5	69	12	659	808	-	179,800	207	986	-	751
Windward Islets											
Bo'sun Bird	47	-	-	-	-	-	8,400	10	-	-	6
Windward	-	-	-	163	207	-	-	20	28	-	134
Crescent	-	-	-	28	5	-	-	36	60	-	8
Atibu	-	-	-	-	-	-	-	-	-	-	-
North Pig	-	-	-	31	17	-	-	76	3,194	-	110
Pig	-	-	-	14	118	-	-	82	1,928	-	164
Skull	-	-	-	-	-	-	-	-	-	-	-
North Brothers	-	-	-	25	9	-	-	23	40	-	69
Brothers	-	-	-	25	-	-	-	8	15	-	50
Noddy Rock	-	-	-	-	-	-	-	80	-	-	-
North Arundel	-	-	-	*	*	-	-	-	-	-	*
Arundel	-	-	-	37	*	-	-	11	249	-	227
Tridacna	-	-	1	111	-	-	-	11	230	-	396
South	-	-	-	0	-	-	-	163	-	-	381
South Nake Islets											
Pandanus	-	2	-	32	26	-	-	26	-	-	52
Danger	-	-	-	139	-	-	-	33	33	-	37
Booby	-	7	-	52	-	-	-	2	1	-	6
Coral	-	1	-	28	2	-	-	6	-	-	15
Lone Palm	-	2	-	48	-	-	-	-	-	-	9
Kota	-	-	1	12	1	-	-	-	-	-	3
Mouakena	-	3	-	8	-	-	-	-	-	-	-
Central Leeward Islets											
Mannikiba	-	-	-	184	287	-	-	161	176	-	195
Blackfin	-	-	-	*	4	-	-	37	-	-	11
Matawa	-	-	-	5	1	-	-	3	-	-	13
Emerald	1	-	-	3	230	-	-	7	150	-	83
Shark	-	-	-	*	118	-	-	37	125	-	44
Scarlet Crab	-	-	-	-	-	-	-	1	-	-	2
Nautonga	-	-	-	11	2	-	-	7	32	-	10
Azure	-	-	-	7	2	-	-	-	-	-	2
Reef-Flat	-	-	-	-	-	-	-	-	-	-	-
Bird	-	-	-	29	6	-	-	42	329	-	48
Fishball	3	-	-	-	-	-	*	5	-	-	-
Southern Leeward Islets											
Raurau	-	-	-	10	31	-	-	1	-	-	2
Eitei	-	-	-	17	14	-	-	6	-	*	18
Pisonia	-	-	-	26	14	-	-	-	-	-	10
Kimoa	-	-	-	21	3	-	-	-	2	-	7
Ana-Ana	-	-	-	0	-	-	-	-	-	-	-
Total Estimated Pairs	56(+1)	189	15	2,221	2,427	56	188,200	1,491	8,392	-	3,957

* Breeding confirmed in 1989 or 1990.

Table 2. Stages in the breeding cycle of the Red-tailed Tropicbird, Caroline Atoll, 27-29 September 1988 (ages after Stonehouse 1962).

Nest Stage:	Juv.	Remiges	Scapulars	Downy	Egg	Pairs on Territory
Approximate Age in Days From Laying:	90-133	69-89	58-68	44-57	0-43	-
No. Nests:	18	4	5	6	21	2

that laying was ending. On 24 May 1990, many nests contained eggs and downy chicks (75% nests with chicks) and pairs were still courting.

On Christmas Island, peak laying generally occurs from June to October (Schreiber & Ashmole 1970), later than those parts of the 1988 and 1990 breeding seasons we observed on Caroline.

MASKED BOOBY (*Sula dactylatra*) Figs. 4, 5; Pl. 2

The Masked Booby is widely distributed in the Atlantic, Indian, and Pacific Oceans. Clapp (1967) estimated that 19,100 Masked Boobies bred in the Line and Phoenix Islands, with about 13,000 of them in the Line Islands, mostly (ca. 9,000) on Jarvis.

Distribution and habitat preference: Eighty-four percent of Masked Booby nests (159) were on the windward, rubbly shores of Long and Nake Islands, extending to the north end of the atoll. Fifteen additional nests were scattered along the lagoon edges of 5 South Nake Islets (Table 1). Nests consisted of bare scrapes with exposed sand, usually within a sparse ground cover of *Portulaca* and *Heliotropium* (Pl. 2). Over half the nests were amassed in one open colony on Nake that extended nearly 1,000 m, beginning approximately 150 m south of Transect 2 and extending about 50 m north of Transect 4 (Pt. I, Fig. 8). Here a nearly unbroken *Heliotropium* mat 30-80 m wide, with patches of *Tournefortia*, occupied the area between the leading edge of the *Tournefortia* scrub and the beach crest. Nests were 20-30 m apart in the densest section (near Tr. 3). All nests were exposed to the sun, unlike those of the Brown Boobies. Some adults and juveniles roosted under the scrub; guano deposits indicated regular occupancy.

A loose group of 7 breeding pairs was scattered on a broad plain of low herbs along a partially filled old interislet channel 370 m south of the north end of Long Island (Tr. C, Pt. I, Figs. 8, 40). Four more pairs nested in coral rubble along the channel separating Nake and Long,

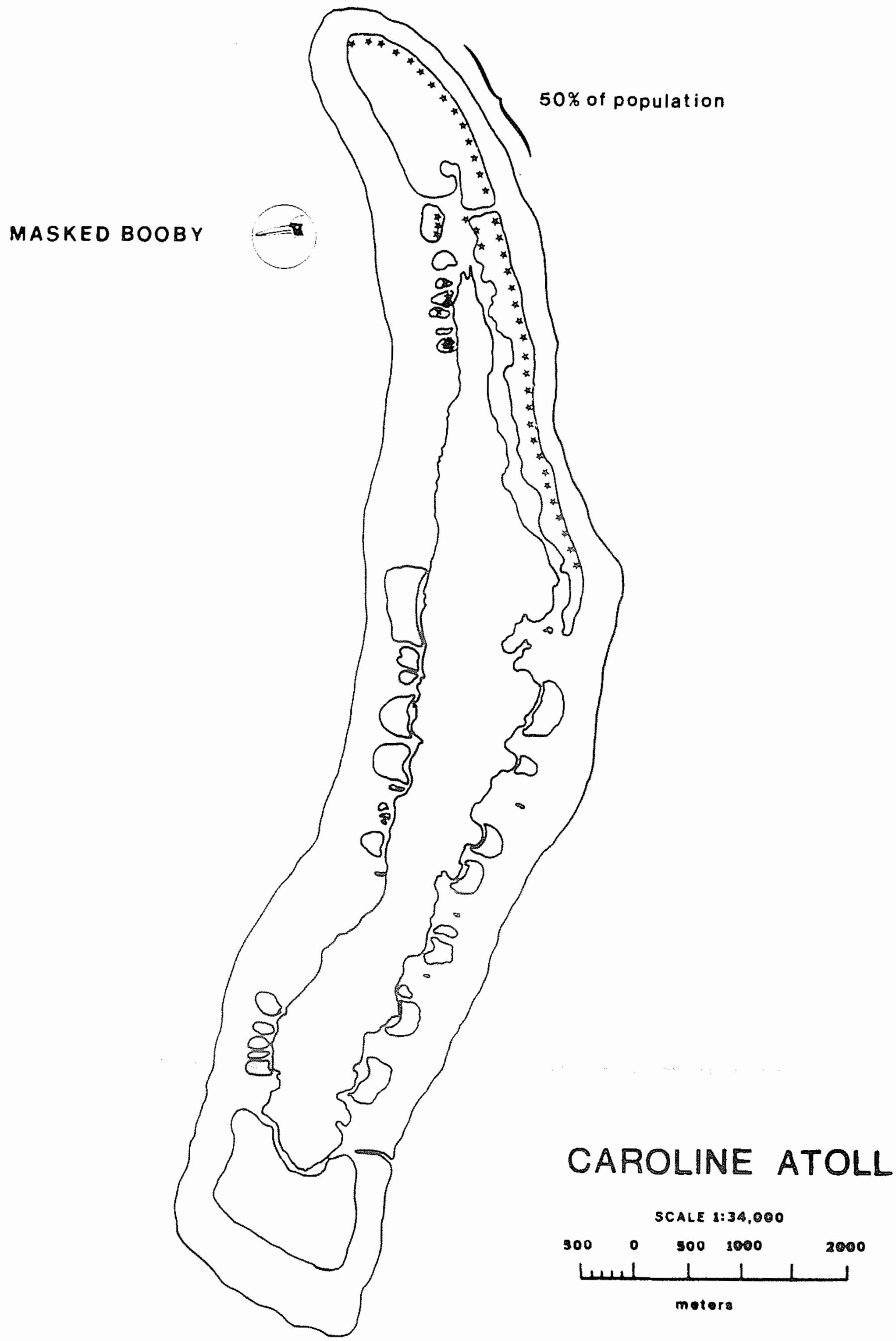

Figure 4. Distribution map of breeding Masked Boobies on Caroline Atoll, September 1988.

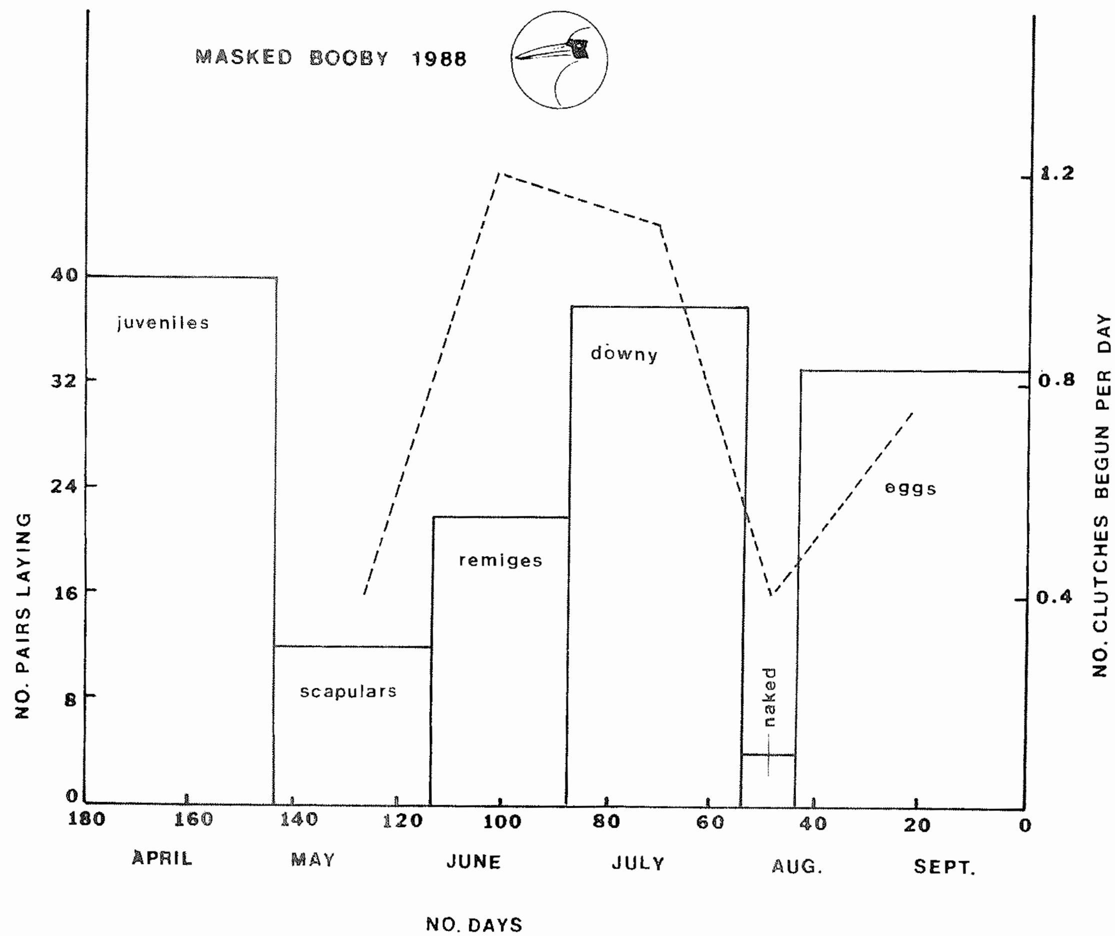

Figure 5. Approximate laying dates for Masked Booby nests found on Caroline Atoll in September 1988. See Fig. 3 for explanation.

one pair with a downy young only 2-3 cm above high-tide flow on an "islet" between fingers of the channel, a precarious location where nesting surely must fail in stormy periods. No birds were seen there in March and May 1990, following a severe storm in February 1990. Four pairs nested singly along a leeward 1,000 m stretch of lagoon shore on the northern end of Long (Fig. 4); hardpan was the primary substrate.

Numbers: In September 1988 we found 189 Masked Booby pairs (Table 3), including those on territory (with or without nest scrapes) and juveniles (with or without attending adults). We found no "clubs" of nonbreeding birds. We covered most of the habitat favored by this species except the northern 300 m of Nake Island; in 1990 a few scattered pairs nested there. Our population estimate, including pairs we might have missed, was approximately 200 breeding pairs. Other population estimates were "ca. 10" birds (Clapp & Sibley 1971a) and 50 ± 15% (Grossman & Grossman 1974). In 1965 POBSP biologists (F. Sibley, pers. comm.) surveyed all locations where we found breeding pairs. Thus, 200 pairs represents a major increase in the population on Caroline Atoll.

Phenology: In June 1965 only 4 Masked Booby nests containing eggs were found (Clapp & Sibley 1971a), indicating that nesting began in May or June. On 9-10 September 1974, Grossman & Grossman counted 23 nests containing "eggs and nestlings" on windward Long and part of Nake. We found nests in all stages in September 1988 (Table 3, Fig. 5). The large age class in April may include some juveniles that could fly (i.e. were older than 180 days). We may have undercounted naked chicks, not wishing to expose them to the sun by frightening the brooding adult. Laying began in April or earlier, peaked in June and July (Fig. 5), and continued until our survey in late September. The 34 pairs on territory, many with nest scrapes (Table 3), indicated that laying was still in progress and would continue into October.

Table 3. Stages in the breeding cycle of the boobies of Caroline Atoll, 21-29 September 1988.

Species	Flying Juv.	Juv.	Scapulars	Remiges	Downy	Naked	Eggs	Pairs on Territory
	Nest stage[1]/Approximate age in days from laying							
Masked	>164	145-164	115-144	89-114	55-88	45-54	0-44	
Brown	>164	144-164	114-144	88-114	54-88	44-54	0-44	
Red-footed	-	>150	111-150	75-110	54-74	45-53	0-45	
	No. nests in each stage							
Masked	-	40	12	22	38	4	33	34
Brown	1	-	-	-	-	-	3	8
Red-footed	many	-	-	-	29	-	919	1,270

[1] For descriptions of nest stages see C. B. Kepler (1978).

In March 1990, 31 pairs were on territory or were attending nests, eggs, or older chicks, indicating that a new breeding season was underway as the previous season was ending. By May 1990 there were 63 nests, mostly with eggs, and there were no older chicks. Thus, the 1990 season augments the 1988 data and suggests an annual cycle with egg laying beginning slowly in February and March, peaking in June and July, and declining to a low ebb from December to February.

The large number of fledged juveniles and nests with older chicks, in both September 1988 and in March 1990, indicated that the 1988 and 1989 breeding seasons were very successful. It also suggested that potential predators (rats and coconut crabs) posed little hazard to this hardy species.

BROWN BOOBY (*Sula leucogaster*) Fig. 2

This widely distributed pantropical species has an estimated population in the Line and Phoenix Islands of about 3,200 (Clapp 1967, Perry 1980), with over half of them (2,000) recently found on Malden Island, in the Southern Line Group. However, all other estimates of this species on Malden from 1964 to 1980 (the 16 years after pigs were eliminated) are below two hundred.

Distribution and habitat preference: Breeding Brown Boobies on Caroline were restricted to the windward edges of *Tournefortia* scrub and forest, generally within 15-20 m of high water. In 1988 we found nests on 4 islets (Fig. 2, Table 1). Long, with 12 pairs, was the only islet supporting more than a single pair. They were located on the northern two-thirds of the island: 4 pairs formed a loose colony near the head of Transect A (Pt. I, Fig. 8). All nests were under *Tournefortia* bushes approximately 3 m tall. In March 1990, we found 20 pairs of Brown Boobies, all on windward Nake as far as the islet's northern extremity. There was no evidence of nesting on Long Island. On May 22, 1990, only 3 nests, all with eggs, were found on Nake.

On 22 September 1988, we saw 2 birds plunge-diving with Masked and Red-footed Boobies approximately 500 m west of South Island. On the atoll, flying Brown Boobies were observed soaring only along the windward beaches. Two birds roosted on the south-central beach of South, and another was found roosting on Kota.

Numbers: We counted 15 pairs during perimeter surveys in 1988, yet found none on the transects. Since we covered virtually all the windward beaches (Pt. I, Fig. 9), we are confident that fewer than 20 pairs nested on the atoll. Our population estimate for 1990 was 25 pairs.

The POBSP (Clapp & Sibley 1971a) found 3 nests on Nake in June 1965, estimating a population of 15 birds, while the Grossmans (1974) found 8 nests on Long Island, estimating a similar population. Even though our surveys triple the known population, the Brown Booby remains a rare seabird on Caroline.

Phenology: With the exception of one recently fledged juvenile, all nests contained eggs in September 1988 (Table 3). Clapp & Sibley (1971a) found eggs in June; the Grossmans found eggs in September. In March 1990, the 20 pairs were all on nests whose contents ranged from eggs to an older juvenile. However, 2 months later, only 3 nests, containing eggs, could be found. These data from 4 years suggest that the species may have trouble rearing young. More juveniles should have been encountered, especially in May 1990. However, cyclonic weather in February 1990 brought torrential rains and severe winds (Falconer, pers. comm.) which defoliated and uprooted the strand vegetation of Long and Nake (Pt. I, Pl. 33), deposited storm blocks on the windward reef flats and tons of sand over the existing beaches and old interislet channels of Long (AKK, pers. obs.). Brown Booby eggs and chicks would have experienced great difficulty at this time, as the region hardest hit was their sole nesting area. During February 1990, 640 mm (25.2") of rain fell in 10 days (Pt. I, App. II). Predation by Polynesian rats or coconut crabs could also limit reproduction on the atoll.

RED-FOOTED BOOBY (*Sula sula*) Figs. 6, 7

This pantropical booby numbers over 55,000 individuals in the Line Group (Clapp 1967, Perry 1980), making it one of the most important regions in the world for this species. Caroline holds the fifth largest known Red-footed Booby colony (see Nelson 1978). The largest known colony (140,000 pairs) is found on Tower Island (Galapagos): three of the 5 biggest colonies occur in the Line Group.

Distribution and habitat preference: In 1988, the Red-footed Booby bred on 28 islets, ranging in size from Nautonga (0.34 ha) to Nake (107.46 ha) (Fig. 6). On the Windward Islands, Red-foots occurred from Nake to Tridacna, absent only from the smallest islets (Noddy Rock, Skull Islet, Motu Atibu). The species was also widespread on the leeward islets, extending from Pandanus to Eitei. The tiny islets (Fishball, Azure, Reef-flat) were not occupied.

Red-foots are tree nesters whose distribution on Caroline closely matched that of *Tournefortia* scrub and forest. They sometimes utilized smaller *Pisonia* or *Cordia* trees where they intermingled with *Tournefortia*, and occasionally built nests in the tallest (>15 m) *Pisonia*. They nested in smaller *Tournefortia* patches within the peripheral scrublands, especially those not directly exposed to the trade winds. They clearly avoided smaller islets because of the lack of suitable *Tournefortia* in which to breed. They nested inward from the vegetated edges of the islets, generally at 3-6 m in height, and were distributed in broken rings around the smaller motus in areas of moderate winds. A higher percentage of the population occurred on perimeter surveys than on cross-island transects.

Red-foots were absent from South Island, which was primarily covered with *Cocos* (Pt. I, Figs. 50, 51). Even though *Tournefortia* occurred on all its coastlines, no boobies nested in them. Ana-Ana was also unoccupied: the presence of a family of 4 people, a cat, and a dog (all removed in 1991) undoubtedly discouraged nesting attempts. Red

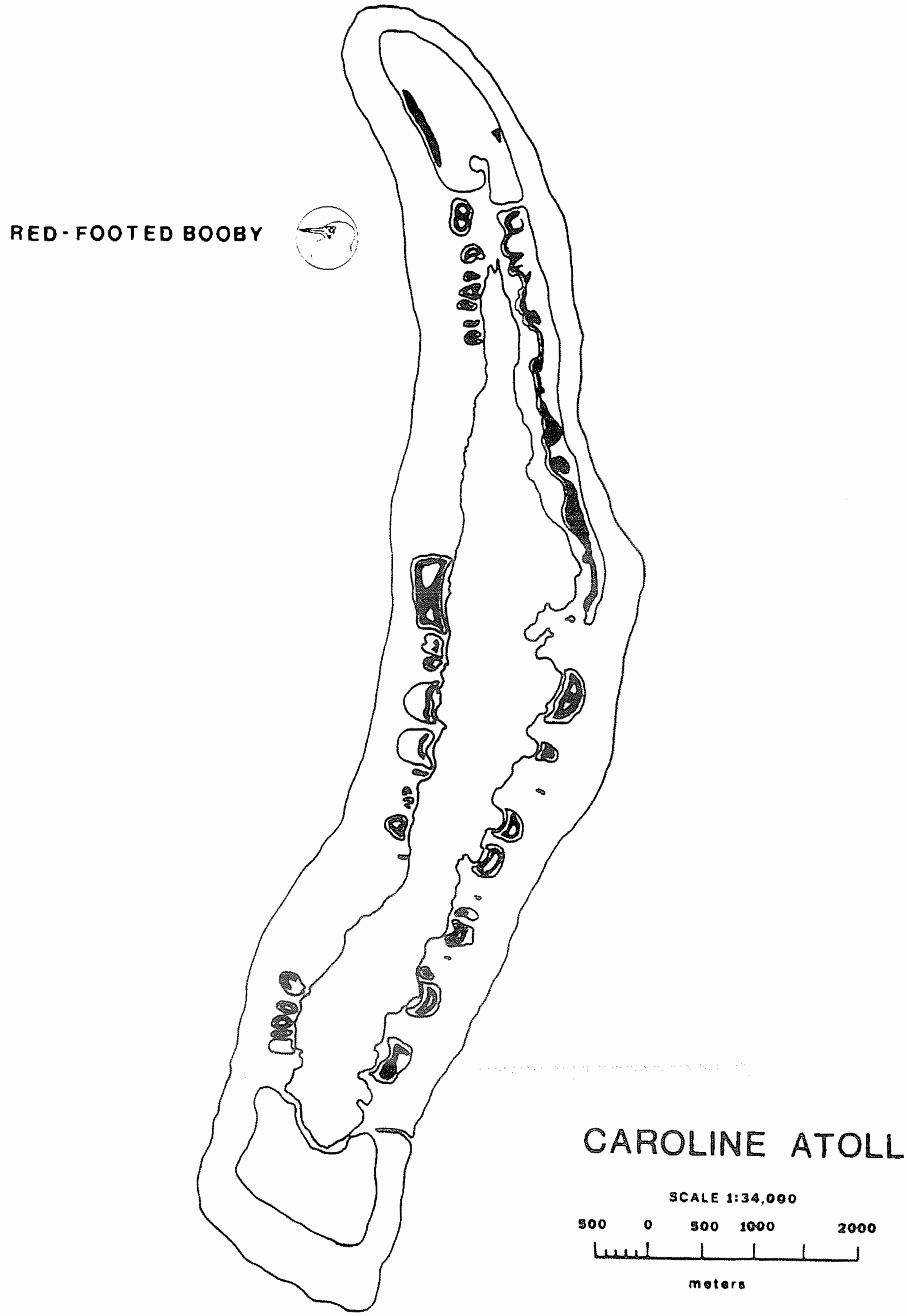

Figure 6. Distribution map of breeding Red-footed Boobies on Caroline Atoll, September 1988.

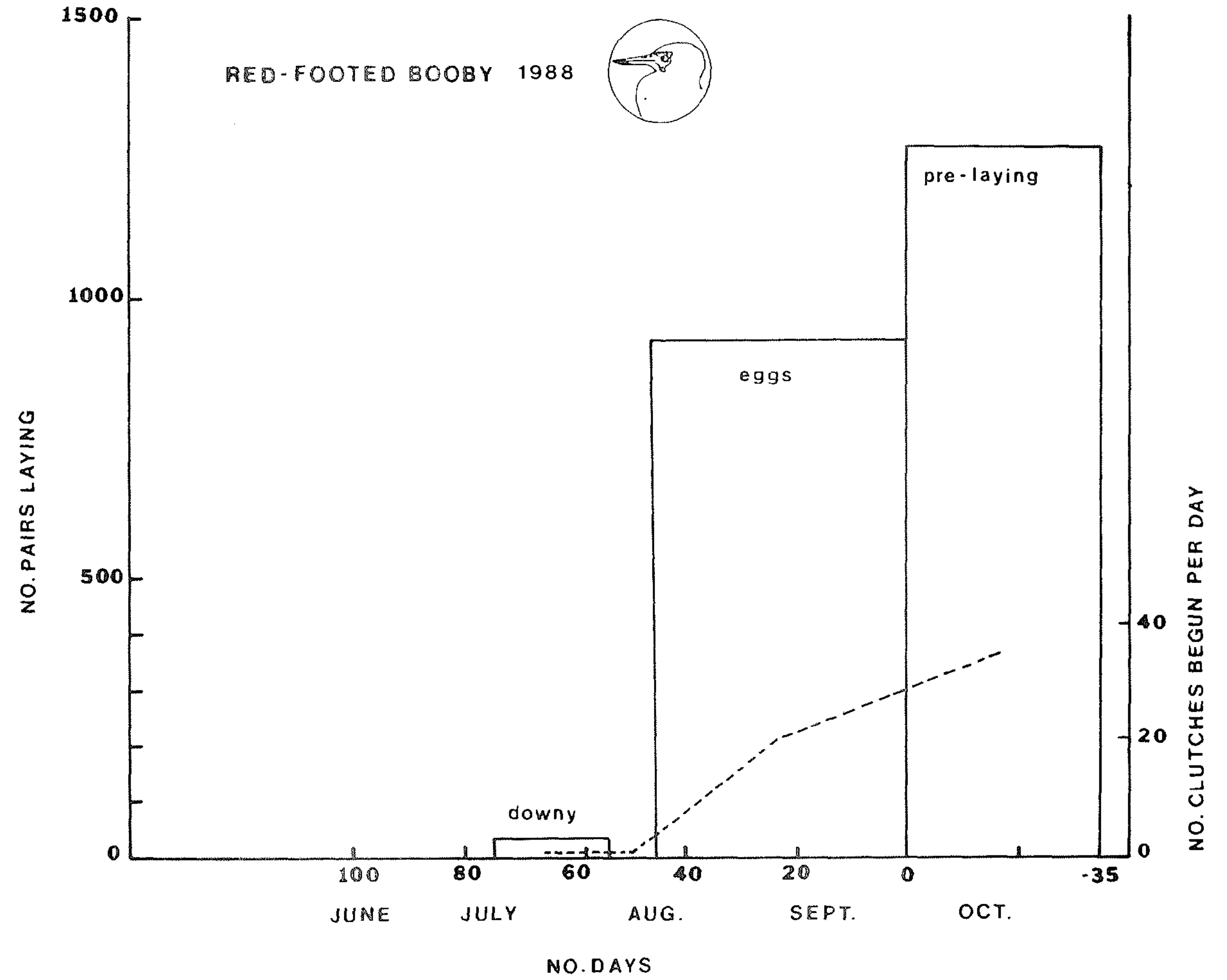

Figure 7. Approximate laying dates for Red-footed Booby nests found on Caroline Atoll in September 1988. See Fig. 3 for explanation.

foots also avoided the mixed forests of south Nake, which contained much *Cocos* and *Pandanus* (Pt. I, Fig. 37). Red-footed Boobies were thus found only in Caroline's indigenous woodlands, primarily in *Tournefortia* >2 m tall; they avoided anthropogenic plant communities and man.

Red-foots used a wider range of habitats for roosting. Nonbreeding birds were found throughout the taller indigenous trees, even in leeward situations where *Pisonia* and *Cordia* overhung the lagoon (as on Long Island).

Numbers: The POBSP (Clapp & Sibley 1971a) estimated 5,000 ± 25% Red-foots on Caroline in June 1965, with about 2,000 ± 25% nesting pairs. The Grossmans estimate was 3,000 ± 25% and 2,500 pairs in September 1974. In 1988 we sampled systematically more than 7% of the available habitat on all motus except Crescent (4.6% sampled) and North Arundel, and estimated that 2,221 pairs of Red-footed Boobies nested on 27 of Caroline's islets (Table 1). We found an additional 1,234 roosting, nonbreeding birds. We know (C. Kepler 1969, Nelson 1978) that fewer boobies remain in their colonies during the day than at night. Thus an unknown fraction of the population was at sea when we conducted our counts. Impressive flights of Red-footed Boobies returned each evening: 3-4 birds arrived for each one that had remained behind, many undoubtedly mates of incubating birds. To approximate the number of returning nonbreeding birds, we doubled the number of roosting adults to allow for an additional 1,234 adults and juveniles. Thus, our conservative estimate was at least 7,000 individuals.

Because Red-footed Boobies were so dependent upon *Tournefortia*, we determined the nesting population on each islet by multiplying the number of nests found on transects by the ratio of sampled to total *Tournefortia* area. Perimeter counts (Pt. I, Fig. 9) were used if the number of Red-foots observed exceeded the number calculated from the cross-island transects.

Long Island held the greatest number of nests (659), mostly in the leeward *Tournefortia* and *Tournefortia-Pisonia* edge. Bird densities were typically highest on the largest islets: Windward and Tridacna, the largest Windward Islets, held 163 and 111 nests, respectively; and Mannikiba, the biggest leeward islet, harbored the largest population (184) of the entire leeward side. There were exceptions, however: Pandanus, with 4 times the area of *Tournefortia* of any of the South Nake Islets, held fewer birds than 3 much smaller islets (Table 1).

Tournefortia scrub and forest covered approximately 125.25 ha (Pt. I, Table 9). Overall, there were 1.75 Red-footed Booby nests/1,000 m^2 of *Tournefortia* forest. Nest densities for occupied islets by island groups (Table 4) showed that Red-foots favored areas less exposed to the trade winds: most nests on the windward motus were protected by well-developed *Pisonia* forests. The exposed Central Leeward Islets held the lowest nest densities (1.2 nests/1,000 m^2), far less than on the South Nake Islets (5.3/1,000 m^2), which are protected by the northern edge of Long. The greatest densities (7.8 nests/1,000 m^2) occurred on the South Nake Islets south of Pandanus.

Table 4. Density of Red-footed Booby nests in occupied *Tournefortia* habitats on islet groups, Caroline Atoll, September 1988.

Islet Group	Number Occupied Islets	Estimated Number Nests	Area of *Tournefortia* (m^2)	Nests/1,000 m^2 of Available Habitat
Nake	1	496	300,650	1.6
Long	1	659	322,000	2.0
Windward Islets	8	434	251,900	1.7
South Nake Islets	7	319	59,800	5.3
Central Leewards	6	239	197,500	1.2
Southern Leewards	4	74	39,600	1.9
Total	27	2,221	1,170,550	1.9

Broadly speaking, Red-foots breed in well-dispersed colonies. A record density of 600 nests/1,000 m^2 on Tromelin Island (Indian Ocean) is exceptional. Elsewhere, 53 pairs/1,000 m^2 on Tower Island (Galapagos), 40/1,000 m^2 on Moku Manu (Oahu, Hawaii), and 27/1,000 m^2 on Half Moon Cay (Honduras) are more consistent high-density colonies (Nelson 1978). Only on tiny Motu Kota (Pt. I, Fig. 52), with 12 nests in 303 m^2 of *Tournefortia* (40/1,000 m^2), did we find such density, and for this reason we named the islet "Kota" (Gilbertese for Red-footed Booby).

Phenology: In September 1988, we located 339 nests. Of the 152 whose contents could be determined, 87 were empty, 63 contained eggs, and 2 held downy chicks. We saw dozens of flying juveniles along the windward coasts. Most pairs were building or guarding their nests during a prelaying stage that lasts from 11-35 days (Nelson 1969). Of the pairs with nests, 57.2% had yet to lay and 41.4% had laid their eggs between mid-August and late September (Fig. 7). Applied to the total breeding population, approximately 1,270 nests were in the prelaying stage and would be expected to produce eggs throughout October. An additional 919 nests had a mean laying date in early September (Fig. 7). Red-footed Boobies were synchronous with Brown Boobies but delayed relative to Masked Boobies.

In June 1965, nests containing prelaying adults, eggs, and young in all stages indicated that the birds were in the midst of a protracted breeding season extending from January to June. In September 1974, eggs and "young at nearly all stages" were present. Our data reveal that no successful nesting occurred in May-June 1988. Data from March and May 1990 indicate that nest-building began in January (or earlier), with eggs laid from January to May. However, perimeter counts and cross-island transects on 11 windward motus found virtually all Red-footed Boobies either nest-building or sitting on eggs. Chicks were found only on the leeward islands. This asynchronous breeding suggests that breeding activities were curtailed by the cyclonic weather two weeks earlier, which was particularly violent on the windward beaches harboring Brown Booby nests. Red-footed Boobies in other tropical locations have variable, opportunistic breeding seasons that depend upon food availability (Nelson 1978; F. Sibley, pers. comm.); our data suggests that similar pressures could be operating at Caroline.

Color morphs: Red-footed Boobies are polymorphic (Nelson 1978). The basic plumages are brown or white, with brown morphs having many combinations of tail, back, scapular, foot, and bill colors. A variety of brown forms and white forms occurred on Caroline, with a ratio of 9:1 (337 brown to 35 white), which contrasts sharply with Nelson's (1978) statement that "in the Line and Phoenix Islands all birds are white morphs." Most of the dark morphs were the "white-tailed" form (see Nelson 1978, pp. 660-661). The variations and proportions of plumage types show clinal change in the Line and Phoenix Islands (F. Sibley, pers. comm.), thus the question of plumage morphology needs much more study in the Central Pacific.

GREAT FRIGATEBIRD (*Fregata minor*) Figs. 8, 9 and Pt. I, Pl. 42

The Great Frigatebird breeds at widely scattered locations throughout tropical waters in the Atlantic, Pacific, and Indian Oceans. It is known to breed on all of the Line Islands except Starbuck (Perry 1980).

Distribution and habitat preference: Great Frigatebirds nested on 25 islets, including Nake, Long, and most of the larger islets (Fig. 8, Table 1), ranging in size from Azure (0.20 ha) to Nake (107.46 ha). Every occupied islet had some *Pisonia* forest, even if only a single tree (Azure). The larger islets lacking *Pisonia* forest (Arundel, 7.34 ha, Tridacna, 9.08 ha) lacked frigatebirds in 1988, although frigatebird chicks were present on Arundel in early 1989 (Anne Falconer, pers. comm).

Although Great Frigatebirds were similar in nest requirements to Red-footed Boobies, there were significant differences: the frigates tended to nest higher in, and closer to the outer edge, of the canopy (although nests were found as low as 1.3 m). Nest sites were more sheltered from the wind than those of Red-foots, and in locations where the birds could take flight easily. Such site preferences may explain the association with *Pisonia*. *Pisonia* reaches 21 m on Caroline, taller than other tree species, providing a windbreak on most islets. The largest colonies (Nake, Long, Pig, Mannikiba) were found leeward of these stands. We found nests in *Tournefortia*, *Pisonia*, and *Cordia*. They were often in the *Tournefortia*-*Pisonia* interface, generally in the taller *Tournefortia*. One colony on south Long overhung the lagoon in a dense *Pisonia* stand. Frigates were not found in any anthropogenic forests and were absent from then-inhabited Ana-Ana.

Numbers: The previous population estimate for Great Frigatebirds on Caroline was 10,000 birds (Clapp & Sibley 1971a, Perry 1980). The Grossmans (1974) estimated 5,000-8,000 birds, with 4,000-6,000 nests.

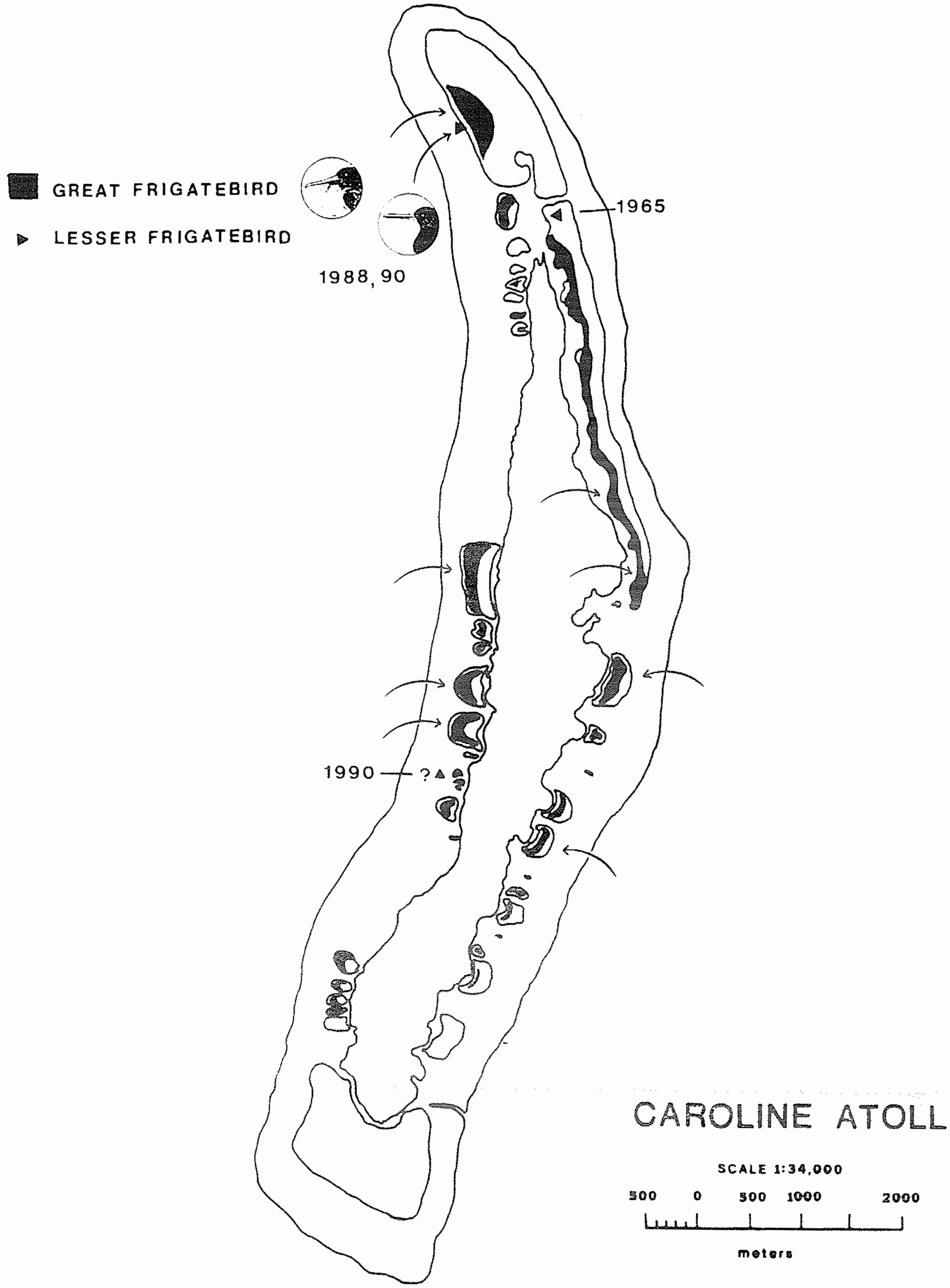

Figure 8. Distribution map of breeding Great and Lesser Frigatebirds on Caroline Atoll, September 1988.

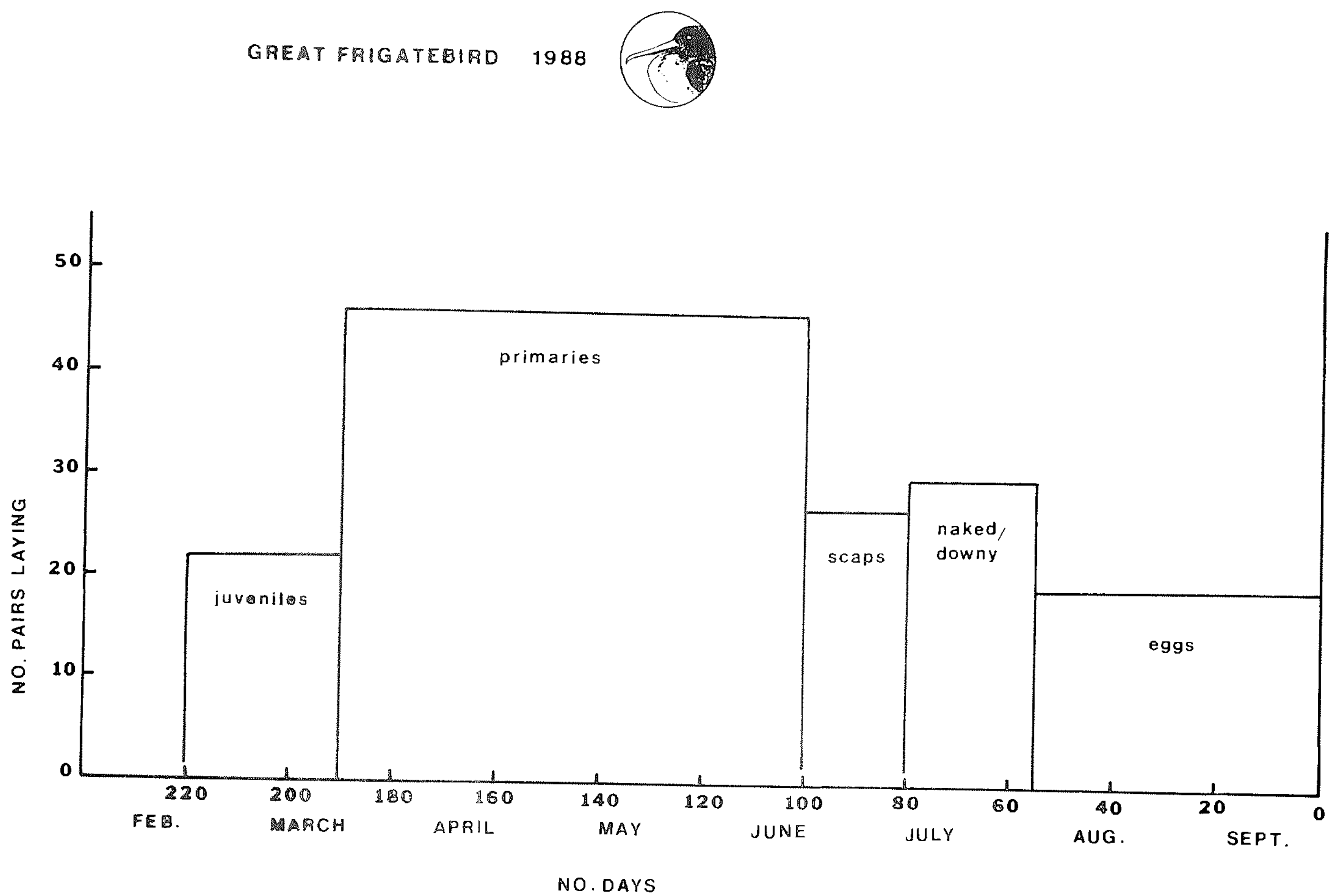

Figure 9. Approximate laying dates for Great Frigatebird nests found on Caroline Atoll in September 1988. See Fig. 3 for explanation.

We calculated that 2,427 pairs bred or attended territories. An additional 617 birds roosted, thus the entire population was approximately 5,471 individuals. A large but undetermined number of birds soared over the atoll throughout the day, and an uncountable number of birds, including fledged juveniles that would ultimately return to the island to nest (Diamond 1971), were undoubtedly at sea. Because this species is difficult to count accurately, it is unclear if the population has changed since 1965.

Phenology: In frigatebirds, the scapulars, which first appear at 81 days in *Fregata magnificens* (Diamond 1973), erupt before the primaries. Because we lack chick stage data for *F. minor* and *F. ariel*, we have modified ages from Diamond (1973) for *magnificens*, using the hatching times for *F. ariel* and *F. minor* from Nelson (1976), and fledging ages from Diamond (1975b), to construct very approximate development stages for the species on Caroline. Since they fledge at an earlier age than *F. magnificens*, we have reduced the ages for chicks with erupting primaries for *F. ariel* and *F. minor*, kept the duration of the earlier stages approximately the same, and reduced the period in juvenile plumage.

We found 214 nests in 1988. Of the 144 in which we determined contents, 49 contained eggs or young chicks, 27 held chicks with developing scapular feathers, and 68 contained older chicks (Table 5). The additional 70 adults occupied nests of unknown contents. We saw fewer than 10 displaying males and a high proportion (87%) of nests with chicks, many of them old, indicating that the breeding season was nearly over. A major laying effort had begun in March-April (Fig. 9) and continued into September. In March 1990, an abundance of flying juveniles and occasional larger chicks down to the downy stage indicated that the previous year's breeding season was ending. Of all the seabird species affected by the February 1990 storm, Great Frigatebirds suffered

Table 5. Stages in the breeding cycle of frigatebirds on Caroline Atoll, 21-29 September 1988.

	Nest stage/Approximate age in days from laying					
Species	Juv.	Primaries	Scaps.	Downy	Naked	Eggs
Great	191-220	101-190	81-100	56-80[1]		0-55
Lesser	181-210	91-180	71-90	56-70	46-55	0-45
	No. nests in each stage					
Great	22	46	27	30[1]		19
Lesser	4	13	4	5	0	0

[1] Duration of naked and downy chick stages are lumped because it was often impossible to see into canopy nests.

the most obvious mortality. We found at least 10 adults and flying immatures recently dead, either draped in partly defoliated *Tournefortia* shrubs or lying on the ground. A small number of males were beginning another courtship cycle. By May 1990, courtship and egg-laying were still underway, and nests contained eggs or small chicks up to the "remiges" stage. Peak laying on Christmas Island (Pacific Ocean) occurs from March-May (Schreiber & Ashmole 1970), the same laying cycle observed on Caroline in 1988 and 1990.

LESSER FRIGATEBIRD (*Fregata ariel*) Figs. 8, 10

The Lesser Frigatebird is a pantropical species. It breeds and disperses widely within the tropical Pacific (Sibley & Clapp 1967). One of the largest populations in the world (30,000-85,000) breeds on McKean Island, in the Phoenix Group (Garnett 1983). Lesser Frigatebirds breed on 4 of the Line Islands, with the population on Malden (7,000) the largest in the archipelago (Perry 1980).

Distribution and habitat preference: In June 1964, Lesser Frigatebirds were found nesting in one compact colony on the leeward north end of Long (Clapp & Sibley 1971a). In September 1974, adults and flying immatures were observed flying and resting (Grossman & Grossman 1974), but no nests were found, most likely because the western side of the atoll was not surveyed. A population of 200 was estimated. We found a single colony in leeward *Pisonia* forest on western Nake (Fig. 8), both in September 1988 and May 1990. The birds nested high (to 18 m) in the *Pisonia* and *Pisonia-Cordia* edge facing an open *Tournefortia* savannah. Although primarily composed of *F. ariel*, a few *F. minor* were scattered along all but the eastern edge of the colony. West of the birds, across the open forest, *F. minor* and *Sula sula* nested in a mixed colony in a denser stand of *Tournefortia*. Birds were seen soaring over Nake, Long, and the leeward islets but were not found roosting or nesting away from the colony on Nake. However, in March 1990, approximately 650 Lesser Frigatebirds were swarming above and roosting on Motu Nautonga in a tight cluster, possibly preparing for nesting.

Numbers and phenology: POBSP biologists estimated a population of 1,000 Lesser Frigatebirds on Caroline in June 1964, with 400 ± 10% breeding: only eggs were found (Clapp & Sibley 1971a). On Christmas Island, *F. ariel* laid in May and June in 1959, 1963, 1964, and 1967 (Schreiber & Ashmole 1970). Of 46 nests found in 1988, we could inspect the contents of only 26: all contained feathered chicks (Table 5). Laying dates ranged from March through July (Fig. 10), with a peak from April to June. Our limited data on Caroline's Lesser Frigates indicates, therefore, that they may be synchronous with those on Christmas. In larger Central Pacific colonies, large subpopulations of this species have differing breeding regimes (F. Sibley, pers. comm.).

Because we did not determine the colony limits, we cannot provide a population estimate. There was a minimum of 200 birds in 1988 (46 nests, plus roosting and flying individuals) and ca. 1,000 in 1990.

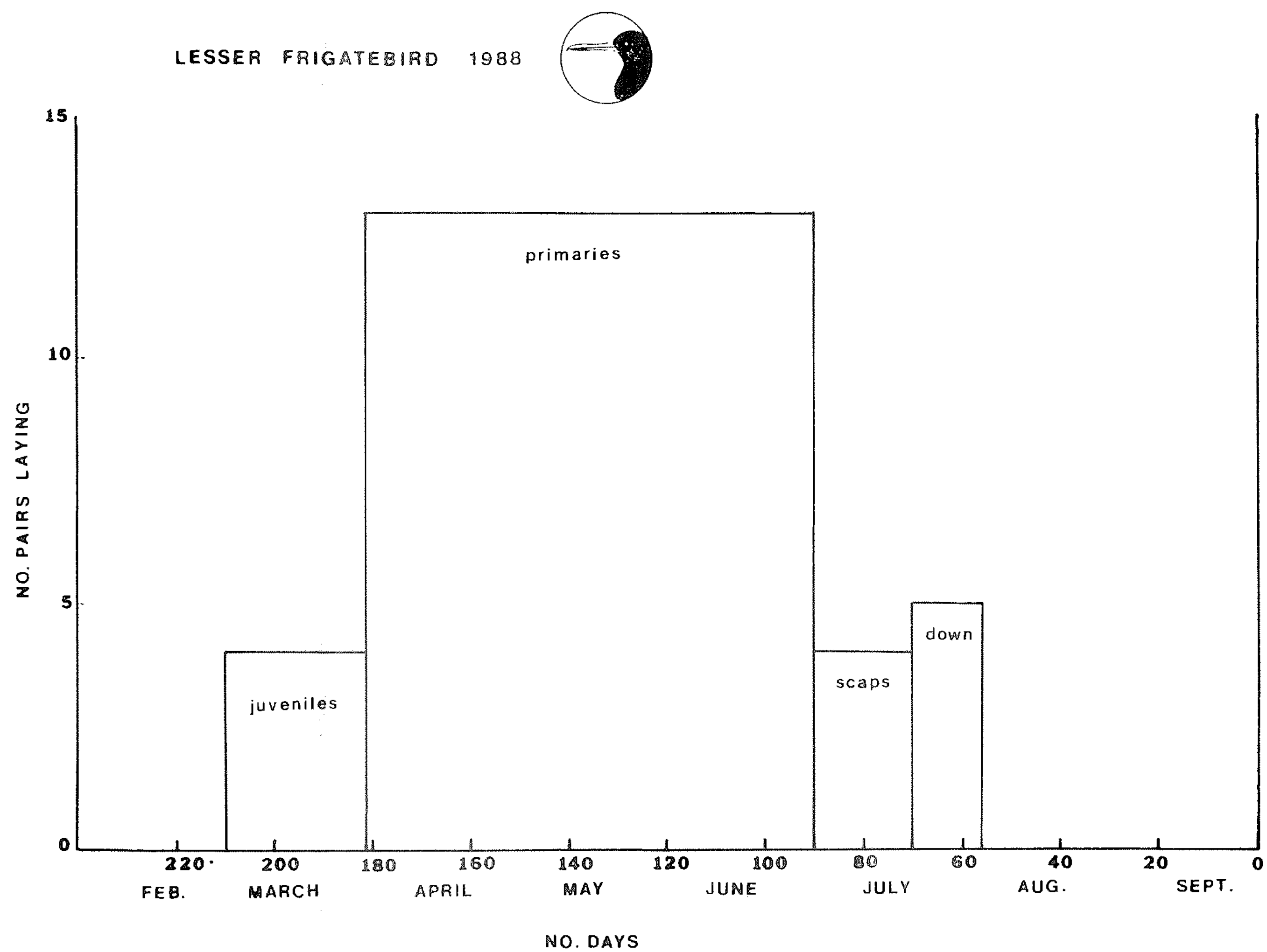

Figure 10. Approximate laying dates for Lesser Frigatebird nests found on Caroline Atoll in September 1988.

SOOTY TERN (*Sterna fuscata*) Figs. 11, 12

This tern is the most widespread and abundant tropical seabird in the world. Under favorable conditions it forms immense colonies numbering into the millions. It is known to breed on 7 of the Line Islands: the largest population in the Pacific is found on Christmas Island (15,000,000 at highest count), and 3,000,000 have been recorded on Starbuck (Perry 1980).

Distribution and habitat preference: To date, 21 colonies from 10 islets are known for the years 1965, 1974, 1988, 1989, and 1990 (Fig. 11). In September 1988, we found 3 colonies, 2 on the northern half of Long and one on Bo'sun Bird Islet; all fit the general habitat description in Clapp & Sibley (1971a). Colony A, nearly square, was 210 m on a side. Eggs were placed under a savannah-type *Tournefortia* scrub, from 1-4 m tall with approximately 60% canopy cover. The substrate was coral rubble mixed with sand, covered by *Heliotropium* (5%), *Portulaca* (1%), *Laportea* (<1%), and *Lepturus* (<1%), typical of old interisland channels. Colony 1 was located in a broad sandy corridor with 2 large "groves" of *Tournefortia*. The northern subpopulation extended 116 m along the windward beach, but 248 m along the lagoon. The southern subpopulation began 28 m further south along the beach, fronted the seaward reef for 86 m, and was shaped like a blunt triangle, its apex pointing toward the lagoon. Most chicks were under *Tournefortia*, which consisted of shrubs 2-4 m high with 80% canopy cover. The substrate was also older beach sands mixed with coral rubble, and covered with *Portulaca* (40% cover), *Lepturus* (<5%), and *Heliotropium* (<5%). The Bo'sun Bird colony, a rough oval approximately 55 m wide by 70 m long, was under 2-3 m high *Tournefortia* with 75% cover, on coral rubble/sand sparsely carpeted with *Portulaca* and *Heliotropium*.

Numbers: Populations were determined by measuring colony dimensions, then counting eggs and/or chicks in 9 m^2 sample plots located at random points along a compass line. Because juveniles moved as we approached, they were counted 6 m ahead of us in estimated 3 m x 6 m plots. The Colony 1 subcolonies (North, South) were treated separately.

Colony size (rounded) in 1988 ranged from 127,000 ± 30,000 "nests" (Colony A) to 1,500 ± 750 new eggs on Bo'sun Bird Islet (Table 6). There were an additional 6,900 ± 1,600 nearly-fledged chicks in the Bo'sun Bird colony, resulting from eggs laid 3 months earlier.

The total number of eggs and chicks was 188,000 ± 40,000. Actual numbers of adults are difficult to estimate, but in other studies have exceeded the number of eggs and young by factors of more than 2 because innumerable eggs and chicks were lost, colonies often overlapped, and many nonbreeding adults joined the prebreeding swarms or associated with breeding birds. Schreiber & Ashmole (1970), relying on POBSP data from Johnston Atoll (North-central Pacific), estimated that 4 adults were present for each egg laid. POBSP data from Johnston (Amerson & Shelton 1976) indicated that about 600,000 adults were present in a colony with 105,000 eggs, or approximately 5.7 adults/egg. If we assume that real

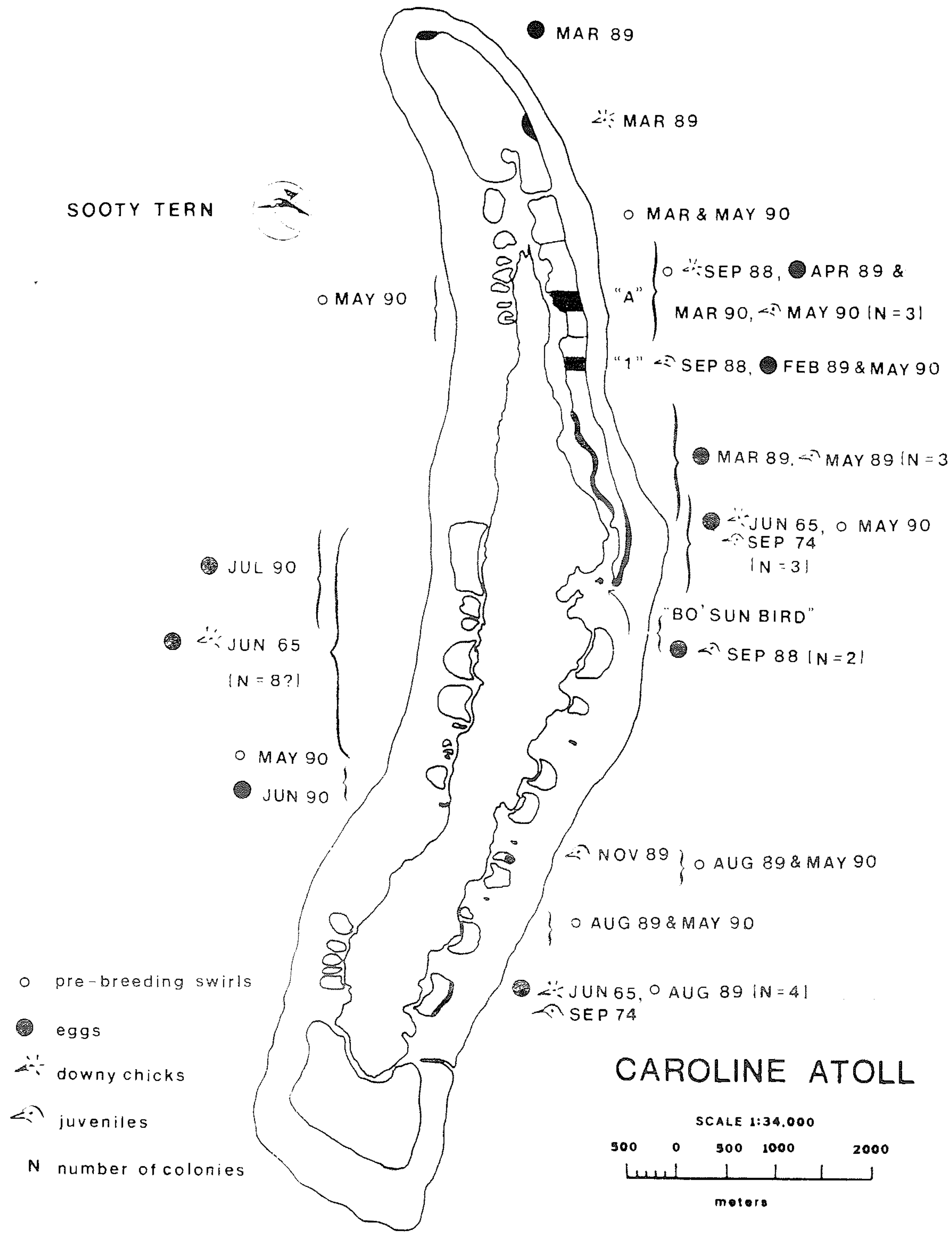

Figure 11. Distribution map of breeding Sooty Terns on Caroline Atoll, September 1988 to July 1990.

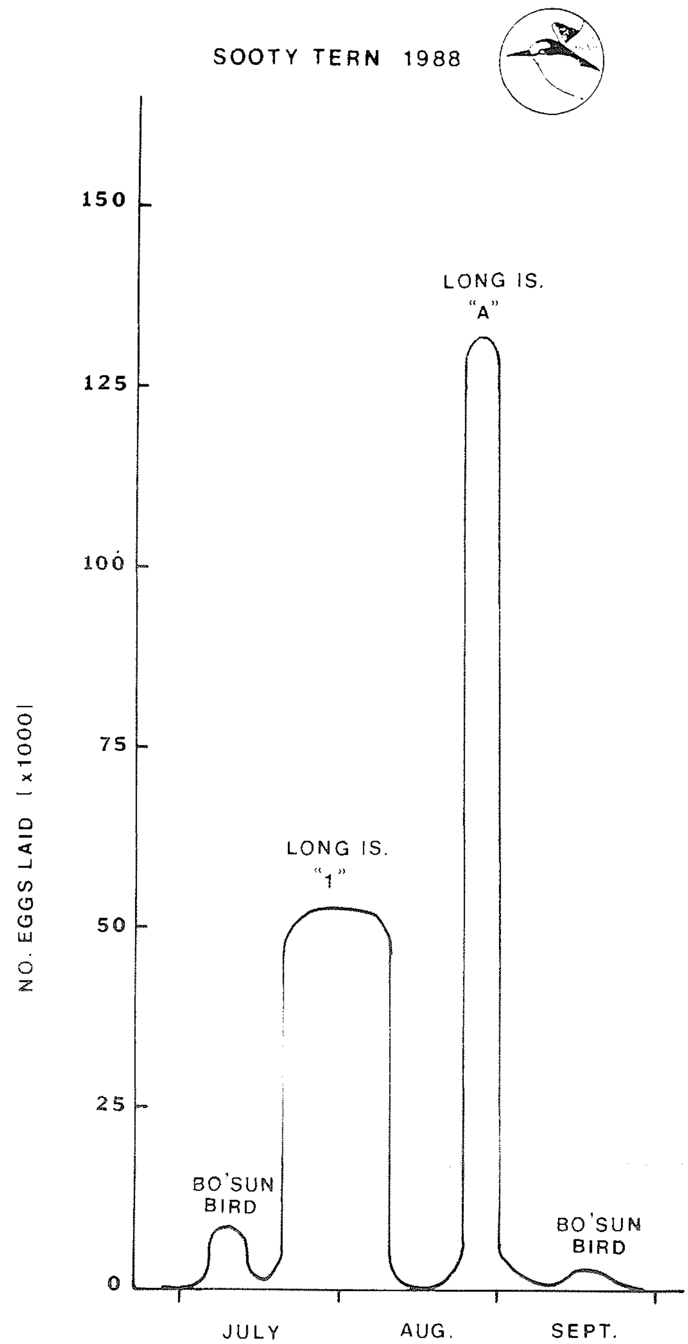

Figure 12. Approximate laying dates for Sooty Tern young found on Caroline Atoll in September 1988. See Fig. 3 for explanation.

Table 6. Sooty Tern colonies on Caroline Atoll, 27-28 September 1988.

Colony Location	Area	Calculated Population (Mean Pairs ± SE)	Nest Stage	Approx. Weeks From Laying
Long Island, A	44,100 m^2	127,449 ± 30,429	hatching eggs, downy chicks	4-5
Long Island, 1 N	24,200 m^2	41,382 ± 5,808	chicks with short tails, juv. plumage	7-10
Long Island, 1 S	6,400 m^2	10,944 ± 1,536	"	7-10
Bo'sun Bird Islet,				
old	3,375 m^2	6,883 ± 1,575	fledglings	11-12
new	3,375 m^2	1,538 ± 758	new eggs	1-2
Total	75,075 m^2	188,196 ± 40,106		

numbers of terns in our colonies lay midway between 4 and 5.7 times the number of eggs and chicks, then the number of Sooty Terns using Caroline Atoll would have ranged between 720,000 and 1,100,000 birds (911,800 ± 21%). This is twice the estimate provided by Clapp & Sibley (1971a), even though we found fewer colonies. However, if the POBSP had used the criterion of 4 adults present for each egg laid, their total population figures would have exceeded ours, hence the 2 estimates are not strictly comparable (F. Sibley, pers. comm.).

In March 1990, laying was just beginning in 2 colonies on Long Island, (625 m x 150 - 315 m wide and 180 m long x 160 m wide). Enormous numbers of birds, both on the ground in densities up to 9 or 10 pairs/m^2 and in the air, made it impossible to calculate a reasonable population figure. According to Anne Falconer, these 2 colonies were very successful. Similarly, counting was difficult in May 1990 when 6 large prebreeding swirls hovered like huge clouds of gnats over discrete islets and islet groups (Fig. 11). Our 1988 estimate of approximately one million birds is probably a conservative count for the atoll as a whole on an annual basis.

<u>Phenology</u>: The incubation period in Sooty Terns is about 4 weeks (Dinsmore 1972). Young fledge 7-8 weeks after hatching, although fledging ages, dependent upon food supply (Schreiber & Ashmole 1970), are highly variable.

Four separate Sooty Tern colonies had been started over the 12-week period prior to our study in 1988 (Table 6). On Bo'sun Bird Islet a new wave of laying was just beginning in an open area immediately southwest of most of the colony, while nearly fledged chicks scurried about beneath the *Tournefortia*. Undoubtedly many young had already fledged, so many more eggs would have been laid in early July by this colony than indicated (Fig. 12). The 2 colonies on Long were established at different times: the short-tailed juveniles in Colony 1 preceded the large number of eggs, hatching eggs, and downy chicks of Colony A by 3-4 weeks.

The July-September laying period on Caroline in 1988 is very different from the bimodal breeding (May-June, December-January) reported from Christmas Island, Pacific Ocean (Schreiber & Ashmole 1970), and the May laying dates noted for Caroline by the POBSP in 1965. In September 1974, "innumerable large unfledged chicks and juveniles" were present in colonies at the tip of Long Island and on Tridacna Islet (Grossman & Grossman 1974). Additional data (Anne Falconer, pers. comm.) indicate that Sooty Terns may lay any time (Fig. 11), certainly January through September (1988 to 1990). Severe storms, which destroyed large Long Island colonies in February 1990, were likely responsible for reinitiating breeding activities on the leeward side of the atoll within the next few months. A great deal more research will be needed on Caroline before the breeding seasons for this species are fully understood. The phenomenon of several colonies on each island breeding at different times is considered the norm for the Line and Phoenix Groups (F. Sibley, pers. comm.), so the situation on Caroline is not unusual.

BROWN NODDY (*Anous stolidus*) Fig. 13

This tern, primarily a tree nester, is widely distributed throughout the warm oceans of the world. It is abundant in the Line and Phoenix Groups, with an estimated total population exceeding 40,000 birds. Brown Noddies are most abundant on Palmyra Island (10,000 birds).

Distribution and habitat preference: The Brown Noddy is second only to the White Tern in the number of motus (28) upon which it is known to breed (Fig. 13). It utilized the smallest (Noddy Rock, 0.02 ha) and largest (South, 104.41 ha) motus, nesting upon coral rubble and in plant communities ranging from the simplest herb mats to *Tournefortia*, *Pisonia*, *Cordia*, *Cocos*, and the mixed anthropogenic forests of South and Nake. Most pairs were well dispersed, nesting from the outer edges of *Tournefortia* to the central, inner branches of *Pisonia*, and from the ground to the crowns of 25-m *Cocos*. When nesting sympatrically with Black Noddies in *Pisonia*, the Brown Noddies typically occupied portions of branches closest to the trunk. Brown Noddies nested almost solitarily in the *Cocos* canopy on South, were found within dense colonies of Black Noddies and White Terns in tall *Pisonia* forests, with Red-footed Boobies and Great Frigatebirds in *Tournefortia*, and amidst Sooty Terns and Red-tailed Tropicbirds (Bo'sun Bird Islet). Apart from a few ground nesters on Raurau and Fishball, the only ground-nesting colony (80 nests) was located on a *Portulaca* mat on Noddy Rock--a site free of predators, although flooded during storms.

Brown Noddies often formed loose roosting "clubs" on the atoll's beaches. Aggregations of 15-20 birds were found on the west coast of South and on Sandy Inlet, south-central Nake.

Numbers: Clapp & Sibley (1971a) estimated a population of 1,000 birds in June 1965, with about 800 birds breeding (with eggs and young). The Grossmans estimated 400 ± 15% in September 1974. We estimated a total population of 1,491 breeding pairs (Table 1). Because nests high in

Figure 13. Distribution map of breeding Brown Noddies on Caroline Atoll, September 1988.

Cocos palms were difficult to detect, we undoubtedly overlooked many, thus our estimate of approximately 3,000 birds is conservative. Although larger than the population estimated by POBSP (Clapp & Sibley 1971a), uncertainties about the 1965 survey coverage (F. Sibley, pers. comm.) prevent us from knowing if Caroline's population has changed over the past 25 years.

Phenology: This is another species whose breeding cycle is irregular in the Central Pacific: during the 1963-1965 POBSP surveys, egg-laying was found in every month of the year somewhere in the Line and Phoenix Groups (F. Sibley, pers. comm.). On Christmas Island, which has received more attention than any other Central Pacific island, the timing of egg laying varies between colonies. In general, peak laying occurs from March to May, and from November to December. On Caroline, mating and nest-building were found in March 1990, but by May only a few eggs had been laid. Eggs and young were found in June 1965 (Clapp & Sibley 1971a) and in September 1988 (present study). Only eggs were present in September 1974. We found 246 nests in September 1988 and determined the contents of 106: 103 held eggs, 3 held downy chicks. The incubation period is 35-37 days (Dorward & Ashmole 1963), so all viable eggs had been laid within the previous 40 days--mid-August to late September. Because many nests were being built, we feel confident that laying continued into October. Clearly more research is needed to determine whether laying occurs in regular cycles.

BLACK NODDY (*Anous minutus*) Fig. 14

The Black Noddy is widely distributed in the tropical Atlantic and Pacific. It is abundant in the Line and Phoenix Groups, with populations of 16,000 estimated in the Phoenix Islands (Clapp 1967) and over 46,000 in the Line Group. Centers of abundance are Palmyra (20,000) and Christmas (14,500) (Perry 1980).

Distribution and habitat preference: The Black Noddy is a tree-nesting species that on Caroline prefers tall stands of *Pisonia*. The largest colonies (61% of the population) were found in the grand *Pisonia* forests (to 25 m) on Pig and North Pig. We found breeding birds on 18 motus, with populations exceeding 800 pairs in the *Pisonia* on Nake, Long, North Pig, and Pig (Fig. 14). The only significant colony not primarily associated with *Pisonia* was found on Tridacna, where approximately 230 pairs nested in the tallest (ca. 8 m), most central *Tournefortia-Morinda* forest. Black Noddies always nested in dense colonies near islet centers and were integral components of these plant communities: their droppings, coating the ground with a film of guano, constantly enriched the islet's meager soils.

Numbers: Clapp & Sibley (1971a) estimated that 7,000 ± 25% birds were on Caroline. The Grossmans (1974) estimated 500 ± 20%. During our visit the population was much larger: 5,122 pairs were estimated for Pig and North Pig alone (Table 1). Basing our numbers primarily on the densities of sampled colonies in *Pisonia*, we estimated that nearly 8,400 pairs were nesting during our 1988 visit. Our population estimate approached 17,000 birds, to which an unknown number of nonbreeding birds

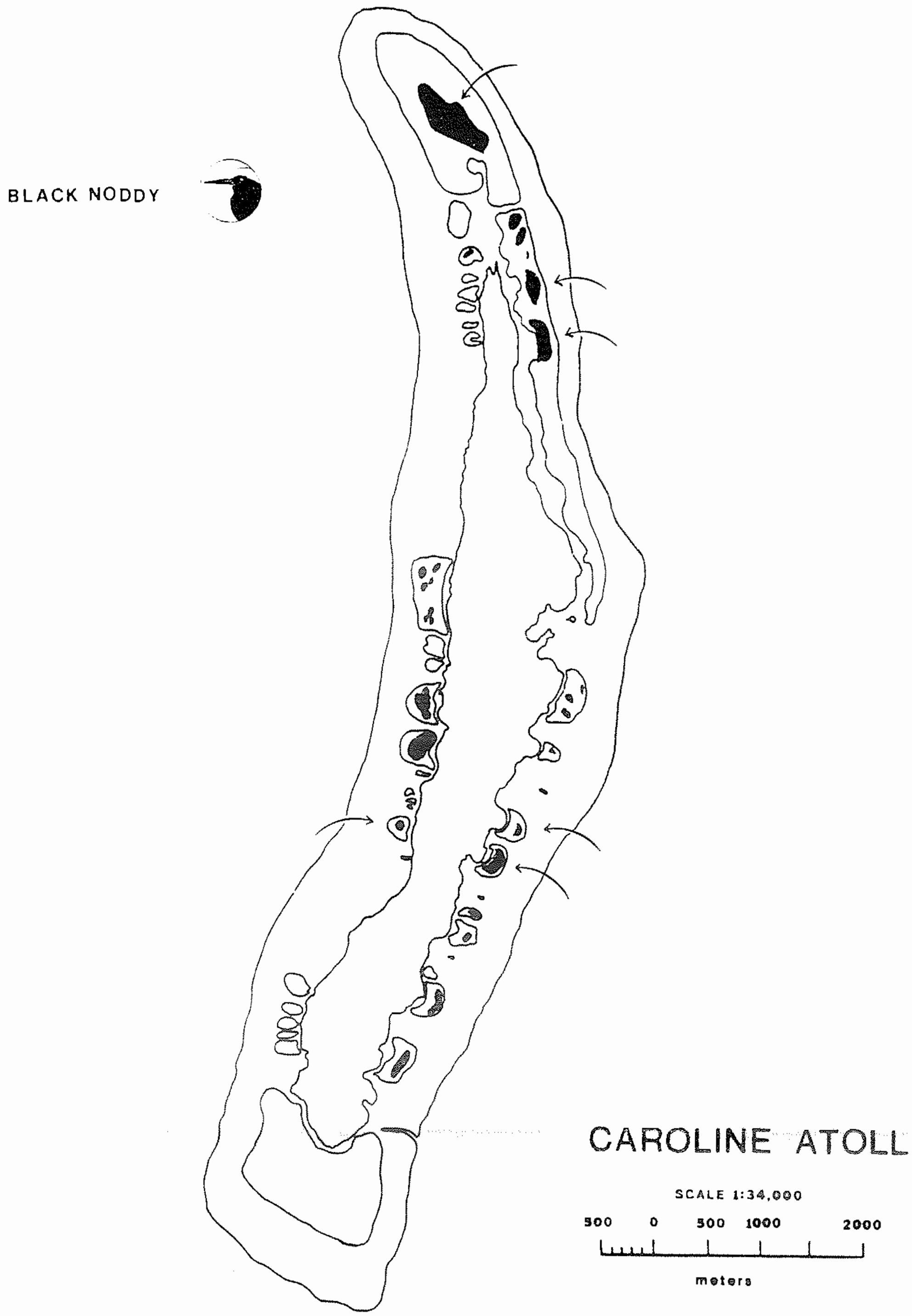

Figure 14. Distribution map of breeding Black Noddies on Caroline Atoll, September 1988.

could be added. These values place the Caroline population far above that for Christmas, making it the largest known population in Kiribati.

Phenology: Black Noddies were just beginning a new breeding season, as was also found in September 1974. On 27 September we observed hundreds of birds gathering *Tournefortia* leaves floating along the windward shore (Long) or flying with fresh leaves to their nests (Pig, North Pig). Of the 1,085 pairs counted on transect, 536 (49%) perched as pairs, were defending nest sites, or were building nests. An additional 273 pairs were attending nearly-completed nests but were not incubating. The remaining 276 pairs were incubating, thus 75% of the pairs had not laid eggs. The contents of 230 nests were unknown, although we assumed they contained eggs because of the incubating positions of the adults. Of 46 nests whose contents were visible, 45 held a single egg, and one contained a downy chick less than 5 days old.

The breeding seasons for Black Noddies on Christmas Island and Johnston Atoll peak in April and May (Schreiber & Ashmole 1970, Amerson & Shelton 1976), where pairs are highly synchronous, laying most of their eggs within a 2-3 month period. The Caroline colony, also synchronous, but beginning egg-production in September, would be expected to peak in October/November, 6 months out of phase with the colonies further north. In 1990, however, Black Noddies were just beginning to mate and nest in March, and by May some were still sitting tightly on nests, while others had chicks in all stages. This was most likely the result of the stormy weather which affected all seabirds.

BLUE-GRAY NODDY (*Procelsterna cerulea*)

Blue-gray Noddies nest widely across the Pacific from the Kermadec Islands to Hawaii. They are scattered throughout the Line and Phoenix Groups. In the Line Islands, they were formerly known to breed only on Christmas and Malden (Perry 1980). Eggs are placed in nests minimally provided with twigs and may be on coral rubble, sheltered under vegetation, or under coral slabs to depths of one meter (Rauzon et al. 1984).

The Blue-gray Noddy was recorded as "present" on Caroline by Perry (1980). Clapp & Sibley (1971a) noted birds over the lagoon but saw none on land. When we approached Caroline, we saw 2 from the ship and later observed 3 flying across the lagoon. We also saw 3 birds perched on reef flats of the leeward motus Nautonga and Eitei. A third bird flushed repeatedly from a small clearing around a pile of bottles on Raurau, but we failed to find a nest. In March and May 1990, we observed Blue-gray Noddies on all of the Southern Leewards, plus Azure and Nautonga in the Central Leewards.

In summer 1990, Alexandre Falconer, resident on Caroline at that time, found one small chick, attended by its parents, on an open expanse of coral rubble on Motu Eitei, the first breeding record for Caroline. Eitei is adjacent to Raurau, which we predicted was the most likely breeding location for this species.

Blue-gray Noddies must breed in very small numbers on Caroline. Nests are hard to find, given their cryptic placement, the small number of birds present, and the extent of open habitat (67.7 ha of herb mats and 41.4 ha of consolidated coral rubble). F. Sibley (pers. comm.) suggests that Blue-gray Noddies are extremely vulnerable to predators, since they were observed on 12 of 20 islands visited in the Line and Phoenix Groups, but nested on only three. Where they did nest, Blue-gray Noddy colonies contained hundreds or thousands of birds.

WHITE TERN (*Gygis alba*) Fig. 15, Pl. 3

The White Tern is a widely-distributed pantropical species occurring in moderate numbers throughout the Line and Phoenix Groups. Perry (1980) estimated 17,050 birds for the Line Islands, and Clapp (1967) estimated 10,000 birds in the Phoenix Group.

Distribution and habitat preference: White Terns, the most widely distributed breeding bird on Caroline, nested on 32 of the 39 motus (Fig. 15), avoiding only those which were tiny and sparsely vegetated.

White Terns nested from one to 15 m above ground, wherever a branch or frond provided a relatively stable platform in *Tournefortia* (Pl. 3), *Pisonia, Cordia, Pandanus* (Pt. I, Pl. 35), or *Cocos*. They did not form dense colonies but were scattered throughout each motu, normally selecting sites sheltered from the prevailing trade winds. They utilized isolated trees, scrub, or forest. An unusual departure from the White Tern's usual mode of "nesting" was an egg laid in an old Black Noddy nest, 6 m up in an 8-m-tall *Tournefortia* on Tridacna Islet.

White Tern densities varied from islet to islet (Table 7). At one extreme we found only 2 nests on Raurau (0.07/1,000 m^2). Densities on

Table 7. Density of White Terns on occupied islets by islet group, Caroline Atoll, September 1988.

Islet Group	# Islets	Vegetated Area (ha)	# White Tern Pairs	Density (pairs/ 1,000 m^2)
Nake	1	66.63	1,094	1.64
Long	1	49.60	751	1.51
South	1	86.10	381	0.43
Windward Islets	9	36.09	1,164	3.23
South Nake Islets	6	8.50	122	1.44
Central Leeward Islets	9	33.56	408	1.22
Southern Leeward Islets	4	6.47	37	0.57
All Occupied Islets	31	286.88	3,957	1.38

Figure 15. Distribution map of breeding White Terns on Caroline Atoll, September 1988.

other islets ranged from 0.75/1,000 m^2 (Shark) to 6.67/1,000 m^2 (Nautonga) with a mean density of 1.38 pairs/1,000 m^2 of woodland. Overall, the lushly vegetated Windward Islets supported the highest densities. Although White Terns also nested in anthropogenic forests, their densities were low: we believe that their low densities on South Island and the Southern Leewards (Table 7) are attributable to man. Of South's 104.47 ha of vegetated land, only 4.2 ha (4.4%) was native woodland (Pt. I, Fig. 50); fully 84% was either *Cocos* (18.3 ha) or dying *Cocos-Ipomoea* (62.5 ha) forest. Although most of the Southern Leewards are covered in virgin forests, central Ana-Ana has been partly cleared (0.21 ha) to accommodate thatched huts and a garden. The activities of a family of 4, with a dog and cat (until October 1990), apparently depressed the White Tern population on Ana-Ana and, perhaps, even on nearby islets. We found no White Terns on Ana-Ana during our visit, although the Falconers, who vacated the atoll in summer 1991, assured us that they occasionally nested.

<u>Numbers</u>: We used the total woodland area of each islet, coupled with transect data, to calculate bird populations (Table 1). More birds were found on the largest islets except South Island (see above). We estimated 1,094 pairs for Nake, 751 pairs for Long, and nearly 400 pairs for Tridacna; these 3 islets accounted for over half the population (and over half the indigenous woodlands). We estimated that 3,957 pairs bred on Caroline, which doubles the numbers of Clapp & Sibley (1971a) and Perry (1980) and exceeds by 3,000 the largest population formerly known for the Line Islands.

<u>Phenology</u>: Of 569 pairs of White Terns recorded on transect, 437 were roosting without obvious signs of eggs or chicks, 107 were incubating, and 25 had chicks (often adults were not present). Of the 25 chicks recorded, 17 were downy, 7 retained extensive traces of down with remiges, and one was almost ready to fly. Incubation takes about 36 days (Ashmole 1963); young may require from 40-96 days to fledge (Gibson-Hill 1950, Ashmole 1968). Nearly all chicks were less than 4 weeks old.

On Christmas Island, Schreiber & Ashmole (1970) found that peak laying occurred in April-August each year, with some laying in each month. On Caroline, Clapp & Sibley (1971a) noted that about half of the birds had eggs, half had young in June 1965. In September 1974, White Terns had eggs only (Grossman & Grossman 1974). In March 1990, we found very few eggs and downy chicks, but in May a larger number of pairs were breeding, with eggs and chicks in all stages. Again, the February storm had most likely interrupted breeding activities, as only 2 juveniles were found on the windward side. These were in the interior *Pisonia* forests of Brothers and North Brothers Islets, which suffered less damage than motus further north. Therefore, although White Terns on Caroline do lay during the peak period on Christmas Island, laying appears to be heaviest after mid-August.

D. OTHER BIRDS ON CAROLINE ATOLL

Seven species other than seabirds have now been recorded on Caroline. Six of them are migrants (5 shorebirds and Long-tailed Cuckoo). The few shorebirds encountered (except for Bristle-thighed Curlews) and their lack of increased numbers in the fall suggest that there is only a small migration to Caroline. The Reef Heron is apparently resident, although no nest has been found.

REEF HERON (*Egretta sacra*)

We found 15 Reef Herons scattered on 8 islands: Nake (1), Long (2), Pig (1), Brothers (3), South (2), Mannikiba (2), Matawa (1), and Emerald (2), as well as on the open reef flats (1). Although birds were found on both the seaward and lagoonward sides of the islets, most were along the lagoon edge, as also found by POBSP in 1965 (Clapp & Sibley 1971a) and the Grossmans (1974). We estimated that approximately 30 birds were using the atoll. We found no signs of breeding. Of the 15 individuals we observed, 5 were dark, 8 were white, and 2 were of the pied morph.

LESSER GOLDEN-PLOVER (*Pluvialis dominica*)

This plover used the beaches and herb mats, generally to seaward. In September 1988, we found them on Nake (1), Long (4), Tridacna (4), and Mannikiba (1), estimating a total population of 20-30 birds, the same number found by POBSP (Clapp & Sibley 1971a). In March 1990, we observed 8, and in May, 3, all in winter plumage. In September 1974, 3 were seen on the windward coast (Grossman & Grossman 1974).

WANDERING/GRAY-TAILED TATTLER (*Heteroscelus incanum* or *H. brevipes*)

In September 1988, we located 18 tattlers on 6 different islets: Nake (3), Long (3), Crescent (1), Arundel (2), South (7), and Emerald (2). All birds were either alone or in pairs and generally remained in the intertidal zone, although they often foraged on herb mats close to the beach scrub. The total population was approximately 40 birds. Those few birds heard were all *H. incanum*. We saw 6 tattlers in March 1990 and several in May of the same year. The Grossmans (September 1974) observed 12 on the windward coast and around the lagoonward shore of the windward islets and South.

RUDDY TURNSTONE (*Arenaria interpres*)

One turnstone was found on the windward beach of Motu Mannikiba in September 1988, and 5 on atoll beaches in March 1990. The Caroline population probably does not exceed 15 birds.

BRISTLE-THIGHED CURLEW (*Numenius tahitiensis*) Pt. I, Pl. 22

The Bristle-thighed Curlew, common in the Line and Phoenix Groups, is a widespread migrant to atolls of the Central and South Pacific during the boreal winter (Pratt et al. 1987). The species is considered rare (Johnsgard 1981, Marks et al. 1990) and is a candidate for the U.S. Fish and Wildlife Service Endangered Species List (Gill 1990). Clapp & Sibley (1971a) estimated 20 birds for Caroline Atoll in June 1965; the Grossmans (1974) saw 4 on the windward coasts.

We counted 83 birds on 12 of Caroline's islets in 1988, including the 3 large islands (Nake, Long, South) and motus in the Windwards, Central Leewards, and Southern Leewards. In March 1990, we saw 20 curlews on 10 islets during incidental observations throughout the atoll, bringing the total number of islets on which they have been recorded to sixteen (41%). On our return trip (May 1990) we only saw 3 curlews (8 motus visited). Undoubtedly, curlews occur throughout, utilizing essentially all plant communities (for details, see Pt. I, Sect. E). Although they are most conspicuous on the beaches and reef flats, higher numbers may actually forage inland during the day. Small numbers of curlews remain all year, being least common from April to August and most abundant after September/October (R. and Anne Falconer, pers. comm.). This correlates with preliminary information from Rangiroa Atoll, Tuamotu Archipelago (Gill 1990; Gill & Redmond, in prep.).

Unvegetated perimeter habitats: On a complete perimeter count of South Island in 1988, we found 29 curlews. Twenty-one were foraging and loitering on the windward east coast, principally above the beach crest on coral rubble interspersed with herb mat. Similarly, 14 of 20 curlews found on Long and the Windward Islets foraged along the windward beach crest, with only 6 birds found on the lagoonward shores. Curlews were equally common on windward and leeward shores in the leeward islets, occupying habitats composed of coral rubble and sand. While the numbers indicate that curlews preferred windward shores, they may be biased because most birds were seen there in the late afternoon (13, 14, 19). Perhaps they use the relatively open areas for roosting and foraging at dusk. Our largest flock (14, Sandy Inlet, Nake) was found at 16:00, foraging on compacted, silty sand at the lagoonward end of the inlet, while single curlews dotted the interislet channels and shallow tidal reef flats (Pt. I, Pl. 22).

Vegetated habitats: We found Bristle-thighed Curlews on natural herb mats, in *Tournefortia* scrub, *Pisonia* forest, and in *Cocos* habitats, both in the healthy peripheral plantations and within the dying *Cocos-Ipomoea* woodlands (Pt. I, Fig. 36, Pl. 34). One was captured in a mist net under a dense *Cocos* canopy. Disintegrating plantations in the center of South (54 ha) held a large population: calculated numbers produced an estimate of 154 curlews. They foraged over the *Ipomoea*-strewn ground (interspersed with *Boerhavia* and *Phymatosorus*), frequently using broken-topped coconut trunks as lookouts. We also found 5 curlews on transects in *Pisonia* forests up to 20 m tall on Nake (calculated population, 41). They were foraging on the relatively open, although dimly lit, forest floor (Pt. I, Pl. 42).

Numbers: From the 1988 data we estimated a population of 300± curlews: 41 birds in *Pisonia*, 154 in *Cocos-Ipomoea*, 43 on the beaches of South, 14 at Sandy Inlet, Nake, and 62 scattered over the remainding motus. Because 154 were calculated from a single flock of 7 curlews on one transect on South, there may be a bias in our population estimate. However, this habitat covers 80 ha, 77% of South's total area, and incidental observations made off-transect indicated that curlews commonly foraged in *Cocos-Ipomoea* woodlands. We believe that our estimated density, about 1.5 birds/ha, is reasonably correct.

Bill length: Bristle-thighed Curlews show great variation in bill length immediately after the breeding season. Because birds of the year migrate south before their bills reach adult length (R. Gill, pers. comm.), the ratio of "long" to "short" bills provides a rough estimate of juvenile survival. Of 31 curlews seen in September, 20 were clearly adult length, 7 were conspicuously shorter, and 4 were "intermediate" (probably young birds). All March and May birds had long, adult-sized bills.

Some subadults remain on their Pacific wintering grounds for up to 3 years, during which time they pass through a flightless phase (Gill 1990, Marks et al. 1990). No flightless birds were seen.

Foraging: We saw one curlew chase and capture a small Polynesian rat at dusk on the south shore of South Island. The bird bashed the rat on the coral rubble, then ran rapidly about with the rat dangling from its bill. After about 5 minutes, the bird swallowed the rat with vigorous gulps.

Polynesian rats, abundant on Caroline (especially in *Pisonia* and *Cocos*-dominated habitats), remain within the forest during the day, but many move to the beach crest and tide line at dusk. They provide abundant potential prey for curlews, which can easily capture them on the open rubble. The synchronous appearance of rats and curlews at the beach-woodland interface at dusk may be part of the foraging strategy of this large shorebird. The presence of curlews beneath the forest canopy may also be partly associated with this source of food.

SANDERLING (*Crocethia alba*)

One Sanderling in winter plumage was seen at water's edge on the windward beach of Long Island on 27 September 1988. Although Sanderlings are well-known fall migrants in the Line and Phoenix Islands (Clapp & Sibley 1967, 1968), this is the first record for Caroline Atoll.

LONG-TAILED CUCKOO (*Eudynamis taitensis*) Fig. 16

The Long-tailed Cuckoo breeds in New Zealand and winters in the southwest Pacific. The center of its winter range lies in central Polynesia, but birds have been recorded as far as Palau in the northwest and Pitcairn Island in the southeast. Although occurring throughout French Polynesia and the Cook Islands, it had not been recorded from the Line Islands prior to our expedition (Bogert 1937; Clapp & Sibley 1971a, 1971b; Pratt et al. 1987; Ellis et al. 1990).

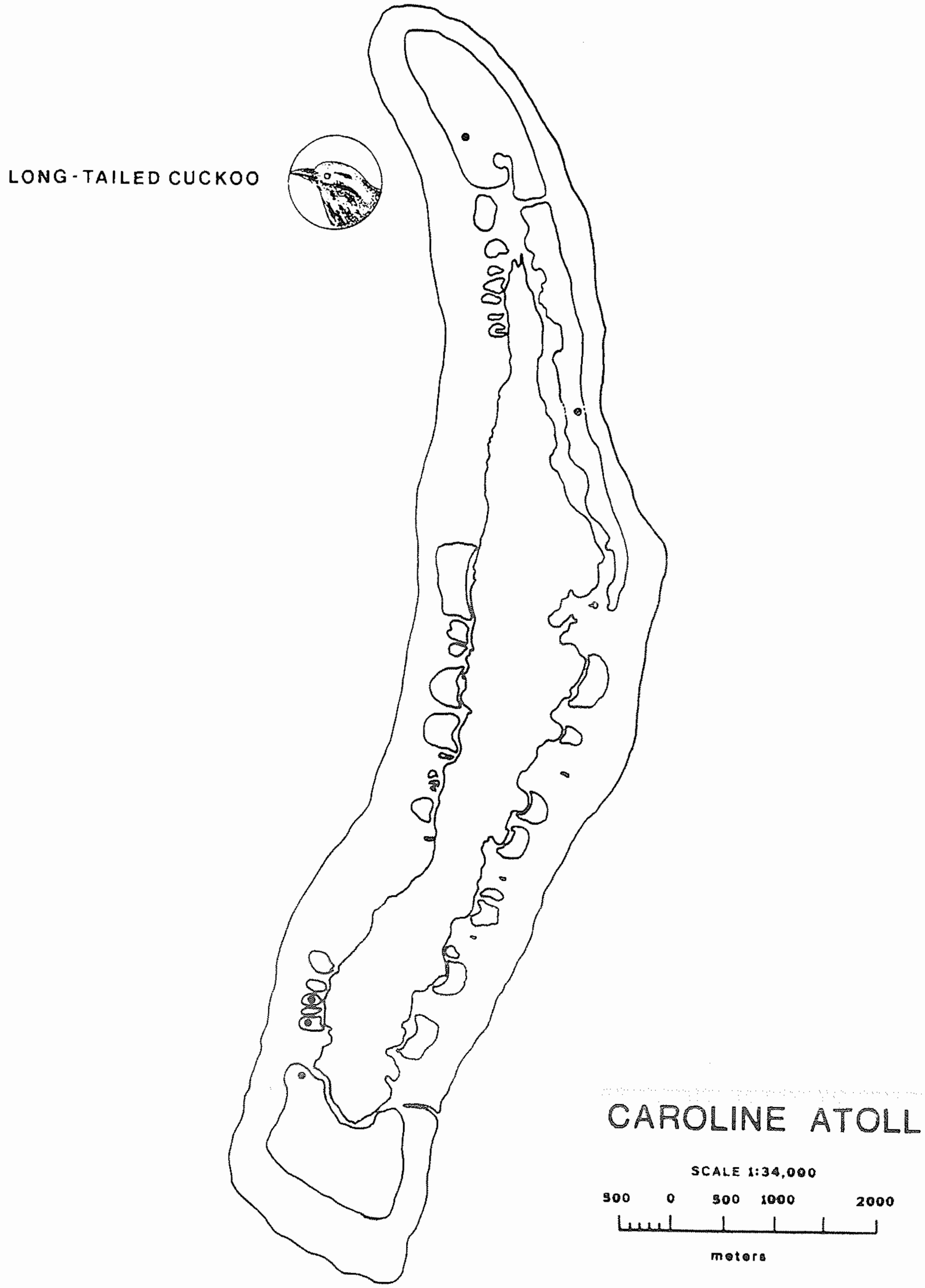

Figure 16. Preliminary distribution map of the Long-tailed Cuckoo on Caroline Atoll. The species most likely utilizes all well-wooded motus.

We found Long-tailed Cuckoos on 4 of Caroline's 39 motus (Fig. 16). We heard its distinctive mono- and disyllabic call notes on South, Long, and Pisonia, identified one on Nake, and on 28 September collected a male in a mist net on Transect 4, Long Island (USNM 607191). Soon after our return home we sent a description and photograph of this species to the Falconers: they, and AKK, have since seen them several times on Motu Ana-Ana in March, April, and May 1989-90.

All the cuckoo sightings were at canopy or subcanopy level, and 3 of the 4 1988 birds were in *Pisonia* forests. The individual on South foraged in a *Cocos* canopy 21 m tall. The netted male flitted secretively within an undisturbed, tangled low-canopy (4-6 m) *Pisonia-Tournefortia* interface. We suspect that this elusive migrant occurs throughout the mid-to-upper levels of Caroline's forest canopy.

These records establish the Long-tailed Cuckoo as a winter visitor to Caroline Atoll. Our observations on 4 motus in 8 days, including the southernmost, northernmost, windwards, and leewards, indicate that many individuals were present. A March 1990 first sighting on Vostok (J. Phillips, pers. comm.) further suggests that the species disperses regularly to the Southern Line Group.

E. OTHER VERTEBRATES

Lizards

Although "small lizards" were observed on Caroline in 1825 (Paulding 1931), it wasn't until 1965 that the first collections were made (Clapp & Sibley 1971a). We collected 4 lizard species, increasing the known terrestrial herpetofauna from 3 to 6 (Table 8). Although all are indigenous, the azure-tailed skink (*Emoia cyanura*) is particularly widespread in Oceania, and is suspected of being partly dispersed by man (Brown 1956, Crombie & Steadman 1986). Recent data from Flint suggest that *E. cyanura* may have been introduced by Tahitian copra laborers this century (Kepler, in prep.). The same situation may be true on Caroline, especially since this easily-indentifiable species was not seen or collected by POBSP personnel in 1965 (Table 8). All but 2 of the lizard species known from the Line Islands (Crombie 1990) have now been found on Caroline. It is perhaps noteworthy that we added 3 species to the atoll list but failed to find 2 species collected in 1965. Since both groups collected lizards opportunistically, rather than systematically, there is evidently much need for further study in this area.

Turtles

We found 3 Pacific green sea turtles (*Chelonia mydas*), a threatened species (McKeown 1978), at Caroline in 1988. Two were swimming over the lagoon reef flats, one west of Arundel, the second east of Ana-Ana. The third was in the open sea about 100 m west of South Island near the "boat entrance." Ron Falconer has seen up to 7

Table 8. Lizards collected on Caroline Atoll, 1965-1988.

Species	Specimens: Clapp & Sibley 1971a	Present Study
Mourning gecko *Lepidodactylus lugubris*	USNM 158355-57	USNM 299773
Polynesian gecko *Gehyra oceanica*	USNM 158353-54	--
Snake-eyed skink *Cryptoblepharus poecilopleurus*	--	USNM 299772
Moth skink *Lipinia noctua*[1]	USNM 158358	
-- *Emoia impar*		USNM 299768-70
Azure-tailed skink *Emoia cyanura*	--	USNM 299771

[1] USNM 158358 has recently been reidentified by R. I. Crombie as *Lipinia noctua*, not *Emoia nigra*, as reported in Clapp & Sibley (1971a).

turtles in the lagoon in a single day. In April and May 1990, AKK saw workers from Tahiti capture and kill a minimum of 4 green turtles in the lagoon, and 2 more were in fishtraps on our departure. Two others entered the lagoon during the following 4 months (R. Falconer, pers. comm.).

In March 1990, AKK and G. Wragg found 3 old nests, presumably of this species, on the northwest coast of Nake within 100 m of the northern tip of the islet. These are the first known turtle breeding records for the atoll. Young (ca. 1922) notes that the copra plantation laborers ate green turtles from September to December each year, and members of the Line Islands Expedition (Grossman & Grossman 1974, Vickers 1974) saw fresh turtle tracks either on South or Nake. The February 1990 storm added large amounts of sand to Caroline's shorelines, providing potential new habitat for turtle nesting.

Terrestrial Mammals

None of the terriers (see Pt. I) that were introduced to control rats on South Island early this century (Young ca. 1922) have survived (F. Sibley, pers. comm.; R. Falconer, pers. comm; pers. obs.). In May 1990 the Falconers kept a dog and cat on Motu Ana-Ana. The dog regularly visited all the Southern Leewards and accompanied the family in their sailing canoe throughout the atoll. As a result of our recommendations, the cat was removed from Caroline in October 1990. The dog, with the family, vacated Caroline in summer 1991.

Bennett (1840) noted "rats of a red-brown color," the first reference to rodents on Caroline. Dixon (1884) found that rats were "not numerous" and that they nested "just at the base of the fronds" of the coconuts. Two specimens collected by the POBSP proved to be *Rattus exulans* (Clapp & Sibley 1971a), an uncommon mammal restricted to South Island.

The 19th and 20th century settlers found rats (presumably *R. exulans*) to be extremely abundant and very destructive to the coconut plantations; they contributing greatly to the twice-abandonment of copra enterprises on Caroline (Young ca. 1922, Maude ca. 1938). They voraciously devoured both growing and fallen nuts, as well as dried copra. Being arboreal, they also lapped the juices of the flower stalks, preventing nut development. In 1920 alone, over 4,600 were trapped on South (Maude ca. 1938). Thousands more were killed by terriers introduced in a vain attempt to control them.

We found rats on almost every islet, especially in or near coconut palms and *Pisonia* trees. We recorded them during daylight hours on most transects. Each night at our campsites on Long and South we noticed groups of 10-20, so tame as to approach within one meter while we were eating. Rats evidently undergo wide population fluctuations, as they were less abundant in March and May 1990 than in September 1988.

We suspect that rats periodically reach most motus, and that those apparently lacking rats (such as Noddy Rock) are too small and/or depauperate to support a resident population. Because *R. exulans* is a known seabird predator (C. Kepler 1967, Fleet 1972, Norman 1975), the restriction of some species (i.e. Red-tailed Tropicbird) to small islets may be due to rat populations on larger islets.

Rats were an abundant nuisance on Ana-Ana; the Falconers trapped over 1,300 animals in 2 years and, like the pioneers before them, relied upon a dog to help keep them at bay.

Marine Mammals

On March 14, 1990, members of the Line and Phoenix Islands Expedition observed a minimum of 10 Pacific bottlenose dolphins (*Tursiops gilli*) in the open sea about 500 m off the southeast corner of South Island.

F. COCONUT CRABS

The coconut crab (*Birgus latro*, Coenobitidae), the largest terrestrial invertebrate on earth, ranges throughout the tropical Indo-Pacific (Pt. I, Pl. 21). It is highly esteemed as a source of food throughout its range, and for this reason is rare or absent on or near most inhabited islands. Because it is heavily exploited by man, it is under consideration for endangered species status (E. Reese, pers. comm.).

Since March 1990, dozens of Caroline's coconut crabs have been killed for food and for preservation in formalin as curios for the Tahiti tourist market. Because of the increasing numbers of visitors to Caroline, it is important that Caroline's coconut crabs receive protection.

History: A Californian malacologist, C. D. Voy, was the first to collect coconut crabs (*Birgus latro*) on Caroline in 1875 (Pilsbry & Vanatta 1905). They are not mentioned again until 1910, when Young (ca. 1922) wrote that "hundreds of great Coconut Crabs were seen: 40 large ones were caught by the crew of the schooner in an hour" on South Island. Young also noted that coconut crabs were considered a great nuisance by plantation laborers, who killed them mercilessly. Evidently they dug up newly planted nuts and snipped off emerging shoots. On smaller motus, visited less frequently than South, Nake, and Long, these depredations were difficult to control. Thus the small motu plantations were abandoned soon after initial planting, resulting in a remarkably rapid recovery of the original vegetation (see Pt. I, Sect. G). Today large crabs once again burrow beneath the boles of well-maturing *Pisonia* forests which their ancestors helped recreate less than 70 years ago.

It is hardly credible that these enormous crabs, the dominant terrestrial animal of the atoll environment, could have been overlooked by almost all visitors prior to the 20th century. The only plausible explanation is that coconut crab populations were reduced drastically each time Caroline was inhabited: 1846 to at least 1852, 1885 to 1901, and 1916 to 1929. Voy collected them in 1875, 10 years before initial land clearing began; Young noted them in a 1910 visit 9 years after the first abandonment of the plantations, and again from 1916 on when copra enterprises were begun anew. From 1916 to 1920 land clearing was far more extensive, involving most of the area of the Windward Islets and Nake (Pt. I, Table 13), and thus a very large number of homeless coconut crabs would have been evident at that time. Again, mass slaughter reduced their numbers until the main group of copra-cutters left in 1929. Since then, occasional Polynesian and other visitors have taken crabs, but since the island was basically uninhabited for 60 years, their numbers have recovered substantially. "Great numbers" were seen in 1974 (Gilbert and Elllice Is. Govt. 1974). However, activities since 1990 do not bode well for the species (see Sect. G). It is of interest in this regard that members of the 1934 Mangarevan Expedition saw no coconut crabs on nearby Flint Island (R. Fosberg, pers. comm.), nor were they mentioned in an historical summary paper on Flint by Maude (ca. 1942), but some were found at the southern tip of the island in 1906, which at that time was covered in virgin mixed broadleaf forest, including large *Pisonia grandis* trees, within whose boles the crabs burrowed (E. Campbell 1908; A. Kepler, in prep.). Today Flint has perhaps the greatest density of coconut crabs in the world (A. Kepler

1990b). Human pressures have likely operated on Flint as on Caroline (A. Kepler, in prep.).

Distribution and habitat preference: In 1988 and 1990, coconut crabs were abundant in the *Cocos* plantations of South and Nake, and present, in varying densities, on 12 other motus (Fig. 17). Although generally associated with *Cocos*, we found them in woodlands of *Pisonia, Cordia*, and *Tournefortia*, as well as on rubble beaches (especially after dusk). Although capable of surviving without coconut palms, these crabs appear to seek them out. In the open understory of the tall plantations, or in groves of only one or 2 palms, telltale piles of shredded coconut husk fibers (Pt. I, Pl. 53) disclosed the crab's presence.

Because the prevalent coarse rubble substrates on Caroline are hard to burrow into, coconut crabs occupied a variety of shelters: mounds of fallen coconuts and rotting palm fronds (to 1.5 m high), piles of rubble pushed against tree roots, sand burrows, tunnels within the *feo* (Pt. I, Pl. 21), or large cavities in the boles of mature *Pisonia* trees. Coconut crabs also use a variety of shelters on the Tokelau Islands (Yaldwyn & Wodzicki 1979), Flint, and Palau (AKK, pers. obs.).

Numbers: Though conspicuous and slow-moving, coconut crabs are very difficult to count. Environmental variables such as rainfall, tide, lunar cycle, and population size and age classes all affect their activity (Reese 1965; Helfman 1977a, b). Although unable to conduct mark-recapture studies, we did make incidental observations on the numbers of individuals seen during transect and perimeter surveys. Coconut crabs are generally nocturnal, but we often found them during daylight, at times exposed on coral gravel beaches close to the waterline. E. Reese (pers. comm.) suggests that the abundance of rats occupying the same habitat may "force" the crabs to be more diurnal, as has been reported from the Indian Ocean. Our estimate of the population on Caroline is approximately 2,200 individuals, based on the number of daytime observations, the area covered, and the fact that only one out of every 3 or 4 individuals may be present on any given night (Helfman 1977b, Reese 1987).

Foraging: Since the first detailed description of coconut crabs in 1705, their shy, curious habits have been the subject of folklore, speculation, and misinformation (see Reyne 1939). No scientist has yet published a documented account of a coconut crab actually opening a coconut (Helfman 1979), which is widely held to be their consummate foraging behavior. Helfman is convinced that they do so, as he has found piles of coconut fiber and observed crabs walking with husked, opened nuts in places where he was the only other possible coconut husker. We repeat Helfman's (1979) assertion that coconut crabs *do* husk fallen coconuts. The piles of finely separated fibers (Pt. I, Pl. 53) we encountered are totally different from those produced by stick or machete husking, the 2 methods commonly employed by Pacific peoples. The crab tears virtually every fiber off individually, a process so painstakingly slow it probably takes days. We did not observe this on Caroline, but in March 1990 AKK, on uninhabited Flint Island, observed a large male coconut crab that had just husked a coconut and was enlarging

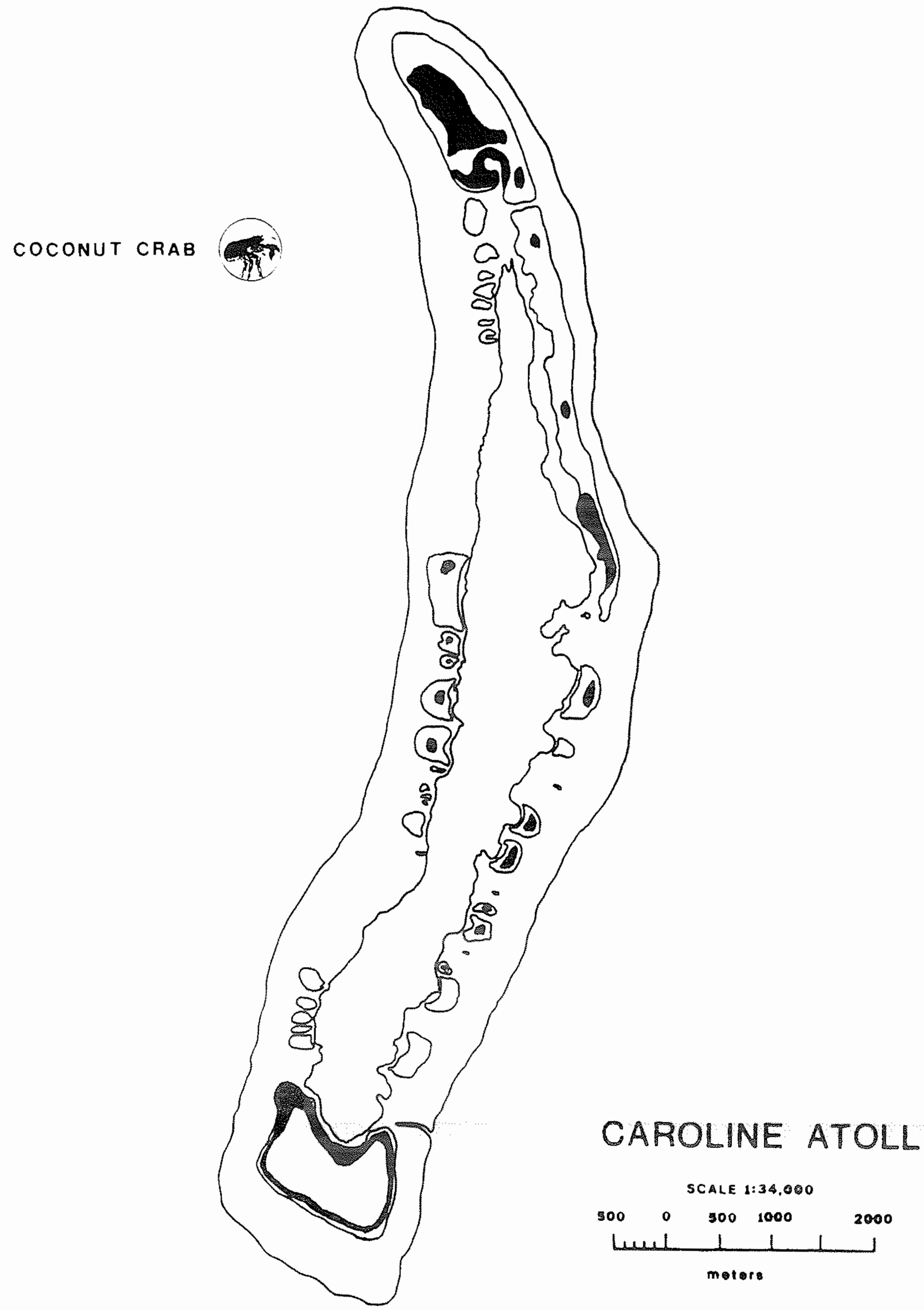

Figure 17. Distribution map of coconut crabs on Caroline Atoll.

a small crack in the center of the smooth nut in a manner similar to that described by Gardiner (1907) in Reyne (1939, p. 297). In June 1992, AKK also encountered large males eating coconut meat and husking fibers in the Southwest Palau Islands, Micronesia.

On Caroline we observed the aftermath of coconut crab-Sooty Tern predation or scavenging. On Brothers Islet, several entrances and pathways leading to coconut crab holes were strewn with the feathered skeleta of adult Sooty Terns (and possibly Brown Noddies), along with numerous, freshly snipped branches of *Pisonia* up to 0.7 m long (Pt. I, Sect. H). This was also recorded on Tridacna Islet by Clapp & Sibley (1971a) for Sooty Tern eggs and chicks, and by Helfman (1979) and Reese (1987) on Enewetak, Micronesia.

Sizes: Living in a rich environment free of predators, coconut crabs attain huge sizes on Caroline. The bodies of the largest males were as wide as a full-sized, unhusked coconut, giving them weights of at least 4 kg (G. Helfman, pers. comm.). Thorax widths for 10 crabs (2 females with eggs, 8 males) averaged 129 mm. The thorax of the largest male measured 200 mm across, making it, along with many measured on Flint in 1990 (A. Kepler 1990b), one of the largest recorded coconut crabs in the world (the previous record was 178 mm in Helfman 1977a), with an age estimated to exceed 40 years (E. Reese, pers. comm.).

G. CONSERVATION: ATTRIBUTES OF INTERNATIONAL SIGNIFICANCE

Caroline's exceptional attributes need to be elucidated, for the atoll has remained essentially unknown, even to some who have evaluated its worth (King 1973; Stoddart 1976; Garnett 1983, 1984). There are few, if any, islands remaining in the Pacific that can claim the impressive array of natural features exhibited by Caroline (Nicholson & Douglas 1969). We believe that it is imperative that this atoll, which has managed to escape large-scale, permanent human disturbance, should remain undeveloped.

Currently Caroline is uninhabited and has been since ca. 1930 except for a single family from 1987-1991. There are no roads, vehicles, stores, jetties, or services (water, sewage, or food), and no communication. There is no passage into the lagoon or safe sea anchorage.

Lack of Major Disturbances

Man's presence anywhere--especially on pristine or near-pristine islands--generally brings rapid, often irreversible, changes. One of the most important of Caroline's attributes is its relative lack of disturbance and very few exotic plant species. Aside from obvious human impacts on South, Nake, and Ana-Ana, the majority of its motus are dominated by indigenous vegetation and its reefs are basically pristine. There is no obvious pollution to alter the chemistry of the lagoon, beyond the flotsam and jetsam that litter the beaches. It is thus an exceptionally clear and clean ecological laboratory that presents a lagoon ecosystem before extensive disturbance by man, providing marine biologists with opportunities to study undisturbed natural communities; for example, the maze of patch reefs in the lower half of the lagoon has the highest recorded density of living *Tridacna* (20/.25 m^2) ever recorded (Sirenko & Koltun 1992). This is one of the few undisturbed world populations of this species (Pt. I, Pl. 25). In addition to conventional ecological studies, biomedical research could investigate the causes and treatment of ciguatoxicity of fishes and crabs. Such topics are increasingly important as more islands are subjected to disturbance and pollution. For example, the abundant red snapper (*Lutjanus vaigiensis*) and red spotted crab (*Carpilius maculatus*), both notoriously poisonous, are safe to eat on Caroline. Caroline, lacking the problems and pollution that beset many other Pacific islands, could serve as a "control island."

Terrestrial Ecosystems

Caroline's motus of varied age and size classes provide excellent examples of substrate and vegetation development, accompanied by an increasing diversity of bird life. On account of its relatively low human disturbance and rapid forest recovery, especially since 1920, Caroline is thus also an outdoor laboratory for terrestrial ecosystems: many motus have recovered so remarkably they are almost indistinguishable from those which have remained pristine, while others are in different stages of recovery resulting from varied management (or non-management) practices.

Caroline's concentric pattern of plant community development and the relationships of these communities to motu size, shape, and location on the atoll rim could continue to provide insight into evolutionary processes on atolls that are left undisturbed.

Physiography

Caroline offers many opportunities for geological research, under reasonably unmodified conditions. Valuable clues as to the nature of underground water supplies may lead to a better understanding of the regulation of water supplies on inhabited islands. Notable physiographic features include inland upraised reefs (*feo*) and deep sand deposits, coalesced islets, exposed older reefs, lithified beachrock, a conglomerate platform, a "perched lagoon," patch reefs, a nonfunctional *hoa*, and changes in motu size and shape during the past century.

Flora

Caroline's insular flora, typical of central equatorial islands in their natural state and covering 70% of the atoll's land area, is of both national and international importance. The 26 extant plant species are 89% indigenous (possibly 92%), an extremely high figure for anywhere in the world. Six of the 7 plant communities are natural. Lushly wooded, Caroline possesses tall *Pisonia grandis*) forests (Pt. I, Pl. 43), reaching 21 m and occurring on 29 islets. Although less majestic than the prime forests of Washington and Fanning (Northern Line Group)[1], which enjoy a heavier rainfall, those on Caroline are notable: Caroline's 62 ha of *Pisonia* forest may well cover a larger area than on any other Pacific atoll.

Caroline also possesses significant stands of the hardwood *kou* (*Cordia subcordata*), which ranges from Africa to Polynesia, but is now rare in the Pacific. Caroline's groves (Pt. I, Pl. 26), although small and often mixed with other indigenous trees, total 26 ha, possibly the greatest area on any Pacific atoll. The extensive presence of tree heliotrope (*Tournefortia argentea*) is also notable: scrub and forests of this species form 40% of the atoll woodlands (Pt. I, Pl. 47). Caroline's large groves are some of the most unmodified in the Pacific, as elsewhere *Tournefortia* is typically restricted to coastal fringes surrounding anthropogenic plantations (personal observations; Wiens 1962; R. Fosberg, pers. comm.).

Caroline, and its neighbor Flint, are also ideal islands in which to monitor the transition from *Cocos* plantations to a more natural state: rainfall regimes, intensity of management, underground water reserves, slightly differing plant communities, and a wide range of island/islet sizes have resulted in marked differences in revegetation pattern only 60 years after the atoll was abandoned.

Seabirds

Associated with Caroline's plant communities are 11 species of breeding seabirds numbering well in excess of 1,000,000 individuals. Almost every islet harbors nesting populations of up to 9 species (Fig. 18). The populations of most of these species are of national importance (Table 9). For example, Caroline has the fifth largest Red-footed Booby colony in the world. Its Black Noddy and White Tern (Pl. 3) populations are the largest in Kiribati. Under the 1975 Republic of Kiribati Wildlife Conservation Ordinance (amended in 1979), all known seabirds, migrant shorebirds, and endemic land birds are "fully protected throughout the Gilbert Islands" (Garnett 1983, p. 128). However, their protected status is in doubt on Caroline, due to attempts to commercially develop the island. Caroline deserves protection similar to the 5 closed areas on Christmas Island and the 7 island sanctuaries in the Line and Phoenix Groups (Garnett 1983), preferably accompanied by on-site enforcement.

[1] In 1992, these forests were evidently altered considerably by immigrant Gilbertese and cyclonic weather.

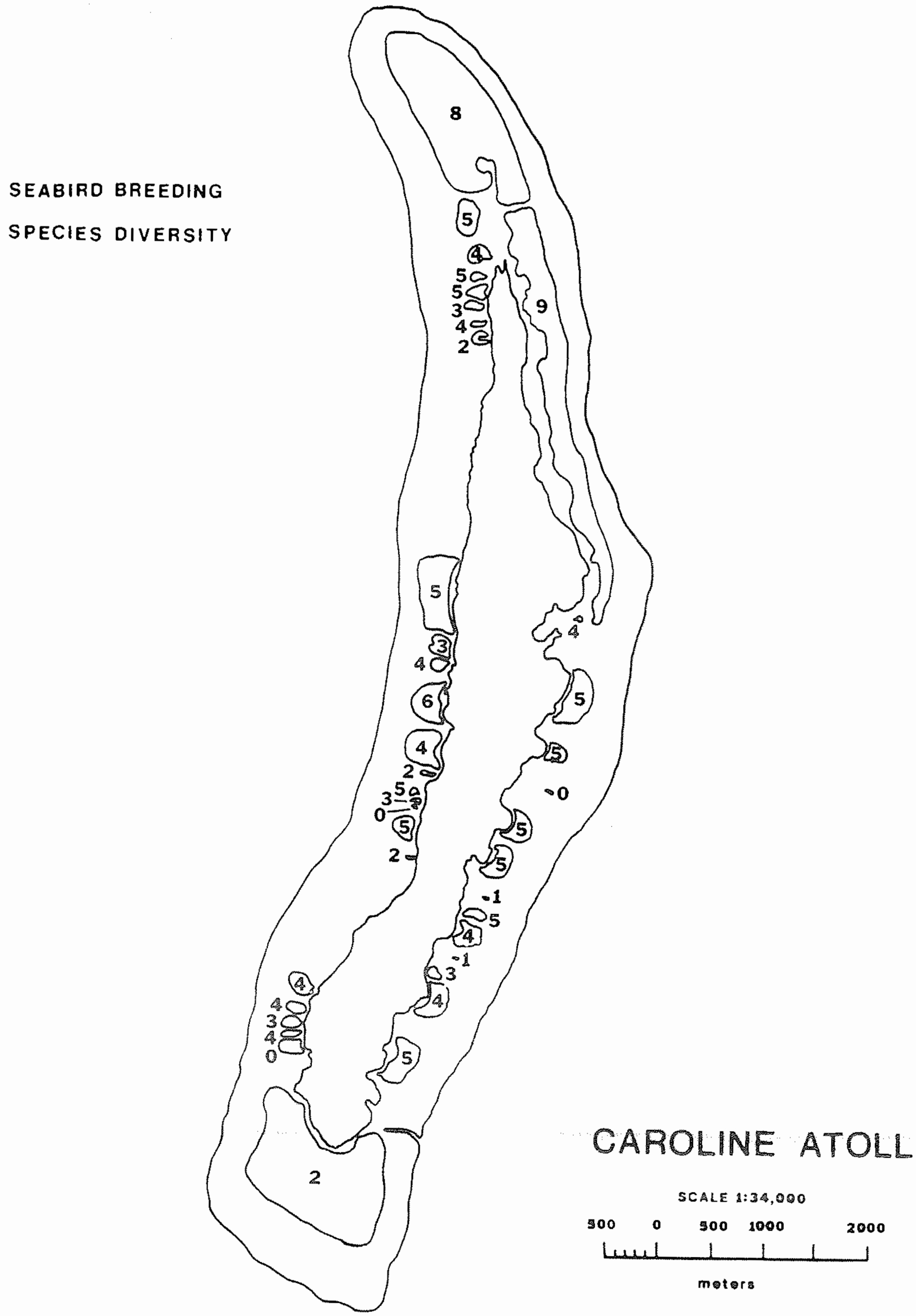

Figure 18. Seabird breeding species diversity by islet, Caroline Atoll.

Table 9. Comparative abundance of Caroline's breeding seabirds in the Line Group.

Species	Estimated Population	Comparative Abundance in the Line Group
Red-tailed Tropicbird	300[a]	Second largest population
Masked Booby	400	Fourth largest population
Brown Booby	40	Third largest population
Red-footed Booby	7,000	Third largest population
Great Frigatebird	6,100	Third largest population
Lesser Frigatebird	200+	--
Sooty Tern	912,000	Third largest population
Brown Noddy	3,000	Third largest population
Black Noddy	17,000	Largest population (largest in Kiribati)
Blue-gray Noddy	<10	--
White Tern	8,000	Largest population (largest in Kiribati)

[a] Based upon nest count in 1990.

Shorebirds

Caroline is an important wintering ground for the Bristle-thighed Curlew, a rare shorebird and candidate for the U.S. Fish and Wildlife Service Endangered Species list. Some subadults remain all year on the atoll. As adult curlews pass through a flightless phase on their Pacific wintering grounds, islands such as Caroline provide a predator-free environment for this vulnerable phase of their life history.

Coconut Crabs

Caroline is exceptional in harboring a robust population of coconut crabs (Fig. 17; Pt. I, Pl. 21). These large invertebrates are abundant in the *Cocos* plantations of South and Nake and are found in good numbers in the indigenous *Pisonia* forests on most larger motus.

Turtles

Although green turtles are not abundant on the atoll, worldwide populations of these marine reptiles have suffered so greatly from overexploitation that remote, predator-free islands such as Caroline provide important, though small, sanctuaries. Since 1978 the Pacific green sea turtle has been reclassified by the United States Department of the Interior as threatened and the Pacific hawksbill sea turtle as endangered.

Archaeology

From an archaeological point of view, Caroline houses one intact Tuamotuan *marae* (ancient religious site) and another smaller site, partly destroyed by storms. The main site (Pt. I, Fig. 3, Pl. 36), basically undisturbed since the 1870s, is a relic of prehistoric occupation worthy of protection and study, being the only one of its kind in the Line and Phoenix Islands.

<u>Current Conservation Status</u>

Caroline Atoll is owned by the government of the Republic of Kiribati and does not enjoy any legal protection (Garnett 1983, Ministry of the Line and Phoenix Islands, pers. comm.). Over the last 50 years it has been leased to private individuals who have scarcely altered the atoll. The benign management of the past is no guarantee for the future, and from October 1989 to the present, pressures to develop the atoll have mounted rapidly. Proposed schemes included an airstrip, a blasted channel through the reef, a hotel, a casino, logging, and commercial harvest of fish and lobsters. In March 1990, commercial harvesting of fish, the taking of coconut crabs, and illegal killing of green turtles began, emphasizing that no island, however remote, is guaranteed protection through isolation.

In addition, during the past 3 years Caroline has become more visited than ever before, mostly without the knowledge or consent of the Kiribati government. During 1990 yachts were present almost the entire year, and in 1989 a cruise ship landed tourists who visited several seabird colonies during midday heat. At this time Polynesian crewmen presented some passengers with fresh tail feathers from Red-tailed Tropicbirds (B. Danielsson, pers. comm.). There are many reasons why Caroline is inappropriate for resident tourists or development (remoteness, distance from medical aid, no regular water supply, no passage into the lagoon, mosquitos, etc.; see A. Kepler 1990a). Caroline could support a limited number of ship-based ecotourists each year, but indiscriminate visitation by yachts or other craft, such as developed into an increasing problem at Suvarov, in the Cook Islands (G. MacCormack, pers. comm.), should be discouraged.

Recommendations for an international preserve began in January 1989. During the 1990 ICBP expedition to the Line Islands, team leaders discussed conservation matters with Kiribati government officials and key scientists in French Polynesia. We obtained photodocumentation of illegal land clearing and wildlife disturbance during the last 2 visits to Caroline (A. Kepler 1990a, b, c). As a result, the Kiribati government considered altering their plans for the development of Caroline in favor of wildlife preservation.

In 1990 and 1991, The Nature Conservancy of Hawaii attempted to establish a triple-island preserve on Caroline, Vostok, and Flint through negotiations with Kiribati officials on Tarawa. These negotiations failed, and the Kiribati government leased Caroline (and Flint) for 55 years to the person responsible for the schemes and illegal activities noted above.

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APPENDIX

Preliminary List of Arthropods

The knowledge of Arthropods on Caroline is limited to 15 Lepidopterans collected by Dr. Palisa during the Solar Eclipse Expedition (Dixon 1884), a scant list of common insects (beetle, gnat, etc.) in the same paper, and a preliminary collection of 82 specimens made by Graham Wragg and AKK in 1990. The latter, identified by David Preston and Scott Miller (B. P. Bishop Museum, Honolulu, Hawaii), contained no endemics, consisting primarily of widespread Pacific species and immatures identifiable only to family level.

Although our collection is also scant, it is the second collection of Arthropods from Caroline and the only one containing species other than Lepidoptera: *Isometrus maculatus* (scorpion), *Scolopendra subspinipes* (centipede), *Anoplolepis longipes* (long-legged ant), Isopoda, lepidopterans (larvae and pupa), dermestid beetles (larvae and adults), cockroaches (Dictyoptera), Hibboboscidae adult (Diptera), Isopoda, Nitidulidae (immature and adults, Coleoptera), Curculionidae (Coleoptera), immature Hemiptera (Lygaeidae), Scolopendriidae immature, spiders (Arachnida).

Plate 1. Incubating Red-tailed Tropicbird, Bo'sun Bird Islet, Caroline Atoll, 25 September 1988. The nest scrape is in fine coral rubble under a *Tournefortia* shrub.

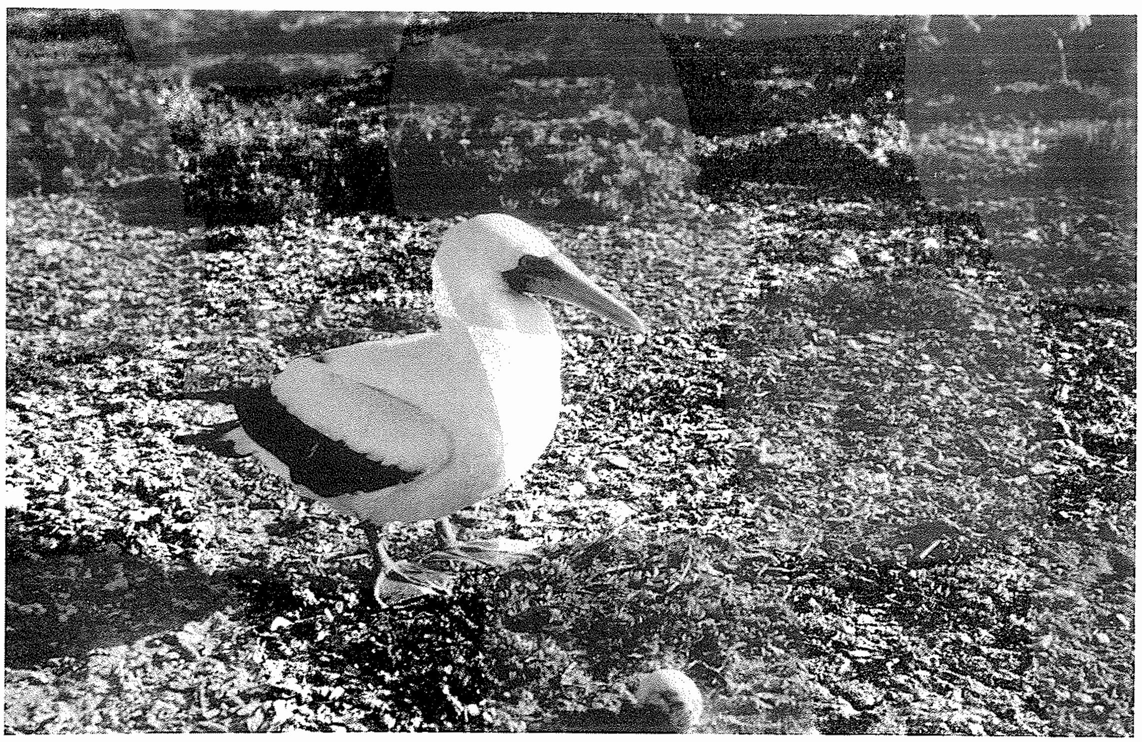

Plate 2. Masked Booby adult with egg on coarse coral rubble substrate with *Portulaca* mat, Nake Island, Caroline Atoll, 26 September 1988.

Plate 3. White Tern adult with egg in typical nest site, a dead *Tournefortia* branch, South Island, Caroline Atoll, 23 September 1988.