



Pelagic Studies of Seabirds
in the
Central and Eastern Pacific Ocean

WARREN B. KING, EDITOR

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ABSTRACT

King, Warren B., Editor. Pelagic Studies of Seabirds in the Central and Eastern Pacific Ocean. *Smithsonian Contributions to Zoology*, number 158, 277 pages, 170 figures, 1974.—Seven papers by various authors on the pelagic distribution of several seabirds in the central and eastern Pacific Ocean based largely on the researches of the Pacific Ocean Biological Survey Program, 1963-1968. "Introduction," by Patrick J. Gould, introduces these and future papers in this series. He discusses the methods and procedures used by the POBSP in gathering and recording data on observations of seabirds, outlines the areas under surveillance, and provides a general account of the oceanography and marine biology of the areas under discussion as a background to understanding the movements of seabirds in relation to their environment. "Sooty Tern (*Sterna fuscata*)," by Patrick J. Gould, presents the POBSP's records of this most abundant tropical and subtropical Pacific species. Its distribution at sea depends on erratic food availability, location of breeding islands, breeding schedule, and postbreeding dispersal patterns. "Wedge-tailed Shearwater (*Puffinus pacificus*)," by Warren B. King, gives data on the distribution of the northern, predominantly white-breasted and the southern, dark-breasted morphs of this species. Subtropical populations migrate extensively, for example between the Hawaiian Islands and the Pacific coast of Middle America; tropical populations are apparently nonmigratory. "Black-footed Albatross (*Diomedea nigripes*)," by Gerald A. Sanger, discusses the distribution and frequency of sightings on a seasonal basis of this ship-following seabird, both in general terms throughout its range and in detail in certain areas, for example, the CalCOFI study covering an eight year period off California and Baja California. Its winter range overlaps largely with, but lies slightly to the south of, its summer range. "Laysan Albatross (*Diomedea immutabilis*)," by Gerald A. Sanger, analyzes observations of this species and relates its seasonal distribution and abundance to its oceanographic environment. This species is more abundant in the western and central Pacific, whereas the Black-footed Albatross is more abundant in the central and eastern Pacific. "The Storm Petrels (Hydrobatidae)," by Richard S. Crossin, summarizes the POBSP's data on eighteen species or subspecies of storm petrels based on sightings and collected specimens. Pelagic distribution is related to breeding cycles, location of breeding sites, and marine environment. "Red-tailed Tropicbird (*Phaethon rubricauda*)," by Patrick J. Gould, Warren B. King, and Gerald A. Sanger, discusses seasonal distribution and abundance of this species relative to its breeding cycle. This species disperses widely from its breeding islands, for example, from the Hawaiian Islands to the Pacific coast of Middle America. "Recoveries of Banded Laysan Albatrosses (*Diomedea immutabilis*) and Black-footed Albatrosses (*D. nigripes*) in the Pacific Ocean," by Chandler S. Robbins and Dale W. Rice, summarizes the seasonal distribution of pelagic recoveries of 324 banded Laysan Albatrosses and 399 banded Black-footed Albatrosses. Different age groups of each species concentrate in somewhat different areas, and, although range overlap between species is almost complete, each has its own distinctive seasonal distribution pattern.

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Pelagic Studies of Seabirds in the Central and Eastern Pacific Ocean

Introduction*

Patrick J. Gould

In 1963 the Smithsonian Institution initiated a research project to study the ecology of certain areas of the Pacific Ocean. The activities and objectives of this project, called the Pacific Ocean Biological Survey Program (POBSP), have been summarized by Humphrey (1965). The present paper is the first in a series summarizing at-sea bird observations made by the POBSP, although a number of papers have already been published incorporating some POBSP at-sea observations (Amerson, 1969; Gould, 1967; Gould and King, 1967; King, 1967; King, 1970; King and Gould, 1967). The following introduction is rather lengthy so that subsequent papers herein and elsewhere may avoid needless repetition of material relevant to all of them.

POBSP efforts were concentrated primarily on a $4\frac{1}{2}$ million-square-mile area of the central Pacific between 10°S and 30°N , and 148°W and 180° . The birds of this area have received the greatest attention, although plants, arthropods, mammals, fishes, reptiles, and other forms have figured in the research as well. The energies of the POBSP were divided between periodic visits to the islands of the Leeward Hawaiian chain, the Line group, the

Phoenix group, and observations in the open ocean. Peripheral island groups such as the Tokelaus, Marshalls, Gilberts, Wake, and the Pribilofs were visited less frequently.

On island surveys POBSP personnel estimated the breeding and roosting populations of each seabird species, described the breeding status of each, made representative collections of the plants and animals (with special attention to vagrants), and marked large numbers of as many species of birds and mammals as possible. In the course of this work, POBSP personnel have banded over 1,800,000 birds of 56 species. On two atolls, Johnston and Kure, POBSP maintained continuous surveillance. A large proportion of the birds on these islands was banded, and uninterrupted breeding biology studies were conducted.

Late in 1966, field work was expanded eastward to include a survey area off southern California and northern Baja California. Observers also accompanied many cruises (south to as far as 20°S and east to as far as 135°W) of project EASTROPAC. This latter project was an intensive oceanographic investigation of the eastern tropical Pacific Ocean by Chile, Ecuador, Mexico, Peru, and the United States, sponsored and coordinated by the U.S. Bureau of Commercial Fisheries.

Observations at sea have been made in the central and eastern Pacific to determine the identity,

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occurrence, and abundance of seabirds. Data on atmospheric and oceanographic conditions were collected concurrently on some cruises to provide a broad ecological foundation. POBSP personnel made continuous observations, normally from sunrise to sunset, but sometimes around the clock, on cruises along replicate tracks and straight-line transects in all months of the year. On most island survey cruises, personnel made observations en route to, from, and between the islands. Furthermore, data on the population and breeding phenology of seabirds from island surveys added to the understanding of the distribution and densities of birds at sea. In addition, the use of plastic leg streamers and feather dye applied by island workers increased the chances of assigning an island of origin to marked birds observed or collected at sea.

SURVEY AREAS

Data were gathered systematically from the north-central, south-central, and eastern Pacific during all months of the year. In these areas, ships followed replicate cruise tracks or concentrated their efforts within a small area of ocean so that the abundance and distribution of birds could be documented seasonally in great detail. Cruises also went into peripheral areas but less regularly (Figure 1). Although the seasonal movements of birds in these peripheral areas cannot be shown in as much detail, the resulting data broaden the total coverage.

The north-central Pacific is defined herein as the area between 10°N and 30°N, and between 148°W and 180°. The only islands within this predominantly tropical oceanic area are the Hawaiian group and Johnston Atoll. This area is within the North Pacific Trade Wind Zone which is characterized by mild temperatures and remarkably constant winds from the northeast, normally between 10 and 25 knots. Anticyclonic high pressure cells move from west to east between 35°N and 50°N and generate the trade winds. These cells break down occasionally, more frequently in winter than in summer, at which times southerly and westerly winds bring warm moist air and increased rainfall.

The north-central Pacific is within the large North Pacific Central water mass. This is bounded on the east by the southward flowing California Current, the westward extension of which flows into the North Equatorial Current. The southern

border of the North Equatorial Current forms a divergence with the Equatorial Countercurrent between 9°N and 12°N depending on the season. The Kuroshio Current and the North Pacific Current border the water mass on the west and north, respectively. The North Pacific Central water mass in the Hawaiian Islands area has a high surface salinity, up to 35.3 parts per thousand, decreasing toward the south to 34.1 parts per thousand. Surface water temperatures range in summer from 25°C in the north (26°N) to 27°C in the south (10°N), and in winter from 20°C in the north to 25°C in the south. A summary of north-central Pacific oceanography is found in Seckel (1962).

The flow of water through the Hawaiian Islands is to the southwest. The large submerged bases of the islands deflect the water and cause eddies to form in the lee of the islands, which result in local areas of nutrient turnover and enrichment (Sette, 1955). Seabirds are often associated with such areas. The leeward Hawaiian Islands, Johnston Atoll, and, to a lesser extent, the main Hawaiian Islands, have large seabird breeding colonies. In the spring and summer, when most of the species of this area are breeding, high densities of seabirds are found at sea near the islands. The oceanic areas within 100 miles of these islands provide most of the food resources that make possible the large colonies.

The south-central Pacific, as herein defined, extends from 10°N to 10°S and from 150°W to 180°. Within this area are the Line Islands, the Phoenix Islands including Howland and Baker, and the Tokelau Islands. Northeast trade winds predominate in the northern part of this area, and southeast trade winds predominate in the south. The narrow zone of light, variable wind between the two trade wind systems is called the doldrums. It is characterized by low atmospheric pressure, warm, humid air, and more abundant rainfall than in the trade wind zones. In January the doldrums are farthest south, being found at 5°N at 150°W and 5°S at 170°W. In July they are found between 5°N and 9°N (Riehl, 1954:13, fig. 1.9). The belt of high rainfall (up to 118 inches per year) moves north and south seasonally with the doldrums.

The oceanographic conditions of the south-central Pacific are dominated by the equatorial current system which includes the easterly setting Equatorial Countercurrent, and the westerly setting

North Equatorial and South Equatorial currents. The boundaries of these currents change seasonally and annually (Barkley, 1962). They are strongest in summer as the result of stronger and more constant trade winds. In winter the width of the currents decreases and the surface flow is weaker. In general the North Equatorial Current is north of 9°N, the Countercurrent lies between 4°N and 9°N, and the South Equatorial Current is south of 4°N. Surface temperatures range between 26° and 29°C, and surface salinities between 34.4 and 35.8 parts per thou-

sand. For a more thorough treatment of the oceanography of the area see Barkley (1962). Ashmole and Ashmole (1967) present an excellent review of the general biology of birds and their food organisms in the equatorial current system.

The uninhabited islands of the south-central Pacific support large breeding seabird populations, and pelagic areas close to islands maintain high seabird densities. In addition, high seabird densities are normally found along the southern boundary of the Equatorial Countercurrent where local

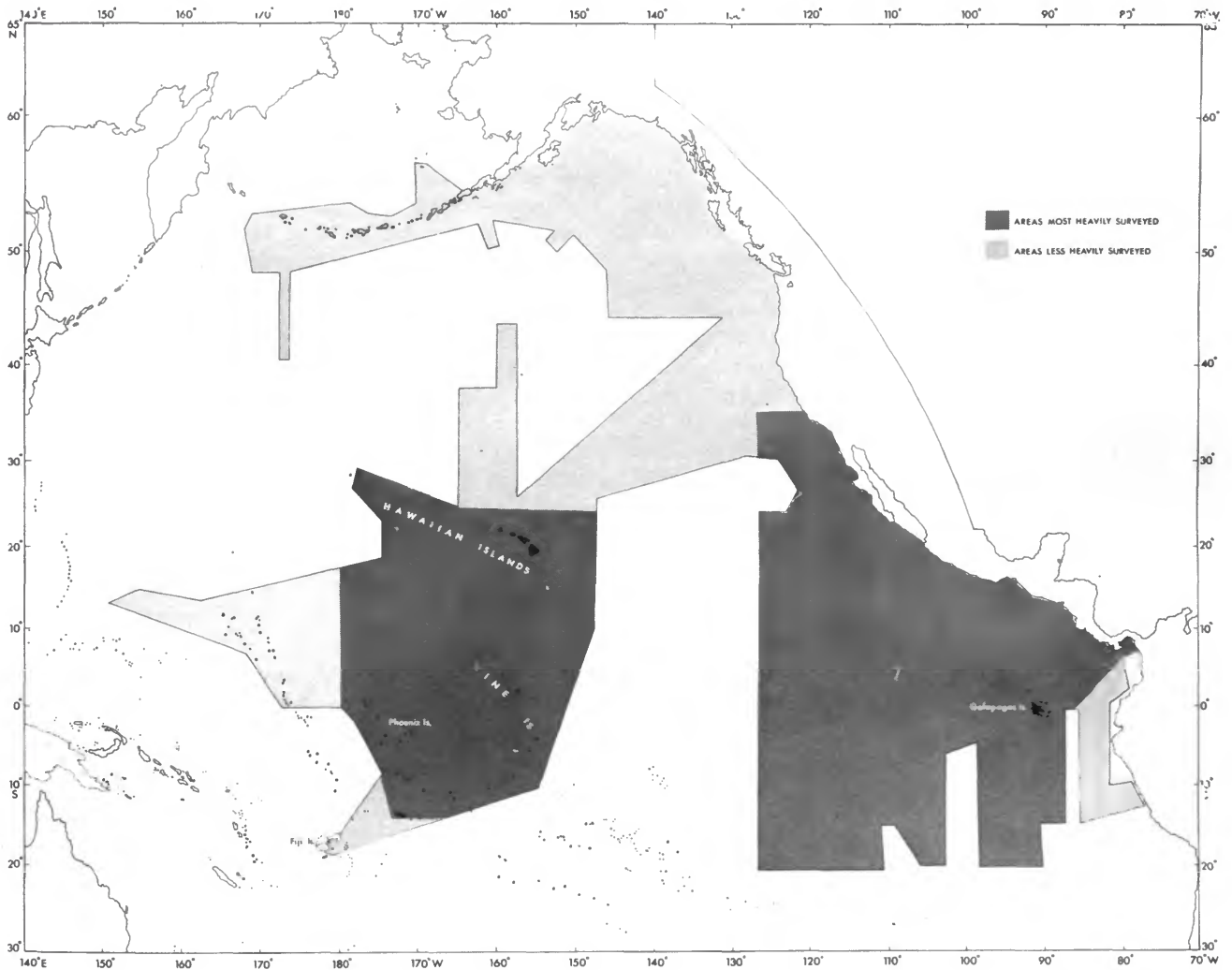


FIGURE 1.—Area covered by POBSP observations.

concentrations of food organisms are caused by convergence of that current with the South Equatorial Current (Ashmole and Ashmole, 1967:57).

The eastern Pacific is herein defined as the expanse of ocean between 35°N and 20°S, and between the American Continental coast and 135°W. Most of the islands in this area occur within 100 miles of the coast but a few are oceanic. The surface water conditions of this area are dominated by the California Current in the north and the Peru Current in the south. These currents, especially the latter, carry relatively low temperature surface waters toward the equator. This results in cooler surface temperatures in this area than are found farther west at the same latitudes.

METHODS AND PROCEDURES

Observers maintained daily watches on ships moving through areas of interest. When two or more observers were available, watches began before sunrise and alternated every two to four hours until sunset. If only one observer was present, one- or two-hour rest periods were taken occasionally. Nocturnal observations were made whenever possible. In no case was an inexperienced observer expected to make identifications without the supervision of an experienced observer. However, in 1963 all observers were relatively inexperienced and for this reason the 1963 data (8 cruises) are included only as supplemental material in this report.

All birds seen were recorded in a daily field log. The following information was included: time of sighting, identification (to species or subspecies when possible), number of birds, direction of flight, behavior, and special comments (e.g., description, association with other species, fish activity). When weather conditions and ship schedules permitted, specimens were collected to verify sight identifications and to show the range of individual birds and, by inference, of whole populations. All specimens are in the collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Records were kept of all position fixes and of interpolated hourly positions. On a few cruises bathythermograph and other oceanographic recordings were also taken. Preliminary reports were made of each trip and these, along with the raw data obtained, are on file at the National Museum of Natural History.

Line transects provide the basis for data collection and analysis. Densities were calculated in birds per mile (BPM) or birds per hour (BPH). In this report only the former value is used. Since the majority of observations were made at a speed of approximately 10 knots, it is necessary only to multiply all BPM figures by 10 to get an idea of BPH values.

In order to store and analyze data, an electronic data processing system was designed (King, Watson, and Gould, 1967). This system can simultaneously analyze data pertaining to sighting, environment, and location and duration of observation. The system was programmed to calculate and list the abundance of each species. For each day of each cruise, the total diurnal miles traveled and the total number of a species seen were used to calculate relative densities for the entire day. All sightings were tied to the noon position of the ship.

The BPM units were plotted by month on maps, one per month, for all data from January 1964 through April 1968. Contour lines were drawn on the maps, connecting points of equal bird density. In most cases a linear gradation of bird density was assumed between any two points (i.e., noon positions). Exceptions to this were when several positions with significantly different densities (greater or less than the next contour increment) occurred within a relatively small area. This may have been because of different densities noted during a given month or a given year, or because of different densities noted among the four years for a given month. In such cases, the contours were drawn according to the arithmetic mean of the densities within the area. Thus, the maps represent the monthly average distribution and density for all four years. All midday positions are indicated by dots, and varying density is indicated by degrees of shading.

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Reginald Creighton and Warren Minami developed and operated the automatic data processing program. Anne K. Poulson prepared most of the illustrations. Mae H. Esterline gave editorial advice. All work was under the direction of Philip S. Humphrey.

All the observations to be presented were made by *POBSP* personnel as well as by many other collaborators. On innumerable occasions logistic and technical support has been generously provided by the United States Coast Guard, the United States Navy, the Bureau of Sport Fisheries and Wildlife and Bureau of Commercial Fisheries of the U. S. Department of Interior, the State of California Department of Fish and Game, the State of Hawaii Division of Fish and Game, the Scripps Institution of Oceanography, and the institutions and countries involved in the *EASTROPAC* investigations. We are grateful to all the participants who have made this series of papers possible.

Sooty Tern (*Sterna fuscata*)*

Patrick J. Gould

Introduction

SUMMARY OF PUBLISHED PELAGIC DISTRIBUTION.—The Sooty Tern is one of the most numerous and characteristic seabirds of the tropical and subtropical Pacific Ocean, occurring widely at sea during all times of the year. Birds have been recorded south to 40°S on both sides of the Pacific, and north to southern Japan and southern Baja California. Population estimates of breeding colonies for mid-central Pacific Islands visited by the POBSP indicate total numbers in that area to be in excess of 30 million birds (Table 1). Data from the eastern Pacific are fewer and less precise but indicate many thousands of birds are present. Vast numbers occur throughout the Atlantic and Indian Oceans as well.

Appendix Table A is a summary of published information on Sooty Tern distribution in the Pacific Ocean. It can be seen that at-sea records are spotty, both with respect to time of year and to geographical area. It is apparent, however, that Sooty Terns range widely at sea throughout the tropical and subtropical Pacific. Mörzner Bruyns (1965) found them common to abundant in November within the Equatorial Countercurrent (6°–8°N) across most of the Pacific. Although he recorded the largest numbers near islands and coastal areas, he found them most consistently, on a day-to-day basis, across the large open stretch between 145°W and 115°W. King and Pyle (1957) found these terns most abundant near islands and coastal areas. They observed birds only sporadically along the northern edge of the Equatorial Countercurrent

(ca. 10°N) in November between 156°W and 120°W, and from mid-October to mid-November between Manzanillo, Mexico, and the Marquesas Islands. In early December they recorded Sooty Terns every day between the Marquesas and the Line Islands.

Distributional extremes in the south Pacific are represented by one specimen from Rio Valdivia, Chile, ca. 40°S (Murphy, 1936:1132) and three records along the Wellington coast of New Zealand, ca. 40°S (Falla, et al., 1967:165). In the north Pacific extreme records are from: the Alijos Rocks, ca. 25°N (McLellan, 1926:283), north of the leeward Hawaiian Islands, ca. 33°N (POBSP), and Japan, 35°N (Austin and Kuroda, 1953:450–451).

Factors influencing Sooty Tern distribution (e.g., feeding habits) have been studied by Ashmole (1963a), and Ashmole and Ashmole (1967). In the latter study they found that these terns fed mainly on fish and squid between 2 and 8 centimeters in length. They suggest that Sooty Terns are capable of utilizing food sources up to 700 miles from breeding islands, and that Christmas Island birds often feed at great distances from land during the breeding season. Nocturnal feeding has been documented by Mörzner Bruyns and Voous (1965) and by Gould (1967).

BREEDING PHENOLOGY.—At-sea distribution and densities of Sooty Terns are greatly influenced by the timing of breeding activities. A brief summary of these activities is thus necessary to the understanding of data presented later in this paper.

Sooty Terns breed, or have bred, on almost all islands in the tropical and subtropical Pacific between latitudes 29°N and 32°S. The timing of the breeding cycle is apparently quite variable (Hutchinson, 1950; Chapin, 1954; Ashmole, 1963a). For colonies within the Hawaiian Islands the breeding

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TABLE 1.— *Maximum number of Sooty Terns recorded on islands in the central and eastern Pacific*

<i>Island</i>	<i>Number</i>	<i>Source</i>
CENTRAL PACIFIC		
Hawaiian-Leeward		
Kure	48,000	POBSP
Midway	353,000	"
Pearl and Hermes Reef	40,110	"
Lisianski	1,000,000	"
Laysan	2,000,000	"
Gardner Pinnacles	1,000	"
French Frigate Shoals	250,000	"
Necker	50,000	"
Nihoa	100,000	"
Moku Manu	20,000	"
Manana	200,000	"
Johnston Atoll	600,000	"
Line Islands		
Palmyra	750,000	"
Fanning	thousands	"
Christmas	15,000,000	"
Jarvis	1,900,000	"
Malden	10,000	"
Starbuck	3,000,000	"
Caroline	500,000	"
Phoenix Islands		
Canton	100	"
Enderbury	400,000	"
McKean	250,000	"
Phoenix	250,000	"
Birnie	1,500	"
Hull	3,000,000	"
Howland	375,000	"
Wake	1,750,000	"
Marshall Islands		
Taongi	20,000	Amerson, 1969:23
Bikar	7,500	Amerson, 1969:37
Taka	60,000	Amerson, 1969:50-51
Eniwetok	16,000	Amerson, 1969:116
Ailinginae	5,000	Amerson, 1969:141
Jaluit	30	Amerson, 1969:196
EASTERN PACIFIC		
Isabel	thousands	McLellan, 1926:283
Revilla Gigedos	thousands	Gifford, 1913:20
Clipperton	2,000	Stager, 1964:365
Islas Frailes del Sur	200	Wetmore, 1965:457
Cocos	30	Hundley, 1962:114
Culpepper	thousands	Lévéque, 1964a:39-40
San Felix	large numbers	Millie, 1963:566

cycle is annual and regular, the dates of peak laying generally falling within the same four-week period in most years. Dates of egg-laying, however, occur progressively later on the chain from Oahu

northwestward to Kure Atoll. On Manana, close to Oahu, the peak of egg-laying occurs during the last week in March or the first week in April. On Kure, at the northwestern end of the leeward Hawaiian chain, egg-laying begins in May.

On Johnston Atoll the peak of egg-laying comes in the middle of March. Birds first appear over the island at night, nearly three months prior to the time of laying. Numbers swirling over the island at night build up gradually to the time of egg-laying, when birds are present throughout the day as well. Maximum numbers on, or over, the island coincide with the hatching peak in the middle of April. Most fledging takes place in June. Fledglings generally leave the island by the first of August, and most adults leave by the end of August. The Johnston population is composed of approximately 300,000 breeding birds, and a roughly equivalent number of subadults and nonbreeding adults. The relative proportion of subadults and nonbreeders to breeding adults increases from June to the end of the cycle. Sooty Terns are virtually absent from Johnston Atoll from mid-September to the end of December (Shelton, in. prep.).

In the Line island group, the breeding cycle appears to be semiannual. Birds that successfully rear a chick breed again in 12 months, but those that fail nest again in only 6 months. The egg-laying peaks are in December and June. This cycle has been documented on Christmas Island by Ashmole (1965) and appears to hold true for other islands of that chain as well, although there may be exceptions or complicating factors in some populations.

The timing of the breeding cycles of Sooty Terns on Wake Island, and in the Phoenix, Marshall, and Gilbert chains, and on islands in the eastern Pacific is not understood. Some islands may have two or more individual colonies, each breeding at different times. Many may have a non-annual cycle. A discussion of breeding cycles and associated problems may be found in Ashmole (1963a).

ACKNOWLEDGMENTS.—I would like to give special credit to Warren B. King and Gerald A. Sanger who have worked with me in analyzing all at-sea bird data obtained by the POBSP and Philip C. Shelton who has provided data and comments on the population dynamics of Sooty Terns on breeding islands. Charles A. Sklar plotted the majority of the noon positions on the maps, and Helen H. Quinn typed the final draft.

TABLE 2.—*Sample size of POBSP Sooty Tern observations*

Observation	1964	1965	1966	Total
Sightings	1,547	1,665	782	3,994
Birds	19,070	20,738	11,287	51,095

I am indebted to William B. Robertson, Jr., and George E. Watson for their critical reading of the manuscript and their many helpful suggestions.

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Behavior

In this section all data, except when specifically stated otherwise, were collected within the following parameters: (1) at sea over 50 miles from land, (2) within approximately three-fourths mile of the ship, (3) in the north-central Pacific Ocean, (4) from 1964 through 1966, (5) from diurnal observations (sunrise to sunset). These parameters have been purposely chosen. Observations near land have been excluded because it was often impossible to get a clear idea of what was happening when birds were "too numerous to count": birds seem to be everywhere, moving in all directions, joining groups, leaving groups, flying high, flying low, etc. In such situations it was impossible to follow individual birds or flocks, or to understand behavioral patterns and interactions. The parameter of three-fourths mile from the ship was chosen because, although Sooty Tern flocks could be seen at greater distances, they could not be counted accurately, nor could they be observed well enough for behavioral studies beyond that distance. Moreover, single birds cannot be observed at greater distances so that the inclusion of distant birds would over-emphasize effects created by flocking. The north-central Pacific was the most uniformly covered large area, and had by far the largest number of observations made within it; also, Sooty Terns breeding in this area have an annual rather than semiannual cycle. Only the years 1964, 1965, and 1966 were included because of the spottiness of coverage in the north-central Pacific during other years. Within these

parameters a total of 51,095 birds in 3994 sightings was recorded (Table 2).

At this point it seems advisable to define a few special terms which will be used in the following discussion. A "sighting" refers to a single bird or two or more birds acting as a unit. A "flock" is considered to be the association of five or more individuals. "BPS" (birds/sighting) is a good index of the gregariousness or flocking tendency of a species. A "mixed" flock or sighting is one that contains more than one species, while a "pure" flock or sighting is one which contains only one species. "Searching" birds are those actively hunting for food, while "traveling" birds appear to be moving towards a specific goal.

FEEDING.—Ashmole and Ashmole (1967) have discussed the feeding ecology of Sooty Terns, considering particularly the kind of food taken and how it is captured. Our observations are in general agreement with theirs. Sooty Terns, searching for food, generally remain from 10 to 20 meters above the water surface. When the food source appears, they descend, simultaneously, and begin wheeling rapidly and erratically in circles. At this time there does not appear to be any coordination between individuals within a flock, although small groups may act in unison for short periods. When the food source descends, the flock rises to its original position and follows until the food returns to the surface or until it disappears. In a feeding flock working over a large area, terns in one section may be flying high, following locally deep food, while those in another section may be low and actively feeding.

"Air dipping" and "contact dipping" (Ashmole and Ashmole, 1967) appear to be the preferred feeding techniques, although "plunge to surface" is frequently used if the food source remains near but under the surface. The latter technique has been recorded only once in the Sooty Tern literature (Watson and Lashley, 1915). In POBSP observations, the "plunge to surface," although actually causing the water to splash up and obscure the bird momentarily, is never powerful, nor is it made from any great height. It never results in complete submergence of the bird, nor do the wings ever appear to cease beating. The feet do not seem to be utilized.

FLOCKING.—Sooty Terns were recorded in sightings of from 1 to 3000 individuals. The overall BPS ratio was 13, the highest value for any seabird

TABLE 3.—Percent of sightings and numbers of Sooty Terns in different sighting classes

Birds per sighting	Percent of all sightings				Percent of all birds			
	1964	1965	1966	mean	1964	1965	1966	mean
1.....	36	35	32	35	3	3	2	3
2.....	20	21	21	21	3	3	3	3
3.....	9	9	10	9	2	2	2	2
4.....	4	5	6	5	1	2	2	2
5.....	3	4	4	4	1	2	1	1
6.....	3	2	3	2	1	1	1	1
7.....	1	1	1	1	1	1	1	1
8.....	1	1	2	1	1	1	1	1
9.....	1	1	1	1	0.5	1	1	1
10+.....	22	21	20	21	86.5	84	86	85
1-4.....	69	70	69	70	9	10	9	10
5-55.....	25	24	26	25	37	35	30	35
56-105.....	4	4	3	4	27	27	16	24
106+.....	2	2	1	2	26	28	45	31

species regularly feeding over 50 miles from land. Although 90 percent of all individuals were found in flocks, flocks comprised only 30 percent of the sightings in all years. Indeed, sightings of single birds (35 percent) far outnumbered sightings of any other group size. Singles and groups of two ac-

counted for 56 percent of all sightings (Table 3).

The RObsp data agree with Ashmole and Ashmole's (1967:97) statement that "most tropical sea birds depend partly or entirely on schools of predatory fish (mainly tunas) to drive their prey close to the surface and so make it available." Although Sooty Terns have been observed feeding in the absence of predatory fish, many actively feeding flocks were directly associated with such schools. The sudden, and often relatively short-term, appearance of feeding tuna apparently places a premium on the ability of Sooty Terns to join feeding flocks containing other species. Seventy-seven percent of all Sooty Terns, and 24 percent of all Sooty Tern sightings, were associated with one or more seabird species (Table 4). Almost all species normally occurring in the area were involved, but the degree of their involvement was related to their gregariousness and their status within the area. For example, 70.6 percent of all mixed flocks containing Sooty Terns also contained Wedge-tailed Shearwaters (*Puffinus pacificus*). Conversely, King (p. 65, herein) found that 77 percent of all mixed flocks containing Wedge-tails contained Sooty Terns. Wedge-tails are the next most abundant species in the area and have a high BPS ratio (King, p. 64 herein). On the other hand, Sooty Shearwa-

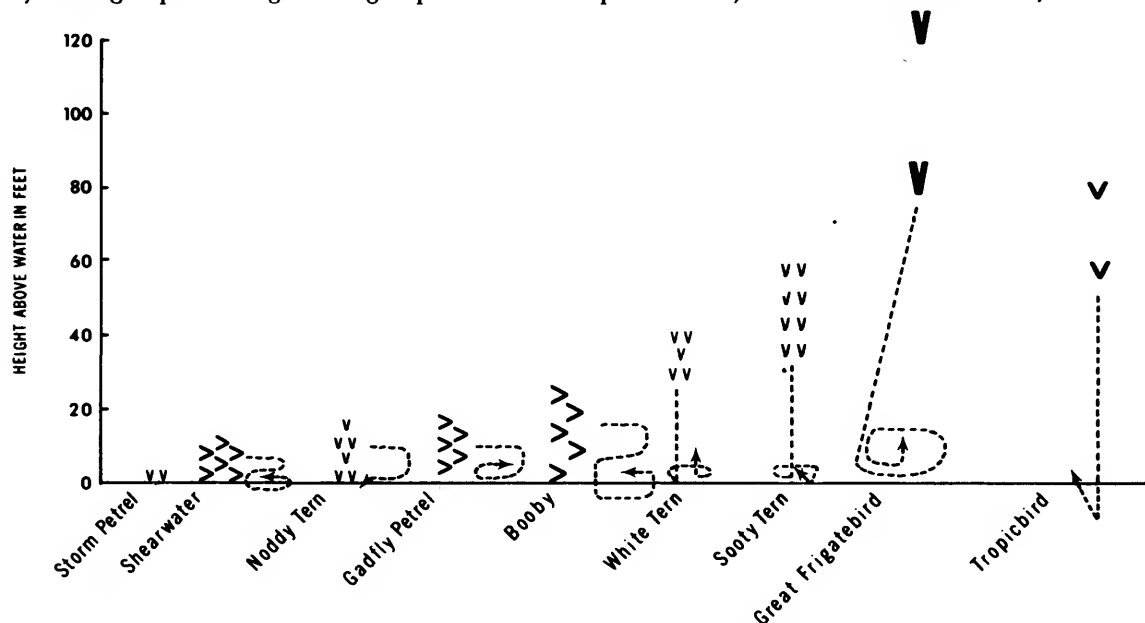


FIGURE 2.—Schematic representation of a mixed feeding flock showing the general stratification of selected species and their general pattern of movement while feeding.

TABLE 4.—Percent of association of Sooty Terns with other seabird species, 1964–1966

Species	All sightings	Mixed Sightings	General at-sea status
<i>Puffinus pacificus</i>	16.4	70.6	abundant most of the year
<i>Pterodroma externa</i>	7.4	32.0	common summer and fall
<i>Gygis alba</i>	4.8	20.8	uncommon throughout year
<i>Pterodroma nigripennis</i> ..	3.9	16.8	common summer and fall
<i>Fregata minor</i>	3.3	14.2	uncommon throughout year
<i>Puffinus griseus</i>	1.1	4.5	abundant spring and fall migrant
<i>Anous stolidus</i>	1.0	4.4	rare throughout year
<i>Puffinus puffinus</i>	1.0	4.3	uncommon spring, summer and fall
<i>Sula sula</i>	1.0	4.1	common winter
<i>Bulweria bulwerii</i>	0.7	2.8	uncommon spring, summer and fall
<i>Pterodroma neglecta</i>	0.7	2.8	uncommon throughout year
<i>Sula dactylatra</i>	0.6	2.5	common winter
<i>Puffinus nativitatis</i>	0.5	2.3	uncommon spring, summer and fall
<i>Phaethon rubricauda</i>	0.5	2.2	common throughout year
<i>Oceanodroma leucorhoa</i> ..	0.4	1.8	abundant winter
<i>Sterna lunata</i>	0.4	1.5	uncommon spring, summer, and fall
<i>Stercorarius pomarinus</i> ..	0.3	1.2	uncommon spring and fall migrant
<i>Puffinus carneipes</i>	0.2	1.0	rare spring and fall migrant
<i>Pterodroma alba</i>	0.2	1.0	rare throughout year
<i>Pterodroma phaeopygia</i> ..	0.2	0.6	rare summer and fall
<i>Stercorarius longicaudus</i> ..	0.2	0.6	rare spring and fall migrant
<i>Fregata ariel</i>	0.1	0.4	rare throughout year
<i>Pterodroma hypoleuca</i>	0.1	0.4	rare throughout year
<i>Phaethon lepturus</i>	0.1	0.4	uncommon throughout year
<i>Puffinus bulleri</i>	0.1	0.4	rare spring and fall migrant
<i>Puffinus lherminieri</i>	0.1	0.3	rare throughout year
<i>Puffinus tenuirostris</i>	0.1	0.3	abundant fall migrant
<i>Pterodroma inexpectata</i> ..	0.1	0.3	uncommon spring and fall migrant
<i>Sula leucogaster</i>	0.1	0.2	rare throughout year
<i>Catharacta species</i>	0.1	0.2	rare spring and fall migrant
<i>Anous tenuirostris</i>	0.1	0.2	rare throughout year

ters (*Puffinus griseus*) were abundant at certain seasons and had a high BPS ratio, but were found in only 4.5 percent of all mixed flocks containing Sooty Terns. This difference between two highly flocking and abundant species is explained by the fact that Wedge-tails are resident in the area while Sooty Shearwaters are primarily passing through on migration and rarely stop to feed.

The association of Sooty Terns with other seabird species appears to be mainly one of a common interest in the same food source. While within mixed feeding flocks, Sooty Terns maintain a definite spatial position in accord with the feeding abilities and techniques of all species involved. (Figure 2).

We have a number of records of Sooty Terns being harassed by Pomarine Jaegers (*Stercorarius*

pomarinus), Long-tailed Jaegers (*Stercorarius longicaudus*), Great Frigatebirds (*Fregata minor*), and Lesser Frigatebirds (*Fregata ariel*).

The largest Sooty Tern flock ever recorded by the POBSP occurred on 20 May 1966, some 200 miles south of Oahu. On this day a feeding flock of 4300+ birds, including Wedge-tailed Shearwaters, Pale-footed Shearwaters (*Puffinus carneipes*), Christmas Shearwaters (*Puffinus nativitatis*), Manx Shearwaters (*Puffinus puffinus*), Bulwer's Petrels (*Bulweria bulwerii*), Great Frigatebirds, Brown Noddy Terns (*Anous stolidus*), Black Noddy Terns (*Anous tenuirostris*), and 3000+ Sooty Terns was observed. The birds were concentrated over eight to twelve Fin-backed Whales (*Balaenoptera physalus*) and about 200 porpoises. The fringes of the flock stretched for approximately three miles.

Although we have no direct information on how much time individual birds spend feeding, searching, or traveling, the fact that the great majority of all birds observed were in mixed flocks, usually an indication of current or recent feeding, suggests that the greatest percent of their time is spent feeding or actively searching for food, with the former outweighing the latter. There is certainly a tendency for Sooty Terns to occur in larger flocks while feeding (Table 5). Our observations indicate that mixed, nonfeeding groups are composed mostly of searching birds. Pure, nonfeeding groups may be either searching or traveling; the activity cannot always be determined. Pure flocks of up to 140 birds and mixed flocks of up to 125 birds have been recorded traveling. Single birds and small groups have been observed both searching (moving slowly, dropping occasionally to the water surface, and investigating other birds in the water), and traveling. The distinction between searching and traveling, however, sometimes breaks down (traveling birds may stop to feed if the stimulus is strong enough), or it is sometimes even meaningless (many traveling birds may be headed for a distant feeding flock).

It was difficult to obtain direct evidence on how flocks form, how long they are maintained, and what happens when the food source being utilized disappears. In discussing the feeding behavior of Brown Noddies and Sooty Terns, Watson (1908: 193) wrote: "The birds feed singly or in groups, usually in groups. The group may be composed of both noddies and sooties and may contain sometimes as many as 50 to 100 individuals. All during the day groups of noddies and sooties may be seen at work. As the minnows cease to jump above the surface of the water, the group disbands and scatters in every direction. An instant later, as an attack is made upon the minnows in some other locality, the birds immediately rush there and renew their feeding." POBSP observations include a number of isolated observations documenting various stages in this process. The following entries, with annotations enclosed in brackets, are abstracted from the POBSP original daily log sheets. They are arranged in a subjective order from "searching" birds through "feeding" birds (including birds traveling toward already formed feeding flocks), to flocks "breaking up."

TABLE 5.—Total Sooty Tern sightings and numbers in mixed and pure, feeding and nonfeeding, situations

Situation	1964	1965	1966	Mean
Percentage of sightings				
Mixed				
Feeding	14	14	14	14
Nonfeeding	8	10	8	9
Pure				
Feeding	2	2	5	3
Nonfeeding	75	74	74	74
Percentage of total numbers				
Mixed				
Feeding	58	54	69	59
Nonfeeding	16	24	8	18
Pure				
Feeding	6	3	10	6
Nonfeeding	18	19	13	18
BPS ratio				
Mixed				
Feeding	51	48	70	53
Nonfeeding	24	30	16	25
Pure				
Feeding	33	22	28	28
Nonfeeding	3	3	3	3

SEARCHING

- 05 March 1964. 0700 Hours. 16°48'N, 169°06'W.
3 ST [Sooty Terns], [flying at] ca. 30-40 feet. One bird separated and circled a dead albatross in the water, then joined other two.
- 08 March 1964. 1103 Hours. 14°50'N, 169°40'W.
1 ST. Investigated downed [dead in water] albatross and continued NE.
- 07 June 1964. 1441 Hours. 18°11'N, 166°10'W.
2 ST. One shot [ship circled to retrieve downed bird]. At 1450 Hrs. 12 ST circled and looked over downed bird.
- 02 April 1964. 1612 Hours. 20°41'N, 159°17'W.
2 ST flying SW joined and circled with 6 ST circling at 1615 Hrs., then all 8 departed SW. No feeding was observed.
- 04 July 1964. 0600 Hours. 16°40'N, 169°18'W.
Flock of 26 ST and 1 WTS [Wedge-tailed Shearwater]. Original group of 14 joined by 6 then 6 more. Birds were not actively feeding but flew around as if food were near by.

FEEDING

- 10 May 1964. 1900 Hours. 15°04'N, 170°37'W.
30± ST. Very high, maybe 1000 feet up. Some of them seem to be gathering to move on, but then descend sud-

- denly as feeding flock. Big fish, probably tuna 5' or more long and some about 3' long jump at least 6' clear of water.
- 22 July 1964. 1110 Hours. 18°46'N, 150°59'W.
Feeding flock containing 90± ST, 2 WTS, 8 JFP [Juan Fernandez Petrel, *Pterodroma externa*], 1 WT [White Tern, *Gygis alba*]. Three separate groups joined up, each with about 30 ST.
- 11 March 1964. 1656 Hours. Near Johnston Atoll.
Feeding flock in formation started with 4 birds on their way south starting to circle and dive. Within minutes, 8 other Sooties came in, seemingly from all directions to join them. No fish action noted and feeding over area of about ¼ mile length (or diameter). [Ship continuing to move at ca. 8 knots.] 1700 Hours: 25+ ST moving low towards above flock. 1702 Hours: 40± ST at ca. 50' moving to join above? 1702 Hours: 10± ST low, moving right under above. 1705 Hours: 2 ST moving low toward above flock.
- 18 May 1965. 1500 Hours. 20°14'N, 154°02'W.
Feeding flock of 50 ST, 8 WTS, and two unidentified shearwaters or petrels. Original flock of 20 joined by 10 individuals and then by group of 25 or so.
- 06 September 1964. 1645 Hours. 17°34'N, 167°03'W.
30± ST, 8 WTS, 1 GFB [Great Frigatebird]. Feeding over fish jumping out of water. 1640 Hours: 13 ST at 50' going to above flock. 1646 Hours: 10 ST, 1 GFB, circling. 1648 Hours: 11 ST flying towards 1645 flock. 1656 Hours: 8 ST flying towards 1645 flock.
- 12 May 1964. 0715 Hours. 15°30'N, 171°33'W.
Flock of 55±1 ST and 3 WTS. Actively feeding. Large tuna-type fish jumping under flock. Flock was originally only of about 30 birds but soon increased to final number. At one point flock broke up into two groups, one of about 25, the other about 30. One group was soaring around high on port side of ship, the other was low, flying on starboard.

BREAKING UP

- 11 April 1964. 0825 Hours. 15°07'N, 171°24'W.
16±2 ST feeding. 3 birds left flock as we approached.
- 18 July 1964. 0905 Hours. 21°48'N, 162°27'W.
Flock of 50±10 ST, 6 WTS, 2 BFB [Blue-faced Booby, *Sula dactylatra*], 1 WT, 1 GFB, feeding—but breaking up into small groups. 0915 Hours: flock of 30 ST, 10 WTS, 1 RFB [Red-footed Booby, *Sula sula*], 2 CIS [Christmas Shearwater], and 1 WT, undoubtedly was once part of last flock; we saw birds from last flock join this one.
- 13 May 1964. 1705 Hours. 16°25'N, 170°51'W.
17 ST, 5 to 50' [above water]. Not feeding, but apparently looking for food source—group tended to split up but constant movement was to E[ast].
- Most shearwaters and gadfly petrels tend to sit on the water in either compact or loose aggregations after heavy feeding. It is well known, however, that Sooty Terns are incapable of spending long periods in such a fashion (Watson and Lashley, 1915:39–41). Sooty Terns do, however, alight occasionally at sea, either on a floating object or actually on the water. All such POBSP records are listed below. Omitting the bird knocked down by shot and the three sitting on turtles or flotsam, 0.3 percent of all sightings and 0.16 percent of all individuals recorded by the POBSP were on the water. These estimates, however, are undoubtedly low since most birds tend to rise before they can be detected.
- 19 August 1965. 0920 Hours. 13°53'N, 173°01'W.
One Sooty Tern was knocked down by shotgun blast and sat in the water for 12 minutes then flew at the approach of the ship.
- 23 October 1965. 0940 Hours. 01°16'S, 173°38'W.
One adult and one immature Sooty together on water, immature being fed by the adult.
- 23 October 1965. 1730 Hours. 02°00'S, 172°52'W.
One adult, one immature were collected while sitting on the water.
- 10 November 1965. 17°51'N, 164°09'W.
In a feeding flock containing ca. 15 Sooty Terns (at least four being immature), one adult and one young were noted as "on water together."
- September-October 1964.
"Three different times during the trip I saw Sooty Terns sitting on the water. A total of 6 birds were observed, always in twos. Each pair contained an immature bird and an adult. In one case both the immature and the adult were observed on the water. In the other two cases just the immature was on the water with the adult hovering overhead. In all cases the birds flew off as the ship approached. I never saw them land on the water so I can't say how long they stayed there. The longest I observed them was about 5 seconds." (POBSP, Robert Standen)
- 12 May 1965. 0744 Hours. 16°44'N, 162°16'W.
10 and 25 Sooty Terns. "Two separate flocks sitting on the water. They were gliding around and at first appeared to be Wedge-tails from their flight pattern. Birds were flying and then sitting down again. They were not feeding."
- 01 September 1967. 0930 Hours. 01°44'N, 98°04'W.
75± ST. All adults, seemed to have fresh plumage. Most circling high 200'±, some close to water. About 8 of them were sitting on the water.
- 14 June 1967. 1425 Hours. (Atlantic Ocean) 12°42'N, 81°06'W.
2 adult ST sitting on water with wings closed—quite happy 10–15 seconds that I saw. (POBSP, Richard Chandler)
- February 1968.
"On February 13 both shipboard observers saw a single flock of 22 adult Sooty Terns resting on the water about 10 miles south of Johnston. When first seen all were together on the water spaced two to six feet apart. As the ship approached two or three birds rose off the water and

began hovering over the remaining 20. These remained on the water for at least another minute before the ship scared them into flight. The time lapse between the first sighting and flushing was about two minutes, but it was obvious that the birds had been there quite a bit longer." (POBSP, Brian Harrington)

07 July 1967. 0955 Hours. 18°35'N, 104°53'W.

One Sooty Tern sitting on a turtle.

10 July 1967. 1433 Hours. 17°08'N, 101°05'W.

One Sooty Tern standing on head of turtle.

18 August 1966. 1713 Hours. 32°06'N, 163°42'W.

One adult Sooty Tern sitting on fish ball [float].

DISCUSSION.—Sooty Terns occur over the entire pelagic area of the north-central Pacific. They are distributed primarily as singles and small groups interspersed with a few small flocks and even fewer large flocks. Over 90 percent of all individuals, however, are found in flocks. The degree of flocking is probably greatest in areas of food abundance. Single birds and small groups generally appear to be searching. Their flight is usually slow, indirect, and often high above the water. They frequently drop to just above the surface, apparently investigating possible food items. When available food is spotted the bird or birds descend and begin feeding. This change in behavior pattern is distinct and easily recognizable to the human eye. Other birds within visual range probably can detect and identify the new pattern and are attracted to it. Birds heading towards a feeding flock fly in a relatively fast and direct manner distinct from that of searching birds. It is possible that this type of flight may provide a clue to other birds which were not aware of the newly formed feeding flock. Similar behavioral differences are also found in other flocking seabirds (e.g., Wedge-tailed Shearwaters) and it seems probable that Sooty Terns could recognize such behavioral changes in other species and act accordingly.

As a feeding flock grows it becomes visible to more distant birds. The eventual size of the flock would thus be controlled, primarily, by the length of time that food is available. The total number of terns within range of the food supply would, however, have a restricting effect, since distant birds might be hard put to detect the presence of food and to reach it before it disappeared. When the food source disappears, Sooty Terns rise high into the air and disperse, either by fragmenting into two or more smaller groups each going in a separate direction, or by all going in the same

direction but becoming widely separated. Subsequent fragmentation of groups or continued separation of individuals may eventually result in the dispersal of all birds over the ocean as individuals. If another food source is discovered before a flock has fragmented or separated completely, the group, whatever size it has been reduced to, becomes the nucleus of a new feeding flock. As the length of time between feedings increases, sightings of single birds should increase since flocks would have had more time to disperse. The relative frequency of sightings of single birds, as opposed to sightings of groups, should thus provide an estimate of food availability and tuna school density in a given pelagic area.

Distribution and Abundance

Figures 17–28 (pp. 34–45) summarize monthly POBSP Sooty Tern sightings in the Pacific Ocean. They attempt to show gross distributional patterns and in most cases tend to de-emphasize local or short-term variations. Only at-sea sightings are included, although these may include sightings within a few miles of land. Sightings cover the period January 1964 through April 1968, and contour lines are drawn without regard to year. Densities are recorded in BPM units.

NORTH-CENTRAL PACIFIC.—Sooty Terns are present in the north-central Pacific throughout the year. At least one bird was recorded during 74.5 percent of all days of observation from 1964 through 1966. Only during January 1964, December 1965, and August 1966, were birds seen on fewer than 50 percent of all observation days (Figure 3).

Densities throughout the year ranged from a low of 0.0 BPM to a high of 54.5 BPM. Densities greater than 10.0 BPM were uncommon and, with one exception, always occurred within 50 miles of land. This exception, however, was the second highest density ever recorded within the study area (27.1 BPM). The highest density figure, 54.5 BPM, is somewhat unreliable since observations on that day covered only four miles and lasted somewhat less than one hour (Table 6).

With the fledging of chicks in August, Sooty Tern numbers near islands decrease markedly. Lowest maximum densities near the Hawaiian Islands and Johnston Atoll occurred in October

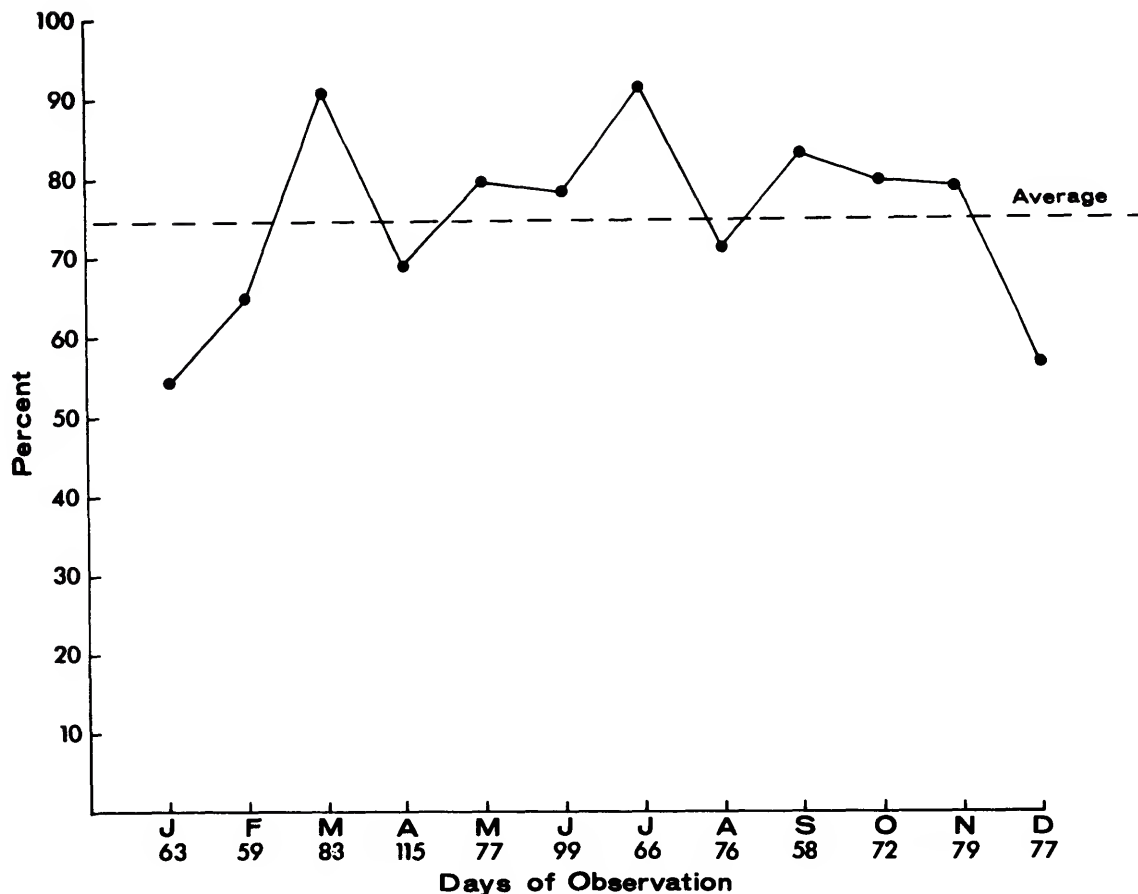


FIGURE 3.—Percent of observation days on which one or more Sooty Terns were recorded in the north-central Pacific during 1964-1966.

(Table 7). In the area as a whole, however, densities were lowest in November and December, even though densities near the Hawaiian Islands and Johnston Atoll increased slightly. Densities over 50 miles from land began increasing in June with an influx of newly fledged birds. From June through November, immature birds became increasingly abundant and wide-spread throughout the north Pacific. We have a few records which indicate that newly fledged birds accompany their parents when they leave the breeding colony, i.e., the six sightings of an adult and immature sitting on the water listed in the behavior section. The record of an adult feeding an immature over 100

miles from land on 23 October 1965 is certainly conclusive.

Increasing densities in January and February, particularly near breeding islands, were the result of birds returning to these islands for the next breeding season. From September through December, and especially during September and October, densities in areas over 50 miles from land were generally greater than those within 50 miles. This was particularly noticeable in two widely separated areas where at-sea densities reached as high as 9.0 BPM. The first area was 200-300 miles west-southwest of Oahu. This is apparently a rich feeding area favored by many species of seabirds, particu-

TABLE 6.—Date and location of all Sooty Tern densities of 10.0 or greater BPM recorded within the north-central Pacific, 1964–1966

(Observation = within 50 miles of "Location")

Density (BPM)	Location	Date	Miles of observation
10.0	Oahu	6 Jun 66	28
10.2	Johnston Atoll	5 Jun 66	141
10.4	Oahu	5 Jul 66	23
10.9	Oahu	5 Jun 64	73
11.0	French Frigate Shoals	17 Jun 64	108
11.5	Oahu	4 May 65	40
11.8	Laysan	20 Jun 66	39
12.4	Johnston Atoll	13 Apr 65	117
12.8	Oahu	13 Jul 64	51
12.9	Johnston Atoll	31 Jan 66	22
14.5	Laysan	5 Aug 65	80
16.1	Johnston Atoll	5 Jul 65	127
23.2	Lisianski	14 Jul 65	33
26.9	Oahu	31 May 65	104
27.1	at-sea, 17°54'N, 158°48'W	20 May 66	117
54.5	Oahu	2 Jul 65	4

larly those breeding in the leeward and main Hawaiian Islands. The second was 700–800 miles south-southeast of Oahu. This area may be occupied by birds from more southerly breeding localities (e.g., Line Islands) as suggested by King (1970:54), although it is somewhat north of the Equatorial Countercurrent which Ashmole and Ashmole (1967:66) considered a likely feeding ground for Christmas Island birds.

During this winter period, a strange pattern of occurrence was found in the area between 50 and 300 miles southwest of Johnston Atoll. During the day, Sooty Tern densities decreased through November and December to a low of 0.0 BPM in January, and then increased again in February. Nocturnal observations in the same area, on the other hand, revealed few terns in November and December, but large numbers in January and February. This occurred in all three successive years of our investigations in this area (Table 8). Nocturnal counts were primarily of birds heard near the ship. Densities listed in Table 8 are conservative, particularly with respect to diurnal sightings, since birds can be seen at greater distances than they can be heard. Although Sooty Terns are often attracted to the ship's lights, particularly on

TABLE 7.—Maximum Sooty Tern densities (BPM) in the north-central Pacific

Month	Near Hawaiian I.	Near Johnston Atoll	50+ miles from land
Jan	4.8	12.9	4.9
Feb	6.7	5.0	6.7
Mar	6.9	7.9	8.0
Apr	5.6	12.4	6.4
May	26.9	7.2	27.1
Jun	11.8	10.2	3.9
Jul	54.5	16.1	9.4
Aug	14.5	2.8	8.0
Sep	1.0	3.5	9.0
Oct	0.1	0.2	7.1
Nov	1.0	1.3	2.6
Dec	1.5	2.3	5.0

TABLE 8.—Winter Sooty Tern densities 50–300 miles southwest of Johnston Atoll, 1963–1967

Year	Nov	Dec	Jan	Feb
Birds per 100 miles of diurnal observations				
1963–1964	23	1	0	1
1964–1965	1	17	0	0
1965–1966	32	1	0	8
1966–1967	3	10	0	41
Mean	14	8	0	20
Birds per 100 miles of nocturnal observations				
1963–1964	2	0*	2*	0*
1964–1965	13*	2	55	30
1965–1966	9	0	62	23
1966–1967	1	5	5	47
Mean	2	3	32	40

*Months in which less than 100 miles of observations were made.

stormy nights, they are still difficult to observe. The chances of counting the same birds twice are much greater at night than during the day. In this case, however, most of the nocturnal birds appeared to be traveling in a specific direction, rather than circling the ship, thus reducing the chances of duplicate recording.

Two additional features were also apparent. First, there was a definite nocturnal activity cycle. Sooty Terns were first heard about an hour after sunset and increased in numbers to maximum

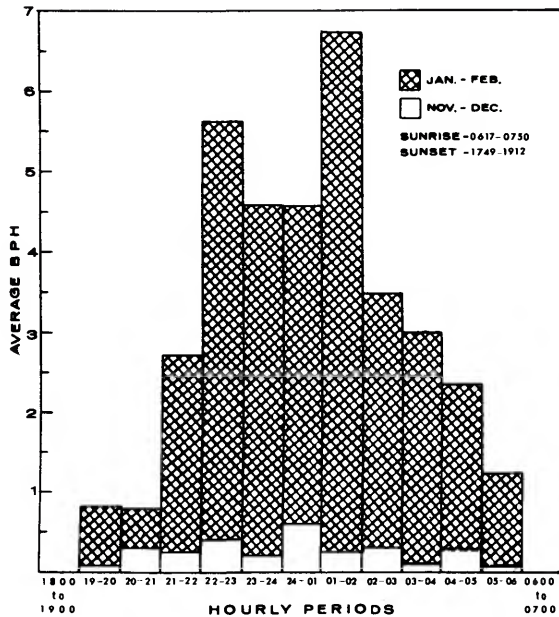


FIGURE 4.—Nocturnal abundance cycle for Sooty Terns from 50 to 300 miles southwest of Johnston Atoll during 1963–1967.

densities between 2200 and 0200 hours. Numbers then declined to zero about an hour before sunrise (Figure 4). This was especially noticeable in January and February, but was also true in November and December. Second, a majority of the nocturnal terns heard south and west of Johnston Atoll was apparently moving north and northwest towards the atoll, or towards other breeding islands farther north and northwest in the Leewards. The number moving in southerly directions was almost nil. Unfortunately, adequate records for nocturnal direction of movement are available only for January and February of 1966 (Figure 5).

A similar nocturnal-diurnal pattern occurred on the breeding island at Johnston Atoll. Lowest numbers of Sooty Terns occurred in October and November when only a few individuals and small flocks visited the island briefly and irregularly. These were probably wandering pelagic birds that happened to pass the island and were temporarily attracted to it, primarily at night or just at dusk. They rarely landed on the island. Potential breeding birds were first observed at the island between late November (1964–1965) and late December

(1963). In 1966 flocks first occurred near the island during the first two weeks of December. These birds first gathered offshore at night, then began settling on the island in small groups. These groups grew until much of the land was occupied. This development took several weeks, generally lasting through mid-February, during which no more than a few wandering birds were over the island during the day. All of those on the ground at night left shortly before dawn. Finally, the birds began to stay on the island during the day, after which courtship and egg laying followed in quick succession (POBSP, Philip Shelton). Sooty Terns occurred within 50 miles of the atoll in fair numbers during the day throughout this period, especially in January and February.

Several causative and perhaps interrelated factors have been suggested to explain the day-night differences in January-February densities. Although none of these explanations is complete in itself, one or more may provide part of the answer.

1. At this time of year Johnston birds are known to avoid land during the day, and to be attracted to it at night. Birds may react toward ships in the same way, thus avoiding diurnal detection at sea.

2. Sooty Tern migration may be rapid and nocturnal. Birds may "pile up" in preferred feeding areas during the day and complete the last leg of their migration in a single night.

3. Most Sooty Terns may remain within 50 miles of Johnston during the day even though they avoid close approach to land.

4. The area southwest of Johnston is probably very poor in available food. Terns leaving Johnston before dawn may pass through the area before sunrise and return through the area after sunset. A lack of food would deter them from pausing within the area.

5. The January and February nocturnal aggregations may represent prebreeding swirls from Johnston Atoll. W. B. Robertson of the National Park Service (pers. comm.) informs me that early prebreeding swirls at the Tortugas often do not seem to be oriented toward the colony site. Instead they may occur anywhere around the general area and, quite possibly, well outside the area.

Although egg-laying commences in late February on Johnston Atoll, at-sea densities of Sooty Terns continued to increase through March in the surrounding waters. This was consistent with a con-

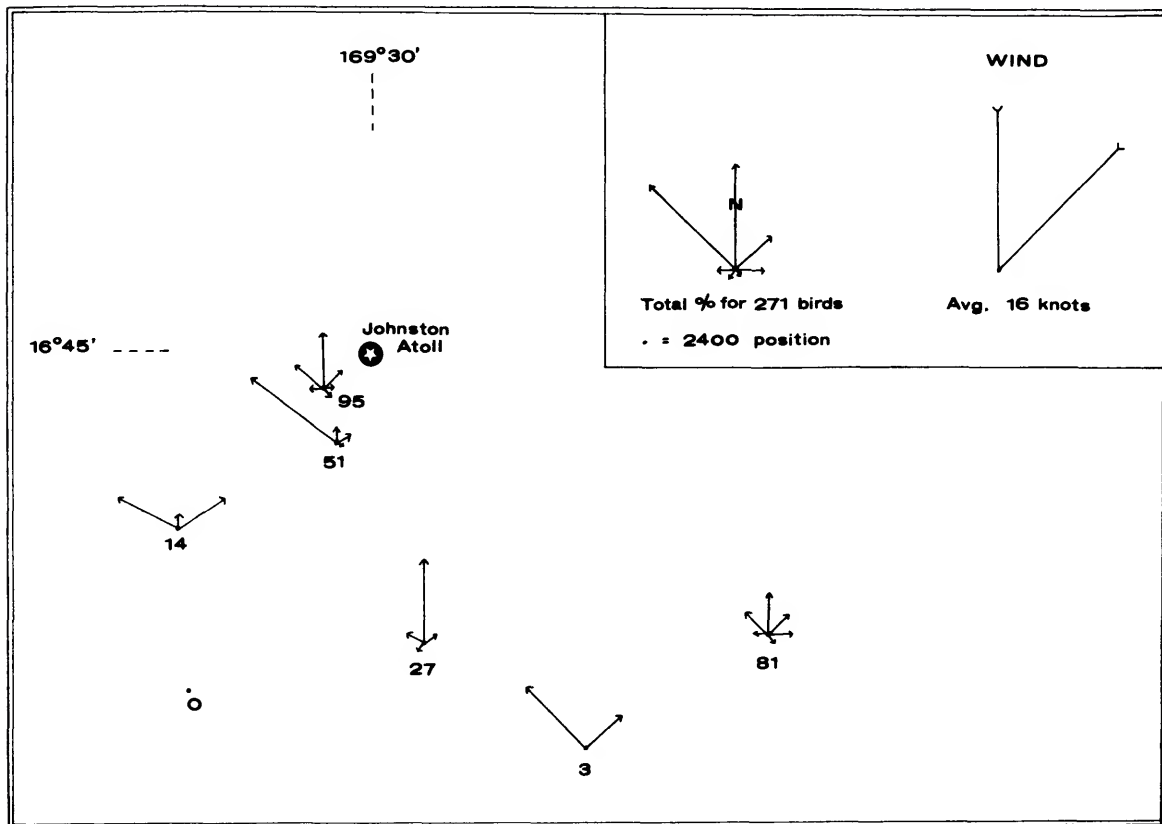


FIGURE 5.—Nocturnal flight directions for Sooty Terns southwest of Johnston Atoll during January-February 1966. (Arrows indicate direction in percent, numbers indicate sample size.)

tinued increase of birds on the island. Maximum island and at-sea densities were generally maintained through July, although some terns began leaving Johnston Atoll in early June.

During the northern summer, densities in the 1-5 BPM range were common over 50 miles from land, and ranged from 0.0-8.0 BPM. Densities up to at least 26.9 BPM were recorded within 50 miles of the breeding islands at this time. The largest single concentration of Sooty Terns recorded by the POBSP north of the equator, however, occurred on 20 May 1966, at 17°54'N, 158°48'W, some 200 miles south of Oahu.

Repeated observations to the northeast of the Hawaiian Islands illustrate the seasonal expansion and contraction of Sooty Tern distributional limits in the north central Pacific (Figure 6). During the

nonbreeding season, in particular November-December, birds were rarely recorded over 100 miles northeast of Hawaii. With the return of the birds and the beginning of nesting activities (March-April), distributional limits were extended, and by July-August, when chicks were being fed, birds were found up to 600 miles northeast of Hawaii. The northernmost sighting in the central Pacific was of two adult-plumaged birds recorded at 33° 06'N, 164°08'W on 9 August 1966.

To summarize, at-sea densities of Sooty Terns in the north-central Pacific Ocean are reflections of breeding island densities. The annual cycle is represented by a fairly smooth curve, with lowest density in November-December and highest density in June (Figure 7).

To clarify the distributional patterns of birds

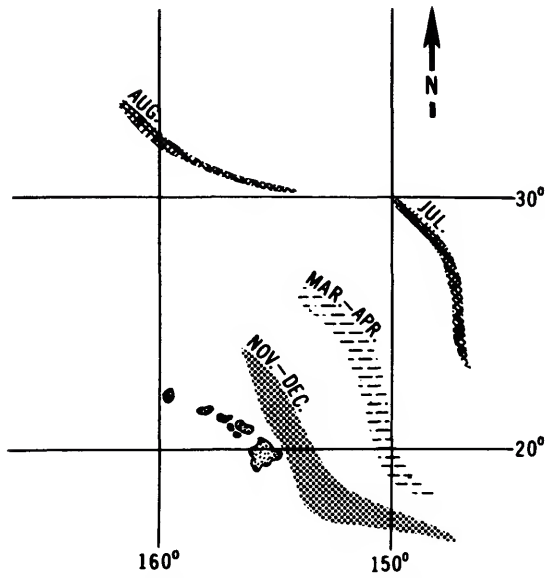


FIGURE 6.—Seasonal variation in the distributional limits of Sooty Terns northeast of the Hawaiian Islands.

within the central Pacific, the POBSP initiated an intensive banding program. Since March 1963, over 1,200,000 Sooty Terns have been banded. These include birds from nearly all major breeding colonies on the main and leeward Hawaiian, Line, and Phoenix (including Howland) island groups, as well as on Johnston and Wake atolls. Greatest numbers have been banded on Johnston (over 250,000), Laysan (over 130,000), and Howland (over 100,000). Colored vinyl leg streamers were also placed on birds from Johnston (orange) and Howland (blue). A special effort was made on all POBSP field trips, both at sea and on islands, to look for streamered and banded birds. In addition, a program of intensive advertisement of our efforts, including appeals for help in locating banded and streamered birds, was made throughout the inhabited areas of the tropical and subtropical Pacific.

As of December 1968, we have processed 1027 interisland and at-sea recoveries and 339 at-sea streamer sightings of Sooty Terns. These represent

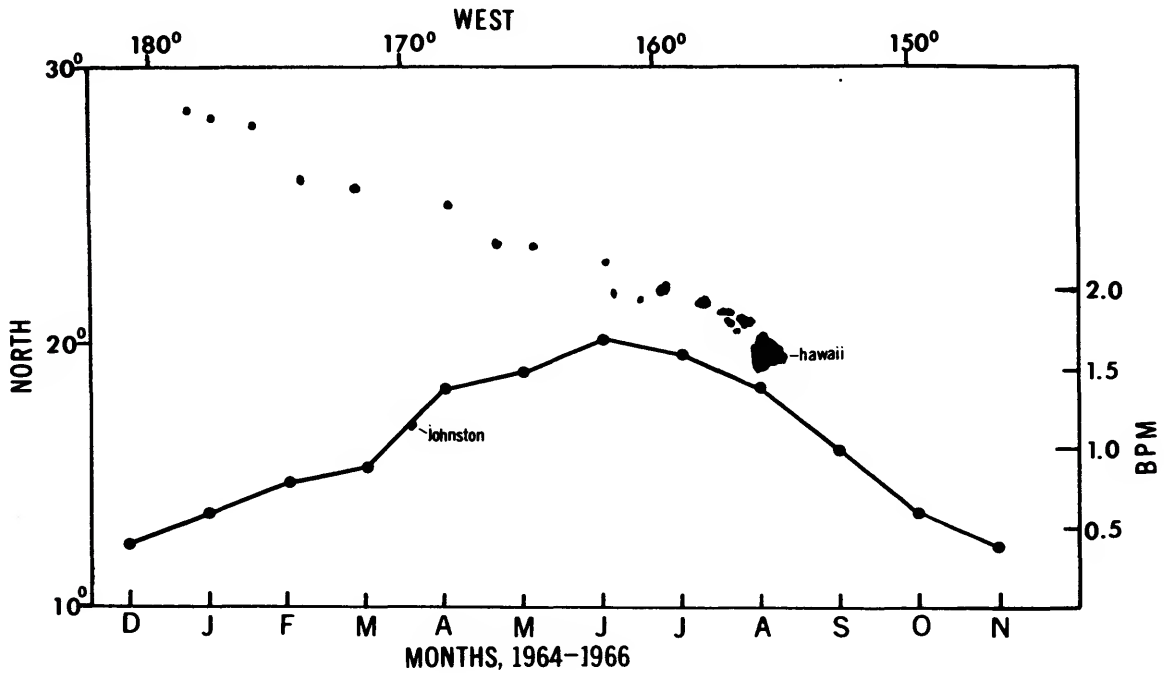


FIGURE 7.—Annual at-sea density cycle for Sooty Terns in the north-central Pacific.

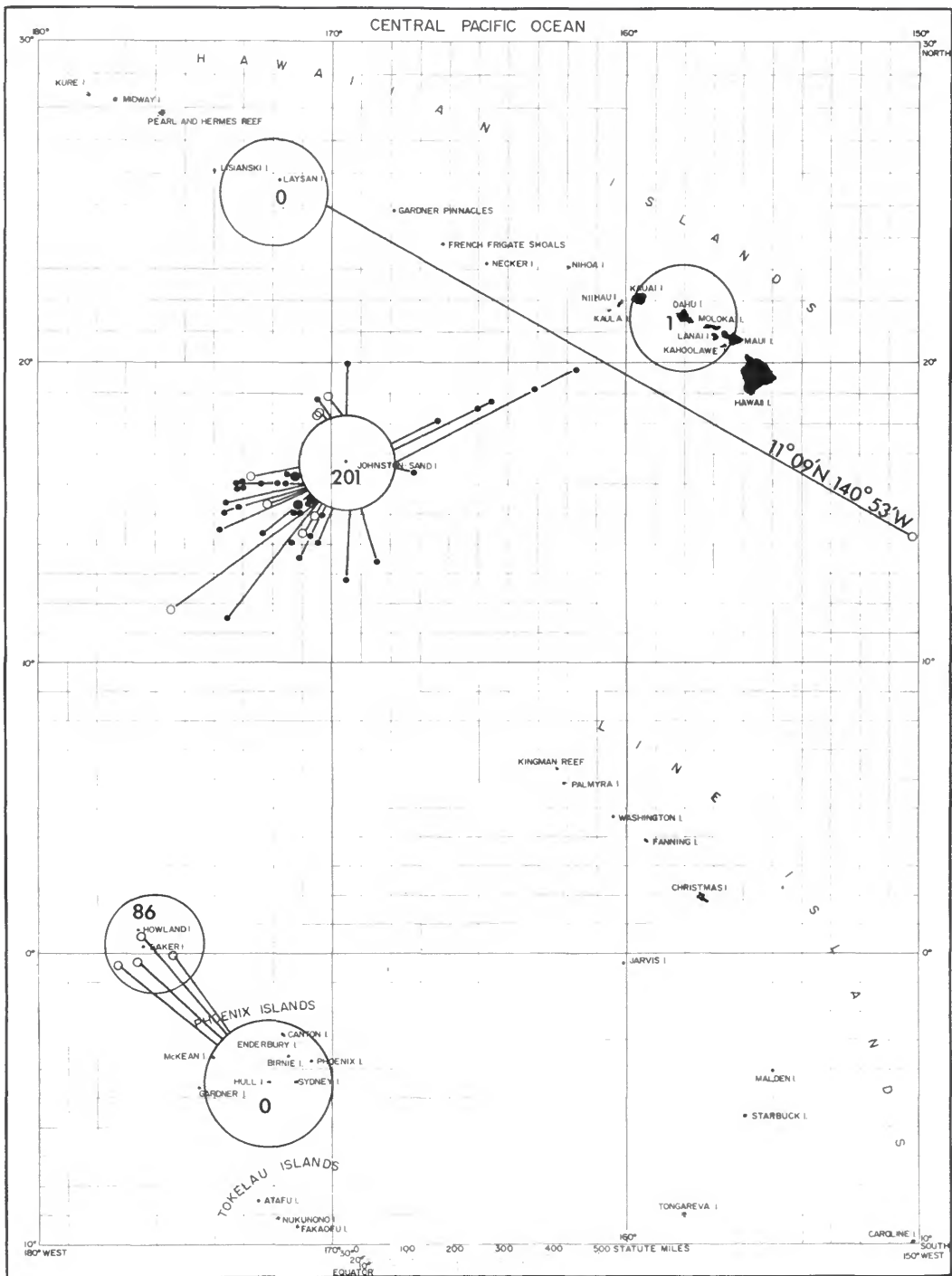


FIGURE 8.—Distribution of banded and streamered Sooty Tern sightings.

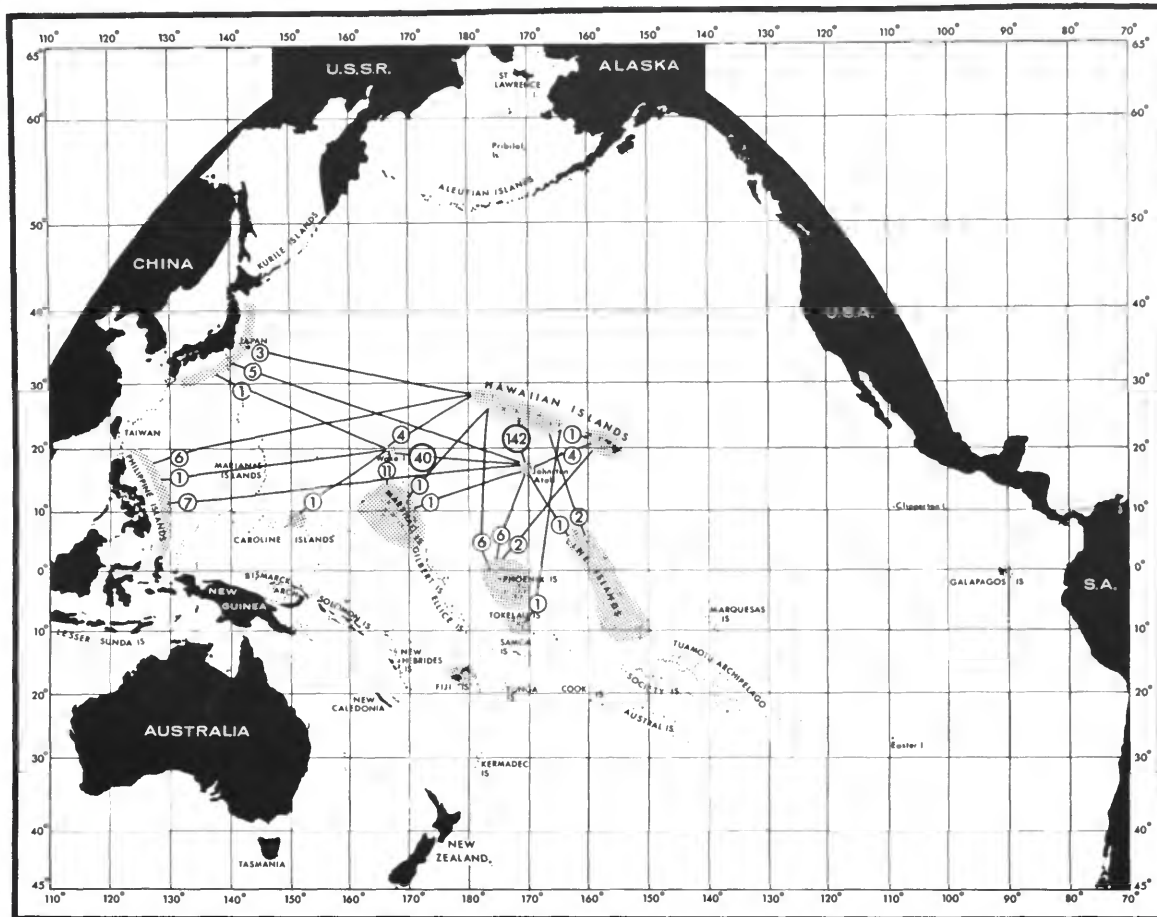


FIGURE 9.—Interisland movements of Sooty Terns banded in the north-central Pacific.

less than 0.01 percent of the total number banded. Over one-half of the interisland recoveries represent elapsed times greater than one year and 68 percent were short-distance movements within island groups (e.g., between Kure and Midway atolls). It is thus too early to attempt a detailed analysis of the banding data. Since some of these records provide insight into the confusing pelagic dispersal of Sooty Terns, however, a brief summary is presented here.

Two hundred and thirty-five orange-streamered birds have been observed at sea (Appendix Table B). All were in the central Pacific north of 11°N. Similarly, orange-streamered birds have been seen and handled on most islands in the same area, but none have been observed on islands farther south. No blue-streamered birds have been recorded north

of 02°N. Ninety-six percent of all orange-streamered birds were recorded during the breeding season (March-August). Of these, 70 percent were within fifty miles of Johnston Atoll even though over 80 percent of all observation time in that general area was spent over 50 miles from the atoll. During the breeding season, four streamered birds were sighted over 275 miles from Johnston (one adult in August, 278 miles SE; one immature in August, 287 miles SW; one adult in August, 392 miles SW; and one adult in March, 392 miles SW). We have 10 records of 13 streamered birds feeding at distances up to 225 miles from Johnston (April-June). Recently fledged streamered birds have been found over 100 miles from the breeding colony only during August (3 birds: 180, 226, and 287 miles SW). During the nonbreeding season (September-

February), three of a total of eight orange-streamer sightings were over 50 miles from Johnston (two in September, 394 and 481 miles NE; and one in December, 299 miles ENE). The remaining five were found in September, January, and February, and were probably late departing or early arriving birds.

Twelve banded birds (10 from Johnston, 1 from Oahu, and 1 from Laysan) have been recovered at sea (Appendix Table C). As with the streamer sightings, all were from the central Pacific north of 11°N. All but three were recovered over 100 miles from the site of banding. One immature banded on Laysan in August was recovered four months later 1170 miles to the southeast. Another, banded on Johnston in July, was recovered four months later 460 miles to the southwest. Figure 8 is a spatial summary of all at-sea streamer sightings and band recoveries.

The above data suggest that during the breeding season, Johnston-based Sooty Terns may forage up to 300 miles from the breeding colony, but that the greatest numbers remain within 50 miles. At the end of the breeding season, adults and immatures disperse widely at sea and many disappear from the north-central Pacific. Four late fall and early winter orange-streamer sightings show dispersal from Johnston of birds to the northeast (three) and to the southwest (one). The one late fall record from Laysan was to the southeast.

Figure 9 summarizes interisland movements of Sooty Terns involving the main and leeward Hawaiian, Johnston, and Wake islands. Unfortunately, few of these recoveries involve known status birds (e.g., breeding, nonbreeding), or elapsed times less than the length of one breeding season. It is thus impossible to connect the islands of banding and recovery with meaningful directional arrows.

TABLE 9.—*Interisland Sooty Tern movements occurring within six months of banding*

Banding and recovery locations	Recovery month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Hawaiian banded:												
Hawaiians	-	-	-	-	-	2*	1*	-	-	-	-	-
Leeward banded:												
Leewards	-	-	-	-	-	2	2	9	-	-	-	-
Johnston	-	-	-	-	-	-	1	1	-	-	-	-
Japan	-	-	-	-	-	-	-	-	2	-	-	-
Philippines	-	-	-	-	-	-	-	-	-	-	-	1
Johnston banded:												
Leewards	-	-	-	-	-	1	3	16	-	-	-	-
Japan	-	-	-	-	-	-	1*	-	1+1*	-	-	-
Philippines	-	-	-	-	-	-	-	-	-	-	1	-
Wake banded:												
Johnston	-	-	-	-	-	-	2	2	-	-	-	-
Carolines	-	-	1*	-	-	-	-	-	-	-	-	-
Japan	-	-	-	-	-	-	-	1*	-	-	-	-
Phoenix banded:												
Phoenix	3	8	-	-	1	-	3	-	2	-	-	-
Leewards	-	-	-	-	-	1	-	-	-	-	-	-
Line banded:												
Leewards	-	-	-	-	-	-	-	1	-	-	-	-
North Pacific banded:												
North Pacific	-	-	-	-	-	5	9	28	-	-	-	-
Western Pacific	-	-	1	-	-	-	1	1	4	-	1	1
South Pacific banded:												
South Pacific	3	8	-	-	1	-	3	-	2	-	-	-
North Pacific	-	-	-	-	-	-	-	1	-	-	-	-

*Banded as locals or immatures.

Table 9 summarizes all recoveries made less than 6 months after time of banding. It is apparent, however, that there is considerable interisland movement between islands of the north-central Pacific. Birds banded on Johnston regularly occur on Wake and in the main and leeward Hawaiians and vice versa. Similarly, much movement occurs between islands of the south-central Pacific. A certain amount of interchange between these two areas has been recorded, but our eighteen records probably exaggerate its amount. The lack of orange-streamer sightings in the southern islands, and blue-streamer sightings in the northern islands, particularly on frequently surveyed islands such as Howland and Johnston, indicate that some of the north-south band recoveries may be due to misread band numbers. Unfortunately, none of the north-south band recoveries have been substantiated by the collection of the bird or the removal of its band. The relatively large number of these north-south records, however, indicate that such movements may occur.

Twenty-eight *POBSP*-banded birds have been re-

covered in the western Pacific. Ten were reported as being associated with typhoons, and three with stormy weather. Another three were reported exhausted when found. By comparing the dates and localities of recapture with typhoon and tropical storm tracks in the western Pacific (Joint Typhoon Warning Center, 1965, 1966, 1967; DeAngelis, 1968, 1969), a total of 20 can be directly associated with typhoons and tropical storms (Table 10). This indicates that at least a majority of banded birds recovered in Japan and the Philippines was driven there by storms. By analyzing the origin and pathway of these storms, it is possible to make assumptions as to the area these Sooty Terns were carried from and thus determine at least part of their non-breeding range.

Typhoons in the northwest Pacific appear to originate in the area between 5°N and 20°N, and between 170°E and the Philippines. The United States Naval Oceanographic Office (1964:42) describes the typhoon tracks in this area as follows:

... the greater number of typhoons conform to the usual tropical cyclone track pattern and move initially westward or

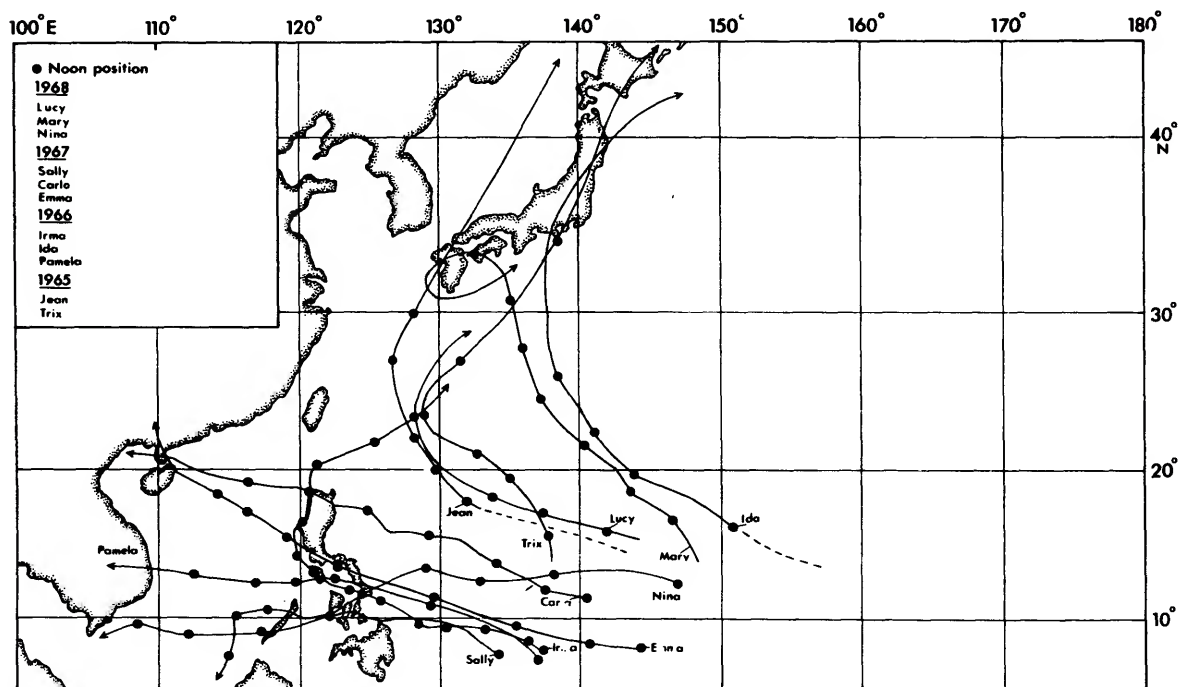


FIGURE 10.—Tracks of typhoons which blew banded Sooty Terns to the western Pacific.

TABLE 10.—*Sooty Tern recoveries from the western Pacific*

<i>Recovery location</i>	<i>Date</i>	<i>Remarks</i>	<i>Banding location</i>	<i>Date</i>	<i>Age</i>
Leyte, Philippines (ca. 11°N, 126°E)	7 Mar 65	tropical storm Vera off Leyte on 7 Mar 65; bird exhausted by "typhoon" winds	Johnston	8 May 64	local
Southern Honshu, Japan (34°40'N, 135°56'E)	7 Aug 65	typhoon Jean moved north over Kyushu 5 Aug 65; birds "typhoon-driven"	Wake	1 May 65	nestling
Honshu, Japan (37°40'N, 139°10'E)	18 Sep 65	typhoon Trix over eastern Honshu on 17 Sep 65	Johnston	11 May 65	local
Southern Leyte, Philippines (ca. 10°N, 125°E)	before 17 Dec 65	typhoon Faye passed about 250 mi NE of islands on 23 Nov 65	Laysan	9 Aug 65	adult
Masbate, Philippines (ca. 12°N, 122°E)	before 22 Dec 65	as above; bird exhausted	Johnston	26 May 65	local
Isabela, Philippines (prob. 10°35'N, 124°E)	before 10 Mar 66	no typhoons or tropical storms since Faye passed 250 mi NE on 23 Nov 65	Johnston	28 May 65	local
Near Ticao, Philippines (12°30'N, 123°50'E)	20 Mar 66	as above	Johnston	7 Jun 65	local
Tarlac, Luzon, Philippines (ca. 15°30'N, 125°E)	20 May 66	typhoon Irma over SW Luzon on 18 May 66; bird in wake of typhoon Irma	Midway	27 Jul 65	nestling
Southern Honshu, Japan (34°50'N, 138°20'E)	25 Sep 66	typhoon Ida passed over Honshu on 24 Sep 66; birds "typhoon-driven"	Johnston	22 Mar 66	adult
Honshu, Japan (35°19'N, 139°22'E)	25 Sep 66	as above; no recapture data	Midway	12 Jun 66	breeding adult
Honshu, Japan (35°00'N, 138°20'E)	25 Sep 66	as above; bird "typhoon-driven"	Lisianski	17 Jun 66	adult
Southern Luzon, Philippines (ca. 15°N, 121°E)	4 Jan 67	no typhoons or tropical storms since Pamela on 27 Dec 66; raining	Johnston	13 Mar 66	adult
Eastern Samar, Philippines (12°N, 125°20'E)	11 Jan 67	as above; bird exhausted	McKean	19 Jul 64	adult
Mawmawan, Philippines (ca. 10°N, 124°E)	4 Feb 67	as above; bird in heavy rain in front of "typhoon"	Johnston	15 Jun 66	adult
Philippines (no location specified)	? Feb 67	as above; bird "storm-driven"	Wake	15 Jun 66	nestling
Southern Leyte, Philippines (ca. 10°N, 126°E)	3 Mar 67	typhoon Sally passed over central islands on 3 Mar 67	Howland	19 Jul 66	adult
Toledo City, Philippines (ca. 10°20'N, 124°E)	4 Mar 67	as above; bird at height of typhoon Sally	Christmas	12 Mar 66	nestling
Negros Island, Philippines (09°10'N, 123°10'E)	4 Mar 67	as above; male bird	McKean	21 Sep 65	local
Southeast Luzon, Philippines (13°30'N, 123°10'E)	6 Mar 67	as above; bird weak	Howland	16 Aug 66	local
Northern Luzon, Philippines (ca. 15°40'N, 121°E)	17 Oct 67	typhoon Carla passed over northern Luzon on 17 Oct 67; after typhoon Trining	Midway	27 Jul 65	nestling
Southeast Luzon, Philippines (ca. 13°20'N, 123°20'E)	3 Nov 67	typhoon Emma passed over southern Luzon on 3 Nov 67; stormy	Johnston	14 Jun 67	local
Southern Luzon, Philippines (ca. 14°15'N, 121°15'E)	4 Nov 67	as above; "typhoon-driven"	Midway	22 Jul 64	local
Eastern Samar, Philippines (11°40'N, 125°20'E)	4 Nov 67	as above; bird after typhoon Welling	Midway	8 Sep 64	immature
Honshu, Japan (35°20'N, 139°35'E)	26 Apr 68	cannot be accounted for by typhoons or tropical storms	Laysan	6 Aug 65	adult
Shikoku, Japan (ca. 33°30'N, 133°30'E)	3 Jul 68	last stages of typhoon Lucy passed about 250 miles S of Shikoku on 2 Jul 68	Johnston	8 Mar 64	adult
Shikoku, Japan (ca. 33°30'N, 133°30'E)	28 Jul 68	typhoon Mary passed over Shikoku on 28 Jul 68	Johnston	20 May 68	local
Shikoku, Japan (ca. 33°30'N, 133°30'E)	29 Jul 68	as above	Johnston	2 May 66	adult
Negros, Philippines (ca. 10°N, 123°E)	25 Nov 68	typhoon Nina passed over Negros on 24 Nov 68	Midway	13 Jun 66	adult

west-northwestward from the source region. Those that reach higher latitudes, normally north of 15°N, have a tendency to recurve and move in a northeasterly direction over or to the east of Japan. A considerable number, however, travel almost due westward and eventually dissipate over the Philippines or the China coast. At the height of the typhoon season over the western Pacific (July through October) the majority of these storms passes to the north of the Philippines moving toward Taiwan, the Japanese Islands, and the China coast. . . . During the so-called slack season (December through February) many continue on a westward course and enter the South China Sea.

Figure 10 shows the typhoon and tropical storm tracks that can be associated with POBSP band recoveries in the western Pacific. All originate in, or immediately southeast of, the Philippine Sea, and all pass through it. Thus, the Philippine Sea must constitute at least part of the nonbreeding range of north-central Pacific Sooty Terns. The only typhoon that can be associated with birds from the Line and Phoenix islands was Sally in 1967. This was the most southern of all Sooty Tern-bearing typhoons, and had the southwesternmost point of origin. No northern birds were reported as a result of this storm. Lane (1967), however, reports the recovery of a Sooty Tern originally banded on Roach Islet, Lord Howe, New South Wales, 28 November 1962, from southern Leyte, Philippines, on 4 March 1967. This is the same recovery date and area as two of our recoveries associated with typhoon Sally. This suggests that the nonbreeding ranges of south-central and north-central Pacific terns are essentially allopatric. Unfortunately, literature records from this area are scarce. Brinkley (in Bourne and Radford, 1961) recorded seven birds in August at 22°N, 124°E. In late October, Mörzer Bruyns (1965) recorded two groups of 50 birds each at approximately 9°N, 131°E, three groups of 40, 10, and 3, near 7°N, 142°E, and possibly two birds at 7°N, 150°E. He did not, however, find any terns in late October or early November near the Palau, western Caroline, or Marshall islands. Records for the timing of the breeding cycle in the Carolines are lacking so that we do not know whether the birds he observed were of that population.

EQUATORIAL CENTRAL PACIFIC.—Sverdrup, et al. (1942:709) point out that the Equatorial Countercurrent is remarkably well developed in the Pacific Ocean, present at all seasons, lies always in the northern hemisphere, and is farther north in the

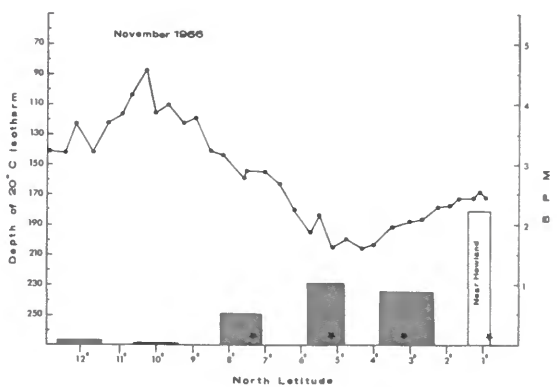
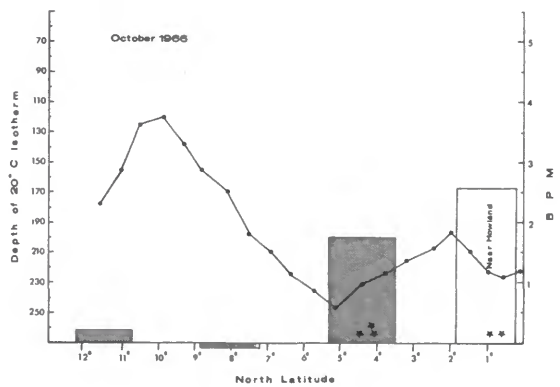
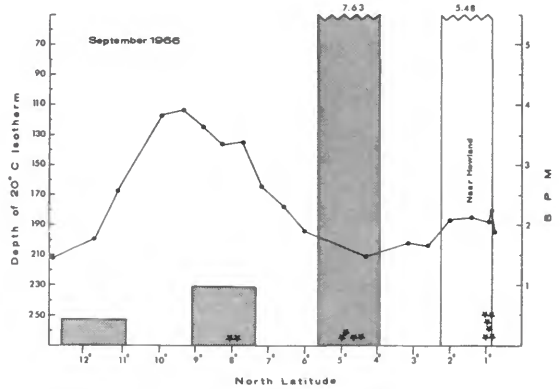
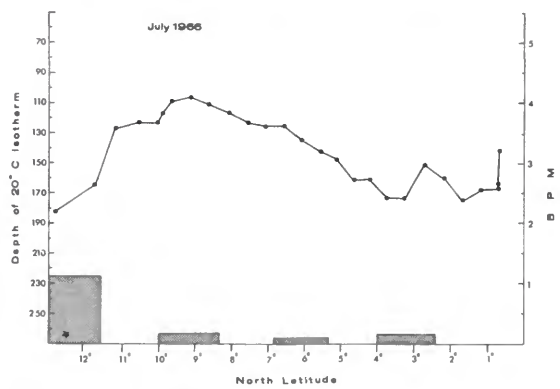
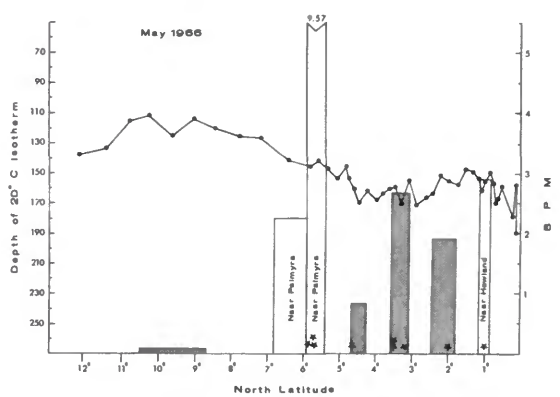
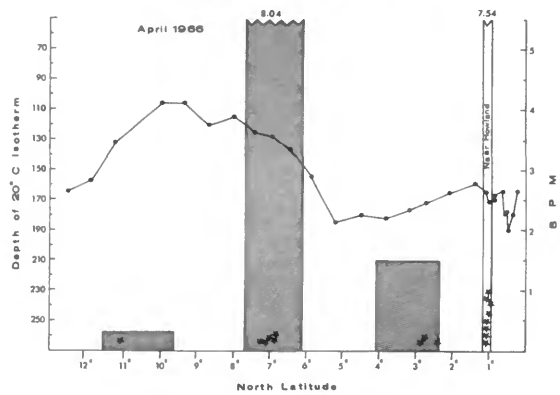
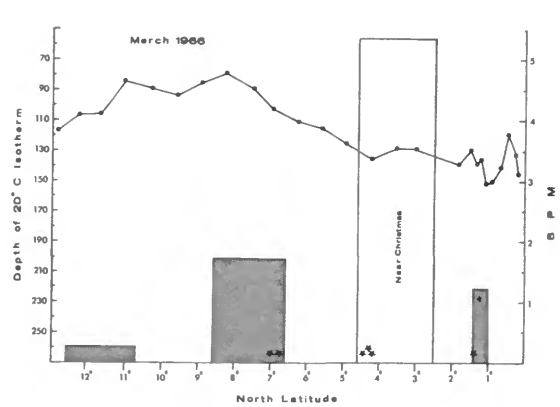
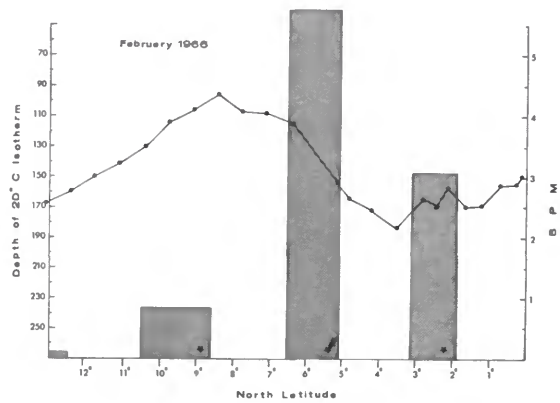
northern summer. Barkley (1962:5) shows that the borders of this current generally lie between 4°–5°N and 9°–10°N. North of the Countercurrent is the westward flowing North Equatorial Current, while south is the westward flowing South Equatorial Current. Data from the Carnegie Expedition (Sverdrup, et al., 1942:711) state that

within the Equatorial Countercurrent descending motion takes place at the southern boundary and ascending motion at the northern boundary, and between the Equator and the Countercurrent descending motion takes place at the boundary of the Countercurrent and ascending motion at the Equator. Thus, two cells appear with divergence at the northern limit of the Countercurrent and at the Equator, and with a convergence at the southern boundary of the Countercurrent.

Ashmole and Ashmole (1967) have discussed the distribution of seabirds with relation to the equatorial currents in the central Pacific. They make several points which are relevant to the following discussion: (1) Most tropical seabirds depend, at least in part, on schools of fish to drive their prey close to the surface. (2) Upwelling waters are generally rich in nutrients and zooplankton. (3) As water moves away from divergence areas, phosphate and zooplankton decrease and forage animals increase. (4) In the equatorial current area fish schools are generally most abundant within the Countercurrent. They (1967:107) conclude that "localized concentrations of plankton and nekton produced by convergence and sinking of surface waters at 'fronts' which have been suggested as exerting important effects on the distribution of surface schools of tunas in the open ocean, may also provide favorable feeding grounds for many oceanic birds." Other authors, among them King and Pyle (1957) and Mörzer Bruyns (1965) have shown some of the effects of oceanic currents in the central Pacific on the density and distribution of seabirds.

From January 1964 through 1967 twenty cruises were made by the POBSP across the equatorial currents (0°–13°N) between 148°W and 180°. Surface water temperatures ranged between 25.5° and 30.6°C with the majority falling between 27.0° and 29.5°C. Barkley (1962) presented averaged temperatures for this area of 27° to 28°C., and averaged salinities of 34.30 to 35.40 ppt.

→
FIGURE 11.—Sooty Tern density in relation to equatorial currents in the central Pacific between longitudes 148°W and 180°.



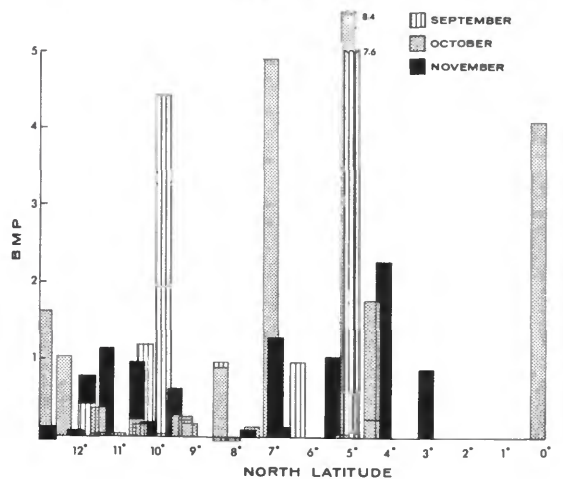
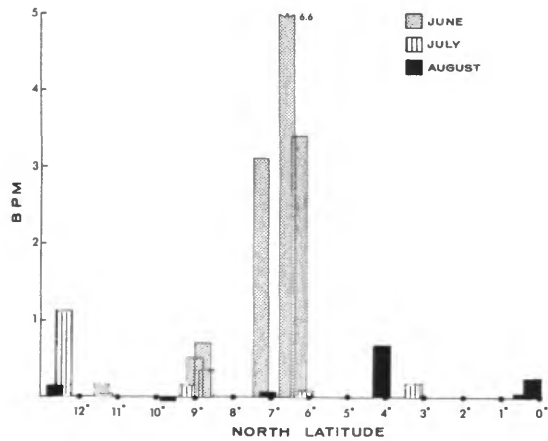
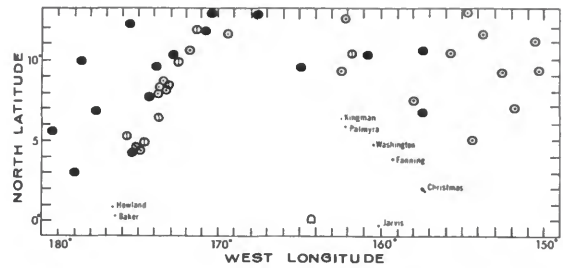
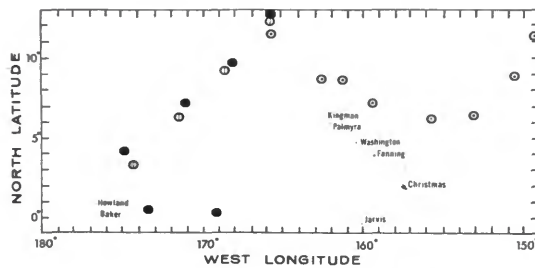
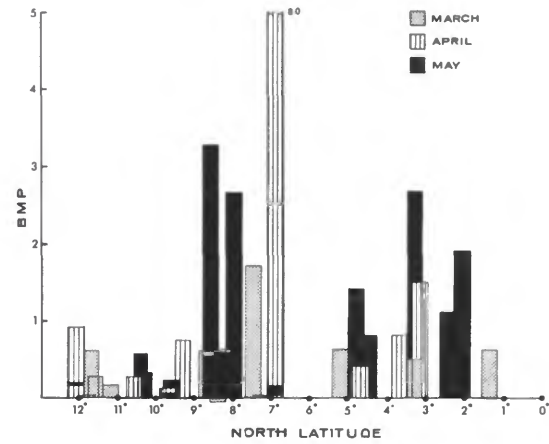
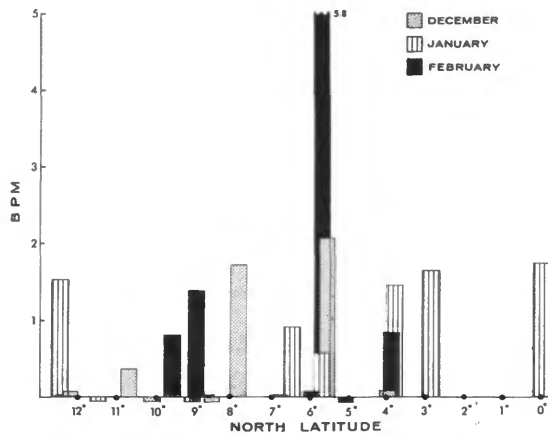
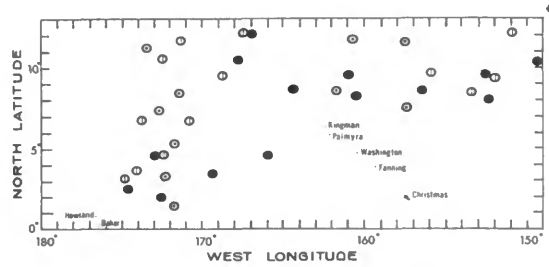
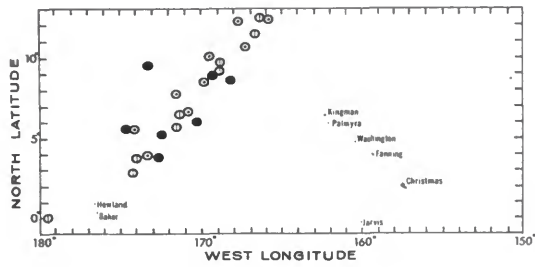


Figure 11 shows latitudinal variation of Sooty Tern densities plotted against the depth of the 20°C isotherm for five 1966 cruises. The slope of this isotherm can be used as a rough indication of the position of major currents. Figure 12 presents density data for all 20 cruises on a seasonal and monthly basis, while Figure 13 shows a composite of all 1965–1966 densities and an average density per each degree of latitude.

Ignoring areas under the immediate influence of islands (i.e., areas within 50 miles of Howland, Christmas, and Palmyra) Sooty Terns are more abundant within the Equatorial Countercurrent than in either the North or South Equatorial currents. The South Equatorial Current has greater Sooty Tern densities than the North Equatorial Current, possibly because of the more direct influence of islands and/or the convergence at its northern border. It is within the convergence area that greatest over-all densities have been recorded (Figure 13). Our data thus support the assumptions reached by the Ashmoles. Our data also suggest, but are too few to prove, a seasonal shift in high densities from the convergence area (4°N–5°N) in the fall, to the northern Countercurrent area (7°N–9°N) in the spring. Intervening seasons are intermediate, with greatest winter densities recorded in the area of 5°N to 6°N, and greatest summer densities in the area of 6°N to 7°N. The more northerly position of high density in spring and summer might be explained if many of the terns in the Countercurrent area were part of the northern islands' (e.g., Johnston Atoll) breeding population. Unfortunately, there have been no band returns or color-streamer sightings from this area. It seems quite probable that Sooty Terns in the equatorial currents are from islands in both the north and south central Pacific and that the influence of each area varies with the season and with the local breeding schedule.

Within the equatorial currents lie a number of islands, most of which support large Sooty Tern colonies. These include the Line Islands: Kingman Reef (06°24'N), Palmyra (05°52'N), Washington (04°43'N), Fanning (03°52'N), Christmas (01°51'N) and Jarvis (00°23'S), and two islands often consid-

ered part of the Phoenix group: Howland (00°45'N), and Baker (00°13'N). The latter two islands have been intensively investigated by the POBSP with respect both to island and at-sea bird populations.

The POBSP observations show a very close relationship between the breeding schedule and densities on Howland Island, and at-sea densities within a 100-mile radius of it (Figure 14). Peak at-sea densities occurred during each of the two major egg-laying periods in 1966–1967. The large numbers of birds at sea during September and October 1965 while island populations were at their lowest are thought to be due to birds from other populations moving into or through the area. The only evidence for this was the collection within the area in October of three immature and one adult Sooty Terns originally banded on Hull Island three to eight weeks earlier. At-sea collections and sightings of banded or color-tagged birds during all other surveys were of Howland-marked birds.

SOUTH-CENTRAL PACIFIC.—Pelagic observations were conducted on 13 POBSP surveys to the south-central Pacific from March 1964 through February 1967. During most of these trips many days were spent in the Phoenix Islands. Twelve trips continued south to eastern Samoa and one to the Fiji Islands. Two general cruise tracks were used, one by way of the Tokelaus and Swain's Island, and the other by way of Rakahanga and the Danger Islands. Table 11 summarizes the distribution and abundance of Sooty Terns during these trips. The area of coverage was too restricted, and the timing of observations too unevenly spaced to allow more than the following brief summary.

Sooty Terns were abundant at all times of the year on and around the Phoenix Islands. Highest densities were recorded from September through February, particularly October to December. Annual at-sea abundance cycles in this area, however, cannot be evaluated because of the variation in the timing of breeding cycles between the islands, and because of the nearness of these islands to one another and our inability to assign island origins to birds observed at sea. These factors prevented relating a daily at-sea density to a particular island. Also May–September records are few while October–April records are numerous. South of the Phoenix Islands these terns became progressively less abun-



FIGURE 12.—Sooty Tern density across the equatorial central Pacific.

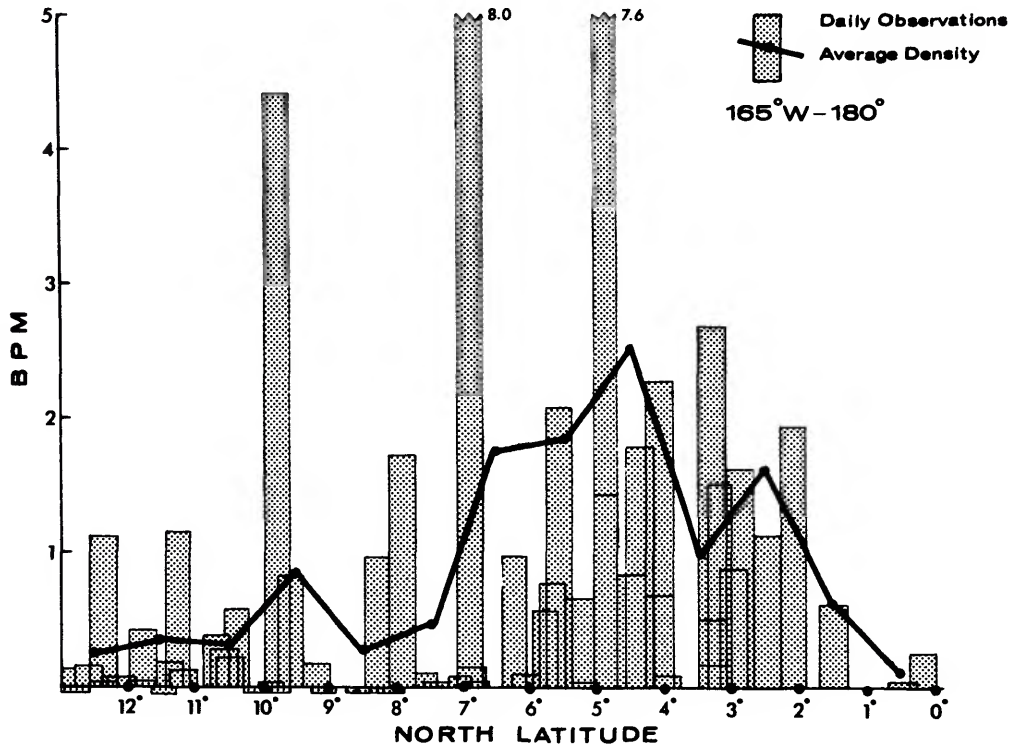
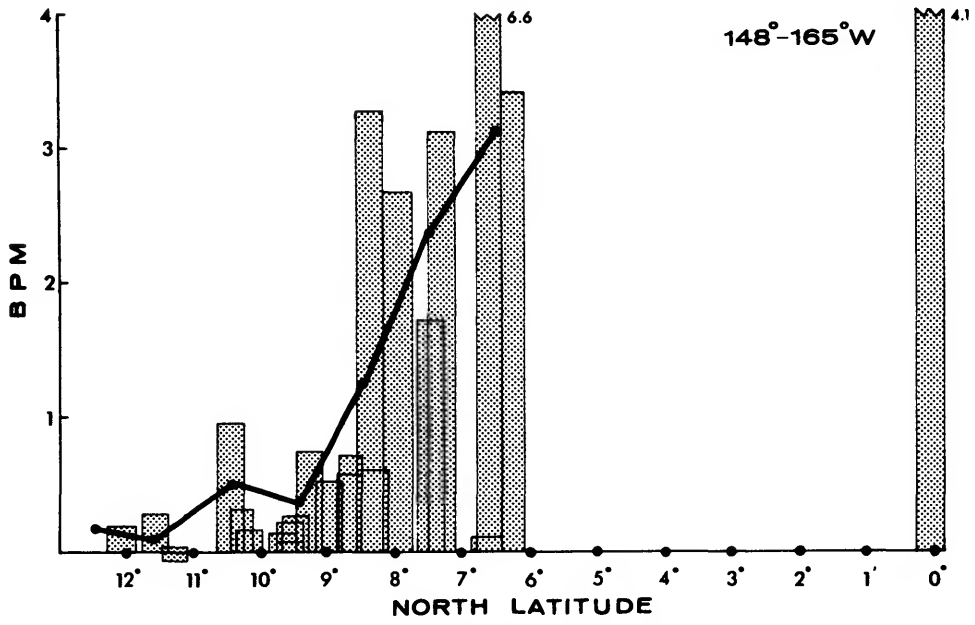


FIGURE 13.—Summary of Sooty Tern densities across the equatorial central Pacific during 1965-1966.

HOWLAND ISLAND

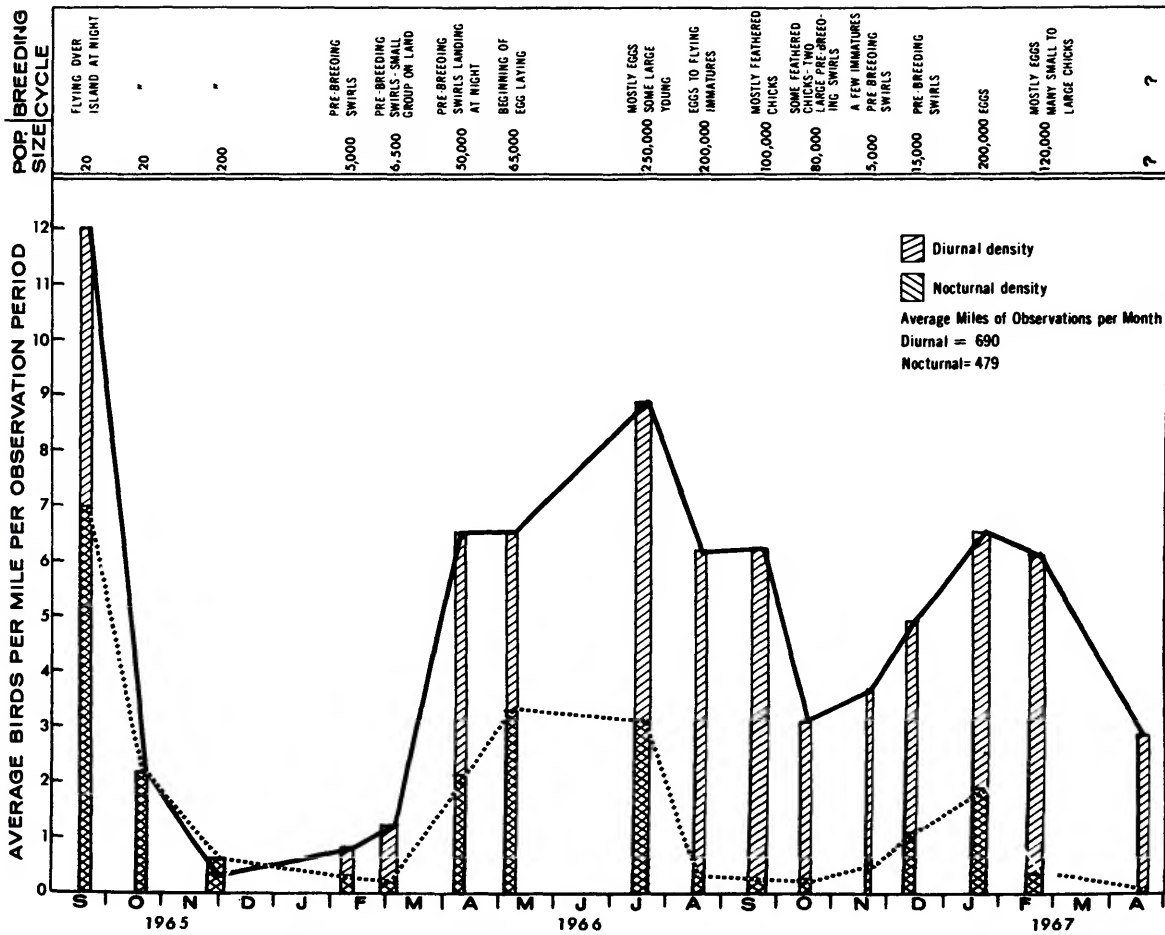


FIGURE 14.—Correlation of at-sea densities (within 100 miles of Howland) of Sooty Terns with the breeding schedule and population fluctuations of Howland Island.

dant, being seen on fewer days as well as in smaller numbers.

Movements of banded and streamered birds from this area are summarized in Table 10, Appendix Tables B, C, Figures 8, 10, and 15. These records are discussed under the section dealing with north-central Pacific banding results, and under the discussion of Howland Island in the equatorial central Pacific.

EASTERN PACIFIC.—Surveys in the eastern Pacific north of 30°N have been conducted from December 1966 through April 1968 off southern Califor-

nia and northern Baja California, generally on a semimonthly basis. South of 30°N surveys have been made in cooperation with EASTROPAC. POBSP personnel recorded observations during nine cruises. Three of these ran concurrently in January-March 1967, one in June-July 1967, two concurrently in August-September 1967, one in October-December 1967, and two concurrently in February-April 1968. The survey pattern was based on north-south cruise tracks along specific longitudes. Two of these tracks (119°W, 112°W) were followed five times each; two (105°W, 98°W) were followed

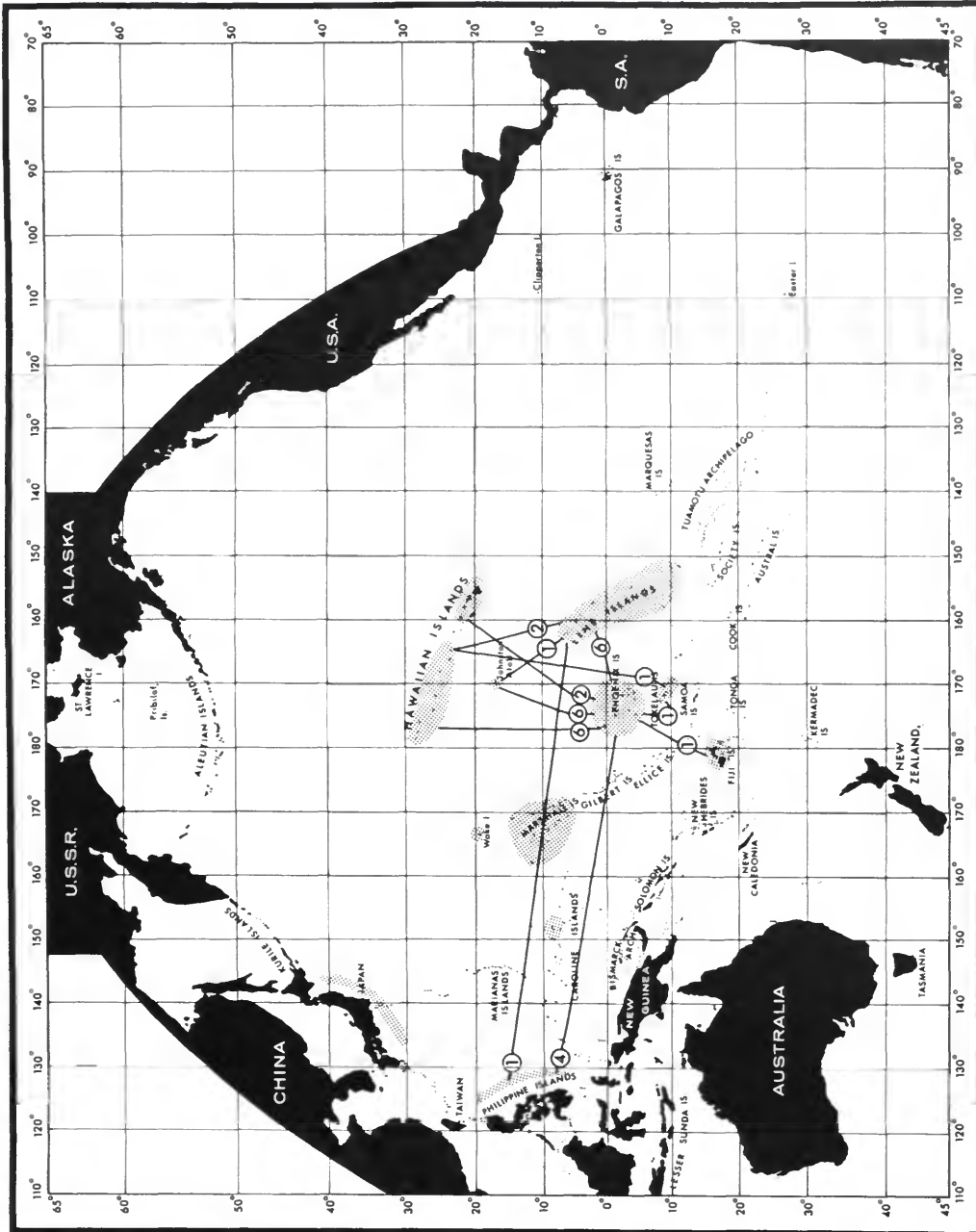


FIGURE 15.—Interisland movements of Sooty Terns banded in the south-central Pacific.

TABLE 11.—*Distribution and occurrence of Sooty Terns within 100 miles of south-central Pacific islands from March 1964 through February 1967*

Area	Days observed (No.)	Days recorded (No.)	Days recorded (%)	Average density (BPM)	Range of density (BPM)	Months of observations
Phoenix Islands	51	51	100	3.9	0.02–34.6	all except Jun and Aug
Tokelau I.	20	17	85	0.7	0.0–3.4	all except Jan and May
Rakahanga I.	2	1	—	0.3	0.0–0.6	Jun
Danger I.	3	3	—	0.3	0.03–0.7	Mar and Jun
Swains I.	17	13	76	0.1	0.0–1.0	all except Jan, May, and Dec
Wallis I.	2	2	—	0.6	0.04–1.2	Feb
E. Samoa	15	4	27	0.1	0.0–1.1	all except Jan, May, Sep, and Dec
Horn I.	2	2	—	0.1	0.02–0.2	Feb
Fiji I.	3	3	—	0.1	0.01–0.3	Feb
Total/average	115	96	83	1.9	0.0–34.6	all months

four times each; one (92°W) was followed twice; and three (126°W, 96°W, 88°W) were followed once.

Sooty Terns have never been recorded north of 26°N in the eastern Pacific, and POBSP personnel have not found them north of 22°N. Our data from the eastern Pacific are not complete enough to show much in the way of annual trends. Observations, for example, do not exist for May and December, and are minimal for January and April. Figures 17 through 28 summarize all POBSP records for the eastern Pacific (pp. 34–45).

Sooty Terns were generally common (1–5 BPM) in the Equatorial Countercurrent, particularly west of 110°W to 126°W, and along the Mexican coast from Acapulco north to the Gulf of California. Densities greater than 5 BPM were recorded on

only five days (Table 12). These were also either along the Mexican coast or in the Equatorial Countercurrent. We have never recorded Sooty Terns north of 15°46'N except at the mouth of the Gulf of California where birds have been seen north of 21°49'N. Anthony (1898), Kaeding (1905), Gifford (1913), and McLellen (1926) recorded Sooty Terns as breeding on the Revilla Gigedo Islands (19°N, 111°W) in the northern spring. However, during four days of POBSP observations within 150 miles of these islands (11 February, 20–21 March, 15 September) no Sooty Terns were seen. Brattstrom and Howell (1956) did not record this species there in March or November.

Only in February and March were observations made south of 20°S. During these two months Sooty Terns were common (1–5 BPM) in southern waters from 5°S to 14°S in the more western area (119°W–126°W), with scattered birds recorded to 19°48'S at 121°31'W. In August, Sooty Terns were likewise common from 5°S to 10°S, the southern limit of our observations.

Equatorial currents were probably as influential on Sooty Tern distribution and abundance in the eastern Pacific as they are in the central Pacific. There are, however, several important differences between the two areas. These appear to be significant in their effect on Sooty Terns. Wyrski (1966, n.d.) characterizes the Equatorial Countercurrents east of 120°W as clearly developed from May to December and absent from February through April. From May to December, west of 110°W, its bound-

TABLE 12.—*Date and location of Sooty Tern densities (BPM) greater than 5.0 in the eastern Pacific*

Date	Noon position	Area	Density
2 Feb 67	9°38'N, 119°00'W	Equatorial Countercurrent	8.8
22 Feb 67	22°18'N, 109°17'W	mouth of Gulf of California	7.8
5 Jun 67	17°56'N, 102°55'W	coast of Mexico	18.5
7 Jul 67	18°38'N, 104°48'W	coast of Mexico	6.1
5 Sep 67	7°42'N, 112°06'W	Equatorial Countercurrent	9.0

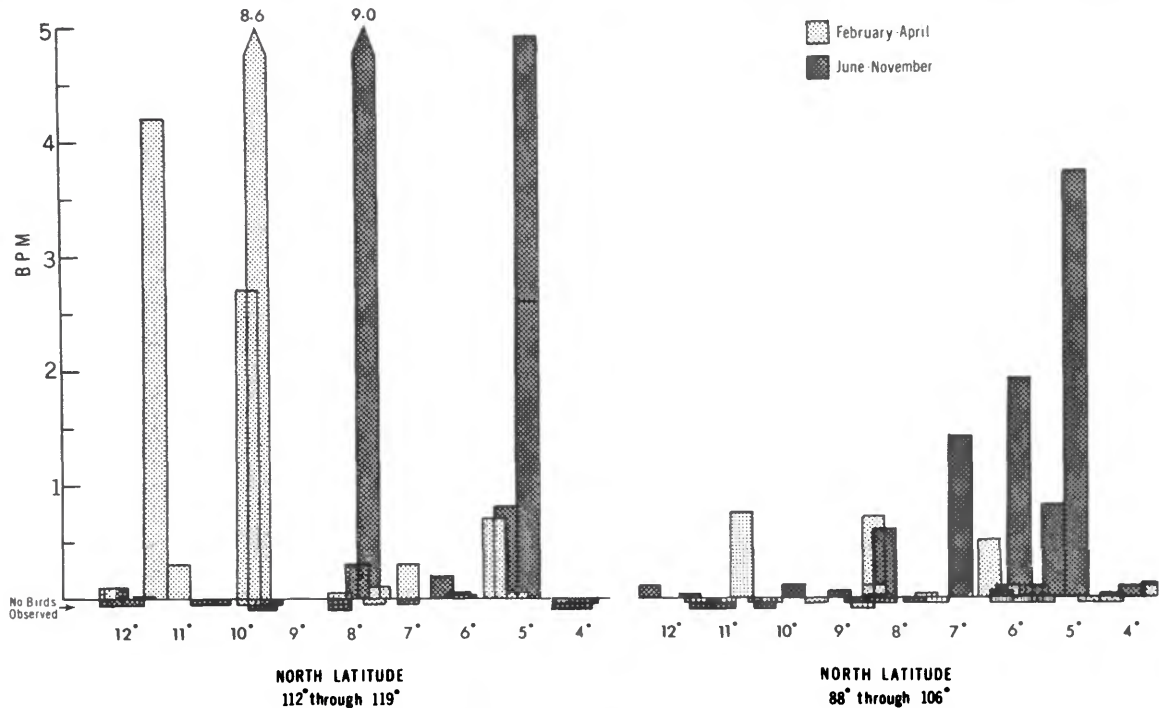


FIGURE 16.—Sooty Tern density across the Equatorial Countercurrent in the eastern Pacific.

aries vary between 4°N to 6°N and 8°N to 12°N, while east of 110°W there is a southward shift so that at the end point the boundaries lie south of 4°N and 10°N. From February to April surface water flow is to the west and northwest between the South Equatorial and North Equatorial currents.

Figure 16 summarizes data from our nine cruises across the Equatorial Countercurrent. The distribution and abundance of Sooty Terns appeared to change in response to changes in the Countercurrent as described by Wyrtki. In both seasons Sooty Terns were found across the entire current area. Density centers, however, differed markedly. During the season when the Countercurrent was not present, high densities were found only west of 110°W (the two highest densities were at 119°W) and only north of 9°N. (If the Countercurrent were developed, this position would be at its northern boundary which is contrary to what would be expected from the Ashmole's discussion and from the observed distribution of central Pacific terns.) Eastern Pacific distribution, however, may be the result of the west and northwest flow developed through

this area at this time of year. During the season when the Countercurrent was clearly developed, high densities were mainly at the convergence along the southern border of the Countercurrent (ca. 5°N). It is also pertinent to note that during both seasons highest densities were recorded west of 112° W where the currents are generally stronger and well developed.

Sooty Terns appear to be present throughout the year in the eastern Pacific. Our fragmentary data suggest that during the spring (February-April) greatest numbers occur west of 110°W, while during the fall (August-November) high densities also occur over much of the area east of 110°W. This would be in accord with fall nesting on the Galapagos Islands and Clipperton Atoll, and with a westward dispersal at the conclusion of the breeding season. Such an hypothesis for breeding stations is consistent with central Pacific Sooty Tern distribution patterns. We would expect to see color-streamed birds if central Pacific birds were moving into the area. Unfortunately, only a few birds have been collected so that the chance of recover-

ing banded birds has been exceedingly small. It is, however, possible that birds from French Polynesia enter the area. This is suggested by the large numbers of birds found from 5°S to 15°S, and from 119°W to 126°W in February and March. All traveling flocks observed at this time were heading east.

Summary and Conclusions

Sooty Terns are abundant and widely dispersed throughout the tropical and subtropical Pacific Ocean. The perimeter of peripheral breeding localities marks the normal limits of their pelagic dispersal. Within this area they may be found over almost any part of the ocean at any time of the year. The occurrence of Sooty Terns beyond the normal limits of their range is generally the result of major climatic disturbances, such as typhoons and cyclones in the western Pacific, and possibly of fluctuations in oceanic currents and water masses. The regularity of stragglers in such areas as Japan is due to the regularity of these disturbances.

Sooty Tern densities fluctuate widely in both space and time. Factors affecting these densities are complicated, often interacting, and sometimes obscured by the presence of two or more populations which are indistinguishable in the field. The following factors are deduced in this investigation, but this list is not exhaustive:

Food Availability: Over a greater part of the ocean, Sooty Terns are generally few and scattered, with occasional high densities shifting from area

to area in response to an erratic food supply. In such areas, tern densities vary directly with the length of time food is available. In areas where food is regularly available (e.g., the Equatorial Countercurrent), tern densities are uniformly higher.

Breeding Island Proximity: During the breeding season Sooty Terns are island-oriented; highest densities generally occur within 25 miles of breeding islands. Individual breeding birds, however, may forage up to 300 miles at sea away from breeding colonies.

Breeding Schedule: At-sea densities vary directly with the breeding cycles on nearby islands; highest at-sea numbers occur at the peaks of the nesting seasons. In the north-central Pacific (Hawaiian-Leewards and Johnston), the at-sea density and island nesting cycles are annual and regular. In the south-central Pacific (Line and Phoenix islands), breeding is semiannual or irregular, and at-sea densities may be high at any time depending upon the status of nearby breeding colonies.

Post-breeding Dispersal: During the nonbreeding season birds may be rare or absent in some parts of the Pacific. After the young fledge, Sooty Terns become ocean-oriented, and densities near islands decrease; birds appear to remain in the general area of the breeding islands for up to a month before moving to nonbreeding areas. Central Pacific Sooty Terns of all age groups disperse westward; many north-central birds reach the Philippine Sea, which constitutes at least part of their nonbreeding range. Nonbreeding ranges, as well as breeding ranges, of north-central and south-central Pacific Sooty Terns appear to be allopatric.

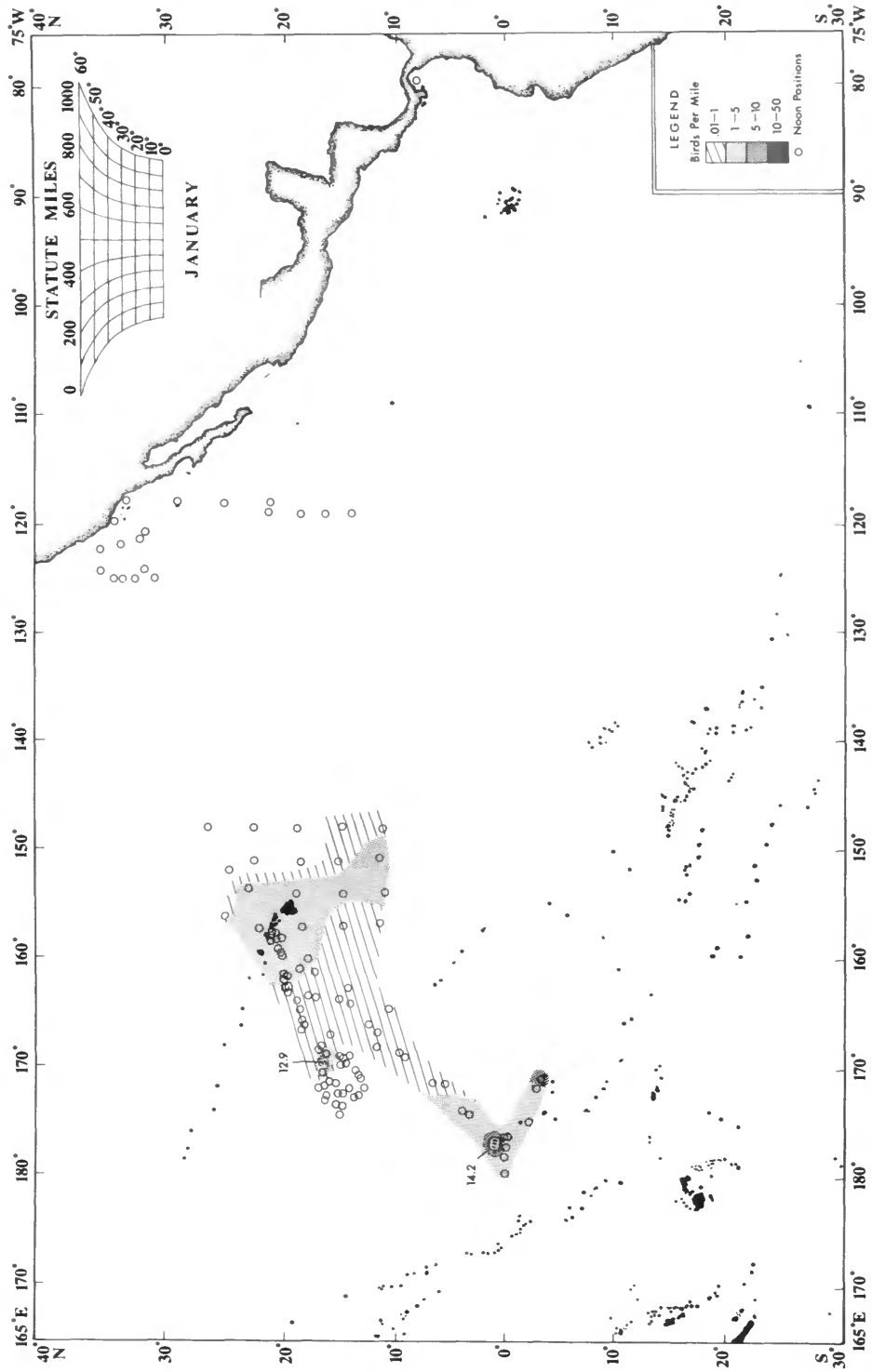


FIGURE 17.—Distribution and density of Sooty Terns in the central and eastern Pacific Ocean in January.

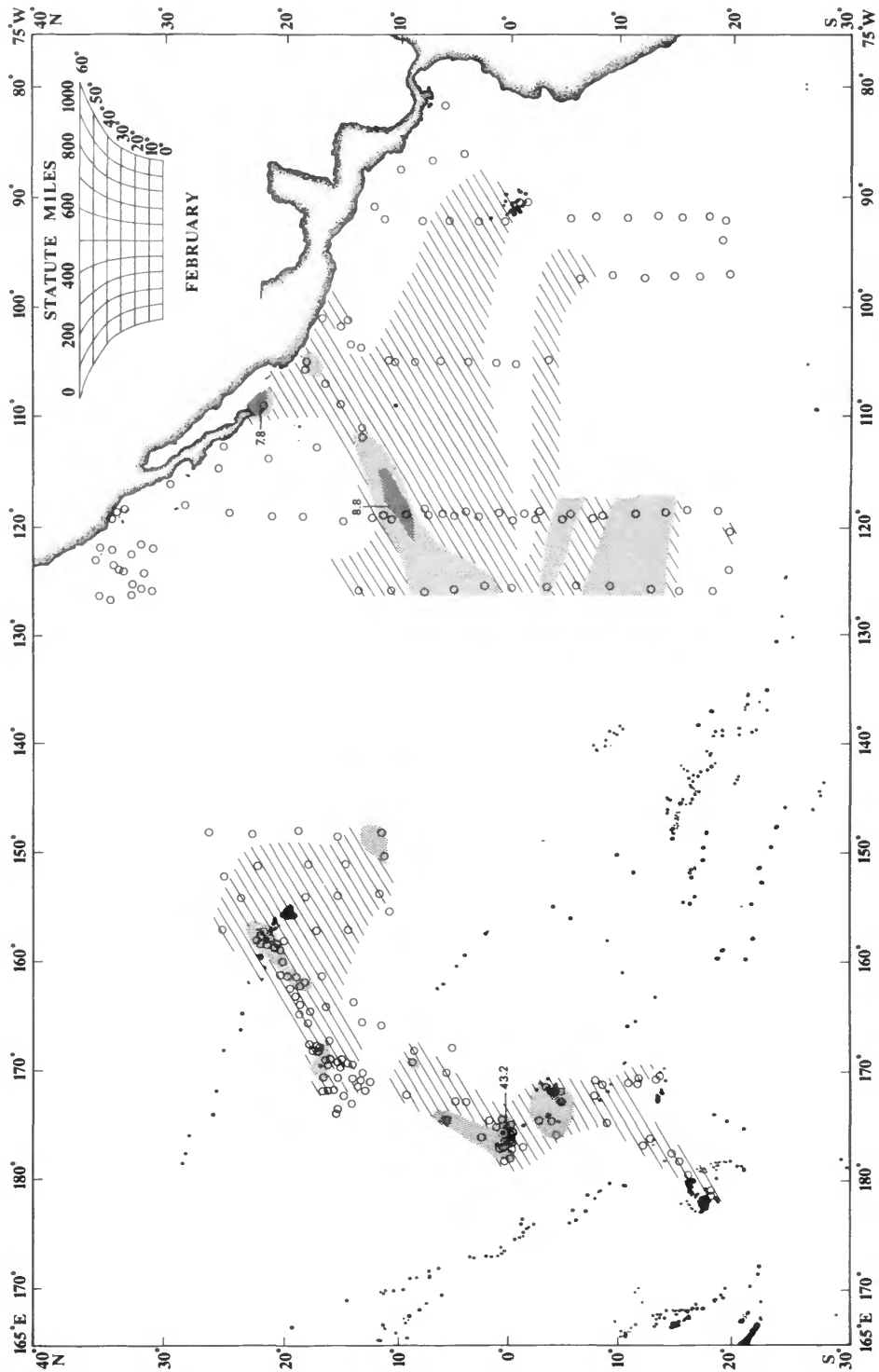


FIGURE 18.—Distribution and density of Sooty Terns in the central and eastern Pacific Ocean in February.

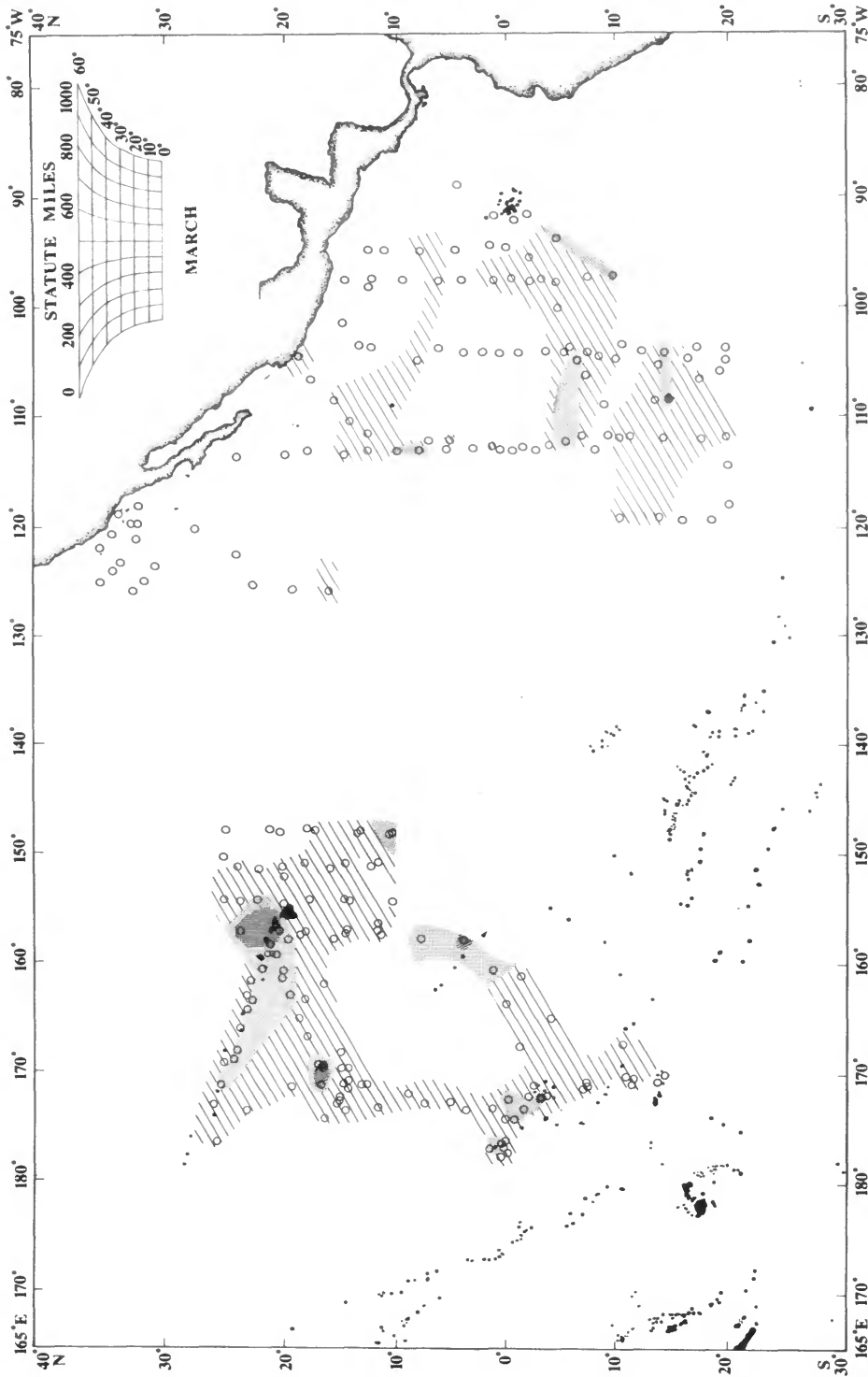


FIGURE 19.—Distribution and density of Sooty Terns in the central and eastern Pacific Ocean in March.

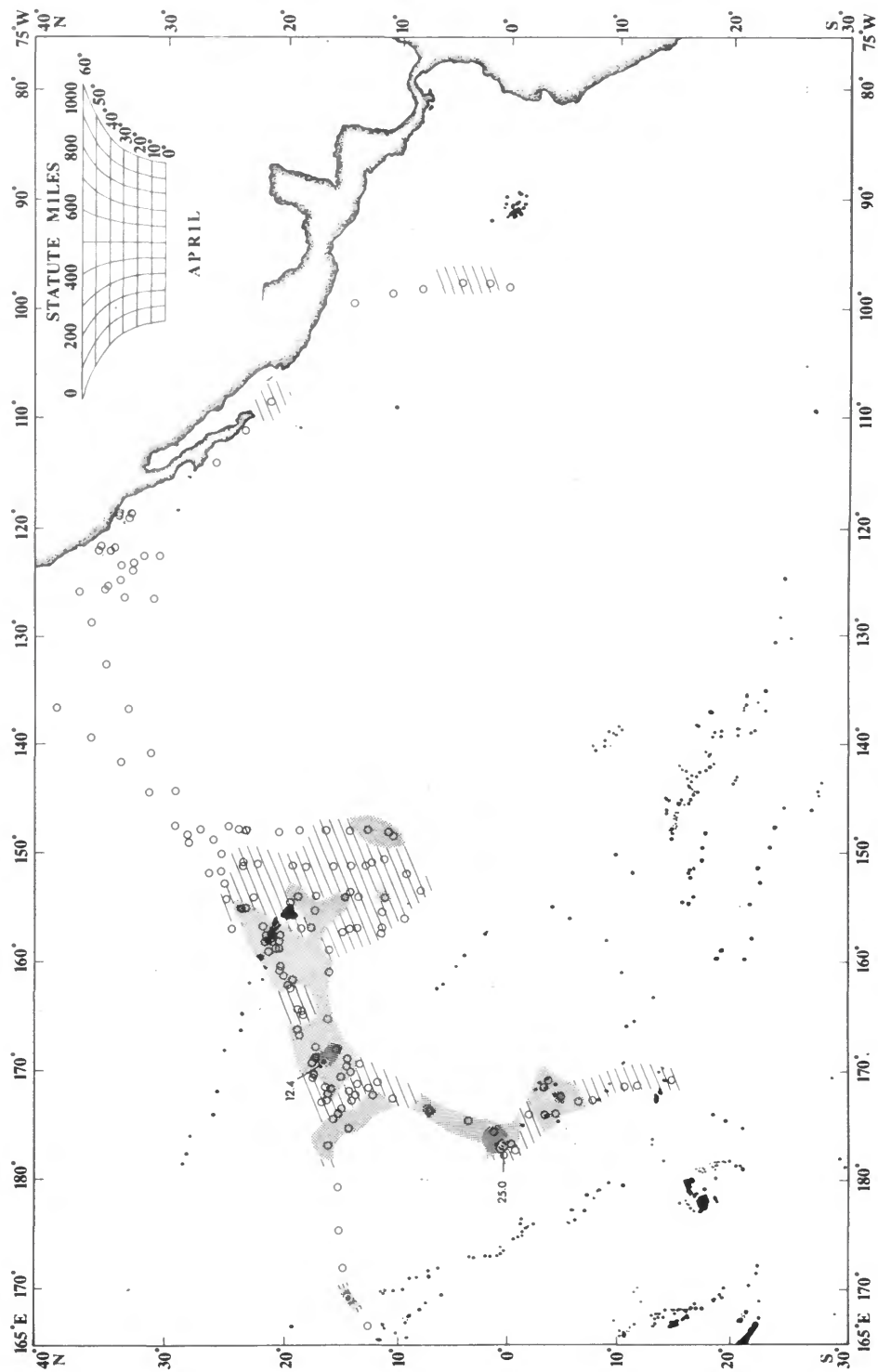


FIGURE 20.—Distribution and density of Sooty Terns in the central and eastern Pacific Ocean in April.

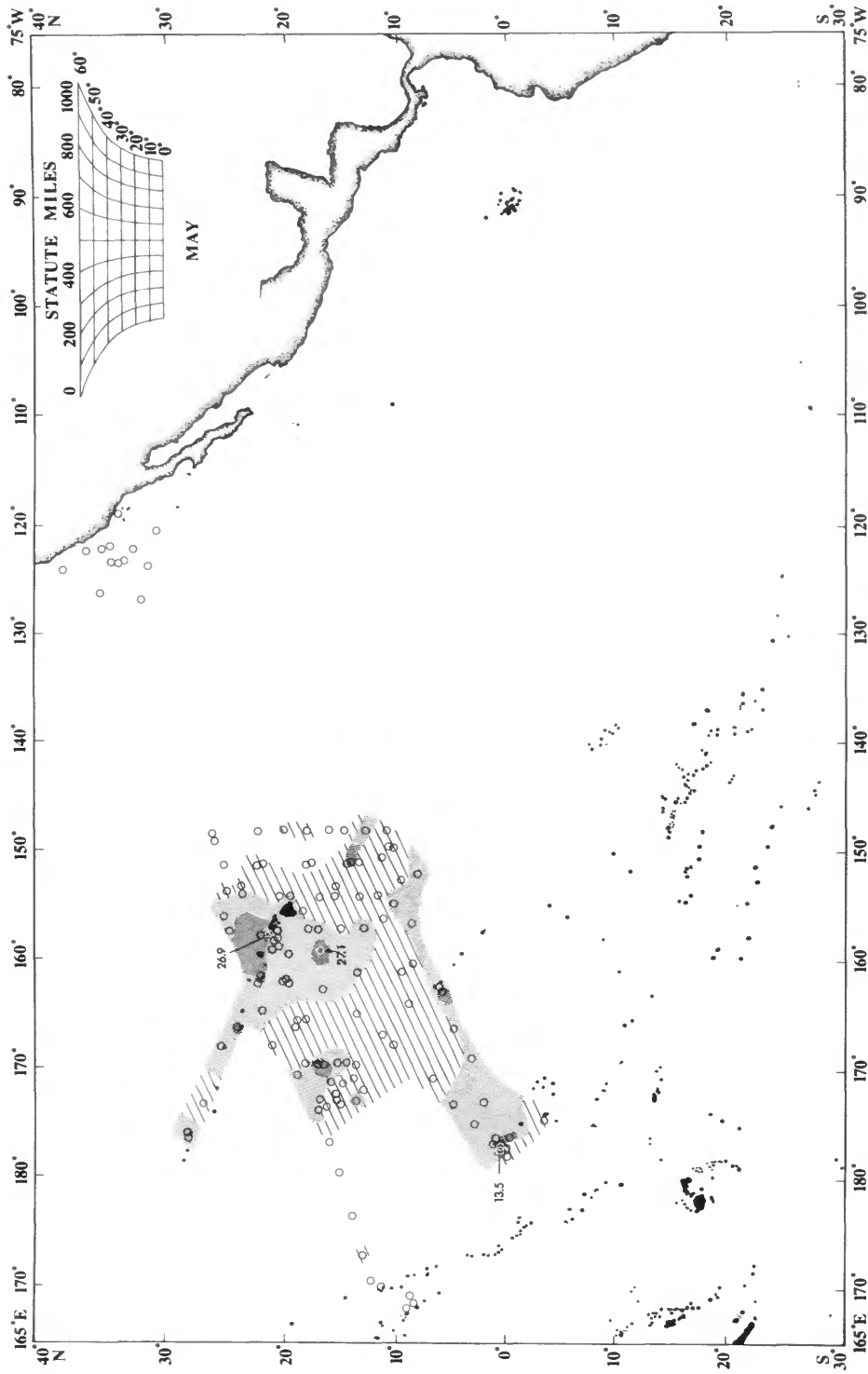


FIGURE 21.—Distribution and density of Sooty Terns in the central and eastern Pacific Ocean in May.

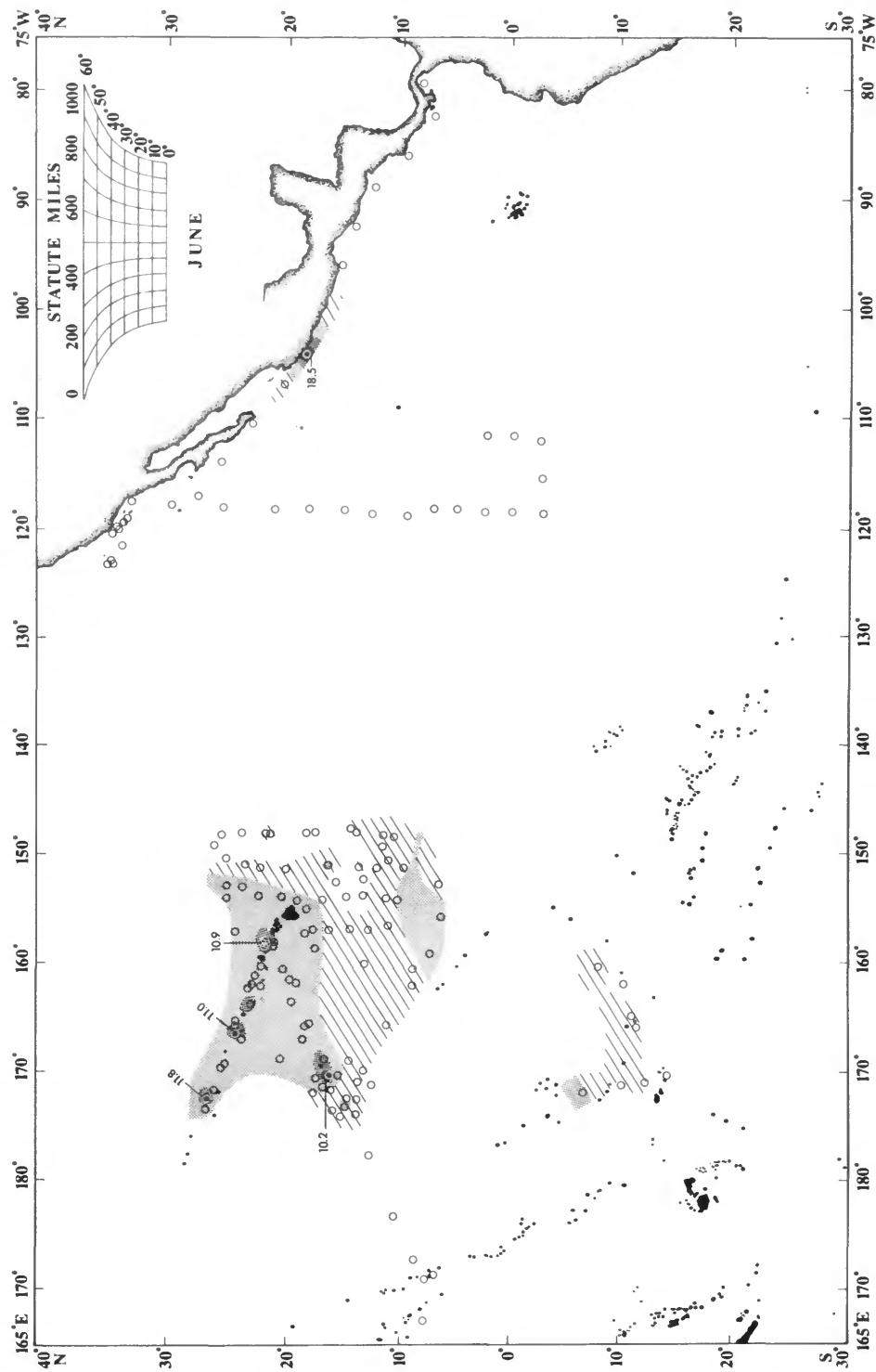


FIGURE 22.—Distribution and density of Sooty Terns in the central and eastern Pacific Ocean in June.

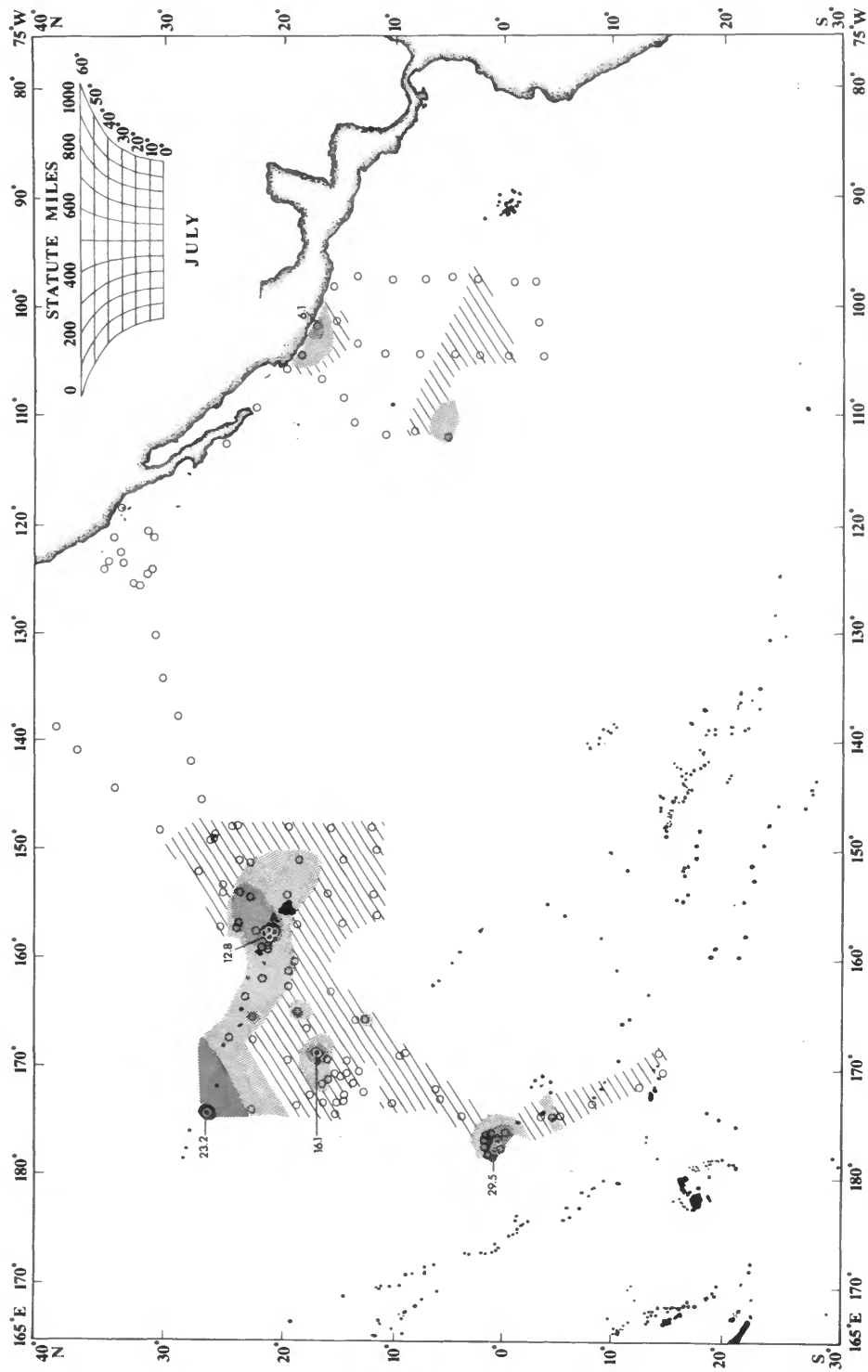


FIGURE 23.—Distribution and density of Sooty Terns in the central and eastern Pacific Ocean in July.

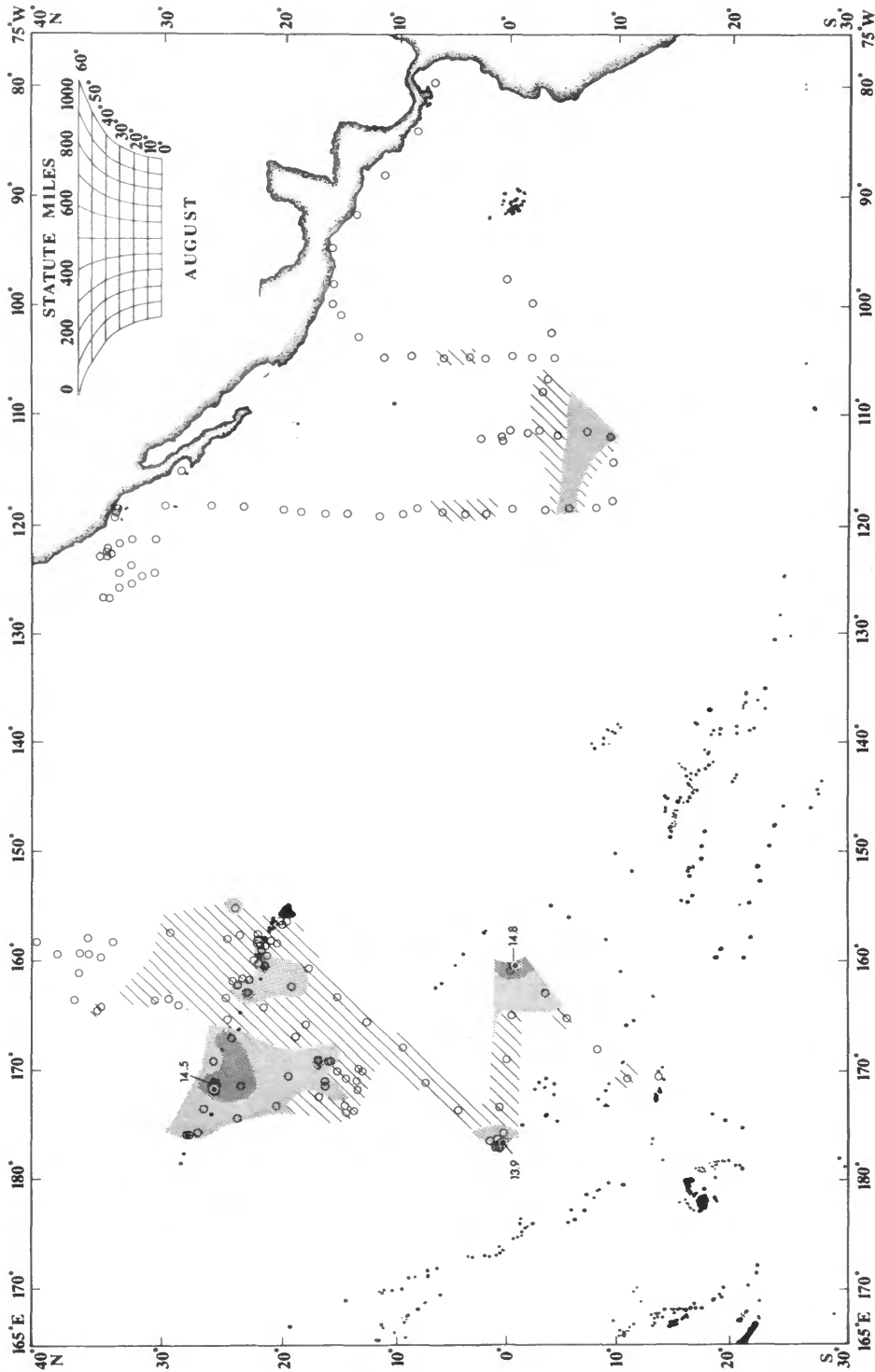


FIGURE 24.—Distribution and density of Sooty Terns in the central and eastern Pacific Ocean in August.

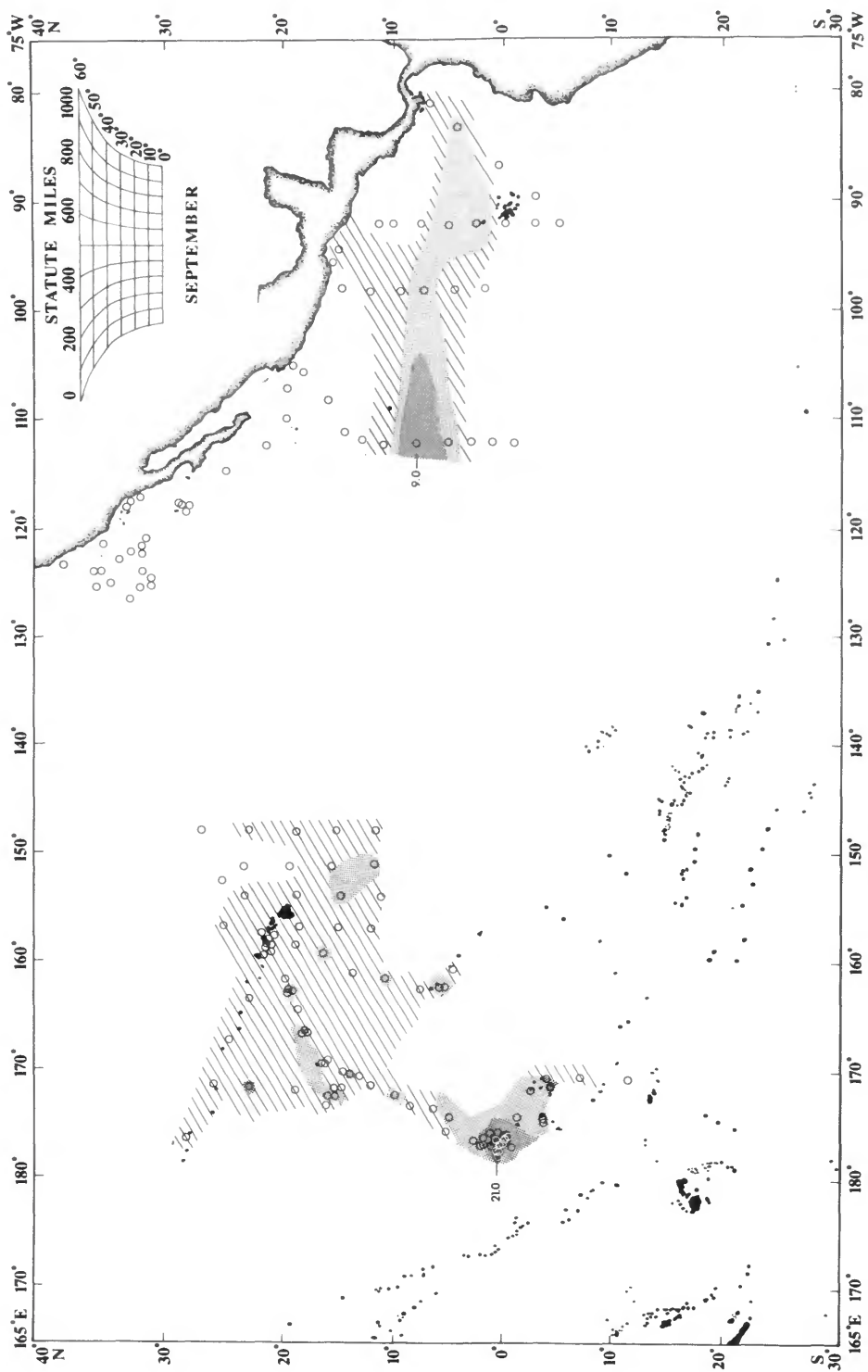


FIGURE 25.—Distribution and density of Sooty Terns in the central and eastern Pacific Ocean in September.

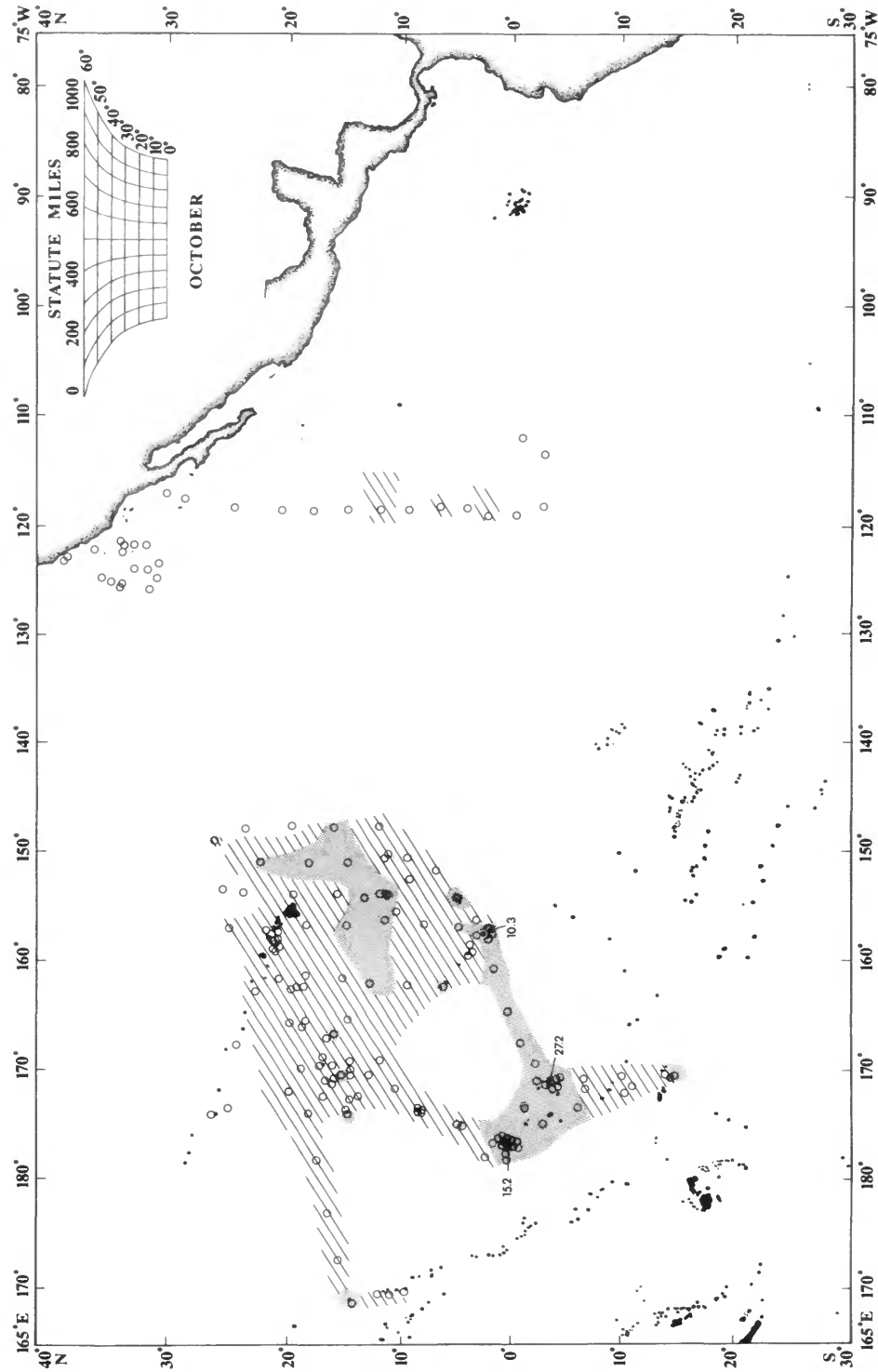


FIGURE 26.—Distribution and density of Sooty Terns in the central and eastern Pacific Ocean in October.

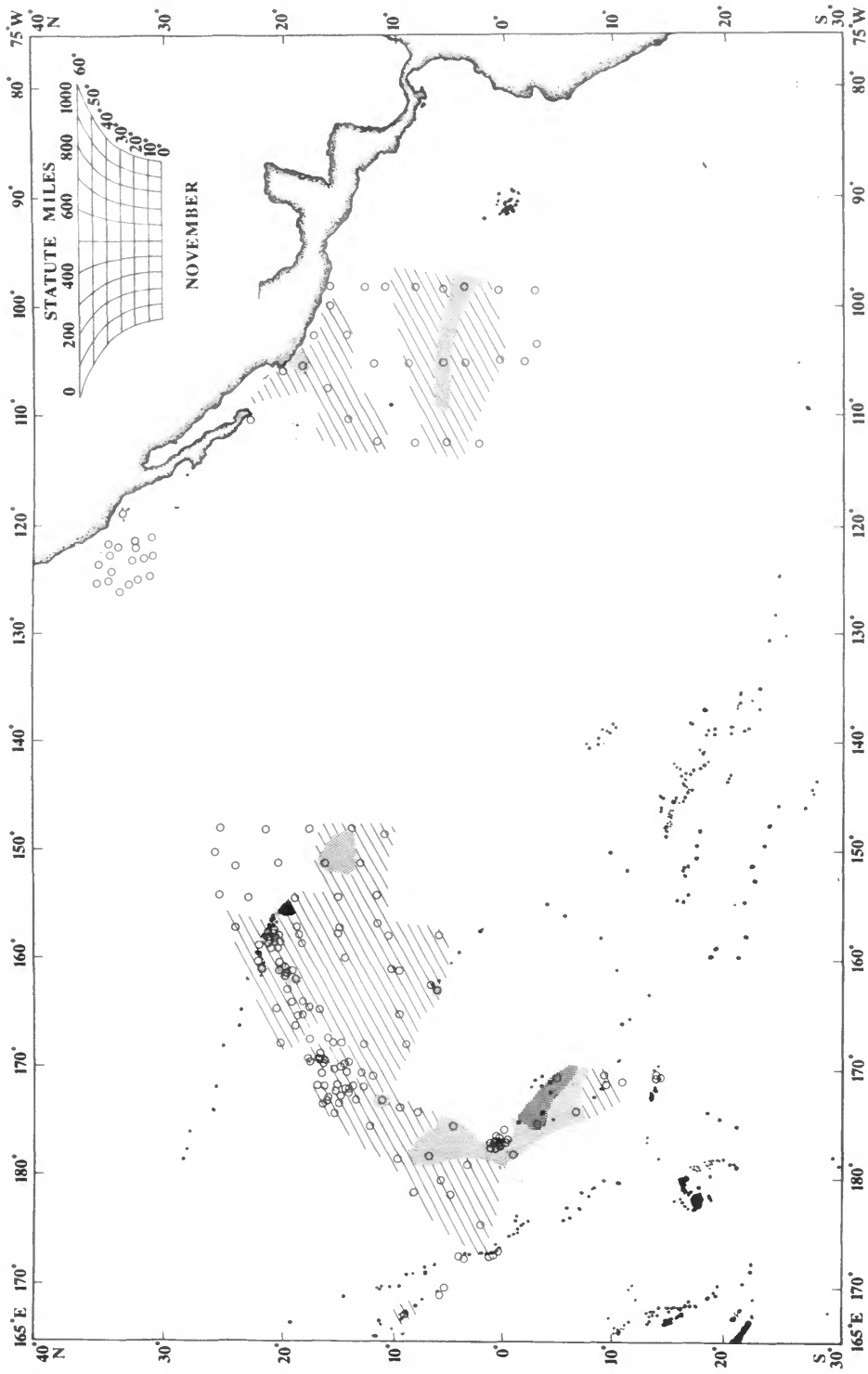


FIGURE 27.—Distribution and density of Sooty Terns in the central and eastern Pacific Ocean in November.

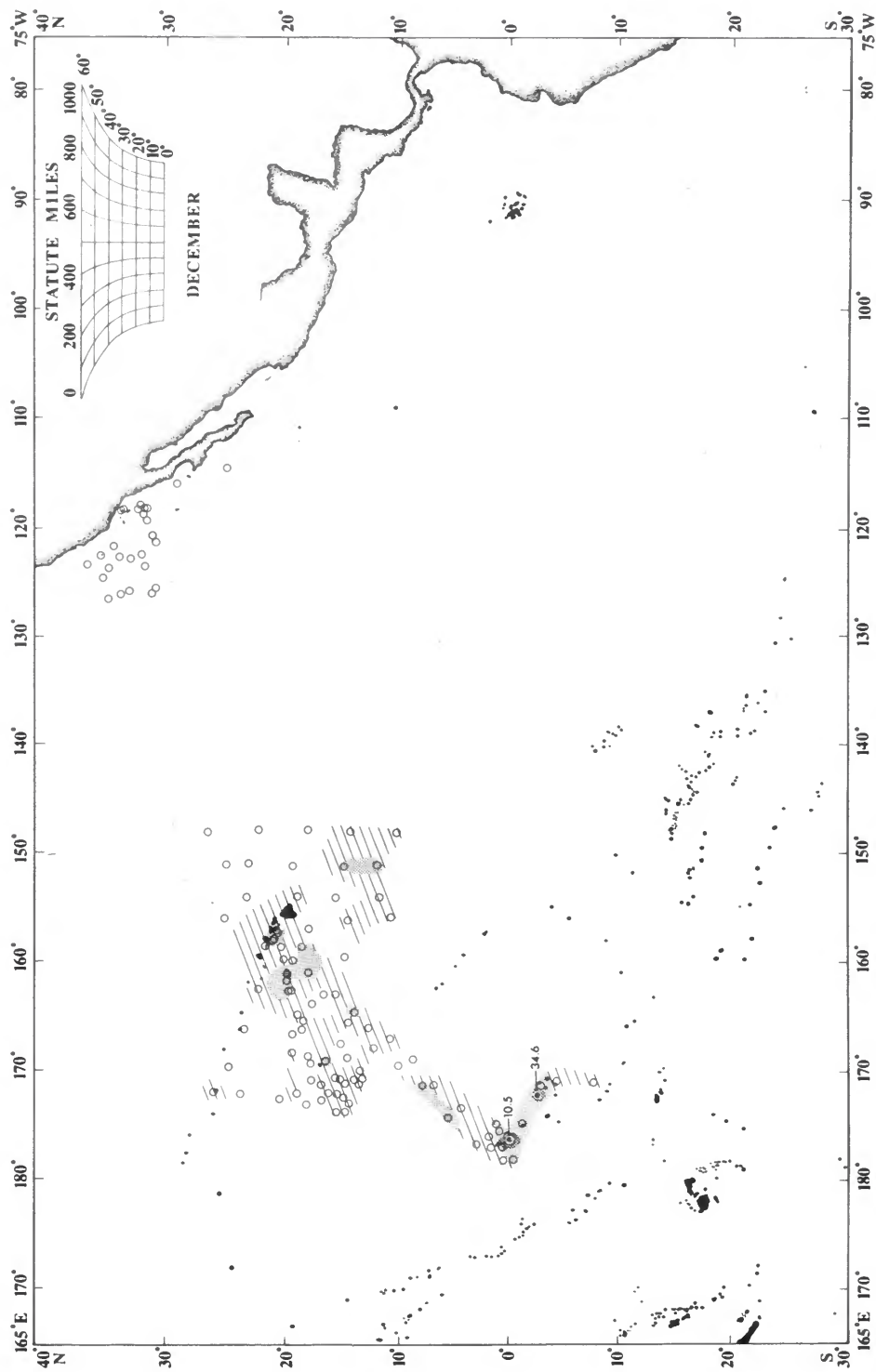


FIGURE 28.—Distribution and density of Sooty Terns in the central and eastern Pacific Ocean in December.

Appendix

TABLE A.—Summary of published data on Sooty Tern distribution

Location	Date	Remarks	Source
EAST-CENTRAL PACIFIC			
Roca Alijos	24 Apr 25	probably breeding, specimens taken	Hanna, 1926:28
Coast of Mexico ca. 20°N	mid-Oct 53	abundant	King and Pyle, 1957:37
Between Manzanilla and the Marquesas I.	24 Oct-24 Nov 55	seen occasionally	" " " " "
Roca Partida	22 May 25	probably breeding, specimens taken	McLellen, 1926:283
Oneal Rock	1925	some	" " "
Isabel I.	24 May 25	thousands, large numbers of almost fully grown young	" " "
Clipperton I. Panama	Aug 58	estimated 2000 breeding	Stager, 1964:365
	breeds on Islas Frailes del Sur and ranges the adjacent waters of the Gulf of Panama and the open sea		Wetmore, 1965:456
7°46'S, 120°W	4 Nov 55	flock of 25-30	King and Pyle, 1957:37
7°09'N, 81°08'W	28 Aug 64	many	Jones, 1965:67
7°N, 131°W	9 Nov 60	groups of 1 and 40	Mörzner Bruyns, 1965:63-64
7°N, 125°W	10 Nov 60	one group of 50	" " " "
7°N, 116°W	11 Nov 60	groups of 1, 20, 20, and 10	" " " "
7°N, 101°W	13 Nov 60	one possible Sooty Tern	" " " "
7°N, 93°W	14 Nov 60	groups of 10-50 continuously through the afternoon	" " " "
Pedro Gonzales I.	7 Sep 61	one seen by D. R. Paulson	Wetmore, 1965:457
7°N, 82°30'W	21-22 Dec?	1, more	Mitchell in Bourne, 1965:37
3°N, 93°30'W	4 Jan 63	3	Morris in Bourne, 1965:36-37
2°50'N, 120°W	8 Nov 55	flock of 14 associated with a convergence front in the upper layer of the ocean	King and Pyle, 1957:37
SOUTHEAST PACIFIC			
Central and South America		recorded breeding from the Tres Marias and Revilla Gige- dos south to the northern Galapagos Islands, also at San Felix Island, Chile	Murphy, 1936:1121
10°15'S, 101°53'W	28 Nov 62	1	Worgan in Bourne, 1964:37
10°30'S, 103°20'W	27 Nov 48	1, in surface water temperature 27.4°C	Fleming, 1950:181
Independencia Bay, Peru	13 Jan 25	many noted by Murphy, sighting coinci- dent with a general warming of the water in this area	Murphy, 1936:1132
San Felix	18 Feb 35	Chapin noted moderate-sized flocks	" " "
Near Mas Atierra	19 Dec 13	Beck noted birds flying toward the island	" " "
Near San Felix I.	10 Oct 62	some birds flying away from the islands in the morning and toward the islands in the evening	Millie, 1963:566
100 mi S of San Felix I.	9 Oct 62	flock of 20 flying toward San Felix in afternoon	" " "
Between Valparaiso and the Juan Fernandez I.	7 Dec 13	observed feeding with shearwaters by Beck	Murphy, 1936:1132
33°S, 74°W	5 Dec 13	4 specimens taken by Beck	" " "
Rio Valdivia, Chile	2 Aug 1855	1 specimen	" " "
NORTHWEST PACIFIC			
Japan and Taiwan		occasional summer straggler to southern Japan; breeds on the Bonin, Riu Kiu, Senkaku Retto, and Marcus islands; recorded also from Borodino Island and Formosa [Tai- wan]	Hachisuka, et al., 1958:222

TABLE A.—Summary of published data on Sooty Tern distribution—Continued

Location	Date	Remarks	Source
Honshu, Japan	25 Apr 04	plus two undated records	Austin and Kuroda, 1953:450-451
Izu I.	undated	1	" " " " "
Honshu, Japan	10 Jul 04	1	" " " " "
" "	24 Aug 07	1	" " " " "
" "	4 Sep 50	1	" " " " "
Shikoku	undated	1	" " " " "
Kyushu	undated	2	" " " " "
WEST-CENTRAL PACIFIC			
26°57'N, 126°07'E	31 May 29	5 or 6	Jespersen, 1933:206
26°36'N, 121°20'E	10 Jun 29	flock of about 50 (species?)	" " " "
25°26'N, 124°18'E	30 May 29	flock of about 30	" " " "
24°55'N, 122°01'E	12 Jun 29	few	" " " "
22°N, 124°E	16 Aug 60	7	Brinkley in Bourne and Radford, 1961:25
19°N, 163°05'E	18 Mar 60	large flocks	Mitchell in Bourne and Radford, 1961:25
135 mi W of Wake I.	6 Mar 45 (or 46)	4	Dixon and Starrett, 1952:271
Micronesia		found in the Mariana, Palau, and Caroline islands	Baker, 1951:161
14°30'N, 113°43'E	19 May 29	flock of about 100	Jespersen, 1933:206
9°N, 131°E	27 Oct 60	two groups of 50	Mörzer Bruyns, 1965:63-64
7°N, 142°E	29 Oct 60	three groups of 40, 10, and 3	" " " "
Philippines		recorded from Siquijor and Sulu Islands	Delacour and Mayr, 1946:77
1°01'N, 119°01'E	14 Aug 29	flock of about 150-200 (species?)	Jespersen, 1933:206
0°02'N, 129°47'E	30 Jul 29	flock of about 58 (species?)	" " " "
0°09'S, 159°50'E			
0°44'S, 136°46'E	21 Jul 29	several	" " " "
1°18'S, 138°35'E	25 Jul 29	many in flocks	" " " "
4°22'S, 128°50'E	24 Mar 29	several (species?)	" " " "
8°25'S, 119°42'E	6 Apr 29	fairly common	" " " "
8°30'S, 134°30'E	27 Sep 63	many	Mitchell in Bourne, 1965:37
9°S, 123°E	26 Sep 63	scattered flocks	" " " "
SOUTHWEST PACIFIC			
SW Coral Sea		vast numbers breeding in this area	Hindwood, et al., 1963:28-30
15°10' 151°39'E	11 Sep 62	8	Norris, 1967:46
to 15°20'S, 151°41'E			
15°57'S, 151°50'E	8 Sep 62	6	" " "
to 15°38'S, 151°39'E			
16°10'S, 157°14'E	20 Aug 61	ca. 50	" " "
16°47'S, 152°27'E	8 Sep 62	8	" " "
to 17°03'S, 152°48'E			
New Caledonia	12 Dec 57	present	Gibson, 1960:18
19°44'S, 156°33'E	22 Aug 61	6	Norris, 1967:46
to 19°50'S, 156°33'E			
20°02'S, 153°31'E	17 Aug 61	3	" " "
to 19°41'S, 153°36'E			
20°26'S, 153°09'E	7 Sep 62	ca. 200	" " "
to 19°32'S, 153°05'E			
20°48'S, 164°13'E	26 Nov 28	larger flock far out (species?)	Jespersen, 1933:206
21°55'S, 173°21'E	8 Jul 62	20	Norris, 1967:46
22°07'S, 154°20'E	23 Aug 61	ca. 30	" " "
to 22°18'S, 154°13'E			
22°39'S, 166°28'E	29 Nov 28	fairly numerous	Jespersen, 1933:206
23°21'S, 153°24'E	14 Sep 62	10	Norris, 1967:46
to 23°36'S, 153°26'E			
26°16'S, 161°24'E	19 Dec 57	one flock	Gibson, 1960:18
27°S, 176°30'E	14 Feb 63	2	Morris in Bourne, 1965:37
29°06'S, 154°01'E	1 May 60	7	King in Bourne, 1964:37

TABLE A.—Summary of published data on Sooty Tern distribution—Continued

Location	Date	Remarks	Source
29°54'S, 178°30'E	23 Nov 64	singles and small flocks in water temperature 70° F	Edgar, et al., 1965:42
29°56'S, 156°37'E	25 Feb 29	few	Jespersen, 1933:206
30°55'S, 155°17'E	20 Dec 57	present	Gibson, 1960:18-19
Off Sydney	17 Feb 29	1 specimen	Jespersen, 1933:206
Lord Howe I.	regular breeding cycle beginning in September each year		Hindwood, et al., 1963:30
New South Wales	undated	rare straggler	Goddard and Hindwood, 1951:170
New Zealand	breeding on Lord Howe, Norfolk, and the Kermadec islands		Falla, et al., 1967:165
Near Sydney	May 1892	1 specimen	Goddard and Hindwood, 1951:170
Sydney Harbor	undated	several specimens	" " " " "
Queenscliff	3 Feb 34	1 immature specimen	" " " " "
Near Sydney Head	11 Dec 42	1 bird observed	" " " " "
Dorrigo	25 Jun 50	2 cyclone-driven birds, 1 collected	" " " " "
North I.	Feb-Apr	7 records following northerly gales	Falla, et al., 1967:165
" "	late Jul-Aug	6	" " " " "
34°32'S, 172°31'E	30 Jul 61	1 bird landed on ship	Jenkins, 1962:33-34
CENTRAL PACIFIC			
Central Pacific	reported as breeding or as having bred on every island group except the New Hebrides and the Solomons		King, 1967:76
23°30'N, 162°W	12 Apr 64	present	Lamb <i>in</i> Bourne, 1966:33
Honolulu	24 May 59	50	Peakall, 1960:202
Oahu	undated	many groups all around the coast	" " "
Pearl Harbor	27 May 60	hundreds	King <i>in</i> Bourne, 1964:37
20°23'N, 158°52'W	26 May 60	5	" " " "
20°31'N, 157°27'W	13 Jan 60	30	" " " "
Marshalls	Oct-Nov 64	occurred near and between breeding atolls	Amerson, 1969:302
"	Jun 66	" " " " " " "	" " " "
"	Apr 67	" " " " " " "	" " " "
7°N, 159°W	5 Nov 60	groups of 2 to 200, one group with immatures present	Mörzer Bruyns, 1965:63-64
7°N, 145°W	7 Nov 60	groups of 1 and 10	" " " "
7°N, 138°W	8 Nov 60	groups of 1, 10, and 3	" " " "
7°N, 179°E	3 Nov 60	three groups of 100	" " " "
Gilberts	Nov 64	20 seen between Makin and Maiana	Amerson, 1969:302
02°15'N, 169°17'W	27 May 59	1	Peakall, 1960:202
Hull I.	28 May 59	ca. 1000 seen fishing in small groups	" " "
8°40'S, 136°54'W	1 Oct 28	few	Jespersen, 1933:206
8°30'S, 156°30'W	6 May 64	large flock over a school of tuna	Mitchell <i>in</i> Bourne, 1966:33
Marquesas I. to Palmyra I.	early Dec 55	observed daily at sea	King and Pyle, 1957:37
Marquesas I.	2 Oct 28	fairly common	Jespersen, 1933:206
" "	late Nov 55	abundant in and around these islands	King and Pyle, 1957:37
SOUTH-CENTRAL PACIFIC			
10°08'S, 142°01'W	5 Oct 28	few	Jespersen, 1933:206
10°41'S, 172°22'W	2 Nov 28	flock of about 10 (species?)	" " "
11°44'S, 144°10'W	6 Oct 28	still a few (one possible flock of 50)	" " "
14°39'S, 174°27'W	8 Nov 28	small flock	" " "
18°07'S, 179°47'W	13 Nov 62	120	Worgan <i>in</i> Bourne, 1964:37
18°40'S, 176°21'W	8 Dec 57	1	Gibson, 1960:18
20°57'S, 158°58'W	21 Oct 28	few (species?)	Jespersen, 1933:206
27°06'S, 177°41'W	13 Dec 28	2 and 2	" " "
29°45'S, 176°57'W	14 Dec 28	1 specimen	" " "
31°35'S, 176°25'W	15 Dec 28	few	" " "

TABLE B.—*At-sea sightings of streamered Sooty Terns*

Date	Time	No.	Behavior	N lat.	W long.	Miles from origin	Age
JOHNSTON STREAMERED							
1963							
5 Aug	0704	1	flying E	15°45'	169°19'	55 SSE	adult
1964							
5 Mar	1040	1	flying E	16°43'	169°21'	9 ESE	"
"	1110	1	feeding	16°41'	169°23'	8 SE	"
"	1148	1	not noted	"	169°22'	9 SE	"
"	1400	1	"	16°22'	169°21'	25 SSE	"
11 Mar	1607	1	flying N	16°40'	169°31'	5 S	"
14 Mar	0659	1	not noted	16°57'	169°39'	14 NNW	"
"	0713	1	flying SE	"	169°36'	13 NNW	"
"	0719	1	flying NNE	"	"	"	"
"	0736	3	flying N	"	"	"	"
"	0837	2	flying SSE	"	"	"	"
9 Apr	0930	1	not noted	14°07'	171°49'	211 SW	"
"	1431	1	flying NE	16°03'	171°51'	144 SW	"
"	1751	1	flying NE	15°26'	173°24'	187 SW	"
13 Apr	1520	1	feeding	16°20'	171°37'	125 WSW	"
"	1810	5	"	"	171°20'	109 WSW	"
14 Apr	1630	1	flying NE	17°05'	169°16'	24 NE	"
"	1335	4	feeding	17°31'	168°08'	90 NE	"
7 May	1002	5	"	16°54'	169°00'	30 NE	"
"	1026	1	flying NE	16°52'	169°05'	24 NE	"
"	1146	1	not noted	16°47'	169°46'	16 W	"
"	1530	1	flying SE	16°20'	169°23'	26 SSE	"
"	1600	1	flying E	16°16'	169°22'	30 SSE	"
8 May	1218	1	flying SE	13°54'	169°24'	174 S	"
10 May	1428	4	feeding	15°36'	170°02'	76 SSW	adult
15 May	1205	1	not noted	16°55'	169°21'	13 NE	"
"	1315	1	feeding	16°59'	169°11'	23 NE	"
"	1423	1	flying SE	17°04'	168°58'	36 NE	"
"	1603	1	flying NNE	17°09'	168°47'	48 NE	"
"	1636	1	flying SE	17°11'	168°44'	51 NE	"
7 Jun	1713	1	flying S	18°05'	166°28'	177 ENE	"
8 Jun	0622	1	flying ENE	17°06'	168°27'	63 NE	"
"	0720	1	flying NNW	16°59'	168°38'	52 NE	"
"	0735	1	flying ENE	"	168°41'	50 NE	"
"	1151	1	flying WSW	16°42'	169°19'	11 SE	"
"	1154	1	flying ENE	"	169°20'	"	"
"	1157	3	not noted	"	"	"	"
"	1300	1	flying NE	16°36'	169°27'	10 SSE	"
"	1304	1	flying SE	"	"	"	"
"	1547	1	flying ENE	16°07'	169°20'	39 SSE	"
11 Jun	0714	1	flying SE	15°32'	169°57'	79 SSW	"
16 Jun	0824	1	flying NE	20°02'	169°27'	200 N	"
11 Jul	1345	1	feeding	15°58'	170°52'	91 SW	"
"	1420	1	"	16°05'	170°46'	84 SW	"
"	"	1	"	"	"	"	immature
5 Aug	0700	1	flying NNW	18°30'	165°03'	278 NE	adult
6 Aug	0702	1	flying N	16°54'	169°00'	30 NE	"
"	0928	1	not noted	16°42'	169°23'	7 SE	"
"	0933	1	flying SE	16°41'	169°21'	7 SE	adult
8 Aug	1640	1	flying E	14°01'	170°46'	180 SSW	immature
10 Aug	1650	1	not noted	14°26'	172°31'	226 SW	"
11 Aug	1050	1	flying NW	16°24'	170°51'	80 SW	"
12 Aug	1250	1	not noted	14°42'	173°57'	287 SW	"

TABLE B.—*At-sea sightings of streamered Sooty Terns—Continued*

<i>Date</i>	<i>Time</i>	<i>No.</i>	<i>Behavior</i>	<i>N. lat.</i>	<i>W long.</i>	<i>Miles from origin</i>	<i>Age</i>
1965							
13 Apr	1507	2	not noted	16°18'	169°25'	28 S	adult
19 Apr	1215	1	feeding	15°37'	173°41'	225 SW	"
"	1630	4	"	16°06'	173°07'	218 WSW	"
20 Apr	0955	10	"	17°28'	170°31'	73 NW	"
"	1345	1	"	16°17'	172°25'	172 WSW	"
15 May	1130	1	not noted	13°32'	169°49'	195 S	"
21 May	1415	1	feeding	18°50'	170°24'	137 NNW	"
17 Jun	0430	1	not noted	15°07'	169°35'	97 S	immature
"	1045	1	feeding	15°22'	170°14'	93 SSW	"
"	"	1	"	"	"	"	adult
21 Jun	1710	2	flying S	17°44'	169°53'	63 NNW	"
5 Jul	0956	1	flying NE	17°07'	168°06'	83 NE	"
11 Jul	1710	1	feeding	15°40'	173°39'	247 WSW	"
15 Aug	0740	9	flying SE	16°54'	169°44'	16 NW	"
"	"	1	flying SE	"	"	"	immature
"	1018	1	flying NW	16°32'	169°34'	13 SSW	adult
"	1143	1	feeding	16°20'	169°30'	25 S	"
22 Aug	1414	9	not noted	16°43'	"	2 S	"
"	1418	2	feeding	16°44'	169°29'	1 S	adult
"	1419	3	not noted	"	"	"	"
"	1451	5	feeding	16°46'	169°25'	5 E	"
"	1507	1	not noted	16°48'	169°23'	8 E	"
"	1508	17	feeding	"	"	"	"
"	"	2	"	"	"	"	immature
"	1530	1	"	16°50'	169°20'	11 ENE	adult
"	1630	1	not noted	16°54'	169°14'	17 ENE	"
"	1700	1	feeding	16°56'	169°12'	20 NE	"
"	1905	3	"	17°03'	169°02'	32 NE	"
8 Sep	0850	1	"	19°47'	161°47'	481 NE	"
"	1700	1	"	19°15'	163°10'	394 NE	"
10 Sep	1515	1	not noted	16°43'	169°31'	2 SSW	"
1966							
31 Jan	1745	1	flying NE	16°28'	169°39'	19 SSW	"
6 Mar	0853	1	flying N	16°34'	170°53'	80 W	"
8 Mar	0852	1	flying NE	11°38'	173°34'	392 SW	"
1 Apr	0642	1	flying W	16°47'	167°21'	124 E	"
"	1754	2	"	16°43'	169°29'	4 SSE	"
2 Apr	0805	1	feeding	15°05'	170°25'	113 SSW	"
"	1215	1	"	14°22'	170°40'	160 SSW	"
"	1710	1	"	13°40'	171°03'	209 SSW	"
4 Apr	1024	1	not noted	16°02'	171°11'	107 SW	"
"	1030	1	flying NW	16°03'	171°10'	106 SW	"
"	1430	1	feeding	16°28'	171°08'	95 WSW	adult
5 Jun	0731	2	flying S	16°18'	169°15'	30 S	"
"	0733	1	"	"	"	"	"
"	0744	1	not noted	16°17'	169°17'	"	"
"	0756	5	feeding	16°16'	169°19'	31 S	"
"	0809	12	"	16°15'	169°22'	"	"
"	0821	3	"	16°14'	169°23'	32 S	"
"	0830	3	"	16°13'	169°25'	33 S	"
"	0837	11	"	16°12'	169°26'	34 S	"
"	0923	1	not noted	16°08'	169°34'	38 S	"
"	1027	18	feeding	16°02'	169°45'	45 SSW	"
"	1659	3	"	15°33'	170°45'	101 SW	"
"	1849	4	flying NE	15°23'	171°02'	122 SW	"
"	1851	2	flying E	"	171°03'	"	"

TABLE B.—*At-sea sightings of streamered Sooty Terns—Continued*

Date	Time	No.	Behavior	N lat.	W long.	Miles from origin	Age
1966							
10 Sep	1458	1	flying N	16°42'	170°13'	42 W	"
3 Dec	1016	1	feeding	18°44'	164°44'	299 ENE	"
1967							
8 Jan	1153	1	not noted	16°38'	169°11'	19 ESE	"
12 May	1429	1	feeding	18°14'	169°12'	89 N	"
1968							
12 Feb	1200	2	"	16°35'	168°35'	54 E	"
HOWLAND STREAMERED							
1966							
14 Jul	0832	1	flying SE	0°53'	176°44'	8 NW	"
"	0845	1	"	0°54'	176°45'	9 NW	"
17 Jul	0846	1	flying NW	0°45'	176°31'	7 E	adult
20 Jul	0830	1	flying NE	0°41'	176°38'	7 S	"
"	1017	1	flying E	0°24'	"	24 S	"
"	1144	2	"	0°14'	176°36'	34 S	"
"	1617	1	flying NW	0°34'	176°41'	15 SSW	"
"	1724	1	flying S	0°41'	176°40'	8 SSW	"
21 Jul	0936	1	not noted	0°27'	176°32'	22 SSE	"
"	1645	3	feeding	0°38'	176°36'	10 SSE	"
"	1649	1	flying W	"	"	"	"
14 Aug	1010	1	feeding	0°31'	"	18 S	"
"	1025	1	"	0°30'	176°35'	"	"
15 Aug	0845	1	"	0°40'	176°28'	15 S	"
16 Aug	0930	1	"	0°34'	176°40'	14 SSE	"
17 Aug	0649	1	not noted	0°40'	176°48'	12 SW	"
"	1659	2	"	0°42'	176°47'	11 SW	"
"	0923	3	"	0°45'	176°44'	4 SW	"
"	0948	1	flying ENE	0°44'	176°48'	12 W	"
"	1015	1	flying NE	0°42'	176°52'	14 WSW	"
"	1044	1	flying SE	0°40'	176°57'	20 WSW	"
"	1059	3	feeding	0°39'	176°59'	22 WSW	"
"	1117	1	flying NE	0°38'	177°01'	24 WSW	"
"	1135	3	feeding	0°37'	177°04'	28 WSW	"
"	1204	1	flying S	0°34'	177°12'	32 WSW	"
"	1320	1	not noted	0°26'	177°22'	50 WSW	"
"	1330	1	flying S	0°25'	177°23'	51 WSW	adult
"	1415	3	feeding	0°22'	177°30'	58 WSW	"
"	1440	3	"	0°21'	177°34'	62 WSW	"
"	1500	2	"	0°20'	177°37'	66 WSW	"
"	1515	1	not noted	0°19'	177°39'	68 WSW	"
19 Aug	0850	1	"	1°28'	177°00'	46 NNW	"
16 Sep	0808	1	flying N	0°52'	176°47'	7 NW	"
19 Sep	1035	1	feeding	0°29'	175°51'	52 SE	"
"	1425	5	"	0°42'	176°26'	15 SE	"
20 Sep	1522	1	not noted	0°52'	176°35'	7 NNE	"
"	1543	1	"	"	176°37'	6 N	immature
22 Sep	1736	1	"	"	"	"	adult
23 Sep	0430	1	"	0°48'	176°23'	8 S	"
"	1040	1	feeding	0°18'	176°27'	32 SSE	"
"	1710	1	"	0°07'	176°01'	54 SSE	"
16 Oct	1015	1	not noted	1°05'	176°46'	17 NNW	"
12 Dec	1652	1	flying SE	0°58'	176°39'	11 N	"
1967							
18 Jan	1153	1	flying E	0°45'	177°35'	56 W	"
18 Feb	0836	1	feeding	0°49'	176°29'	9 E	"

TABLE C.—*At-sea recoveries of banded Sooty Terns*
(table based on distance between banding and recovery localities; ? uncertain, — not noted)

Original data			Recovery data				
Date	Age	Location	Date	Age	Sex	Elapsed months	Miles
HOWLAND ISLAND							
2 Feb 65	adult	1°00'N-175°47'W	9 May 66	adult	—	15.2	52 ENE
"	"	0°11'N-176°30'W	14 Aug 66	"	♂	18.4	38 S
1 Feb 65	"	0°12'N-176°36'W	9 Apr 66	"	♂	14.3	35 S
19 Jul 65	"	0°15'N-176°40'W	"	—	—	8.7	33 S
2 Feb 65	"	0°17'N-176°31'W	21 Jul 66	adult	♂	17.6	32 S
12 Jul 66	"	"	"	"	♂	0.3	"
"	"	"	"	?	?	"	"
18 Jul 66	"	"	"	adult	♀	0.1	"
"	"	"	"	?	?	"	"
12 Oct 64	"	1°17'N-176°34'W	15 Jul 66	adult	♂	21.1	28 N
2 Feb 65	"	0°42'N-176°17'W	17 Jul 66	"	♂	17.5	22 ESE
1 Feb 65	"	0°47'N-176°59'W	13 Jul 66	"	♂	17.4	22 W
23 Jul 64	"	0°48'N-176°59'W	9 Dec 66	"	♂	28.5	21 W
12 Jul 66	"	"	"	"	♀	4.9	17 W
19 Jul 66	"	1°01'N-176°39'W	22 Apr 67	?	?	9.1	13 N
21 Jul 66	"	0°44'N-176°27'W	23 Sep 66	adult	♀	2.1	12 ESE
17 Aug 66	immature	0°38'N-176°34'W	18 Sep 66	immature	♀	1.0	11 SSE
1 Feb 65	adult	"	19 Sep 66	adult	♂	19.6	"
21 Jul 66	"	0°44'N-176°27'W	23 Sep 66	"	♀	2.1	12 ESE
9 Oct 64	"	0°50'N-176°26'W	17 Jul 66	adult	♂	21.3	5 ENE
1 Feb 65	"	"	"	"	♂	15.5	"
12 Jul 66	"	"	"	"	♀	0.2	"
2 Feb 65	"	near Howland	17 Jan 67	?	?	23.5	1 W
HULL ISLAND							
26 Sep 65	"	0°27'S-177°31'W	20 Oct 65	adult	♀	0.8	400 NW
24 Sep 65	immature	0°34'N-176°20'W	22 Oct 65	immature	♂	0.9	390 NW
"	"	0°02'S-176°37'W	17 Oct 65	"	♂	0.8	370 NW
25 Sep 65	"	0°14'N-175°52'W	22 Nov 65	"	♀	1.9	360 NW
JOHNSTON ATOLL							
8 Jul 66	"	11°57'N-175°49'W	13 Nov 66	"	?	4.2	460 SW
3 Feb 64	adult	16°18'N-172°57'W	20 May 65	adult	♀	15.6	202 WSW
30 Jan 64	"	15°44'N-172°20'W	18 Apr 65	"	♀	14.6	175 WSW
8 Jun 64	"	14°36'N-171°03'W	16 Apr 65	"	♀	10.3	158 SW
27 Apr 65	"	18°58'N-170°16'W	21 May 65	"	♂	0.8	141 NNW
1 Aug 63	"	18°49'N-170°24'W	"	"	♀	21.7	135 NNW
25 Jul 63	"	18°43'N-170°31'W	"	"	♀	21.9	132 NNW
22 Jul 64	"	14°59'N-170°37'W	16 Apr 65	"	♀	8.8	124 SW
11 Feb 64	"	17°42'N-169°47'W	20 Apr 65	"	♀	14.3	60 NNW
21 Apr 66	"	16°44'N-169°11'W	8 Jan 67	?	?	8.6	18 E
LAYSAN ISLAND							
9 Aug 65	immature	11°09'N-140°53'W	before 6 Dec 65	?	?	3.9	1,170 SE
MANANA, OAHU							
20 Mar 64	adult	at sea, Hawaiian area	mid-Oct	?	?	31.0	0 to 400

Wedge-tailed Shearwater (*Puffinus pacificus*)*

Warren B. King

Introduction

The material contained in this report was gathered in the course of intensive biological investigations in the central and eastern Pacific by the Pacific Ocean Biological Survey Program (POBSP), Smithsonian Institution, Washington, D. C. Humphrey (1965) has given a general summary of the activities and objectives of the program, and Gould (pp. 1-5) has discussed the methods and materials and areas of coverage of the program.

At-sea work began in 1963 and was concluded in 1969. This report is one of a series of studies of the pelagic distribution of Pacific seabirds. By the end of 1968 POBSP personnel observed 81,740 Wedge-tailed Shearwaters during 2747 days (26,457 hours) and 259,710 miles of observation.

The Wedge-tailed Shearwater (*Puffinus pacificus*) is an abundant, wide-spread species in the tropical and subtropical Pacific and Indian oceans; it may be encountered far from land most of the year. In the central Pacific its population is approximately one-half million birds (Table 13). It also breeds on numerous islands in the western Pacific from the Bonin, Volcano, and Pescadore islands in the north, along the east coast of Australia to Montague Island near Bass Strait in the south. In the eastern Pacific it breeds only on San Benedicto Island of the Revilla Gigedo group.

Its marine range is only slightly larger than its breeding range in the Pacific, although in the Indian Ocean its marine range appears to extend farther north than its breeding range (Bailey, 1968). In the eastern Pacific it has been recorded from

Baja California south to the Gulf of Guayaquil, Ecuador. In the western Pacific it has been recorded from the Izu Islands south of Japan to the South China Sea and the Tasman Sea.

The northernmost records are a sighting (POBSP,

TABLE 13.—Maximum estimates by POBSP (1963-1968) of Wedge-tailed Shearwaters on islands in the central Pacific*

Island	Number
Kure	6,230
Midway	3,000
Pearl and Hermes Reef	22,400
Lisianski	60,000
Laysan	200,000
Gardner Pinnacles	100
French Frigate Shoals	13,600
Necker	2,000
Nihoa	25,000
Islets of the Main Hawaiian group	70,000
Johnston	2,500
Christmas	6,000
Canton	40
Phoenix	10,000
McKean	500
Taongi	12,000+
Bikar	6
Taka	12
Eniwetok	3
Wake	6

*Estimates are of birds "using" the islands, including breeding birds, nonbreeders, and, in some cases, chicks. Estimates of nocturnal burrowing birds are notoriously inaccurate so that many of these estimates may be low by 100 percent or more. On the basis of total number of birds handled in one year during banding operations on islands on which coverage was thorough (Kure, Johnston), POBSP experience indicates that most initial estimates should be doubled or trebled. Above estimates, however, give a good idea of order of magnitude of the populations.

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Paul Woodward) at latitude 35°26'N, longitude 164°17'W in August 1966 and a typhoon-driven bird found 30 September 1959 in Fukui, Japan, near the Sea of Japan at latitude 36°N (Anonymous, 1960). The southernmost record is a U.S. Fish and Wildlife Service (USFWS) band return record from Cook Strait, New Zealand, on 8 November 1965; the light-phase bird had been banded as an adult 19 September 1963 on Johnston Atoll by POBSP personnel. Another Wedge-tailed Shearwater, also light-phase, was reported by Falla (1962) from Makara, Wellington, also in Cook Strait. On tenuous grounds Falla assigned this bird to one of the north Pacific light-phase breeding islands, rather than the Shark's Bay, Western Australia, breeding grounds where light-phase birds occur as well.

Murphy (1951) recognizes two subspecies, *P. p. pacificus* Gmelin, an all-dark form from the Kermadec Islands, Norfolk Island, and Kandavu Island of the Fiji group, and *P. p. chlororhynchus* Lesson, a slightly smaller form, from all other islands in the Pacific and Indian oceans. The latter occurs in both light-phase and dark-phase morphs, and occasionally in an intermediate form. The light-phase morph predominates in all breeding colonies north of 10°N except the Marianas, where only dark birds occur, and in the Revilla Gigedos. These breeding grounds include:

island or group	latitude	longitude	light-phase pop. (%)
San Benedicto	19°N	110°W	33 or less
Main Hawaiians	19°-22°N	154°-160°W	97
Northwestern			
Hawaiians	23°-28°N	162°-179°W	99+
Johnston Atoll	16°N	169°W	95
Northern Marshalls	11°-14°N	162°-170°E	93
Bonins, Volcanos	24°-27°N	140°-142°E	99+
Pescadores	20°N	119°E	99?

Light-phase birds make up about one percent of the Phoenix Islands' population. Light-phase birds have not been reported in any other breeding colonies in the south Pacific. The figure of 33 percent light-phase birds for the Revilla Gigedos comes from Murphy's (1951:9) comment that "in certain colonies, as at the Revilla Gigedo Islands, both dark- and white-phase birds are found together in a respective ratio of about two to one." The comment was probably paraphrased from Anthony (1898:313), who was speaking of the birds "about" San Benedicto and Socorro Islands, not particu-

larly of the birds "on" either island. Anthony's (1900:251) statement that "by far the greater number were in dark plumage," refers to breeding birds on San Benedicto, and Loomis (1918:143) quotes Bunnell's notes which say that "the white-breasted ones were a very small proportion of the total number" just offshore or on the island of San Benedicto. At the risk of reading information into these comments, it would seem that the proportion of light- to dark-phase birds on San Benedicto may be smaller than one to two.

BREEDING PHENOLOGY.—The breeding season is from April to November in northern subtropical Pacific breeding localities, and October to May in southern subtropical localities. Birds are most abundant at sea near their breeding areas during these months. When the birds of the year fledge, young and old alike disperse from the general vicinity of the breeding islands, so that numbers encountered nearby at sea are only a small fraction of those seen during the breeding season. The routes of dispersal are not yet known.

Birds from tropical Pacific breeding stations are often present near their breeding islands year round, and their breeding cycle may extend beyond the eight months of the subtropical breeders.

In the Hawaiian group, Johnston Atoll, and the northern Marshalls, the Wedge-tailed Shearwater breeds synchronously on an annual cycle. Birds appear first on their breeding islands at night in early March. In the Hawaiian group maximum numbers occur in May, although on Johnston Atoll numbers increase gradually to an August peak. Eggs are laid in mid-June. Nonbreeders visit the islands sporadically and usually account for more than half the population on an island at any given time. Eggs hatch in early August and by mid-August the chicks are left alone in their burrows during the day. By early November neither breeding nor nonbreeding adult birds visit the island, and by the middle of November the young have fledged and no birds remain. From September to November large flocks are often encountered off the shore of breeding sites. Birds presumably form such flocks prior to migration.

The gonadal development cycle of light-phase birds was determined on the basis of measurements of 75 males collected at sea in all months but January and of 79 females from all months but January, October, and November (Figure 29). Gonadal de-

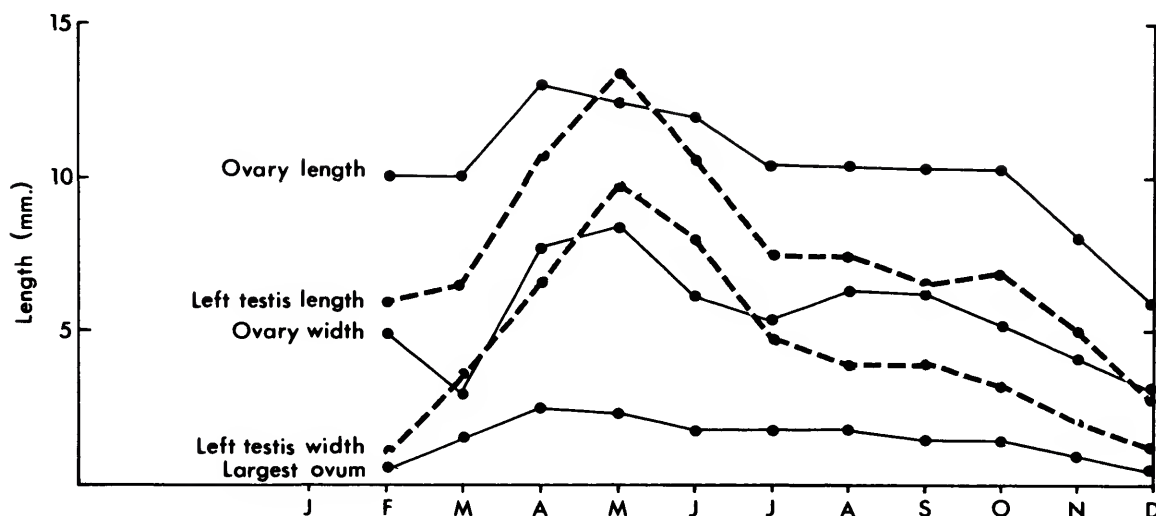


FIGURE 29.—Monthly gonad dimensions of light-phase Wedge-tailed Shearwaters collected at sea.

velopment apparently begins with the birds' return to the vicinity of their breeding islands and reaches a peak by May, a month before eggs are laid. After May, gonads decrease in size, but the decrease stops between July and October during which gonad sizes hold constant; thereafter they shrink rapidly to minimum size during winter. There is little indication from the data of any distinction between adults and subadults on the basis of gonad size. An exception was that two of four birds collected on the equator in April had gonads very much smaller than the mean dimensions, suggesting they might have been subadults. The other two, and several others taken later in the year south of 10°N latitude where subadults might be expected to be found, showed gonadal development not appreciably different from monthly averages.

Birds from Christmas Island breed on a schedule similar to that of Hawaiian birds although it is somewhat more prolonged (Schreiber and Ashmole, 1970), but it is not known if the birds disperse after breeding.

In the Phoenix Islands the breeding cycle is annual but the peaks are not clearly defined (POBSP). The cycle is five months ahead of the cycle in the Hawaiian group. Breeding birds arrive at their islands in September and eggs are laid in late November or early December. Peak populations are found on the islands at this time, although more

than half of the birds present are nonbreeders. Eggs hatch in early February and by March the adults visit the islands only sporadically at night to feed their chicks or to roost. Most adults leave the islands in early May, followed by most of the fledged young two weeks later. By early June few birds are left on the islands except small roosting populations which remain during the nonbreeding season.

The breeding cycle of San Benedicto Island appears to be roughly synchronous with that of the northwestern Hawaiian group on the basis of the only available information: two egg dates, 31 May and 26 July (Anthony, 1900:252; Loomis, 1918:142).

SUMMARY OF PUBLISHED PELAGIC RECORDS.—The appendix summarizes the status of the Wedge-tailed Shearwater in the Pacific Ocean. Because few observers are familiar with the distinguishing characteristics of this species, many of the pelagic records are ambiguous; they could refer to one or more species that resemble either light- or dark-phase Wedge-tailed Shearwaters.

In the eastern Pacific Wedge-tailed Shearwaters have never been identified with certainty south of the Gulf of Guayaquil (latitude 3°S) (Lévêque, 1964b:53-54). They have been reported several times along the Middle American coast from Panama to Mexico near Manzanillo. Murphy's (1958) record of both light- and dark-phase birds off north

ern Baja California in December is exceptional; they have not otherwise been reported north of 21°N (Loomis, 1918), fully 500 miles farther south. Records from the eastern Pacific have been obtained mainly in the northern spring and fall.

Mörzer Bruyns (1965) saw Wedge-tailed Shearwaters over the Equatorial Countercurrent across most of the Pacific in November, dark-phase west of the Line Islands, and mixed from there east; King and Pyle (1957) found them in the Countercurrent between the Line Islands and Mexico in October.

In the southwest Pacific several authors (Jespersen, 1933; Fleming, 1950; Gibson, 1960; Mitchell, *in Bourne*, 1965; Morris, *in Bourne*, 1965; Norris, 1967) have noted scattered individuals or small groups of dark-phase birds between Samoa and Australia throughout the year.

ACKNOWLEDGMENTS.—In addition to all the co-operators who have made this paper possible (p. 5) special thanks are due to Gerald A. Sanger and Patrick J. Gould who were closely involved in analyzing the data. The latter was almost solely responsible for the section entitled "Density and Distribution within Equatorial Currents."

I am also indebted to William R. P. Bourne, Roger Bailey, and George E. Watson for their critical reading of the manuscript and their many helpful suggestions and comments.

Distribution and Abundance

Figure 34–57 (pp. 68–91) show monthly densities of Wedgetailed Shearwaters in the central and eastern Pacific based on POBSP observations between 1963 and 1968. Densities are expressed in terms of birds per linear mile of observation, and located on the monthly map at the ship's noon position. Areas of similar daily densities are contoured to show the relative abundance of the species in all areas of the Pacific where POBSP observations have been made. In cases where parallel ocean transects were made on cruises spanning two months, the contouring takes into account the distribution and abundance reflected in adjacent areas even though the data came from different months. Because of their geographical and, often, phenological distinctness, light-phase and dark-phase birds are treated separately.

DENSITY AND DISTRIBUTION WITHIN EQUATORIAL CURRENTS

The Equatorial Countercurrent is an eastward-flowing current, bounded on the south by the westward-flowing South Equatorial Current and on the north by the westward-flowing North Equatorial Current or the California Current Extension, depending on the longitude.

Sverdrup, et al. (1942:709) point out its salient features, i.e., it is a well-developed, northern hemispheric phenomenon, whose boundaries fluctuate with the seasons, moving north with the northern summer. Data from the Carnegie Expedition discussed by Sverdrup, et al. (1942:709–711) show that at latitude 140°W the countercurrent lies between 3°N and 10°N. Due to a distinct transverse circulation superimposed upon the major flow direction, a divergence occurs at the northern boundary of the countercurrent and at the equator, while a convergence occurs at the southern boundary. They speculate, on the basis of the plankton collections of the Carnegie Expedition, that divergences are of high productivity. Similarly, convergences concentrate plankton and organisms that feed on plankton along narrow fronts (Ashmole and Ashmole, 1967). Other authors, e.g., Murphy (1936) and Mörzer Bruyns (1965), have noted some of the effects of oceanic currents on density and distribution of birds.

In the central Pacific Wedge-tailed Shearwaters may be found throughout the current areas. In general the dark-phase population predominates in the area south of 10°N, the area generally covered by the Equatorial Countercurrent and the South Equatorial Current. The dark-phase population moves north in conjunction with the northward movement of warm waters during the northern summer months.

North of the countercurrent, light-phase birds predominate, although small numbers may sometimes be encountered as far to the south as the equator or farther. These may represent migrants or nonbreeding visitors since they occur primarily during the nonbreeding period of the light-phase population.

CENTRAL PACIFIC.—From January 1964 through February 1967, sixteen cruises were made by the POBSP across these equatorial currents in the area bounded by longitudes 165°W and 180°. Surface

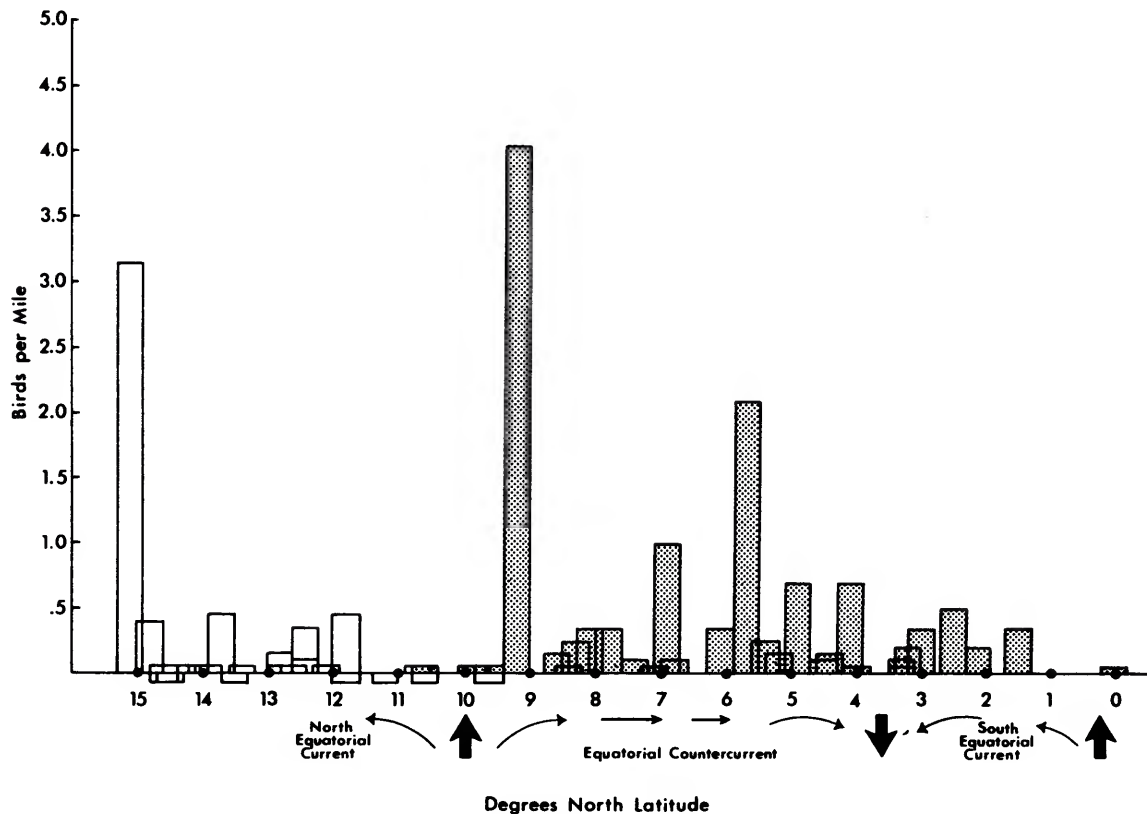


FIGURE 30.—Density of Wedge-tailed Shearwaters in relation to latitude across the equatorial currents in the central Pacific (165°W to 180°), all months, 1966. (Shaded bars = dark phase; white bars = light phase.)

water temperature ranged from 25.5° to 30.6°C throughout the period of study; the vast majority of samples fall between 27°C and 30°C. Lowest temperatures were generally found north of the countercurrent and highest temperatures south. Within the countercurrent temperatures remained remarkably constant.

Small densities of Wedge-tailed Shearwaters were recorded throughout the current area at all times of the year; a few notable concentrations occurred between 4°N and 7°N in winter and spring, and at 9°N in July. A July peak, composed of 99 percent dark-phase birds, occurred during the period of northward movement of the dark-phase population. A concentration in the fall at 15°N can best be explained in terms of the attraction of Johnston Atoll, a nearby breeding site. Unlike Sooty Terns, whose pattern of distribution in the

Equatorial Current area does not conform to any boundaries (Gould, p. 32 herein), Wedge-tailed Shearwaters appear to be most abundant within the borders of the Equatorial Countercurrent. This is best exemplified by Figure 30, in which all the data from 1966 are combined. Data from 1966 were used because data were complete enough to permit identification of the countercurrent on the basis of water temperature samples.

EASTERN PACIFIC.—In the eastern Pacific the Equatorial Countercurrent is generally well defined east to 90°W longitude from June through December, but diffused or absent during the rest of the year. Its southern boundary remains relatively stable at 4°N to 6°N; its northern boundary fluctuates between 8°N and 12°N. It is farthest north during the northern summer (Wyrki, 1966; n.d.).

Figure 31 shows densities for six cruises through

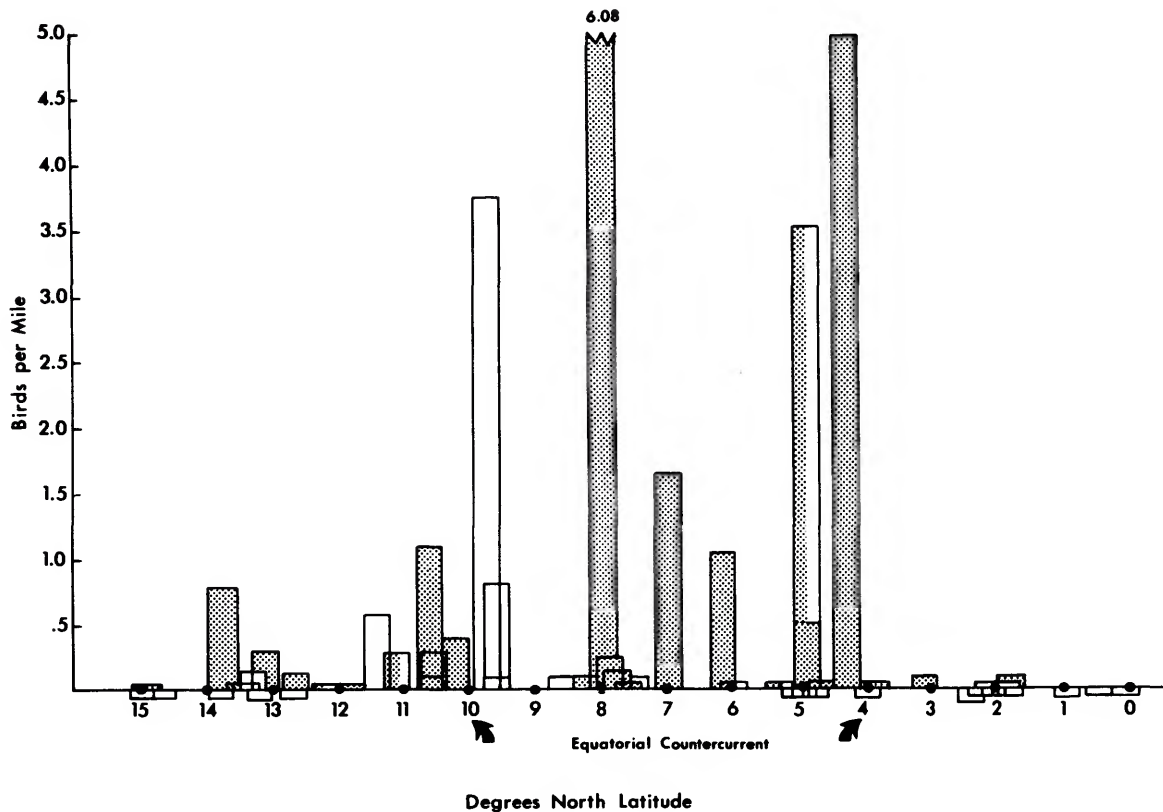


FIGURE 31.—Density of Wedge-tailed Shearwaters in relation to latitude across the Equatorial Countercurrent in the eastern Pacific (97°W to 126°W), 1967. (Shaded bars = dark phase; white bars = light phase.)

the area bounded by 97°W and 126°W during 1967. Surface water temperatures show a different pattern for these cruises than for the central Pacific cruises. Temperatures remained between 25.5° and 28.8°C in latitudes south to ca. 6°N . At 6°N , temperatures began to drop rapidly; at ca. 2°N readings were between 23.8° and 25.7°C , dropping in one instance to 20.7°C near the equator at 97°W .

Both color phases occur within this area, and, although the data base is too small to provide a complete picture, it appears that light-phase birds (possibly nonbreeding sojourners from the central Pacific) predominate in the northern winter, while dark-phase birds (possibly from the Revilla Gigedo population) predominate during the rest of the year.

All large concentrations were found between 4°N and 10°N . In February and March highest densities were near 10°N . Due to the unstable condition of the countercurrent at this time, its boundaries cannot be defined clearly. In June and July highest densities were from 4°N to 5°N , corresponding fairly closely with the southern boundary of the countercurrent; smaller concentrations were found at 7°N and from 10°N to 11°N , the former being just north of the southern boundary of the countercurrent, and the latter just south of the northern boundary. In the fall (September) only one large concentration was noted, at 8°N , somewhat south of the northern boundary of the countercurrent. In the eastern Pacific, especially in the northern summer when the Equatorial Countercurrent is strongest, Wedge-tailed Shearwaters

reach highest densities near and within the borders of that current.

RANGE OF SEA SURFACE TEMPERATURES AND SALINITIES AT WHICH WEDGE-TAILED SHEARWATERS WERE OBSERVED

The Wedge-tailed Shearwater is distributed throughout most of the tropical central and eastern Pacific Ocean, and, thus, it is not surprising to find that the range of sea surface temperatures and salinities at which the species was observed is roughly as broad as the recorded temperatures and salinities of the area. Sea surface temperatures were recorded on a sufficiently large number of cruises to provide a substantial amount of data from which to draw conclusions; salinity determinations were far fewer, and the data are less conclusive.

The water samplings within five minutes of the hours of 0800, 1000, 1200, 1400, and 1600 were assumed to give a fairly accurate measure of the temperature and salinity for one hour before and one hour after the hours mentioned. All sightings made one hour before to one hour after were assigned the temperature and salinity values of said hours. Since each sample covers two hours of observation, the ratio of birds to samples divided by 2 yields a bird per hour of observation figure.

TEMPERATURE.—Sightings made when no sea surface temperatures were taken, or more than one hour before 0800 or after 1600, account for slightly more than one-half the data. Temperature correlations apply to 34,073 of 82,000 Wedge-tailed Shearwaters observed during the study. Table 14 shows the number of birds observed in conjunction with each whole degree of temperature centigrade, the number of water samples at each temperature, and the ratio of birds to samples.

Table 14 suggests that Wedge-tailed Shearwaters showed no great sensitivity to temperature as long as it was above 21°C. The lowest sea temperature at which Wedge-tailed Shearwaters were observed was 15.0°C. Two individuals were seen at this remarkably low temperature; otherwise the lowest temperature was 20.8°C, and the highest was 33.0°C.

SALINITY.—Far fewer salinity measurements were made, too few to show anything but the range of salinities over which Wedge-tailed Shearwaters were observed. Table 15 shows the number of birds,

TABLE 14.—Relative abundance of Wedge-tailed Shearwaters at various sea surface temperatures

Temperature (°C)	Number of birds	Number of water samples	Birds/Sample
20.....	0	56	.00
21.....	13	66	.20
22.....	502	75	6.56
23.....	278	98	2.84
24.....	5,193*	133	39.05
25.....	1,618	445	3.64
26.....	11,642	853	13.65
27.....	6,596	900	7.33
28.....	5,579	814	6.85
29.....	1,185	340	3.49
30.....	1,398	276	5.07
31.....	69	14	4.93
Total.....	34,073	4,070	

*Includes a single sighting of 3500 individuals. This sighting is unusually large, and accounts for the inflated birds/sample figure at 24°C.

TABLE 15.—Wedge-tailed Shearwaters observed at various sea surface salinities

Surface salinity (parts per thousand)	Number of birds	Number of water samples	Birds/Sample
33.0-33.3.....	4	4	1.00
33.3-33.7.....	18	11	1.64
33.8-34.1.....	17	31	0.55
34.2-34.5.....	84	46	1.83
34.6-34.9.....	158	49	3.22
35.0+.....	87	38	2.29
Total.....	368	179	

the number of samples, and the birds per sample in each of six salinity ranges. Table 15 shows a fairly even spread across the recorded salinity range, with a tendency toward greater abundance at salinities 34.6 parts per thousand and above. The lowest recorded salinity at which Wedge-tailed Shearwaters were seen was 32.60 parts per thousand; the highest was 36.54 parts per thousand.

SPECIMEN RECORDS, MOLT, AND BAND RECOVERIES

SPECIMEN RECORDS.—The POBSP secured specimens of Wedge-tailed Shearwaters at sea in both

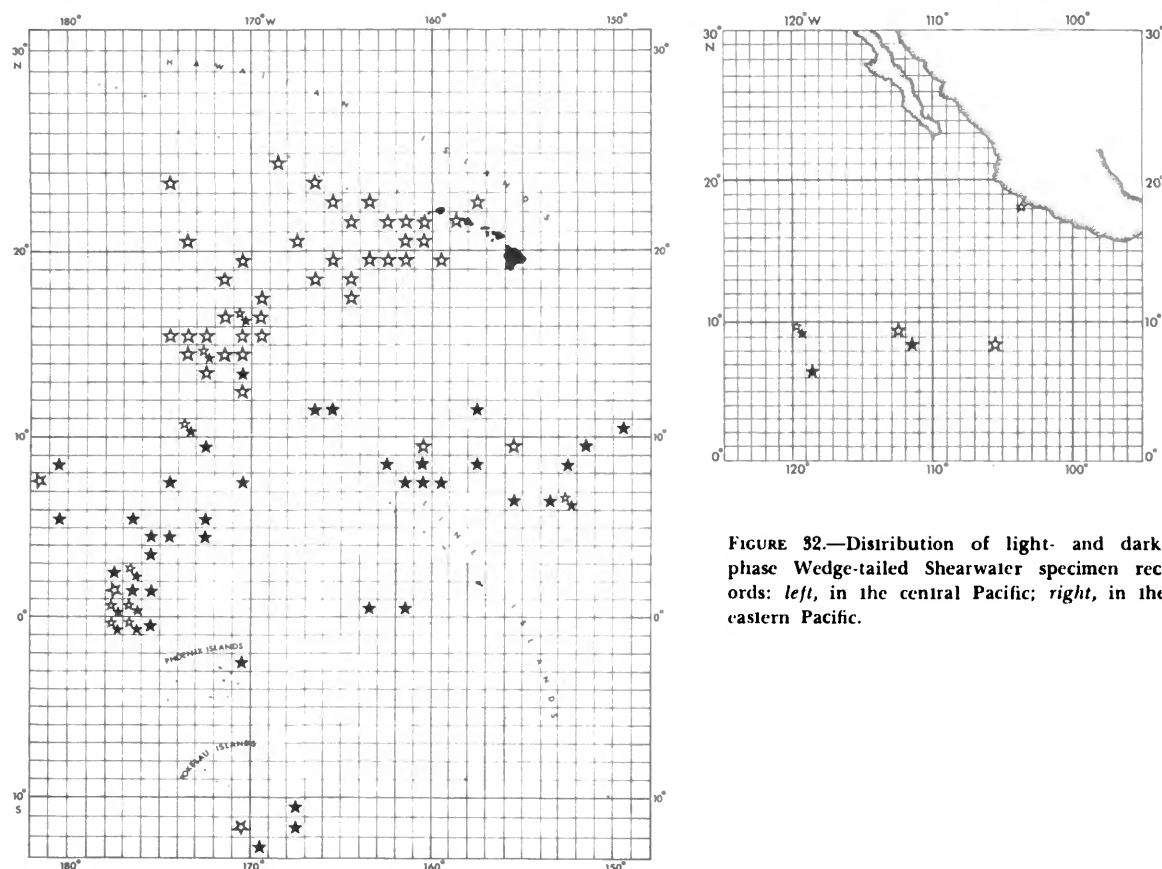


FIGURE 32.—Distribution of light- and dark-phase Wedge-tailed Shearwater specimen records: *left*, in the central Pacific; *right*, in the eastern Pacific.

the central and eastern Pacific. Table 16 lists the numbers of specimens of the two color phases collected each month. Figure 32 shows the location, by degree squares, where specimens were obtained; color phases are differentiated.

TOPOGRAPHY AND SYNCHRONY OF MOLT.—Primary molt proceeded distally from one locus. It was far more symmetrical than rectrix molt. The primaries on either wing were almost invariably at identical stages of growth. Growth differentials of one-half of a feather length were noted rarely. In distal primary molt (primaries 7 to 10) only one feather was replaced at a time. Growth of a distal primary was nearly completed as the next one began to grow. Several inner primaries can be replaced simultaneously.

Rectrix molt was most intense during later primary molt. It was only marginally symmetrical, usually more in the number and spacing of replaced

feathers than in their position. For example, rectrices 2 and 4 might be growing on the left, and rectrices 3 and 5 on the right. Rectrix replacement followed no fixed sequence. Usually one or two, and up to five, of the six rectrices on each side were replaced simultaneously.

Contour feather molt probably started at the same time as, but was more protracted than, primary molt. Head and nape feathers were replaced first, followed by scapular and rump feathers. New head and nape feathers of light-phase birds were gray and soft; old ones were browner and coarser. Newly replaced scapulars had conspicuous pale scallops at their tips. These pale scallops were most conspicuous in light-phase birds in December (presumably first-year birds), slightly less so in adults in April. Most December light-phase birds had gray vermiculations on the crissum, flanks, and sides, similar to those of adult Pink-footed Shearwaters

TABLE 16.—*Specimens of Wedge-tailed Shearwaters collected by the POBSP each month*

Area and color phase	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
CENTRAL PACIFIC													
Light phase	0	3	1	12	32	25	18	30	24	2	1	16	164
Dark phase	3	3	2	20	7	17	10	2	10	5	11	3	93
EASTERN PACIFIC													
Light phase	—	—	3	—	—	1	—	—	—	4	—	—	8
Dark phase	—	1	—	—	—	—	1	—	—	1	—	—	3
Total	3	7	6	32	39	43	29	32	34	12	12	19	268

(*Puffinus creatopus*). Such vermiculations were present infrequently in light-phase birds from other months.

First-year birds probably retain their juvenal plumage for 15 months. Adults molt primarily during their nonbreeding season, although replacement of contour feathers extends throughout the breeding season. Since adults and subadults are present together on islands, and most likely also at sea, most age-classes were probably sampled in the POBSP collections. Thus, it is likely that molt occurs simultaneously in all age-classes after the first year.

SCHEDULE OF MOLT.—*Light-phase Birds:* No light-phase birds were collected at sea in January. Few were seen in the central Pacific, but they were common in the eastern Pacific. In early February in the eastern Pacific POBSP personnel (Woodward, pers. comm.) reported that they had noticeable gaps in their primaries, indicative of molt of the inner primaries. The three central Pacific specimens from February had no molt of remiges, rectrices, or contour feathers; two had gray vermiculations on flanks and abdomen. These three were probably first-year birds with 3-month-old plumage since March and April specimens, presumably adults growing their 9th or 10th primaries, were in the midst of rectrix replacement and had replaced head, nape, and some scapular contour feathers. Some March specimens collected on the northwestern Hawaiian Islands were completing growth of their 10th primaries. In April seven of twelve specimens taken at sea had completed remex and rectrix molt, but all were still replacing contour feathers. In May only one of 32 specimens had not completed flight feather molt, but contour

feather molt was continuing in the scapulars and on the rump. No flight feather molt occurred on any bird from June to December. However, all sixteen December specimens had fresh plumage, including remiges and rectrices with a silvery sheen and prominent white scalloping on scapular and lower back feathers. (The scalloping was noticeable from a considerable distance at sea.) Their remiges had broad vanes and blunt tips with small sharp central points, similar to those of May specimens, indicative of unworn feathers. There was no indication of remex replacement in the small sample of October and November birds, so I conclude that the December birds, which were all from the central Pacific, were fledglings and that adults and subadults had already left that area. Although the date of onset of molt is not known, adults and subadults might have already started to molt their worn plumage by December. These December birds were the only ones that followed ships regularly (see "Behavior").

Dark-phase Birds: The molt cycle in dark-phase birds is more complex than it is in light-phase birds because of the geographical and temporal overlap of populations at sea. There was some rectrix or remex molt in 40 out of 96 birds, and in all months but May. Using the clear-cut molt cycle of the light-phase birds as a model, it is difficult to explain the molt cycles of dark-phase birds. Phoenix Islands' birds lay eggs in November and December; they should start flight-feather molt in May and complete it in October. Many specimens conform to this schedule. Five of 17 June birds were growing primaries 4, 5, or 6; 7 of 10 July birds were growing primaries 6, 7, 8, or 9; several August birds and 7 of 10 September birds were growing primaries 9

or 10, and all 5 October birds had completed or nearly completed molt.

Christmas Island birds lay eggs in June and July. They would be expected to begin molt in November and to complete it in April. Seven birds collected in November were growing primaries 3 to 7; two January birds were growing primary number 8; 17 of the 20 April birds and all May birds had completed molt of flight feathers. These birds conform to the Christmas Island schedule.

There are still a number of dark-phase specimens that conform to neither of these schedules. The large number of birds molting at all times of the year suggests two explanations: either most birds are from local populations (e.g., Line and Phoenix islands) and are present around their breeding islands a greater part of the year and molt is more protracted than in their subtropical, light-phase counterparts, or the central Pacific is invaded by postbreeders from other populations. The two theories are not mutually exclusive. I suspect both are true.

BAND RECOVERIES.—Between 1963 and 1969 POBSP personnel banded 75,285 Wedge-tailed Shearwaters, 65,806 in the Hawaiian Islands, Johnston Atoll, and the northern Marshall Islands, and 9,479 in the Line and Phoenix islands. Nineteen banded birds were recovered at sea by August 1969. Three had been banded on Johnston Atoll; the remainder had been banded on islets off the northeast coast of Oahu.

The only significant recovery is the southernmost record from Cook Strait, New Zealand, described in the introduction. Recoveries of birds banded on Johnston Atoll were within 300 miles southwest or northwest of Johnston Atoll. Birds banded on islets off Oahu were recovered within 100 miles in all directions of Oahu. All recoveries were made between April and October—the breeding season.

On 11 October 1964 a bird that had been marked with an orange plastic leg streamer on Johnston Atoll was seen at latitude 9°25'N, longitude 152°55'W, about 1250 miles southeast of its place of marking. Although it is tempting to suggest that this is evidence for migration, individuals doubtless range thousands of miles searching for food, so that this location might well be included within the possible foraging range of the Johnston Atoll population.

DISCUSSION

In the central Pacific light-phase distribution and abundance at sea were quite evidently tied to the breeding cycle of the birds on the Hawaiian Islands and Johnston Atoll. During the northern winter light-phase bird abundance was lowest and, although there was a poorly defined density center at the Equatorial Countercurrent, for the most part the few birds that were recorded were scattered. In February light-phase birds were virtually absent from the central Pacific north of 10°N (7 individuals in 4 years). Data from March showed birds reentering that area, and from April through November a typical distribution pattern prevailed with only minor irregularities; maximum densities during this period were recorded consistently within 100 miles of the breeding islands.

In the eastern Pacific the timing was reversed. Light-phase birds were most abundant from October to February (a maximum of 10.6 BPM south of Guatemala in February), and least abundant from March to September. Greatest densities were recorded between 6°N and 12°N, the area of the Equatorial Countercurrent, and the normal light-phase range did not appear to extend very much farther north or south. The northern limit appeared to be approximately 25°N latitude.

I conclude that the eastern Pacific is a major wintering ground for light-phase birds from the Hawaiian group. I suspect they migrate there along the Equatorial Countercurrent and return via the North Equatorial Current.

The at-sea distribution and abundance of dark-phase birds cannot be tied as readily to their breeding cycles. In the first place the two populations that breed in the central Pacific do so at opposite seasons. (Increasing density in the eastern Pacific concurrent with the beginning of the breeding season on Christmas Island suggests that the bulk of eastern Pacific dark-phase birds in the northern summer do not come from Christmas Island.) Secondly, both populations number in the tens of thousands, rather than hundreds of thousands as does the Hawaiian population. Thirdly, there are many more dark-phase colonies across the Pacific than there are light-phase colonies. Thus, assigning islands of origin to any group of dark-phase birds encountered at sea is, at our present level of knowledge, only conjecture.

Several tendencies in dark-phase distribution are worth noting. The first is the repeated association of high densities with the Equatorial Countercurrent area, not only in the central Pacific but also in the eastern Pacific. The second is the extent and timing of the northward penetration of dark-phase birds. This penetration began in April at the same time that light-phase birds were once again becoming numerous to the north. It increased in scope and intensity to a peak in July and August, during which time dark-phase birds were found nearly as far north (to ca. 23°N) as light-phase birds. Numbers decreased thereafter until there were almost no dark-phase birds to be seen north of 10°N during December, January, and February. In other words, the distribution and abundance pattern of dark-phase birds north of 10°N in the central Pacific paralleled that of light-phase birds.

A parallel situation occurs in the Indian Ocean (Bailey, 1968). During the northern winter, the breeding season for Wedge-tailed Shearwaters in the western Indian Ocean, the birds are distributed most abundantly along the Equatorial Countercurrent. In summer, when the countercurrent weakens or is absent, birds move north to the Bay of Bengal and the Arabian Sea in substantial numbers.

In the eastern Pacific light-phase and dark-phase birds occupied roughly the same area, but they reached maximum abundance at different times of year. Both phases reached greatest densities between the Equatorial Countercurrent and the coast of Mexico near Manzanillo. Light-phase birds generally were not seen south of 4°N, whereas dark-phase birds were seen occasionally as far south as POBSP observations were made (to latitude 20°S in some months). Light-phase birds were most abundant between October and February; dark-phase birds attained highest densities from June to September. It is likely that a few birds of both phases, probably nonbreeders, were present throughout the year in the eastern Pacific.

The implication of an abundance cycle in the eastern Pacific of dark-phase birds similar to that of light-phase birds, although several months out of phase, is that dark-phase birds from yet unspecified breeding sites perform an annual translongitudinal migration also. Even if all the dark-phase birds encountered in the eastern Pacific were from the Revilla Gigedos, which is quite unlikely, they must be making an extensive migration, for there are

fewer dark-phase birds to be found in the eastern Pacific from October to May than from June to September.

Several sources (Jespersen, 1933; Dixon and Starrett, 1952; MacDonald and Lawford, 1954; Mörzer Bruyns, 1965) indicate the presence in the western tropical Pacific between New Guinea and the Marianas, and in the Philippine Sea, of large numbers of dark-phase Wedge-tailed Shearwaters from April to October. POBSP personnel saw light-phase birds between the Tokelau and Samoan islands at 12°S latitude in February. Dixon and Starrett (1952) also suggest that light-phase birds are present, at least south of the Marianas, in January and February although these may have been any of several other species, especially Streaked Shearwater (*Calonectris leucomelas*). Thus there may be in the western Pacific a situation directly analogous to that of the eastern Pacific in which both phases are present but with abundance peaks in different seasons.

Behavior

FEEDING.—Wedge-tailed Shearwaters have been observed feeding on the surface, under the surface, and in the air. The method most frequently noted by POBSP observers, at least for diurnal flocks, was "contact dipping," to use the terminology of Ashmole and Ashmole (1967). Second in frequency was "feeding on the surface," third was "air dipping," and fourth was "air diving."

In contact dipping birds flew close to the surface, wings held back as if to hover, sometimes touching the surface with outstretched feet. Head and neck were plunged down several inches into the water. Forward momentum was regained by vigorous wing beats and foot paddling. Usually when a fish was caught it was eaten without interrupting flight although birds stopped on the surface occasionally, presumably to swallow heavy prey. This was the only method of feeding observed at night (Gould, 1967), although it is likely that feeding on the surface was used too.

Feeding on the surface was often accomplished from a sitting position but sometimes a surface dive was employed, although rarely forcefully enough to submerge a bird completely under water. Wing tips and tail usually remained out of water.

Air dipping was seen infrequently. It involved

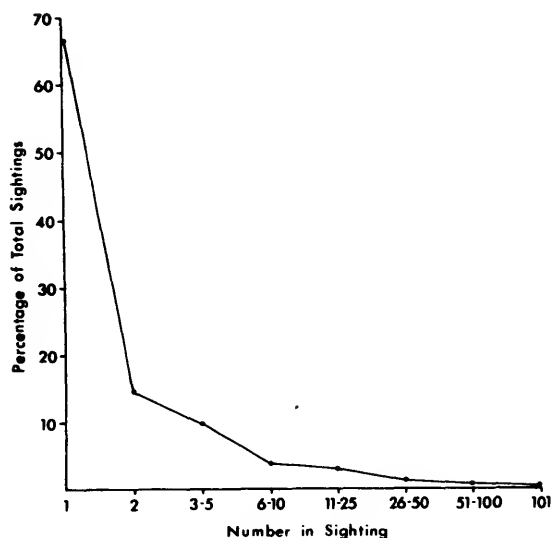


FIGURE 33.—Number of Wedge-tailed Shearwaters per sighting in a sample of 1000 sightings in which this species was recorded.

pursuit of a flying fish above the surface of the water, sometimes accompanied by vigorous foot strokes for increased speed.

Air dives were rarely observed. They involved a dive into the water "just about like the boobies" (POBSP, Dayle Husted). No further description is available.

There were no observations to indicate that birds swim any distance under water, in spite of adaptations for this purpose such as laterally compressed tarsi and compact plumage (Kuroda, 1954; Storer, 1960).

FLOCKING.—Figure 33 shows the number of Wedge-tailed Shearwaters counted or estimated per sighting in a random sample of 1000 sightings in which the species was observed. A sighting is defined here as the observation of one or more birds acting as a unit. Occasionally it was difficult to decide whether birds seen at the same time were associated or not. This was especially true close to breeding areas where streams of birds of several species could be seen coming and going at the same time.

Most sightings (66.9%) were of single birds. Progressively fewer sightings were made of larger groupings. Only 0.3 percent of sightings contained 100 or more birds. However, the largest number

seen in one sighting was 3500. This was part of a large milling mass of birds near Kaula Rock. Of 70 flocks containing 100 or more Wedge-tailed Shearwaters, the mean number for that species was 307. Fifty out of 70 (71.4%) flocks of more than 100 Wedge-tailed Shearwaters were within one day's travel (100 miles or less) of the Hawaiian Islands.

ASSOCIATION WITH OTHER SPECIES.—Casual observations at sea suggest that birds of some species tend to occur individually, others tend to associate frequently with other members of the same species, and still other species tend to occur in mixed-species aggregates. Wedge-tailed Shearwaters usually travel singly or in small groups, but feed most frequently in large mixed-species flocks.

Data on association of Wedge-tailed Shearwaters in all sightings between 1963 and 1969 were analyzed to determine the relative tendency for the species to occur alone or in conjunction with other species. Data showed that Wedge-tailed Shearwaters associated with members of other species in 57.8 percent of the sightings, and were alone or with other Wedge-tailed Shearwaters in 42.2 percent of the sightings (Table 17).

To understand why more Wedge-tailed Shearwaters were seen in mixed-species aggregates than alone, it is important to look at the behavior of the respective groups. The categories of behavior for which information was recorded systematically included sitting on the water, feeding, searching, following the ship, displaying, parasitism, dispersing, and traveling. The behavior of birds at sea, however, is sometimes difficult to characterize. Searching and dispersing are closely related to feeding. Searching implies that a flock of birds has formed and is about to feed when schooling fish break the surface. Dispersing implies that a flock was feeding a short time before observation, but inability to

TABLE 17.—Sightings of Wedge-tailed Shearwaters in association with other species and alone

Status	Average number		
	Number of birds	Number of sightings	of birds per sighting
Associated	47,276	3,225	14.66
Unassociated	34,561	14,743	2.34
Total	81,837	17,968	4.56

TABLE 18.—Number and percentage of sightings in which various species were observed feeding with Wedge-tailed Shearwaters (n=1285)

Species	Number	Percentage
<i>Puffinus pacificus</i> (alone)	85	6.6
<i>Sterna fuscata</i>	994	77.4
<i>Anous stolidus</i>	241	18.8
<i>Gygis alba</i>	239	18.6
<i>Sula sula</i>	213	16.6
<i>Pterodroma externa externa</i>	192	14.9
<i>Fregata minor</i>	112	8.7
<i>Pterodroma hypoleuca nigripennis</i>	104	8.1
<i>Sula dactylatra</i>	90	7.0
<i>Puffinus puffinus newelli</i>	75	5.8
<i>Sula leucogaster</i>	45	3.5
<i>Puffinus griseus</i>	43	3.3
<i>Bulweria bulwerii</i>	43	3.3
<i>Pterodroma externa cervicalis</i>	40	3.1
<i>Sterna lunata</i>	31	2.4
<i>Anous tenuirostris</i>	30	2.3
<i>Fregata ariel</i>	28	2.2
<i>Pterodroma neglecta</i>	26	2.0
<i>Puffinus nativitatis</i>	24	1.9
<i>Oceanodroma leucorhoa</i>	20	1.6
<i>Stercorarius pomarinus</i>	17	1.3
<i>Puffinus carneipes</i>	15	1.2
<i>Puffinus lherminieri</i>	15	1.2
<i>Pterodroma alba</i>	13	1.0
<i>Phaethon rubricauda</i>	11	0.9
<i>Procelsterna cerulea</i>	10	0.8
<i>Stercorarius longicaudus</i>	8	0.6
<i>Diomedea immutabilis</i>	7	0.5
<i>Phaethon lepturus</i>	7	0.5

find more surfacing fish was resulting in disintegration of the flock. Wedge-tailed Shearwaters were not known to display at sea, nor were they subject at sea with any regularity to parasitic attacks by jaegers (*Stercorarius* spp.), skuas (*Catharacta skua*), or frigatebirds (*Fregata* spp.).

Wedge-tailed Shearwaters not actively involved in any other behavioral activity were assumed to be traveling. Thus, it is not surprising that in only 2172 sightings (12.1%) was a behavior noted other than that of traveling.

Of behavioral categories other than traveling, feeding was probably of greatest significance, because, next to traveling, the greatest number of sightings were of feeding birds (1285 sightings). An additional 295 sightings were noted as searching and 16 were dispersing. Significant interspecific relationships can be shown best by analyzing the spe-

cies content of the 1285 sightings of feeding birds. I disregarded searching and dispersing birds in this analysis because of the possibility that these behaviors were misinterpreted by the observers. Table 18 lists the number and percentage of sightings in which various species were in feeding association with Wedge-tailed Shearwaters. Wedge-tailed Shearwaters fed without other species present only 6.6 percent of the time; 93.4 percent of the time they fed in association with other species, especially Sooty Terns (*Sterna fuscata*).

In mixed feeding flocks in the tropical Pacific Ocean, Wedge-tailed Shearwaters and the noddies (*Anous* spp.) fly lowest, usually no higher than 10 meters above the water. Boobies (*Sula* spp.) usually fly between 10 and 30 meters and Sooty Terns and White Terns (*Gygis alba*) fly between 20 and 60 meters above water level. Frigatebirds can be found substantially higher, perhaps as high as 120 or 160 meters. These are the approximate levels at which these species fly during the periods when the schooling fish are not surfacing. The longer the periods between surfacing, the higher the Sooty Terns and frigatebirds tend to fly, and the more dispersed the typical feeding flock becomes. When fish once again break the surface it is difficult for an observer to tell which component of the flock spots them first, but an observer quickly learns to watch for a characteristic flash of white as the Sooty Terns bank from horizontal flight, exposing their white underparts against the sky, in a dive toward the surfacing fish. It is visible to an observer perhaps a mile or more away, appearing like snowflakes dancing on the horizon. The presence of frigatebirds over the terns confirms the suspicion that a flock has gathered and is or has been feeding.

Wedge-tailed Shearwaters utilize a modified dynamic soaring technique in flight, less efficient than the soaring of albatrosses because of higher wing loading and lower aspect ratio. However, they take advantage of the differentials in windspeed at different elevations over the waves caused by surface friction, and are, therefore, more or less tied to the air layer in which windspeed differentials are greatest. Sooty Terns and frigatebirds, on the other hand, either soar statically or propel themselves by constant wingbeats, and are not tied as closely to the surface of the water.

Sooty Terns are in a good position to act as the "eyes" of the flock, both because they are high

above the water and because their greater abundance permits a greater area of ocean to be kept under surveillance for surfacing fish. If human observers can take advantage of the Sooty Terns' dives to the surface as an indication of feeding activity, it is not unreasonable to suspect that birds do the same. Although the behavioral pattern of Sooty Terns may bring increased numbers of other species to the feeding area, competition for food is probably minimal because food is superabundant for the short periods when it is available.

The ephemeral nature of the food supply suggests that, up to a point, more, rather than fewer, birds help to make the supply of food more readily available. Ashmole (1963, postscript) suggested that although tropical seabirds may be limited in their abundance by the availability of food, their effect on the abundance of the food organisms is probably negligible. This is probably also true in areas of food concentration (for example, in the upwellings of the Peru current, where birds' search efficiencies are undoubtedly much higher than for tropical oceans as a whole), where breeding adaptations permit more rapid growth of offspring and population sizes commensurate with predictable abundance of food (see Nelson, 1968, for a comparison of breeding adaptations of boobies within and without such an area of predictable food abundance). Seas surrounding breeding islands in areas without unusual food abundance may support seabird concentrations large enough to cause competition for available food resources. In the face of such competition some species, such as Sooty Terns and Wedge-tailed Shearwaters, can, if necessary, exploit seas at greater distances from their breeding islands than can others, e.g., noddies and boobies. Traveling greater distances for food places more importance on the role of search time in the species' energy budget than in birds of areas of food abundance, and the resulting breeding strategies tend to be more conservative, e.g., fewer offspring, longer incubation stints, and longer fledging periods.

Of significance is the relatively low percent of participation in feeding sightings of the Sooty Shearwater *Puffinus griseus*, Bulwer's Petrel *Bulweria bulwerii*, Leach's Petrel *Oceanodroma leucorhoa*, and the two tropicbirds *Phaethon* spp., all of which are more abundant than is suggested by Table 18. The first species, and its traveling companion the Slender-billed Shearwater *Puffinus*

TABLE 19.—Sightings of sitting birds that included Wedge-tailed Shearwaters (n=465)

Species	Number	Percentage
<i>Puffinus pacificus</i> (alone)	382	82.2
<i>Pterodroma externa</i>	34	7.3
<i>Anous stolidus</i>	9	1.9
<i>Puffinus puffinus newelli</i>	7	1.5
<i>Sula sula</i>	6	1.3
<i>Puffinus puffinus auricularis</i> or <i>P. p. opisthomelas</i>	4	0.9
<i>Sula leucogaster</i>	3	0.6
<i>Puffinus griseus</i>	3	0.6
<i>Pterodroma hypoleuca nigripennis</i>	3	0.6
<i>Sula dactylatra</i>	3	0.6

tenuirostris, seldom stops to feed in the tropics during its transequatorial migrations. The other species are all more or less solitary feeders.

SITTING ON WATER.—Wedge-tailed Shearwaters frequently sit on the water during the day. Of 465 sightings of sitting birds which included Wedge-tailed Shearwaters, 382 (82.2%) sightings were of Wedge-tailed Shearwaters only. Other species most frequently associated with Wedge-tails were Juan Fernandez Petrels *Pterodroma externa externa*, and White-necked Petrels *P.e. cervicalis*. These petrels, not readily distinguished from one another on the water, were frequently seen sitting on the water singly and in rafts up to ten birds during the months of June to October undergoing heavy molt. They were frequently joined by Wedge-tailed Shearwaters. Table 19 gives the frequency with which other species were seen to sit on the water with Wedge-tailed Shearwaters.

Wedge-tailed Shearwaters seem to sit on the water most frequently under two conditions. The first is in association with flocks in which individuals have finished feeding and are resting on the water in small rafts. The second is evidently prior to migration. Rafts of up to 700 or more Wedge-tailed Shearwaters have been seen, mainly near the Hawaiian Islands in November when the young of the year are fledging; the age-structure of the rafts is not known.

FOLLOWING SHIPS.—Wedge-tailed Shearwaters were recorded following ships 20 times. I will omit an analysis of the other species involved in these sightings because of the difficulty in determining if an individual bird was actually following, or if it

passed aft of the ship, turned, and ran with the ship and the other birds for a short while. Also, if the ship provided the stimulus that led the birds to follow, then the association of the various species would be purely accidental.

There can be no doubt, however, that Wedge-tailed Shearwaters occasionally followed ships for 30 minutes or more. They followed ships most readily in November and December in the vicinity of the Hawaiian Islands, and the birds that followed always seemed to have very fresh plumage. They may have been fledglings, attracted to the ship because of food smells emanating from it. Normally Wedge-tailed Shearwaters did not follow ships, although they did not seem to avoid them as did some other species, e.g., Sooty and Slender-billed Shearwaters.

Summary

The Wedge-tailed Shearwater breeds on numerous islands in the tropical and subtropical Pacific Ocean. The infrequent sightings of the species at sea belie the fact that it is abundant and widespread. Some of its subtropical populations perform extensive migrations. Birds from the Hawaiian Islands, for example, probably migrate

south to the Equatorial Countercurrent and then east to the coast of Middle America during their nonbreeding season. Molt takes place during the nonbreeding season and is nearly completed when the birds return to the central Pacific to breed. Tropical populations are present at sea near their breeding islands most of the year, and may not migrate.

Consistently high densities of birds were recorded in the vicinity of the Hawaiian Islands, in the equatorial current area between latitudes 4°S and 10°N, and off the coasts of Middle America. Light-phase birds were abundant in the central Pacific during the northern summer and all but absent during the northern winter; the cycle of abundance was reversed in the eastern Pacific. The abundance of dark-phase birds paralleled that of light-phase birds in the central Pacific, but alternated with light-phase birds in the eastern Pacific. Within the equatorial currents birds were most abundant near the boundaries of the Equatorial Countercurrent.

Wedge-tailed Shearwaters are gregarious when feeding, but more solitary when traveling. Three-quarters of the sightings in which this species was noted feeding contained Sooty Terns; Wedge-tailed Shearwaters may rely on the conspicuous diving behavior of the Sooty Terns to help them locate food.

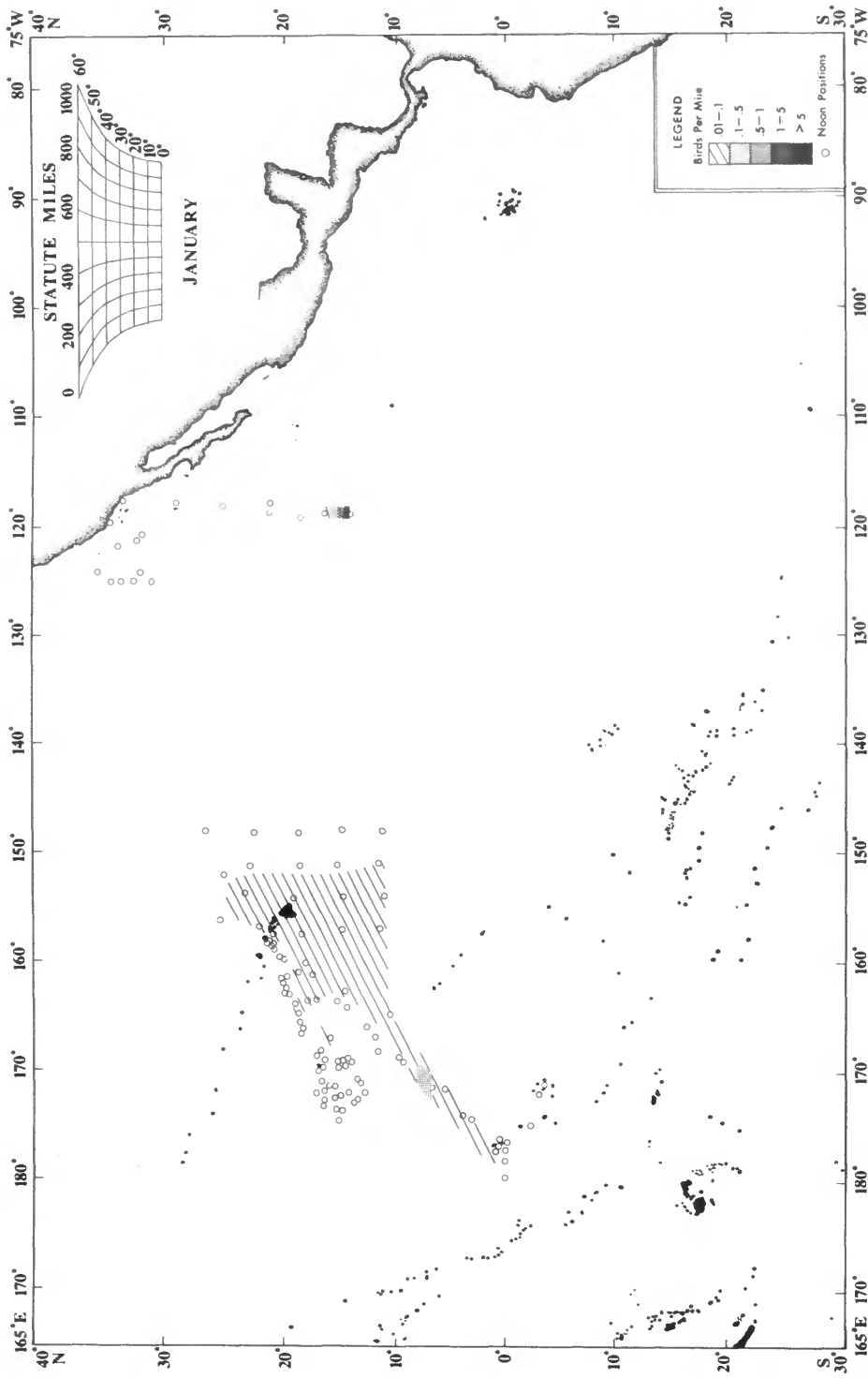


FIGURE 34.—Daily density (BPM) of light-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on 1083 observations in January 1963-1968.

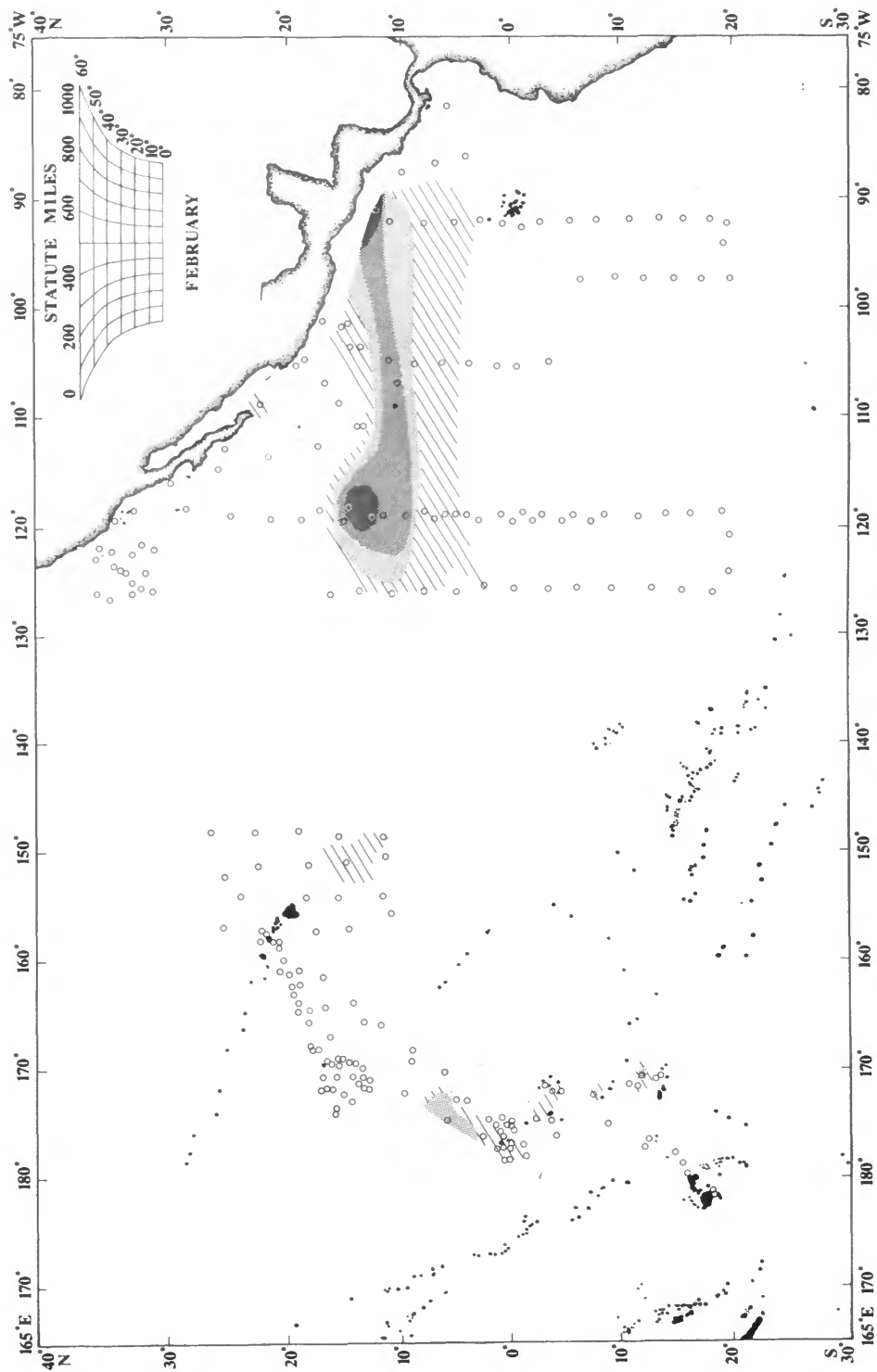


FIGURE 35.—Daily density (σ_t) of light-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on roost observations in February 1963-1968.

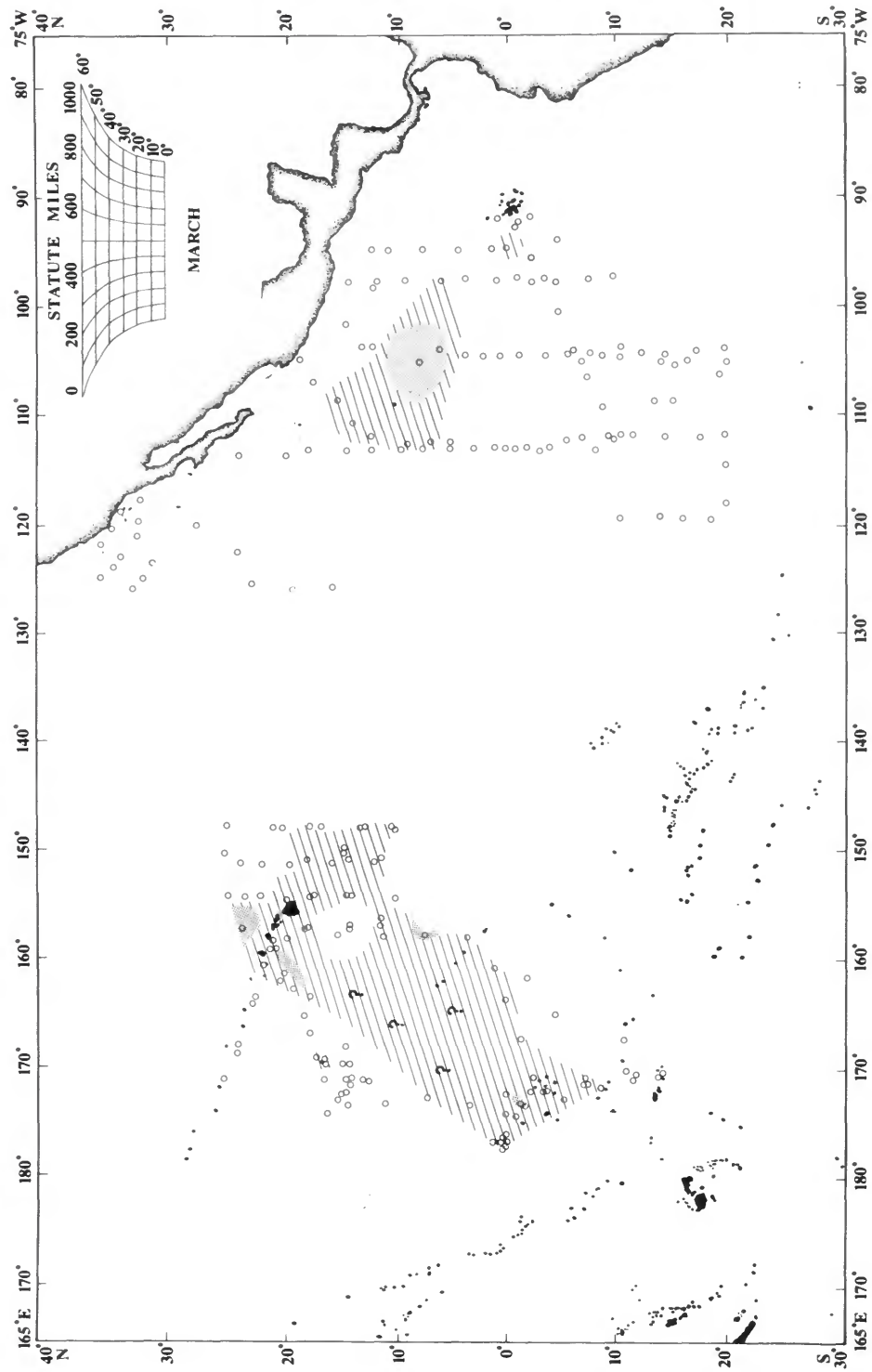


FIGURE 36.—Daily density (σ_t) of light-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on POBS observations in March 1965-1968.

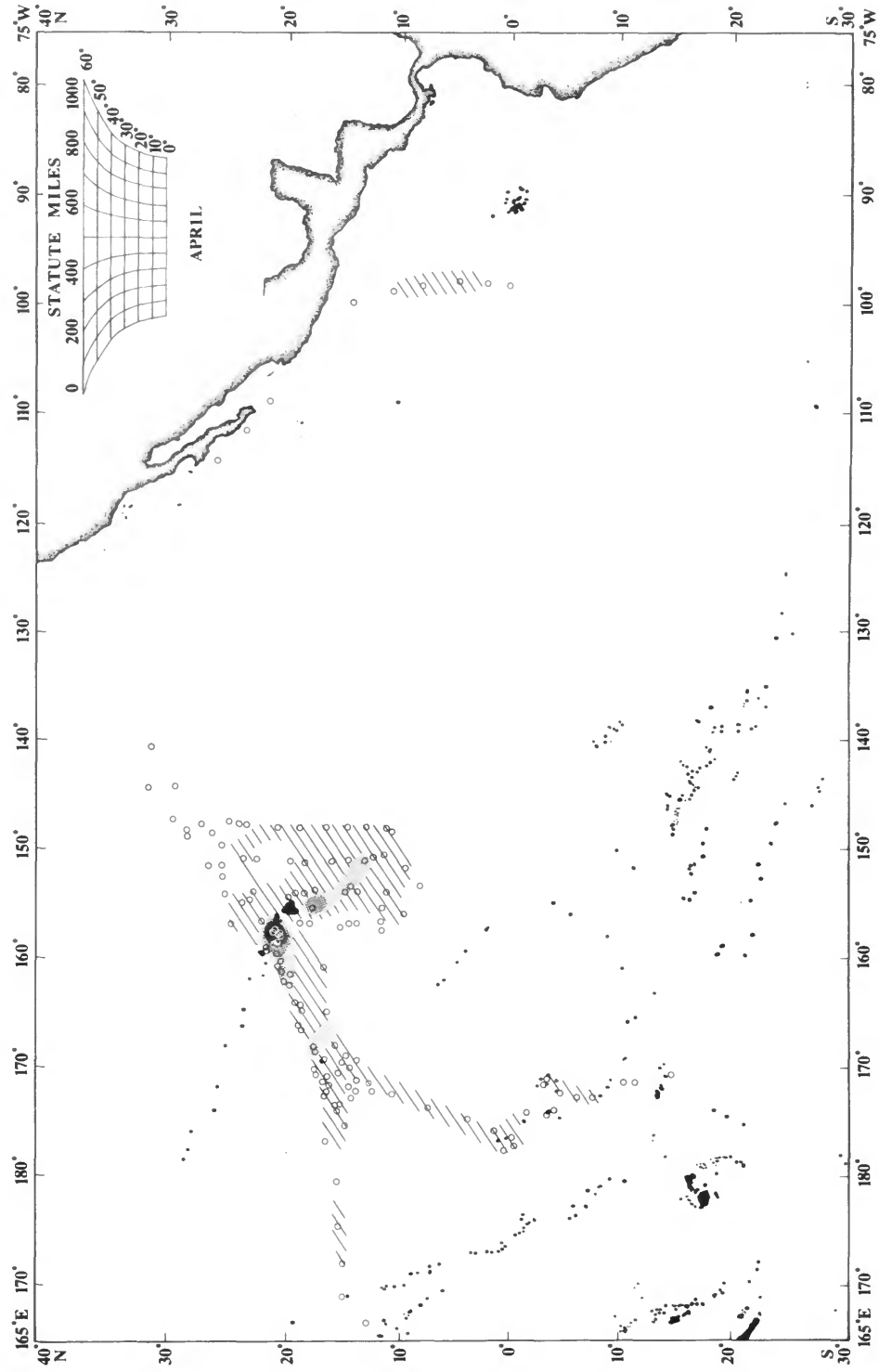


FIGURE 37.—Daily density (σ_t) of light-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on post observations in April 1968-1968.

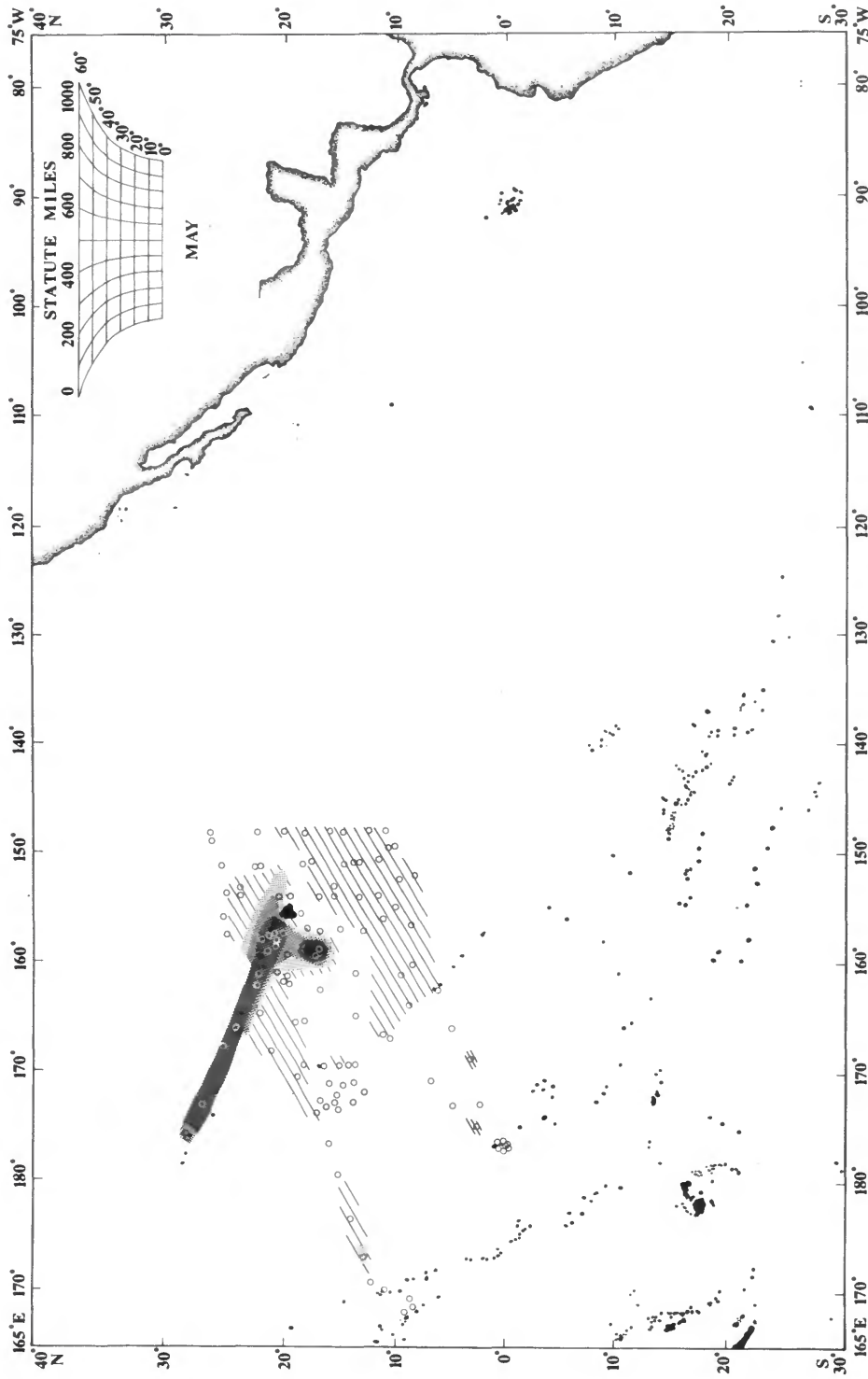


FIGURE 38.—Daily density (σ_t) of light-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on roost observations in May 1963-1968.

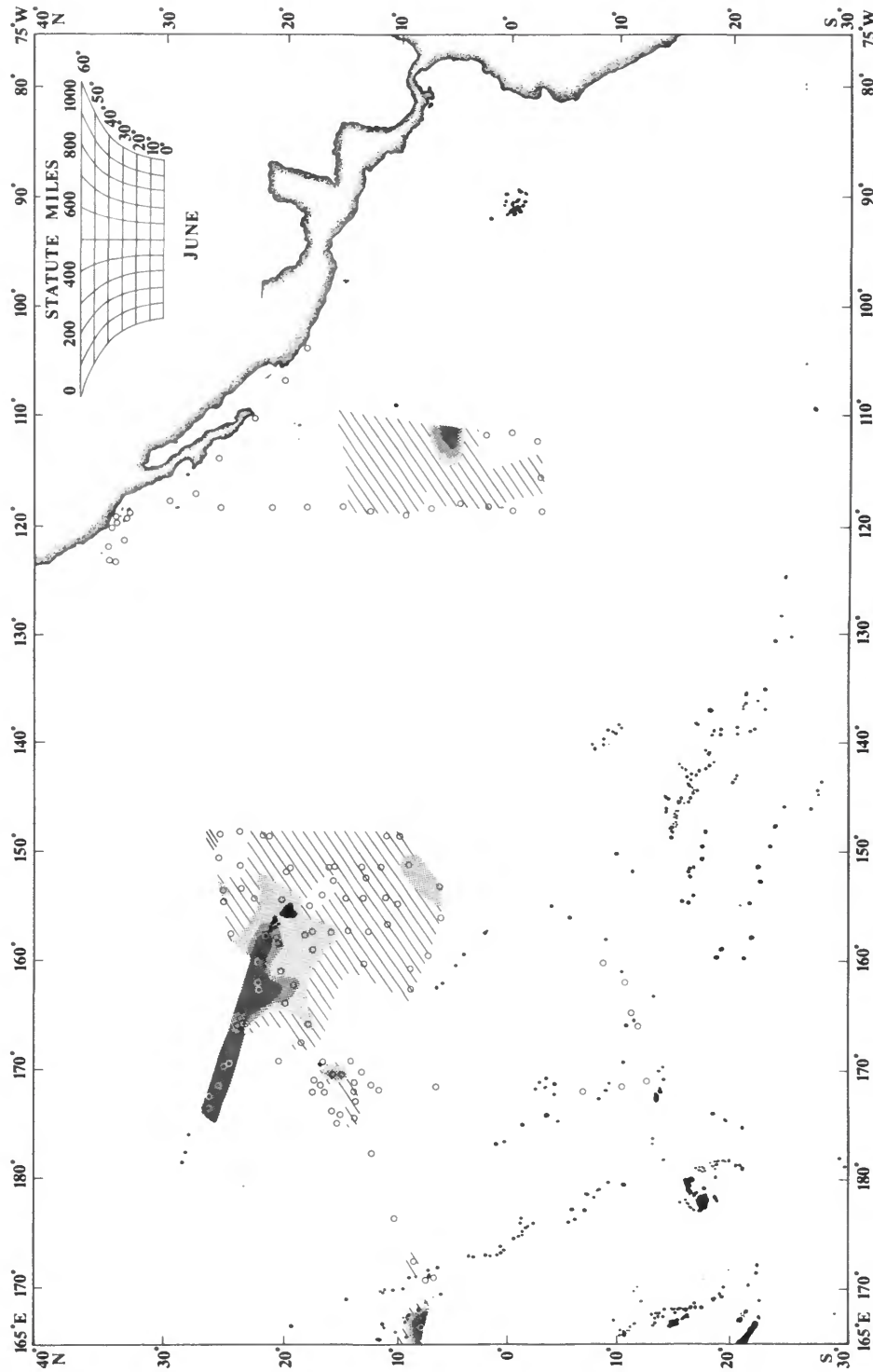


FIGURE 39.—Daily density (σ_{θ}) of light-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on roasp observations in June 1963-1968.

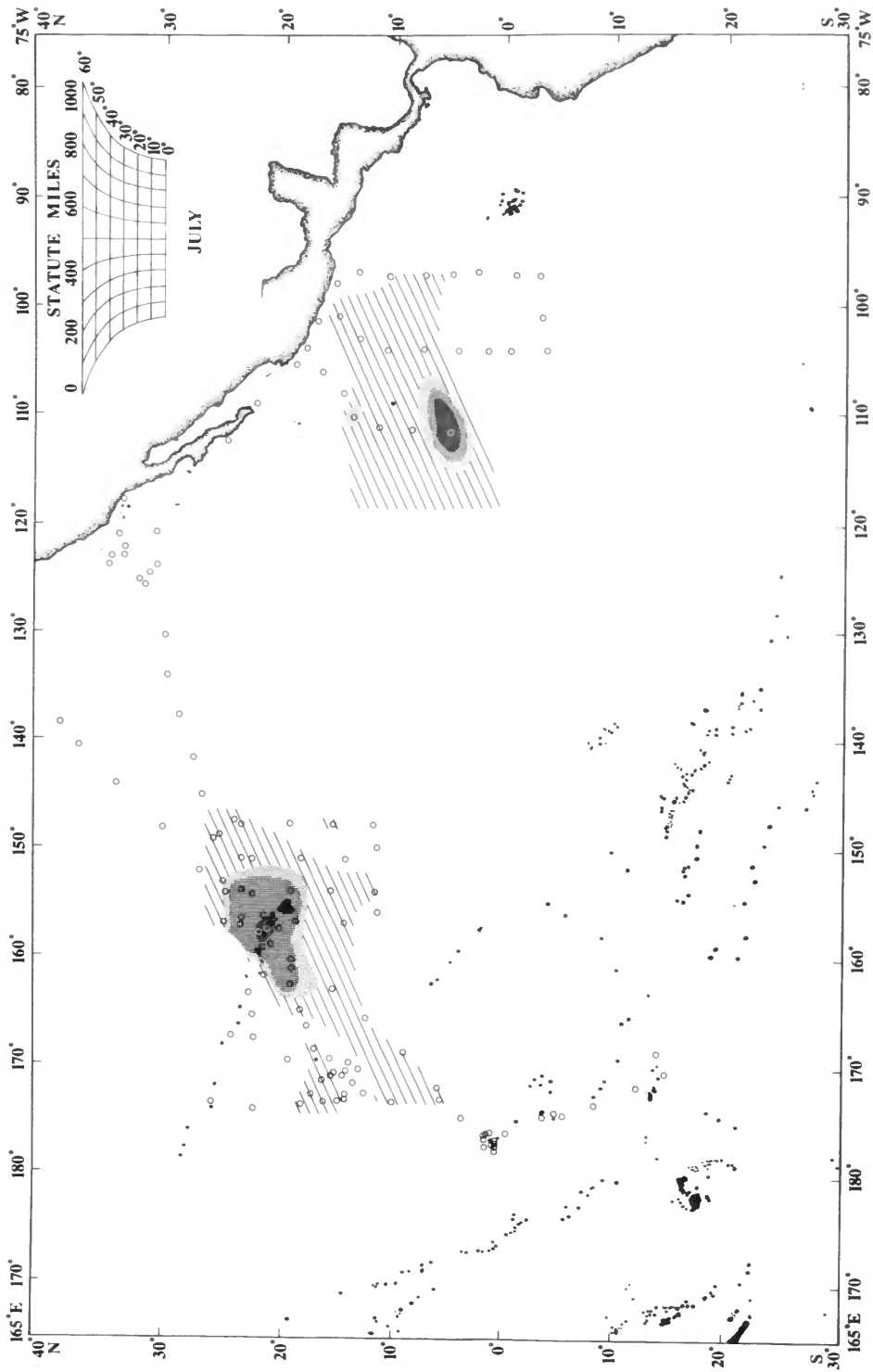


FIGURE 40.—Daily density (σ_t) of light-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on rookery observations in July 1963–1968.

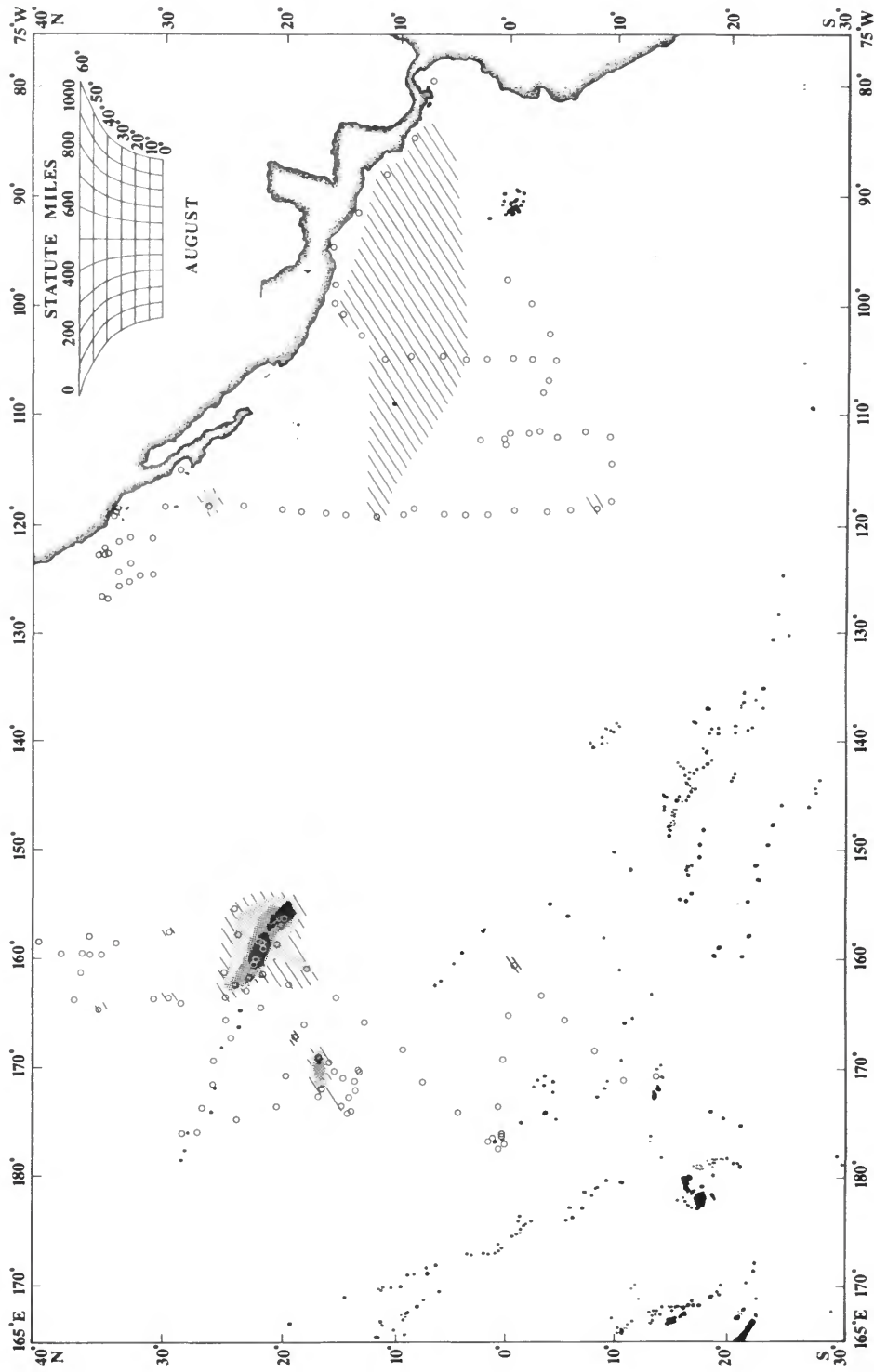


FIGURE 41.—Daily density (σ_{θ}) of light-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on roser observations in August 1963-1968.

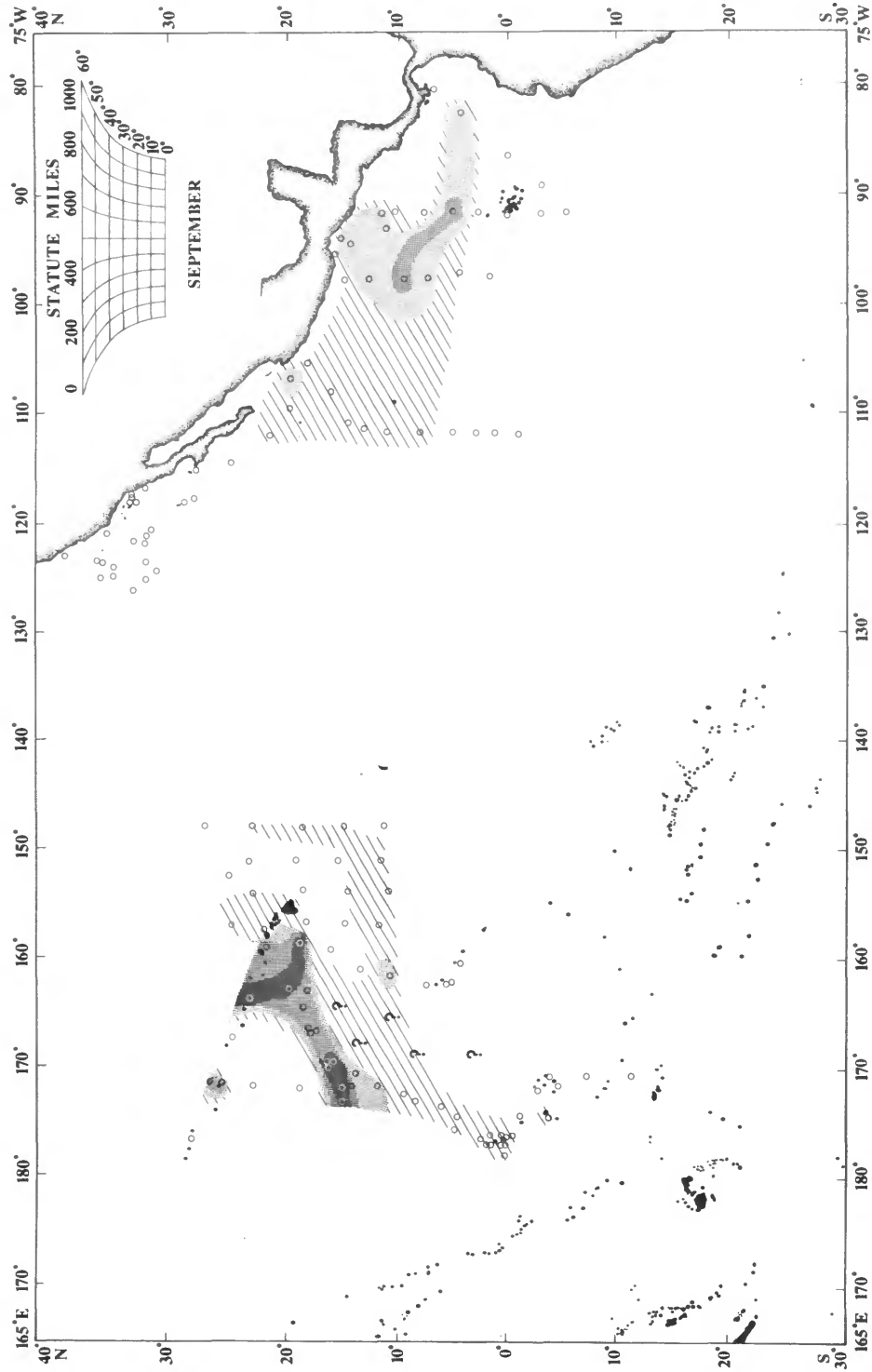


FIGURE 42.—Daily density (bpm) of light-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on roost observations in September 1963-1968.

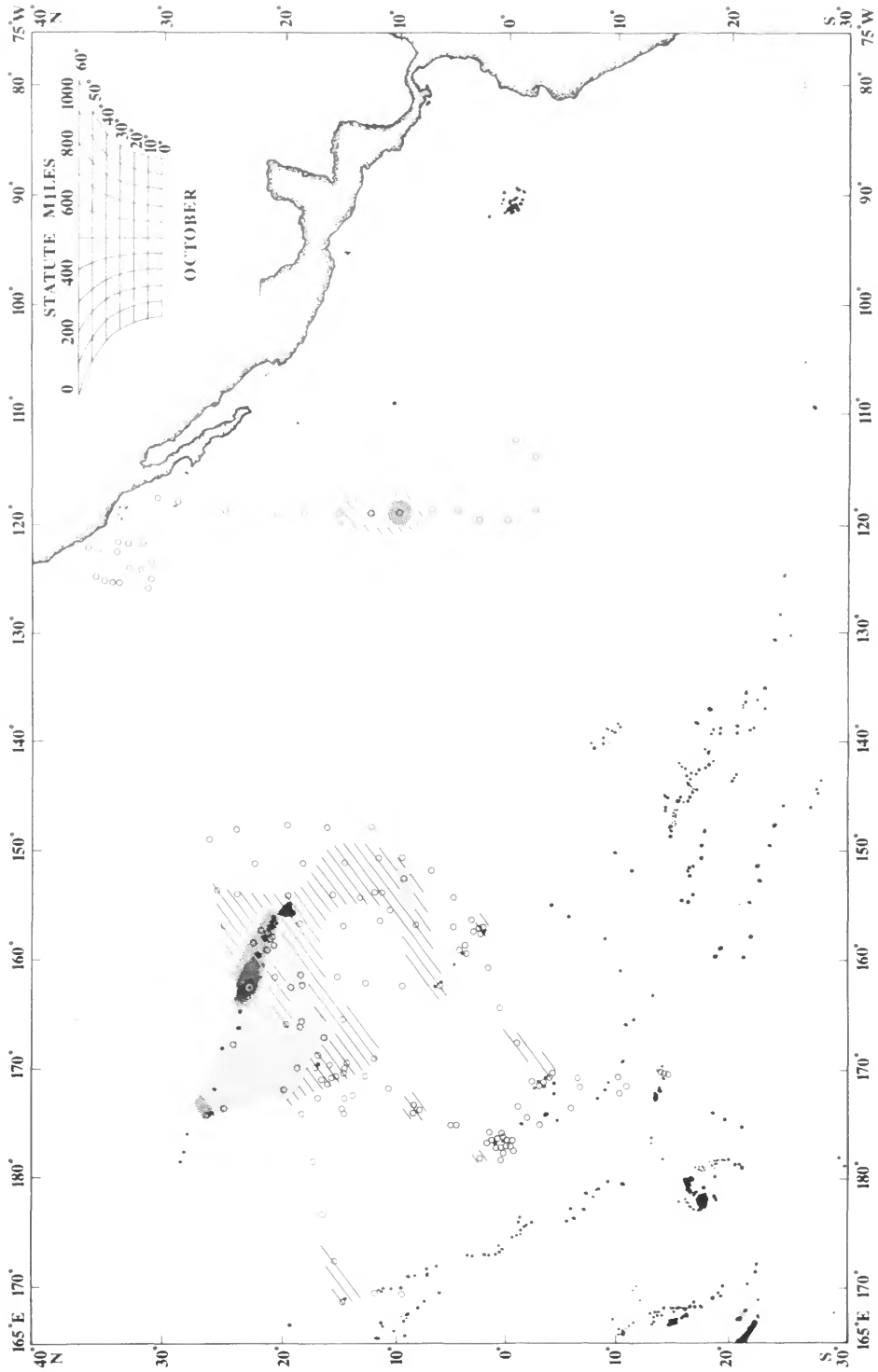


FIGURE 43.—Daily density (σ_t) of light-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on FOSP observations in October 1963-1968.

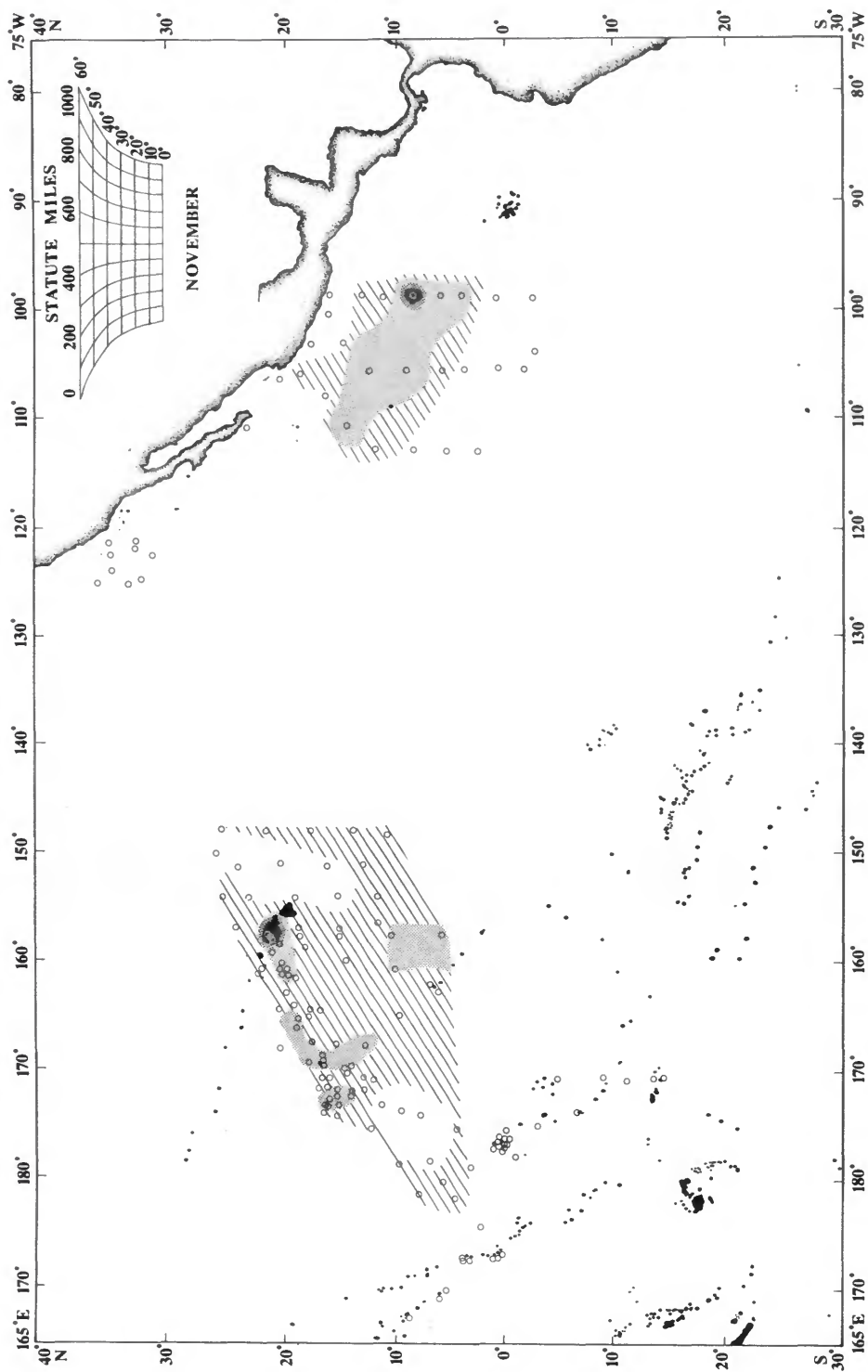


FIGURE 44.—Daily density (σ_t) of light-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on post observations in November 1963-1968.

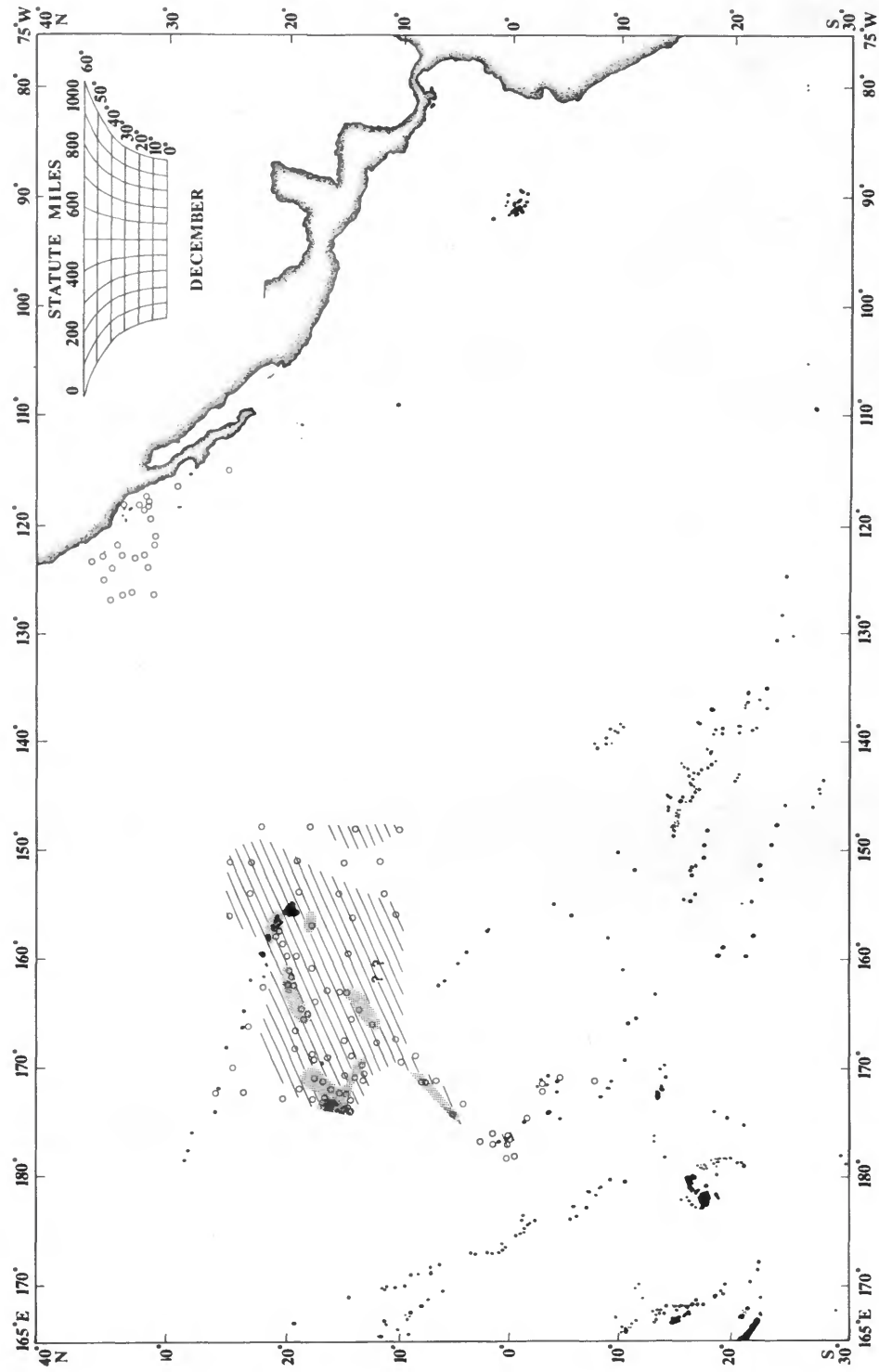


FIGURE 45.—Daily density (σ_t) of light-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on POBSP observations in December 1968-1968.

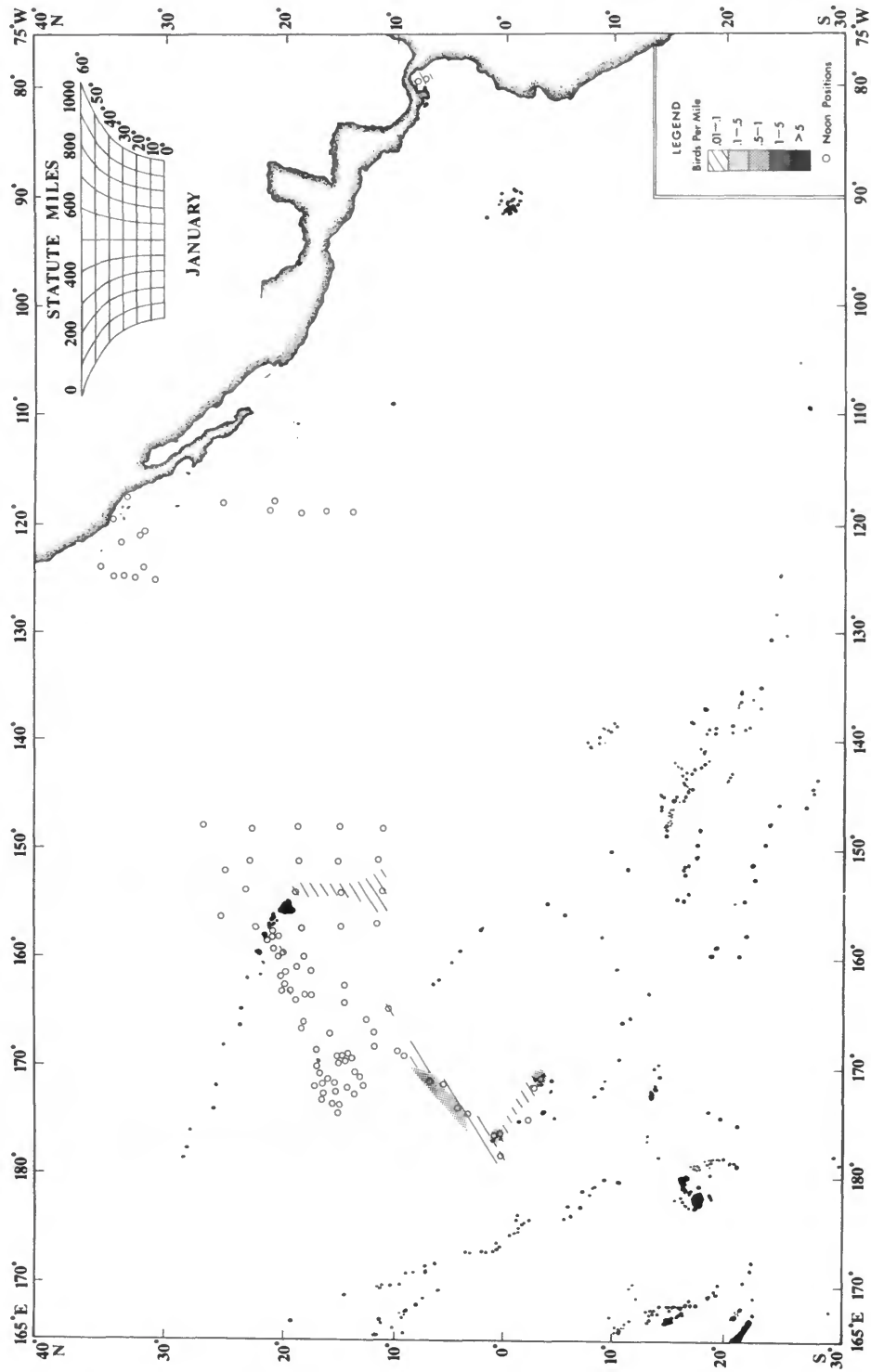


FIGURE 46.—Daily density (BPM) of dark-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on roost observations in January 1965-1968.

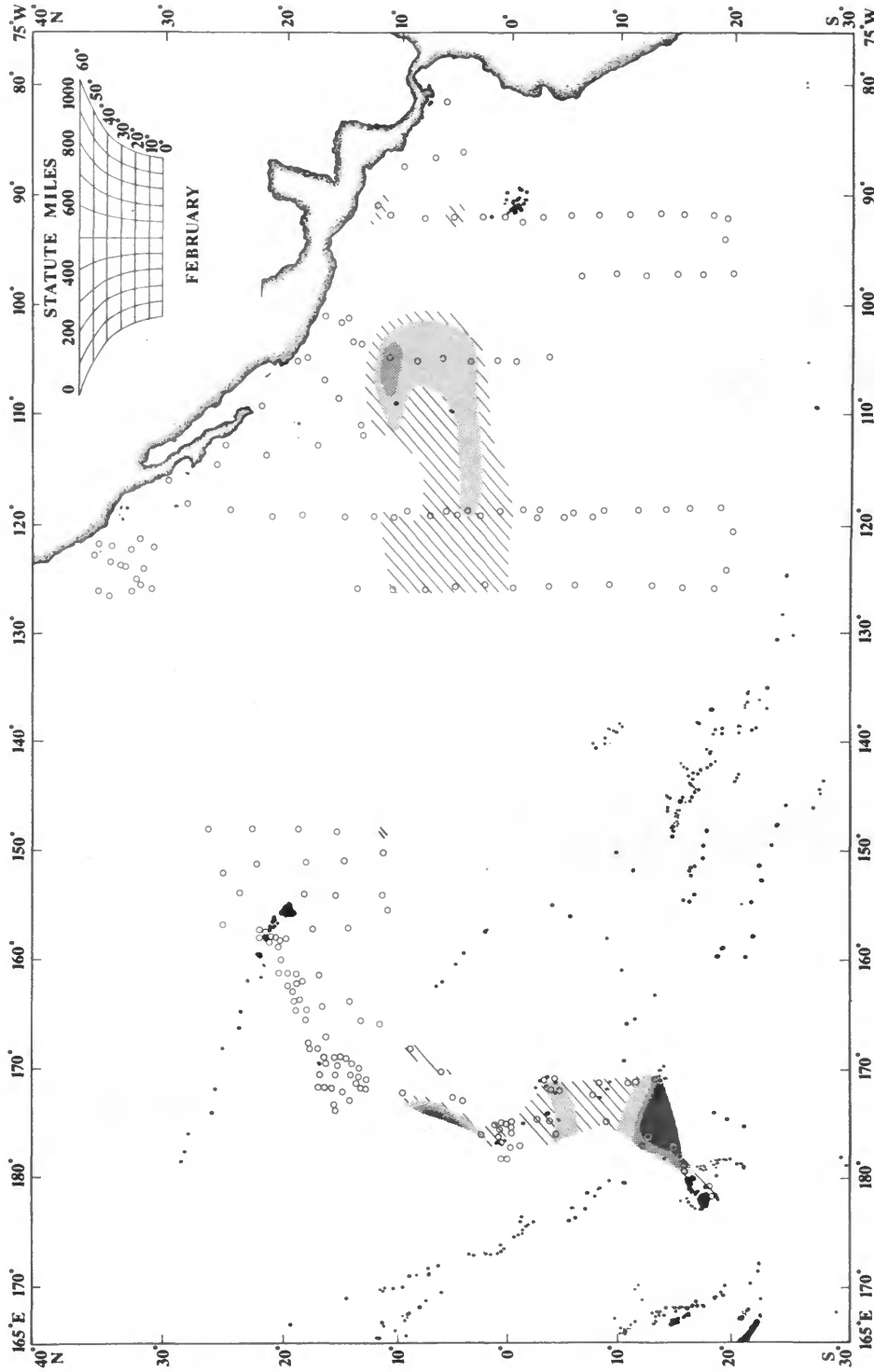


FIGURE 47.—Daily density (σ_t) of dark-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on POSSP observations in February 1963-1968.

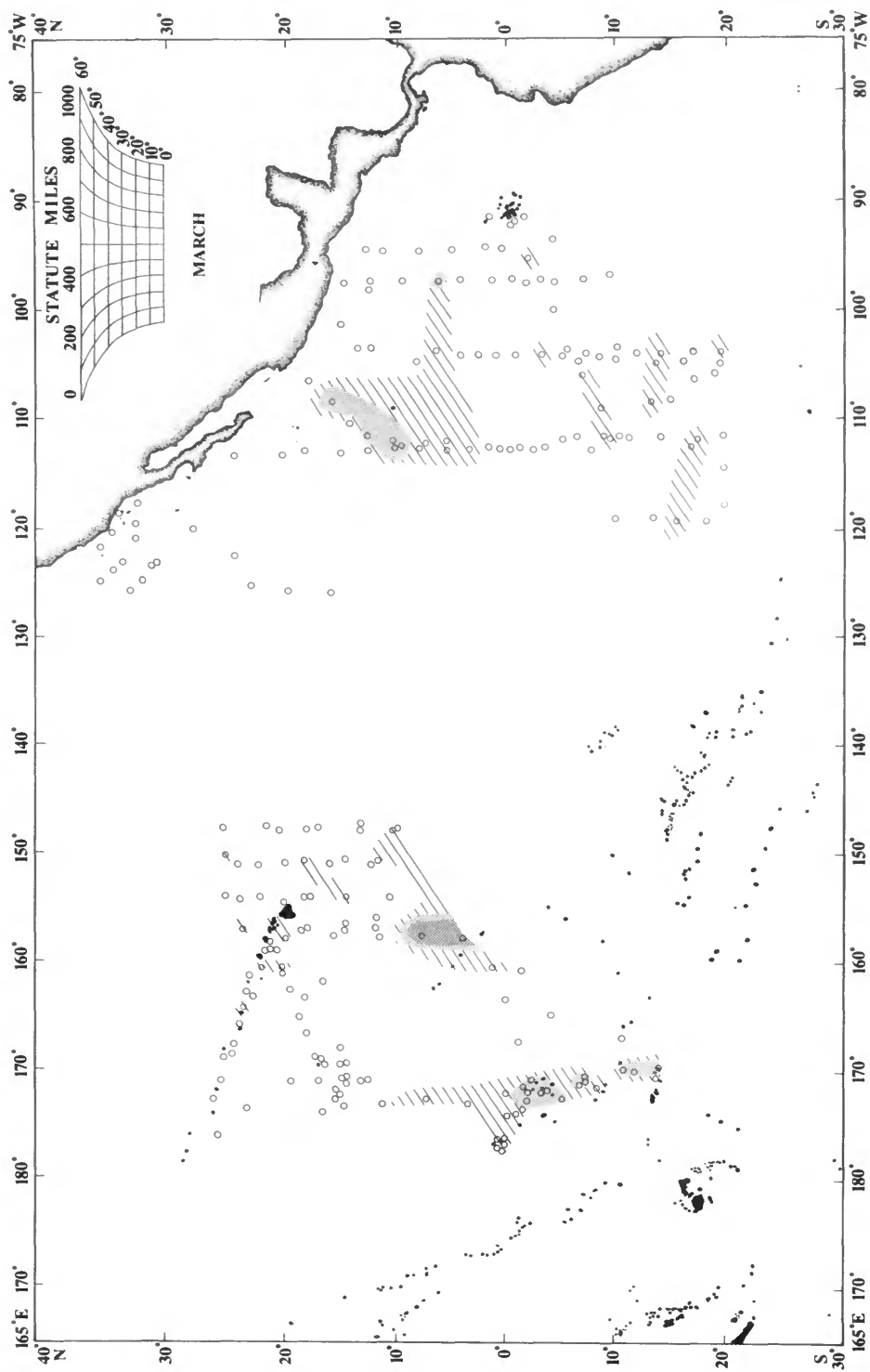


FIGURE 48.—Daily density (σ_t) of dark-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on POSP observations in March 1965-1968.

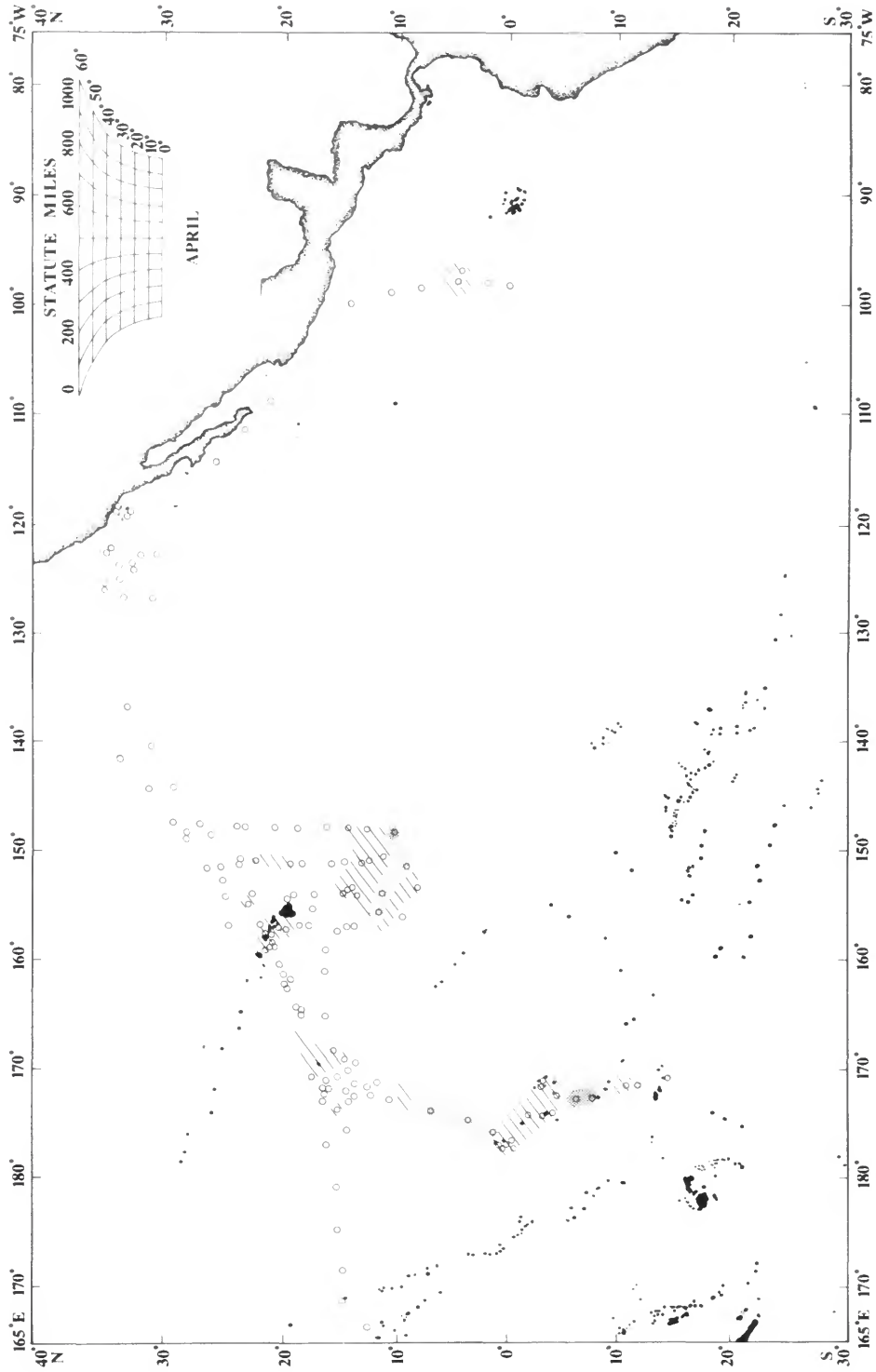


FIGURE 49.—Daily density (σ_t) of dark-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on roost observations in April 1968–1968.

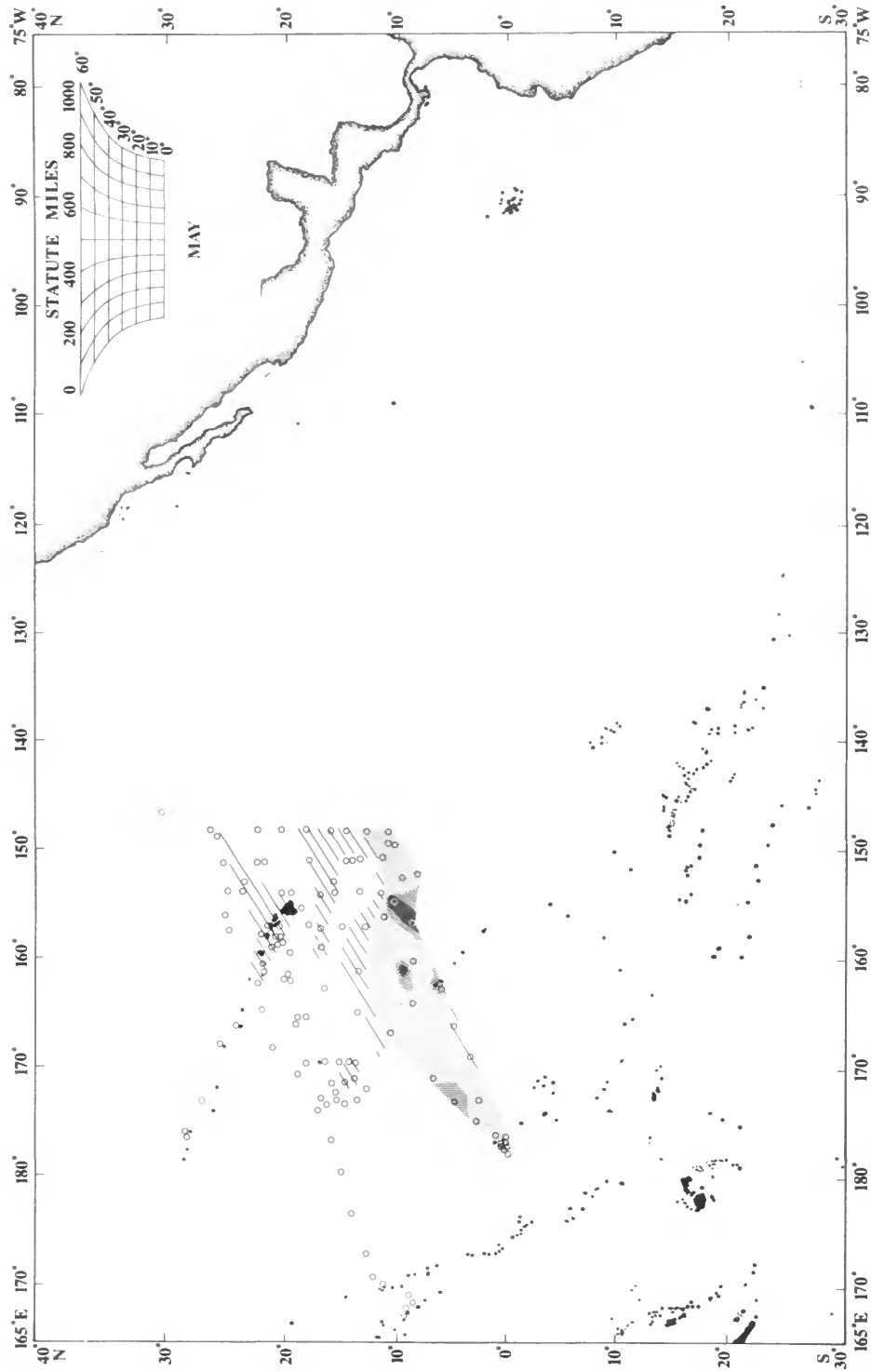


FIGURE 50.—Daily density (σ_{t}) of dark-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on ROSSP observations in May 1968-1968.

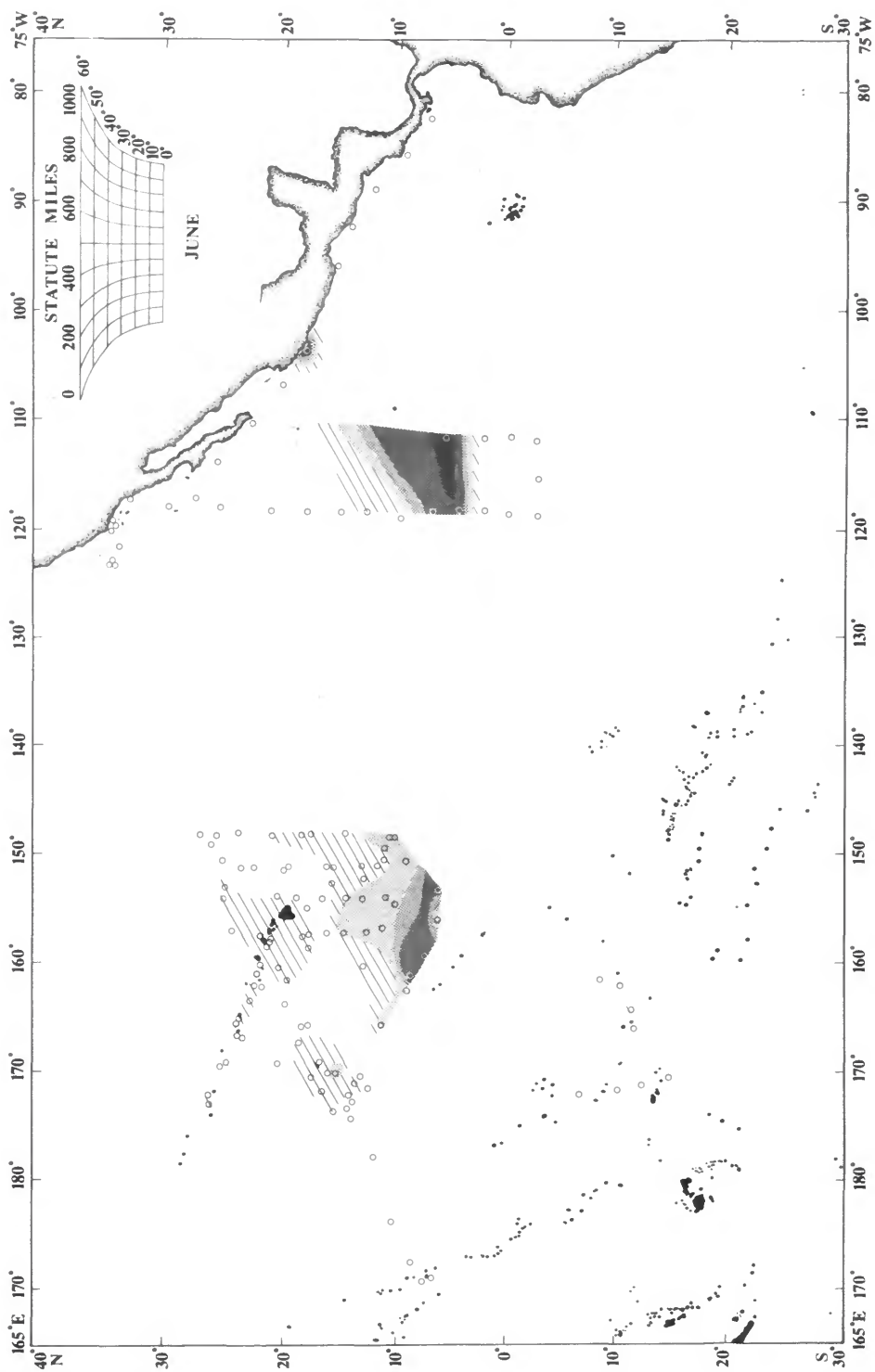


FIGURE 51.—Daily density (σ_t) of dark-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on ROSSP observations in June 1963-1968.

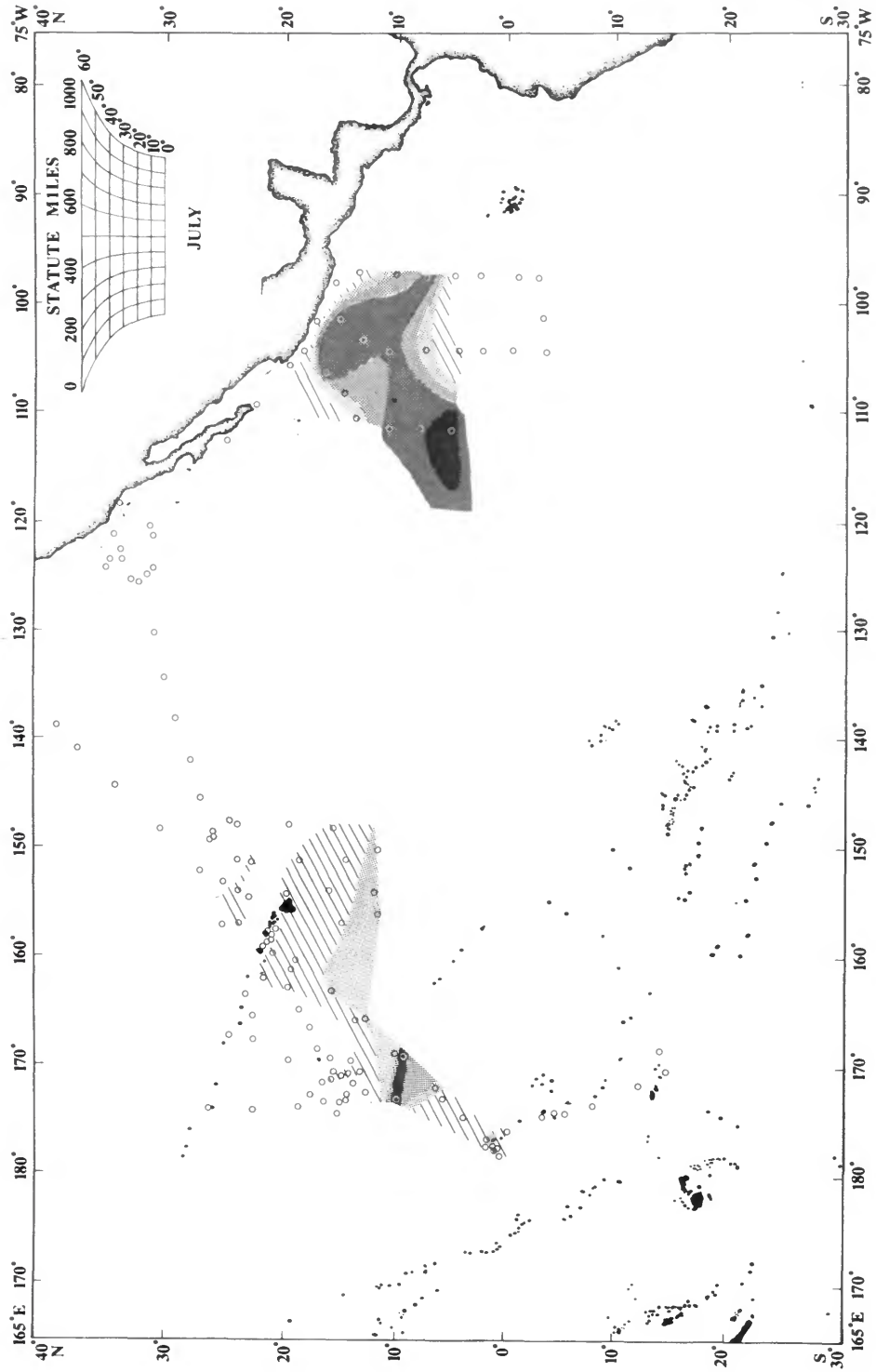


FIGURE 52.—Daily density (σ_{t}) of dark-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on roost observations in July 1963-1968.

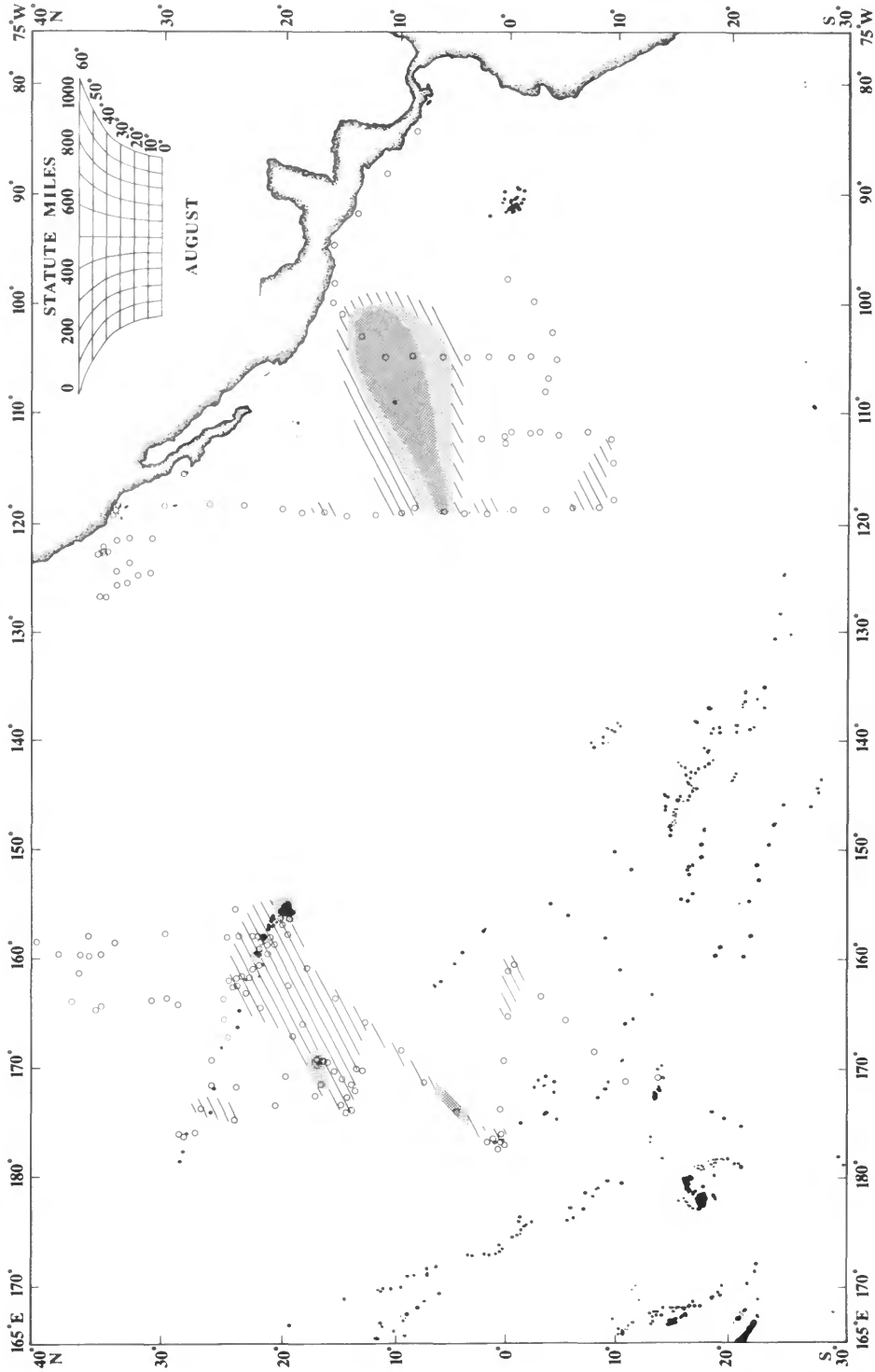


FIGURE 53.—Daily density (σ_t) of dark-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on POSS observations in August 1963-1968.

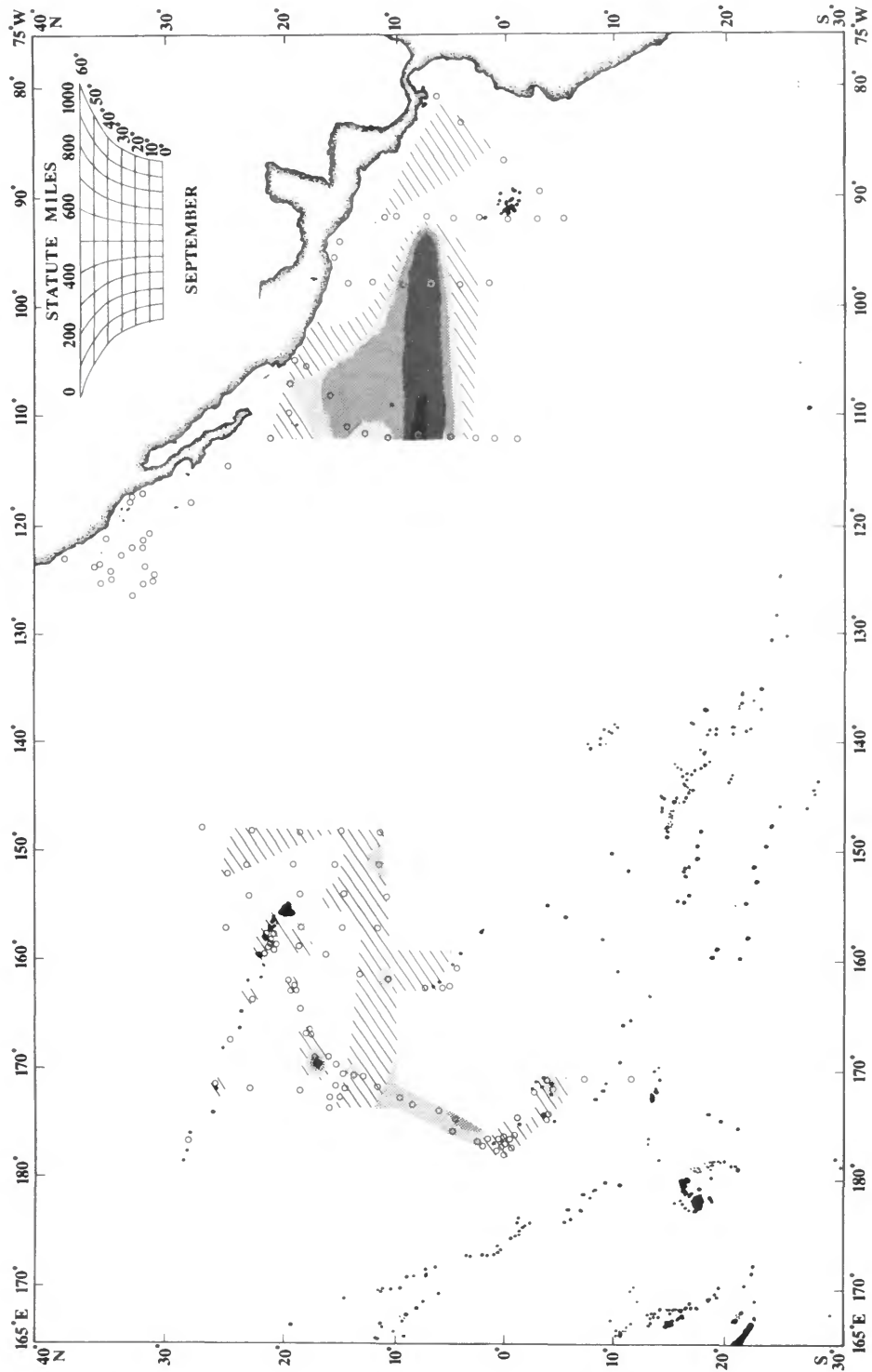


FIGURE 54.—Daily density (σ_t) of dark-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on robsp observations in September 1968–1968.

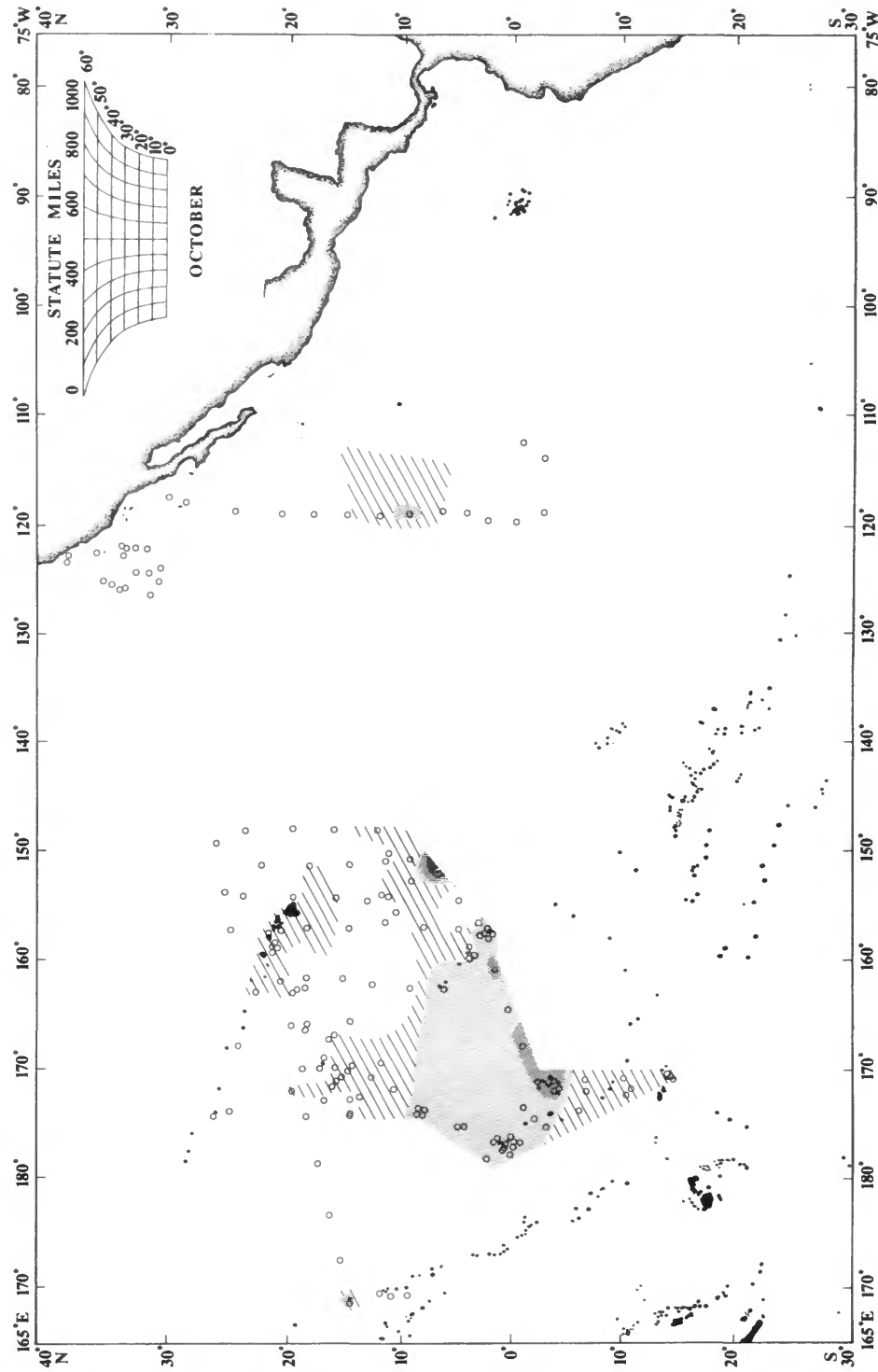


FIGURE 55.—Daily density (σ_t) of dark-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on roost observations in October 1963-1968.

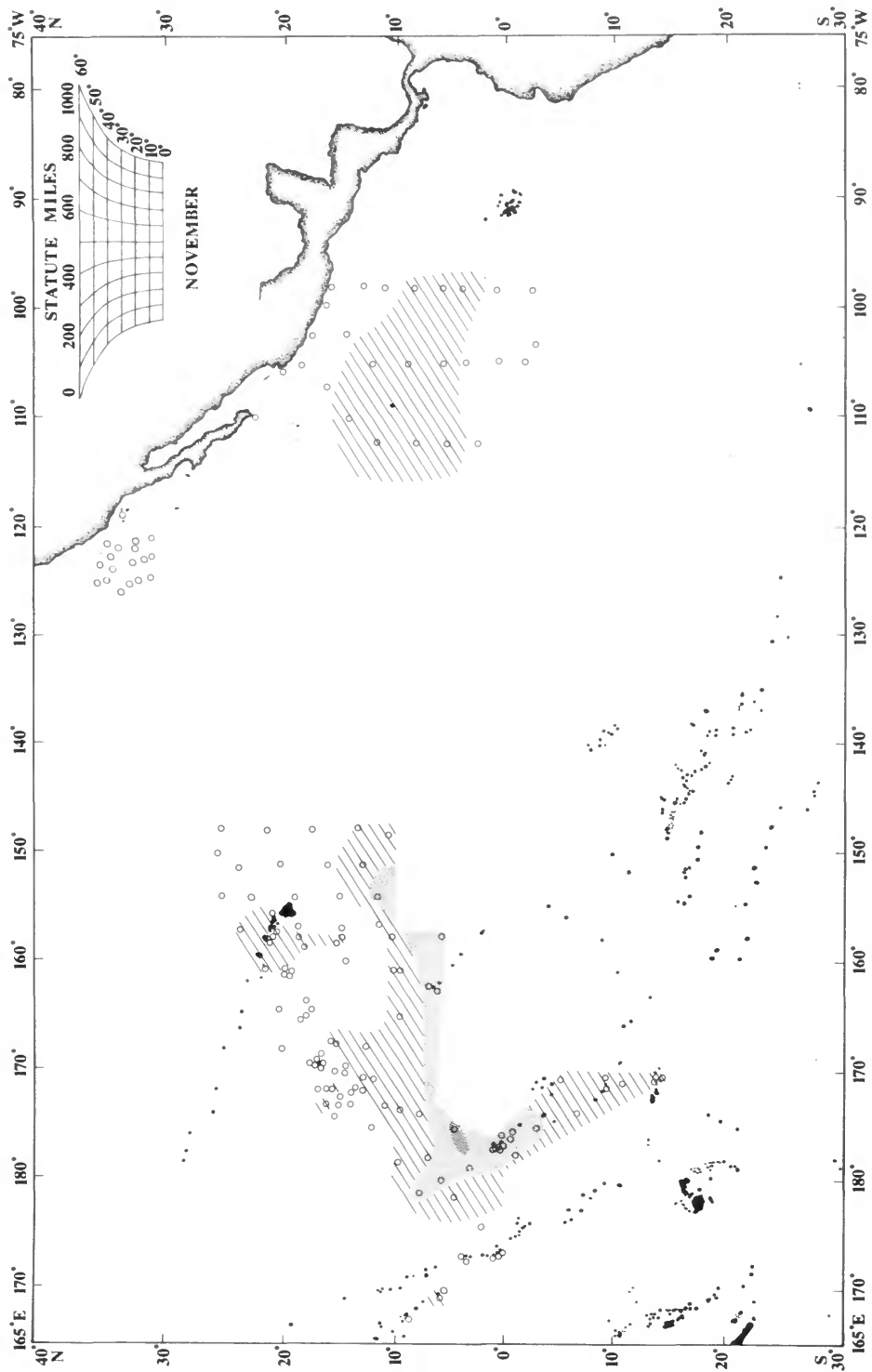


FIGURE 56.—Daily density (σ_t) of dark-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on POBS observations in November 1963-1968.

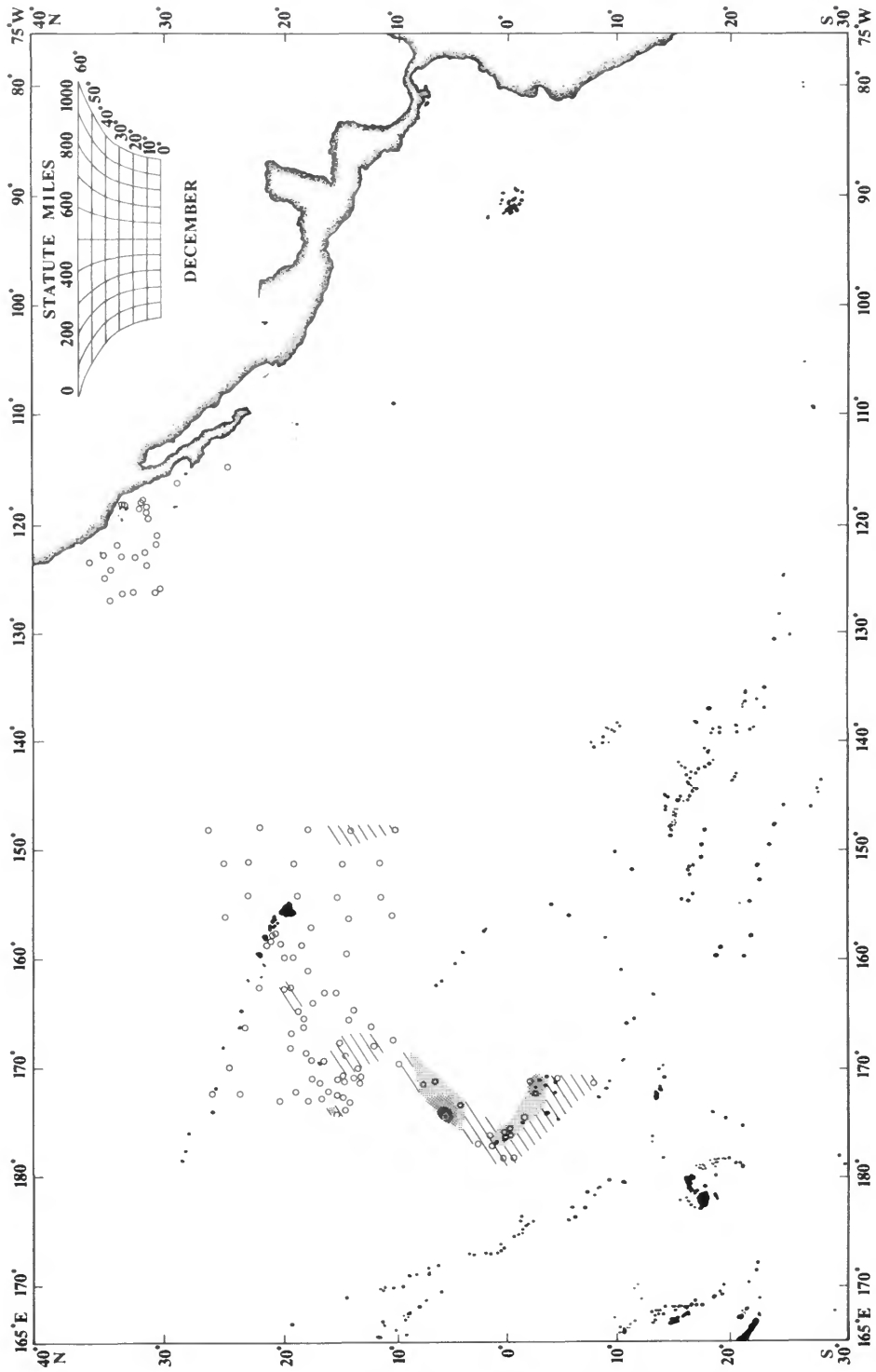


FIGURE 57.—Daily density (σ_t) of dark-phase Wedge-tailed Shearwaters in the central and eastern Pacific based on POSSP observations in December 1968-1968.

Appendix

Summary of published data on Wedge-tailed Shearwater distribution

Location	Date	Remarks	Source
NORTHEAST PACIFIC			
Vancouver, B. C.	not noted	hypothetical, based on 1 specimen, questionable data	Godfrey, 1966:23
EAST-CENTRAL PACIFIC			
Off N Baja California	16 Dec 56	light and dark seen	Murphy, 1958:104
Off Manzanillo, Mexico	24 Oct 55	8	King and Pyle, 1957:35
20°59'N, 111°57'W	23 Jul 05	a few	Loomis, 1918:142
19°37'N, 111°11'W	25 Jul 05	common	" " "
Revilla Gigedos	not noted	thousands	Anthony, 1900:250-251
Revilla Gigedos	not noted	breeds	Brattstrom and Howell, 1956:111-112
16°55'N, 07°23'N to 97°48'W, 112°55'W	28 Sep-18 Oct 05	seen daily	Loomis, 1918:142
Off Cape San Lucas, Mexico	not noted	recorded	Blake, 1953:10
Off Nayarit, Mexico	not noted	recorded	" " "
Off Nicoya Peninsula, Costa Rica	8 Feb 38	3 specimens, 20 miles S of Cabo Blanco	Slud, 1964:31
11°N, 90°55'W	17 Nov 56	many, all light	Murphy, 1958:104
Off Darien, Panama	5 Mar 41	2 specimens at sea 5 km NW of Ensenada, Guayabo	Wetmore, 1965:42
10°18'N, 121°04'W	13 Oct 55	came aboard ship	King and Pyle, 1957:35
Clipperton	not noted	3 specimens, 7 seen in caves and on bank of lagoon	Loomis, 1918:142
9°46'N, 93°30'W	6 Dec 56	seen	Murphy, 1958:104
7°58'N, 108°25'W	27 Oct 55	1	King and Pyle, 1957:35
7°N, 131°W	9 Nov 60	25 dark, 1 pale	Mörzcr Bruyns, 1965:58
7°N, 123°W	10 Nov 60	1 dark	" " " "
7°N, 109°W	12 Nov 60	1 dark, 3 pale	" " " "
7°N, 101°W	13 Nov 60	2 dark	" " " "
7°N, 93°W	14 Nov 60	10-20 dark and 10-20 pale	" " " "
W of Panama	not noted	seen	Harrison in Bourne, 1959:13
S of Panama	not noted	seen	" " " "
4°N, 96°30'W	25 Apr 64	1 of this species or <i>P. nativitatis</i>	Mitchell in Bourne, 1966:19
3°24'N, 84°12'W	23 Nov 58	1	Lévêque, et al., 1966:84
1°40'N, 86°W	3 Sep 56	3	" " " "
1°30'N, 108°30'W	27 Apr 64	1 of this species or <i>P. nativitatis</i>	Mitchell in Bourne, 1966:19
0°30'S, 120°W	29 Apr 64	1 of this species or <i>P. nativitatis</i>	" " " "
NW coast of South America	not noted	occurs regularly	Lévêque, et al., 1966:84
NW of Galapagos I.	7 Aug 62	1 specimen	" " " "
Gulf of Guayaquil	14 Mar 62	seen in numbers, light phase	Lévêque, 1964b:53-54
6°22'S, 117°08'W	23 Nov 57	1 light, probable	Gibson, 1960:16
SOUTHEAST PACIFIC			
13°34'S, 103°59'W	29 Mar 50	2 possibles, dark	Laird, 1951:176-177
23°28'S, 127°31'W	9 Jul 48	3 possibles, dark	Fleming, 1950:175

Summary of published data on Wedge-tailed Shearwater distribution—Continued

Location	Date	Remarks	Source
NORTHWEST PACIFIC			
Off Izu I.	not noted	not uncommon	Austin and Kuroda, 1953:305
WEST-CENTRAL PACIFIC			
Bonin and Volcano I.	not noted	"Comes to land in late Mar. or Apr., some remaining until end of Nov. After breeding, a few stray northward to the waters off Japan."	" " " "
Marcus	not noted	may still breed	King, 1967:118
Pescadores	not noted	seen in May	Cheng, 1955:6
Pescadores	not noted	breeds	Murphy, 1951:9
Philippine Sea	Apr 52	this species or <i>P. carneipes</i> , sometimes in large numbers	MacDonald and Lawford, 1954:19-20
15°57'N, 113°12'E	10,15,28 Jan 61	probables seen	Mitchell in Bourne and Radford, 1962:16
Philippines	not noted	a few stragglers	Delacour and Mayr, 1946:21
Marianas	22 Aug 45	flocks of 21 and 41 (dark-bellied?) 100 miles SW from Sariguan, Marianas	Dixon and Starrett, 1952:269-270
Marianas	Jan-Feb 46	white-bellied birds, possibly this species, off southern Marianas	" " " "
Marianas	not noted	breeds Aug	Baker, 1951:65
Carolines	not noted	breeds	Murphy, 1951:2
7°N, 141°E	29 Oct 60	dark phase in numbers up to 10	Mörzer Bruyns, 1965:58
7°N, 150°E	30 Oct 60	up to 6 dark at Helen Shoal	" " " "
7°N, 157°E	31 Oct 60	1 dark at Ngatik I.	" " " "
7°N, 157°E	1 Nov 60	6 dark N of Kusaie I.	" " " "
10°S, 151°30'E	4 Oct 63	several	Mitchell in Bourne, 1965:19
Off S coast of New Guinea	3 Oct 63	1	" " " "
New Guinea	not noted	1	Rand and Gilliard, 1967:29
New Guinea and Celebes	Jul 29	this species or <i>P. carneipes</i> , very numerous from N point of Celebes, easterly toward the waters N of New Guinea	Jespersen, 1933:196
Solomons	not noted	breeds	Murphy, 1951:2
SOUTHWEST PACIFIC			
17°S, 158°E	24 Oct 63	1	Mitchell in Bourne, 1965:19
Near New Caledonia	18 Dec 57	well represented	Gibson, 1960:18
23°46'S, 151°18'E	16 Nov 61	3 probables, dark	Semple in Bourne and Radford, 1962:16
New Caledonia	Nov 28	several, all dark	Jespersen, 1933:196
New Caledonia	not noted	breeds	Delacour, 1966:20
26°16'S, 161°24'E	19 Dec 57	usually 1 or 2 in sight	Gibson, 1960:18
27°30'S, 154°30'E	26 Oct 63	2	Mitchell in Bourne, 1965:19
30°55'S, 155°17'E	20 Dec 57	some in sight all day, once in hundreds	Gibson, 1960:18-19
Tasman and Coral Seas	Aug 61-Sep 62	numerous dark-phase sightings	Norris, 1967:37-38
East Australia, Lord Howe and Norfolk I.	not noted	breeds Sep to Dec	Mathews and Iredale, 1921:26
Off Sydney, Australia	21 Dec 57	seen	Gibson, 1960:19
Off Sydney, Australia	27 Oct 63	2	Mitchell in Bourne, 1965:19
37°41'S, 134°E	19 Apr 57	1 dark	Gibson, 1960:12
Makara, New Zealand	26 Jan 62	1 specimen, white-breasted	Falla, 1962:278-279
CENTRAL PACIFIC			
N, E, and W of Hawaiian I.	Feb 64-Jun 65	Abundant Mar-Nov, uncommon Dec-Feb	King, 1970:25

Summary of published data on Wedge-tailed Shearwater distribution—Continued

Location	Date	Remarks	Source
Hawaiian I.	27 Apr 45	11 S of Oahu	Cogswell, 1946a:47
	28 Apr 45	14 S of Oahu	Cogswell, 1946a:47-48
	29 Apr 45	5 near Johnston Atoll	Cogswell, 1946a:48
Hawaiian I.	not noted	breeds May-Nov	Richardson, 1957:16
Off Pearl Harbor, Oahu	24 Dec 61	200 light, 3 dark	King <i>in Bourne</i> , 1964:19
150 to 350 miles WSW of Johnston Atoll	30 Apr 45	33	Cogswell, 1946a:48
Off Oahu	24 May 59	5	Peakall, 1960:199
Wake	not noted	migrant (bred formerly)	King, 1967:111
13°30'N, 180°	1 May 45	2	Cogswell, 1946b:53
Marshalls	not noted	breeds	Amerson, 1969:295
9°55'N, 164°48'W	26 May 59	8 of this species or <i>P. carneipes</i>	Peakall, 1960:199
9°43'N, 138°51'W	6 Oct 55	flock of 20	King and Pyle, 1957:35
9°04'N, 143°49'W	4 Oct 55	came aboard ship	" " "
Christmas I.	not noted	breeds Feb-Nov	Schreiber and Ashmole, 1970:368
7°N, 179°E	3 Nov 60	two groups of 200 dark	Mörzer Bruyns, 1965:58
7°N, 180°	4 Nov 60 (E)	2 dark	" " " "
7°N, 166°W	4 Nov 60 (W)	2 dark	" " " "
7°N, 152°W	6 Nov 60	6 pale	" " " "
7°N, 146°W	7 Nov 60	3 dark	" " " "
7°N, 138°W	8 Nov 60	110 dark, 1 pale	" " " "
(N of Marquesas)			
6°N, 153°W	9 Dec 63	1	Mitchell <i>in Bourne</i> , 1965:19
Jaluit	2 Nov 60	10 dark	Mörzer Bruyns, 1965:58
Phoenix	not noted	breeds all months	King, 1967:93
4°-02°30'S, 169°-155°E	Oct 51	small numbers of this species or <i>P. carneipes</i> between Niutao Atoll and the Admiralty I.	MacDonald and Lawford, 1954:19
Marquesas	not noted	breeds	Murphy, 1951:2
SOUTH-CENTRAL PACIFIC			
New Hebrides	not noted	breeds Jan-Jun	King, 1967:105
11°S, 177°W	30 Mar 63	3	Morris <i>in Bourne</i> , 1965:19
11°S, 167°30'W	8 May 64	1 of this species or <i>P. nativitatis</i>	Mitchell <i>in Bourne</i> , 1966:19
Samoa	Nov 28	several, all dark	Jespersen, 1933:195-196
Samoa	not noted	breeds	Murphy, 1951:2
Tonga	not noted	breeds	Davidson, 1931:217-218
14°30'S, 176°E	16 Nov 63	several	Mitchell <i>in Bourne</i> , 1965:19
14°47'S, 170°35'W	27 Feb 63	1 in hand	Jenkins <i>in Bourne</i> , 1965:19
Fiji	not noted	breeds	Murphy, 1951:2
Fiji	Nov 28	several, all dark	Jespersen, 1933: 196
Tuamotus	not noted	breeds	Murphy, 1951:2
Henderson	not noted	breeds	" " "
16°S, 178°W	10 May 64	1 of this species or <i>P. nativitatis</i>	Mitchell <i>in Bourne</i> , 1966:19
16°09'S, 176°42'E	9 Dec 57	occasional	Gibson, 1960:18
17°57'S, 169°52'E	10 Dec 57	seen	" " "
Society	not noted	breeds	Murphy, 1951:2
18°28'S, 172°48'W	6 Dec 57	small flock, dark birds, 1 light	Gibson, 1960:17
19°30'S, 177°30'E	12 May 64	1 of this species or <i>P. nativitatis</i>	Mitchell <i>in Bourne</i> , 1966:19
19°30'S, 178°E	2 Feb 63	1 probable	Morris <i>in Bourne</i> , 1965:19
20°02'S, 175°01'W	25 Feb 63	1 in hand	Jenkins <i>in Bourne</i> , 1965:19
Near Papeete, Tahiti	28 Nov 57	dark birds seen, possibly this species	Gibson, 1960:17
Near Fiji	24 Mar 59	seen	Dixon <i>in Bourne</i> , 1959:11
24°S, 166°30'E	14 May 64	several	Mitchell <i>in Bourne</i> , 1966:19
25°S, 176°30'E	3 Feb 63	1 probable	Morris <i>in Bourne</i> , 1965:19
Australis	not noted	breeds	Murphy, 1951:2

Summary of published data on Wedge-tailed Shearwater distribution—Continued

<i>Location</i>	<i>Date</i>	<i>Remarks</i>	<i>Source</i>
26°15'S, 176°56'W	14 Mar 47	50-60	Fleming, 1950:172
26°28'S, 176°32'W	15 Mar 47	scattered group of 15	" " "
30°S, 175°30'E	4 Feb 63	1 probable	Morris in Bourne, 1965:19
Kermadecs	not noted	breeds Oct-early Jun	Falla, et al., 1967:42
Kermadecs	not noted	breeds Dec-May	Sorensen, 1964:70
33°S, 176°30'E	5 Jun 63	2	Morris in Bourne, 1965:19

Black-footed Albatross (*Diomedea nigripes*)^{*}

Gerald A. Sanger

Introduction

The material contained in this report is a summary of all at-sea observations of the Black-footed Albatross (*Diomedea nigripes*) by the POBSP in the central and eastern Pacific Ocean. Literature records, scattered northern Pacific POBSP records, and data obtained from POBSP island surveys are included for general background information. Humphrey (1965) gave a general summary of the objectives of the program and Gould summarized the areas surveyed and the methods and materials used in data collection and analysis. The reader is referred to these papers for more details.

The Black-footed Albatross is probably the most often seen and best known of the truly pelagic northern Pacific birds. It has been the subject of more papers on distribution and habits at sea than any other northern Pacific seabird. In recent years, intensive research relating to albatross interference with aircraft operation at Midway Atoll has been conducted. While the breeding grounds research has been most fruitful (Rice and Kenyon, 1962a, 1962b; Robbins, 1966), the at-sea studies, because of their general lack of temporal and seasonal scope, have given only general ideas of the overall distribution and ecology.

Rice and Kenyon (1962a:383) conservatively estimated the world's population of Black-foots at 300,000 birds during the period 1956-1958. Robbins (1966:9) noted a sharp decrease in the nesting population at Sand Island, Midway Atoll, through 1963, but felt that there was not enough informa-

tion available on prebreeding and older "unemployed" (=not breeding) birds for a direct comparison with Rice and Kenyon's 1957-1958 population estimate.

BREEDING.—The Black-footed Albatross breeds mainly in the leeward Hawaiian chain (Rice and Kenyon, 1962a). A small colony (ca. 20 birds) exists on Torishima, in the Izu Islands, south of Honshu, Japan (Aronoff, 1960).

The leeward Hawaiian Islands support breeding Black-footed Albatross populations as shown in Table 20. The breeding cycle (see Rice and Kenyon, 1962b) is nearly identical from island to island and from year to year. Table 21 summarizes this information. Breeding birds begin returning to their islands late in October. Eggs are laid between the middle of November and the first week of December; they are incubated for 66 days, and most of the chicks have hatched by the end of January. At

TABLE 20.—*Largest numbers of breeding Black-footed Albatross populations* (all derived from POBSP data except for Kaula, which is from Rice and Kenyon, 1962a:377)

Location	Number of birds
Kure	1,150 ^b
Midway	24,000 ^a
Pearl and Hermes Reef	9,000 ^a
Lisianski	4,000 ^a
Laysan	40,000 ^a
French Frigate Shoals	3,100 + ^a
Necker	375 ^a
Nihoa	100 ^a
Kaula	50 ^a

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* Paper Number 72, Pacific Ocean Biological Survey Program, Smithsonian Institution, Washington, D.C. 20560.

^a Recorded.

^b Estimated.

TABLE 21.—Timing of Black-footed Albatross activities at breeding grounds (adapted from Rice and Kenyon, 1962b)

Activity	Period
Arrival	6 Oct-6 Nov
Egg-laying	3 Nov-30 Nov peak = 21 Nov
Incubation	\bar{x} = 65.6 days
Hatching	15 Jan-7 Feb peak = 25-26 Jan
Departure of fledged chicks	Jun-mid-Jul*

*Parents cease visiting breeding grounds when chicks are fledged, but no sooner.

least one parent is present with the chick continuously through mid-March, when the guard state terminates. During April and May breeding birds are mostly at sea and return only briefly to feed fledging young. By June only young birds are present all day; breeding adults return only long enough to feed their young. Most young have fledged and departed the islands by the middle of July, and toward the end of July all birds are at sea.

SUMMARY OF PUBLISHED PELAGIC OBSERVATIONS.—The Black-footed Albatross is an abundant and commonly seen species throughout much of the northern Pacific Ocean. At sea it ranges from the coasts of China, Japan, and Russia eastward to continental North America, and from the southern Bering Sea and the Gulf of Alaska southward to 18°N off North America, occasionally to 10°N in the central Pacific, and to 19°N off Asia.

The appendix summarizes published data on Black-footed Albatross distribution. Papers on observations from the eastern half of the northern Pacific outnumber those on other areas by a wide margin; a few of these papers warrant discussion.

McHugh (1955) made a detailed analysis of Black-foot distribution off North America in 1949-1950. In 1949 a progressive northerly distributional shift occurred in the spring. The population center lay relatively close to shore off southern California in March, close to shore north of San Francisco in April, and off Oregon and Washington in May, when the center showed a tendency to withdraw from the coast and to disperse over a larger area. Summer months generally showed a decrease in

number of birds, and a somewhat irregular distribution. Birds were present in low to moderate density (\bar{x} = 11-20 birds/sighting, from stopped ship) in an area off the southern California Channel Islands in August, resulting in the highest abundance of the year there. In October there was a high overall density of birds, with a broad, heavy concentration some 200 miles off southern Oregon and northern California. By November the population center had shifted southward far off central California, and overall density had diminished considerably. The 1950 distribution patterns were not clear, but the abundance peak for the entire area was in March; there was evidence of a southerly shift of heavy concentrations of Black-foots from southern Oregon-northern California in May, to central California in June.

In the period June-September of 1937 and 1938, Black-footed Albatrosses were concentrated in a cold tongue of water off the California Channel Islands (Miller, 1940). There were commonly 12-15 birds at oceanographic sampling stations in the cold tongue, but never more than five or six at stations outside this area. None were seen in the Santa Barbara channel. Miller (1942) showed that most Black-foots followed his ship for only a few miles. Of 25 birds marked with paint, 12 followed the ship for 20 miles, seven for 30 miles, three for 40 miles, and only one for 60 miles.

In 1945 Thompson (1951) observed the distribution of *D. nigripes* between Pearl Harbor, Hawaii, and San Francisco, California. Most months showed an increase in abundance as the California coast was approached, except in June, when there was fairly even pelagic distribution, and late November, which showed a bimodal distribution with peaks at ca. 125°W and 150°W, and minimums at 140°W and 155°W. There appeared to be an inverse correlation between surface water temperatures and albatross numbers. This easterly increase was associated with passing from the North Pacific Central Water (Sverdrup, et al., 1942) into the California Current between 130°W and 155°W. The maximum number of birds seen at any one time was 45 at 130°W in October. A parallel increase in albatross and jellyfish abundance was observed, which Thompson (1951) believed was a similar response of the two organisms to the same environmental conditions.

The Black-footed Albatross was the most com-

monly seen and abundant species during seven cruises off Washington and Oregon in 1964–1965 (Sanger, 1970). They were present on 94 percent of the 88 days spent in the area and accounted for 53 percent of all birds seen. Maximum abundance and occurrence were in the summer, and minimums were in the winter. Peak abundance occurred in August 1965 when albatrosses were 2.5 times as abundant as in the previous August. Minimum abundance was in January 1965. Generally, numbers increased with distance from shore, although the maximum number seen at a single sighting (78) occurred just 40 miles off northern Washington in August 1965. Generally there was no difference in abundance or distribution between the areas off Oregon and Washington. For data lumped for all seven cruises there was a general increase in abundance with air temperature and surface water temperature (range: 6°–18°C.). There was no observed relation between albatross numbers and surface salinity, with birds found in salinities ranging from greater than 33 parts per thousand (‰) far offshore to 15‰ just off the mouth of the Columbia River. There appeared to be no relationship between albatross numbers and rate of primary productivity, although the largest number of birds in a single sighting (78) occurred in water with the highest primary productivity rate of all cruises. These data have been incorporated with the POBSP records and are included on the distribution maps.

The literature suggests that Black-footed Albatrosses are less abundant, or less frequently encountered, in the western than in the eastern Pacific. For example, Starrett and Dixon (1946) noted a general absence of albatrosses from the southwestern portion of their range between June 1945 and February 1946, and MacDonald and Lawford (1954) noted that flocks of Black-foots were generally smaller in the western Pacific than the eastern Pacific in 1951 and 1952.

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tion of Oceanography. Furthermore, the mass of CalCOFI data, which is the single most intensive pelagic record ever assembled for the species, would not have been possible without the cooperation of the many CalCOFI sea-going personnel who diligently recorded the sightings. Among these were Robert Counts, David Kramer, James Thraillkill, and Andrew Vrooman, all of the National Marine Fisheries Service, La Jolla, California. To all of these people I express my sincere appreciation.

Distribution and Abundance

SPECIMEN RECORDS

Table 22 summarizes Black-footed Albatrosses collected at sea by POBSP personnel. Most were from the central Pacific; a few were from the western Aleutians and the coast of southern California.

SIGHTING RECORDS

Figures 66–77 (pp. 114–125) are monthly maps of the average Black-footed Albatross distribution for January 1964 through November 1967. Relative abundance, i.e., average number of birds per sighting for each day, is indicated by different degrees of shading. Because of the ship-following habits of the Black-footed Albatross and a consequent disparity in field recording techniques for this species, it was impossible to estimate the actual abundance in the standard units of birds per linear mile of travel. The disparity in field recording techniques was mainly a failure of observers to record the number of birds at set time intervals; some observers recorded hourly counts and others recorded at irregular intervals, or whenever the Black-foot density changed. However, the relative abundance was determined by using a unit of mean number of birds per sighting (mBPS) for each day the species was seen, thus eliminating discrepancies in abundance due to variations in recording techniques.

Three principal areas received consistently good seasonal coverage of Black-footed Albatross distribution: the central Pacific, off the southern California coast to about 126°W, and off the coasts of Washington and northern Oregon to about 140°W. Relative abundance in the former two areas is mutually comparable in every way. In the latter area, however, many counts were made from a stopped

TABLE 22.—*Black-footed Albatross specimens collected at sea by POBSP personnel*

Location	USNM number	Sex	Body weight (gm)	Gonad size (mm)	Date	Collector
47°18'N, 173°13'E	503266 ^b	—	3110+ +	—	9 Oct 65	R. DeLong
47°03'N, 173°16'E	503267 ^a	—	3110+ +	—	9 Oct 65	R. DeLong
33°23'N, 122°18'W	497772 ^c	♀	—	18 x 8	21 Jan 67	B. Harrington
33°23'N, 122°18'W	497773 ^d	♀	—	18 x 8	21 Jan 67	B. Harrington
21°23'N, 167°37'W	496723	♀	2527	20 x 10	22 May 65	D. Husted
20°58'N, 158°06'W	493513	♀	2802	23 x 15	3 Jan 64	—
20°56'N, 158°33'W	492911	♂	3200	26 x 17	3 Dec 63	R. Fleet
20°49'N, 158°52'W	492910	♀	2100	30 x 14	3 Dec 63	R. Fleet
20°23'N, 161°07'W	lost	♀	2533	19 x 11	4 Jan 64	—
19°28'N, 162°11'W	493917	♀	2900+	25 x 17	4 Feb 64	V. Hoeman
18°23'N, 165°12'W	494145	♀	—	45 x 35	9 Dec 64	R. Standen
18°01'N, 166°11'W	496198	♂	—	27 x 5	9 Dec 64	M. Thompson
				20 x 4		
17°20'N, 164°12'W	493819	♀	2610	22 x 25	6 Jan 64	C. Kepler
16°50'N, 169°50'W	495791	—	—	—	15 Jan 65	D. Husted
16°38'N, 169°38'W	493512	♂	2857	14½x7½	12 Feb 64	—
14°46'N, 160°44'W	494144	♂	3000+	16 x 6	8 Mar 64	V. Hoeman
				11 x 6		
12°20'N, 167°41'W	495792	♀	2006	15 x 10	22 May 65	R. Merrill

^a Banded, U. S. Fish and Wildlife Service Number 737-45577 (adult, sex unknown, 8 Nov 63, Green Island, Kure Atoll).

^b Banded, U. S. Fish and Wildlife Service Number 697-73041

^c Banded, U. S. Fish and Wildlife Service Number 757-26257 (local, sex unknown, 12 Jun 66, East Island, French Frigate Shoals).

^d Banded, U. S. Fish and Wildlife Service Number 767-42423 (nestling, sex unknown, 19 Mar 63, Grass Island, Pearl and Hermes Reef).

ship, a fact that may make the counts seem large compared to the other areas due to the increased attraction stopped ships have for Black-foots. All mileage figures refer to statute miles.

January Distribution (Figure 66): The densest concentration of birds occurred in the central Pacific across a broad front at ca. 25°N, between 148°W and 157°W; however, there were no observations along the leeward Hawaiian Islands. Black-foots occurred in most of the area off California farther than 75 miles off the coast, and in areas farther than 100 to 200 miles off the coasts of Oregon and Washington.

February Distribution (Figure 67): In the central Pacific, birds were seen in fair numbers as far south as 11°N, 151°W, although they were peculiarly absent a few longitudinal degrees in either direction. Concentrations were still found across the front at 25°N; no observations were conducted in the Leewards. Scattered birds were seen south to 13°N, 170°W, although there was a conspicuous

absence of Black-foots at similar latitudes between 153°W and 168°W. Off California, overall densities decreased from January; a few birds were observed within 30 miles of the coast. Scattered birds were seen between northern Washington and 53°N in the Gulf of Alaska; these sightings apparently represent the northernmost winter records for the species.

March Distribution (Figure 68): During March, observations were extended westward along the leeward Hawaiian Islands. Correspondingly, extremely dense concentrations of *Diomedea nigripes* were seen in areas near the breeding islands. A maximum of 56 bps was seen near Laysan Island. No Black-footed Albatrosses were seen south of 31°N in the area off California; a few birds were encountered within 25 miles of the coast. No observations were conducted off Washington or Oregon.

April Distribution (Figure 69): Due to two cruises between Hawaii and North America, cover-

age this month was quite broad in area, although the Leewards area was not included. A localized concentration of 10–20 BPS was found some 100 miles north of the main Hawaiian Islands, but the bulk of the Black-foot population was seen north of 25°N. A relatively small concentration of birds was centered at 148°W, 28°N, but between here and northeastward to 130°W, distribution was remarkably uniform. Off southern California, overall densities remained essentially unchanged from March; scattered birds were seen within 25 miles of shore. Between the area off southern California and Oregon, distribution is largely speculative, because noon positions were so far apart. However, there apparently was a broad band (5° wide) of 5–10 BPS density off northern California and Oregon between ca. 127°W and 132°W, with lesser densities to either side. The densest concentrations this month occurred off Washington and northern Oregon.

May Distribution (Figure 70): The most evident feature of May distribution in the central Pacific was the continued northward withdrawal of the population to 20°N. A lone bird was encountered at ca. 13°N. Concentrations were centered at French Frigate Shoals, and some 450 miles northwest of the main Hawaiian Islands. Distribution off California was quite uniform at 2–5 BPS across most of the area. There were no observations off the Washington-Oregon coasts.

June Distribution (Figure 71): A continued northward withdrawal of the population in the central Pacific was evident this month; the southern limits were at 21°N, 160°W, although two widely scattered individuals were seen at the 16°N parallel. The species was observed along the Leewards as far west as Lisianski Island. Off southern California, the overall density diminished greatly. A bimodal distribution was evident off Washington and Oregon, with concentrations of birds found relatively close to shore off northern Oregon and 400 miles off northern Washington.

July Distribution (Figure 72): The Black-foot population continued to move northward, with 28°N marking the southern range limits. Ten to twenty BPS densities were seen some 1000 miles due west of San Francisco, with an apparent density decrease toward the southern California coast. A bimodal distribution was noted off southern California. Concentrations of 10 to 20 BPS were seen

within 75 miles of the coasts of Washington and Oregon.

August Distribution (Figure 73): In the central Pacific, Black-foots were found still farther north than during the previous months. Overall abundance off southern California declined slightly. *Diomedea nigripes* was very abundant off the Washington and Oregon coasts; about half of the region was populated with birds in 10 to 20 BPS densities and a general increase in abundance with distance from shore was noted.

September Distribution (Figure 74): In the central Pacific two widely separated individuals were sighted near Midway Atoll and at 04°30'N, 174°W; the latter sighting is the southern record for the species, excluding the two strays in the southern hemisphere (Oliver, 1955:181). Overall abundance off southern California decreased markedly; a few Black-foots were seen within 20 miles of shore. A region near the western Aleutians was censused this month and low concentrations were encountered over most of the area. There was no observation off the Washington-Oregon coast.

October Distribution (Figure 75): Only one *Diomedea nigripes* was found in the central Pacific this month, near Gardner Pinnacles; however, areal coverage was scanty. Farther north, among and south of the western Aleutians, low densities were still encountered over most of the area. Overall abundance off Washington and Oregon diminished markedly from August, and *Diomedea nigripes* numbers were distributed erratically in the region off southern California.

November Distribution (Figure 76): The species had again returned in some numbers to the central Pacific area, south to 19°N. There was a pronounced decrease in overall abundance off California, while the region off Washington and Oregon showed an increase in Black-foots between 134°W and 139°W.

December Distribution (Figure 77): The population level in the central Pacific increased to an observed all-time high this month. As would be expected, maximum concentrations were found among the leeward Hawaiian breeding islands. Off California, overall density showed an increase over November, and two days of observations off the Washington-Oregon coast revealed a few birds off Oregon but none within 50 miles of the Washington coast.

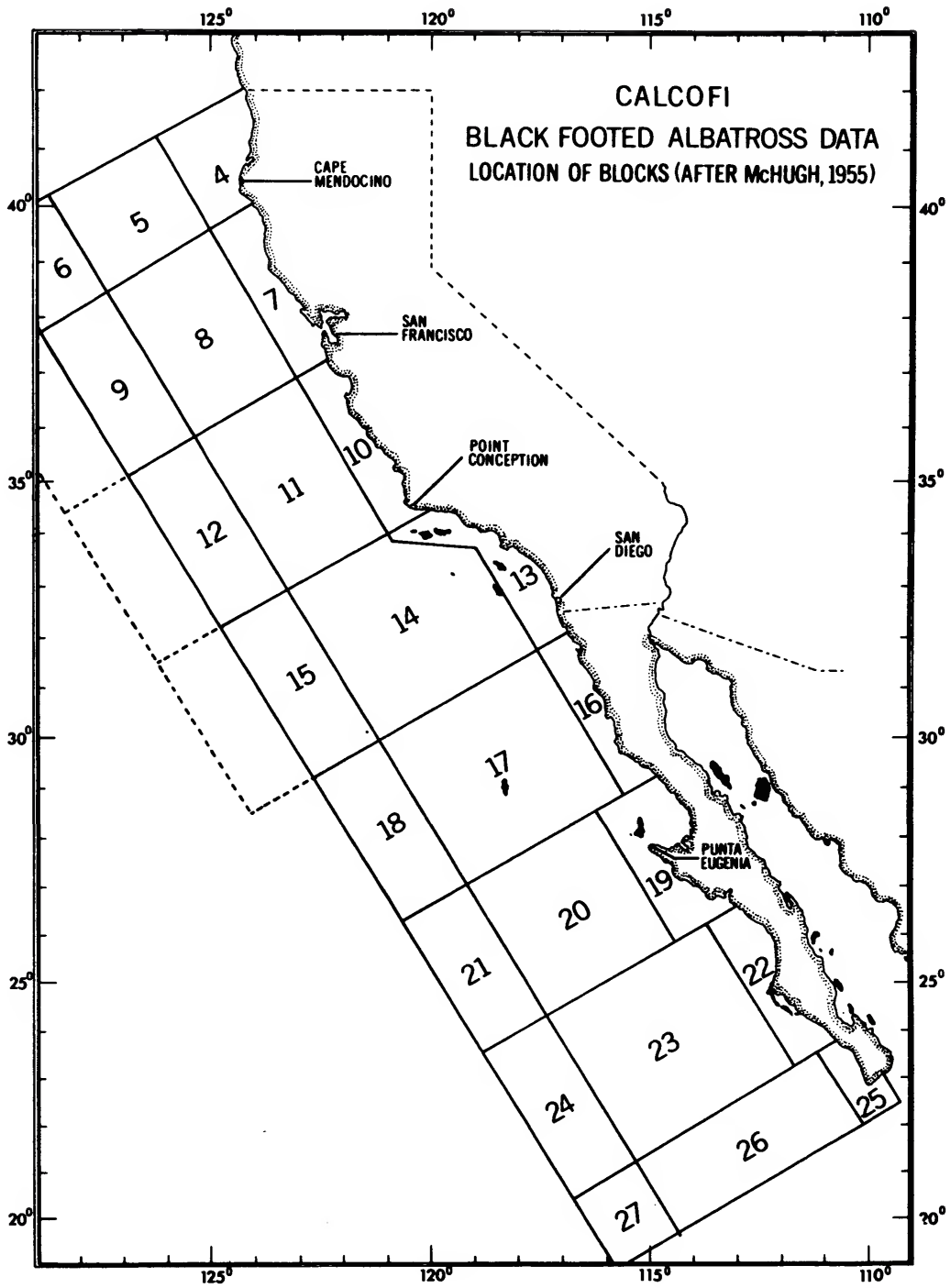


FIGURE 58.—Location of area blocks for analysis of CalCOFI Black-footed Albatross distribution.

BAND RETURN INFORMATION

Robbins and Rice (pp. 232–271 herein) made a detailed analysis of at-sea band returns of Black-footed and Laysan albatrosses including POBSP records. No young Black-foots were captured in the leeward Hawaiian Islands during their first winter of life, but some were captured within a couple of hundred miles of both Japan and the United States. As the birds grew older (through their fourth summer), there was an increasing tendency for band recoveries to occur farther north and east in summer, and closer to the Leewards breeding islands in winter. Once the birds reached breeding age, there was only a slight tendency for more recoveries to occur off North America in summer than off Japan. The relative chances of a tagged bird being caught in either area are unknown.

There are a number of POBSP band returns from various breeding islands from birds that were originally banded on other breeding islands. Thus, this species exhibits some interisland movement; the individuals involved are probably prebreeders.

DISTRIBUTION OFF CALIFORNIA AND
BAJA CALIFORNIA, 1951–1959

In 1949, an interagency oceanographic research program known as the California Cooperative Oceanic Fisheries Investigations (CalCOFI) "was established as a broad and thoughtful inquiry into the environment and the biology of the California Current system" (Ahlstrom, et al., 1967:5). As a regular part of routine survey cruises, the number of Black-footed Albatrosses congregating around the ships was counted at each sampling station. Black-foot distribution has been analyzed for only the first two years of these data (McHugh, 1955), although the albatross counts continued through April 1959. Data subsequent to 1950 are analyzed and discussed here for the first time.

McHugh's (1955) method of analyzing the data was, for the most part, used herein. The survey area was divided into the same series of blocks (Figure 58), and the monthly average of the number of *Diomedea nigripes* counted at each station



FIGURE 59.—Real time graphs of the BPSt for inshore blocks: a, 1951–1953; b, 1954–1956; c, 1957–1959. (Numbers on graphs indicate number of stations contributing to BPSt.)

within a block was calculated as mean number of birds per station (BPSt), using the maximum number of birds seen at any one time during a station and including "zero counts." McHugh (1955) discusses the reasons for averaging the counts from stations within the blocks, rather than considering individual counts at each station. An atlas-type presentation of monthly distribution maps such as McHugh (1955) used would be impractical in this paper because of the large amount of data involved. Therefore the blocks were divided into three north-south strips, inshore (blocks 4, 7, 10, etc.), intermediate (blocks 5, 8, 11, etc.), and offshore (blocks 6, 9, 12, etc.). The seasonal changes in abundance within individual blocks have been analyzed, as well as changes within the entire strips.

SEASONAL CHANGES IN ABUNDANCE WITHIN AND AMONG INDIVIDUAL BLOCKS.—Seasonal fluctuations in birds per station were examined in blocks with the most intensive coverage. These were blocks 10, 13, and 16 in the inshore strip, and 11, 14, and 17 in the intermediate strip. Blocks 12 and 15 in the offshore strip were also considered in this manner because of their proximity to the other blocks, although their coverage was poor. Real time graphs of the BPSt in the inshore blocks are presented in Figure 59, in the intermediate blocks in Figure 60, and in the offshore blocks in Figure 61. In the inshore blocks (10, 13, 16) a north-south density cline is quite evident, as are seasonal cycles in abundance, with peak numbers occurring in late spring-early summer, especially in block 10. A study of the intermediate blocks (11, 14, 17) shows that *Diomedea nigripes* was generally more abundant there than closer inshore. Also evident during most of the period is a north-south population cline (regardless of year or season) and seasonal abundance cycles, with maximum numbers occurring in late spring and early summer. Figure 61 indicates that the highest numbers of Black-footed Albatrosses in the entire area may have occurred farthest off the coast. However, the scanty coverage, both in time and in number of stations, precludes direct comparisons with the blocks closer to shore.

OVERALL DISTRIBUTION AND ABUNDANCE.—Temporal changes in albatross abundance within each of the north-south strips are presented as contoured density real time diagrams (Figure 62). By simultaneously examining the diagrams for all three strips it is possible to see changes in distribu-

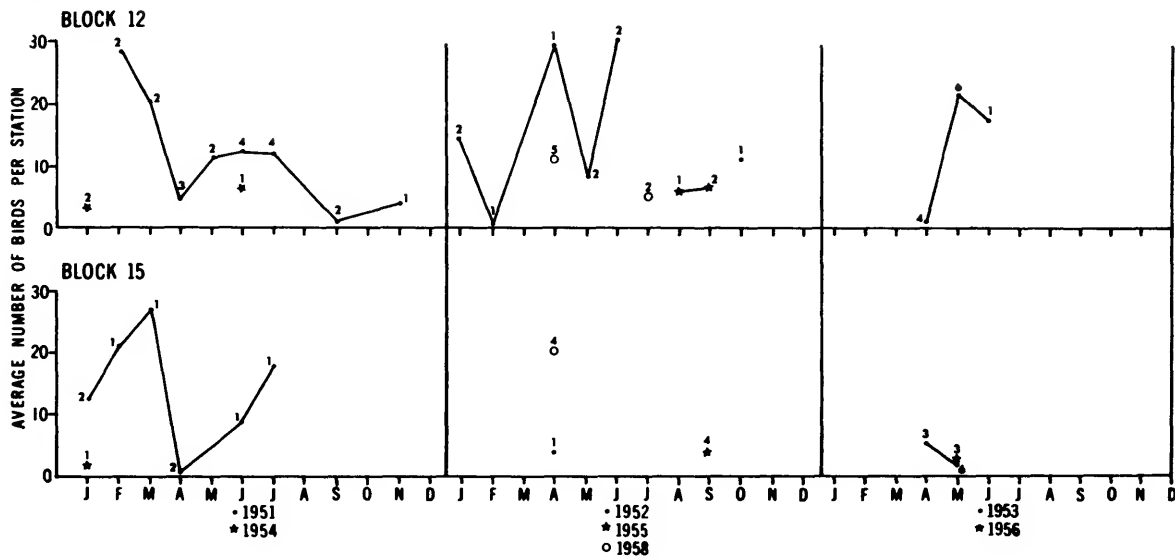


FIGURE 61.—Real time graphs of the BPSt for offshore blocks 1951–1956 and 1958. (Numbers on graphs indicate number of stations contributing to BPSt.)

tion and to infer movement among the three areas. There are a number of salient features to the distribution and abundance evident in each of the strips.

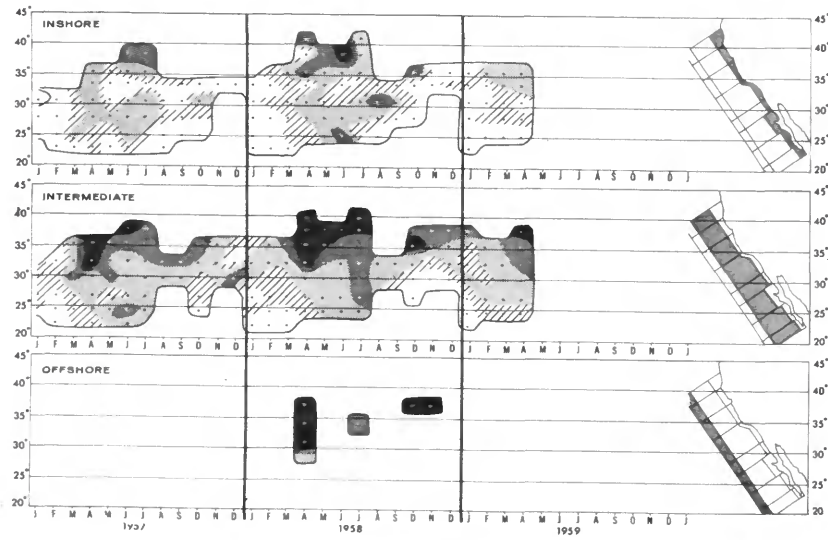
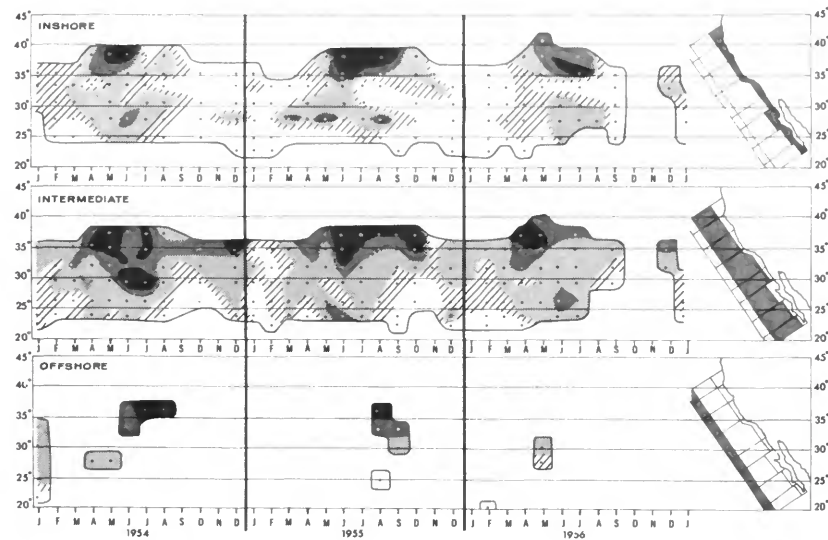
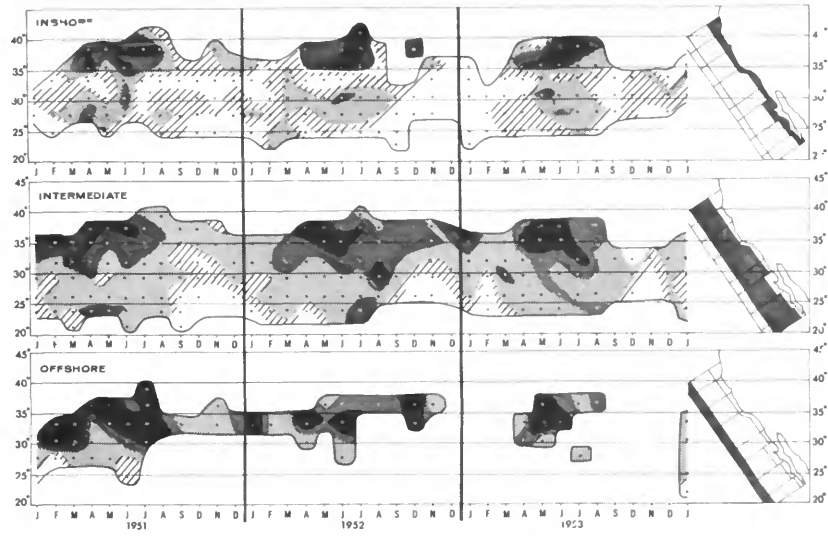
Inshore Strip (upper diagram in Figure 62): Seasonal cycles in abundance are apparent for most years, especially north of Point Conception, California. Black-foots occurred in concentrations of 5 to 10 BPSt mostly between April and July; other months they were absent, or present in concentrations of 5 BPSt or less. Off southern California they were generally absent most of the year, but a few birds showed up sporadically. The year 1958 was unique in that Black-foots occurred in this area continuously from March through September (except for June), although mostly in densities of 1 BPSt or less. In strong contrast, Black-foots occurred during most months north of Point Conception and off northern Baja California.

Concentrations as high as 10–20 BPSt occurred only north of Point Conception; indeed, south of here densities of 5 BPSt or less occurred most of the time. Also quite evident each year was an absence

of birds between 24°N and 30°N in late summer or early fall. This could be due to either a northward migration, or a progressive northward withdrawal to seaward from these latitudes. This phenomenon culminated in a complete withdrawal from the inshore strip in the fall and winter of 1952–1953 and 1955–1956.

Intermediate Strip (middle diagram in Figure 62): The most striking feature here is that Black-footed Albatrosses were continuously present in at least part of this zone for the entire 100-month period (no stations were occupied in October and November 1956). There appeared to be a trend for maximum density to occur between April and July, although in 1955 Black-foot densities of 10–20 BPSt lingered until October north of 32°N. Relatively few birds were found in the strip in August through March. Densities of greater than 10 BPSt were rarely encountered south of ca. 32°N; when they did occur, usually as somewhat anomalous groups, it was from June through August (e.g., at 30°N in August 1952 and June–July 1954). Evident in most years in varying degrees was an exodus from, and return to, the area south of 30°N, from late summer to early winter in the same manner as in the inshore strip. This movement generally started in September south of 25°N and progressed northward to 30°N,

FIGURE 60.—Real time graphs of the BPSt for intermediate blocks: a, 1951–1953; b, 1954–1956; c, 1957–1959. (Numbers on graphs indicate number of stations contributing to BPSt.)



where it peaked in October or November. In December and January low numbers of *Diomedea nigripes* returned to the southern end of the strip but another brief evacuation from the southernmost degrees usually followed. This phenomenon occurred every year for which data are available, except 1958–1959.

At or south of 25°N anomalous patches of 5–10 BPST densities frequently occurred from June through August; examples of this were observed in July–August 1953, June 1955, June–July 1956, and June 1957.

Offshore Strip (lower diagram, Figure 62): As seen in the figures, coverage in the offshore strip was quite spotty compared with those closer to shore, but a few salient features of distribution and abundance are evident. Densities of more than 20 BPST occurred with greater frequency in this strip than in either the inshore or the intermediate zones. There also seems to be a tendency for high densities to occur farther south in this strip than in the other two. These high densities occurred quite erratically, and with no apparent evidence of the cycles which were displayed in the other two strips.

Discussion: South of Point Conception, the relative abundance among the three strips indicates a general increase in abundance with distance from shore, but north of here there is no consistent pattern. A more uniform pattern of distribution among the strips is evident, and sometimes there is even a decrease in abundance with distance from shore. Indeed, north of Point Conception, maximum densities among the strips occurred within the inshore strip in June and/or July of 1952, 1953, 1955, and 1956.

ABUNDANCE AT WEATHER STATION *Victor*

Personnel aboard the USCGC *Winnebago* kept a record of albatross numbers seen while the ship was positioned at Ocean Weather Station *Victor* (34°N, 164°E) from 26 February through 19 March 1967. Figure 63 presents the results of this record. The most birds seen at any time during the day (upper graph) ranged from a low of 2 on 17 March to highs

of 31 birds on 1 March and 30 birds on 12 March. There appeared to be a cycle in numbers of birds, changing from low to high numbers at 5–7-day intervals. The bottom graph of Figure 63 shows that the maximum number of birds usually occurred in the afternoon (1600), but never occurred in the morning (0800).

Analysis of Distribution

GENERAL CONSIDERATIONS

Two major trends in the distribution of Black-footed Albatrosses are evident. First, there is a major latitudinal population shift coincident with the breeding season, i.e., the birds are in the southern part of their pelagic range in winter (breeding season), and in the northern part of their range in summer (Figure 64). This is especially evident in the central Pacific. However, because there is considerable spatial overlap between the two ranges, and some birds are well north as early as April and as late as October, there are Black-foots throughout most of the absolute range at any given time of the year. Secondly, the evidence suggests that this species is predominantly an eastern Pacific bird, although a part of the population regularly occurs west of 180°. For example, the numbers of birds seen in single sightings in the northeastern Pacific are far in excess of similar counts for the northwestern Pacific. Examples of this are: 70 birds 40 miles off San Francisco Bay (McHugh, 1950); 125 birds some 1000 miles southwest of San Francisco, and 53 Black-foots 465 miles off Oregon (Yocom, 1947), 78 birds 40 miles off northern Washington (Sanger, 1970); and 100 Black-footed Albatrosses at Unimak Pass in the Aleutians (ca. 165°W, 54°N) (Arnold, 1948). Although similar counts for the western Pacific are scarce, those available show far lower numbers; Kuroda (1955) saw a maximum of 11 birds 240 miles east of Hokkaido during his summer observations, and Wilhoft (1961) had a maximum cumulative daily total of only 70 birds, some 100 miles northwest of Luzon in the Philippines. Furthermore, a general scarcity of Black-foots has been noted in the western Pacific at various seasons (Starrett and Dixon, 1946; Aronoff, 1960). Trans-Pacific observations (MacDonald and Lawford, 1954; Nakamura, 1963) have revealed generally more Black-foots in the eastern Pacific than in the west



FIGURE 62.—Contoured density real time diagrams of BPST in inshore, intermediate, and offshore blocks: a, 1951–1953; b, 1954–1956; c, 1957–1959.

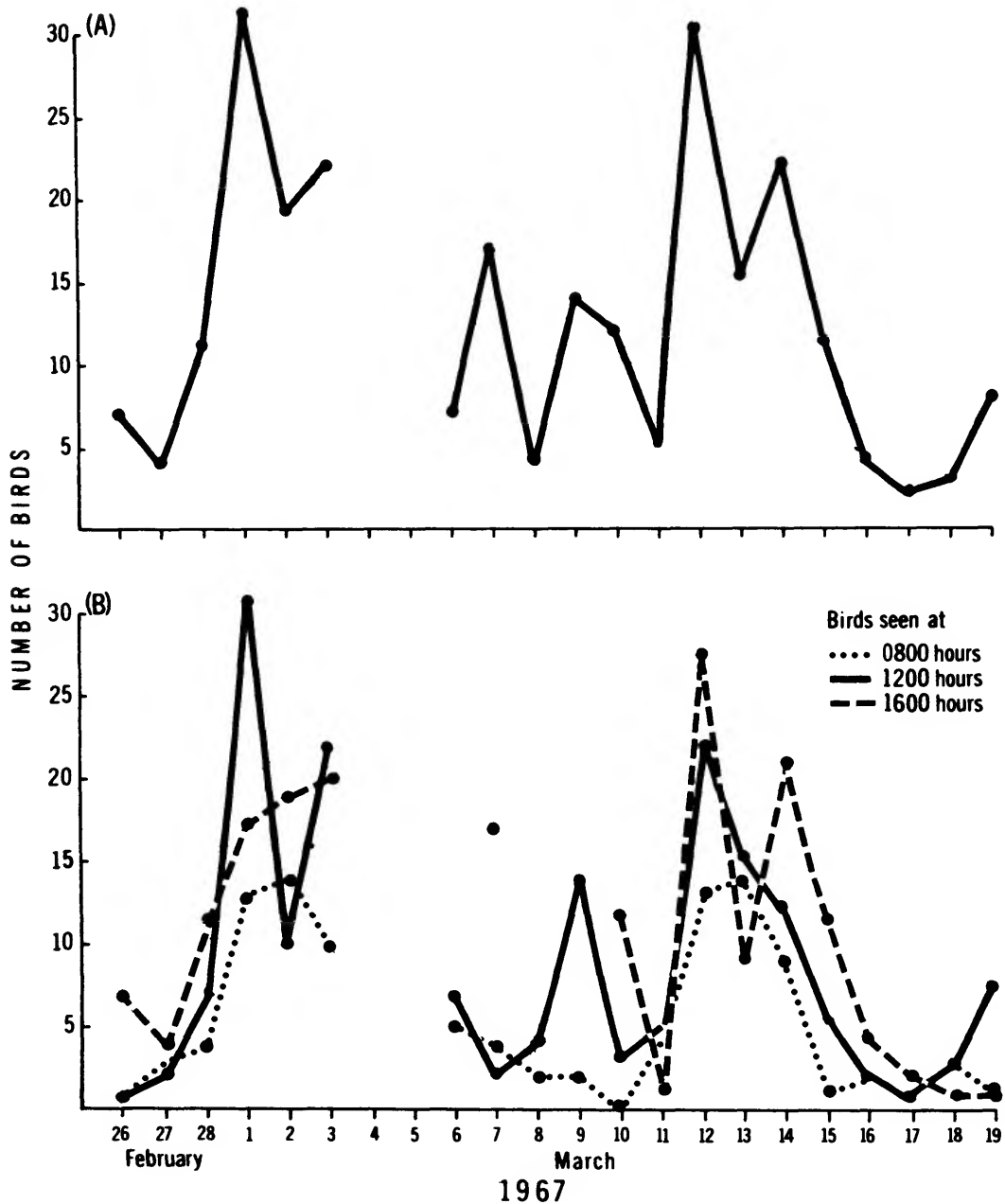


FIGURE 63.—Fluctuation in Black-footed Albatross numbers at Ocean Weather Station Victor (34°00'N, 164°00'E).

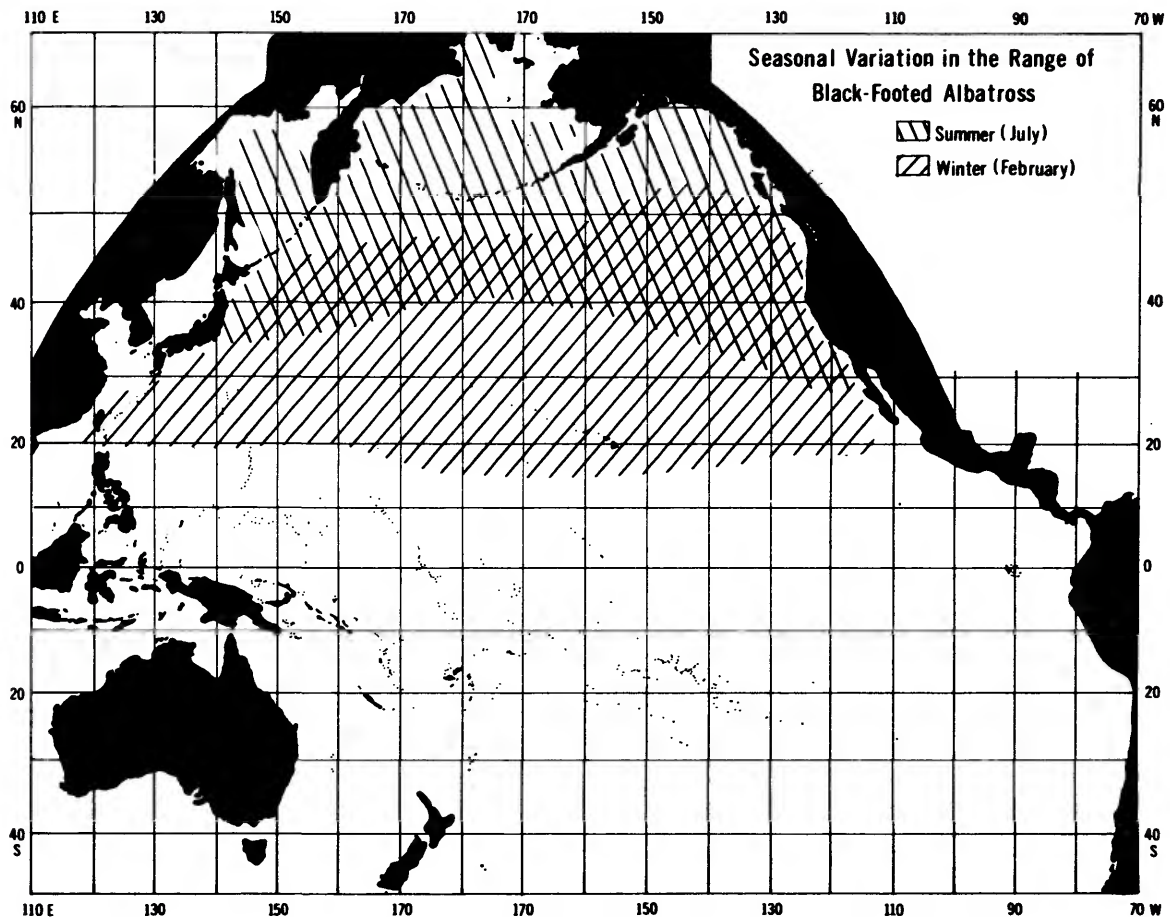


FIGURE 64.—Seasonal variation in the range of the Black-footed Albatross.

(although Austin and Kuroda [1953:299–300] stated that this albatross is common off Japan from April to November, and Hamilton [1958] observed that in June 1955 they were more abundant between Japan and 180° than east of there). Perhaps the most convincing evidence that the majority of the population prefers eastern Pacific waters is obtained from banding studies. Robbins and Rice (pp. 237–238) reveal that band recoveries of pre-breeding young showed a marked tendency to occur in the eastern half of the Pacific in all seasons, as did those for adults during winter. In summer, however, band recoveries of adults occurred with nearly equal frequency off North America and Asia. The relative chances for recovering banded birds in these two areas of the Pacific are unknown.

SEASONAL AND MONTHLY VARIATIONS

Starting in late fall, adult birds begin arriving at the breeding grounds. This would explain, at least in part, the sharp reduction in the number of Black-foots off Washington and Oregon between August and October. The regular late summer-early fall reduction in numbers off southern California and Baja California may be partly due to adult birds leaving for the breeding islands. Except for copulation, breeding activities do not require the simultaneous presence of both parents. "Incubation spans" range up to 18 days, and "guard spans" last about 2½ days (Rice and Kenyon, 1962b). When the guard stage ends in late February, both parents leave the island, returning only briefly to feed the

fledging young. Thus, even during the breeding season, about half of the breeding birds are at sea.

It is uncertain how far parents range from breeding sites, but they probably remain within 1500 to 2000 miles. Evidence to this effect is a dramatic buildup at sea during the breeding season in areas near the main Hawaiian Islands, some 1500 miles east and southeast of the major breeding areas on the Leewards. Robbins and Rice (Figure 148) indicate a host of band returns of adult birds from December through March between 155°E and 170°W, along the latitude of 30°N, and very few elsewhere. This further suggests the tendency for adults to range as indicated above. The Black-foots that occur off Washington, Oregon, and southern California in winter are probably largely nonbreeding immatures, but it is physically possible for the parents to range for food as far away from the breeding grounds as the North American Pacific Coast and return to the breeding grounds within two to three weeks.

Although parent birds are gathering food for the young, and presumably for themselves, they apparently exist under a progressive nutritional deficit during the breeding season. Frings and Frings (1961) noted that the weight of adult Black-footed Albatrosses decreased by about 8 percent over a two-week period in early egg-laying and nesting stages, presumably because of a reduction in heavy fat deposits which birds have prior to that time.

Woodward (1955) shows a dramatic decrease in the number of nonbreeding Black-foots during March and April on Kure Atoll. By late February most breeders are away from the atoll most of the time. The general exodus of birds from breeding islands which takes place in March and April may explain the regular April-May ingression of birds into the area off California as noted in the CalCOFI data. McHugh's (1955) 1949 distribution data certainly suggest a northeastward movement away from the breeding grounds, followed by, and coincident with, a northward movement paralleling the coast. The timing of this movement corresponds to the subsequent CalCOFI data reported here.

After the young albatrosses are fledged in early July, the adults stay away from the breeding grounds permanently and disperse throughout their range. Their distribution is probably governed by the distribution of food organisms, concentrations

of which, at least in the case of immature birds, are possibly found only by random searching.

Overall movements, as indicated earlier in the literature review, show that some birds are in the area of the Aleutians as early as May (Gabrielson and Lincoln, 1959:74), and as late as November (Kenyon, 1950). There seems to be no clear-cut trend in the winter movements in the far northeast Pacific. Rice and Kenyon (1962a) estimated that about 14 percent of the Black-foot population (one- and two-year-old birds) winter at sea.

DISTRIBUTION IN RELATION TO THE ENVIRONMENT

CURRENTS AND WATER MASSES.—The southern limits of Black-foot distribution generally coincide with the southwestern sweep of the California Current in the eastern Pacific Ocean off Baja California and the North Equatorial Current in the central Pacific Ocean. Although there are few data available for the western Pacific it seems likely that Black-foots usually do not range south or west of the North Pacific or the Kuroshio Currents, which may explain the scarcity of birds reported by Starrett and Dixon (1946). La Touche (1934) and Cheng (1955) both stated that this species occurs off China. It is common in the Bering Sea in summer, considerably north of the major northerly currents, the West Wind Drift and the Alaskan Stream. In winter the species apparently does not range very far north of the Kuroshio-Oyashio convergence in the northwest Pacific, nor of the subarctic current (ca. 50°–55°N) in the northeastern Pacific.

Thompson (1951) found that Black-foots tended to be more abundant in the California Current off California than in eastern North Pacific Central Water. Within the California Current, Miller (1942) found Black-foots concentrated within "tongues" of cold water off the southern California Channel Islands. Sverdrup, et al. (1942) explain that these tongues are caused by intense upwelling of deep water along the coast which are swept southward along the surface by the California Current. The point of upwelling in Miller's description would have been at Point Conception, California.

Reid, et al. (1958:30) note that upwelling along the North American coast is seasonal, being "strongest off Baja California in April and May, off southern and central California in May and June,

off northern California in June and July, and off Oregon in August." Thus, while the initial increase in abundance of Black-foots close to the central California coast (north of Point Conception) is correlated with the departure of adults and nonbreeding birds from the breeding islands in March and April, it seems quite possible that this high density of Black-foots is prolonged by the enriching process of upwelling in May and June. Further, the decrease in upwelling off the central California coast in July might well be a factor in the reduction in Black-foot numbers usually noted at this time.

Farther north off Oregon, upwelling also occurs close to the coast in August, and Black-footed Albatrosses are apparently concentrated there then (Gerard Bertrand [Oregon State University], pers. comm.). The large concentrations of birds found by Yocom (1947) are well within the California Current, but the observed abundance was probably distorted by the fact that his ship spent several days in the same location, thus creating a strong attraction factor.

Sanger (1970) observed a concentration of 78 Black-footed Albatrosses relatively close to shore over the continental shelf in August 1965, but over an 18-month period there was a general increase in abundance with increasing distance from shore; however, observations in nearshore areas may have been inadequate for a direct comparison with offshore data. P. W. Martin (1942) implied an abundance of Black-foots off British Columbia in summer over offshore banks. The large concentration of birds observed in Unimak Pass in the Aleutians (Arnold, 1948) could well have been coincident with local island-induced upwelling or tidal currents. In the western Pacific, Kuroda (1955) saw his highest numbers of *Diomedea nigripes* in the coastal waters off Honshu, approximately west of the Kuroshio-Oyashio convergence, in June and July.

SURFACE WATER TEMPERATURE.—There has been much discussion on the relationship between Black-footed Albatross distribution and surface water temperatures. Kuroda (1955) considered the species to be warm water adapted in his study of the birds between Japan and the western Bering Sea. Thompson (1951) observed a seeming inverse correlation between temperature (mostly 15°–25°C) and albatross numbers between Oahu and California. Hamilton (1958), Wilhoft (1961), and Nakamura (1963) all present temperature data which are in-

conclusive. In oceanic waters off Washington and Oregon, relatively high surface water temperatures (range over 18-month period, ca. 6°–17°C) were associated with relatively large numbers of Black-foots, and low temperatures were associated with small numbers (Sanger, 1970). In the central Pacific near the main Hawaiian Islands, King (1970: 91) observed Black-foots in low densities when surface water temperatures were greater than 23°C (range of ca. 22°–27°C).

The POBSP data correlating water temperature and albatross occurrence show no clear-cut trends for individual months; sample sizes (number of days of observation) are often small and the data are therefore insufficient to present graphically. In most months the data apparently simply reflect the range of surface temperatures encountered on the cruises. The only month that indicates a trend at all is March, which shows an inverse correlation between Black-foot numbers and water temperatures from 20° to 28°C. This is in line with temperature data of King (1970) and Sanger (1970), which suggest that the species is most often found in relationship to surface water temperatures ranging from ca. 14° to 22°C.

A detailed analysis of the relationship of albatross abundance and water temperatures in the CalCOFI area is beyond the scope of this paper; however, a few brief generalizations can be made. Ten-meter water temperatures were obtained at the same time the albatross counts were made (California Marine Research Committee, 1963). The warmest temperatures generally occurred off southern California and Baja California in September and October, followed by rapid cooling through March. Off southern Baja California (ca. 26°30'N in the inshore strip), the 10-year mean October 10-meter temperature was 23°C; it can reasonably be assumed that the surface temperature was warmer by a few, perhaps several, degrees. Thus, the usual fall evacuation by Black-foots from the zone south of 30°N in the inshore and intermediate strips may have been the result of a negative reaction by the birds to increased water temperatures. Similarly, the fact that the birds consistently reentered this zone in winter may have been a result of cooling water temperatures. Just off Point Conception (CalCOFI station 80.60), the coldest 10-meter temperatures occurred between February and May (10-year mean ca. 12.5°C), and the warmest from Au-

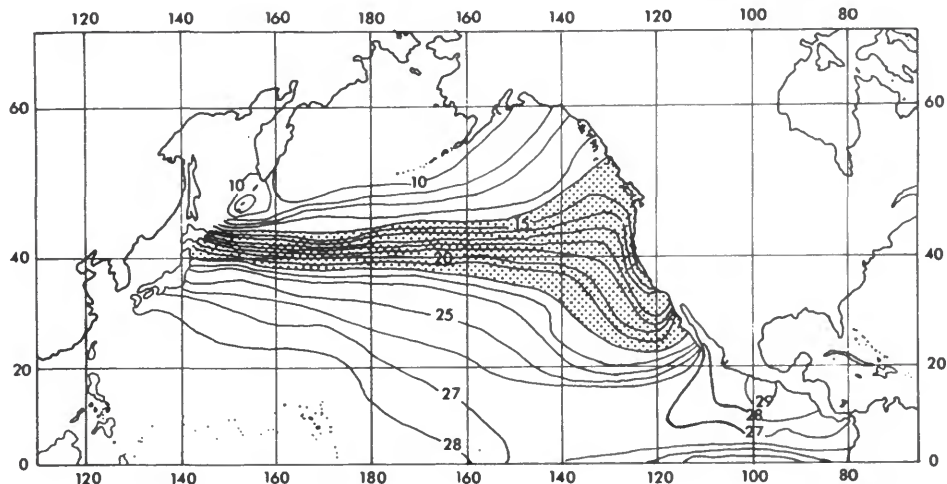


FIGURE 65.—The area bounded by the surface isotherms of 14° and 22°C (after Muromtsev, 1958).

gust through October (10-year mean ca. 17.5°C). The peak Black-foot numbers occur just north of here as the water temperature is warming (in June), although the entire annual range of temperatures is within the "preferred" temperature range noted above.

The apparent disparity in abundance of the Black-footed Albatross between the western Pacific (fewer birds) and the eastern Pacific (more birds) may possibly be explained by the species' apparent preference for a certain range of surface water temperatures. It was noted above that Black-foots were most often found within a surface temperature range of ca. 14° to 22°C. Assuming that the species disperses randomly within, and actively associates with, waters in this temperature range, one would expect to find more birds in the eastern Pacific than in the western Pacific. Figure 65, the average summer surface temperature in the North Pacific (after Muromtsev, 1958), shows that the region encompassed by the isotherms of 14° and 22°C is more than two times as large east of 170°W than west of that meridian. Thus, if the Black-foot indeed does actively associate within a 14° to 22°C surface water temperature range, one would expect most of the population to be found in the eastern north Pacific.

The absolute range of surface water temperature in which this species has been observed is from 3.4°C in the Gulf of Alaska in March 1967 (Uni-

versity of Washington data), to 30°C in the western Central Pacific in August 1960 (Wilhoft, 1961).

SURFACE SALINITY.—King (1970) observed an apparent direct relationship between Black-foot numbers and surface salinity in the central Pacific (within a range of ca. 33.5‰ to 35.0‰). He felt, however, that this resulted from the fact that, within his study area, the species' geographic range occurred north of waters with a lower surface salinity. Off the Washington and Oregon coasts there was no observable relationship between Black-foot numbers and surface salinity (Sanger, 1970), although Black-foots were occasionally found in salinities far below normal sea water salinities (e.g., 14.98‰).

AIR TEMPERATURE.—Air temperatures are closely correlated with ambient surface water temperatures in the ocean. One would expect, therefore, to find similar relationships between Black-foot numbers and these two parameters, and this indeed is the case. King (1970:89) observed a pronounced inverse correlation between air temperatures and Black-foot numbers from 16° through 29°C. Few birds were seen at temperatures warmer than 22°C, and none above 27°C. Sanger (1970) noted a direct relationship between air temperature and Black-foot abundance within a range of 7° to 18°C, and Kuroda (1960) believed that within an overall range of 7.0° to 22.5°C the species preferred air temperatures from 17° to 22.5°C.

WEATHER CONSIDERATIONS.—Wind is probably the most significant feature of the weather affecting albatross distribution. Since albatrosses are dependent upon the wind for mobility, it stands to reason that they would avoid, or be found in lesser numbers in, areas with wind velocities insufficient or marginal to maintain their sailing flight. The average wind velocity decreases as the equator is approached and the doldrum wind conditions are encountered; this fact no doubt plays a significant role in limiting the southern distribution of the Black-footed Albatross. High winds apparently have little or no adverse effect on the Black-foot, since the species has been noted sailing in winds as high as

70 knots (80 MPH) with no apparent ill effects (Sanger, 1970).

Addendum

After this paper was written in 1968, the important paper of V. P. Shuntov (1968) came to my attention. It is in general agreement with the findings reported here that the Black-footed Albatross is primarily a species of the eastern north Pacific, but with some of the population occurring in the western part. Shuntov indicates the Black-foot ranges in summer and autumn into the Sea of Okhotsk and north into the western Bering Sea to the Gulf of Anadyr, but not as far south in winter as our records in the central Pacific indicate.

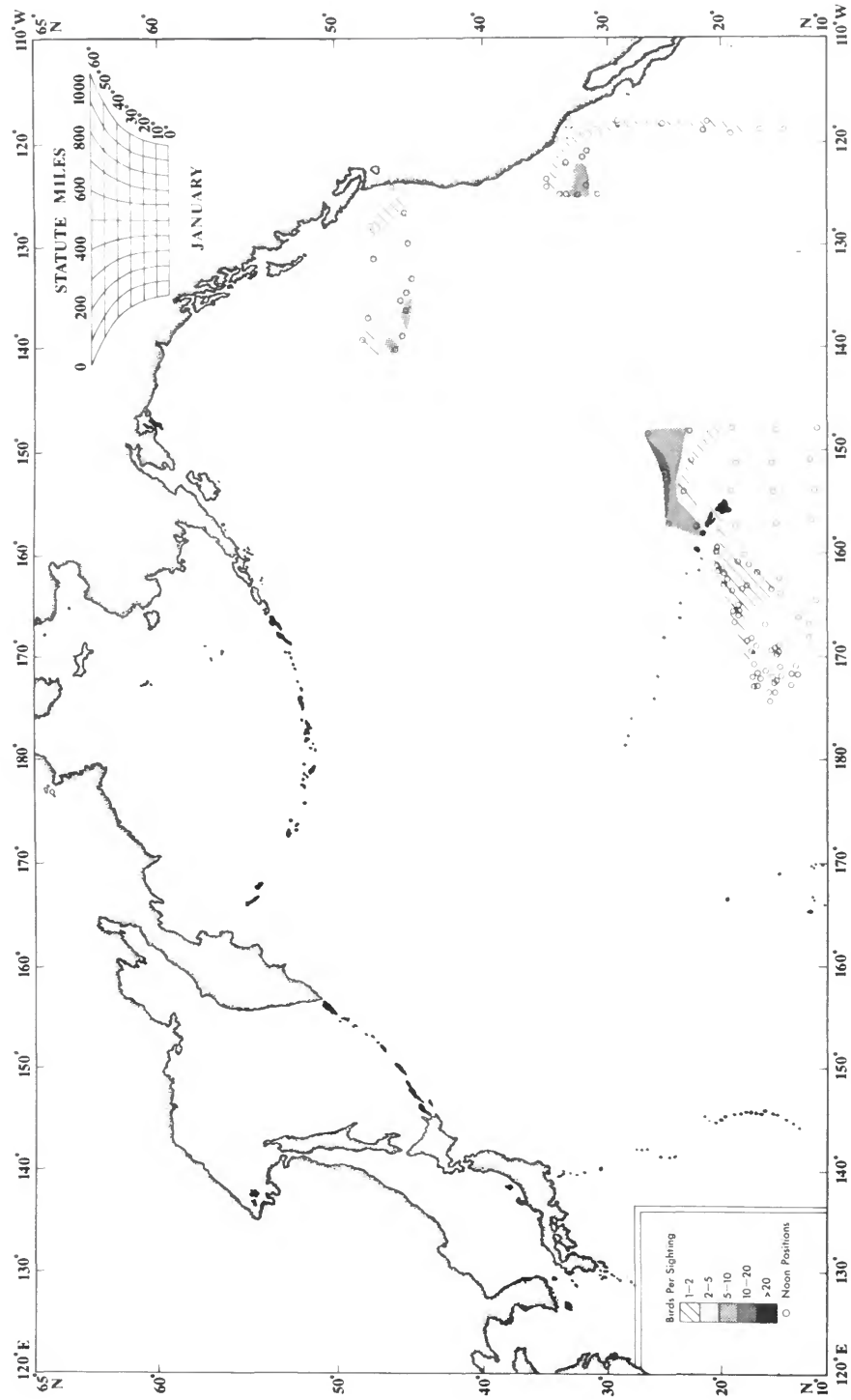


FIGURE 66.—Distribution and density of Black-footed Albatrosses in the Pacific Ocean in January.

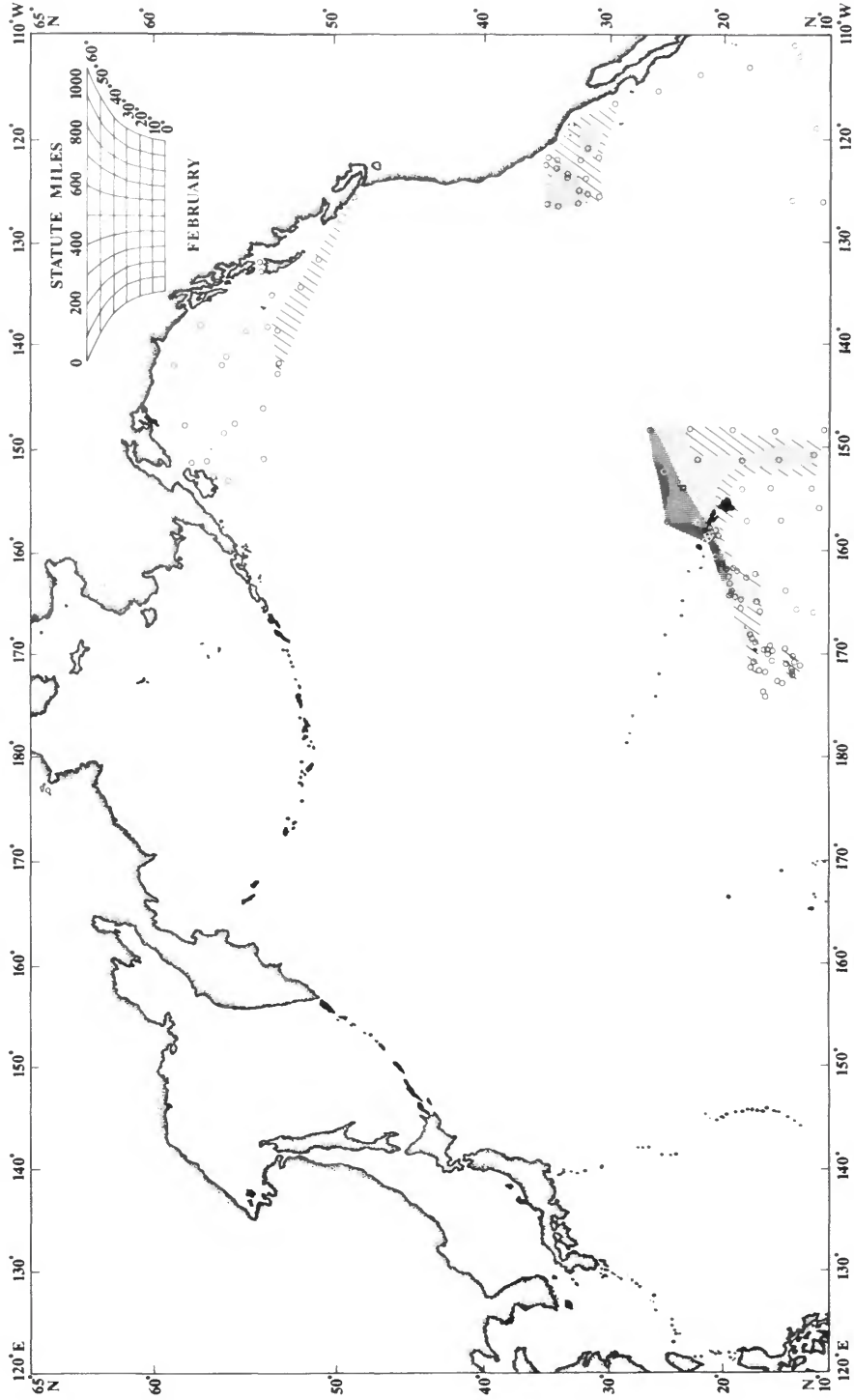


FIGURE 67.—Distribution and density of Black-footed Albatrosses in the Pacific Ocean in February.

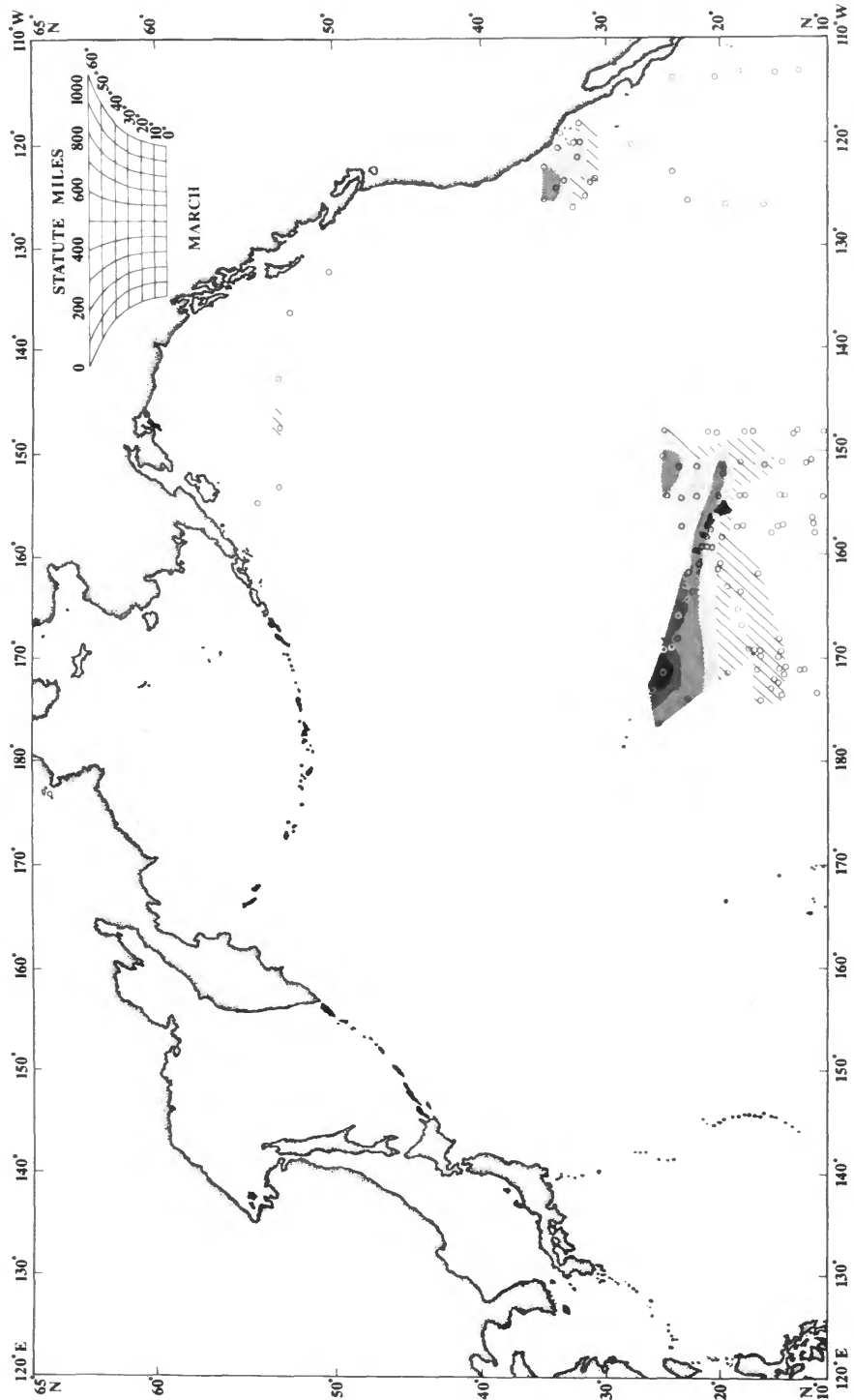


FIGURE 68.—Distribution and density of Black-footed Albatrosses in the Pacific Ocean in March.

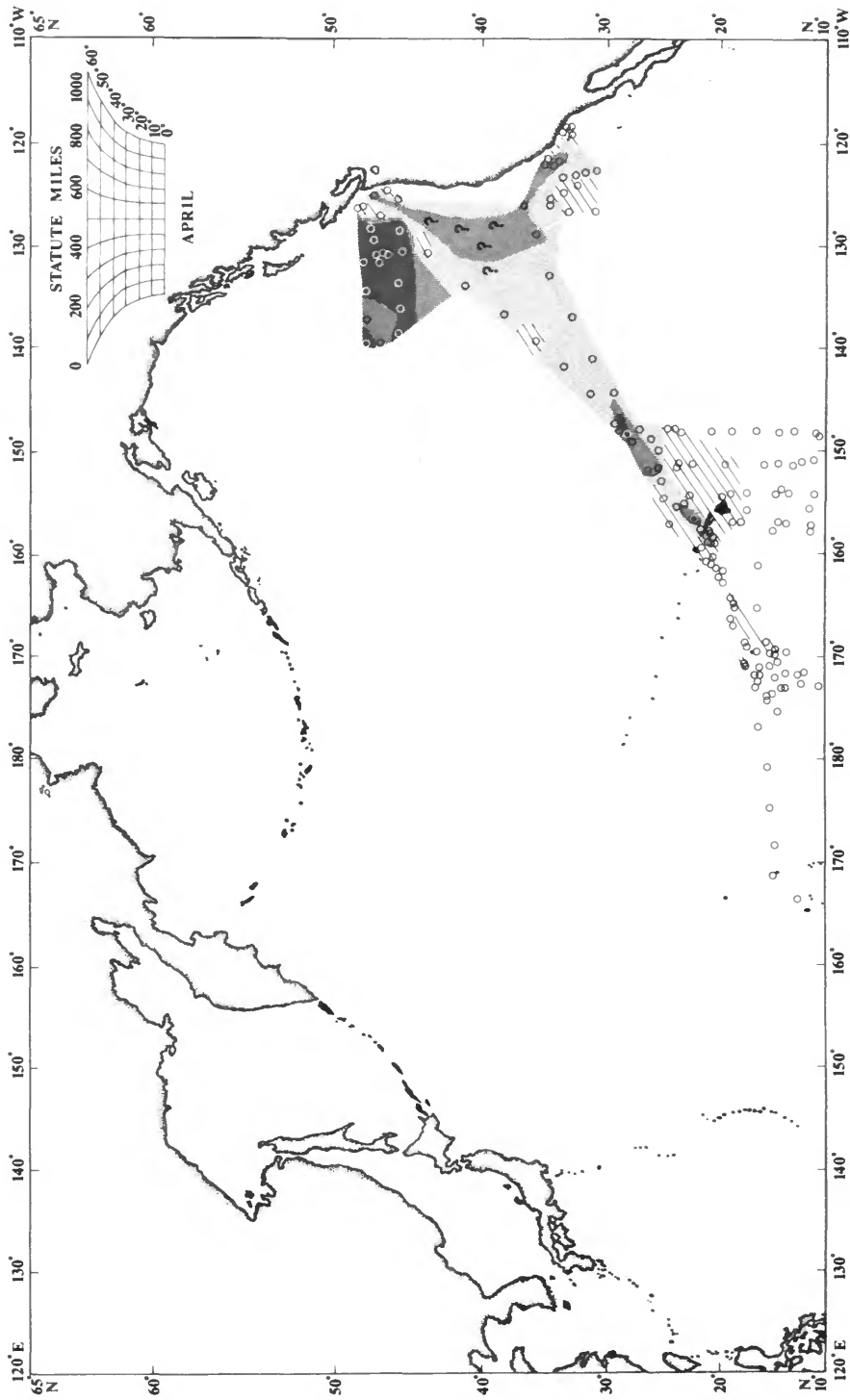


FIGURE 69.—Distribution and density of Black-footed Albatrosses in the Pacific Ocean in April.

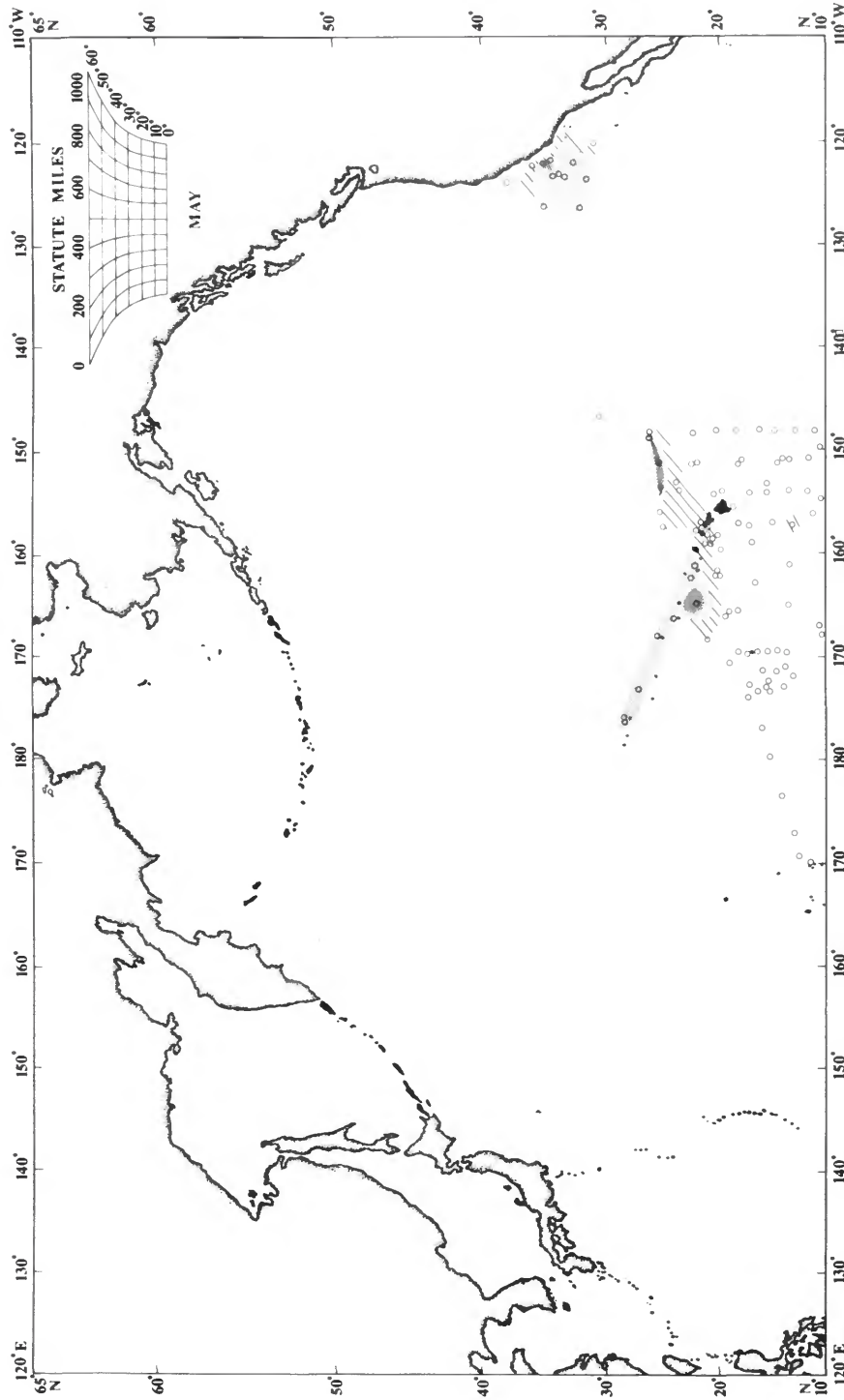


FIGURE 70.—Distribution and density of Black-footed Albatrosses in the Pacific Ocean in May.

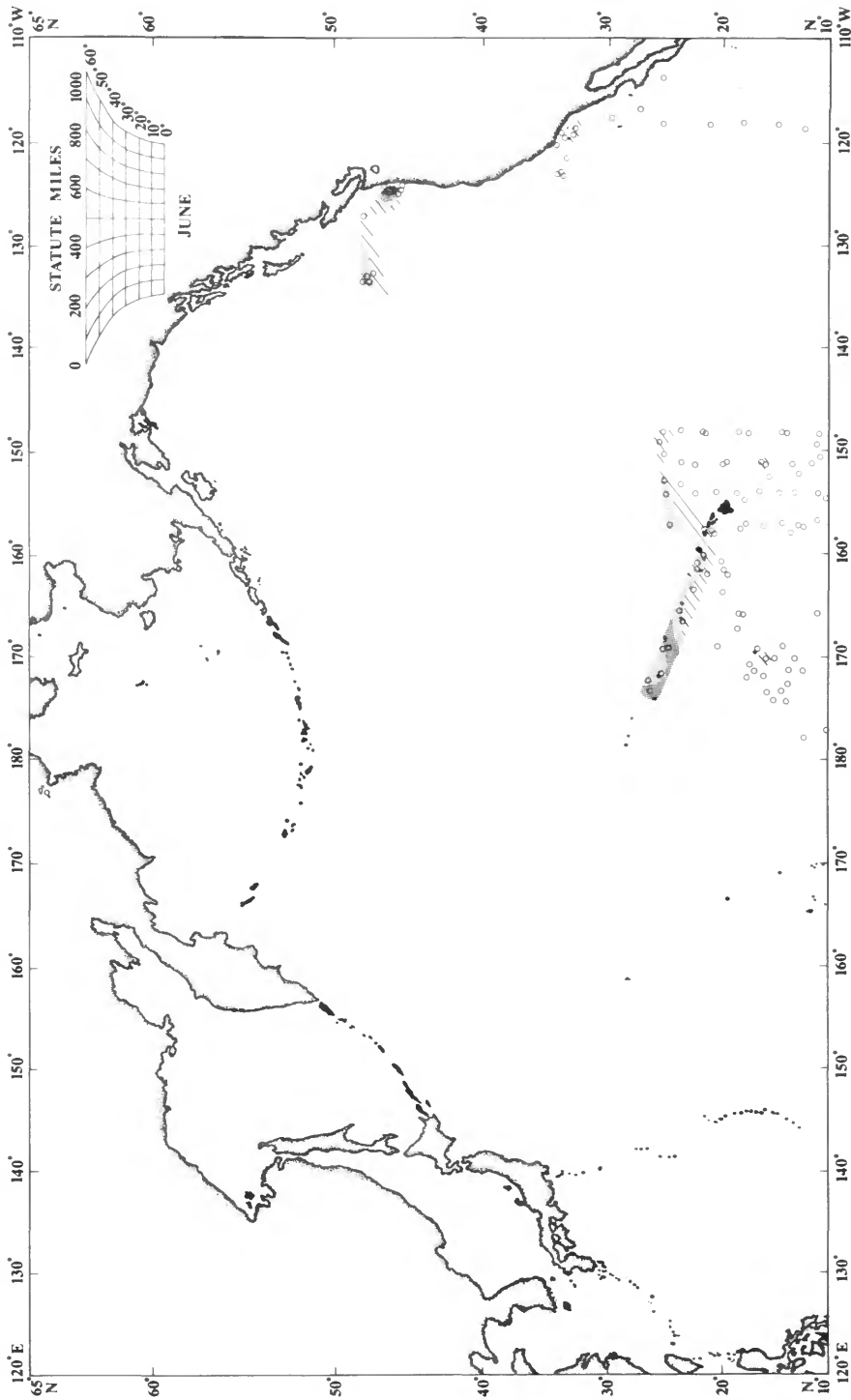


FIGURE 71.—Distribution and density of Black-footed Albatrosses in the Pacific Ocean in June.

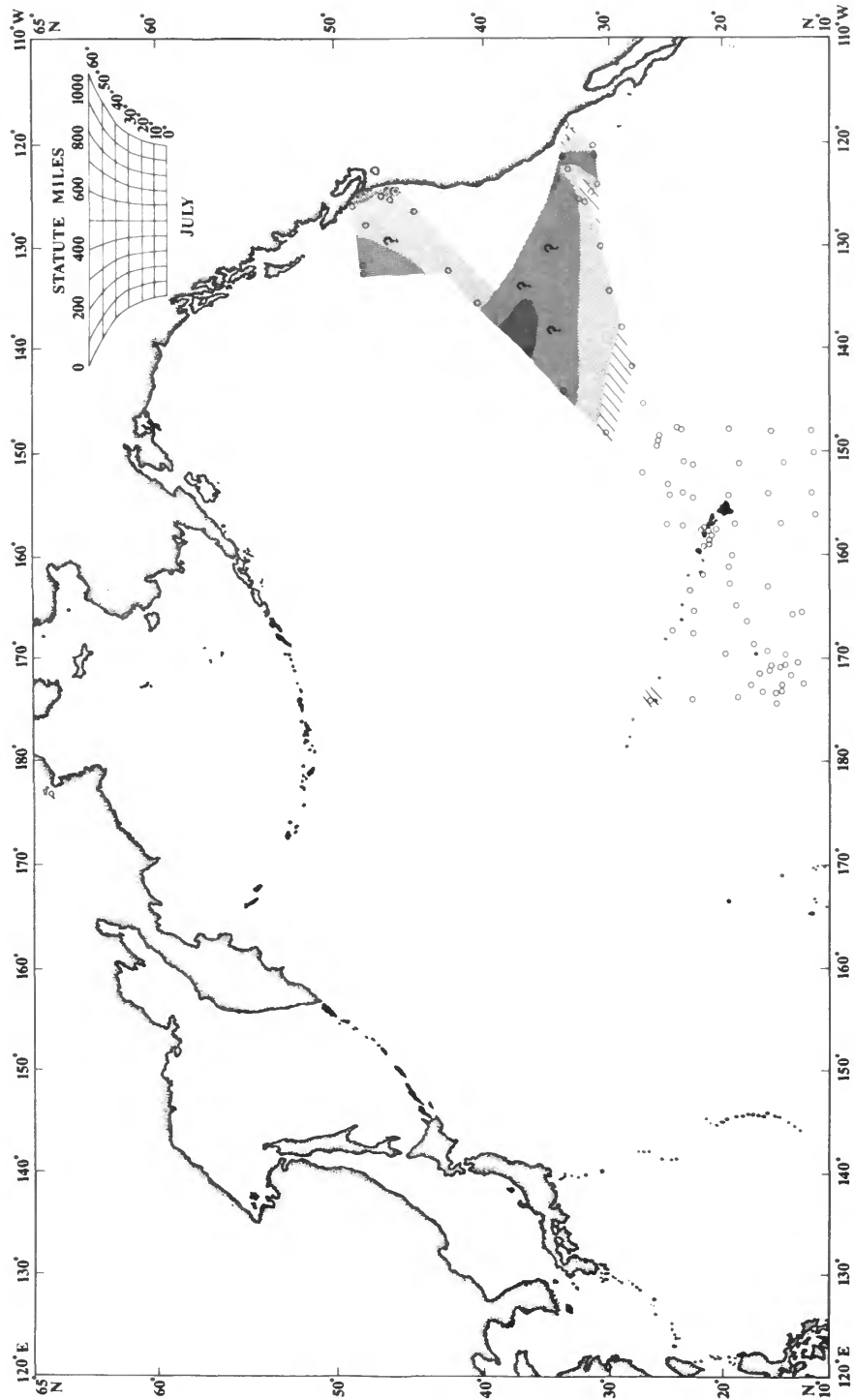


FIGURE 72.—Distribution and density of Black-footed Albatrosses in the Pacific Ocean in July.

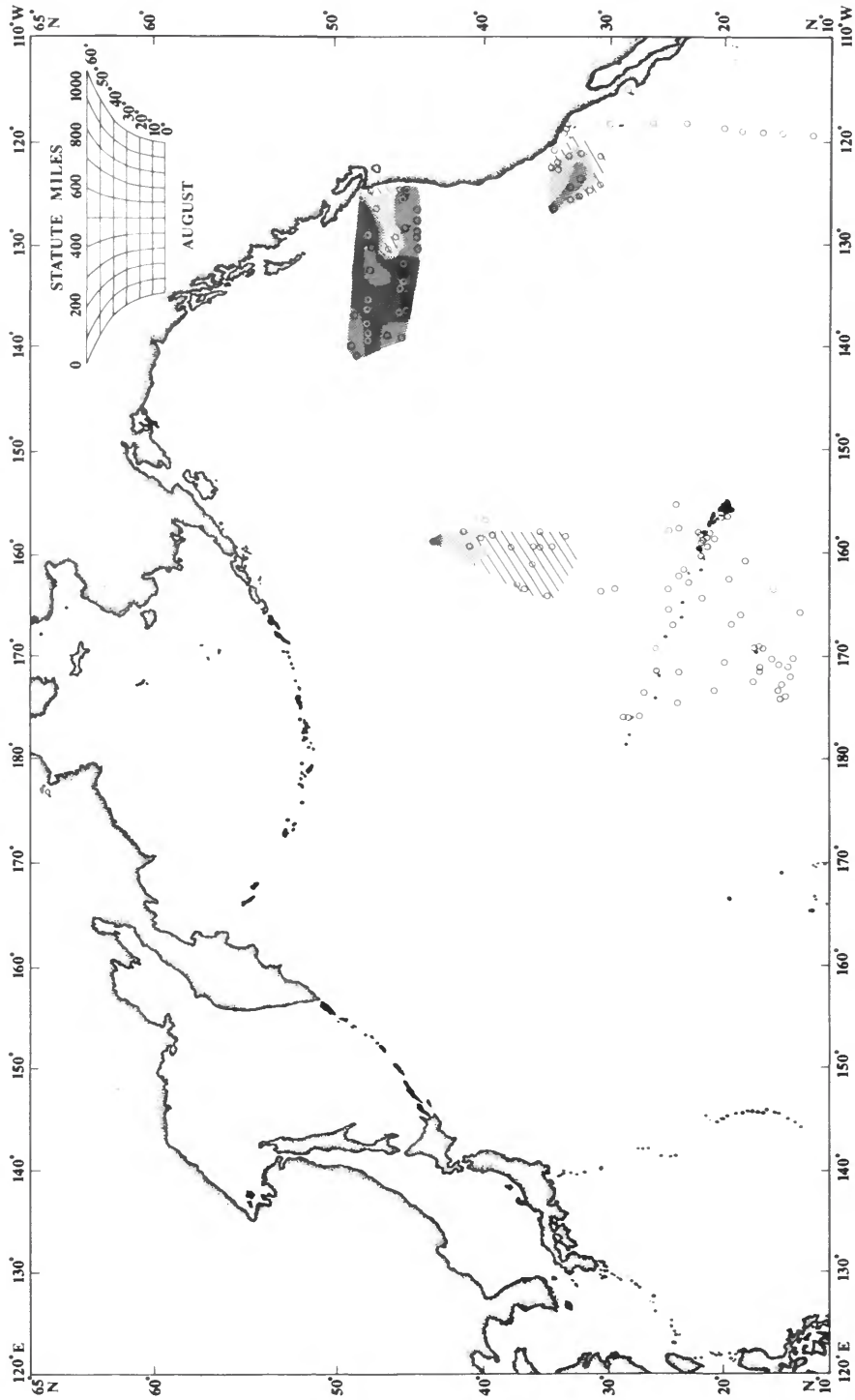


FIGURE 73.—Distribution and density of Black-footed Albatrosses in the Pacific Ocean in August.

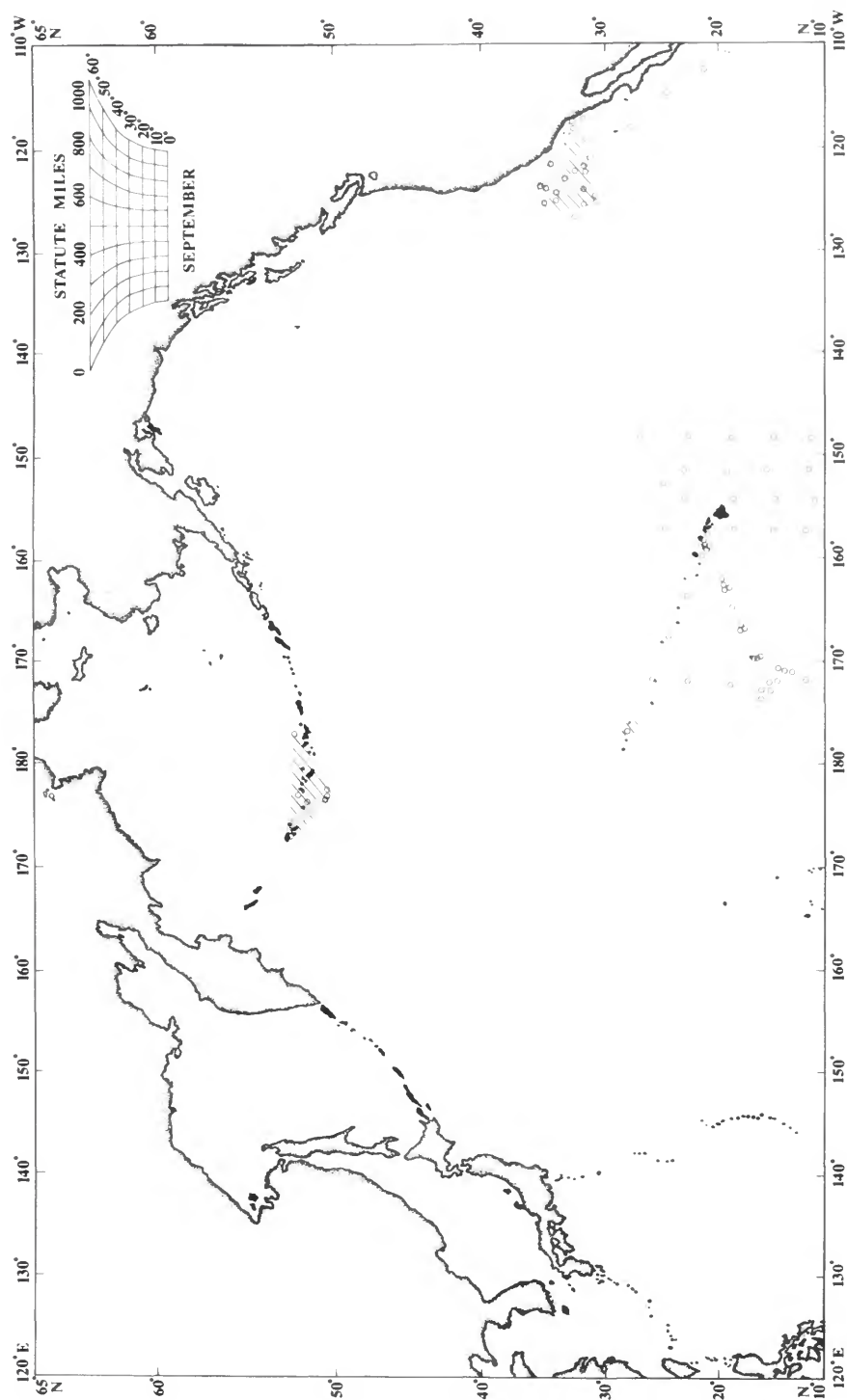


FIGURE 74.—Distribution and density of Black-footed Albatrosses in the Pacific Ocean in September.

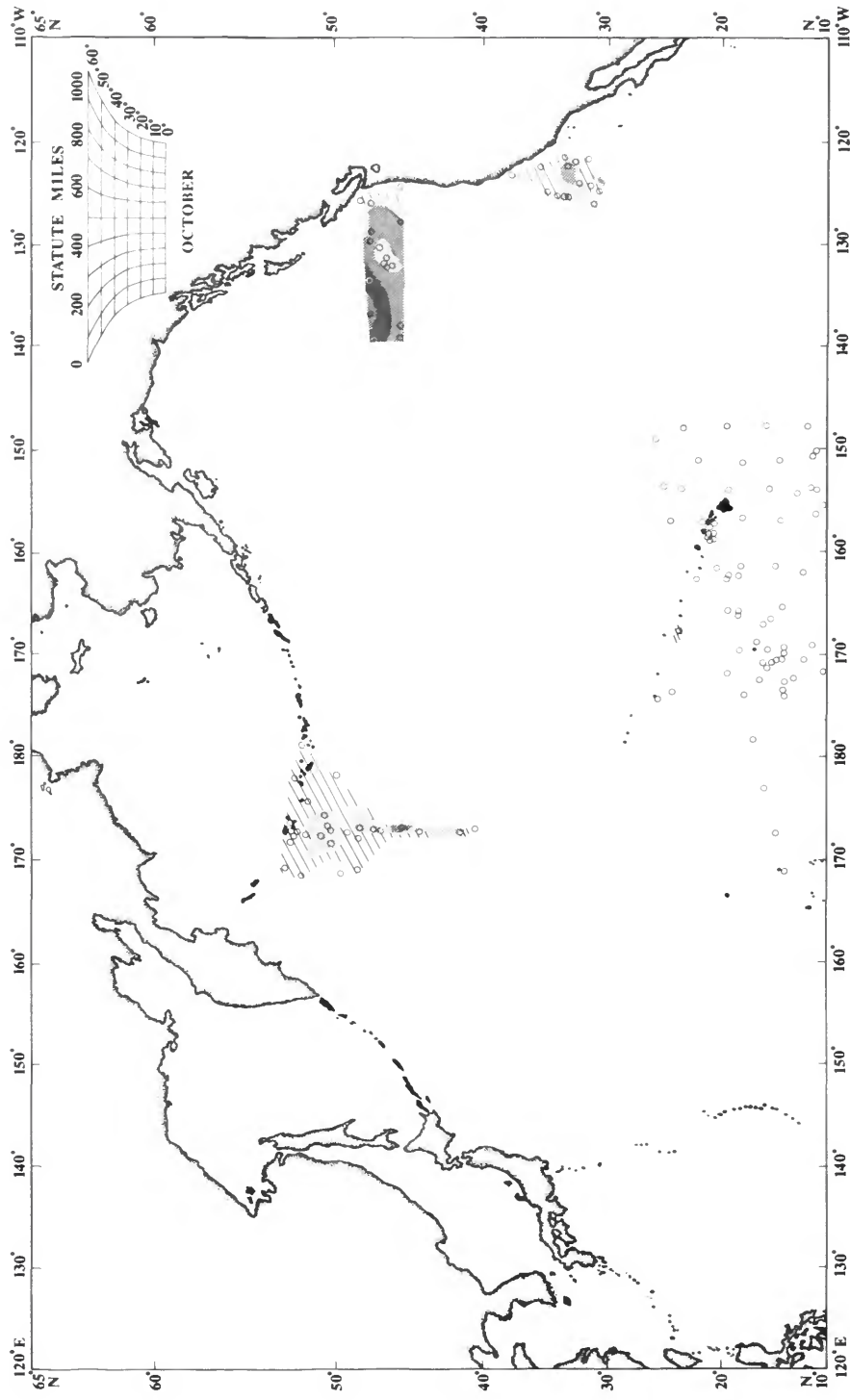


FIGURE 75.—Distribution and density of Black-footed Albatrosses in the Pacific Ocean in October.

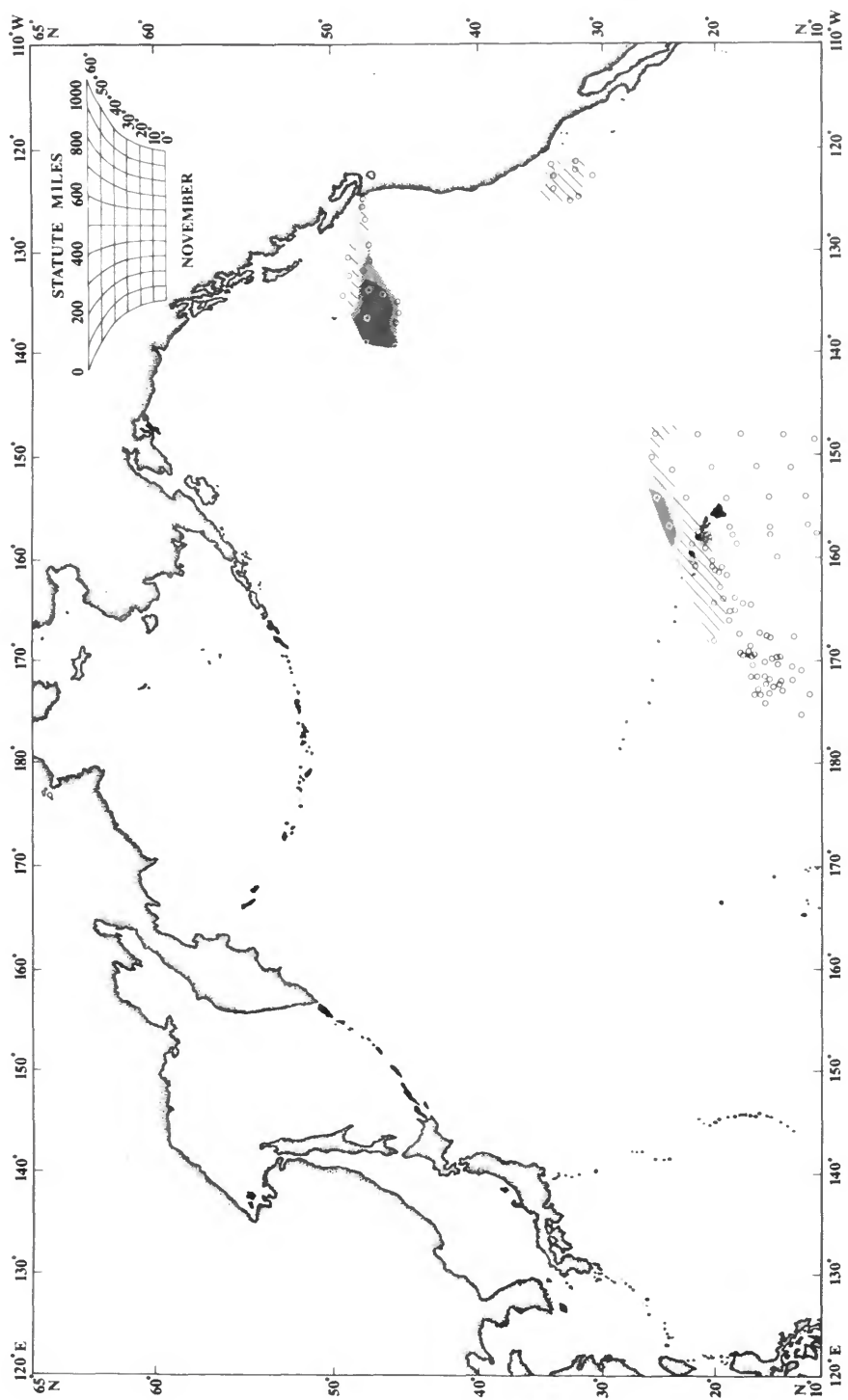


FIGURE 76.—Distribution and density of Black-footed Albatrosses in the Pacific Ocean in November.

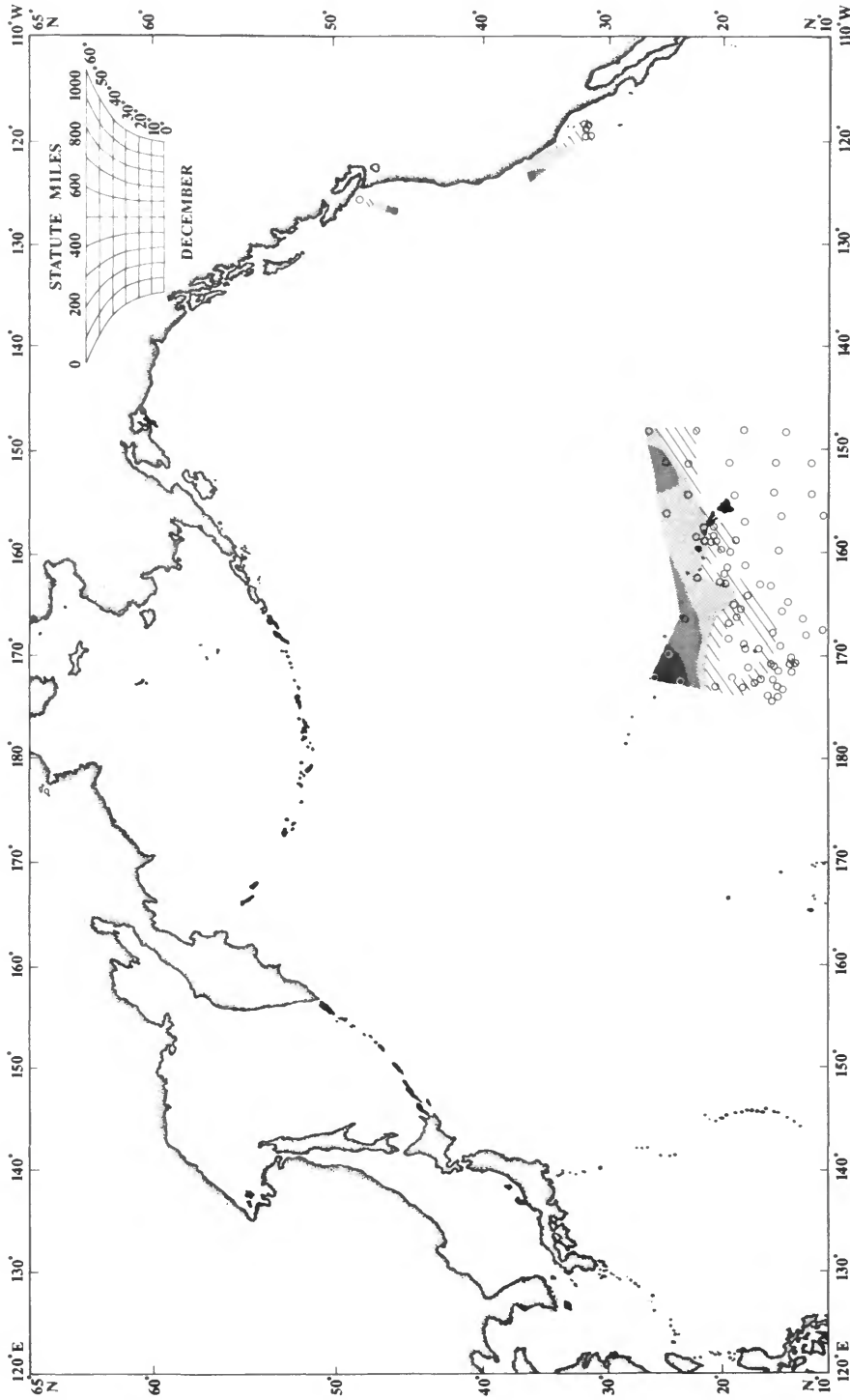


FIGURE 77.—Distribution and density of Black-footed Albatrosses in the Pacific Ocean in December.

Appendix

Summary of published data on Black-footed Albatross distribution

Location	Date	Remarks	Source
NORTHEAST PACIFIC			
Point Barrow, Alaska	5-11 Jul 1898	the authors note, without comment, 11 specimens reportedly collected here; since the expedition during which these birds were collected was in the north Pacific 5-11 July 1897, it seems possible that specimens were collected then and not a year later at the extremely extralimital site of Point Barrow	Gabrielson and Lincoln, 1959:74
Gulf of Alaska and Bering Sea	May-Oct		" " " "
Between Unalaska and the Pribilofs, Bering Sea	Jul 47	some present in this area	Kenyon, 1950:98
Unimak Pass, Aleutians	9 Jun 43	100 at once	Arnold, 1948:556-557
Bristol Bay, Alaska	no date	ranges nearly to 58°N in this region	Murie, 1959:35
From S of Shumagin I. (Alaska), W into southern Bering Sea at 75 mi N Seguam I.	8-11 Jun 43	continuous between these points	Arnold, 1948:556-557
From 47 mi NW Semisopochnoi I., Aleutians, to 30 mi W Cape Spencer, Alaska	20 Jun-10 Aug 43	continuously seen in this area	" " "
Southern Bering Sea	Oct 47, Nov 48, May 49		Kenyon, 1950:98
900 mi SE Unalaska to the Farallon I. off San Francisco	Nov 48	continuously in sight, following ship; up to 10 seen at once	Kenyon, 1950:97
Great Circle route, San Francisco to Yokohama, return via Honolulu to Los Angeles	Aug 59, Mar 61	abundance slightly higher in NE Pacific than NW; maximum at once, 11 at 155°W on Great Circle route, 14 at 164°E on return	Nakamura, 1963:239-245
Off British Columbia and in Gulf of Alaska	Sep 52-May 54	seen each of five cruises, most common Sep-Oct, least common Nov-Dec	Poole, 1966:71
British Columbia	no date	in pelagic waters; numbers increase as spring progresses, a tendency to flock in summer	Godfrey, 1966:20-21
Off British Columbia	Apr-late Sep	"constant companion of fishermen on offshore banks"	Martin, 1942:27
60 mi inside Str. of Juan de Fuca, Washington	no date	1	Poole, 1966:71
51°44'N, 138°48'W-49°56'N, 128°16'W	25 Jul 44-27 Jul 55	4-10 seen daily	Motoda and Fujii, 1956, t.3
Washington	14 Apr-30 Oct	"a common migrant or wanderer" "well offshore"	Jewett, et al., 1953:66
Trans-Pacific and off Washington	Jun 55	numbers ranged from 0 at 180° to ca. 7.5/hr off Washington; mean daily abundance 8.5 over six days E of 180°	Hamilton, 1958:160-162

Summary of published data on Black-footed Albatross distribution—Continued

Location	Date	Remarks	Source
48°27'N, 126°32'W– 43°08'N, 179°08'W	9–20 Aug 55	seen daily, up to 12 following ship at once	Motoda and Fujii, 1956, t.3
Cobb Seamount, 290 mi off Washington	Aug 50	presence of Black-foots briefly mentioned	Powell, et al., 1952:52
Off Washington and Oregon	1964–1965	comprehensive seasonal data; see text herein	Sanger, 1970:342–349
Central California to northern Washington	1949–1950	comprehensive seasonal data; see text herein	McHugh, 1955:375–381
Southern California to northern Washington	Dec 48	5–15 followed ship within 30–175 mi off the coast	Kenyon, 1950:98
Off Washington and Oregon	1963	presence off coast to 130°W during all seasons	Sanger, 1965:1
100 mi off Washington Oregon	Feb-Mar 51 apparently regular summer visitors	present from here to Hawaii not abundant off Oregon	MacDonald and Lawford, 1954:14–15 Gabrielson and Jewett, 1940:80
Off central and northern California	1949	increasing abundance over previous 20–odd years noted	McHugh, 1950:153
130° W off San Francisco	Oct 45	45 seen at once is maximum of period	Thompson, 1951:228–229
EAST-CENTRAL PACIFIC			
California	apparent increase during summer	“especially along the edge of the continental shelf throughout the length of the state”	Grinnell and Miller, 1944:40
Off southern California	1949	increasing abundance over previous 20–odd years noted	McHugh, 1950:153
Southern California	Jun–Sep 1937, 1938	concentrated offshore of Channel Islands in “cold tongue” of water; commonly 12–15 birds at oceanographic stations in cold tongue but never more than 5–6 outside this area; none seen in Santa Barbara Channel	Miller, 1940:231–232
34°40'N, 129°50'W	24 Feb–19 Mar 45	abundant, maximum of 65 seen at once	Yocom, 1947:518
34°00'N, 131°31'W	10 Apr–1 May 45	abundant, maximum of 50 seen at once	“ ” “
34°00'N, 131°31'W	24 May–15 Jun 45	abundant, maximum of 95 seen at once	“ ” “
32°N(ca.), 132°34'W	Jul 59	cumulative total of 30 near here	Wilhoft, 1961:258–260
31°40'N, 136°00'W	22–27 Jun 45	abundant, maximum of 73 seen at once	Yocom, 1947:518
Baja California	1949–1950	comprehensive seasonal data; see text herein	McHugh, 1955:375–381
Mexico	not noted	off Baja California and in the Revilla Gigedo I.	Friedmann, et al., 1950:15
Off Mexico at 22°N, 109°W	15 Jun 54	seen south to here	Poole, 1966:71
NORTHWEST PACIFIC			
Along Aleutians between Unalaska and 175°E	Oct, Nov 47	a few seen	Kenyon, 1950:98
Between Kiska and Attu, and the USSR	Jun 43	absent	Arnold, 1948:556–557
Japan	Apr to Nov (year?)	common offshore in summer	Austin and Kuroda, 1953:299
Off Hokkaido	Dec (year?)	none seen	Kuroda, 1963:234
43°05'N, 175°42'E	22 Aug 55	2 seen in distance	Motoda and Fujii, 1956, t.3
42°57'N, 171°04'E	23 Aug 55	2 seen in distance	“ ” “ “

Summary of published data on Black-footed Albatross distribution—Continued

<i>Location</i>	<i>Date</i>	<i>Remarks</i>	<i>Source</i>
42°51'N, 162°08'E– 42°45'N, 151°28'E	25–27 Aug 55	none recorded here	" " " "
Off Honshu and Hokkaido	4 Jun– 14 Jul 54	fairly concentrated close to shore; rare N to 200–300 miles off southern Kamchatka; maximum number of 11 just N of Hokkaido	Kuroda, 1955:292
Japan to Washington	Jun 55	from Japan to 180°, mean daily abundance was 15.5 over four days, vs 8.5 over six days from 180° to Washington	Hamilton, 1958:160–162
Between Torishima I. and Tokyo	Apr 58	occurred relatively infrequently	Aronoff, 1960:277
Honolulu to Yokohama	May 20	present from a day out of Honolulu to a day before arriving Yokohama	La Touche, 1934:430
32°39'N, 160°37'E	16 Sep 64	1	Jones, 1965:71
34°36'N, 141°31'E	Apr 51	westernmost record of authors	MacDonald and Lawford, 1954:15
WEST-CENTRAL PACIFIC			
China coast	winter–spring	"Off the China coast during the winter and spring; in the Taiwan Straits at the end of the year, according to Swinhoe."	Cheng, 1955:5
Formosa Channel	year round	common in Formosa Channel	La Touche, 1934:430
Western Pacific	1951–1952	flocks generally smaller in W Pacific than in E	MacDonald and Lawford, 1954:14–15
West Pacific area 16°05'N, 119°02'E	Jun 45–Feb 46 Aug 60	general absence noted daily total of 70+ birds	Starrett and Dixon, 1946:268–270 Wilhoft, 1961:258–260
New Hebrides to Solomons to western Carolines and from Okinawa to Saipan	Mar, Apr 45	none	Thompson, 1951:233
Saipan to Pearl Harbor	21 Apr 45	first seen at 15°40'N, 176°20'E	" " "
Philippines to Pearl Harbor	Oct 45	none	" " "
SOUTHWEST PACIFIC			
New Holland (Australia)	no date	specific location not indicated, specimen collected	Oliver, 1955:181
Dusky Sound, N.Z.	July 1884	vagrant specimen collected by A. Reischek	" " "
CENTRAL PACIFIC			
Washington to Oahu	Feb–Mar 51	present near Hawaii, with maximum of 18, N of Maui	MacDonald and Lawford, 1954:14–15
San Francisco to Honolulu	May 20	present to two days out of Honolulu	La Touche, 1934:430
Honolulu to San Francisco	25 Jan–1 Dec 45	during most months abundance increases as California coast is approached; see text herein	Thompson, 1951, 228–231
1000 mi SW San Francisco	Jul 64	125; maximum ever seen in single sighting at sea	Yocom, 1947:518
San Francisco to Eniwetok	Aug 45	last seen at 35°N, 151°W	Thompson, 1951:233
Southern California to Hawaii	Jul 59	numbers generally low	Wilhoft, 1961:258–260
North of leeward Hawaiian I.	Mar 51	most plentiful mid-March; maximum of 60, 600 miles NW of Hawaii	MacDonald and Lawford, 1954:14–15
24°22'N, 163°30'W	25 Aug 60	daily total of 50+	Wilhoft, 1961:258–260
Philippines to Pearl Harbor	Oct 45	none	Thompson, 1951:233

Laysan Albatross (*Diomedea immutabilis*)*

Gerald A. Sanger

Introduction

The material contained in this report is a summary of all at-sea observations of the Laysan Albatross (*Diomedea immutabilis*) gathered by the Pacific Ocean Biological Survey Program (POBSP) in the central and eastern Pacific Ocean. Literature records, scattered northern Pacific POBSP records, and data obtained from POBSP island surveys are included for general background information. Humphrey (1965) gave a general summary of the program's objectives and Gould (pp. 1-5 herein) summarized the areas surveyed and the methods and materials used in the data collection and analysis. The reader is referred to these papers for more details.

An estimated 1.5 million birds constituted the world population of Laysan Albatrosses (*Diomedea immutabilis*) in 1956-1958 (Rice and Kenyon, 1962a:383). Although the Laysan is five times as abundant as the Black-footed Albatross (*Diomedea nigripes*) there has been a grossly disproportionate lack of information on the pelagic habits and distribution of the former species at sea. The Laysan Albatross is a shy bird, usually not strongly attracted to ships. Consequently, it has been seen and studied at sea far less than the gregarious, inquisitive Black-foot. Indeed, until 1950 Laysans were quite erroneously thought to range only to 40°N, but Kenyon (1950) showed them to range as far north as the southern Bering Sea. Recent papers which mention scattered sightings at sea (e.g., Hamilton, 1958; Kuroda, 1955) have expanded our

knowledge, but they also glaringly exposed our ignorance of gross distribution and movements. Pelagic observations of the POBSP in the central Pacific, off southern California, northern Baja California, and in the Aleutians, plus a seasonal study off Washington and Oregon (Sanger, 1970), have gone a long way toward providing an understanding of movement in rather small areas of the north Pacific Ocean. Moreover, large-scale banding studies by the U.S. Fish and Wildlife Service and the POBSP have revealed much about the qualitative distribution of known-age birds at sea.

BREEDING.—The Laysan Albatross presently breeds exclusively in the Hawaiian Islands (Table 23). The population is centered in the Leeward chain, but a small population breeds irregularly on Niihau and a nesting was recorded on Moku Manu off Oahu (Richardson, 1957:16). Fisher (1967, 1971) contributed to our knowledge of the Laysan's breeding biology on Midway Atoll. Rice and Kenyon (1962a, 1962b) gave an account of general breeding distribution and phenology. The breeding pattern follows that of the Black-footed Albatross, but is 10 to 14 days later in starting and finishing. Breeding birds return to the islands the first week in November, eggs are laid at the end of November or early December, chicks hatch at the end of January or early in February, and all birds have fledged and headed out to sea by the second week in August. The proportion of nonbreeding birds on the islands is the same as that of the Black-footed Albatross, about 75 percent.

SUMMARY OF PUBLISHED PELAGIC OBSERVATIONS.—The Laysan Albatross is an abundant species throughout much of the north Pacific Ocean, although rare or uncommon in some parts of its range. Its at-sea range is from the Japanese coast to 150°W and, in winter, almost to the North

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TABLE 23.—*Laysan Albatross breeding populations*

Location	Largest number of breeders ^a	Number of breeding pairs ^b
Kure	3,200 ^d	350
Midway	110,000 ^d	100,055
Pearl and Hermes Reef	30,000 ^d	17,750
Lisianski	8,000 ^d –	30,000
	10,000	
Laysan	300,000 ^d –	130,000
	500,000	
Gardner Pinnacles	14 ^c	2
French Frigate Shoals	1,000 ^d	584
Necker	1,650 ^d	2,500
Nihoa	38 ^c	500
Niihau	no data	500

^a POBSP and U.S. Bureau of Sport Fisheries and Wildlife data.

^b From Rice and Kenyon (1962a:369). A discussion of the disparity between these two sets of figures is beyond the scope of the present paper. The estimates are presented merely to give the reader an idea of the general population size of Laysan Albatross. A more accurate and detailed evaluation of populations will be presented in island accounts currently under preparation (POBSP).

^c Recorded.

^d Estimated.

American Pacific Coast; from the southern Bering Sea and the Gulf of Alaska south to about 28°N in the eastern Pacific, 13°N in the central Pacific, and about 30°N in the western Pacific.

Available data on the life history of the Laysan Albatross prior to 1962 have been summarized (Palmer, 1962:126–130). The previously known marine range and published pelagic records are summarized in the appendix. Information on Laysan distribution adjacent to coastal North America south of Alaska is scanty or nonexistent in major area references (e.g., Godfrey, 1966; Grinnell and Miller, 1944), but a number of recent papers (e.g., Holmes, 1964), supported by a mass of POBSP sightings, show that the Laysan Albatross is indeed common in this area from late fall through early spring. Winter storms are notoriously severe in the northeast Pacific and this fact has no doubt dissuaded bird observers from venturing into the region at this time.

Since the Laysan Albatross is a reasonably distinctive bird, and the only species normally ranging in the north Pacific with which it could be confused (*Diomedea albatrus*) is extremely rare (Sanger, 1972), the sight records as a whole are

TABLE 24.—*Recent specimen records of Laysan Albatrosses off North America*

Area	Date	Remarks	Source
Northern Oregon coast	13 Jul 60	dead specimen on beach	Fredrich, 1961:500
Northern Oregon coast	30 Jan 53	dead specimen on beach	McAllister, 1954:211
Five mi off S. California	6 Feb 58	caught alive from a fishing vessel	Stager, 1958:404–405

probably quite valid. Supporting the sight observations off North America are three recent specimen records (Table 24).

ACKNOWLEDGMENTS.—Many people in addition to those mentioned by Gould (p. 5) helped make this paper possible. Warren B. King and Patrick J. Gould were especially helpful in offering useful criticism on early drafts. George E. Watson read the final draft. Richard H. Fleming initiated the bird observation program for University of Washington Department of Oceanography cruises, which resulted in many sightings; these cruises were supported by various research grants from the U.S. Office of Naval Research and the U.S. Atomic Energy Commission. Robert L. Wisner, Scripps Institution of Oceanography, kindly assembled the California Cooperative Oceanic Fisheries Investigations sightings.

Distribution and Abundance

SPECIMEN RECORDS

Three Laysan Albatrosses have been collected at-sea by POBSP personnel. Two were taken south of the western Aleutians and the third in the central Pacific. Pertinent data for these specimens are listed in Table 25.

SIGHTING RECORDS

Figures 81–92 (pp. 140–151) show average monthly Laysan Albatross distribution in the Pacific Ocean as determined by POBSP sightings. The relative abundance is indicated by a unit of mean number of birds per sighting per day (BPS). In addition to POBSP sight records (1964–1968), sightings during a number of earlier University of Washing-

TABLE 25.—*Laysan Albatross specimens collected at sea by the POBSP*

Location	USNM number	Sex	Body weight (gm)	Gonad size (mm)	Date	Collector
51°19'N, 172°46'E	496197	♂	?	12x3, 11x3	4 Oct 65	R. DeLong
44°25'N, 173°02'E	503268	?	3110	?	13 Oct 65	R. DeLong
13°53'N, 171°05'W	496720	♂	?	11x5	1 Feb 66	R. Crossin, D. Husted

ton Department of Oceanography cruises are included on the maps. These cruises occurred in the Gulf of Alaska in September 1955, May 1956, and April 1957, and in the Aleutians to 173°28'E in August-September 1957. Since the distribution of the Laysan has been so poorly understood in north-eastern Pacific waters, these sightings are listed in detail in Table 27, as well as on the maps.

Laysan Albatrosses were also noted during the CalCOFI oceanographic cruises off California and Baja California from 1951 through 1959 (for details of these cruises see the Black-footed Albatross account, Sanger, this volume). These are listed in Table 26.

January Distribution (Figure 81): In the central Pacific, only scattered individuals were observed southwest of the main Hawaiian Islands to 17°15'N. Birds were undoubtedly abundant in the Leeward Islands, but no trips were made to that area. The species was relatively common and abundant (up to 4.0 BPS) off southern California. It was also seen commonly off Washington and Oregon, and occurred in densities up to 7.3 BPS about 600 miles off northern Oregon.

February Distribution (Figure 82): The frequency of sightings in the central Pacific increased over January (the southernmost sighting occurring at 13°02'N), but the species was still seen on only a minority of all days. A vagrant was noted at 8°30'N by Thompson (1951). Sightings off southern California decreased, with birds being seen on only four days. The northernmost winter record was noted at 53°00'N, 141°30'W in the Gulf of Alaska, on 6 February 1967.

March Distribution (Figure 83): Laysans were observed rather frequently in the central Pacific, and, although scattered birds reached almost 17°N, they were uncommon south of 20°N. One bird, possibly a vagrant, was recorded at 11°30'N, 151°04'W. Observations were conducted along the

Leewards for the first time; birds were found in densities of up to 2.3 BPS. They were seen on only four days off southern California, the southernmost record being at 28°49'N. None were observed in the Gulf of Alaska during five days spent north of 50°N, but scattered individuals were recorded off Washington and Oregon in 1963.

April Distribution (Figure 84): In the central Pacific Laysans were uncommon south to 17°30'N, but relatively common from 23°N to at least 35°N. They were noted on three days off southern California and were seen only at distances greater than 450 miles off Washington and Oregon. They were recorded north to 55°N in the Gulf of Alaska (1957).

May Distribution (Figure 85): Only a single Laysan was seen south of 24°N (18°25'N, 155°28'W)

TABLE 26.—*Laysan Albatross sightings (one bird each) during CalCOFI Cruises, 1951-1959*

Date	Location
22 Feb 51	32°09'N, 125°15'W
20 Jan 53	28°42'N, 116°37'W
10 May 53	31°35'N, 118°30'W
17 Jun 53	37°37'N, 123°37'W
10 Aug 53	40°30'N, 149°45'W
12 Aug 53	44°20'N, 150°18'W
4 Sep 53	51°00'N, 158°40'W
9 Sep 53	41°20'N, 155°13'W
10 Sep 53	40°00'N, 155°00'W
23 Jan 54	24°00'N, 132°00'W
1 Feb 54	33°28'N, 133°26'W*
19 Mar 54	25°18'N, 125°00'W
13 Oct 54	32°04'N, 120°39'W
15 Jul 56	40°00'N, 159°00'W
6-7 Nov 56	29°26'N, 119°45'W
	30°25'N, 117°45'W
8 Dec 56	33°00'N, 120°21'W
1 Feb 58	36°03'N, 122°02'W
10 Apr 58	33°39'N, 122°12'W
24 Apr 59	34°20'N, 122°01'W

*Two birds.

TABLE 27.—*Miscellaneous sight records of Laysan Albatross from the eastern North Pacific.* (observers, except one, from University of Washington)

Date	Location	No. of birds	Observer	Remarks
28 Sep 49	38°00'N, 123°45'W	1	R.C. Miller*	letter of 21 Jan 66 to Sanger
3 Sep 55	53°38'N, 161°28'W	1	unknown	Operation NORPAC
4 Sep 55	50°58'N, 161°09'W	3	"	" "
6 Sep 55	51°06'N, 152°40'W	2	"	" "
5 May 56	50°43'N, 133°48'W	1	C.M. Love	
7 May 56	50°12'N, 142°39'W	1	" "	
8 May 56	50°02'N, 144°12'W	2	" "	
8 May 56	50°02'N, 144°21'W	1	" "	
8 May 56	50°01'N, 144°45'W	2	G.H. Allen	
8 May 56	50°00'N-145°02'W- 50°02'N, 144°56'W	1	C.M. Love	bird stayed with drifting ship for 7.5 hours
9 May 56	51°15'N, 145°03'W	1	" "	
9 May 56	52°02'N, 145°02'W	1	H. Jackson	
9 May 56	52°05'N, 145°02'W	1	" "	
9 May 56	52°31'N, 145°02'W	1	G.H. Allen	
12 May 56	59°17'N, 144°59'W	2	unknown	
13 May 56	59°34'N, 144°30'W	1	"	
29 May 56	54°36'N, 152°46'W	1	"	
1 Jun 56	50°01'N, 144°57'W	1	C.M. Love	
8 Aug 57	50°22'N, 177°38'W	1	P. McCrery	I.G.Y. Expedition
9 Aug 57	50°32'N, 177°29'W	2	H. Jackson	" "
9 Aug 57	50°52'N, 177°35'W	1	P. McCrery	" "
13 Aug 57	50°42'N, 177°12'E	1	G.H. Allen	" "
14 Aug 57	50°40'N, 177°18'E	2	P. McCrery	" "
15 Aug 57	49°44'N, 174°29'E	1	E. Linger	" "
15 Aug 57	49°30'N, 173°29'E	2	R. Rubinstein	" "
16 Aug 57	49°20'N, 173°28'E	2	P. McCrery	" "
16 Aug 57	49°35'N, 173°28'E	1	R. Rubinstein	" "
17 Aug 57	51°08'N, 174°41'E	1	P. McCrery	" "
18 Aug 57	51°13'N, 174°32'E	2	R. Rubinstein	" "
18 Aug 57	51°19'N, 175°05'E	2	E. Linger	" "
18 Aug 57	51°24'N, 175°35'E	1	P. McCrery	" "
20 Aug 57	52°39'N, 180°00'	1	R. Rubinstein	" "
20 Aug 57	52°42'N, 179°41'W	1	E. Linger	" "
24 Aug 57	51°11'N, 173°20'W	1	P. McCrery	" "
25 Aug 57	51°02'N, 171°45'W	1	R. Rubinstein	" "
25 Aug 57	51°02'N, 171°45'W	1	E. Linger	" "

in the central Pacific, but the species was still common in the Leewards. In 13 days of observations off southern California, Laysans were seen on only two days. A single bird was recorded as close as 200 miles off the Washington coast, but most were west of 140°W. In the Gulf of Alaska (1956) the species was seen as far north as 59°34'N, this apparently being the northernmost record for the species.

June Distribution (Figure 86): Laysans were common in relatively low densities (less than 3.2 bps) in the Leewards, but were not seen in the remainder of the central Pacific. None were observed off southern California, and one was seen in the Gulf of Alaska (1956).

July Distribution (Figure 87): Our records show only one sighting in the entire Pacific this month, at 26°15'N, 174°00'W near Lisianski Island.

August Distribution (Figure 88): In the central Pacific there were but two birds sighted in the Leewards (near Pearl and Hermes Reef), and two more at 35°N. None were seen off southern California and only one was observed off Washington, about 750 miles off the coast. In the Aleutians (1957), Laysans were common just south of the islands between longitudes 171°W and 173°E. Two were noted one day in the southern Bering Sea at ca. 52°40'N, 180°.

TABLE 27.—Miscellaneous sight records of Laysan Albatrosses from the eastern North Pacific. (observers, except one, from University of Washington)—continued

Date	Location	No. of birds	Observer	Remarks
25 Aug 57	51°02'N, 171°45'W	1	P. McCrery	" "
13 Sep 57	52°58'N, 150°34'W	1	" "	" "
14 Sep 57	51°53'N, 150°42'W	1	E. Linger	" "
2 Apr 57	55°30'N, 139°00'W	3	unknown	
3 Apr 57	54°20'N, 135°00'W	1	"	
13 Jan 61	48°10'N, 126°42'W	2	C.M. Love	
16 Jan 61	46°22'N, 129°30'W	3	" "	
27 Jan 62	46°41'N, 126°40'W	1	K. Lightwood	
10 Oct 62	42°21'N, 125°25'W	1	C.M. Love	
1 Mar 63	48°14'N, 126°46'W	2	" "	
1 Mar 63	48°13'N, 127°45'W	1	" "	
9 Mar 63	45°34'N, 129°30'W	1	" "	
11 Mar 63	44°16'N, 127°24'W	1	" "	
15 Oct 66	47°04'N, 130°08'W	1	J. Nickerson	
15 Oct 66	46°53'N, 130°31'W	1	R. Robeck	
16 Oct 66	47°00'N, 132°10'W	1	D. Armand	
16 Oct 66	47°00'N, 132°00'W	2	" "	
18 Oct 66	47°00'N, 132°00'W	1	J. Nickerson	
19 Oct 66	47°00'N, 132°00'W	2	D. Armand	
20 Oct 66	46°55'N, 132°12'W	2	" "	
23 Oct 66	46°55'N, 132°00'W	3	" "	
24 Oct 66	47°00'N, 132°03'W	4	" "	
24 Oct 66	47°00'N, 132°00'W	3	R. Robeck	
26 Oct 66	47°00'N, 132°00'W	4	D. Armand	
27 Oct 66	47°00'N, 132°00'W	3	R. Robeck	
30 Oct 66	47°30'N, 129°45'W	2	D. Armand	
13 Nov 66	48°00'N, 131°52'W	2	" "	
14 Nov 66	47°45'N, 131°55'W	2	" "	
19 Dec 66	48°10'N, 125°41'W	1	" "	ca. 35 mi off Cape Alava, Washington
21 Dec 66	46°03'N, 126°40'W	1	" "	
27 Sep 67	53°30'N, 162°00'W	2	V. Wyatt	
29 Sep 67	52°30'N, 160°00'W	2	J. Nickerson	
29 Sep 67	52°07'N, 159°20'W	2	V. Wyatt	
5 Oct 67	50°00'N, 137°00'W	1	" "	
6 Oct 67	47°33'N, 133°00'W	1	" "	
7 Nov 67	48°25'N, 129°18'W	4	" "	

*California Academy of Sciences.

September Distribution (Figure 89): None were seen in the central Pacific or off southern California; one was seen some 35 miles off central California (Robert C. Miller, California Academy of Sciences, pers. comm.). The species was common in the western Aleutians and in the western Gulf of Alaska (1955, 1957).

October Distribution (Figure 90): None were seen in the central Pacific nor off southern California again this month. Off Washington and Oregon, however, Laysans were common in densities of up to 4.0 BPS. One was noted 75 miles off Washington, but most were much farther offshore. South of the western Aleutians, they were common and ex-

tremely abundant. A center of abundance was noted at ca. 45°N, 173°E, where densities of 20 and 30 BPS were recorded on two consecutive days. These are high records for pelagic areas away from breeding islands.

November Distribution (Figure 91): One bird was observed in the central Pacific near Kaula Rock (21°45'N, 160°30'W), but no surveys were conducted in the Leewards. Single birds were seen on three days off southern California and the species was common to abundant to 138°W in areas farther than 150 miles off the Washington and Oregon coasts.

December Distribution (Figure 92): Laysan Alba-

trosses were abundant (up to 10.0 BPS) in the western Leewards, but only scattered sightings were made south to 13°37'N in the central Pacific. Only on 3 out of 33 days were they seen off southern California. Off Washington and Oregon, single birds were noted on two out of an unspecified number of days; one was a scant 35 miles off Cape Alava, Washington.

ANNUAL PELAGIC CYCLE

The appearance of Laysan Albatrosses in pelagic areas of the central Pacific in late November corresponds to their arrival on the breeding islands. Numbers increase at sea around the breeding islands in December and scattered birds are recorded to almost the southern limits of their central Pacific range. From December through May they are seen, though uncommonly, in pelagic areas south to 13°N, with February being the month of peak abundance south of 20°N and the month of most southerly penetration. Birds begin to leave the central Pacific in May and by July and August there is only an occasional bird seen in the northern Leewards. They are unrecorded in September and October. This seasonal shift in distribution is illustrated in Figure 78. It can be seen that this north-south shifting of birds is synchronized across the central and eastern Pacific. The northern range limits also retreat southward in winter, but this is neither as pronounced nor as well documented as it is in the central Pacific.

The occurrence of Laysan Albatrosses in the Gulf of Alaska also appears to be cyclic, with spring being the season of maximum abundance and northward penetration. A few birds occur in the southern part during winter. As spring approaches they move northward and by May can be found in the northernmost part of the Gulf. As summer approaches, they move westward out of the Gulf, and are found with any regularity only west of 160°W; most of the population apparently occurs west of 180°. Thus, the westward movement out of the Gulf of Alaska corresponds to the late spring movement away from British Columbia, Washington, and Oregon (Sanger, 1970).

ABUNDANCE AT WEATHER STATION *Victor*

Figure 79 presents counts of Laysan Albatrosses made by personnel of the USCGC *Winnebago* at

Ocean Station Victor (34°N, 164°E), from 26 February through 19 March 1967. The maximum number of birds seen at any time during the day (upper graph) ranged from none on 17 March to a high of 27 on 15 March. Most counts revealed no more than 14 birds. The maximum number of birds during the day usually occurred in the afternoon (1600), although the high counts were in the morning on three days. This suggests that Laysans were less inclined toward a regular daily activity cycle than Black-footed Albatrosses, who never displayed maximum numbers in the morning in the same area.

BAND RETURN INFORMATION

Routine monitoring of banded birds during surveys of the breeding colonies on the leeward Hawaiian Islands has documented numerous inter-island movements of Laysans. Most of these involve birds moving the short distance between Kure and Midway Atoll, or between Kure and other Leeward locations. Only one bird has been recaptured on land away from the breeding islands. This specimen, banded as an adult on Kure Island, was recovered on Mejit Island (ca. 10°30'N, 171°00'E), Marshall Islands, on 20 May 1965 (Amerson, 1969: 293), but must be regarded as a stray in this extralimital location. This represents the southernmost specimen record for this species.

The ~~POBSP~~ Laysan Albatross band returns are being integrated with those of the U.S. Fish and Wildlife Service (Robbins and Rice, p. 234, herein). Pertinent highlights of this information are summarized here. Recoveries of subadult birds (through the fifth year of life) suggest that they are more inclined to be scattered longitudinally than adult birds, but most recoveries were west of 180°. More than half of the summer adult recoveries occurred between 170°E and 180°, in and just south of the western Aleutian Islands. Almost all of the summer adult recoveries were from north of 40°N between Japan and the Aleutians. In winter, the adult recoveries were mainly south of 40°N, scattered between Honshu, Japan, and Midway Atoll.

Analysis of Distribution

GENERAL CONSIDERATIONS

Two major trends are apparent in the gross distribution of the Laysan which are similar to those

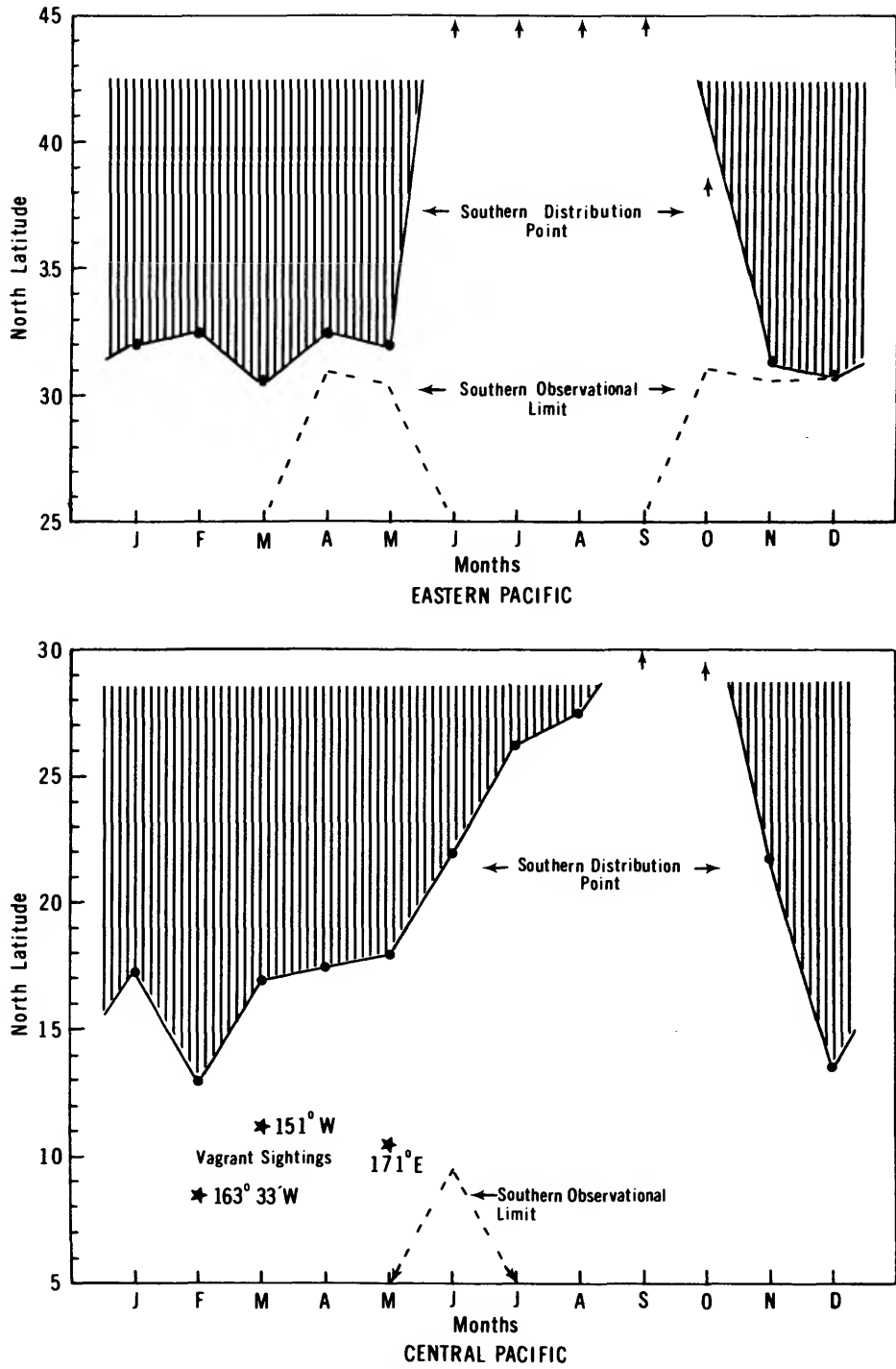


FIGURE 78.—Seasonal and latitudinal shifting of Laysan Albatrosses in the central and eastern Pacific Ocean.

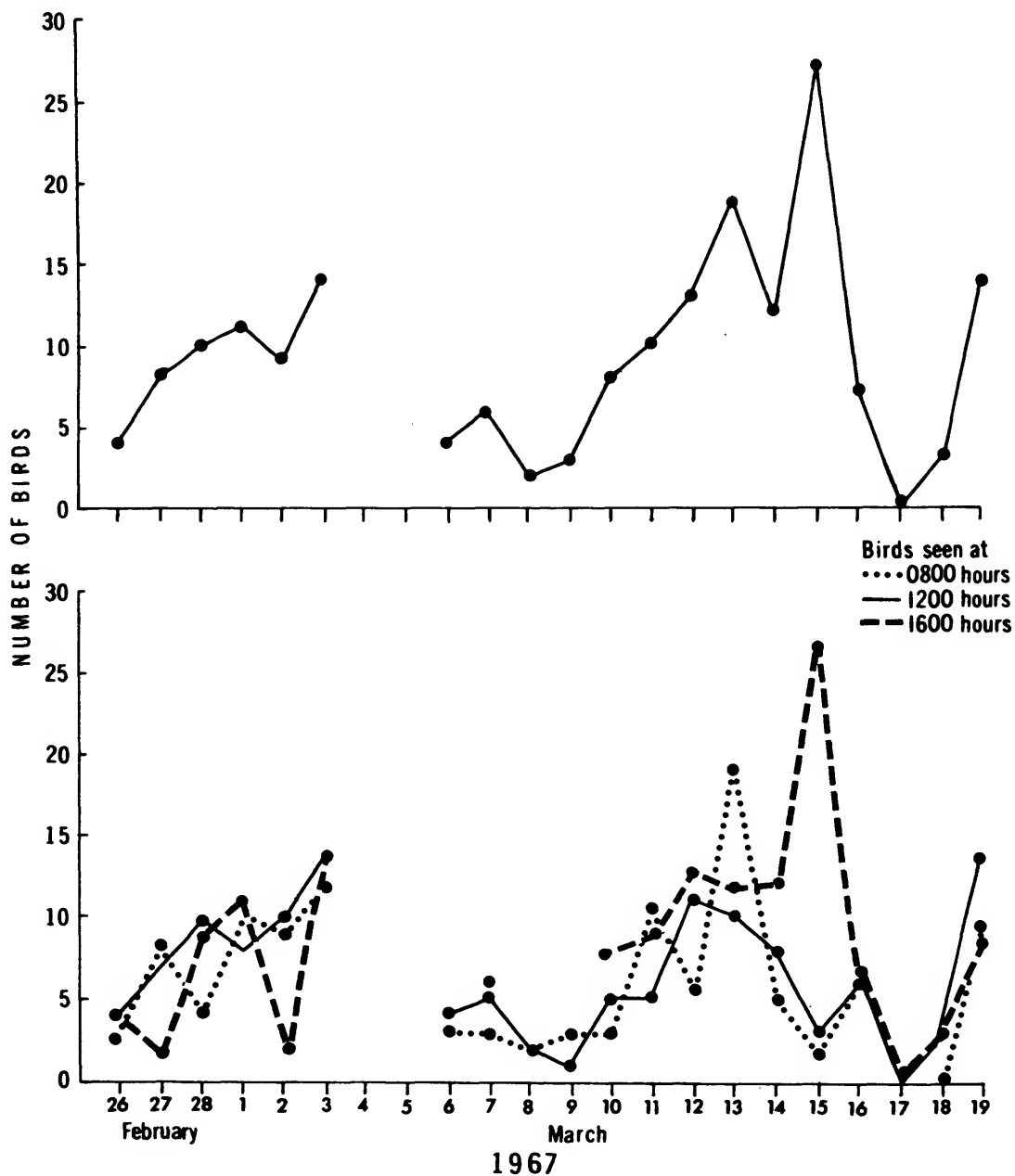


FIGURE 79.—Counts of Laysan Albatrosses made by personnel of the USCGC *Winnebago* at Ocean Weather Station *Victor* (34°N, 164°E) 26 February through 19 March 1967.

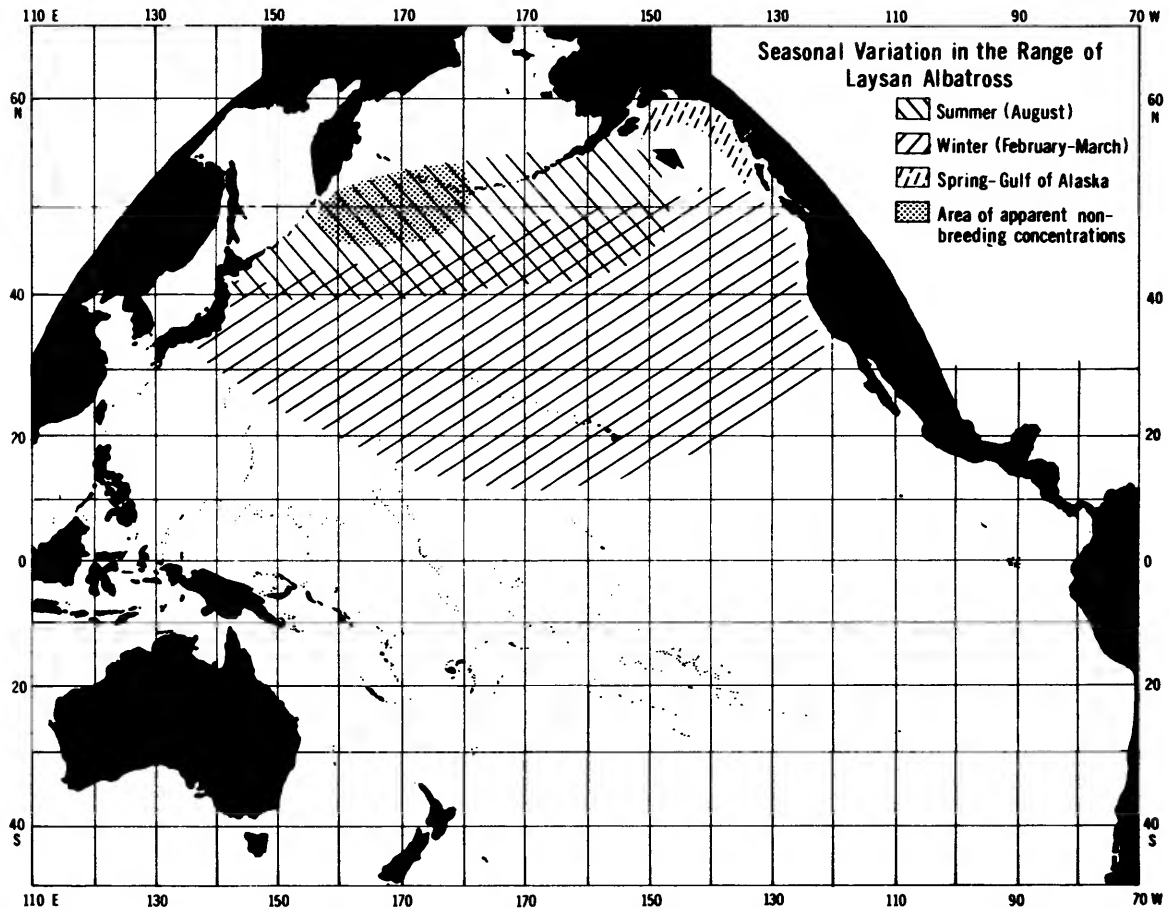


FIGURE 80.—Seasonal variation in the range of the Laysan Albatross.

of the Black-footed Albatross. First, there is a major latitudinal population shift concurrent with the winter breeding season (Figure 80). In summer, they are fairly far north in the Pacific, apparently concentrated off the Kuriles and in the Aleutian Islands. During the winter breeding season, their range shifts considerably farther south (to 13°N). Rare birds have been seen at 11°N (King, 1970:9) and 8°30'N (Thompson, 1951) in the central Pacific Ocean. The second major distributional feature is that the Laysan is predominantly a western and central north Pacific species, in contrast to the Black-footed Albatross which has a more even or eastern distribution.

The movements of breeding adults and older im-

matures are directed toward the breeding grounds in late fall, and away from the breeding grounds and toward feeding areas early the following summer. Moreover, about half of the breeding birds are away from the breeding grounds at any given time during the breeding season; indeed, the recovery of a breeding bird over 2000 miles away 23 days after being banded on its nest shows that breeding birds can range well away from the breeding grounds (Kenyon and Rice, 1958). Curiously, the breeding season range is much broader than that of the nonbreeding season. In winter, Laysans are uncommon off North America from northern Baja California to southern British Columbia, and off Japan as far south as Kyushu. These

birds are no doubt mostly prebreeding immatures, but probably include some adult breeders. Kenyon and Rice (1958) demonstrated the amazing ability of this species to cover vast distances in relatively short periods of time, despite adverse weather conditions.

Banding returns indicate that the postbreeding dispersal of adults and fledged young takes them northwestward from the breeding grounds. Pobs sightings for September and October 1964–1965 indicate that maximum numbers of Laysans may occur in the Aleutians in late summer and early fall. Therefore, the occurrence of Laysans off Japan in summer may be because of a curvilinear migration route to the Aleutians.

DISTRIBUTION IN RELATION TO THE ENVIRONMENT

CURRENTS AND WATER MASSES.—As in the case of the Black-footed Albatross, the gross distribution of the Laysan Albatross (Figure 80) is similar to the distribution of certain major currents and water masses. Winter distribution seems generally to parallel the circulation of the north Pacific cyclonic currents, but individuals wander north of the West Wind Drift and south into the Equatorial Counter-current. Concentrations of birds in summer are apparently mostly within the western Subarctic and Alaskan Gyres, and north of the West Wind Drift (see Dodimead, et al., 1963, for descriptions of these currents and water masses). Summer distribution seems to conform to the Kurilo-Aleutian surface water mass (Muromtzev, 1958:248) with some birds being found in the western part of the "Alaska Bay (=Gulf) surface water." Distribution off Japan (Kuroda, 1960; Robbins and Rice, pp. 236–237, herein) relates well to the Kuroshio-Oyashio convergence, with no birds being found in the warm Kuroshio Current in summer.

SURFACE WATER TEMPERATURE.—The maximum surface water temperature tolerated by most of the population seems to be about 21° to 24°C (70°–75°F) in the central Pacific in winter. In summer, individuals occur as far south as 35°N, where the surface temperature would again be in the 21° to 24°C range (Muromtzev, 1958, fig. 112). However, the surface water temperatures in the western Aleutians, where most of the population apparently summers, is moderately cold, about 8° to 10°C (Muromtzev, 1958, fig. 112). Kuroda (1960)

suggested that the Laysan is the most cold-adapted albatross in northwest Pacific waters. When the Laysan occurs off Washington and Oregon in winter, the surface water temperature generally ranges from 8° to 10°C. Within an observed annual range of about 7° to 17°C in this area, Laysans were found to occur most often in relatively low temperatures, and only three times (all during the same cruise) in water warmer than 14°C (Sanger, 1970). King (1970) noted that albatrosses (both Laysan and Black-foot) were seldom found in water warmer than 23°C in a survey area east and southeast of the main Hawaiian Islands (the data from which are included in this report). As long as the birds are within their physiological temperature tolerances, distribution will probably be dictated by the distribution of preferred food organisms and not by water temperature per se.

AIR TEMPERATURE.—The limits of the Laysan's range seem to parallel the isotherms of about 5° and 24°C regardless of season. The 24°C (75°F) isotherm lies at about 20°N latitude in March and at about 40°N latitude in August in the central Pacific (U.S. Navy, 1956). Both of these latitudes appear to be the southerly limits of most of the Laysan population during the respective seasons (see Figures 81–92). The temperature tolerance of this species is conjectural at this point, but the species has been seen in temperatures ranging from 4.8°C in the Gulf of Alaska in February 1967 to as high as ca. 26°C in the central Pacific (King, 1970:89). Kuroda (1960) observed that Laysan Albatrosses preferred 13° to 15°C temperatures within a range of 6.2° to 22.5°C in the summer in northwest Pacific waters. In waters off Washington and Oregon, Laysans were encountered most often when the air temperature was less than 10°C in an annual range of 6.6° to 18.0°C (Sanger, 1970).

SURFACE SALINITY.—The distribution of Laysans indicates that they occur in waters with moderate to high salinities, and only rarely in low salinity water (less than 32.5–33.0‰). The surface salinity in areas of Laysan Albatross concentrations, i.e., west of 180° and north of 40°N, generally ranges from 33–34‰ (Muromtzev, 1958:374). Seasonal data from off Washington and Oregon show that, indeed, Laysans may avoid relatively low salinity water (Sanger, 1970). In summer, when Laysans are well away from the coast, salinity of less than 32.5‰ (resulting from runoff from the Columbia

River) has been traced westward to nearly 132°W off Oregon (Budinger, et al., 1964:52). Coincidentally, there is no such offshore area of low surface salinity in the northwest Pacific. In winter, prevailing south and southwesterly winds off the Washington-Oregon coasts tend to hold river runoff within a relatively few miles of the coast (Budinger, et al., 1964:69), allowing a maximum eastward invasion of oceanic water toward the coast via the California Current. It is at this time that maximum abundance of Laysan Albatrosses occurs in the area and they occur closest to shore (see Figures 81, 91). In the central Pacific, albatrosses tended to be found in higher salinity water within a range of 33.9‰ to 35.2‰ (King, 1970:96).

WEATHER CONSIDERATIONS.—As in the case of Black-footed Albatrosses (see p. 113), wind is probably the most significant feature of the weather affecting Laysan distribution. The doldrum wind conditions no doubt play a significant role in limiting the southern distribution of the Laysan Albatross.

Addendum

After this paper was completed in 1968, two important papers on the pelagic distribution of Laysan Albatrosses were published, those of V. P. Shuntov (1968) and Fisher and Fisher (1972). Generally, these authors indicate the same distribution patterns reported here, but with certain notable exceptions.

Shuntov, using sightings at sea, has Laysans ranging much farther north in winter than our data indicate, to about 59°N in the Gulf of Alaska, and to about 55°N in the western Bering Sea. Also, contrary to our sightings and those in the literature, Shuntov has Laysans ranging south to only about 21°N in the central Pacific. In summer, he shows Laysans ranging well into the Sea of Okhotsk and north in the western Bering Sea to the Gulf of Anadyr.

The Fishers' paper is based on 109 captures at

sea of birds banded on Midway Island and most of the sightings noted in the literature; omitted for unknown reasons are Sanger's (1970) records off Washington and Oregon. These omissions cast some doubt on the validity of the graphs (Fisher and Fisher, 1972: figs. 3, 5, 7) portraying average monthly longitudinal and latitudinal movements, as does the lack of statistical treatment of the data in the graphs. The inclusion of standard deviations of the means shown in the Fishers' figures 3 and 5 would have given an idea of how representative the means really are. Puzzling is the contention (Fisher and Fisher, 1972:8) for "a probable similarity in the distribution of tunas and albatrosses in the North Pacific. . . ." The facts are that tuna range far south of the southern limit of the Laysan's range (cf., Rothschild and Uchida, 1968), and that Laysans range far north of the northern limits of tuna distribution. The northern part of the tuna range and the southern part of the Laysan's range merely overlap. Fisher and Fisher's (1972:16) curious reference to Seckel's (1970) discussion of weather-sea surface interactions in the area from 0° to 35°N, and 130°W to 170°W, for documenting "turbulence and many eddies between 35° and 40°N and 140° to 160°E," and their erroneous view that warm oceanic waters have low salinity (Fisher and Fisher, 1972:17, 23), suggests that more rigor might have been applied in discussing oceanographic matters. The question raised by the authors of whether their data reflected the distribution of albatrosses or of persons recapturing albatrosses never was convincingly answered, especially in view of the disparity in the distribution of albatrosses and tuna (and therefore tuna fishermen). Longline tuna fishing is by far the most susceptible means of capturing albatrosses at sea because the birds actively go after the baited hooks. These and other flaws notwithstanding, the Fishers have presented an important, useful document, all the more so because they have given evidence for differences in the at-sea distribution of young and adult Laysan Albatrosses.

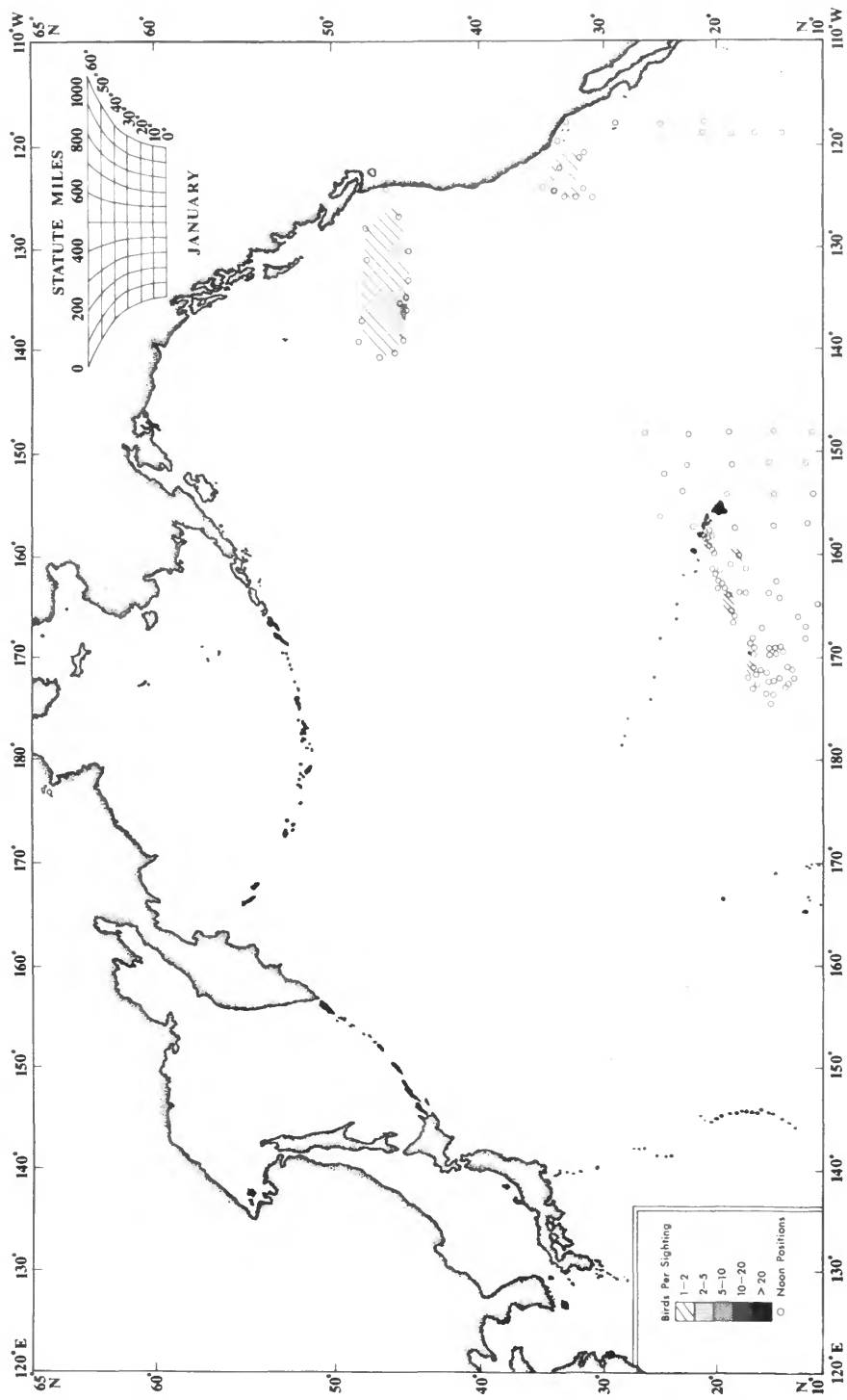


FIGURE 81.—Distribution and density of Laysan Albatrosses in the Pacific Ocean in January.

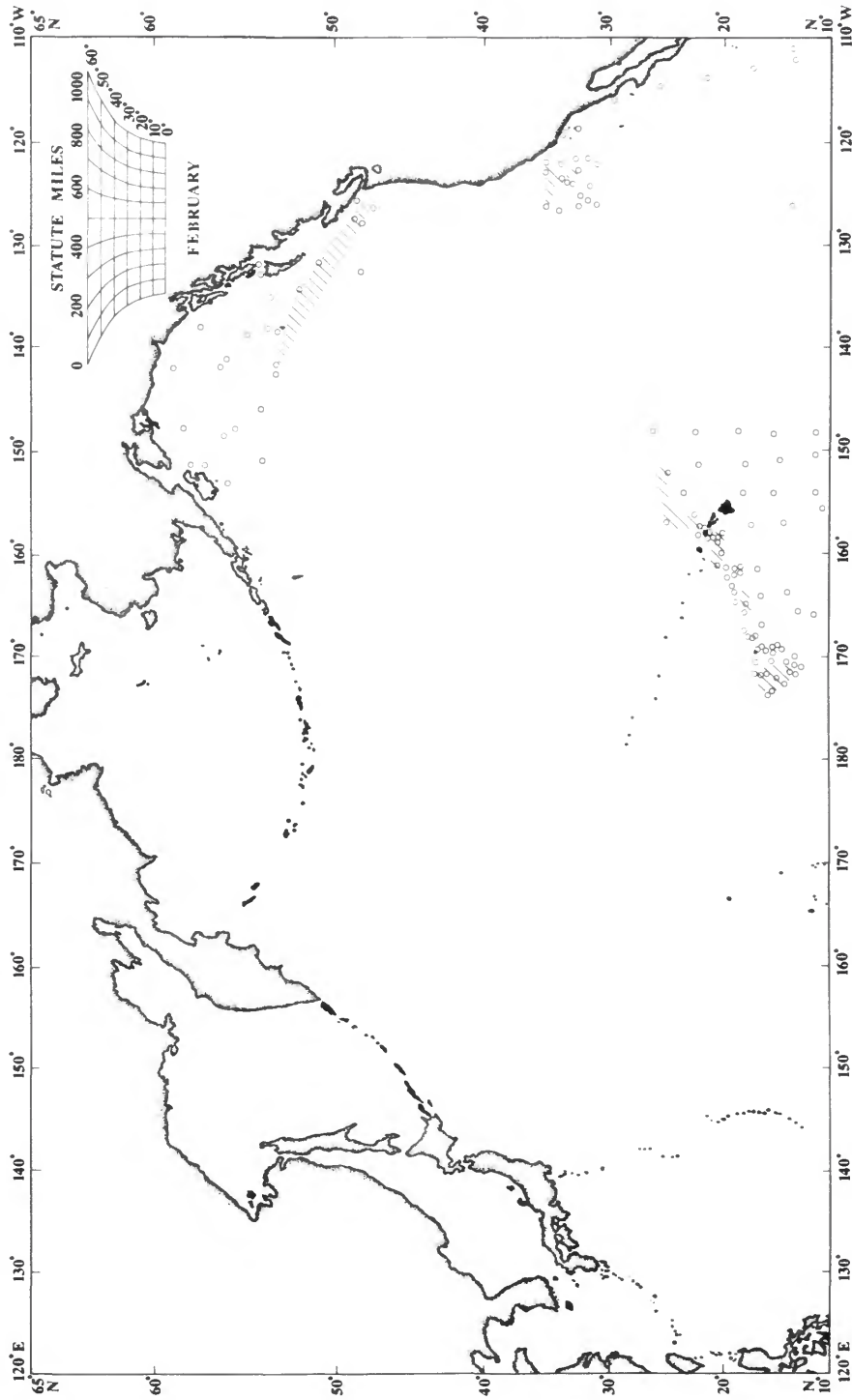


FIGURE 82.—Distribution and density of Laysan Albatrosses in the Pacific Ocean in February.

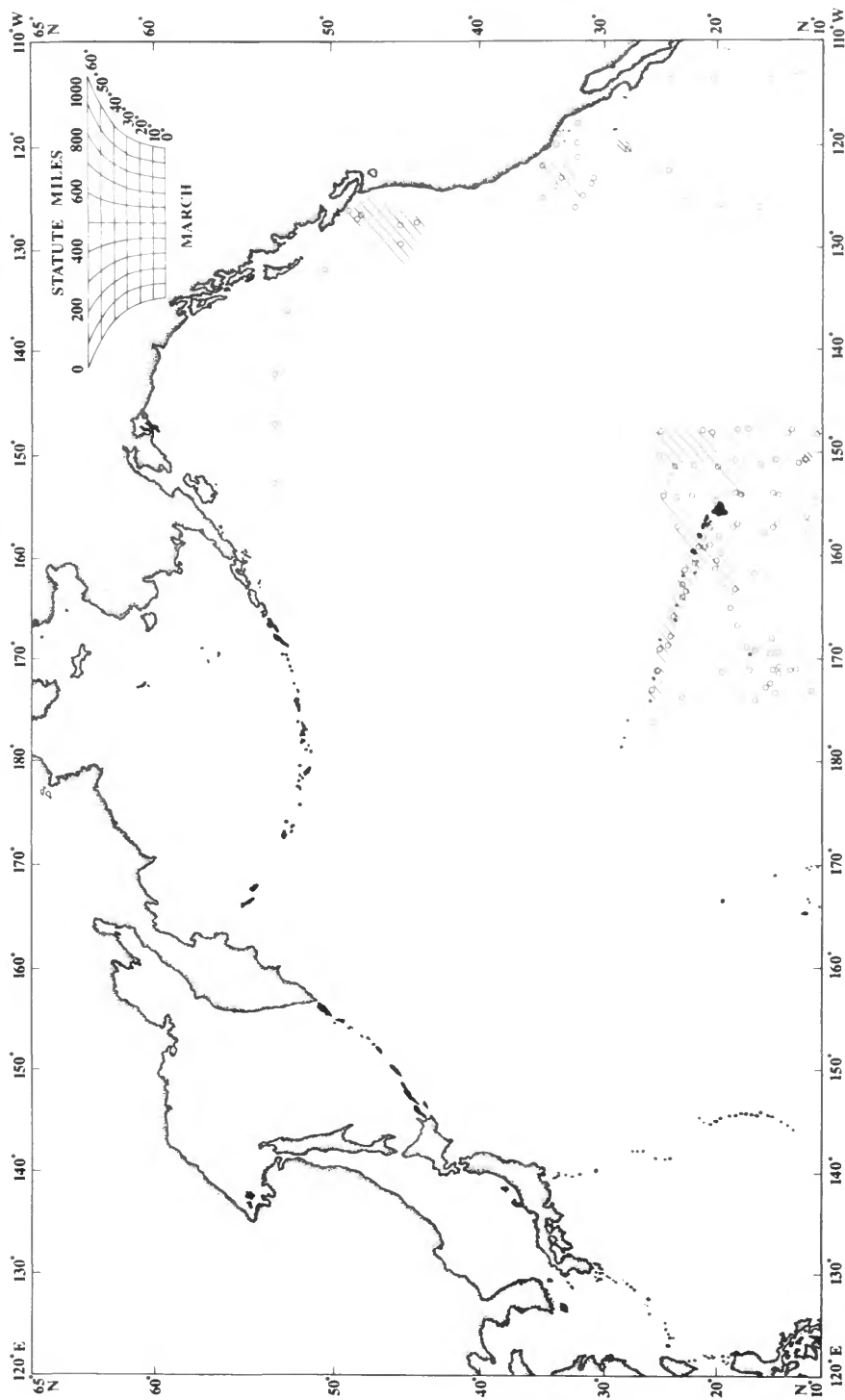


FIGURE 83.—Distribution and density of Laysan Albatrosses in the Pacific Ocean in March.

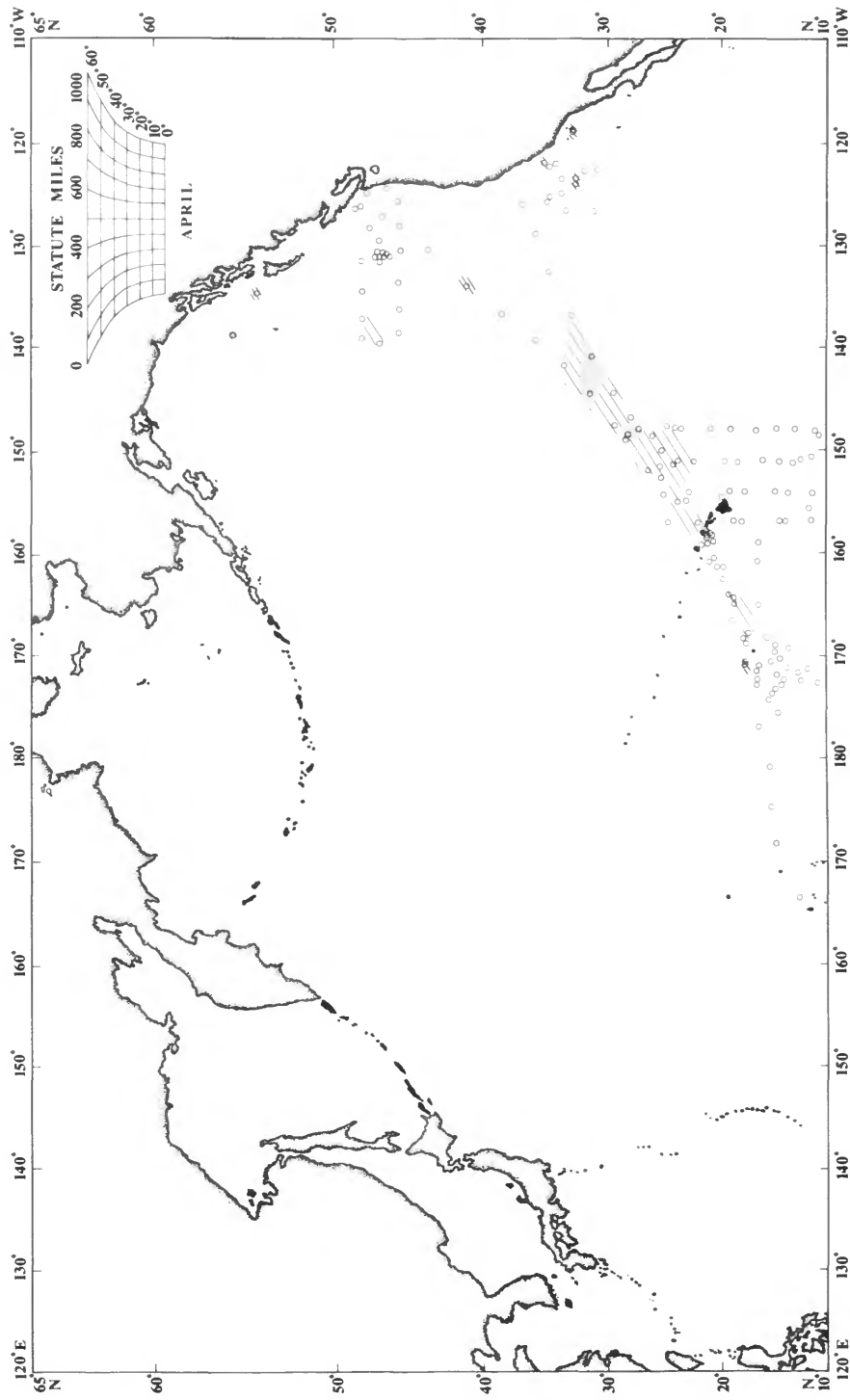


FIGURE 84.—Distribution and density of Laysan Albatrosses in the Pacific Ocean in April.

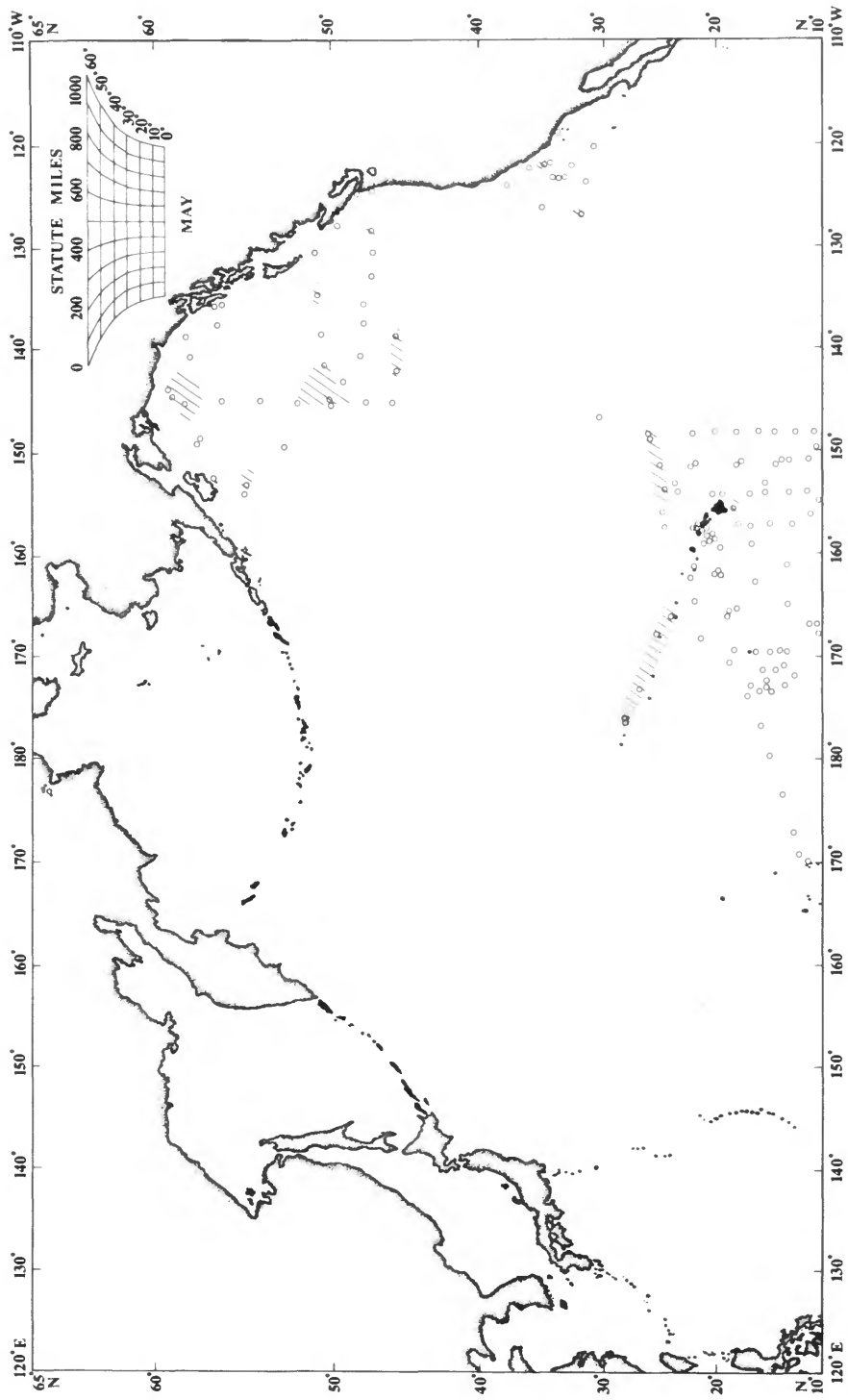


FIGURE 85.—Distribution and density of Laysan Albatrosses in the Pacific Ocean in May.

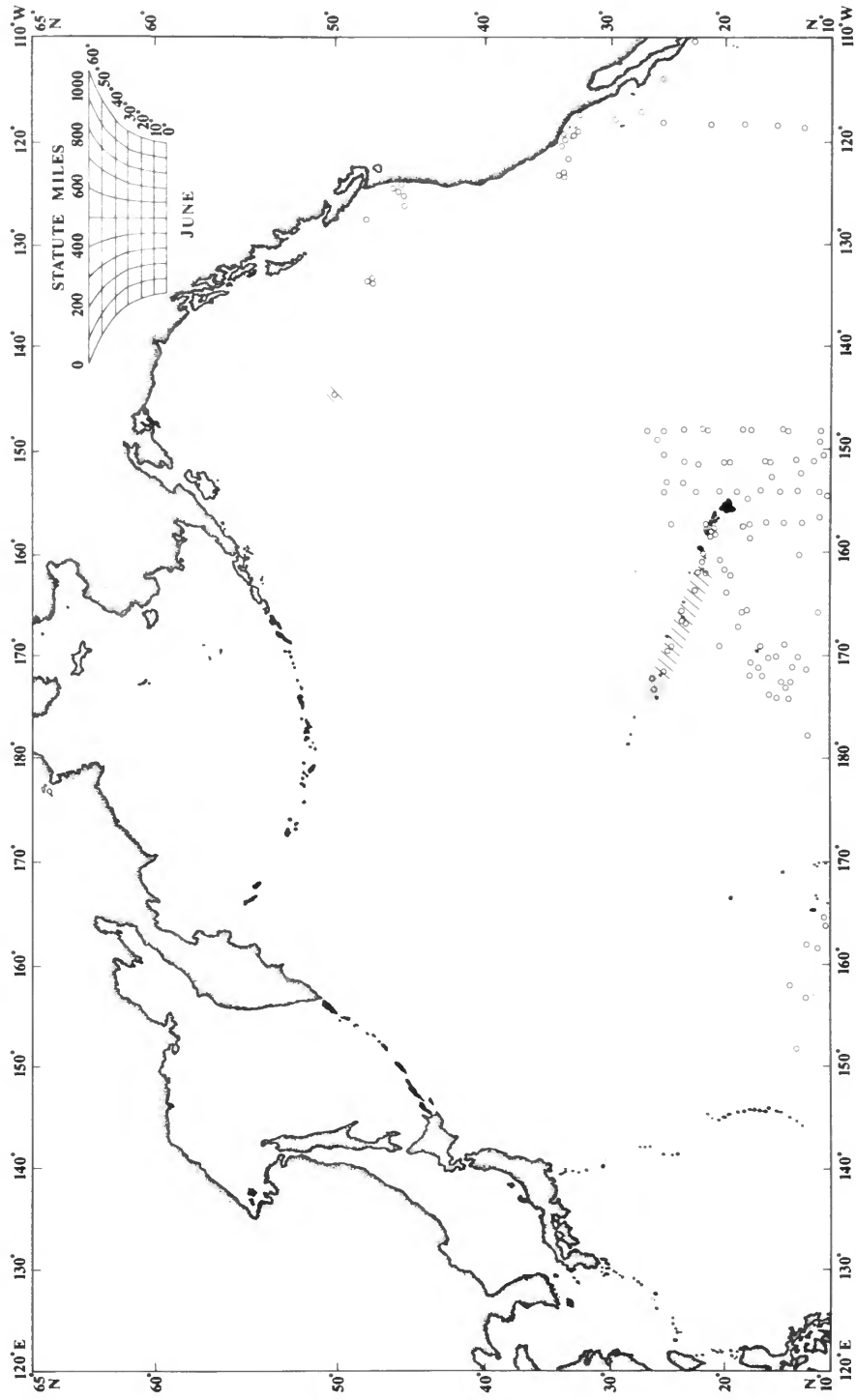


FIGURE 86.—Distribution and density of Laysan Albatrosses in the Pacific Ocean in June.

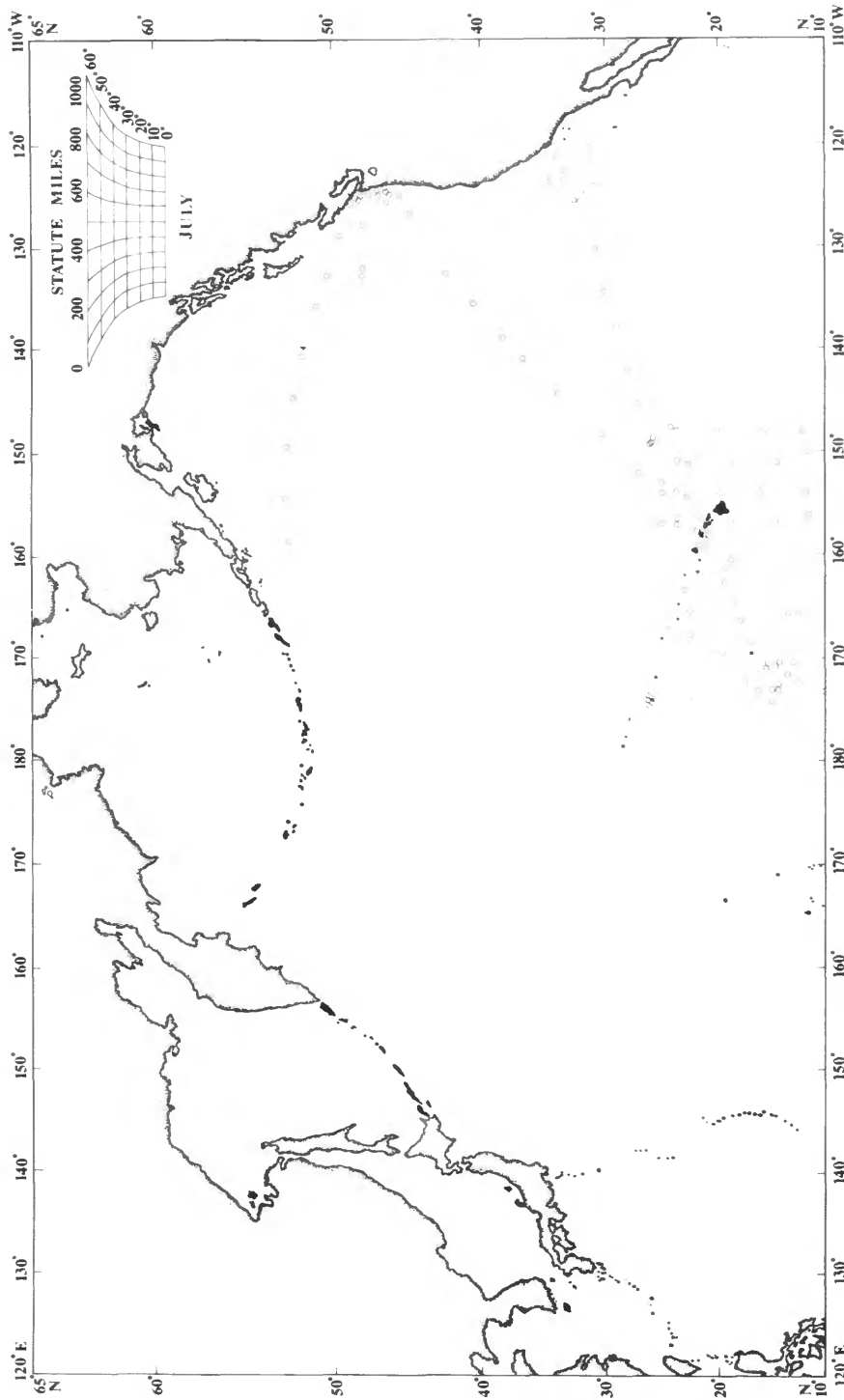


FIGURE 87.—Distribution and density of Laysan Albatrosses in the Pacific Ocean in July.

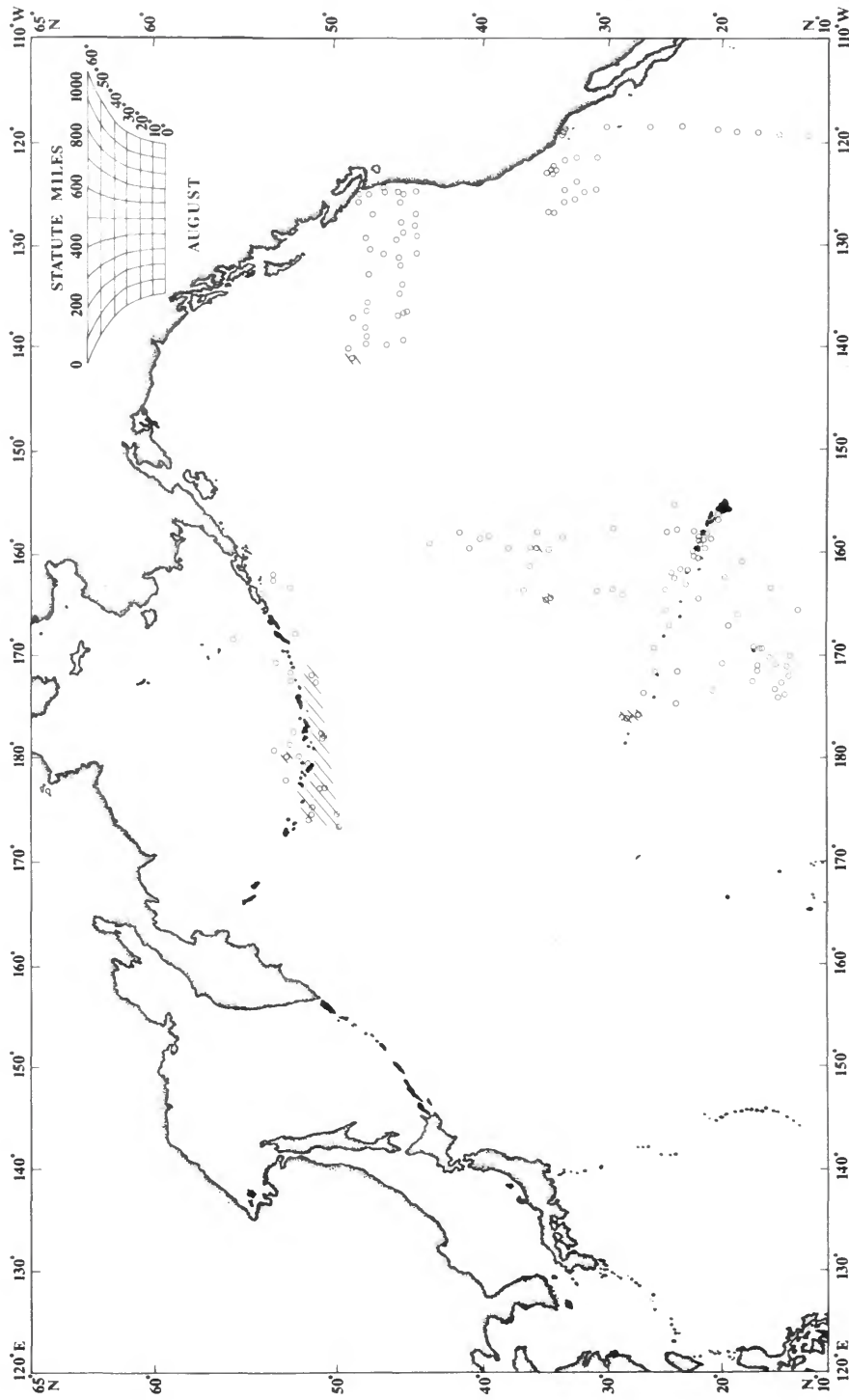


FIGURE 88.—Distribution and density of Laysan Albatrosses in the Pacific Ocean in August.

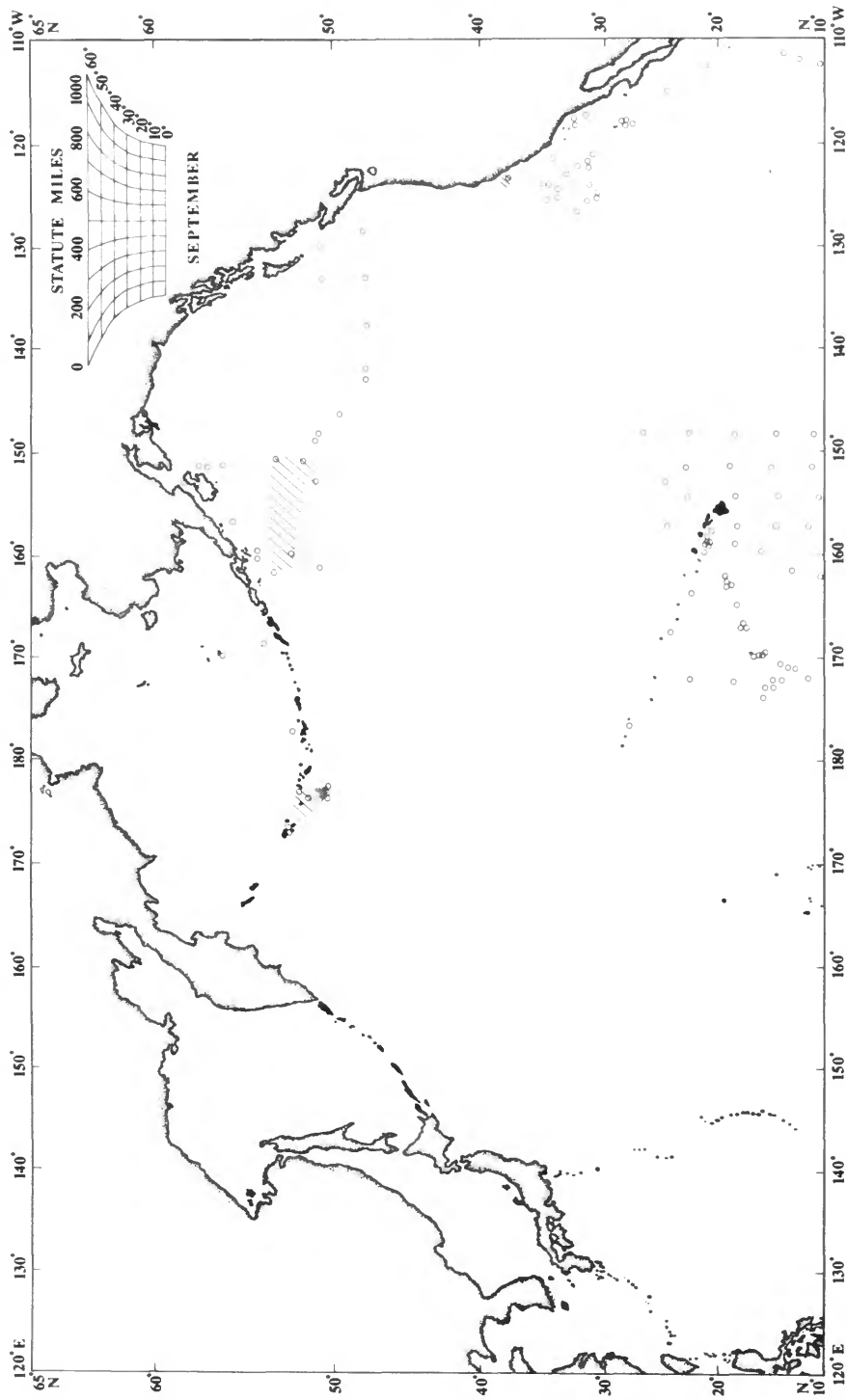


FIGURE 89.—Distribution and density of Laysan Albatrosses in the Pacific Ocean in September.

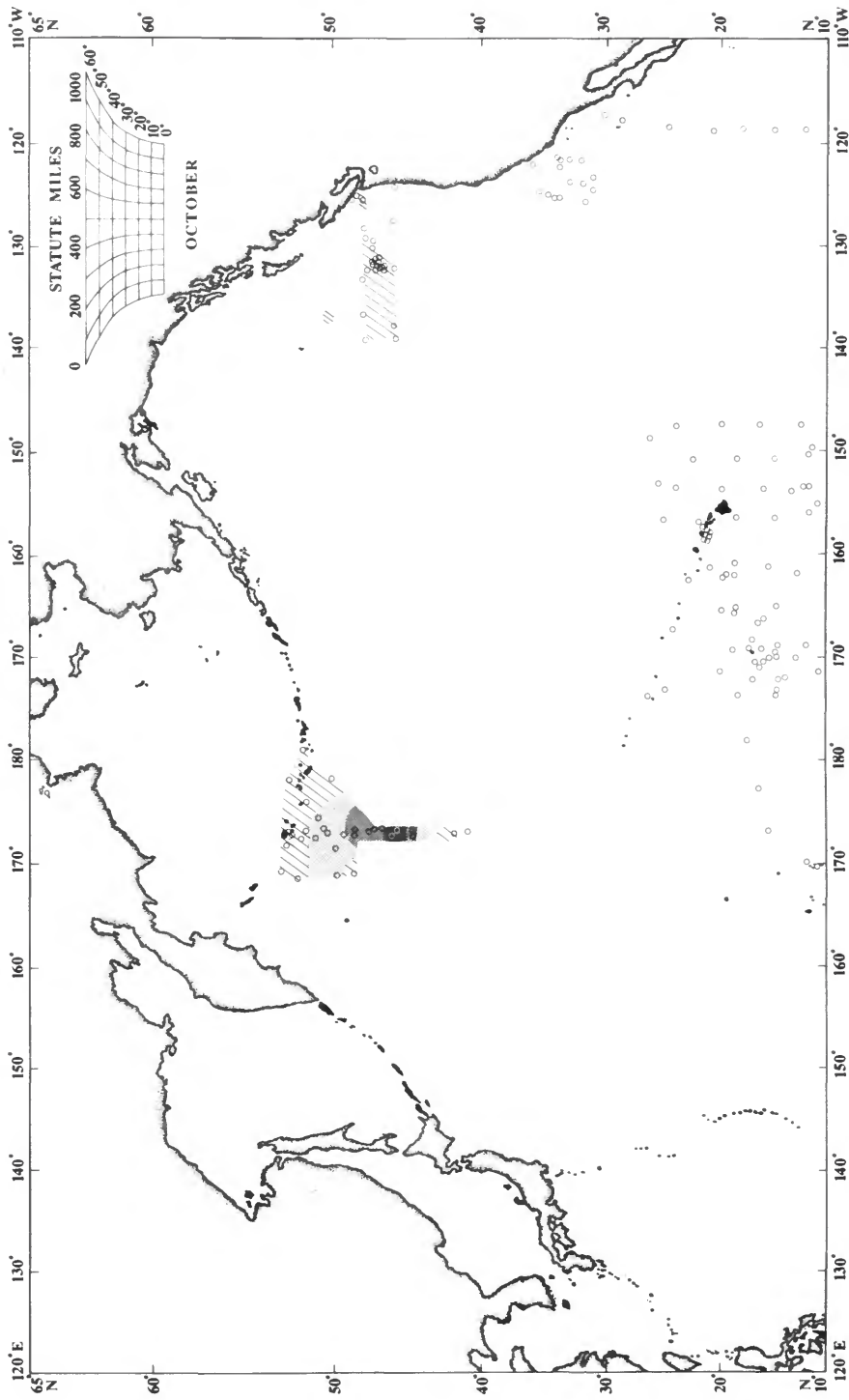


FIGURE 90.—Distribution and density of Laysan Albatrosses in the Pacific Ocean in October.

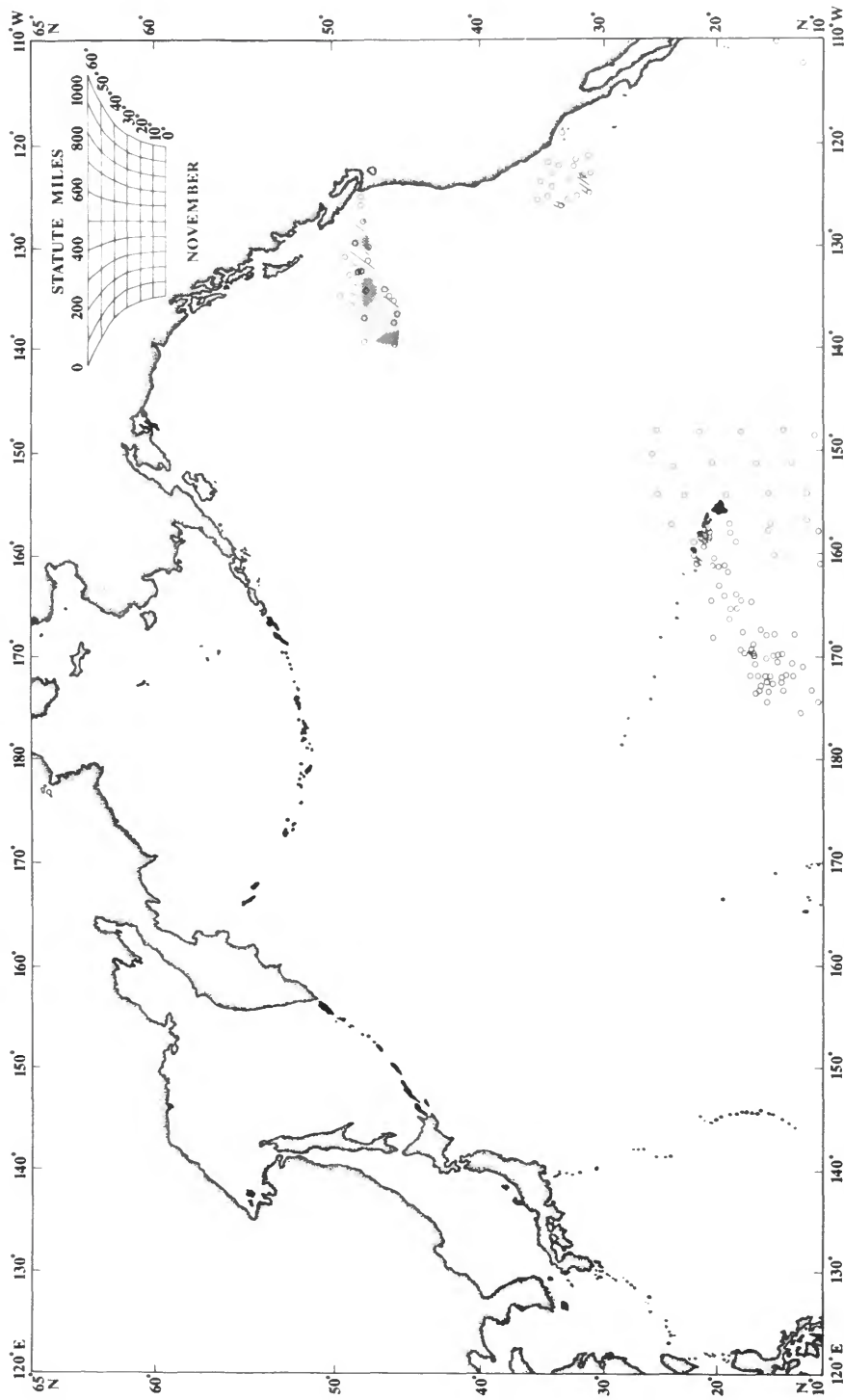


FIGURE 91.—Distribution and density of Laysan Albatrosses in the Pacific Ocean in November.

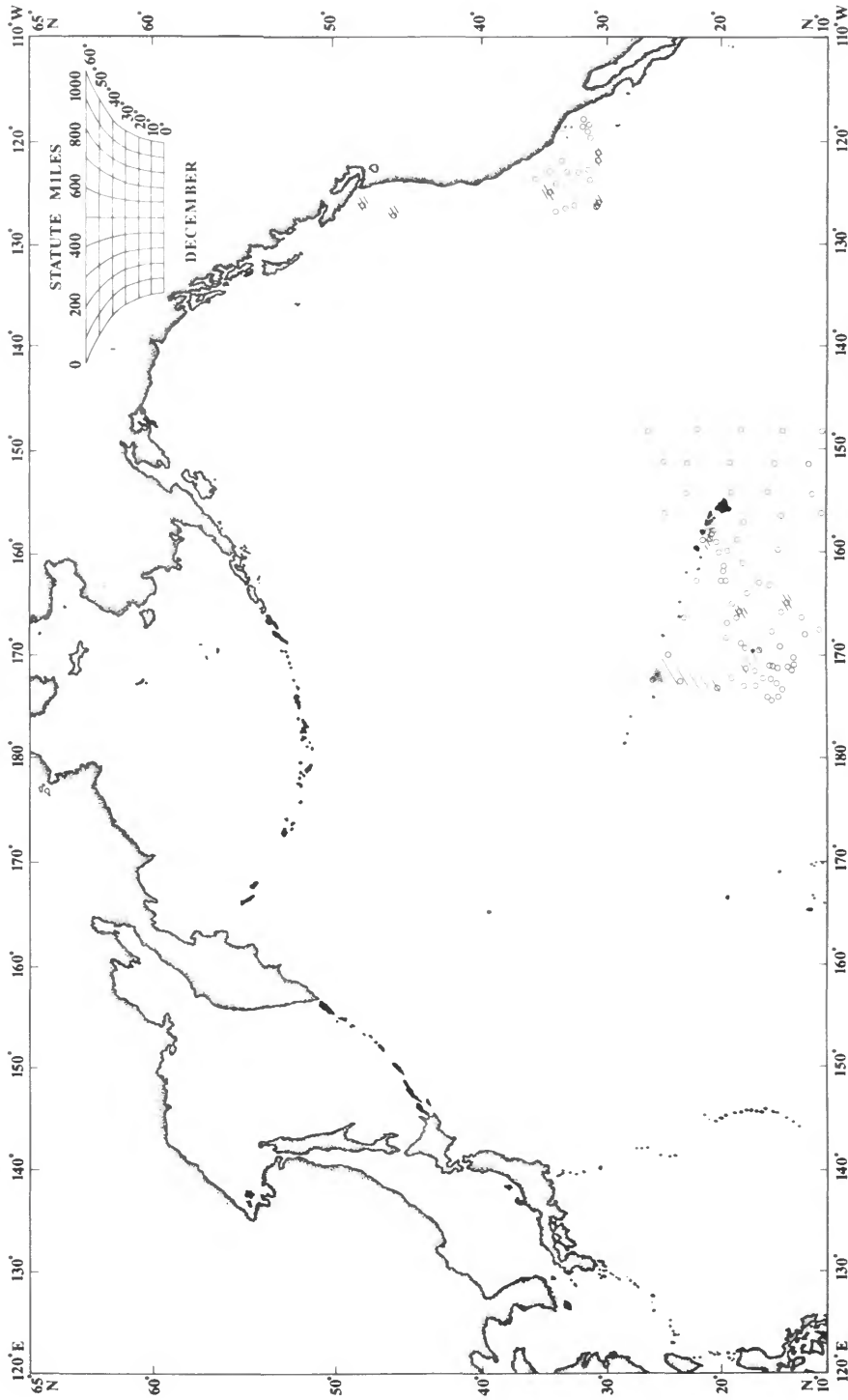


FIGURE 92.—Distribution and density of Laysan Albatrosses in the Pacific Ocean in December.

Appendix

Summary of published data on Laysan Albatross distribution

<i>Location</i>	<i>Date</i>	<i>Remarks</i>	<i>Source</i>
NORTHEAST PACIFIC			
Various sites in the Aleutians, three Gulf of Alaska sightings	May-Oct	possible confusion of early records with Short-tailed Albatross	Murie, 1959:39-40
230 mi E Kodiak I., Alaska	13 Oct 48	individual followed ship for several hours; ship's captain quoted as often seeing Laysans in same area	Kenyon, 1950:100
Various sites in Aleutians	Jun, Jul	sight and specimen records; possibility of several Short-tailed Albatross sightings being Laysans	Gabrielson and Lincoln, 1959:75
90 mi S of Aleutians at 49°51'N, 178°22'W	28 Mar 51	1, apparently the northernmost record for the central North Pacific at this early date	MacDonald and Lawford, 1954:16
Off Vancouver I.	25 Dec 52	2 at 48°N, 133°W, was closest sighting to North America	Poole, 1966:71-72
" " "	10 Dec 53	3 at 49°N, 133°W, were the most seen off North America at this latitude; generally scarcer in NE Pacific than NW Pacific	" " "
Off Washington, Oregon and Vancouver I.	24-27 Feb 58	6 sightings of 1-3 individuals, 60-100 mi off northern Washington and southern Vancouver I.	Sanger, 1965:1-2
Off Washington and Oregon	May 64-Nov 65	comprehensive seasonal data; see text herein	Sauger, 1970:342-343, 349-352
100 mi off Washington to Oahu	Feb 51	seen less often and in fewer numbers than Black-footed Albatross	MacDonald and Lawford, 1954:15-16
50°N, 173°W	23 Sep 54	12 this date; place was maximum for general area; seen north of 52°N several times	Poole, 1966:71-72
48°N, 150°W to 30 mi NW of Farallon I.	30 Nov-6 Dec 48	seen every day during this period; 1 collected 40 mi off northern California	Kenyon, 1950:100
47°15'N, 126°45'W	1 Dec 45	1	Thompson, 1951:234
Along 47°N at 155° and 178°W	Aug 59	155°W, apparently near eastern limits of summer range	Nakamura, 1963:239-245
45°36'N, 124°36'W	1 Oct 63	1	Sanger, 1965:1-2
45°14'N, 127°31'W	16 Mar 63	2	" " "
44°45'N, 132°00'W	16 Dec 63	1	" " "
44°10'N, 135°45'W	15 Dec 63	1	" " "
44°10'N, 132°W	30 Nov 45	2	Thompson, 1951:234
41°N, 137°30'W-24°30'N, 155°W	16-20 Jan 60	"Two or three were always present"	Agnew, J. H. <i>in</i> Bourne, 1961:12
40°32'N, 138°17'W	29 Nov 45	1	Thompson, 1951:234
39°40'N, 139°W	29 Nov 45	1	" " "
37°37'N, 124°53'W	25 Jan 45	1	" " "
EAST-CENTRAL PACIFIC			
North America	when not breeding	only southern range limits, i.e. Baja California, specifically mentioned	Vaurie, 1965:19
Within 45 mi of central California coast	Feb-Mar 58	11 sightings 8 Feb-29 Mar as close as 18 mi offshore	Holmes, 1964:302-303
California, far offshore from Cape Mendocino to San Nicolas I.	Oct-Apr	rare or casual visitant; specimen collected San Nicolas	Grinnell and Miller, 1944:41

Summary of published data on Laysan Albatross distribution—Continued

Location	Date	Remarks	Source
Baja California to Oregon	Feb–Apr 49	several sightings by people on oceanographic cruises; unspecified positions and numbers	McHugh, 1950:153–154
San Geronimo, Guadalupe and San Martin, Baja California	no date	formerly fairly common but not recently seen	Friedmann, et al., 1950:15
34°N, 131°30'W	17 Mar 45	2 stayed near the stopped ship for most of one day; crew members saw other white-bodied albatrosses in the area prior to 1945	Yocom, 1947:510
31°47'N–35°31'N, within 100–300 mi of shore	31 Mar–5 Apr 49	scattered singles and doubles	McHugh, 1950:153–154
31°45'N, 129°W	26 Mar 60	1	Agnew, J. H. in Bourne, 1961:12
NORTHWEST PACIFIC			
SE of Kamchatka Peninsula	16 Aug ?	1 obtained in Kamchatka waters	Dement'ev and Gladkov, 1951:347
45°N, 155°E	22 Oct 53	25, maximum number seen at single sighting; generally more common in western Pacific than other areas	Poole, 1966:72
Off Pacific coast of Honshu and Hokkaido	early spring–late autumn	regular and not uncommon visitor; not as plentiful as Black-foot	Austin and Kuroda, 1953:300
Off Hokkaido, Kuriles, and Kamchatka	Jun, Jul 54	maximum number 14 ca. 240 mi S southern tip Kamchatka; other sightings mostly scattered singles; none seen in western Bering Sea; suggested temperature preference is 7°–8°C	Kuroda, 1955:292
40°N, from 165°E to 172°W	6–8 Jun 55	maximum numbers (2.5 per hr) seen at 180°	Hamilton, 1958:160–162
Coastal Honshu, Japan, from ca. 35°N to 38°30'N	Dec 62	second in abundance only to <i>Rissa tridactyla</i> ; winter banding returns for coastal Japan; suggests wintering birds are nonbreeding young	Kuroda, 1963:234
Off Japan	Apr, May 51	more common here at this time than in NE Pacific in previous February	MacDonald and Lawford, 1954:16
36°N, 141°E	10 Jun 53	6, closest sighting to land during 5 trans-Pacific trips	Poole, 1966:71–72
Off Japan 35°37'N, 142°59'E	apparently May 51	westernmost and southernmost position at which sighted	MacDonald and Lawford, 1954:16
Off Japan	not specified	suggests main summer range off Japan as N of 40°N; main winter range S of 35°N (quoted by Kuroda, 1963:234)	Yamashina, 1942:247 [in Japanese]
34°56'N, 157°00'E	22 Aug 60	only time species seen during 36 days at sea, including 2 days off southern and central Japan	Wilhoft, 1961:260
30°N, 154°E	Mar 61	1	Nakamura, 1963:241–243
29°N, 146°E	22 Mar 60	1	Mitchell, J. B. in Bourne, 1961:12
CENTRAL PACIFIC			
33°N, 166°E–23°30'N, 162°W	9–12 Apr 61	regular occurrence in area implied	Lamb, K.D.A. in Bourne, 1961:12
26°30'N, 151°30'W	12 Apr 60	2	Agnew, J. H. in Bourne, 1961:12
22°N, 170°W	Mar 61	1	Nakamura, 1963:241–243
N, S, and E of Hawaii	1964–1965	see text herein	King, 1970:9
17°44'N, 159°56'W	22 May 59	1, apparently southernmost record for month	Peakall, 1960:199
17°30'N, 171°20'W	22 Apr 45	3	Thompson, 1951:234
8°30'N, 163°35'W	1 Feb 45	1, southernmost record for species	" " "

The Storm Petrels (Hydrobatidae)*

Richard S. Crossin

Introduction

The family Hydrobatidae consists of a group of morphologically similar species distributed over most of the pelagic waters of the earth. At least 15 species and a variable number of subspecies (depending upon the reviewer) are found in the areas of the Pacific Ocean covered in the present work. Many of these species are included in the genus *Oceanodroma* which contains groups of sibling species, often only separable with some difficulty in the hand, and presenting considerable problems to the observer in the field. The pelagic ranges, as well as other aspects of the life histories of most of the Pacific forms, are little known; for some species even the breeding grounds are unknown. Austin (1952) discusses the taxonomy and breeding stations of most north Pacific species but deals little with pelagic distribution or other aspects. Palmer (1962) covers those hydrobatids that occur in North American waters, but the pelagic distribution maps are inadequate. In many cases lack of knowledge of pelagic distribution of a species is admitted by placing a large question mark in an area. For other species range maps are presented with little or no information given as to the type of records (specimens, sightings) used to determine the distribution area shown. Murphy (1936) discusses the forms found in waters off the South American continent, as well as many species found to the north. Despite the considerable ornithological work since these volumes were written, there has been little or no new information gained regarding many species of hydrobatids considered therein.

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The major reason for lack of positive knowledge regarding Pacific Ocean hydrobatids is the logistics problem with which the student of these seabirds must contend; the Pacific is a vast area where ports are few and far between, and shipping is primarily restricted to large commercial or military vessels. Harrison (1962) had a rather exceptional opportunity of making seabird observations while aboard Royal Navy ships. King and Pyle (1957), Szijj (1967), and others have gained information while on trans-Pacific research cruises. The unique opportunities of consistent area observation available to the Smithsonian Institution's Pacific Ocean Biological Survey Program (POBSP) during the course of field work from 1963 to 1968 have added a wealth of new information not only on Pacific hydrobatids, but on Pacific seabirds in general.

In this paper I shall not attempt to summarize all information available from other sources on the forms of hydrobatids under consideration. Rather I shall present the recently acquired POBSP data, with inclusion of previous data only when it seems necessary for cogency. The POBSP data on Pacific hydrobatids covers essentially four categories: (1) pelagic distribution, (2) breeding biology, (3) molt, (4) taxonomy. As might be expected, unequal amounts of information in these categories were acquired for the various species concerned. These data are presented in the species accounts.

Throughout the course of POBSP studies, a variety of vessels were utilized: United States Department of Interior, Bureau of Commercial Fisheries ships; United States Navy vessels; Scripps Institution of Oceanography research vessels; United States Coast Guard ships; leased fishing ships; and others. POBSP observers normally worked in rotating two-man teams who were on watch constantly during daylight hours and occasionally at night. On cruises

with only a single POBSP observer aboard, he usually observed from dawn to dark with intermittent breaks. All bird sightings were recorded with accompanying pertinent data. The recording of time of day at each sighting permitted interpolation of latitude and longitude positions from the ships' cruise charts. Weather and oceanographic conditions were coupled to each sighting when possible, and all information was later transferred to magnetic tape from which rapid summations of data for single species or species groups could be drawn for analysis. For a more comprehensive view of the Automatic Data Processing program, see King, Watson, and Gould (1967). As field work was performed for the most part on a year-round basis, migrational patterns, seasonal movements, and other factors can be analyzed to determine variations present in seasonal timing and areas utilized by the various species concerned. During the course of POBSP activities some 12,574 observations covering 27,140 individuals of the family Hydrobatidae were recorded. Regular and periodic surveys of islands used for nesting within the area of investigation allow for a more complete understanding of the pelagic observations. Specimen collecting accompanied pelagic observations whenever feasible. Artificial oil slicks (see Murphy, 1936:8) were often put out specifically to attract hydrobatids.

During the course of the study 650 specimens of 11 hydrobatid species were collected. Most specimens collected and observations made were of the various subspecies of the Leach's Storm Petrel (*Oceanodroma leucorhoa*). The means, with standard errors and standard deviations, are given in Appendix Tables A to E for all standard measurements of the POBSP specimens of *leucorhoa* races, as well as of other species. All wing measurements are of the chord. In comparing chord measurements with measurements of the flattened wing on storm petrels, I find extremely little difference between the two.

AREA COVERED BY POBSP.—Gould (Figure 1) shows the approximate outlines of the areas surveyed during all POBSP cruises from August 1963 through April 1968. All portions of those areas were not comparably surveyed in regard to total coverage or to time of year. Without question, certain areas received consistent and by far more regular coverage than other areas, which were surveyed only once or very irregularly. By and large, the area surveyed

falls into two major regions: the central Pacific and the central eastern Pacific (hereafter referred to as the eastern Pacific). The former was surveyed almost constantly from 1963 to 1967. The latter was surveyed intensively during 1967 and 1968. Intermittent cruises were also run in the Alaskan area.

FIELD IDENTIFICATION.—As a group, the various white-rumped and dark-rumped storm petrels in the Pacific present as great an identification problem to the field worker as any two groups of sibling species known. I have no doubt that each species has its peculiar identifying characters and that under *ideal* conditions most individuals might be properly identified to species, but sightings in the field are seldom under ideal conditions. In fact, it is unusual when weather, lighting, distance and other factors are satisfactory for positive identification. Most sightings are assigned to species only by inference and deduction.

In 1965 Wilson's Storm Petrels (*Oceanites oceanicus*), a totally unexpected species, were collected for the first time in the central Pacific. No doubt some were seen during late 1963 and 1964, but were erroneously recorded as Leach's (*Oceanodroma leucorhoa*) or Harcourt's Storm Petrels (*Oceanodroma castro*). Continued collecting after 1965 with the resultant procurement of scattered specimens of Wilson's, plus a detailed survey of migration in the central Pacific (Huber, 1971) have shown that these birds apparently move through the Pacific (Marshall Islands area, at least) in considerable numbers, and are scattered throughout the central Pacific in small numbers during the migratory period. Any purely visual identification made of storm petrels in an unknown area is, in my opinion, speculative.

In the central Pacific, identification problems were greatest for Leach's, Harcourt's, and Wilson's Storm Petrels, all white-rumped forms. The latter two were present in fewer numbers than Leach's. Random collecting performed throughout the area allowed for a fairly good estimate of the percentage of each species present.

In the eastern Pacific the situation was considerably different in that both white-rumped and dark-rumped forms were present. Although more species were involved, the majority of these were sufficiently diverse to allow reasonably accurate field identification. General collecting proved even more fruitful here than in the central Pacific, as certain forms, such as the two races of the Gala-

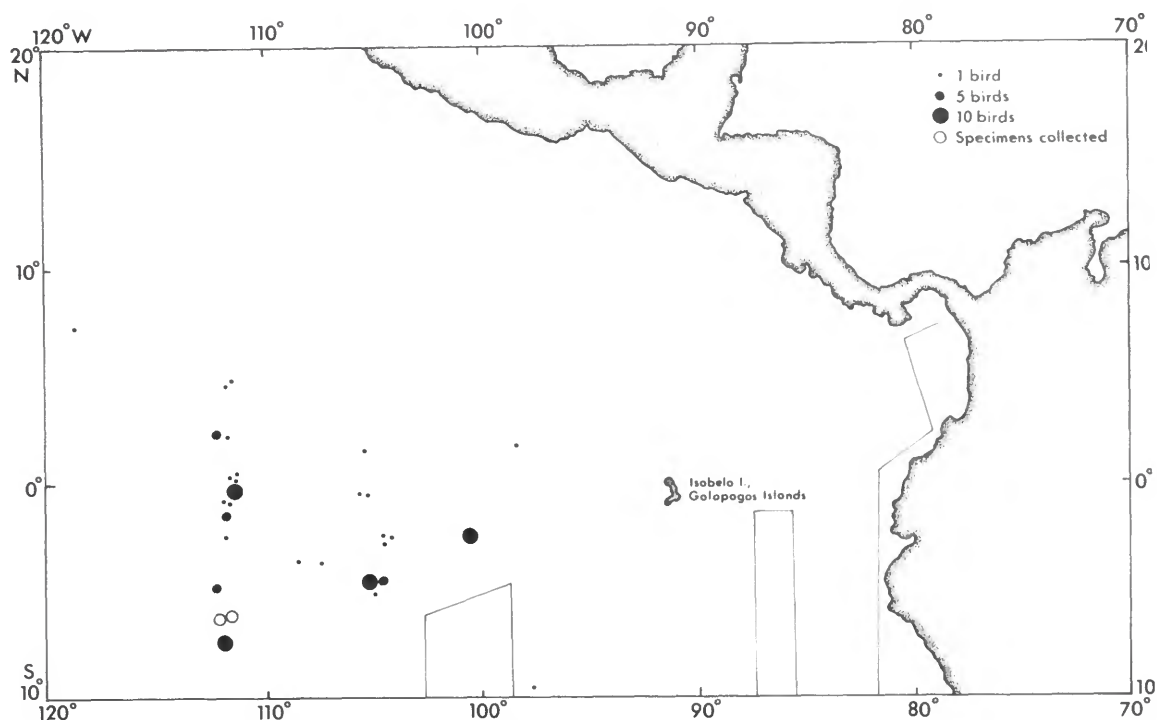


FIGURE 93.—POBSP sightings and specimens of *Pelagodroma marina*.

pagos Storm Petrel (*Oceanodroma tethys*), are readily separable in the hand. Thus in a situation such as this, the ideal is realized in that a collected specimen not only provides positive identification of the species, molt, food, and gonadal information, but allows for designation of the at-sea range of a specific geographic race.

Hence, despite the problems connected with field identification of hydrobatids, observations made during the POBSP surveys can be discussed with a considerable degree of assurance for the following reasons: (1) the observers concerned had an extraordinary opportunity to gain experience in field identification during extensive periods of work at sea under every conceivable condition, and (2) most at-sea observations were backed by random collecting; this constant procurement of specimens throughout various areas provided a constant check on visual observations.

ACKNOWLEDGMENTS.—The following made important observations and collected field data pertinent to hydrobatids during the program; without their

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I also wish to thank the following individuals who aided the writing of this paper in their respective ways. Philip S. Humphrey, as Principal Investigator of the Pacific Program, offered valuable advice and encouraged the writing of the present work. Dean Amadon of the American Museum of Natural History in New York and Joseph R. Jehl, Jr., of the San Diego Natural History Museum made available the hydrobatid specimens in their charge. Carl L. Hubbs of Scripps Institution of Oceanography generously offered me the use of his field notes and preliminary consolidated data on hydrobatids from the eastern Pacific islands, espe-

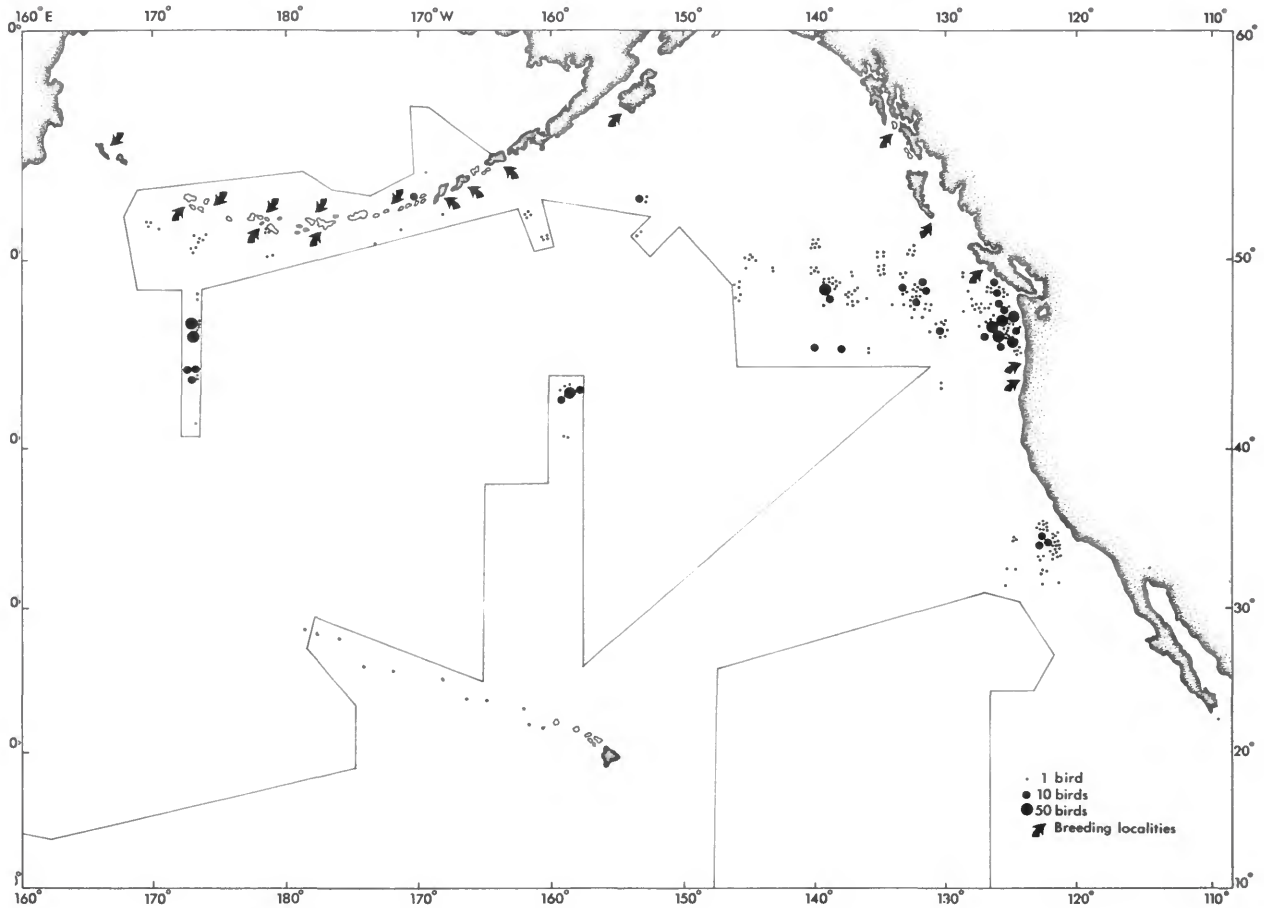


FIGURE 94.—POBSP sightings of *Oceanodroma furcata*. (Breeding localities are largely from Palmer, 1962).

cially Guadalupe. Oliver L. Austin, Jr., reviewed the manuscript and offered valuable suggestions. Ralph Browning donated his time and effort to performing much of the tedious work of measuring specimens. Anne K. Poulson prepared the illustrations.

***Pelagodroma marina* (Latham)**
WHITE-FACED STORM PETREL

PELAGIC DISTRIBUTION.—Most POBSP pelagic records of this basically southern hemisphere hydrobatid are from west of the Galapagos Islands. Prac-

tically all sightings fall within a triangular area with points at 5°N, 112°W; 8°S, 112°W, and 3°S, 100°W (Figure 93). Two adult females were collected by the POBSP on 24 August 1967 at 6°19'S, 111°55'W. Three other specimens taken in the eastern Pacific (two near the Galapagos, one near Ecuador) are mentioned in Murphy (1936:768). Lévêque, et al. (1966) report a specimen collected in September 1930 about 100 miles southwest of the Galapagos, and two sightings in August 1960 and seven sightings in July 1961 about halfway between the Ecuadorian mainland and the Galapagos.

The similarity of south Atlantic (Tristan da

Cunha Islands) and south Pacific (Australia-New Zealand) subspecies makes it difficult to assign origin to specimens collected near the Galapagos. Murphy (1936:768), while implying that some form of this species was probably resident in the eastern Pacific, left the question of origin open. Most likely these eastern Pacific records pertain to members of the Australian-New Zealand populations, which migrate to the South American coast and follow the Peru Current north and west through the Galapagos region. The large number of records west of the Galapagos in August and September (84% and 14%, respectively, of total POBSP sightings for those months) indicate a buildup prior to the return to the Australian-New Zealand breeding grounds where egg-laying takes place in late October. The condition of our August specimens (in terminating stages of complete molt and with moderate fat) is in accord with the condition of other procellariiforms prior to a prebreeding migration. Murphy (1936) and Palmer (1962) summarize the known biology of the species.

Oceanodroma furcata (Gmelin)

FORK-TAILED STORM PETREL

PELAGIC DISTRIBUTION.—This species was observed commonly on all POBSP cruises in the central and eastern Pacific north of 40°N (Figure 94). A region of high density off the California coast between 31°N and 36°N probably consists of birds from the northern California or Oregon populations. An obvious straggler was observed on 22 February 1968 feeding on refuse behind a ship in the company of several Black Storm Petrels (*Oceanodroma melania*) near the southern tip of Baja California. POBSP collected only a few specimens of nominate *O. f. furcata* near the Aleutian Islands; thus most of our pelagic sightings are not referable to race.

Oceanodroma leucorhoa leucorhoa (Vieillot)

LEACH'S STORM PETREL

PELAGIC DISTRIBUTION.—The nominate race of Leach's Storm Petrel is distributed in its at-sea range over much of the Pacific Ocean with a decided center of abundance in the central Pacific. Measurements of normally used characters of all

specimens collected (Figure 95) in this area are compared with known breeding *O. l. leucorhoa* from the Alaskan area in Appendix Table B. It can easily be seen that central Pacific birds fall well within the range for nominate *leucorhoa*. As a whole, the specimens are comparable both in measurements and other more subtle morphological characters with nominate *leucorhoa* from the breeding grounds. However, because of the difficulty involved in separating nominate *leucorhoa* from *O. l. beali*, the presence of a small percentage of the latter in the central Pacific is not to be excluded.

Oceanodroma l. leucorhoa attains greatest winter densities in a broad belt along the equator. Numbers drop rapidly to the south, and south of 12°S only an occasional individual is sighted. Waters to the north of this equatorial high-density area present problems of seasonal density specification. High density in small sectors north of the equatorial complex is probably due to several factors, among which are local, temporary, high concentrations of food. Additionally, late fall and early spring migrants may tend to mass at certain points in the northern sector of the wintering grounds before moving on south or north, as the case may be. Birds are found throughout the central Pacific wintering grounds throughout the year, with decided buildups of wintering birds as would be expected (compare Figure 96 "Summer" with Figure 97 "Winter").

The number of summering birds is considerable, but their age status is uncertain. In the Atlantic population of the nominate race, birds presumably do not breed until three years of age, but two-year old birds may return to the colony during the breeding season (Wilbur, 1969). Wilbur (1969) implies that first-year birds might fly over the colony without entering it; he apparently has no positive evidence for this in the form of banded birds. Huntington (pers. comm.) informed me that of eleven breeding birds banded as nestlings, the youngest were four years old; of thirteen banded birds mist-netted over the colony, breeding status unknown, the youngest were three years old. There may be considerable individual variation among one- and two-year old birds in regard to their return to the breeding colony.

The only other explanation for the large number of birds that summer in the central Pacific is

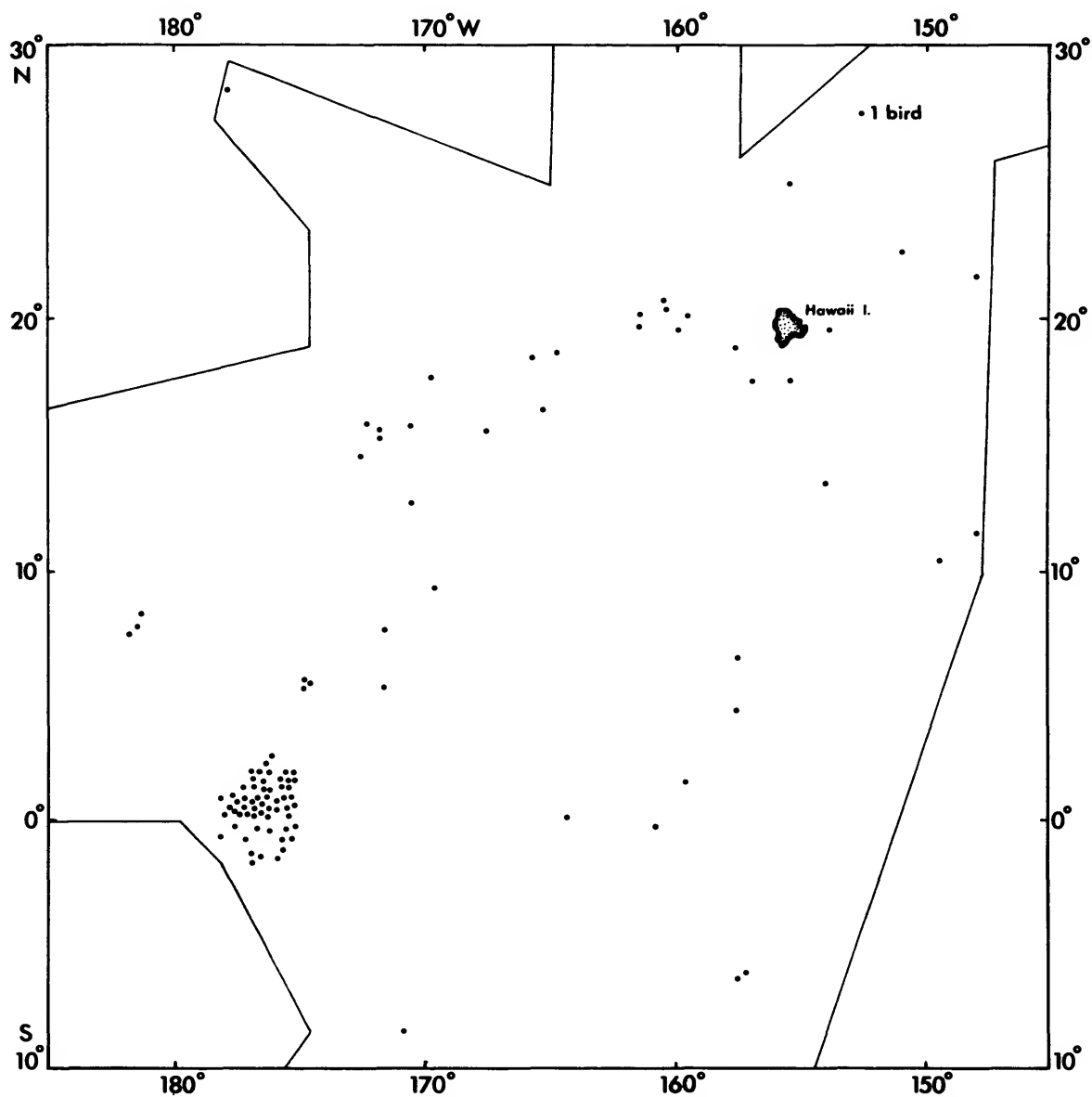


FIGURE 95.—Localities of collected specimens of *Oceanodroma leucorhoa leucorhoa* in the central Pacific.

that for some reason, some adults do not return to the breeding colony every year. Both Huntington (1963) and Wilbur (1969) record that approximately 50 percent of birds banded while nesting one year are found nesting the following year. Unless we assume some birds were missed in the study

plots or had moved elsewhere, this seems to be an exceptionally high mortality rate. Possibly some adults that successfully raise a chick one year do not return to the breeding grounds the following year.

The migrational pattern of nominate *leucorhoa* is largely obscured by the high densities of sum-

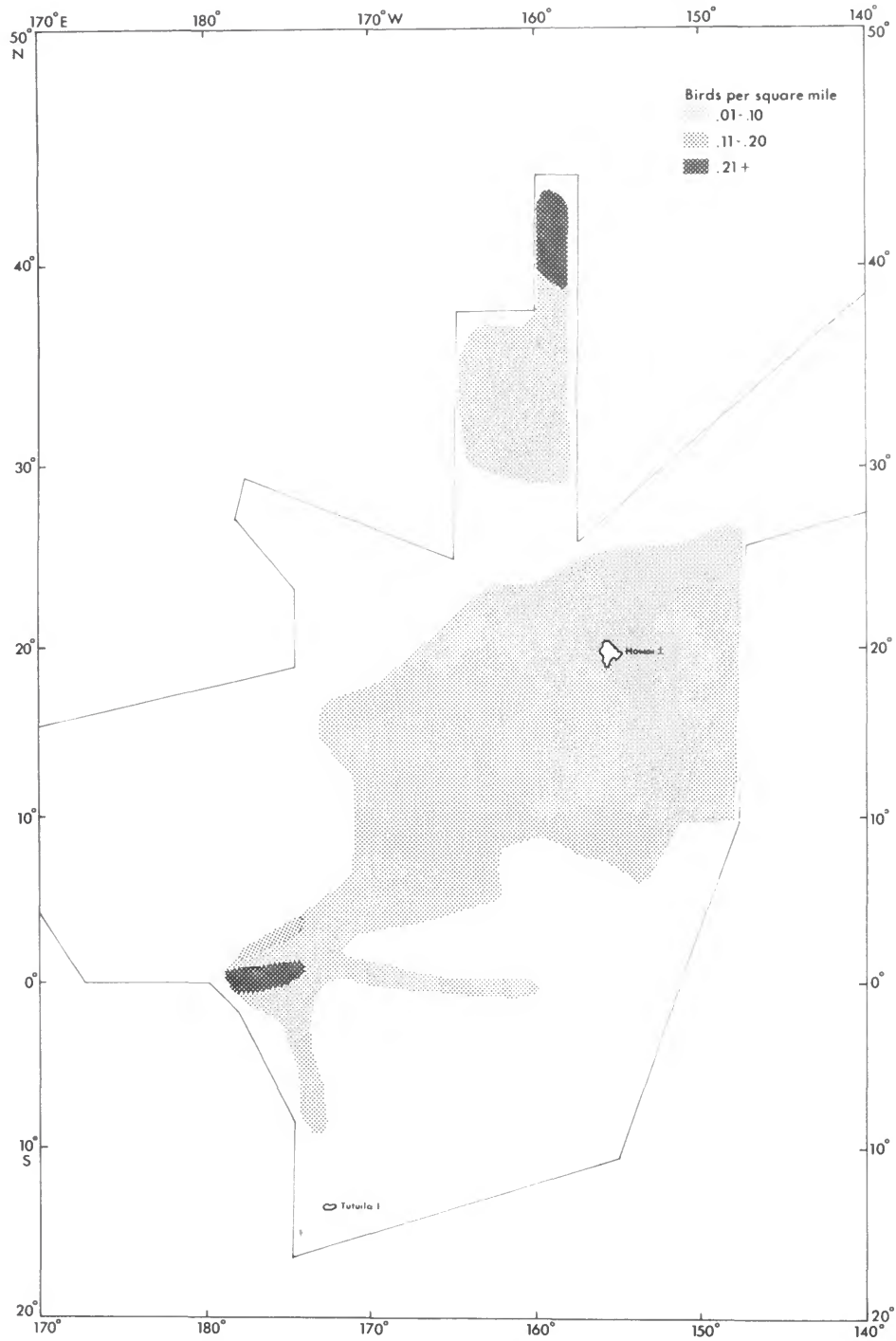


FIGURE 96.—Summer densities (May, June, July, August) of *Oceanodroma leucorhoa leucorhoa*.

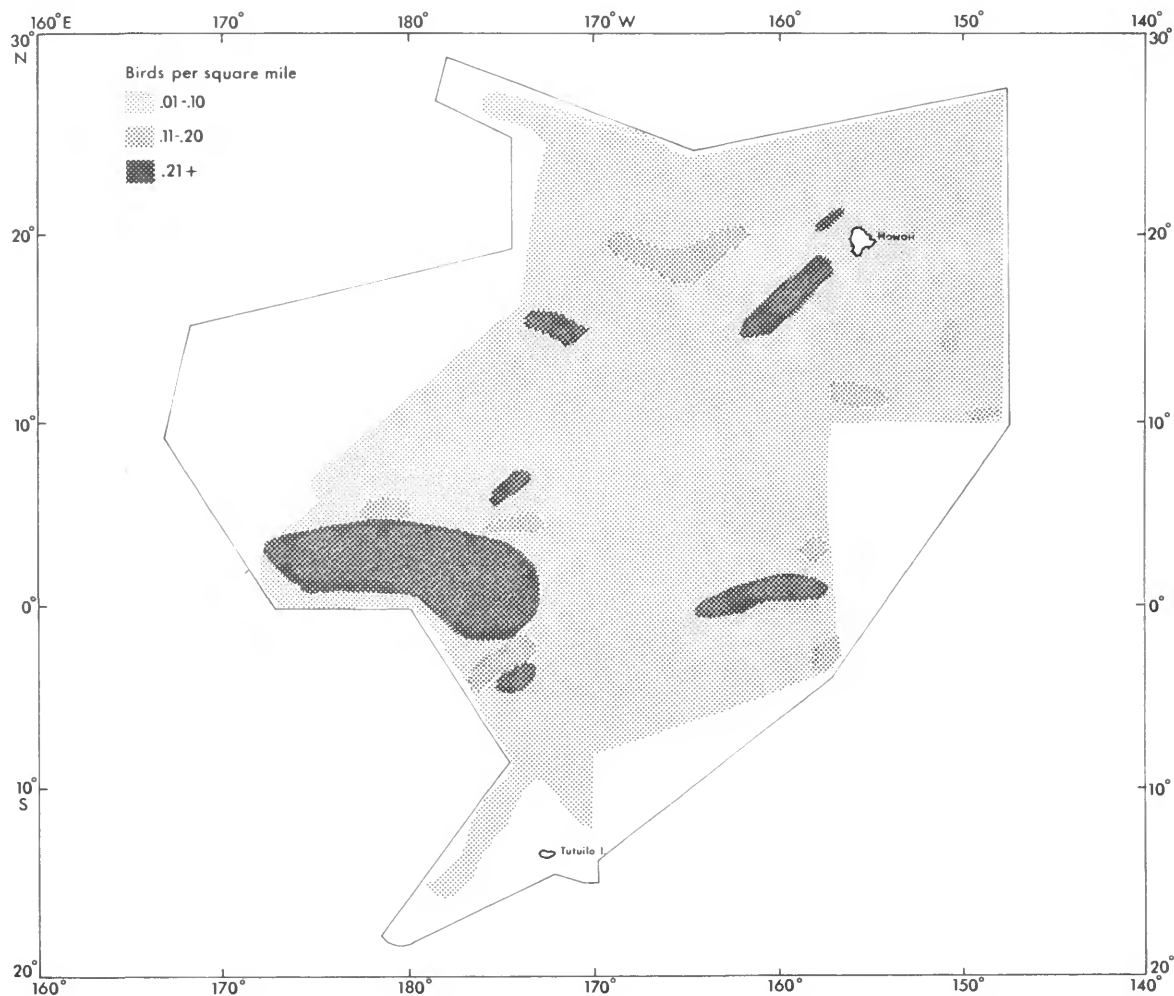


FIGURE 97.—Winter densities (November, December, January, February) of *Oceanodroma leucorhoa leucorhoa*.

mering birds, and is more readily ascertained by field observations of flocking birds rather than by actual increases or decreases in recorded density. The spring migration north begins in March and probably occurs sporadically throughout April, since April densities in the central Pacific are still far greater than in mid-summer when most breeding birds are on the breeding grounds. The fall migration south is also largely obscured by summering birds, but definite density increases are noted southward to the high-density equatorial center as early as September. At this time of year breeding

birds would still be expected on the breeding grounds or at least in more northerly latitudes. These early fall buildups in the equatorial area may either be of birds that have experienced nesting failures, and thus have left the breeding grounds earlier than the successful breeders, or of prebreeders that have spent the summer farther north and have returned to more southerly latitudes for the winter. As it is virtually impossible to distinguish immature prebreeders from adult breeding birds when the latter's gonads are in a winter quiescent stage, collected specimens from these sea-

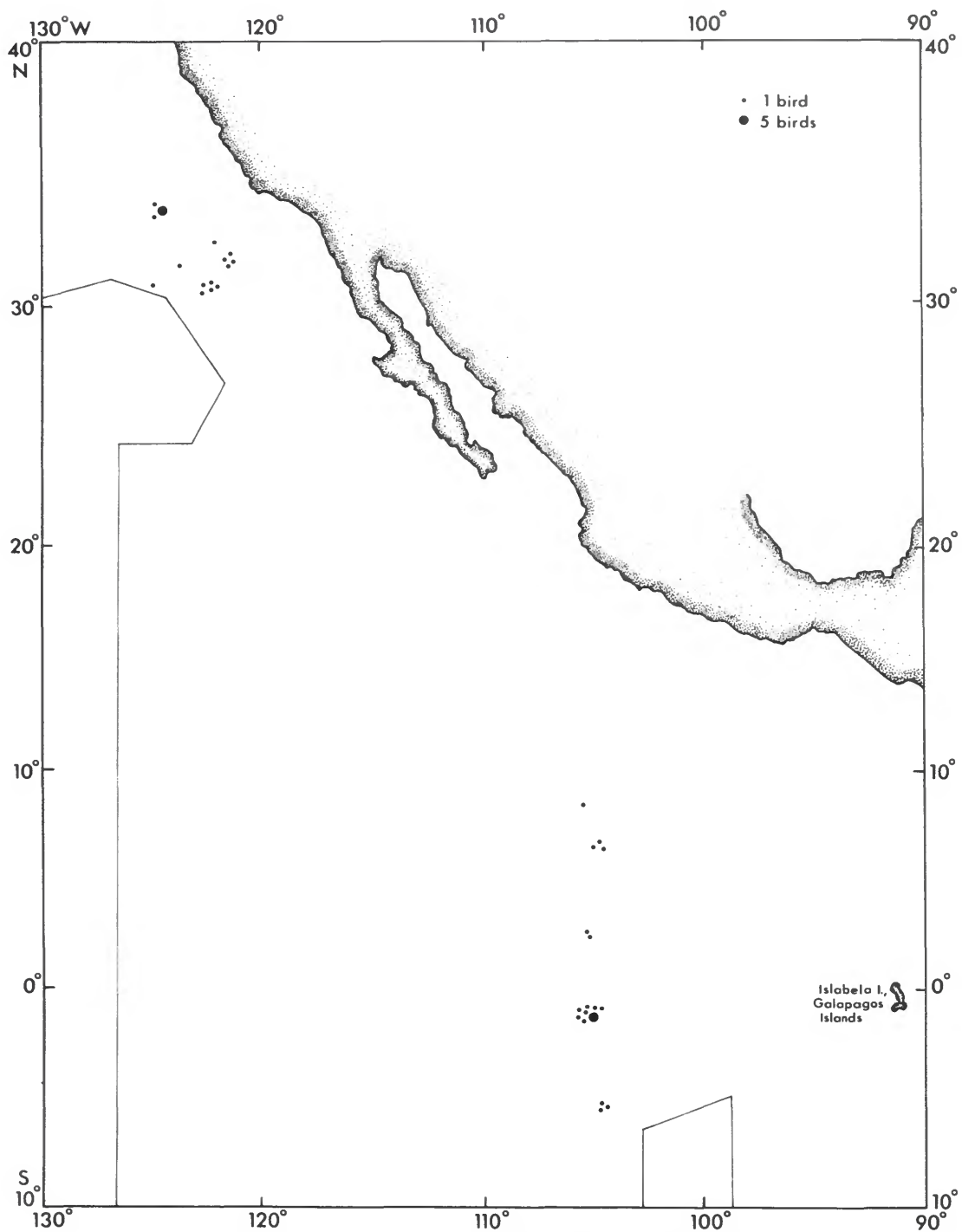


FIGURE 98.—Localities of collected specimens of *Oceanodroma leucorhoa leucorhoa* in the eastern Pacific Ocean.

sons do not lend information as to their recent breeding activities.

Movements and distribution of the nominate race throughout the eastern Pacific are less clear because of the difficulty of separating individuals from the abundant *O. l. beali*, which winters prominently along the western American coast. A few specimens from the eastern Pacific are clearly referable to nominate *leucorhoa* by their greater size; collecting localities of these are shown in Figure 98. Aside from POBSP specimens, Loomis (1918:182) mentions three specimens collected south of the Galapagos Islands whose measurements indicate their allocation to the nominate race. Palmer (1962:227) mentions examples of the nominate form taken off the coast of Ecuador. Comparatively, the numbers of these eastern representatives are low and the equatorial high-density area between 170°W and 175°E is, if not the center of winter abundance, one of the most important of such centers.

TAXONOMY.—Considerable taxonomic work was performed on available POBSP specimens during the course of this study in the hope that the ability to distinguish races of at-sea collected specimens would allow for a clearer picture of their respective at-sea ranges. In some cases this was possible, but many individuals cannot be designated unconditionally to a particular race. Concerning the Pacific races of Leach's, Austin (1952:400) stated: "On dimensions alone these are all weak races. Despite significant differences between the means of some characters, fewer than half the individuals of many of the recognized subspecies are distinguishable." Despite the recently collected large series of most of the races concerned, we are no better off in regard to solving these problems. Austin's (1952) arrangement of the various Pacific subspecies of *Oceanodroma leucorhoa* is followed here. The unusual situation concerning *O. l. socorroensis* at Guadalupe Island and the possible need for revision of the taxonomy of that population is discussed beyond.

In working with fresh series of recently molted birds of all populations, I find that little significance can be attached to the oft-mentioned character of a lead bloom to the plumage of the northern races, which is supposedly most prominent in nominate *leucorhoa*. All races in very fresh plumage show this particular bloom but with considerable individual variation, and this particular cast

is lost quite rapidly, both in living birds and in museum specimens. Freshly molted series of either *O. l. chapmani* or *O. l. socorroensis* show this character as prominently as newly molted nominate *leucorhoa* from the Alaskan area, although the overall plumage is admittedly considerably darker in the southern races. Juvenile *socorroensis* from Guadalupe are especially prone to show this particular character, but drastic differences exist between new and old plumage. When the plumage is several months old the entire feather coat in all races is of a washed-out brown hue in addition to its ragged condition, with hardly a trace of the rich charcoal present in new featheration. Body contour feathers, as well as flight feathers, are badly worn at the end of a plumage sequence. Of the flight feathers, primaries appear to take the most wear. In contour feathers, those about the head and neck appear most subject to wear and at the beginning of a new molt sequence these are often no more than ragged portions of the original appendages.

Only in the case of exceptionally large individuals of *O. l. leucorhoa*, and exceptionally small individuals of *O. l. socorroensis*, can birds of the *leucorhoa* complex be segregated with any degree of certainty. As is evident from the measurements in Appendix Table B, nominate *leucorhoa* from the Alaskan area is the largest of all races. While the average individual of the nominate race has a generally more massive bill, this subtle difference is useful only in direct comparison of specimens, and does not lend itself meaningfully to mensural application.

MOLT.—Members of the nominate race of Leach's that enter the central and eastern Pacific from northern breeding grounds, as well as year-round semipermanent residents there (nonbreeders), are already undergoing a pronounced primary molt by July. This continues in some individuals throughout the fall and winter (to December or even later). In a large percentage of birds the entire primary molt has been accomplished by November, and in exceptional individuals by October (Figure 99). For many others this molt may not terminate until April. It cannot be determined whether individuals finishing primary molt from, say, February through April, are birds that have a very prolonged cycle or whether they are individuals that began molt very late in the year. Primary molt can be clearly ascertained and follows a set pattern of replacement of

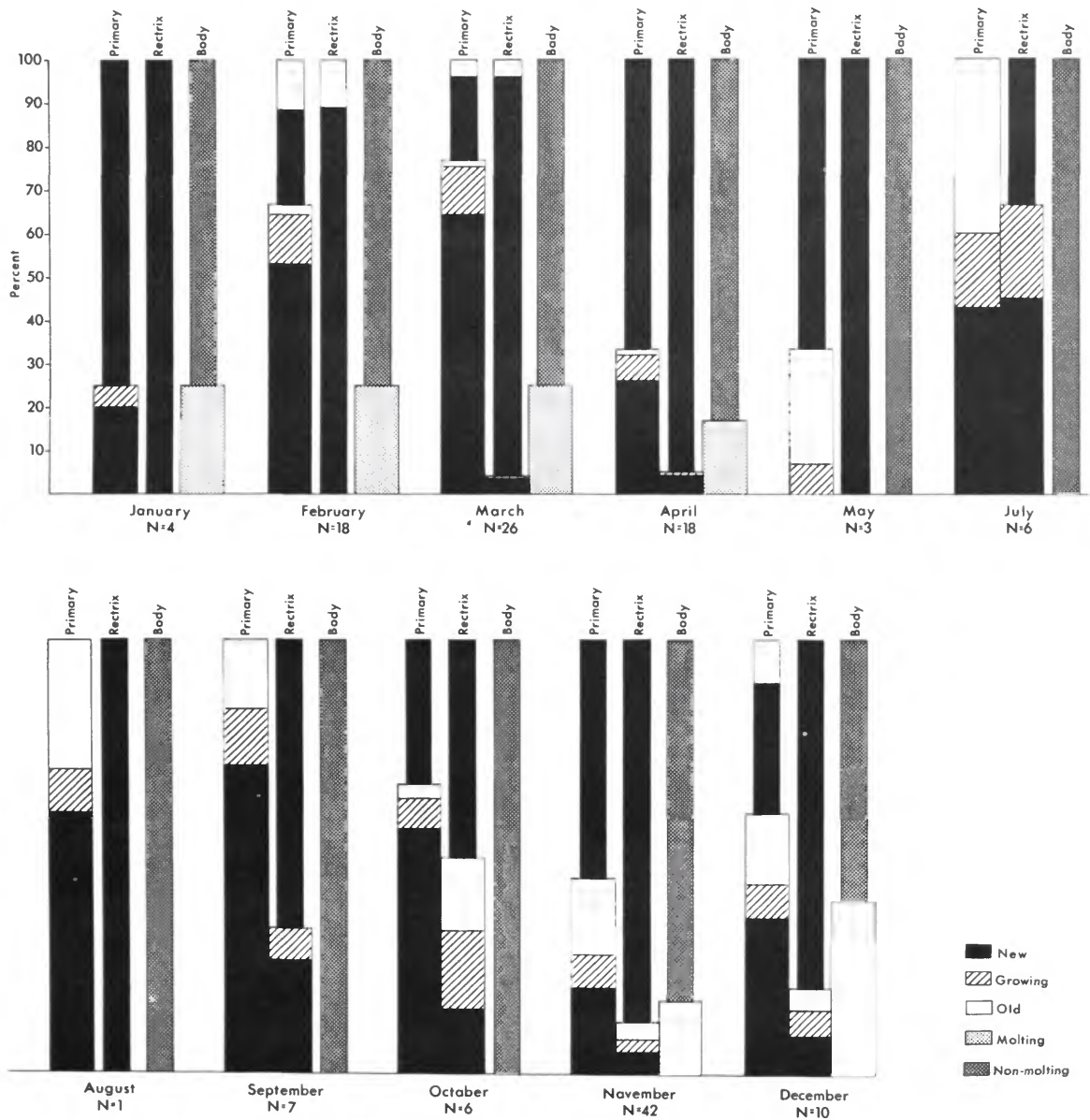


FIGURE 99.—Seasonal molt stages in *Oceanodroma leucorhoa leucorhoa*. The percentages of new, growing, and old primaries and rectrices are calculated from direct count of all birds in each respective sample; narrow portion of bar equals nonmolting percentage of sample, wide portion of bar equals molting percentage of sample. (n = sample size.)

new feathers from the innermost to the outermost primaries with corresponding feather pair members of each wing coincident or very closely attuned. Most individuals of *chapmani* and *socorroensis*, re-

turning to the breeding islands, were in terminal stages or had very recently completed a body and primary molt. Some individuals were still growing the outermost (tenth) primary as defeathering of

the brood patch and gonadal enlargement were occurring. We took no specimens of either *beali* or *leucorhoa* on any breeding grounds except for *willetti* (= *beali*) on the Coronados Islands.

Rectrix molt, like the preceding, is already well along in our July sample of *O. l. leucorhoa*, and is for all practical purposes finished by November. Only a few isolated individuals show any evidence of rectrix molt during the period from January through May. There seems to be no set pattern of rectrix molt except that opposite members of a pair of tail feathers are generally molted at the same, or at nearly the same time.

Investigation of the molt pattern of the secondary feathers was less satisfactory because of the difficulty of working with study skins in these small, long-winged birds. In general, it appears that the outer secondaries begin to molt at about the time the first primaries shed, and molt then proceeds progressively toward the body. Secondary molt is closely parallel to primary molt and is usually terminated before the last primary has finished growing.

Extensive body molt of the contour feathers in the nominate race begins in November and is apparent in a decreasingly smaller number of individuals through April. Body molt is generally distributed over most of the body; the crown and throat regions and the primary and greater coverts are the last areas to replace feathers. The various races of Leach's show certain variations in molt patterns.

No doubt much of the variation in molt between individuals of the nominate race can be attributed to differences between juvenile, immature, and adult breeding birds. However, I cannot satisfactorily separate immature birds from adults on the wintering grounds after the latter's gonads have regressed, except for truly adult females, which form only a small part of our sample. The more extensive lighter margins of the coverts and the scapulars, and the wrinkling of the nostril area in study skins, which are supposed to be good characters for separating juvenile birds from older individuals, are not positive determinants and at any rate these differences disappear within the first year of life. Hence, the monthly samples shown in the molt graphs are unquestionably made up of a variety of age classes.

Oceanodroma leucorhoa beali Emerson

BEAL'S STORM PETREL

PELAGIC DISTRIBUTION.—Our at-sea observations, backed by routine collecting of specimens throughout the eastern Pacific (Figure 100), have determined that *O. l. beali* winters throughout a broad area south of the breeding grounds from north-central California (northern limit of recurrent POBSP cruises) to at least 20°S. South of 10°S decreasingly lower densities are recorded. Within this extensive area the distributional picture is somewhat confused because of the admixture of certain other white-rumped forms, such as a scattering of identifiable nominate *leucorhoa*, *O. l. socorroensis* and two races of Galapagos Storm Petrels (*O. tethys tethys* and *O. t. kelsalli*). Nevertheless dense wintering populations of *beali* are found off both central and southern California and throughout a broad area from ca. 26°N to ca. 8°S, between 90°W and 120°W (Figure 101). Although not readily apparent from the density distribution maps, these are the areas most heavily surveyed by the POBSP. Hence, as is often the case, graphic display of geographical distribution of an organism more often tends to show distribution of the researcher rather than of the organism. The POBSP has not surveyed to the west or south of the areas involved in EASTROPAC cruises. Our summer cruises in the eastern Pacific only extend to ca. 5°S; densities of *O. l. beali* are fairly high to that point (Figure 102).

It may be noted that the density figures in the *O. l. beali* pelagic distribution charts are considerably higher than those for *O. l. leucorhoa* in the central Pacific. Despite the fact that more forms are involved in the eastern area, actual eastern Pacific densities for all races of *leucorhoa* are roughly three times greater than those recorded in the central Pacific. Since the magnitude of observations under varying conditions in both areas would eliminate, or render insignificant, any temporary variations in the data gathering, the differences in density consistently recorded between these two areas must be regarded as real.

TAXONOMY.—Austin (1952) synonymizes both *O. l. beldingi* from the northern California coast, and *O. l. willetti* from the Coronados Islands, with *O. l. beali*. Hence, *O. l. beali* applies to all Leach's Storm Petrels breeding along the North American west coast from extreme southeastern Alaska to the

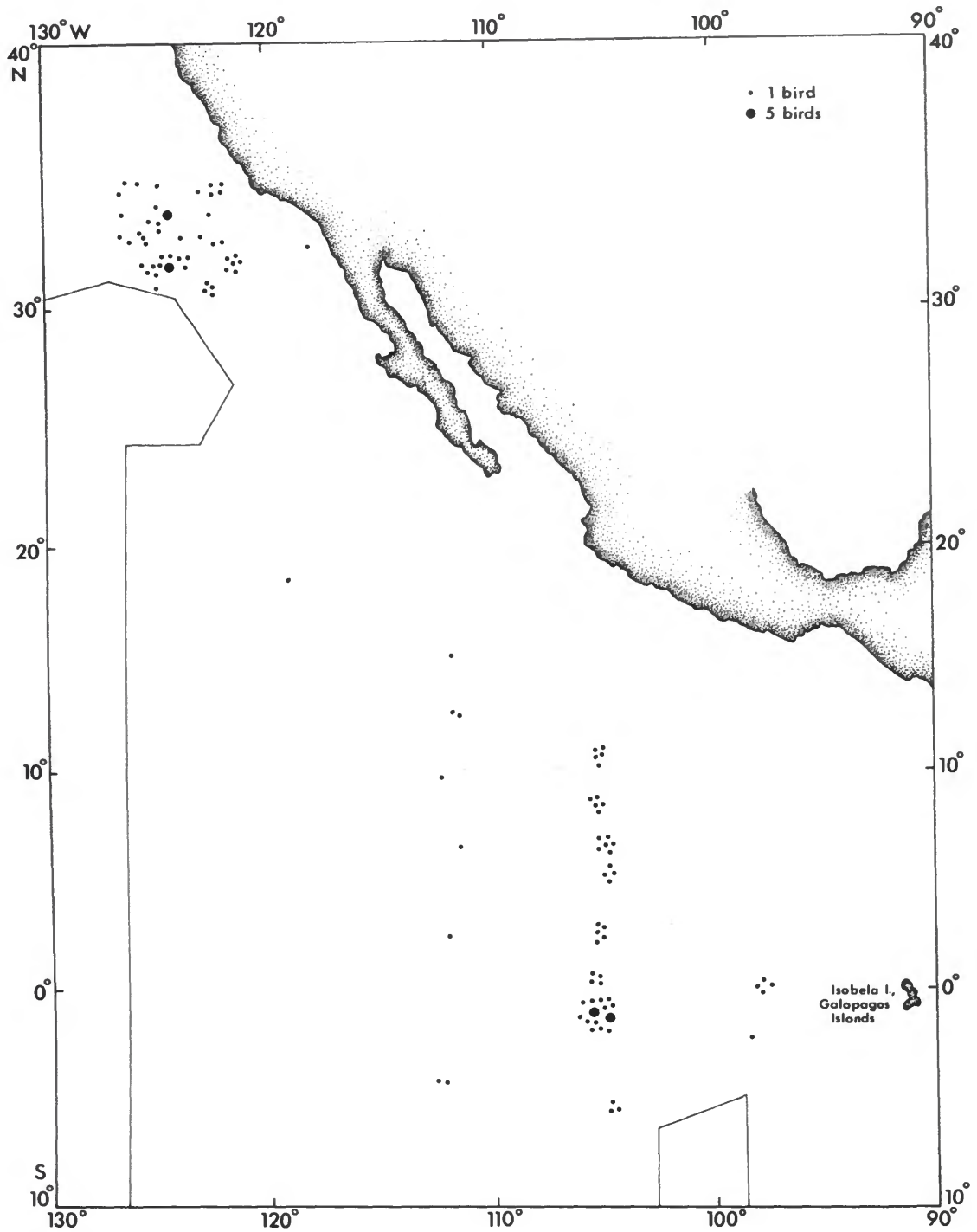


FIGURE 100.—Localities of collected specimens of *Oceanodroma leucorhoa beali*.

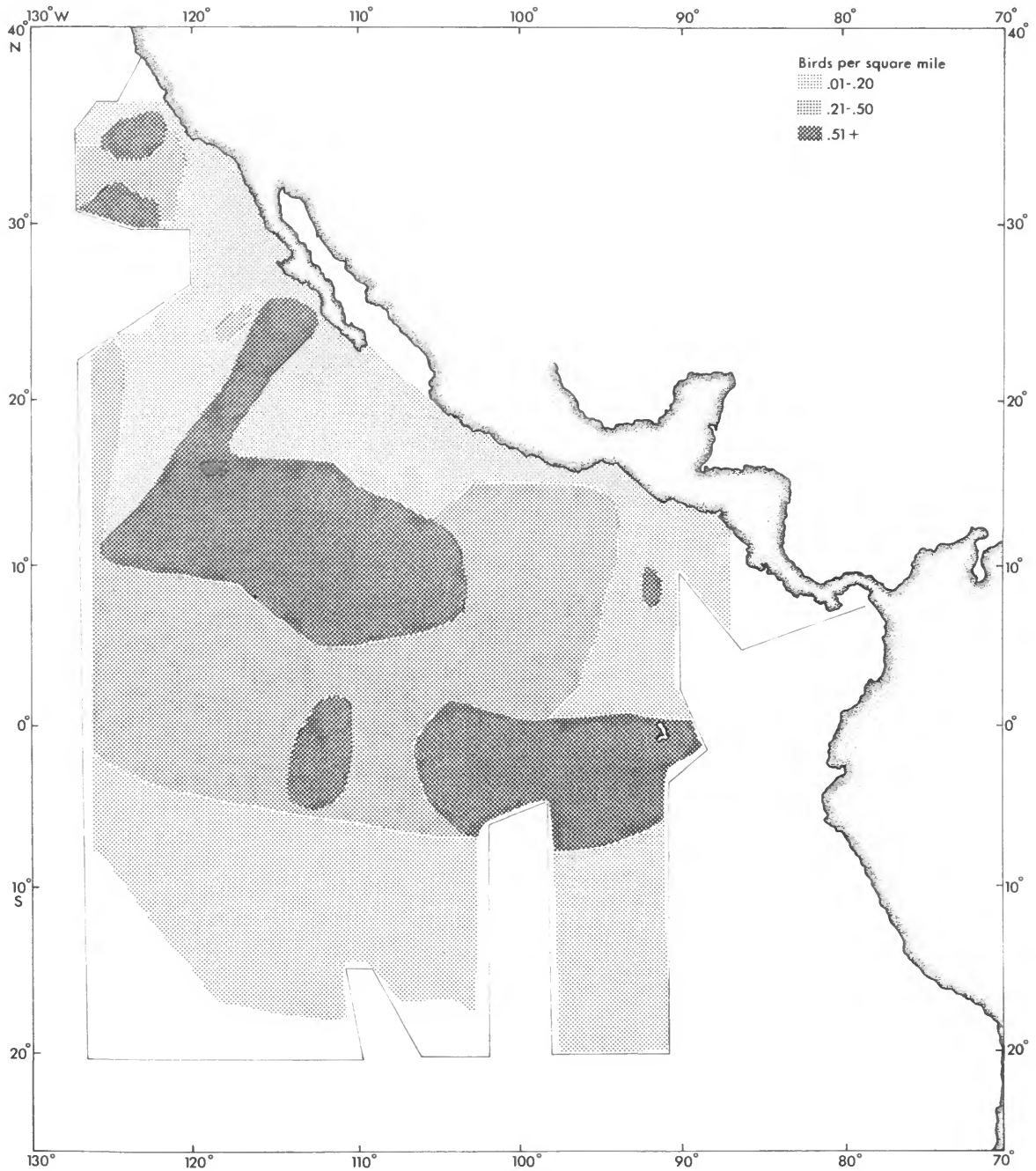


FIGURE 101.—Winter densities (November, December, January, February, March) of *Oceanodroma leucorhoa beali*.

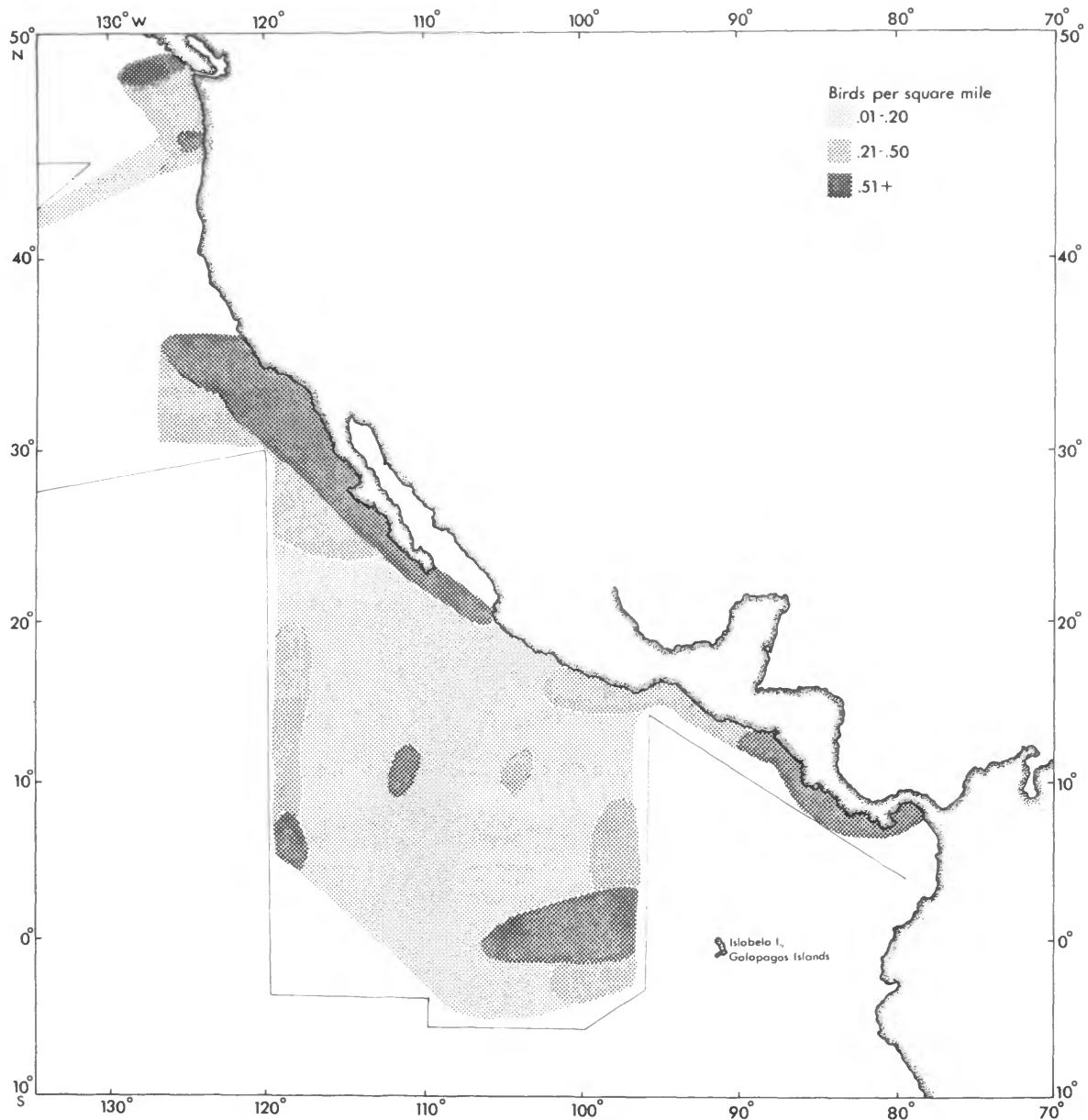


FIGURE 102.—Summer densities (May, June, July, August) of *Oceanodroma leucorhoa beali*.

Coronados Islands just south of the United States-Mexican border. Although this eliminates the confusion involved in attempting to recognize more than one form along the United States west coast, many individuals in this complex cannot be dis-

tinguished from nominate *leucorhoa* to the north; a considerable number of individuals from the Coronados population cannot be distinguished from either dark-rumped *O. l. chapmani* from the San Benitos Islands (along the west-central coast

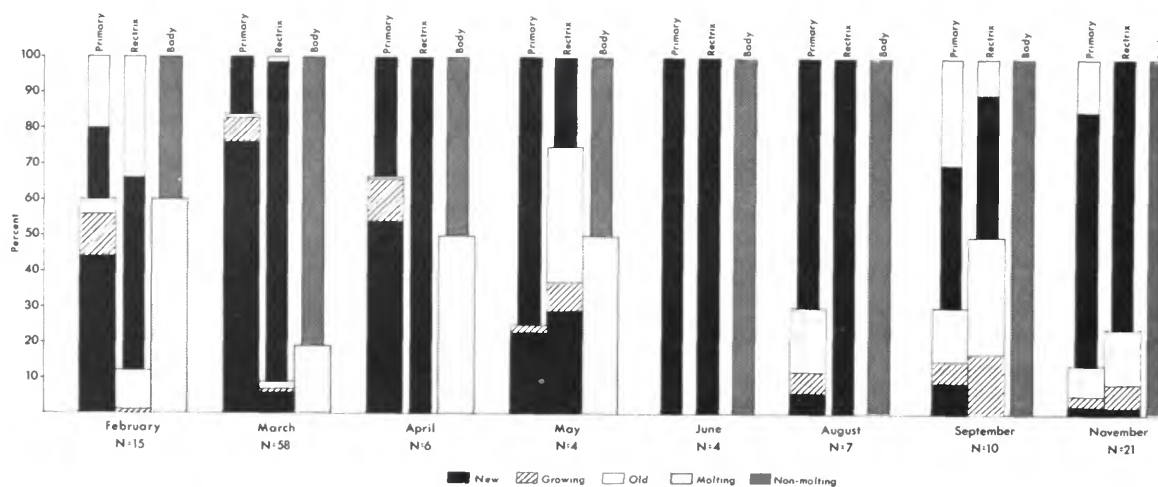


FIGURE 103.—Seasonal molt stages in *Oceanodroma leucorhoa beali*. (See Figure 99 for explanation of symbols.)

of Baja California), or *O. l. socorroensis* of Guadalupe Island.

BREEDING BIOLOGY.—A number of authors record the nesting of *O. l. beali* along the western North American coast; among these are Grinnell and Daggett (1903), Willett (1915), Howell (1920), Bailey (1927), E. W. Martin (1938), and Campbell and Stirling (1968). The consensus of these reports is that *beali* nests from at least April through September. Eggs are recorded from June to August, and young from July to September. An exceptionally early record of the Coronados Island population (= *willetti* of the 1957 A.O.U. Check-list) is that of a three-quarter grown downy young taken 27 April 1929 (specimen in the San Diego Natural History Museum). Other specimens from the Coronados in that institution were collected between 6 July and 5 September. A few of the September birds are small downy young that probably would not have left the island until October. The POBSP captured three dark-rumped birds of the Coronados population in a mist net on the night of 30 June 1968 on Center Island. No nests were found; the population at that time could not have exceeded 100 birds.

MOLT.—The molt sequence of *O. l. beali* is graphically demonstrated in Figure 103. From our collected samples, *beali* appears to have a larger percentage of individuals undergoing primary molt

during the prebreeding months (February–May) than *O. l. leucorhoa*. Fall primary molt (probably concerned with immatures) is terminated more rapidly than in *O. l. leucorhoa*. Rectrix and body molt are basically the same in *beali* and nominate *leucorhoa*.

Oceanodroma leucorhoa chapmani Berlepsch

CHAPMAN'S STORM PETREL

PELAGIC DISTRIBUTION.—The pelagic distribution of this form is little known, and POBSP surveys have not been informative. Although the race is characterized by the fact that all members have a dark rump, its presence at sea is difficult to determine because it is indistinguishable from dark-rumped birds of both the Coronados and Guadalupe Island populations present in the same area. Although we have a considerable number of sightings of dark-rumped birds from both the northern cruise areas and the southern EASTROPAC areas, it is impossible to assign racial designation to these sightings. An admixture of collected specimens of dark-rumped, intermediate, and white-rumped birds of small size from the eastern Pacific are in most cases definitely assignable to *socorroensis*. It is not possible by measurements to separate definitely all dark-rumped *socorroensis* from *chapmani*. We have collected few, if any, *chapmani* at sea. On the basis of the

limited number of small, dark-rumped specimens taken, however, it may be that this race winters much closer to the coast than do *beali*, *leucorhoa*, or *socorroensis*.

BREEDING BIOLOGY.—This dark-rumped form of Leach's breeds predominantly or exclusively on the San Benitos Islands off west-central Baja California. During a POBSP survey of these islands from 26 to 29 April 1968, birds were plentiful on all three islands. At that time they were calling from the air, as well as occupying empty burrows and cavities among the rocks. No eggs were found. Several adults were discovered fatally impaled upon the spines of the rampant cholla cactus (*Opuntia* sp.). A later June survey noted 14 such individuals on one slope.

During a 25 to 27 June 1968 survey, most birds were still calling from empty nest sites; some 20 percent of the population were on fresh to heavily incubated eggs, but no chicks were found. The birds occupy every feasible habitat on the islands for nesting, with possibly the talus slopes and rocky areas preferred. In these habitats they are in competition for nest sites with the Black Storm Petrel and Least Storm Petrel (*Halocyptena microsoma*). Some *chapmani* used abandoned Cassin's Auklet (*Ptychoramphus aleutica*) burrows, but a number were noted digging their own burrows. DeLong (POBSP) records that "despite the apparent weakness of the bony structure of the legs, they dig with great fervor and make the soil fairly fly."

The species' nocturnal and secretive nesting habits make it extremely difficult to arrive at more than a rough estimate of the population size. For the June 1968 survey this was set at 50,000 birds for the island group.

Oceanodroma leucorhoa socorroensis Townsend

SOCORRO STORM PETREL

PELAGIC DISTRIBUTION.—*O. l. socorroensis* were found at sea as far north as 35°N and south to 10°N. A considerable number of specimens were taken southeast of the breeding island of Guadalupe. As *socorroensis* cannot be distinguished in the field with any degree of certainty, all records are based on collected specimens (Figure 104). In late February 1968 near 10°N, and between 100°W and 110°W, sizeable concentrations of *socorroensis* were recorded in mixed flocks composed of *Oceanodroma*

tethys tethys, *Oceanodroma leucorhoa beali*, and a few large specimens that are best referable to *O. l. leucorhoa*. No *socorroensis* were collected below 10°N, although extensive collecting was done throughout the cruise in these longitudes to 20°S. The western limits of the pelagic distribution are unknown. From our evidence, apparently *socorroensis* does not range as widely from the breeding grounds, nor as far from the coast, as do *beali* or *leucorhoa*.

TAXONOMY.—This race is the smallest and most variable in rump color of all forms of *leucorhoa* in the Pacific. The characters of greatest use in separating this from other races are wing and bill length, and the overall slighthness of the bill. Weights, when available, are also useful in demonstrating the small size.

A series of 109 POBSP specimens from the summer breeding population show a range of wing length from 135 mm to 150 mm with a mean of 141.89. Austin (1952) records 25 *socorroensis* with wing length ranging from 141 mm to 157 mm, and with a mean of 148.8 ± .88. Another series of winter breeding birds composed of POBSP specimens as well as specimens from the San Diego Natural History Museum contains 19 males with a wing length range of 141 mm to 150 mm, and 18 females with a range of 140 mm to 147 mm. With this overall range of from 140 mm to 150 mm for both sexes (although close to the 135 mm to 150 mm range for summer *socorroensis*) the winter birds tend to be slightly larger, although there is complete overlap between winter and summer birds. Considering all birds of both winter and summer populations from a sample of 146 birds, the range is 135 mm to 150 mm. This large sample should totally blanket Austin's sample of 25 birds, but his series shows considerably larger measurements in both range and mean. His sample apparently contains both winter and summer Guadalupe birds and also apparent stragglers (probably of *O. l. beali*) taken offshore Guadalupe. For example, several obvious *beali* (by their worn plumage and measurements) taken offshore in winter were found in the series of *socorroensis* in the San Diego Museum.

The winter breeding population on Guadalupe of slightly larger birds is in need of considerable investigation. If this population is sufficiently different to warrant subspecific recognition, the appropriate name would be *Oceanodroma leucorhoa*

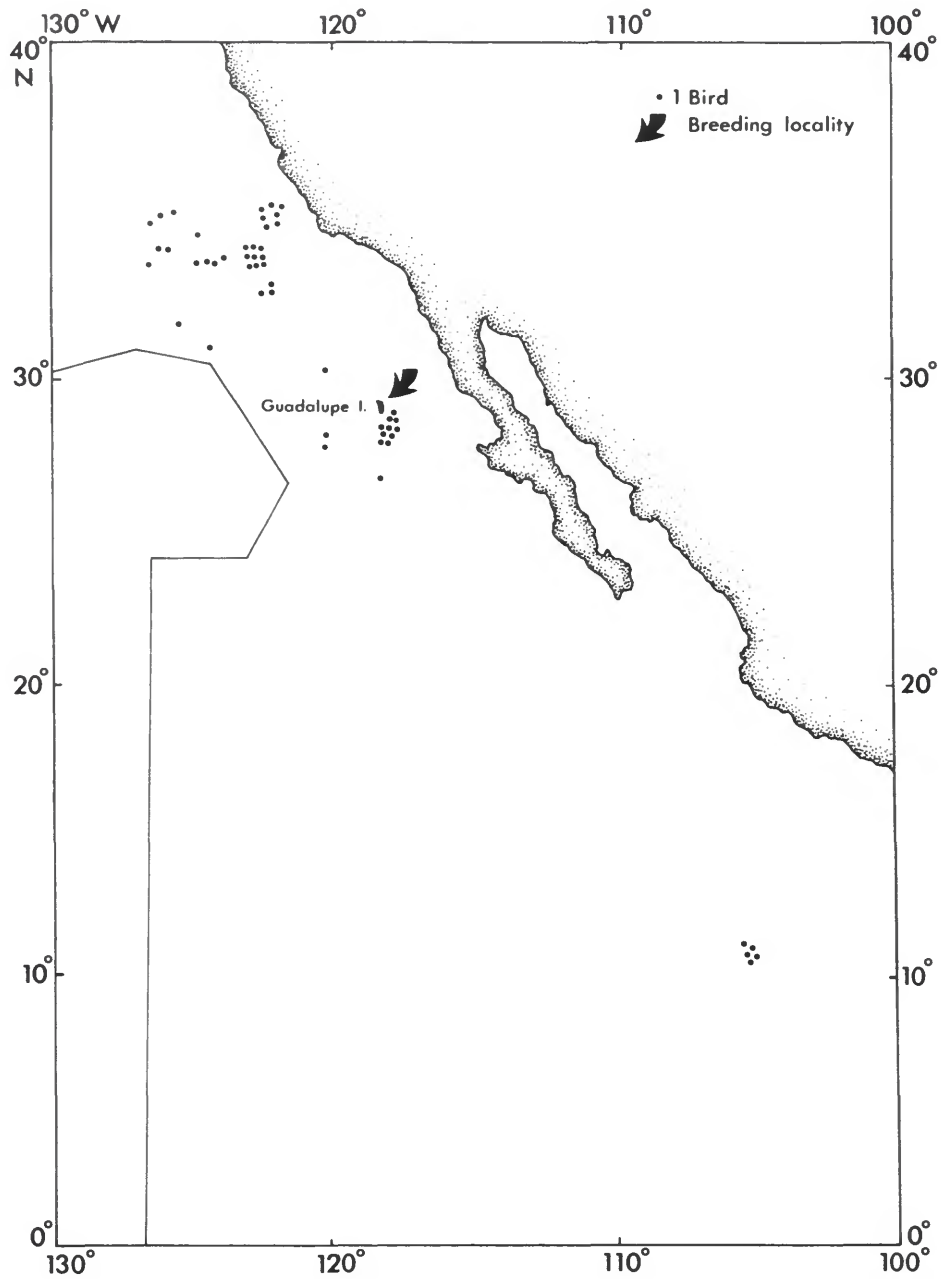


FIGURE 104.—Localities of collected specimens of *Oceanodroma leucorhoa socorroensis*.

kaedingi. For convenience, I will refer to the winter breeding birds as “*kaedingi*” to differentiate them from the currently recognized summer breed-

ing population, *socorroensis*. Besides their slightly larger size, *kaedingi* are, in part, further distinguishable from *socorroensis* by rump color. All 37

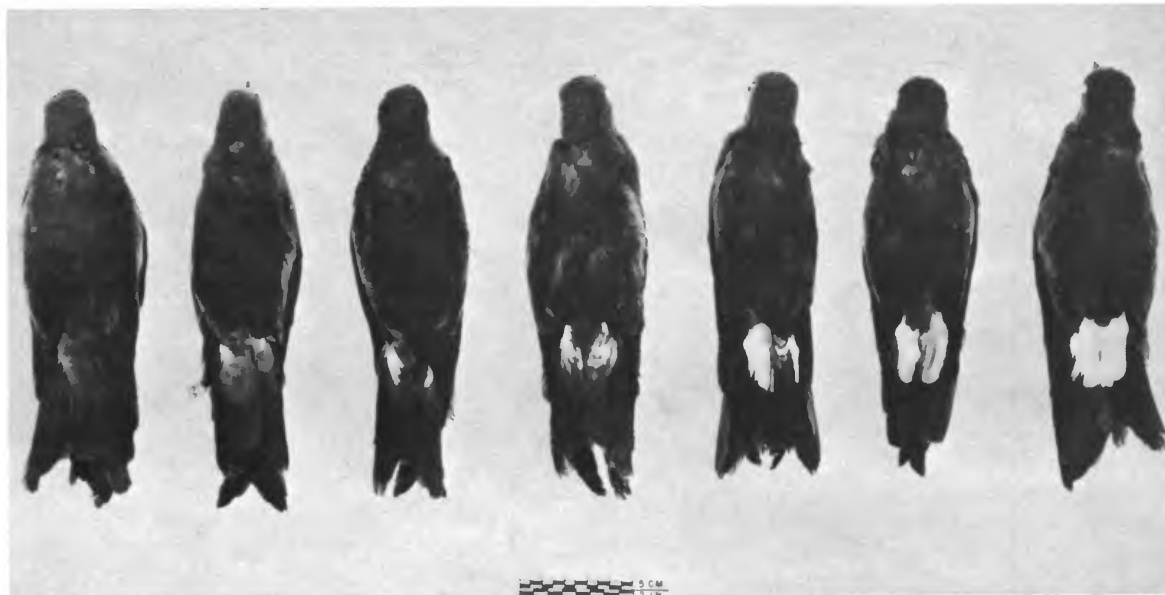


FIGURE 105.—Variation in rump color of *Oceanodroma leucorhoa socorroensis* from Guadalupe Island.

winter-breeding *kaedingi* examined are white-rumped, the amount of white ranging from 2 through 4 on a scale of 0 to 5 measuring the amount of white in the rump. The series of 37 showed the following scale figures: 2 (14%), 3 (40%); intermediates between 3 and 4 (11%); and 4 (35%). Thus an average bird of this population would have rump color of slightly over 3, about comparable to that of *O. l. beali*. Summer *socorroensis*, on the other hand, have rump color ranging from categories 0 through 5, or from pure dark to pure white rumps (Figure 105). Austin's (1952:401) statement characterizing rump color of *socorroensis*, "rump patch variable, almost always with some white, but never as much as in typical *beali*," is not quite true. As discussed in the breeding biology section, 90 percent of the birds breeding on Isote Negro in June 1968 had pure dark rumps. Conversely certain individuals taken off Isote Afuera have a pure white rump; even the feather shafts are white (as in *Oceanodroma castro*), a condition that rarely occurs in any race of *leucorhoa*. Obviously these differences between *socorroensis* and *kaedingi* are insufficient to permit racial designation of most individuals taken away from the breeding island, so at present it is useless to attempt to recognize these two populations as taxonomically distinct.

These differences, however, are neither more nor less than those displayed by most named subspecies of *leucorhoa*. A small- to average-sized *O. l. chapmani* from the San Benitos Islands would be indistinguishable from a dark-rumped *socorroensis* from Guadalupe Island, as would a large *chapmani* be indistinguishable from a dark-rumped "*willettii*" (= *beali*) from the Coronados. Unfortunately we are dealing with populations that show few external morphological differences. Nevertheless the winter breeding population at Guadalupe, whether it is recognized as a distinct race or not, undoubtedly differs physiologically from the summer population. Despite equalizing ocean temperatures, Guadalupe is at a fairly high northern latitude (29°N) with a considerable difference between summer and winter temperatures. The possibility exists that food items available to the young in the surrounding waters differ considerably between winter and summer. To my knowledge *kaedingi* is the only hydrobatid (besides *Oceanodroma tristrami*) in the northern hemisphere that nests in the northern winter.

BREEDING BIOLOGY.—*Oceanodroma leucorhoa socorroensis* breeds only on Guadalupe Island, some 200 miles west of Baja California, Mexico. The POBSP surveys, as well as numerous surveys by Carl

Hubbs of Scripps Institution of Oceanography and other parties, have shown that at least the bulk of the storm petrel population is now restricted to breeding on tiny offshore islets free of introduced predators. The two best surveyed among these islets are Islote Negro and Islote Afuera near the Mexican settlement at the southern tip of the main island. We have indirect evidence that a sizeable population may still breed on the main island proper, but the actual nesting area has not been discovered.

This race of Leach's has presented some of the most puzzling problems of all forms studied. Between 22 and 23 June 1968 the populations on both Islote Negro and Islote Afuera were surveyed. On Islote Negro the estimated population of several thousand birds, judged by several hundred handled at the nest sites, was composed almost without exception of dark-rumped birds. On Islote Afuera, only about a mile and a half away, we estimated more than 90 percent of the population were white-rumped. There appeared to be no morphological difference except rump color between the two populations. This was inferred not only from living birds, but from the series of skins collected at the time. Vocalization recordings of individuals from both populations were taken, but these have not yet been analyzed. Suffice to say that the field workers could discern no differences in the calls of the two populations. To complicate matters even more, a series of about 50 birds collected aboard ship on the night of 28 June immediately off the southeast coast approximately 10 miles from these islets, contained individuals with every conceivable rump color from white through completely dark. Many of these were not in breeding condition, but a considerable number of birds with intermediate-colored rumps had heavily vascularized brood patches, indicating that eggs or young were already present. Had these birds been part of the populations on either Islote Negro or Afuera, it seems certain that they would have been noticed. Hence, this population was suspected of nesting somewhere on the main island. Huber spent about eight hours about the cliffs and among the pines on 29 June, but found no breeding storm petrels.

No explanation is offered regarding the allopatric distribution on adjacent islets of these populations. That chance would be operative in segregating these color morphs appears to be a mathe-

matical improbability, especially in view of the number of individuals involved. The total exclusion of an influx of birds of opposing rump colors can hardly be plausible. For the present, this confusing issue must await a more detailed study.

The nesting stages of the populations on these islets on 22 and 23 June 1968 were as follows:

Islote Negro: The summer breeding population on Islote Negro was estimated to be about 4000 birds. Storm petrels were found nesting over the entire islet, but definite concentrations were found wherever large masses of volcanic rocks were present, these apparently being the most favored sites. Lesser numbers were found nesting in soil burrows, excavated by Black-vented Shearwaters (*Puffinus puffinus opisthomelas*) or Cassin's Auklets, and under dense mats of plant material. The storm petrels themselves also excavated a considerable number of burrows in the hard-packed soil. The tiny entrance holes to many extensive burrows indicated that only storm petrels could have dug them.

Varying amounts of plant material in the form of seed pods or dried stems (usually of the introduced ice plant, *Mesembryanthemum* sp.) were used for nest linings. Nests in rocky areas usually had very little nest lining, the eggs being deposited on the sparse soil or on the rocks in some cases. The population on Islote Negro at this time was approaching its egg-laying peak with an estimated 20 percent of the nests containing fresh eggs. Only a single egg out of about 30 examined showed advanced incubation. The majority of the population appeared to be paired with completed or partially completed nest sites.

An occasional fresh egg was found lying on the ground outside nest cavities. These were presumably inadvertently kicked out by the shearwaters or murrelets, both of which utilized the larger nooks, and rock or soil crevices. Many old storm petrel eggs, presumably of the winter breeding population, were noted in and about active nest sites. It appeared that the two populations frequently utilized the same nest sites. This seems reasonable, as practically every good nest site was occupied by the summer breeders.

Birds vocalized continuously through the night, with a calling frenzy shortly after full dark. Most birds called from burrows; a few called on the wing.

All birds examined (a minimum of 500) on Islote

Negro had dark rumps. The most white noted on any bird was a few feathers at the sides of the rump. In these individuals the feathers were more gray than glaringly white.

Islote Afuera: Islote Afuera supported about 25 percent fewer birds than Islote Negro. The nesting cycle was roughly in the same stage, with a somewhat higher percentage of nests with eggs. This may have been due to the considerably less nest construction necessary, as the vast majority of birds on Islote Afuera occupied natural pockets and crevices in the lava rock instead of excavating burrows in the sparse soil.

At least 90 percent of the birds on Islote Afuera were white-rumped. Other than rump color, no differences could be detected between the populations of the two islets. Except for the following records of immatures, we have few data pertaining to later aspects of the breeding season of *O. l. socorroensis*. Huey (1930) records a juvenile with considerable down still adhering to the plumage that came aboard ship about a mile off Guadalupe on the evening of 27 September 1929, and another with completely downy underparts that came aboard ship 28 September, 26 miles north of Guadalupe. The POBSP found flying young with down on ventral regions sitting around burrows at night on 21 October 1967 on Islote Negro. The latest date for young of this population is a male juvenile with completely downy underside that flew aboard a ship off northeast anchorage, Guadalupe, on 12 November 1954. The three specimens mentioned above are in the San Diego Museum of Natural History. From the above records it can be surmised that young *socorroensis* leave the islands throughout the fall and hence overlap with the winter breeding population, at least from September through November.

Measurements of a series of 20 eggs of the summer breeding populations of Islotes Negro and Afuera are given in Table 28. Eggs of *socorroensis* are white with a wreath of fine reddish brown dots about the large end. The small size of *socorroensis* is reflected in the egg dimensions when compared to those of other races of Leach's Storm Petrel.

WINTER BREEDING POPULATION (*O. l. kaedingi* Anthony).—More confusing is the status of the winter breeding population that arrives on the same islets before all the summer breeders leave (see Hubbs, 1960). No POBSP survey was made during

TABLE 28.—Egg measurements of three subspecies of Leach's Storm Petrel (*Oceanodroma leucorhoa*) (data for *O. l. leucorhoa* and *O. l. beali* are from Palmer, 1962)

Measurement	<i>O. l. leucorhoa</i> (Bay of Fundy)	<i>O. l. beali</i> (NW U. S. coast)	<i>O. l. socorroensis</i> (Guadalupe Island)
Length with SD (n=20)	33.01 ± 1.06	31.46 ± 1.31	29.76 ± 0.72
Breadth with SD (n=20)	23.58 ± 0.57	23.21 ± 0.78	22.19 ± 0.74

the height of the breeding season of *kaedingi*, and we have few specifics pertaining to its cycle. It apparently begins coming to the islets in August, and thus at least a portion of the two populations overlap, as not all the summer breeders have left the islets by this time. On 21 October 1967 on Islote Negro, three pairs were noted during a mid-day survey of the islet. Approximately 30 minutes after sundown birds began appearing, and within an hour an estimated 100 birds were calling from the air and about 400 from rock crevices and burrows. Previous mention is made of *socorroensis* juveniles recorded at this time.

Specimens of juvenile *kaedingi* in the San Diego Museum of Natural History indicate the extent of the breeding season. J. R. Henderson took a three-quarters downy young from a burrow on 31 January 1950 and Carl Hubbs collected similarly sized young under a boulder on Islote Afuera on 11 February 1957. A juvenile with completely downy belly was taken aboard ship by Hubbs at northeast anchorage on 1 March 1965. A POBSP survey found on Islote Negro on 29 April 1967 one large juvenile with down on the venter. It apparently represented the last of the 1966–1967 winter season *kaedingi*. The June 1968 POBSP survey found about ten fully feathered chick mummies on Islote Afuera (presumably birds of the winter breeding population). Only one of these had a dark rump. All previously collected winter birds were white-rumped.

The conditions that cause two or more populations of the same species, or of different species, to utilize the same geographical area for nesting at different times of year appear to be the presence of vast uniform feeding grounds, coupled with very limited land space for breeding. Much the same

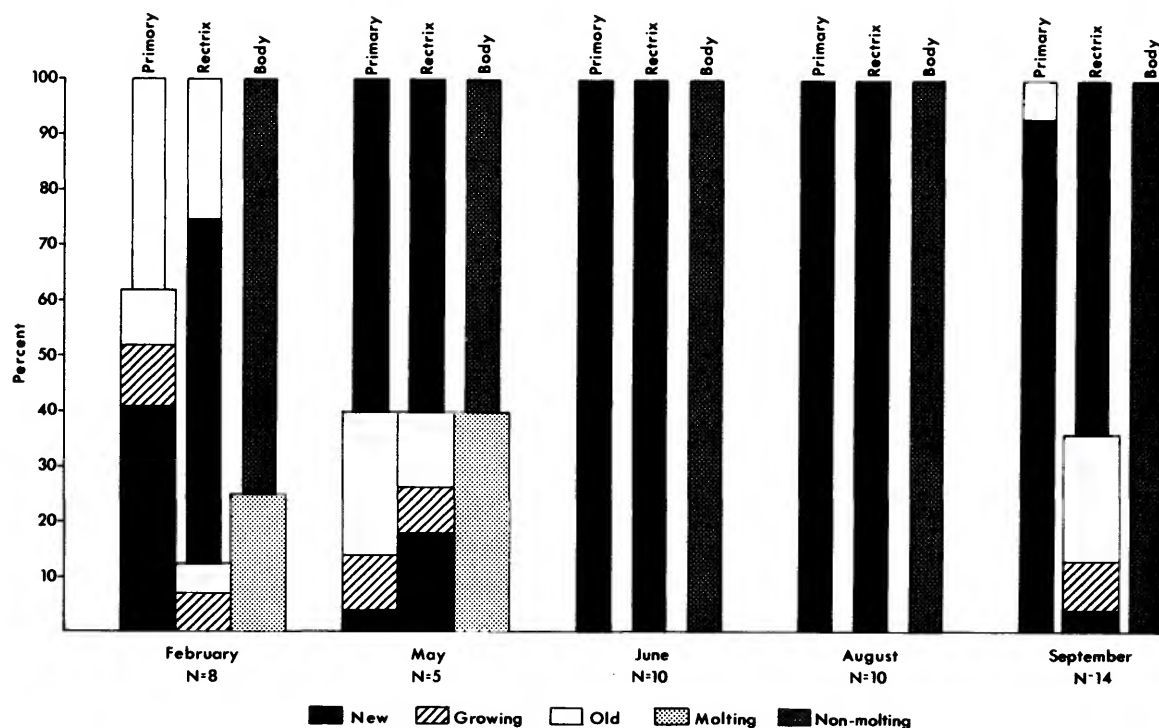


FIGURE 106.—Seasonal molt stages in *Oceanodroma leucorhoa socorroensis*.
(See Figure 99 for explanation of symbols.)

situation occurs at islands across the equatorial Pacific where two or more colonies of the same species breed on the same island at different times of the year. This is most noticeable in the Phoenix and Line groups with the Sooty Terns (*Sterna fuscata*) because the colonies are exceedingly large. However, species that are found breeding all months of the year, yet with a known changeover of marked individuals (such as the White Tern, *Gygis alba*) must be doing the same thing, only in a less dramatic way. How these species arrive at such "shift-work" utilization of an island is little known, but the factors bringing about such a situation are obvious. Aside from a shortage of actual physical space on these small islands, and the possibility of insufficient food in the surrounding waters to support the entire population at any one time of year, the social stresses between individuals would prohibit reproduction if all birds were to occupy the same area at one time.

MOLT.—Our samples, except for late summer, are

too small and disjunct in regard to time of year to be especially meaningful. Data are graphically demonstrated in Figure 106. For the most part, molt sequence closely parallels that of *O. l. beali*.

PREDATION.—Aside from the ever-present danger to storm petrels posed by the Western Gull (*Larus occidentalis*) (primarily avoided by the strictly nocturnal habits of the hydrobatids), Burrowing Owls (*Speotyto cunicularia*) appeared to be the greatest threat to these small Procellariiformes. In order to study predation, numerous remains of owl-eaten storm petrels were collected on Isote Negro during the April 1968 survey and again during the June 1968 visit. Although little of quantitative value can be determined from this study because of the wind-scattered remains, etc., predation was considerable. In April 1967 a downy young storm petrel was found, partially eaten, at the end of a burrow, indicating the possibility that the small owls may enter occupied storm petrel burrows and attack the young. At least one pair of owls each were noted on

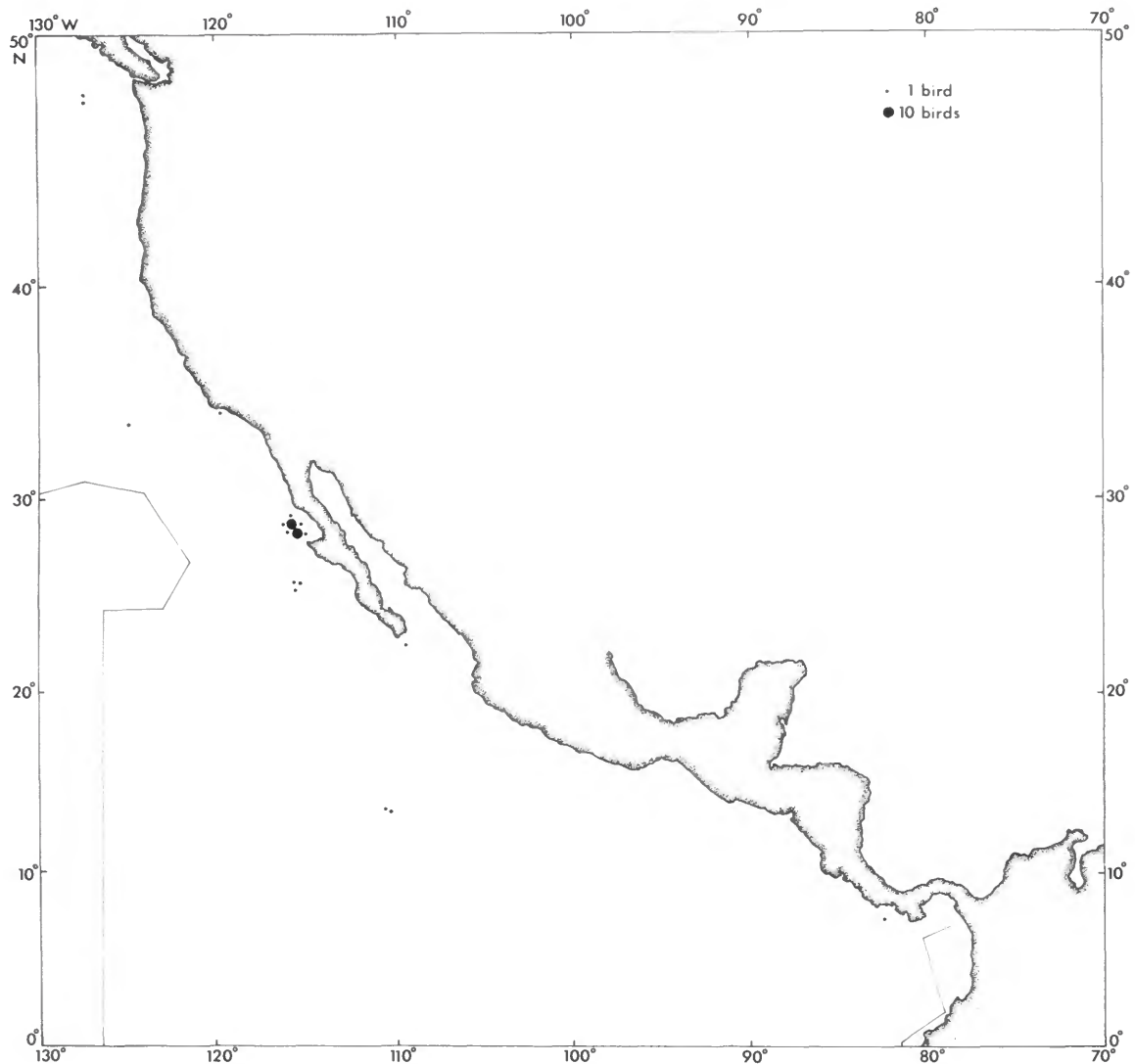


FIGURE 107.—POBSP sightings of *Oceanodroma homochroa*.

Islote Negro and Islote Afuera. During June 1968 the owls were largely feeding upon downy young Xantus' Murrelets (*Endomychura hypoleuca*), which were hatching in great numbers and trying to make their way to water.

Oceanodroma homochroa (Coues)

ASHY STORM PETREL

PELAGIC DISTRIBUTION.—The POBSP records of

this species are few, with low numbers of scattered sightings from ca. 7°N to 47°N; all sightings are along the western North American coast (Figure 107). The most pelagic sightings are of two birds near 13°N about 480 miles from the coast. The only concentration we recorded was off the Baja California coast between 28°N and 29°N during August 1967.

Uncertainty concerning the pelagic range of this species results primarily from difficulties in sep-

arating it in the field from closely similar dark-rumped *Oceanodroma leucorhoa* races such as *O. l. chapmani*, *O. l. socorroensis* and *O. l. willetti* (= *O. l. beali*). It probably occurs in rather low numbers compared with its closely allied forms.

BREEDING BIOLOGY.—A POBSP survey around San Miguel Island in the Channel Islands off the California coast 14 and 15 May 1968, found small numbers of birds on both Castle Rock and Prince Islet, all in empty nest cavities in rock crevices among a colony of Cassin's Auklets. Flight calls of the storm petrels were heard shortly after full dark, but it was impossible to make an estimate of the population size because of the din of surf and calling auklets. The few birds examined at this time had bare or defeathering brood patches.

On another survey of San Miguel from 28 May to 7 June 1968, birds were still courting; one egg each was found on Castle Rock and Prince Islet. The maximum estimate at that time was 100 birds for the San Miguel population. A bright moon at the time seemed to retard the arrival of the birds on the islets and reduced their activity. Perhaps the Western Gulls take advantage of the moonlight to prey upon these petrels as the Great Black-backed Gulls (*Larus marinus*) and Herring Gulls (*L. argentatus*) prey upon Leach's Petrels in the Bay of Fundy (Gross, 1935). Gross notes that on moonlit nights very little storm petrel activity occurs.

In the Coronados Islands Joseph Jehl of the San Diego Natural History Museum collected a few Ashy Storm Petrels in a mist net on Center Island the night of 17 May 1968, but POBSP recorded none during a 30 June to 1 July 1968 visit. No evidence of nesting was found on either visit; apparently very few individuals utilize the Coronados. Orr (1944) gives an excellent summary of what little is known of the breeding biology of this species along the California coast.

From a series of 20 birds collected at San Miguel Island, two show considerable amounts of whitish feathers at the sides of the rumps. This is interesting, not only from the standpoint of the relationship of *homochroa* to *leucorhoa*, but from the fact that selection for dark rumps seem to have affected all hydrobatid forms along the middle western North American coast (an area of excessively high gull predation?).

Oceanodroma castro (Harcourt)

HARCOURT'S (OR MADEIRAN) STORM PETREL

PELAGIC DISTRIBUTION.—The pelagic range of Harcourt's Storm Petrel in the Pacific is rather extensive, as indicated in Figures 108 and 109. The sightings recorded probably represent only a small fraction of the actual birds seen, as those shown represent only sightings considered positive. The more extensively white rump of Harcourt's as opposed to Leach's could often be used to separate these two forms at close range, but undoubtedly the majority of birds of this species were recorded by POBSP personnel only as "unidentified white-rumped storm petrel." Despite the difficulty of distinguishing Harcourt's from other white-rumped forms (especially Leach's and Wilson's), specimens of Harcourt's collected at various points throughout the pelagic range lend credibility to the observations.

In the central Pacific birds were recorded commonly south and southwest of the Hawaiian Islands to 4°S, with one sighting south of 8°S. Birds were also common to the west and northwest of the Hawaiian Islands and it is likely that the species ranges beyond the boundaries shown in the northern sector as birds were observed practically to the limits of POBSP cruises in that area. Although it cannot be determined from the collected specimens, central Pacific records probably represent birds from the Hawaiian population (dubiously distinctive *O. c. cryptoleucura*).

Harcourt's distribution in the eastern Pacific is even more extensive than that recorded in the central Pacific. Sightings were recorded from near Panama west to 120°W and from 25°N to south of 13°S. While it might be logical to assume that eastern Pacific records are attributable to the Galapagos Islands population, we cannot, in fact, assign origin to them. The species obviously ranges so widely at sea that sightings at any point could be of birds from any one of the Pacific breeding stations. Three specimens taken near the Galapagos are most probably referable to the breeding race of that island group (*O. c. "bangsi"*), but as Austin (1952) demonstrates, none of the named Pacific subspecies of this form are separable.

BREEDING BIOLOGY.—The available breeding data for this species are summarized by Palmer (1962). The POBSP was unable to add further information of its breeding status in the Hawaiian Islands.

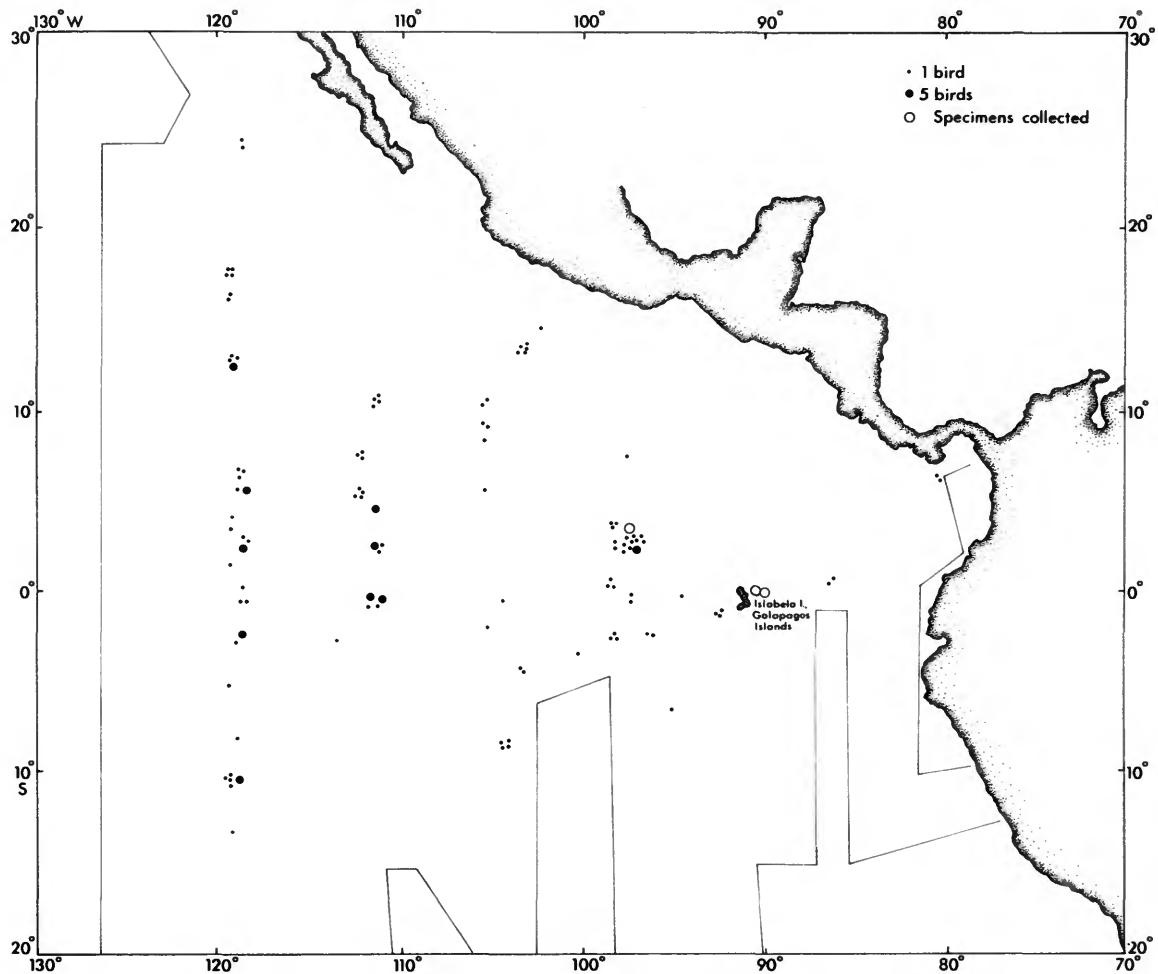


FIGURE 109.—POBSP sightings and specimens of *Oceanodroma castro* in the eastern Pacific.

court's Storm Petrel during a day of collecting on 25 June 1966 just off Kauai Island near the Waimea Canyon area, where I saw a considerable number of birds and collected one specimen, a female with ovary enlarging, but not yet in breeding condition. Birds appeared to be both going to and leaving the island throughout the day, but we could not approach the shoreline closely enough to determine if the birds went to land. The population on Kauai, as judged by the number of specimens and sightings, cannot be large.

MOLT.—The data from the ten specimens collected by POBSP are given in Figure 110. Briefly, our May and June birds collected in the central Pacific,

as well as March birds collected near the Galapagos, are in new plumage without molt except for terminal stages in the rectrices of the May birds. October and November central Pacific birds are in intermediate primary and body molt with very worn, but unmolting, rectrices. Oddly enough, a Galapagos bird collected in late July is in exactly the same stage of primary molt as two November specimens from the central Pacific.

Oceanodroma tethys (Bonaparte)

GALAPAGOS STORM PETREL

PELAGIC DISTRIBUTION.—The Galapagos Storm

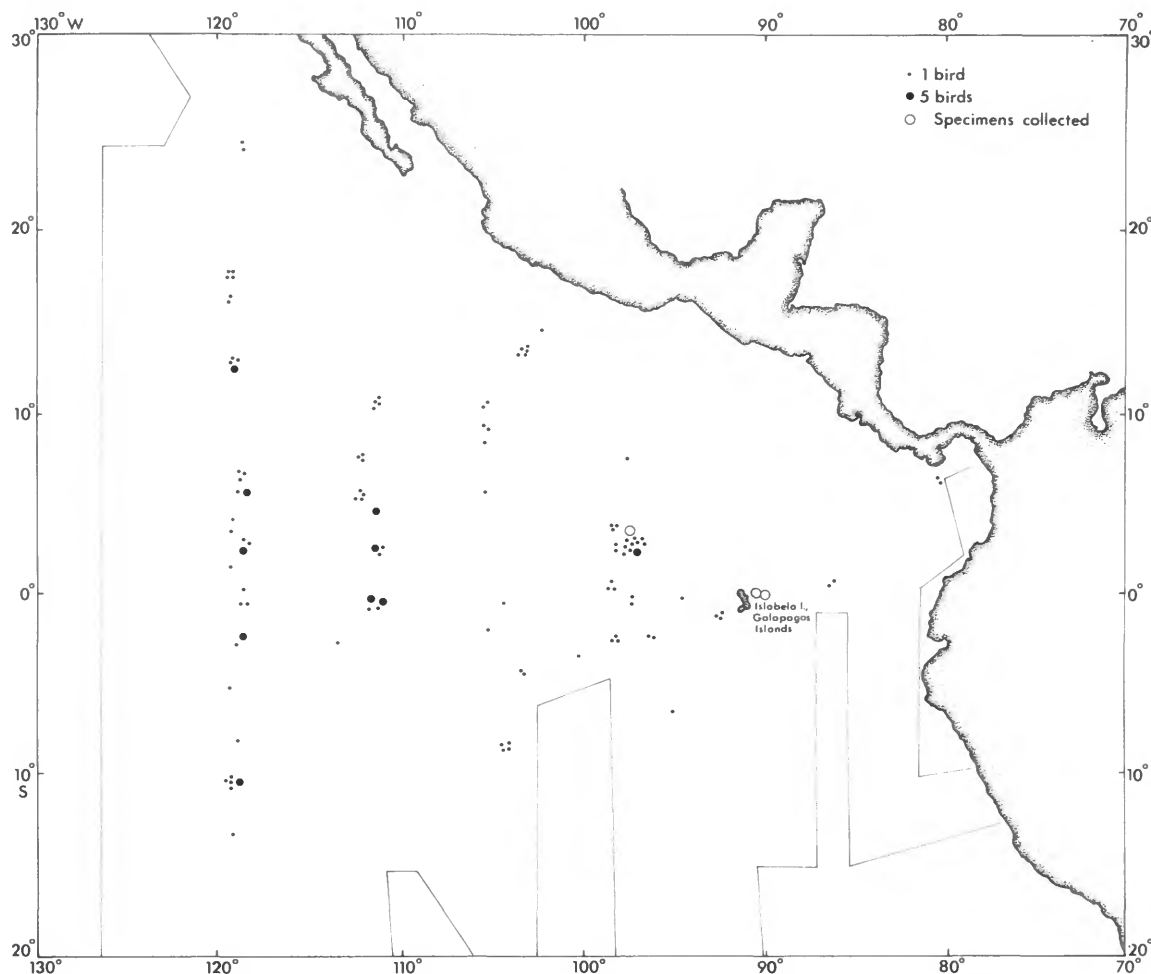


FIGURE 109.—POBSP sightings and specimens of *Oceanodroma castro* in the eastern Pacific.

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GALAPAGOS STORM PETREL

PELAGIC DISTRIBUTION.—The Galapagos Storm

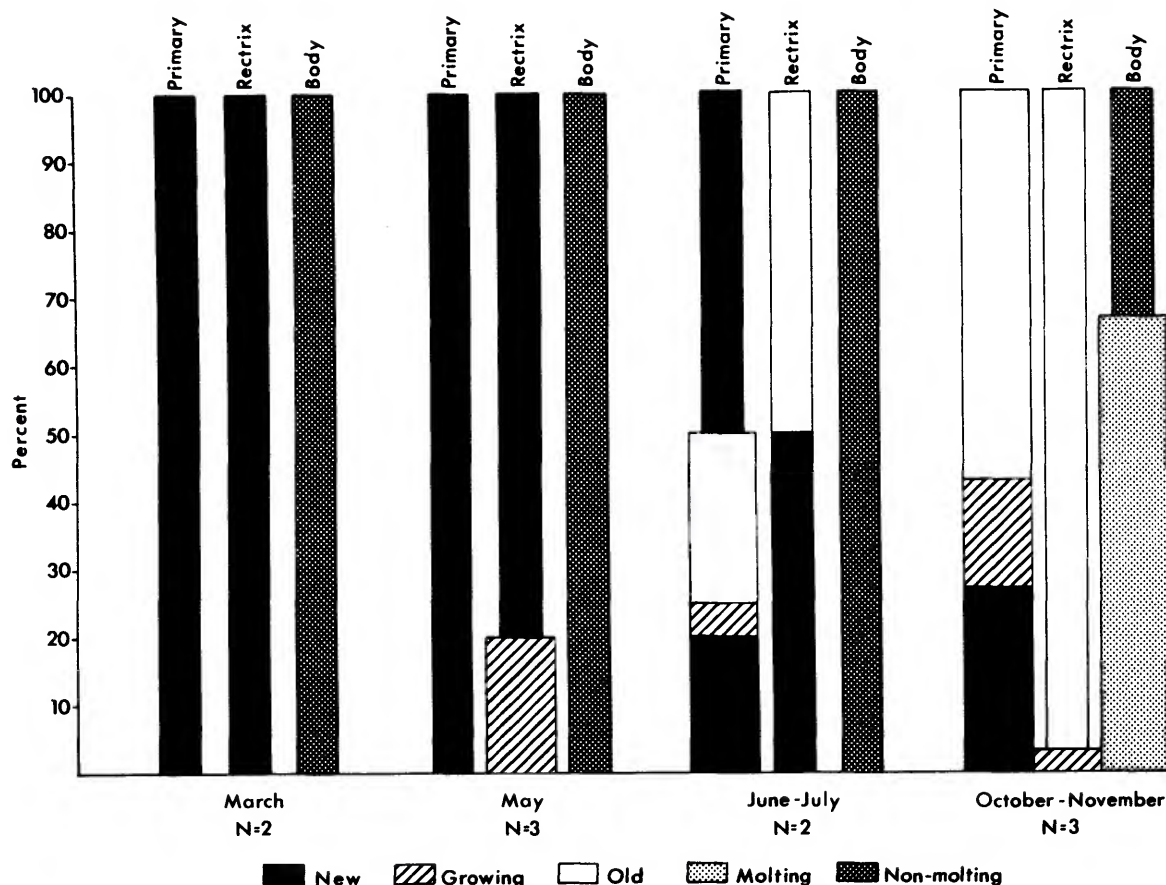


FIGURE 110.—Seasonal molt stages in *Oceanodroma castro*. (See Figure 99 for explanation of symbols.)

Petrel is one of the few white-rumped species in the Pacific that can be identified with a fair degree of certainty under most field conditions. The extremely large, prominent, wedge-shaped white rump, and alternately fluttering and bouncy flight are good characters for distinguishing most individuals from *Oceanodroma leucorhoa*, the species regularly recorded with *O. tethys* over much of the latter's pelagic range. When I first encountered *tethys* at sea, and before I learned some of its more subtle characters, I had difficulty making on-the-spot distinctions between it and equally small, exceptionally white-rumped *O. l. socorroensis*. Part of this difficulty arose from the fact that both forms were in extremely ragged plumage at the time. It may be noted that specimens of both races of *O.*

tethys had medium-gray oil (uropygial) glands, as opposed to the creamy white oil glands of all races of *O. leucorhoa* and of *O. castro*.

Supposedly, the nominate race (*O. t. tethys*) breeds in the Galapagos from April through September(?). The POBSP pelagic specimens of this race are confined to August 1967 and March and April 1968. During the latter period concentrations were especially prominent in a broad band along the equator from about 3°N to 2°S between longitudes 97°W and 105°W. August specimens were taken at 12°N, 120°W. A June specimen in the San Diego Natural History Museum was taken at 15°N, 101°W. Huey (1952) reports a specimen taken by J. R. Pemberton in March 1938 at Roca Partida in the Revilla Gigedo Islands south-southwest of Baja

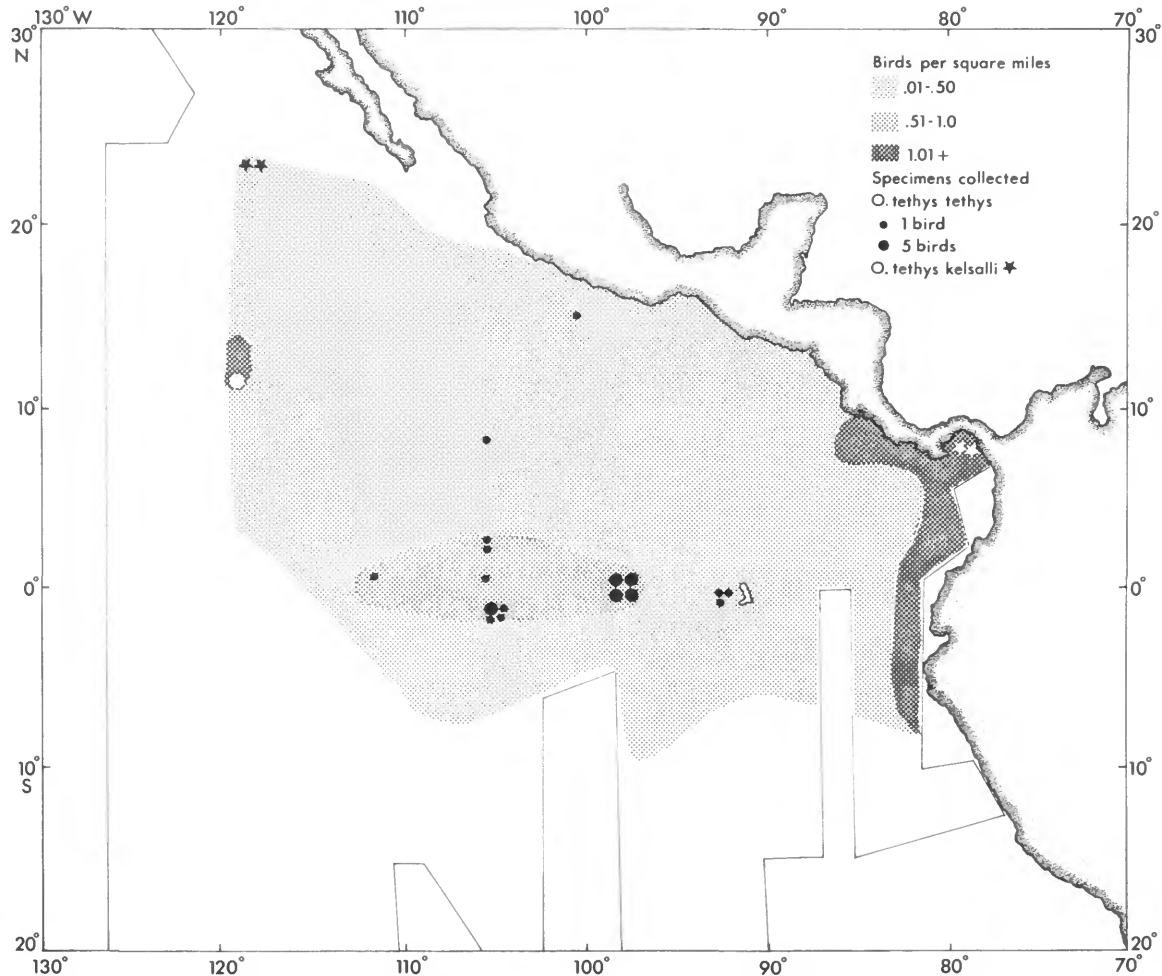


FIGURE 111.—POBSP sightings and specimens of *Oceanodroma tethys*.

California (ca. 19°N). In this same publication Huey reports a male of this race in nonbreeding condition (testes 3 x 2 mm) taken from a colony of *Oceanodroma leucorhoa kaedingi* on Guadalupe Island off Baja California in January 1950. The bird was found in a nest cavity with a downy young *kaedingi*. For whatever reason the bird came to the island, Hubbs (1960) is incorrect in regarding this as constituting a breeding record for the Galapagos Storm Petrel at Guadalupe. I have examined this specimen at San Diego and, except for a short, heavy bill and slightly small wing for *O. t. tethys*, it corresponds well to that form. This locality, at

roughly 29°N, apparently marks the northern limit for the nominate race.

The second-named form of this species, *O. tethys kelsalli* (Lowe), breeds on the Pescadores and San Gallan Islands off the coast of Peru. Northernmost POBSP records of this race are of two individuals collected on 6 August 1967 at 23°03'N, 118°24'W. Moffitt (1938) reports 12 specimens collected at 22°30'N, 112°39'W on 22 July 1905 and another specimen taken at 16°45'N, 110°28'W on 22 September 1933. These birds had traversed northward through most of the recorded pelagic range of the nominate race. Our pelagic sight records (Figure

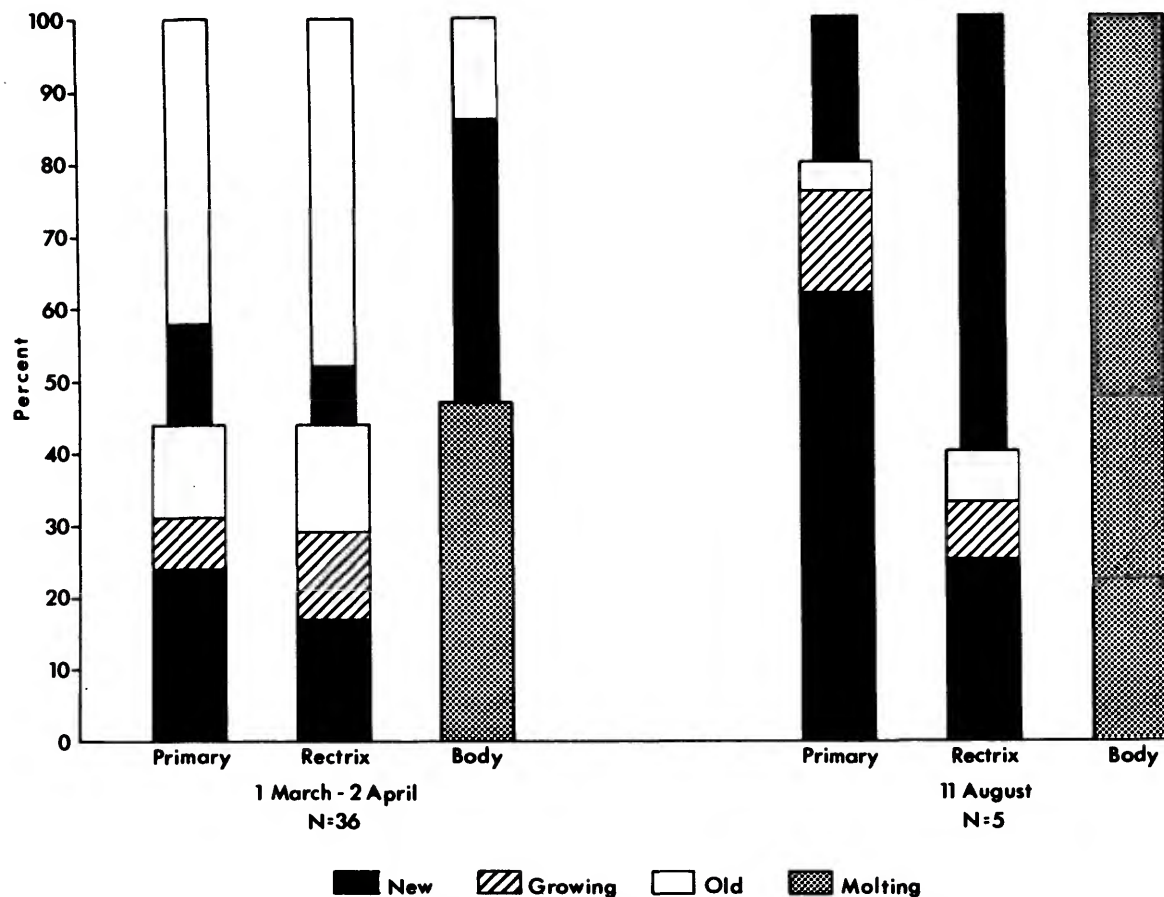


FIGURE 112.—Seasonal molt stages in *Oceanodroma tethys tethys*.
(See Figure 99 for explanation of symbols.)

111) cannot be qualified to race as the two named forms are separable only on mensural differences. The pelagic ranges of the two races show considerable sympatry.

Other POBSP specimens of *O. t. kelsalli* were collected in the Gulf of Panama during August 1968 and June and August 1969. Large numbers of *O. tethys* were observed in the gulf from August through November 1968 and June through August 1969. Although only a relatively few specimens were collected, all are definitely referable to *O. t. kelsalli*. On this basis, it is reasonable to assume that most Gulf of Panama wintering *O. tethys* are of the race *kelsalli*. From November on, *tethys* is absent from the Panama gulf waters, when it is apparently replaced by the Black Storm Petrel and the Least Storm Petrel.

MOLT.—Considerable variation in molt is displayed in two series of *O. t. tethys* collected at sea. A series of 36 taken between 1 March and 2 April falls essentially into two categories:

1. *Molting*: As shown in Figure 112, 44 percent of the birds in this sample are molting in both primaries and rectrices. There was no exact correlation in the progress of molt between these two plumage areas. A few birds still molting the primaries had completed their rectrix molt and vice versa. Hence, although only 44 percent of the sample is involved in each case, the total number of individuals concerned in these combined categories equaled 50 percent of the sample. In practically every case, primary and/or rectrix molt was accompanied by body molt.

2. *Nonmolting*: The remainder of the sample

(50%) not in primary or rectrix molt, was, for the most part, in old, but relatively unworn plumage, indicating that molt had occurred within the previous few months. Definition of plumage condition in rectrices or remiges of birds not in molt is somewhat subjective. When molting, a distinction is easily made between new and old feathers, primarily because the feathers being replaced are obviously old and show considerable wear and discoloration.

The majority of birds in both molting and non-molting categories were adults, judging by gonadal condition. None was in breeding condition, although several may well be considered either to have begun gonadal enlargement or retrogression. The nominate race of *O. tethys* is supposed to have a complete postbreeding molt from July through October (Murphy, 1936:730). It appears from our sample that the duration of the molt cycle is much more extensive. If *tethys* has a molt cycle similar to races of *O. leucorhoa*, a large number of birds would be expected to terminate a molt just prior to the advent of a breeding cycle.

The small series of five birds collected in August are all in finishing stages of complete molt, or in very new plumage. A combination of immatures and adults is represented, judging by gonads. This series substantiates Murphy's (1936:730) statement concerning a postbreeding molt from July through October, but half of the large series taken in March and April certainly do not correspond to this pattern. Obviously we need to know the ages and times of breeding cycles of individual birds before it will be possible to draw conclusions concerning the molt cycle of the species.

Oceanodroma hornbyi (Gray)

HORNBY'S STORM PETREL

PELAGIC DISTRIBUTION.—The few POBSP records of sightings and specimens of this southern hemisphere hydrobatid were recorded in August 1967 in the Peru Current southeast of the Galapagos Islands along the South American coast (Figure 113). Three specimens taken at 3°38'S, 87°01'W were adult females with medium fat, ovaries between 3 and 5 mm, granular. I have no data for a fourth specimen taken south of the above area at 9°29'S, 82°05'W. Murphy (1936:741–743) limits the species to the Peru Current roughly between Valparaiso, Chile, and the equator.

The breeding grounds of *O. hornbyi* are still imprecisely known, but Johnson (1965:108) cites four points of evidence that strongly indicate it nests inland along the Chilean and Peruvian coasts. These are summarized as follows: (1) In 1894, Dr. Darapsky found a fully grown immature specimen (with patches of down still adhering) in a hole in the hills of the coast ranges of the port of Taltal, in the southern Antofagasta Province (specimen in the National Museum of Santiago). (2) In 1923, Wetzel found mummified nestlings in holes in the canyon of the Loa River at the point where it crosses the nitrate desert inland from Tocopilla. (3) Another mummified specimen was found in December 1923 in the nitrate fields of Santa Luisa de Taltal, 30 miles from the coast at an altitude of 5000 feet. (4) The Koepckes took several specimens at night in the streets of Lima, Peru. Some of these had abundant down patches on the abdomen.

Oceanodroma melania (Bonaparte)

BLACK STORM PETREL

PELAGIC DISTRIBUTION.—Abundant observations of this species were made on POBSP cruises along the western American coast from about 38°N to the equator. Sightings below the equator (to 7°S) were few, as were those in the extreme northern sector and at extreme distances from the coast (Figure 114). There was a pronounced movement into the Gulf of Panama during November, which presumably indicates a southward movement after the breeding season. The species was common in the gulf area until June, during which time the Least Storm Petrel was also abundant. Most sightings along the California coast are summer records, but a few birds were recorded above 34°N in December. At sea the Black Storm Petrel is a swift flyer. During collecting activities off the Baja California coast, the birds appeared to have no problem in outdistancing our skiff, which was moving at an estimated 25 knots.

BREEDING BIOLOGY.—*Coronados Islands*: During a POBSP survey on 1 and 2 May 1968, Black Storm Petrels began coming in over the cove on North Island precisely at full dark. Their appearance was in exact correlation with the termination of Western Gull movements and one may be certain that

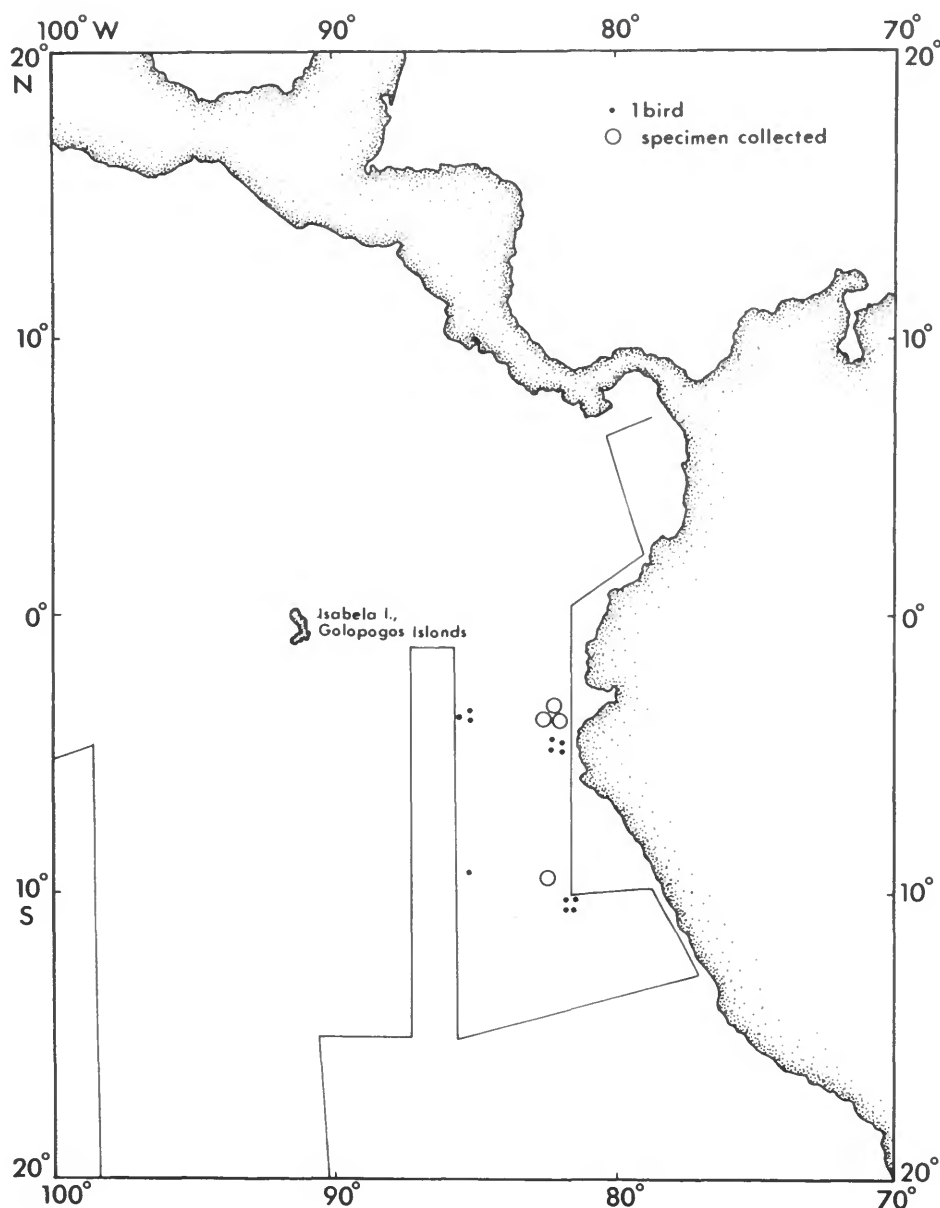


FIGURE 113.—POBSP sightings and specimens of *Oceanodroma hornbyi*.

the timing of these activities is not coincidental. Storm petrel aerial movements and vocalizations were most intense during the first few hours after dark and had essentially stopped by midnight. An increase in flying birds was noted near the beach at about 0100; this possibly represented birds leaving

the island. Two characteristic calls were noted: an aerial call described by most field workers as "puck, puckeroo," and a variable "twitter" uttered only from nest cavities. This latter call may continue for many minutes. The nest sites on North Island were invariably in deep recesses under large boulders

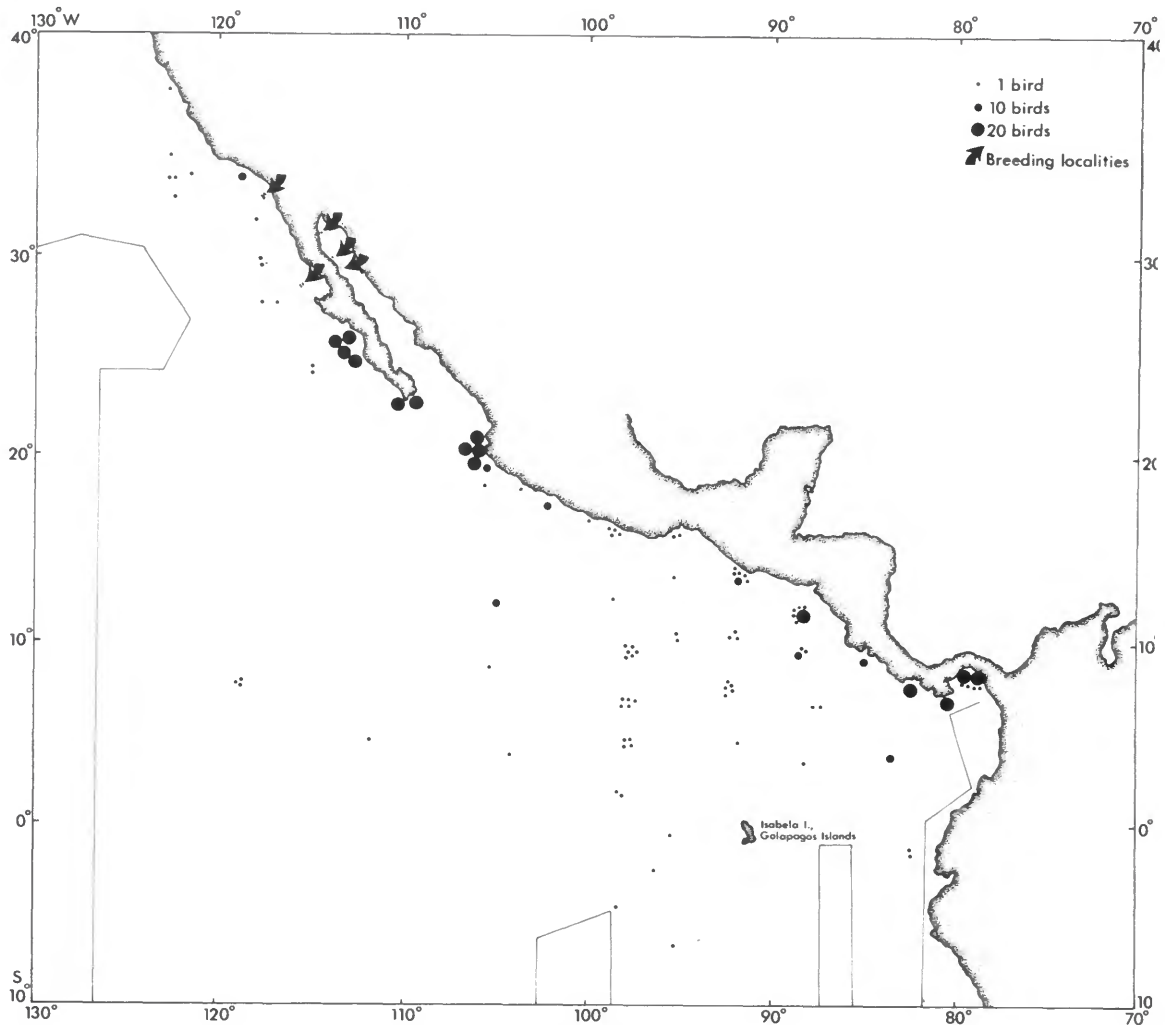


FIGURE 114.—POBSP sightings of *Oceanodroma melania*.

that prevented investigating the nests in most cases. A few such large "fortresses" harbored more than one pair. The four to six nests that could be examined at this time contained both members of the pair, but none had eggs or young. Individuals taken in a mist net had bare or defeathering brood patches. During a visit on 30 June 1968, a few birds were noted on Center Island and a chick, estimated to be only a few days old, was found on North Island. In the San Diego Natural History Museum a series of downy nestlings, ranging in size from small to large, are recorded from the Coronados from 13 August to 5 September.

San Benitos Islands: On a POBSP survey from 26 to 29 April 1968, these petrels were noted coming in over the islands at night, with a peak of aerial movements and vocalizations during the first three hours of darkness. Little activity was noted for the remainder of the night. No evidence of nesting was recorded at that time. During a survey from 25 to 27 June 1968, a sample of nest sites examined showed that birds were on fresh- to medium-incubated eggs, with a few individuals still calling from as yet empty nest cavities. The preferred nesting sites of this species seemed to be under large boulders on talus slopes. In some cases Least Storm

Petrels were found nesting in the same burrows with the Blacks. The Black Storm Petrels were found on all three islands in the San Benitos group, with greatest densities on West Island. A population estimate for the island group at that time was 10,000+ birds. A prime mortality factor was the

abundant cholla cacti throughout the nesting area. Birds flying about in the dark were often impaled upon the spines; on one slope several Black Storm Petrels were found dead in this manner (see comparable data on *Oceanodroma leucorhoa chapmani*).

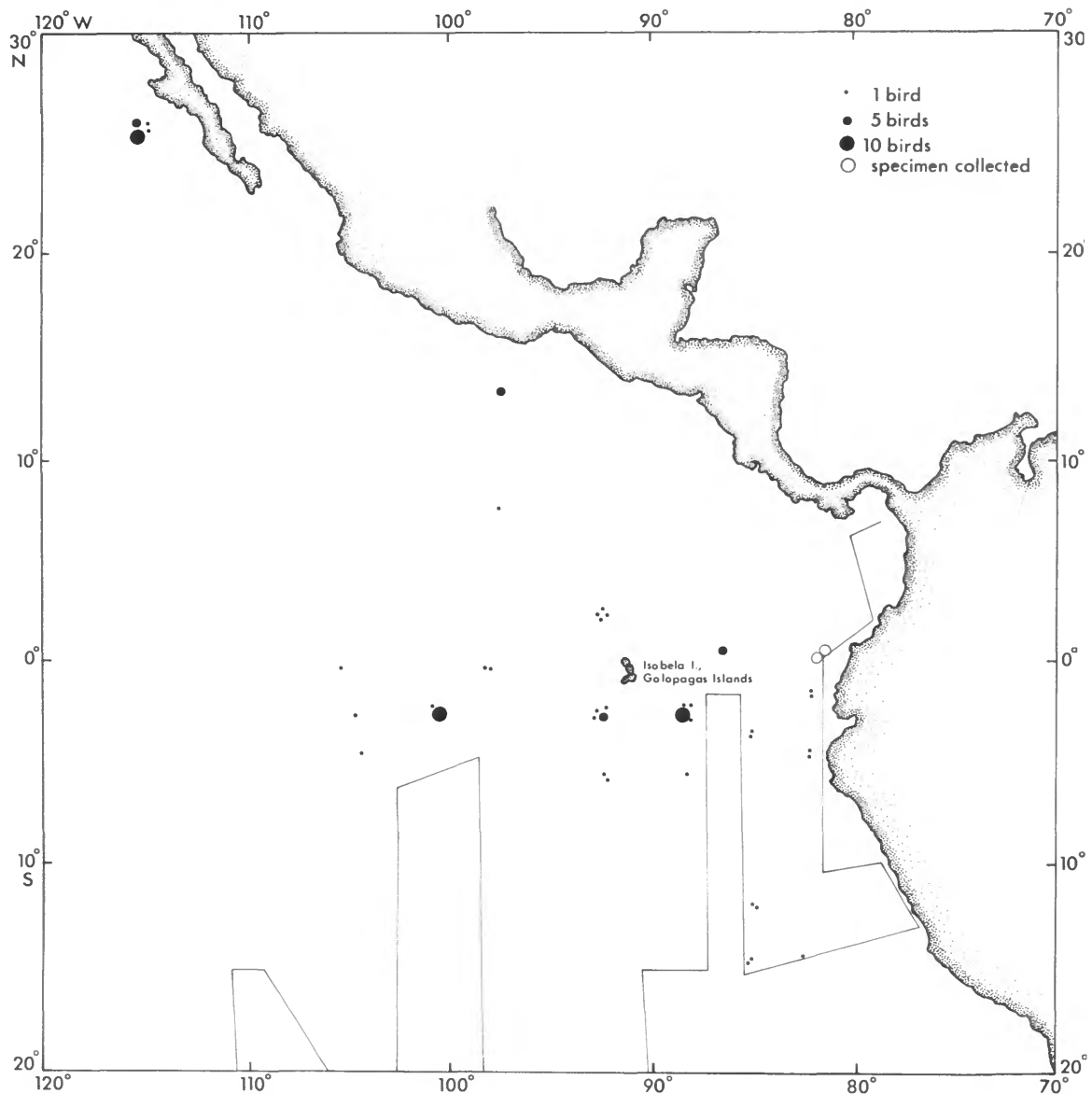


FIGURE 115.—POBSP sightings and specimens of *Oceanodroma markhami*.

Oceanodroma markhami (Salvin)

MARKHAM'S STORM PETREL

PELAGIC DISTRIBUTION.—Most POBSP pelagic sightings of this species are in August and September along a broad equatorial front from the South American coast west through the Galapagos area to 105°W (Figure 115). A group of more northerly sightings off the coast of Baja California may well represent erroneous identifications attributable to the very similar *Oceanodroma melania*. I doubt if the two species can be distinguished in the field, and *melania* would certainly be the more expected form in these northern waters. It may be noted, however, that Murphy (1936:740) cites Loomis (1918:174) as having recorded *markhami* at 13° 28'N, 108° 52'W, and just south of Cocos Island, 5° 33'N, 87° 00'W. Two specimens were collected by POBSP along the South American coast. Both individuals taken on 6 August 1967 at 00° 18'N, 81° 51'W were females with small gonads (and oviducts never used), light fat and heavy contour molt.

The breeding grounds of this species are still unknown. Murphy (1936:739) records several females with fully formed eggs in the oviducts taken by Rollo Beck in early June, 75 to 80 kilometers off the Peruvian coast. He further states that the only islands off the Peruvian coast not thoroughly investigated were the Hormigas de Afuera, which because of their exceedingly low elevation seemed a doubtful nesting site. He suggests the possibility of their nesting inland in the Andes. Johnson (1965:107) notes that Carlos Reed collected a specimen on 1 December off Antofagasta, Chile (23°S) that still had traces of down on the head and abdomen. He also records an immature specimen with abundant down on the breast and abdomen taken between Pica and Matilla, some 30 miles inland from the port of Iquique, Chile.

Oceanodroma tristrami Salvin

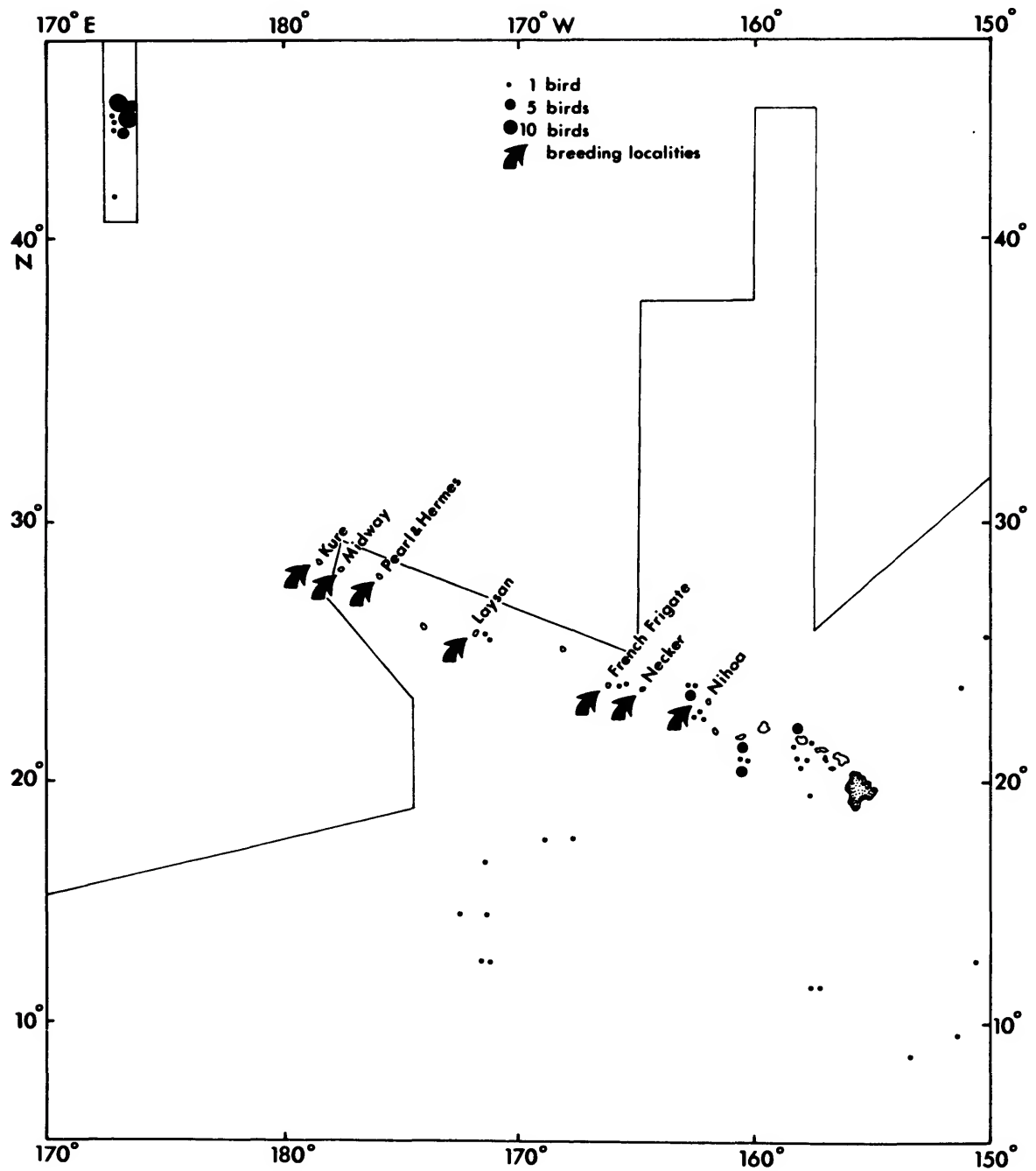
SOOTY STORM PETREL

PELAGIC DISTRIBUTION.—The POBSP pelagic sightings of this species are from various positions around the Hawaiian Islands, with concentrations near the Hawaiian Leewards (breeding sites), as would be expected (Figure 116). A disjunct, high-density concentration was also recorded between 44°N and

45°N near 173°W. The latter records may pertain to *tristrami* populations from the Bonin or Izu islands, or possibly to *Oceanodroma matsudairae* from the Bonin Islands. It is extremely doubtful if *tristrami* could be differentiated from *O. matsudairae* in the field. No specimens are available to clarify which of the two species were seen here, but even if specimens were available, distinctions could not be made between the Hawaiian and Bonin Island populations of *O. tristrami*.

BREEDING BIOLOGY.—Sooty Storm Petrels have a disjunct breeding distribution, with populations at Torishima in the southern Izu Islands (Austin, 1952), the Bonin Islands, and the Hawaiian Leewards. The specific localities in the Leewards are Laysan, Pearl and Hermes Reef, and Midway. Richardson (1957:19) mentions the possibility of their breeding on Necker but gives no details. Bryan and Greenway (1944:96) record the species on Nihoa. Clapp and Woodward (1968:10) report recent POBSP records on Kure Atoll and French Frigate Shoals. The latter cite the collection of three specimens with definitely enlarged gonads on Kure (one each on 1 January 1964, 1 March 1965, and 12 December 1965). The January 1964 bird was one of two observed digging a burrow. Two other birds were observed digging a burrow on 2 April 1964, and one examined in the field between 30 December 1966 and 5 January 1967 had a completely bare brood patch. Others were seen on Kure between November and January during the years 1963 to 1967. Three specimens collected 1 to 3 January 1967 have greatly enlarged gonads. On 14 March 1967, one very small downy chick and another about three-quarters grown were found in shallow burrows under the grass on Whale-Skate Island, French Frigate Shoals. Amerson noted a fledgling here in early June 1967. I believe it very likely that the species will eventually be found nesting on Lisianski Island, which has an extensive habitat comparable to that which supports a sizable population on Laysan. From this latter island POBSP collected three specimens on 22 October 1966 with considerably enlarged gonads. Willett (1919) reports egg-laying on Laysan from 1 to 15 January.

Inadequate POBSP winter surveys in the Leewards, plus the very secretive nature of this storm petrel on the breeding grounds, make it difficult to obtain a clear picture of the breeding cycle. From available data it appears that the species is to be found on

FIGURE 116.—POBSP sightings of *Oceanodroma tristrami*.

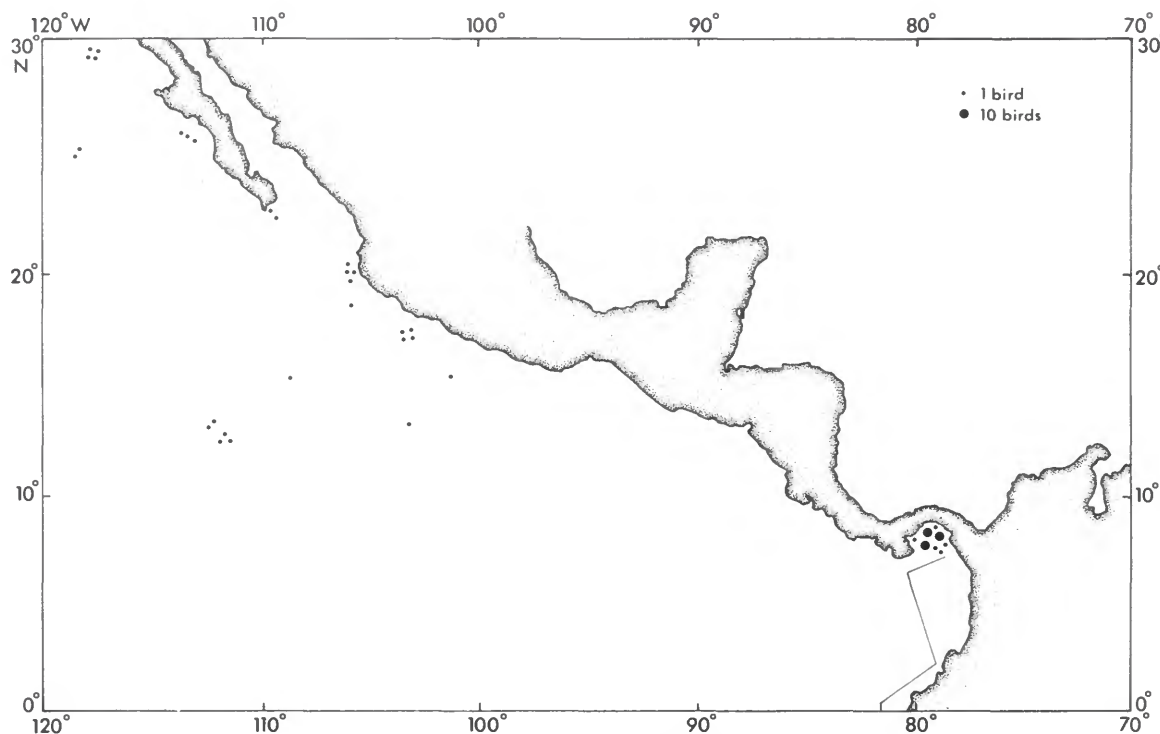


FIGURE 117.—POBSP sightings of *Halocyptena microsoma*.

the breeding grounds during an extended period from at least October to May. Apparently December and January are peak egg-laying months; both young and adults are gone from the islands by mid-May.

Halocyptena microsoma Coues

LEAST STORM PETREL.

PELAGIC DISTRIBUTION.—At sea this species is usually distinguishable from other dark-rumped forms by its tiny size. Although it is normally a more coastal form, it was sighted by the POBSP as far as 600 miles off the Mexican mainland. Large numbers are found in the Gulf of Panama during the winter months (December to April). There appears to be replacement between this species and *Oceanodroma tethys* in the Gulf of Panama. *Oceanodroma tethys* is very abundant from June to November, but completely disappears in the latter month when *H. microsoma* begins showing up in numbers.

A small number of Black Storm Petrels are, however, present during the time the Least is abundant. Other than the concentrations in the Gulf of Panama, the majority of POBSP sightings of the Least Storm Petrel was along the coast of Baja California and the Mexican mainland (Figure 117).

BREEDING BIOLOGY.—The Least Storm Petrel breeds on the San Benitos Islands and on various other islands in the Gulf of California. During a POBSP survey of the San Benitos on 28 April 1968, the only Least noted was one that came aboard ship offshore. During the 25 to 27 June 1968 survey here, Leasts were abundant on all three islands of the group. Nesting was primarily restricted to rock outcrops and talus slopes, and nests were invariably in rock crevices. Occasionally more than one pair were found in suitable cavities and some birds were nesting in the same cavities with the much larger Black Storm Petrels. A few eggs of the Least were found, but most of the birds in June were still in early stages of nest site selection and courting. An

estimate for *Halocyptena* during the June survey was ca. 15,000 birds for the island group. As mentioned in the sections on *O. melania* and *O. l. chapmani*, *Halocyptena* were adversely affected by the abundant cholla cacti on the islands and several birds were found impaled on the spines.

On islands in the Gulf of California, the Least Storm Petrel is frequently mentioned as nesting in association with the fishing bat (*Pizonyx vivesi*). Maya (1969), who studied this bat in the Gulf, felt that a lizard (*Cnemidophorus* sp.) preyed upon the young storm petrels and that the lizards were less prone to inhabit cavities where the bats lived. On Isla Partida (in the northern part of the Gulf of California) R. D. Ohmart (pers. comm.) saw no predation by the lizards on very small storm petrel chicks left unattended by their parents during the daytime. Once after removing an adult storm petrel from its nest, he saw a large scorpion carry away the egg. Ohmart did not feel that the presence of the bat offered any particular advantage to the petrel. It appeared to him that the Least and Black Storm Petrels and the fishing bat clumped to avoid excessive heat and gulls, and possibly to gain in relative humidity. Both eggs and small downy chicks of the Least Storm Petrel were found on Isla Partida from 12 to 21 June 1968. Nests were beneath rocks on the ground or in cavities among rock piles.

Oceanites oceanicus (Kuhl)

WILSON'S STORM PETREL

PELAGIC DISTRIBUTION.—The POBSP pelagic records indicate extremely widespread distribution of this species in the Pacific, with two decided centers of abundance (Figures 118 and 119). The equatorial central Pacific records are practically all confined to October and November; all are of adults with somewhat enlarged gonads and very heavy fat, and in all probability represent birds returning to the Antarctic breeding grounds. An April specimen from this area is probably a straggler from an apparent postbreeding migration that moves north through the Marshall Islands in the spring (Huber, 1971). Our surveys give no clue to northward extent of this movement, nor to the distribution or activities of the birds between April and October.

Large numbers are recorded in the Peru Current along the northwestern coast of South America during August. A fair number of stragglers are recorded throughout the eastern Pacific to at least 31°N. In view of this, the various coastal California records in August (1910, 1935, and 1959) summarized by Nisbet and McCaskie (1960:141) seem not too unusual considering the species' wide dispersal. It should be emphasized that the POBSP sight records shown are only those of fairly positive nature; undoubtedly many more birds were observed which were recorded only as "unidentified white-rumped storm petrel."

Oceanites gracilis (Elliot)

GRACEFUL STORM PETREL

PELAGIC DISTRIBUTION.—Most POBSP sightings of this species were during September near the Galapagos Islands. Other cruises were run about the islands during other times of the year, especially March and April, and relatively few birds were seen. Most of our September sightings were within a hundred miles of the Galapagos (Figure 120). Loomis (1918:181) states that "they were never observed far from land, the greatest distance being about 50 nautical miles." Murphy (1936) has no record of its breeding, but it has been taken just offshore of several of the Galapagos Islands and unquestionably breeds there.

The race *O. g. galapagoensis* obviously restricts itself to the cold waters of the Peru Current just to the west of the Galapagos. The nominate race *O. g. gracilis* appears to be restricted to the Peru Current between Valparaiso, Chile, and Santa Elena, Ecuador (Murphy, 1936).

Fregetta grallaria (Vieillot)

WHITE-BELLIED STORM PETREL

PELAGIC DISTRIBUTION.—The primary distribution of this species in the area covered by POBSP was along 85°W from 06°S to 15°S. Two scattered sightings were recorded at 09°45'S, 117°43'W, and 02°17'N, 104°W (Figure 121).

Murphy (1936:762) recorded that R. Beck took a specimen of *Fregetta grallaria titan* at 04°20'S,

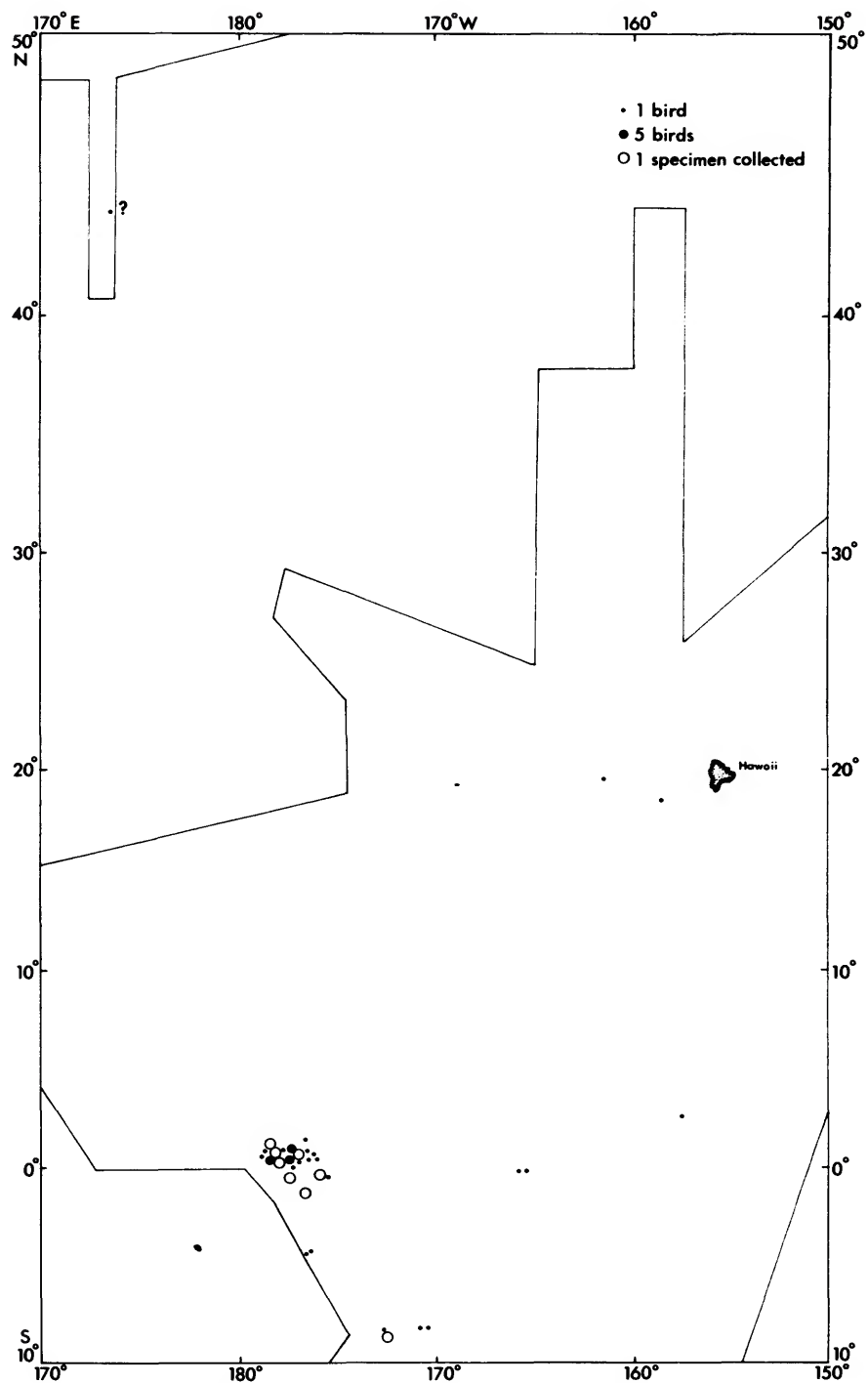


FIGURE 118.—POBSP sightings and specimens of *Oceanites oceanicus* in the central Pacific. (? = doubtful information.)

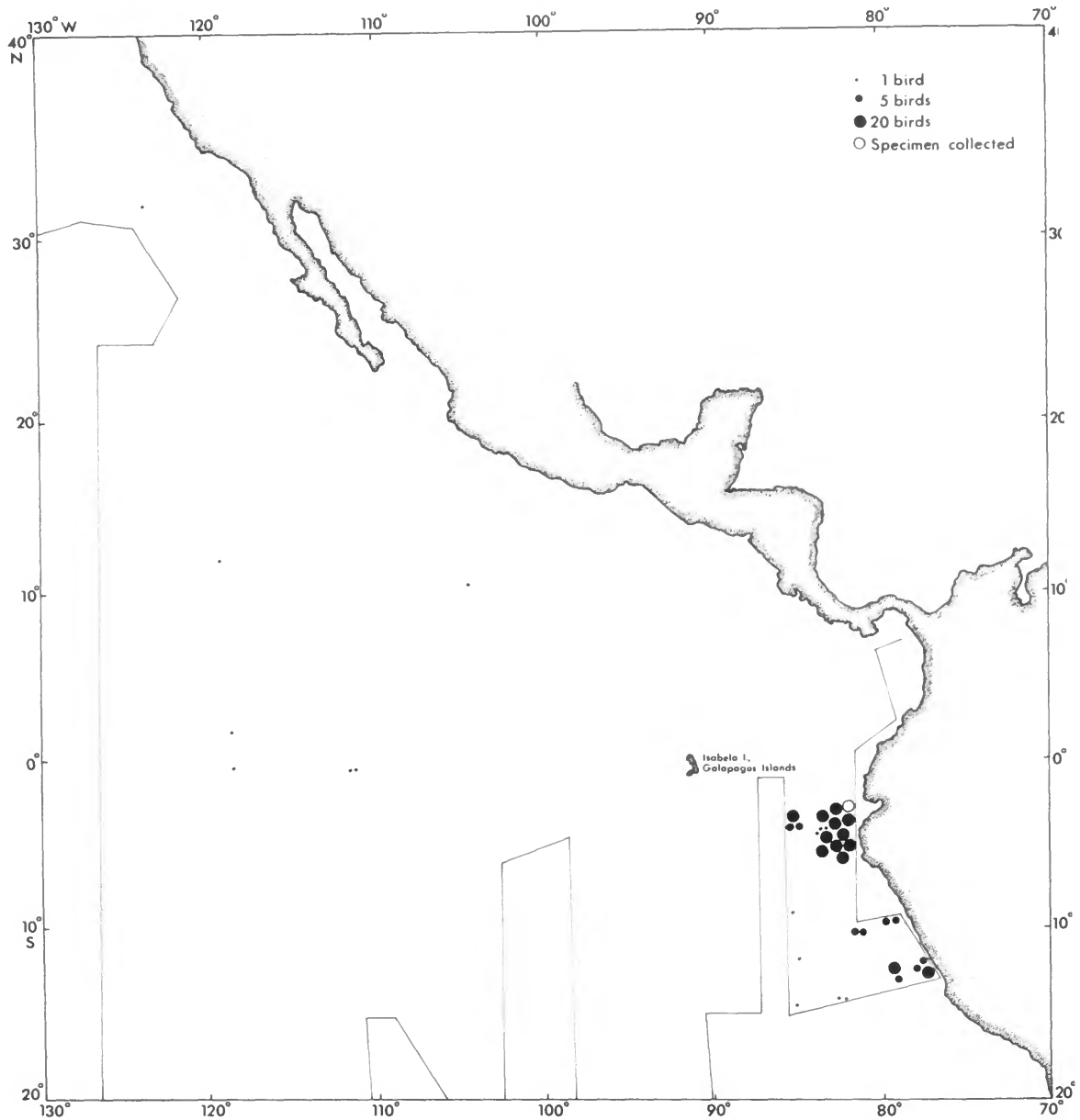
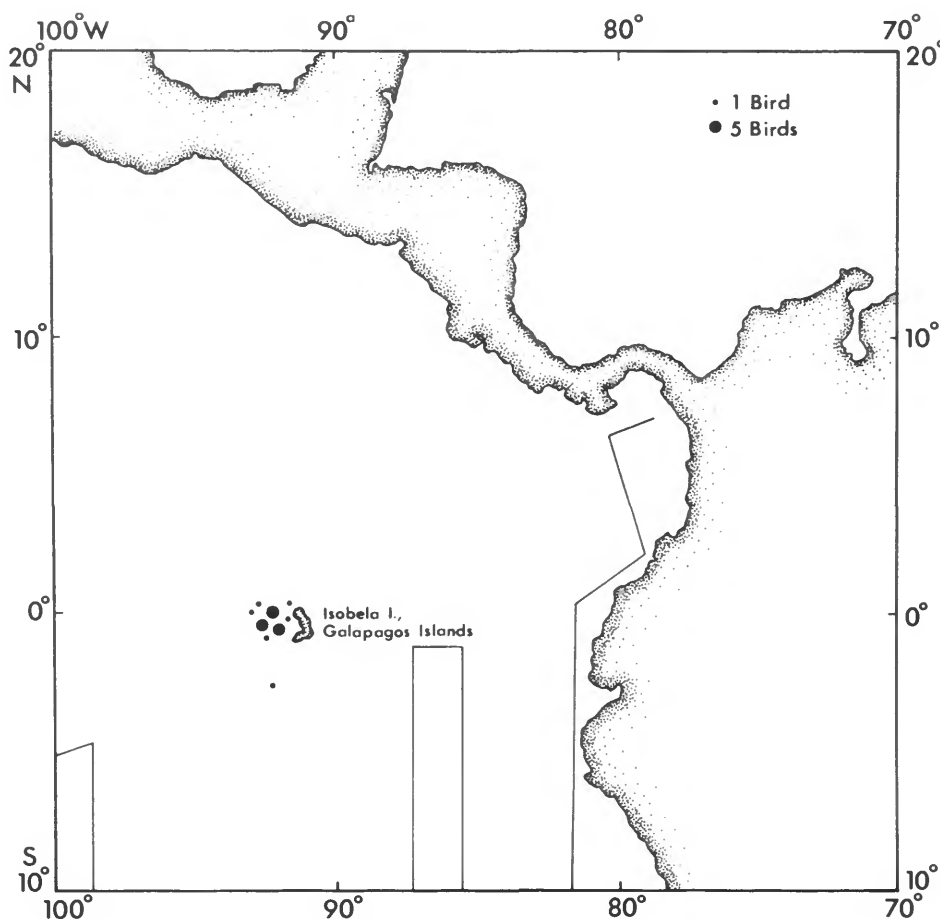


FIGURE 119.—POBSP sightings of *Oceanites oceanicus* in the eastern Pacific.

93°30'W on 11 June 1906, and further stated that no less than ten other examples were seen in the same vicinity during the next few days. The race *F. g. titan* is recorded as breeding at Rapa Island in southern Polynesia. Whether our sightings per-

tain to the race *F. g. titan*, or to the nominate *F. g. grallaria* which breeds at Mas Atierra and Santa Clara of the Juan Fernandez Islands is unknown, since no specimens were collected.

FIGURE 120.—POBSP sightings of *Oceanites gracilis*.*Nesofregatta albigularis* (Finsch)

WHITE-THROATED STORM PETREL

PELAGIC DISTRIBUTION.—This species was widely distributed in the Pacific along equatorial latitudes. The vast majority of sightings in both the central and eastern Pacific is confined to areas between 10°N and 10°S (Figures 122 and 123). Concentrations about the Phoenix and Line islands in the central Pacific are easily referable to the breeding populations of those areas. The equally great concentrations recorded in the eastern Pacific west of the Galapagos Islands are of unknown origin, but most probably from the breeding stations in the Marquesas Islands and Christmas Island. It should

be pointed out that our data represent a considerable range extension to the known pelagic range.

TAXONOMY.—To my knowledge this species does not vary throughout its considerable range, and no subspecies have been proposed. Except for *Oceanodroma tristrami*, *N. albigularis* is approximately the largest storm petrel in the Pacific area (Appendix Table A). Most POBSP specimens are from the Phoenix and Line islands (Christmas Island) populations.

In the Phoenix group, the majority of birds are of the color morph usually described for the species, i.e., dark upperparts and chest band, with white rump, throat and belly. On both Phoenix and McKean islands, however, every conceivable color vari-

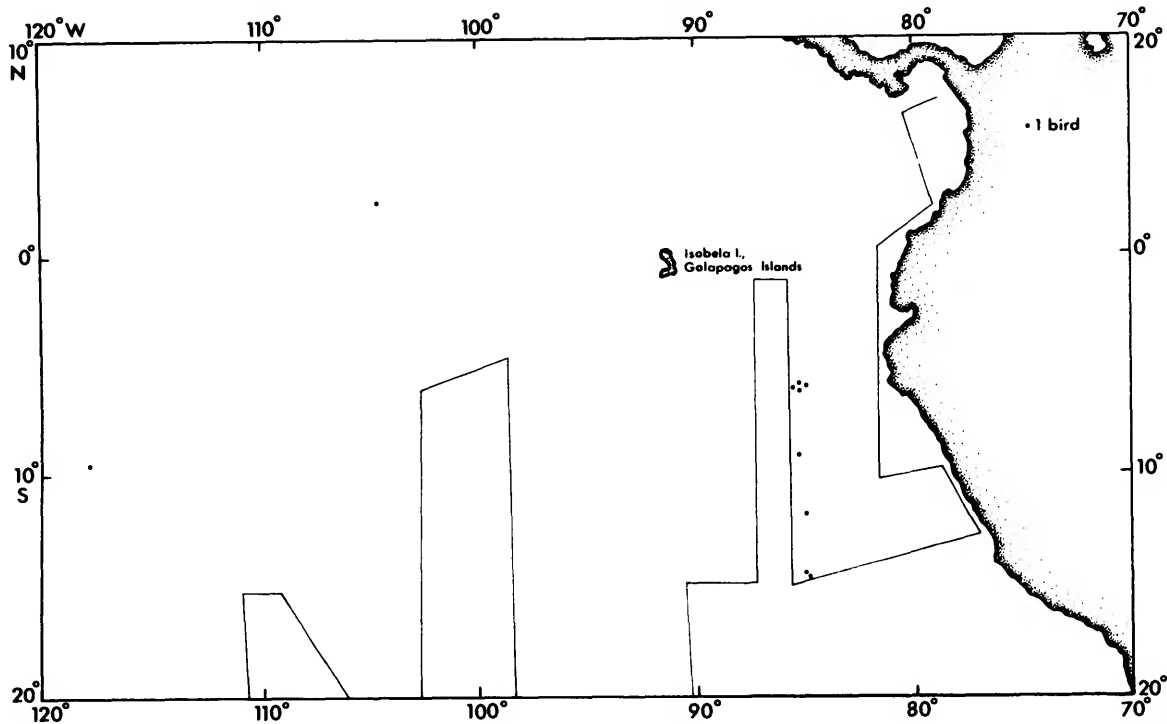


FIGURE 121.—POBSP sightings of *Fregetta grallaria*.

ation between the normal form and totally dark individuals may be found (Figure 124). The "Samoan Storm Petrel" ("*Fregetta moestissima*" Salvin), known from the unique type taken offshore the Samoan Islands, is considered by Murphy and Snyder (1952) to be nothing more than an entirely melanistic example of *Nesofregetta albigularis*. The appreciably larger dimensions (especially wing) than those of any specimens from the Phoenix, Line, Marquesas or New Hebrides islands indicates it may be from a distinct population, possibly breeding somewhere in the Samoan Islands. Bourne (1957) indicates that the unique, all dark specimen of *Fregetta fuliginosa* (Gmelin) from Tahiti (specimen subsequently lost) was probably closely allied to the Samoan form. On Christmas Island about half the population of *Nesofregetta albigularis* shows some dark flecking on the white underparts, but completely melanistic birds have not been seen.

BREEDING BIOLOGY.—Published data on the breeding biology of this species is virtually nonexistent and thus I have entered POBSP data in considerable detail in comparison to other species

whose breeding biologies are well known. The breeding range of *Nesofregetta albigularis* extends from the Line Islands (Christmas Island) and Phoenix Islands (Phoenix and McKean islands) in the central Pacific south to and including the Samoan Islands (?), Marquesas Islands, Fiji Islands, and the New Hebrides Islands. The POBSP surveys covered only the more northern parts of its range, i.e., the Line and Phoenix islands. Since our surveys were fairly complete for the Phoenix group, it is unlikely that *N. albigularis* breeds on islands other than McKean and Phoenix, although we have several sightings of birds flying over Enderbury Island (25 to 27 September, and 9 to 10 October 1966). A specimen was collected on Howland Island on 24 October 1938, but we have no recent sightings.

In the Line Islands, however, islands such as Malden and Starbuck are quite large and our coverage was insufficient to rule out the possibility of birds breeding in those areas. On Malden Island one bird was noted at night on 31 March 1967. Several islets in the lagoon were not thoroughly investigated and might be utilized by this species

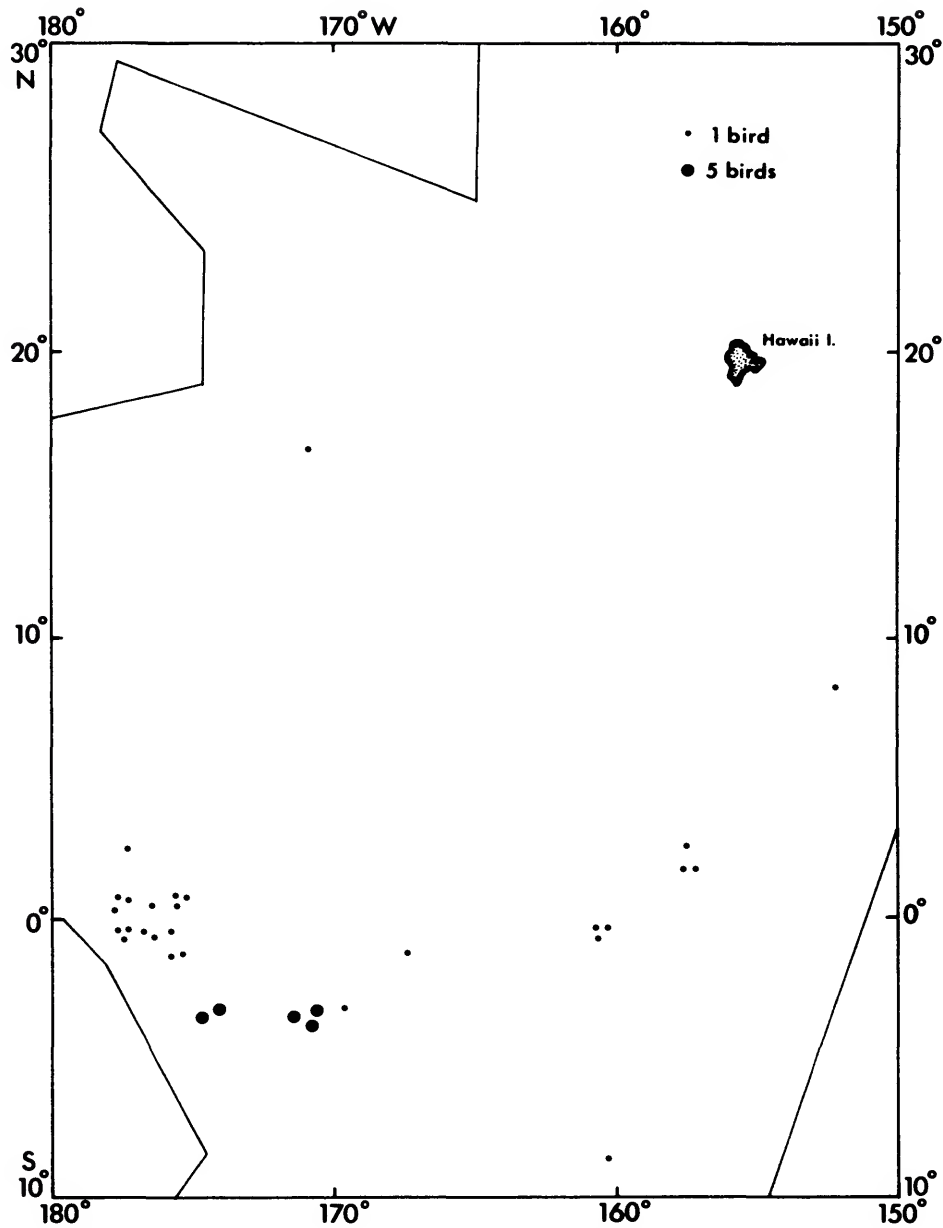


FIGURE 122.—POBSP sightings of *Nesofregatta albigularis* in the central Pacific.

for nesting. Other possible breeding areas are the Gilbert, Society, Tuamotu and Marshall islands (King, 1967:42).

The choice of breeding sites on the three central Pacific islands investigated was much the same. Areas supporting bunch grass (*Lepturus* sp.), large clumps of weeds (*Boerhaavia* sp.) or *Sesuvium*, in

combination with an abundance of loose rocks, were utilized in practically all cases in the Phoenix Islands. Extensive areas of rocky coral slabs without vegetation, as well as areas of continuous short grass or small annuals, were avoided. Old fallen rock walls which were constructed by the early colonists on the Phoenix Islands were often used as

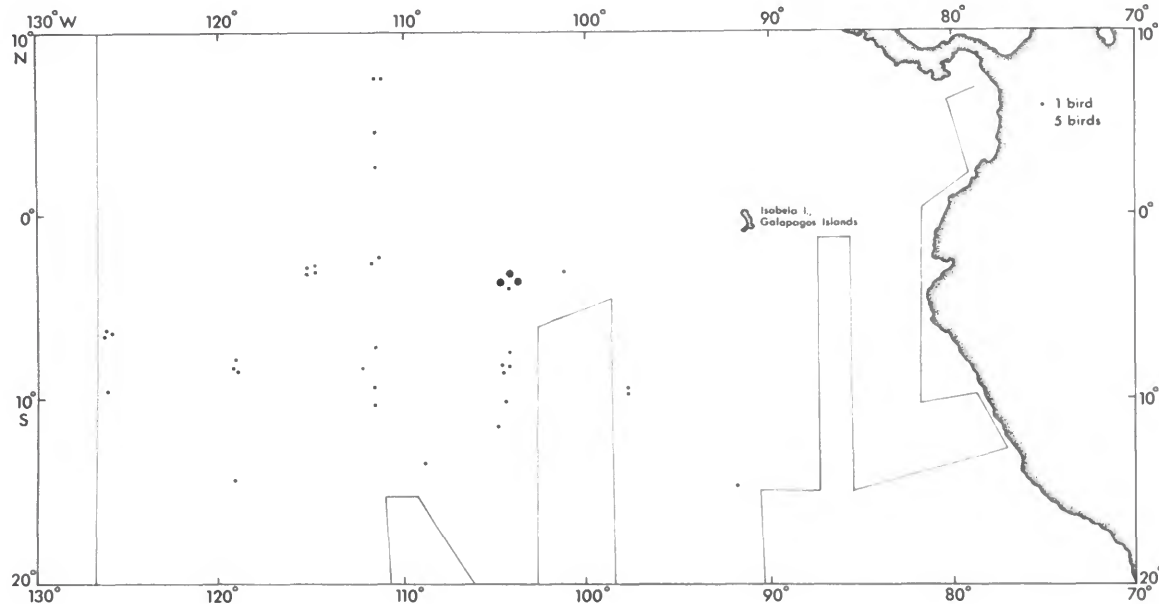


FIGURE 123.—POBSP sightings of *Nesofregatta albigularis* in the eastern Pacific.

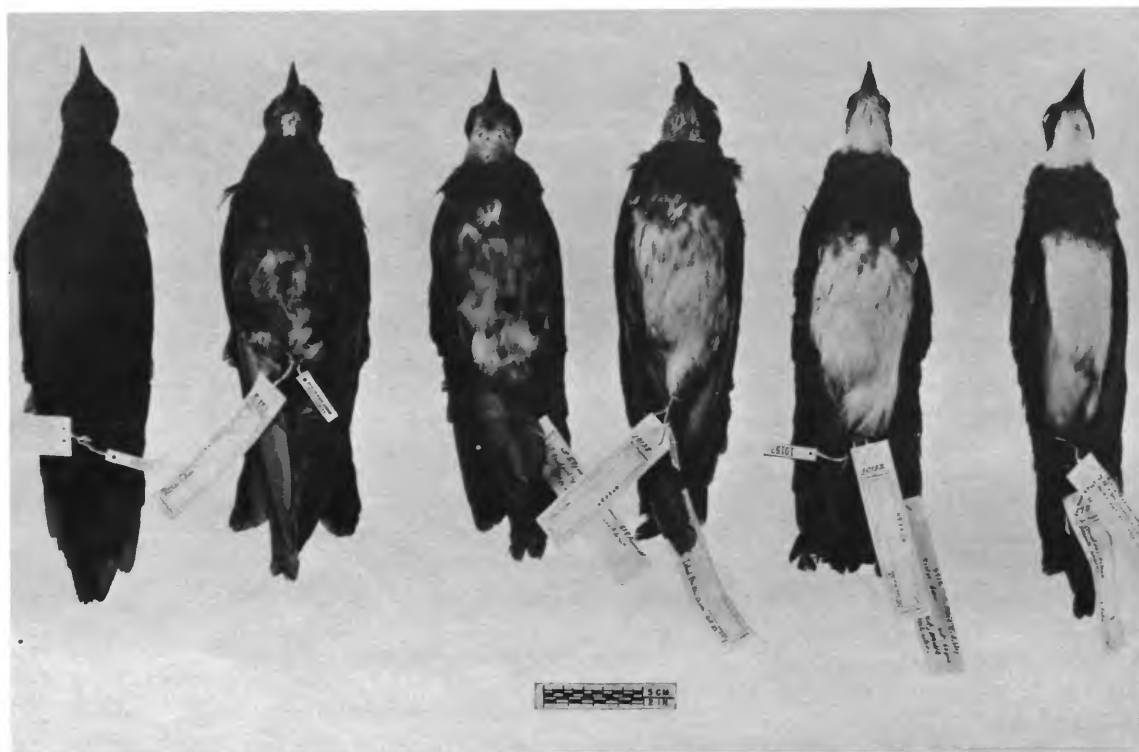


FIGURE 124.—Color variation in *Nesofregatta albigularis* from the Phoenix Islands.

nest sites, although standing walls devoid of vegetation were much more prone to be utilized by Bulwer's Petrel (*Bulweria bulwerii*). On Christmas Island most nests on the small islets were under clumps of overhanging grass (*Lepturus*), in pockets in coral rock shelves also usually sheltered by grass, or in depressions under *Sesuvium*. Regardless of nest site, the actual nests were similar in all cases. The few pieces of nest material (grass, weed stems, feathers, etc.) invariably present were most likely in the nest cavities to begin with; such material is probably manipulated to some extent, but to my knowledge no material is ever carried into the nests by the birds. Incubating birds are usually hidden from view within nest cavities, but an occasional individual will nest in rocks in such a manner that it can be seen. Schreiber (POBSP) noted that tails of incubating birds were often visible in the shallow nest cavities on the islets in Manulu Lagoon, Christmas Island. Under large, extensive grass or weed clumps, the birds usually retreat to the most concealing portion. The nest cavities may be slightly enlarged under clumps of vegetation, but I have never noted any extensive digging performed by this species. Storm petrels often utilize nest cavities dug out by the abundant Audubon's Shearwater (*Puffinus lherminieri*) on McKean and Phoenix islands.

On Christmas Island the nesting areas are primarily limited to five tiny islets in Manulu Lagoon. These are separated by expanses of water from the main island. A few birds nest on the islets of Motu Tabu, Motu Upua, and on at least one islet in Isles Lagoon. Utilization of these retreats is probably a direct result of feral cat predation on the main island.

From banding and recapture data Schreiber (POBSP) estimated the total population using Christmas Island in 1967 at 350 to 450 birds, although this estimate is probably low. Table 29 summarizes the stage of nesting and nest contents recorded in Manulu Lagoon by POBSP and others.

From the above data it can be inferred that the peak egg period on Christmas Island is from September through November, but obviously some portion of the population is nesting at all times of year. This seasonal spread of nesting apparently allows a greater number of birds to utilize the available nesting area than would be possible if

TABLE 29.—*Surveys of nesting Nesofregatta albigularis in the Manulu Lagoon area, Christmas Island, Line Islands*

Date	Nest contents	Source
Jan 59	20 occupied nests (contents?)	Gallagher (1960:494)
Feb 21	eggs and young present	Murphy (1924:12)
Mar 65	30 nests, eggs and chicks	POBSP
Apr 59	1 small, 2 nearly fledged chicks	Gallagher (1960:494)
Jun 65	few nesting	POBSP
Jul 67	3 eggs, 1 small downy chick	"
early Aug 67	14 eggs, 3 chicks	"
late Aug 67	21 eggs, 5 chicks	"
Oct 65	50 (eggs and small chicks)	"
Nov 64	26 eggs, 5 chicks	"
early Nov 67	54 eggs (including 11 abandoned), 9 chicks	"
late Nov 67	37 eggs (including 6 newly abandoned), 9 chicks (including 5 dead)	"
late Dec 67	6 eggs, 25 chicks	"

nesting were limited to a specific time of the year for all individuals. One adult, with an egg, banded on 25 August 1967, on Islet #2 in Manulu Lagoon was found incubating an egg on Islet #1 on 28 November 1967. This meager evidence suggests that the species will reneest within the same year, and, furthermore, a specific nest site is apparently not adhered to. Another adult in an empty nest cavity on 29 August 1967 was incubating an egg there on 4 November 1967; yet another incubating an egg on 17 August 1967 was still incubating on 4 November 1967. The egg in the latter case was probably infertile, but these examples give an idea of the extensive periods that the birds spend on the breeding islands.

Our data for the Phoenix Islands are less complete because of the extremely short surveys made, but the available evidence shows that on McKean and Phoenix, as on Christmas Island, some portion of the population is nesting during every month of the year. Tables 30 and 31 present POBSP data for McKean and Phoenix islands.

Variation and inconsistencies in the data are due partly to different observers and to the extremely inadequate surveys in most cases. It is nonetheless evident that considerable variation is to be found on the same island for a given month during different years (Table 30, February 1964 and 1965). Despite these differences, considering the data as a

TABLE 30.—POBSP surveys of *Nesofregatta albigularis* on McKean Island, Phoenix Islands

Date	Number banded	Population estimate	Nest contents
6-7 Feb 65	94	500	large number beginning to nest
16-20 Feb 64	9	25-30	no eggs or young found
17-19 Apr 66	-	500+	no eggs
30 Apr-1 May 66	-	1000	1 egg
13-15 Jul 68	-	1000 adults, 200 eggs, 200 chicks	sample of 23 nests: 12 eggs, 11 chicks ranging from ca. 4 days old to fully feathered
18-20 Jul 64	56	no data	no data
23-25 Jul 66	-	750	10 eggs, few small and large downy nestlings
14-30 Oct 68 (thorough survey)	13	30 adults	1 egg, 3 large chicks
18-22 Oct 64	6	100	no data
24-28 Oct 63	1	100+, 7 collected	1 egg found

whole, there appears to be a breeding peak on McKean from April through at least July or August, with a definite low in October and probably later. For Phoenix Island we do not have data from monthly surveys in successive years, but certainly the high nesting populations recorded from October through December do not correspond to the breeding situation on McKean. This lack of conformity to a set seasonal or annual cycle has been noted for most species on the equatorial islands. Our surveys indicate that the populations on one island appear to operate independently from those on other islands, regardless of the apparent ecological similarities of the islands or their geographic proximity.

On McKean Island there appears to be a definite separation in the timing of nesting of *Nesofregatta albigularis* and *Bulweria bulwerii*. This was quite apparent during two fairly extensive surveys in July and October 1968. During July, *N. albigularis* was definitely undergoing a peak in nesting with an estimated 1000 adults on the island. Bulwer's Petrel at that time was for all practical purposes absent from the island (one adult calling from an empty nest cavity). During the extensive October survey only about 30 adult White-throated Storm Petrels were present on the island with nine nests (3 with young, 1 with egg, and 5 occupied, but as yet without eggs). Bulwer's Petrel at this time was approaching a peak nesting situation with a very conserva-

TABLE 31.—POBSP surveys of *Nesofregatta albigularis* on Phoenix Island, Phoenix Islands

Date	Number banded	Population estimate	Nest contents
26-28 Jan 67	-	150	1 fresh egg found
23-26 Feb 64	-	100	no evidence of nesting
14-16 Apr 66	-	300+	nesting
26-30 May 65	35	500	nesting, young present
18-20 Jul 64	56	200-300	eggs and nestlings present
29-30 Sep 65	-	2	no evidence
10-11 Oct 66	-	400 (15% nesting)	20 eggs, 5 small downy young, 5 large downy young
3-7 Nov 64	15	100	no data
2-5 Dec 66	-	300 (40% nesting)	50 eggs, 10 small chicks

tive estimate of 1000 birds on the island. The majority of these were calling from empty nest cavities or from nests with fresh eggs; an estimated five percent had small downy young. Both species tend to utilize the same nest sites to a high degree, and this complementary seasonal nesting arrangement apparently affords both populations minimum competitive activity during their respective breeding periods. Food availability in the nearby ocean may also be a factor in creating alternating nesting seasons for these similar species.

On the breeding islands, White-throated Storm Petrels are usually absent during most of the daylight hours (except for those attending to incubation or brooding duties). On several occasions, however, I have seen adults come to nests in full daylight to feed young. This type of behavior is never performed by any of the small hydrobatids in the eastern Pacific, since any individual showing itself during the day would be immediately set upon and devoured by Western Gulls. The rapidity with which the gulls attack storm petrels appears to be the sole reason why storm petrels never appear overland in daylight hours. In the central Pacific, however, *Nesofregatta* appears to be without predators. The frigatebirds (*Fregata ariel* and *F. minor*) were never noted harassing storm petrels, but seemed to restrict their parasitism to larger birds such as boobies, shearwaters, and terns.

Adult storm petrels normally come in over the breeding islands from the ocean from about one-half to three-quarters of an hour before dusk. This seems to be the period of greatest activity, during



FIGURE 125.—Young of *Nesofregatta albigularis* on McKean Island.
(Photo by C. Douglas Hackman.)

which many individuals may be noted flying back and forth over potential or actual nest sites. Birds with active nests seem to circle repeatedly over the general area of the nest site for some time before landing, as do individuals obviously searching for nest sites. When the birds land, they usually do so ungracefully, falling softly and then awkwardly crawling over the terrain toward the nest site or into the nest cavity.

As with other hydrobatids and procellariiforms in general, *Nesofregatta* lays only a single egg. Occasionally a bird is found incubating two eggs, but one is invariably an infertile or abandoned egg from an earlier nesting. Relative to other storm petrels, the eggs are large for the size of the bird. A series of 20 eggs from Phoenix, McKean, and Christmas islands show the following measurements: length (mean with standard error) 37.95 ± 0.41 mm (SD=1.85); breadth 27.45 ± 0.18 mm (SD=0.82). The eggs have a creamy-white background color, with reddish and lavender dots which usually form a prominent wreath about the large end, but are scattered less finely over the entire surface.

The few observations available on marked nests show that both birds are present in the nest cavity

for some time (days?) before the egg is laid. Copulation probably takes place at the nest site. During these times and at least during early incubation, adults utter a soft guttural "grrrrr-grrrrr-grrrrr" call from the nest cavity. Both sexes incubate, but the rate of changeover, as well as the length of the incubation period, is unknown. After the chicks are a few days old the parents only come to the nest to feed them. The young hatch blind, but are profusely covered with medium-gray down which is quite short on the underparts and long on the dorsum. A chick estimated to be five days old had down to 20 mm long on the back. I doubt if the young can use vision in the nest until they are in the large, fully-feathered stage, since the entire orbital region is completely covered by shaggy down. When the chicks are approximately two-thirds grown, they have a definite bi-colored aspect. The dark and light colors correspond roughly to the black and white areas of the adults. This bicolored effect is brought about by the growth of new feathers beneath the down. As the feather coat progresses, more and more down is shed until only patches remain about the head, dorsum and flanks (Figure 125). It is not known how soon the young leave the island after attaining their juvenal plum-

age, but apparently it is rather soon, as birds with traces of down still clinging to the feathers were noted attempting to fly at night; they were at least many yards away from any possible nest site (see comparative data on *Oceanodroma leucorhoa socorroensis* young).

The White-throated Storm Petrel exhibits a peculiar flight at sea which has not been noted in any other species of hydrobatid. On many occasions these birds were seen kicking off waves with considerable force, using their extremely long legs and spatulate feet. The moment their feet hit the water surface, the birds instantly change direction and sharply increase their speed, attesting to the force applied to the water's surface. The usual procedure was for the individual to "kick off" a wave, glide for approximately 20 to 30 seconds and again "kick off." I have on occasion noted a bird parallel a ship for a mile or more in this manner. Both Gallagher (1960) and Schreiber and Ashmole (1970) have noted birds performing this behavior in the quiet lagoon on Christmas Island. Wilson's Storm Petrels often dabble their feet in the water, but this appears to be more of a balancing maneuver than an actual thrust motion as in *Nesofregatta*. This mode of travel might be a means of expending less energy in equatorial regions where wind is often at a minimum. At any rate, the extremely long tarsi and spatulate feet of *Nesofregatta* make possible its unique locomotory behavior.

Discussion

The hydrobatids form a rather homogeneous group widely distributed over the Pacific regions. In many cases their breeding distribution and pelagic movements appear to be random, but undoubtedly reflect patterns that have been dictated by seasonal abundance and distribution of food items, interspecific competition, and the need to occupy the limited breeding areas during favorable periods. These patterns have undoubtedly undergone considerable fluctuation over time; the present view of the family shows a few exceedingly abundant forms and many uncommon to rare species. In the Pacific region, individuals of the combined subspecies of *Oceanodroma leucorhoa* by far outnumber all other species combined.

The northern breeding forms of *O. leucorhoa* show south-north migration patterns and practically

inundate the central and eastern equatorial Pacific during the nonbreeding season (September-March). Wilson's Storm Petrel, a strictly southern hemisphere breeder, shows the inverse north-south movements in the western Pacific and along the South American coast during migration and nonbreeding season from the Antarctic. Another southern hemisphere breeder (White-faced Storm Petrel) demonstrates an east-west pattern, moving east from its Australian breeding grounds to the South American coast, thence north along the Peru Current and west through the Galapagos area with a subsequent return to the Australian region. Possibly Wilson's performs more of a circular route in its north-south movements. A number of forms such as *Oceanodroma leucorhoa chapmani*, *O. l. socorroensis*, and *O. homochroa* apparently do not move any great distance from the breeding islands during the nonbreeding season. For many Pacific hydrobatids the nonbreeding distribution is imprecisely known; for others the stated breeding grounds are merely conjecture.

At sea most storm petrels are either solitary or join with members of their own species. In certain cases two or more species will congregate, often in response to a temporarily plentiful food supply. They normally do not mix with other seabird species, even with their nearest relatives, the procellariids. I believe the presence of storm petrels in mixed feeding flocks of procellariids, terns, boobies, etc., is usually a random occurrence. On many occasions when I have observed storm petrels in the vicinity of mixed feeding flocks, the hydrobatids appeared to lack the intense feeding interest of the other species and usually moved out of the immediate area of intense feeding. It should be stressed that in most cases POBSP observers did not distinguish, in a recorded species association, those members that were actually feeding or traveling together. If members of two or more species were together at the time of initial sighting, they were usually recorded as such. The imprecision of these observations was the result, usually, of the impossibility of detailed notations of individuals in large mixed feeding or traveling flocks where often hundreds or even thousands of birds were concerned. In such cases a gross account of numbers was about the best that could be acquired. Thus the presence of one or more hydrobatids in the immediate vicinity of a flock would be recorded as positive, al-

TABLE 32.—*Intraspecific sociability (number of individuals/number of sightings) in species of Pacific hydrobatids*

Species	Individuals	Sightings	Ratio of sociability
<i>Oceanodroma castro</i>	269	203	1.3
<i>O. leucorhoa</i>	14,355	9,071	1.6
<i>O. furcata</i>	936	235	4.0
<i>O. markhami</i> or <i>O. tristrami</i>	167	121	1.4
<i>O. melania</i>	465	214	2.2
<i>O. homochroa</i>	36	10	3.6
<i>O. hornbyi</i>	12	7	1.7
<i>O. tethys</i>	1,723	443	3.9
<i>Halocyptena microsoma</i>	63	48	1.3
<i>Oceanites oceanicus</i>	443	66	6.7
<i>O. gracilis</i>	22	6	3.7
<i>Pelagodroma marina</i>	79	67	1.2
<i>Fregetta grallaria</i>	10	8	1.3
<i>Nesofregetta albigularis</i>	111	97	1.1
Total	27,140	12,574	2.2

though, as I have often stated from personal observations, this is usually not the case.

The amount of intraspecific sociability can be calculated in a gross manner quite easily from our data. From Table 32 it is immediately apparent that individuals of some species are far more prone to associate intraspecifically than others. Fork-tailed and Wilson's Storm Petrels commonly associate with other members of their respective species. On the wintering grounds Leach's Storm Petrels disperse singly or in very low densities unless a local food source happens to bring large numbers together temporarily. During migration they commonly group and are noted resting on the water in large rafts. Even with our sightings of migratory and feeding flocks included, the low sociability ratio of 1.6 for nearly 10,000 sightings (involving over 14,000 individuals) demonstrates their usual solitary nature. Other species, such as the White-throated Storm Petrel, show this solitary nature to a greater degree and are almost invariably noted singly. For most of the less abundant species, although the available evidence suggests solitary occurrence, we do not have enough observations to demonstrate their overall social behavior at sea.

The solitary nature of most hydrobatid species away from the breeding grounds is perhaps necessary because of the foraging behavior (flight low

over the water with a limited area view) to distribute themselves as widely as possible over their range to take utmost advantage of the widely distributed small organisms which make up their diet. Members of a species, or of several species, will gather readily at an unusual, abundant food source such as an oil slick. At such gatherings I have never noted either inter- or intraspecific hostile behavior between individuals, behavior that certainly some (if not all) species are capable of demonstrating as witnessed by intraspecific battles over nest sites on the breeding grounds (Leach's, Least, Black, and White-throated Storm Petrels).

To my knowledge all members of the Hydrobatidae are strictly surface feeders, that is, they do not submerge the body beneath the surface of the water to obtain food. All Pacific species were observed to glean the surface of the water for floating objects, often with wings held aloft for balance. The foot dabbling behavior with wings held aloft for balance in the Wilson's Storm Petrel is well known and documented. Leach's, Harcourt's, and most especially Least Storm Petrels will hold the wings aloft in a V formation when feeding over an oil slick or other concentrated food source. In this respect they appear as so many butterflies on a wet sand bar. Least Storm Petrels were never noted dabbling their feet the way Wilson's do. They usually feed while resting on the water with wings up until wanting to move. Then with a few quick wingbeats the bird moves to a new position, usually still holding the wings aloft.

The preceding species accounts provide a basis for understanding the distribution and abundance of Pacific hydrobatids and indicate the vast amount of data yet to be gathered concerning these forms. While it is unlikely that a program devoted to pelagic ornithology in the Pacific of the magnitude of the POBSP will occur again in the near future, important contributions can be made to existing knowledge by participation in cruises devoted to any type of pelagic investigation. The great amount of information on hydrobatids gathered during the EASTROPAC cruises is a good example of this.

While it is understandable that we know little or nothing about the breeding biology of many of the southern hemisphere hydrobatids, it is less explicable why information of this sort is lacking for most of the species and subspecies inhabiting the coastal islands of the western United States and Mexico.

There is a decided need in these areas for long range studies with banded birds similar to the investigation of the nominate race of Leach's Storm Petrel on Kent Island, New Brunswick, Canada, which was begun by Gross (1935) and continued by Huntington (1963) and his co-workers.

A fascinating problem awaiting study is the elucidation of the relationships and interactions of winter and summer breeding populations of Leach's Storm Petrel on Guadalupe Island. A second problem is to account for the clumping of completely

dark hydrobatids along the California and Baja California coasts. In the Hydrobatidae, where white patterning is widespread, the lack of this color in so many forms (four species and three subspecies) common to this area can hardly be coincidental. The factor of predation by the various gull species (especially the Western Gull) is probably only part of the reason. The dark rump color predominates in all forms of hydrobatids along the coast of Japan also, possibly for the same reasons.

Appendix

Measurements of POBSP-collected specimens of Pacific hydrobatids
(number of specimens in parentheses, linear characters in millimeters, weights in grams)

TABLE A.—*Various Pacific hydrobatids*

Characters and measurements	<i>Oceanodroma homochroa</i>	<i>O. castro</i>	<i>O. t. kelsalli</i>	<i>O. t. kelsalli</i>	<i>O. melania</i>	<i>O. tristrami</i>	<i>Halocyptena microsoma</i>	<i>Oceanites oceanicus</i>	<i>Nesofregatta albigularis</i>
WING	(20)	(6)	(36)	(4)	(47)	(13)	(11)	(8)	(21)
Range	133-145	148-159	127-141	119-128	163-180	175-195	114-123	148-156	175-193
Mean w/SE	138.40 ± .65	152.00 ± 1.73	133.39 ± 0.49	124.50 ± 2.02	171.96 ± 0.55	183.15 ± 1.70	118.45 ± 0.98	152.50 ± 1.07	186.38 ± 1.16
SD	2.91	4.24	2.92	4.04	3.75	6.14	3.24	3.02	5.30
TAIL	(20)	(6)	(42)	(4)	(44)	(13)	(11)	(8)	(21)
Range	79-89	71-75	58-67	56-61	82-94	109-118	52-60	70-76	89-107
Mean w/SE	83.10 ± 0.67	72.33 ± 0.61	62.26 ± 0.30	59.25 ± 1.11	88.41 ± 0.47	113.54 ± 0.83	57.00 ± 0.80	72.00 ± 0.73	97.48 ± 1.11
SD	3.01	1.51	1.91	2.22	3.10	2.99	2.65	2.07	5.10
CULMEN	(20)	(6)	(41)	(4)	(45)	(13)	(11)	(7)	(20)
Range	13.10-15.10	14.40-15.80	10.60-14.00	10.90-12.00	14.00-16.10	16.30-18.30	9.60-11.60	11.90-13.00	15.70-18.00
Mean w/SE	14.10 ± 0.11	14.85 ± 0.22	12.40 ± 0.09	11.73 ± 0.28	15.22 ± 0.07	17.36 ± 0.18	10.72 ± 0.17	12.50 ± 0.17	16.63 ± 0.13
SD	0.50	0.55	0.60	0.55	0.48	0.65	0.57	0.44	0.57
TARSUS	(20)	(6)	(42)	(2)	(46)	(13)	(11)	(8)	(21)
Range	21.50-23.70	21.50-22.50	20.00-23.60	20.25-21.00	29.00-33.30	25.10-28.60	19.10-22.10	33.40-35.60	40.00-46.60
Mean w/SE	22.46 ± 0.14	22.00 ± 0.15	22.02 ± 0.13	20.75 ± 0.25	31.48 ± 0.14	27.38 ± 0.28	21.00 ± 0.26	34.24 ± 0.26	43.07 ± 0.42
SD	0.63	0.36	0.86	0.35	0.96	1.02	0.85	0.72	1.91
WEIGHT	(20)	(6)	(26)		(44)	(10)	(11)	(7)	(19)
Range	33.3-42.4	40.5-45.0	21.0-33.0		50.0-67.0	58.4-94.0	18.2-21.7	35.0-39.0	57.0-70.0
Mean w/SE	36.90 ± 0.51	42.67 ± 0.68	25.48 ± 0.61		58.95 ± 0.56	82.53 ± 3.04	20.47 ± 0.34	36.71 ± 0.47	62.84 ± 0.96
SD	2.27	1.66	3.12		3.69	9.62	1.11	1.25	4.17

TABLE B.—*Oceanodroma leucorhoa leucorhoa*

Characters and measurements	Central Pacific (at sea)		Eastern Pacific (at sea)		North Pacific (breeding)		Total
	males	females	males	females	males	females	
WING	(43)	(31)	(23)	(12)	(4)	(6)	(119)
Range	144-161	148-166	140-162	144-162	149-158	153-167	140-167
Mean w/SE	153.60 ± .57	155.19 ± .82	151.57 ± 1.22	152.08 ± 1.73	153.75 ± 1.89	157.67 ± 2.03	153.68 ± .45
SD	3.72	4.56	5.86	5.99	3.77	4.97	4.89
TAIL	(52)	(42)	(37)	(36)	(4)	(4)	(175)
Range	76-92	77-93	67-87	73-95	82-89	78-89	67-95
Mean w/SE	83.35 ± .42	84.33 ± .50	81.84 ± .66	84.00 ± .72	86.00 ± 1.47	82.25 ± 2.36	83.43 ± .28
SD	3.05	3.24	4.00	4.34	2.94	4.72	3.72
CULMEN	(54)	(41)	(35)	(36)	(4)	(6)	(176)
Range	15.10-17.50	15.00-16.90	13.70-17.10	13.30-17.00	15.00-16.50	15.00-16.50	13.30-17.50
Mean w/SE	16.01 ± .07	16.02 ± .07	16.00 ± .11	15.89 ± .12	15.78 ± .32	15.62 ± .23	15.97 ± .04
SD	.52	.46	.63	.74	.63	.56	.598
TARSUS	(54)	(41)	(35)	(36)	(4)	(4)	(174)
Range	22.00-25.10	22.10-25.10	20.00-25.00	21.40-25.10	21.70-24.10	23.80-25.00	20.00-25.10
Mean w/SE	23.48 ± .10	23.58 ± .10	23.61 ± .17	23.74 ± .16	23.20 ± .56	24.20 ± .28	23.59 ± .06
SD	.75	.63	1.00	.98	1.12	.57	.84
WEIGHT	(48)	(37)	(30)	(35)			(150)
Range	29.0-49.0	31.0-54.0	25.2-55.1	24.0-57.5			24.0-57.5
Mean w/SE	38.73 ± .63	40.86 ± .78	44.03 ± 1.25	43.17 ± 1.02			41.35 ± .47
SD	4.34	4.74	6.85	6.03			5.77

TABLE C.—*Oceanodroma leucorhoa beali*

Characters and measurements	Eastern Pacific (at sea)		California & Alaska (breeding)		Coronados (breeding)		Total
	males	females	males	females	males	females	
WING	(33)	(34)	(30)	(26)	(15)	(17)	(155)
Range	136-155	139-159	142-155	143-155	144-154	139-155	136-156
Mean w/SE	145.61 ± .78	146.09 ± .75	147.40 ± .71	148.81 ± .65	148.80 ± .78	148.65 ± 1.01	147.24 ± .33
SD	4.48	4.36	3.87	3.31	3.03	4.18	4.15
TAIL	(60)	(66)	(20)	(18)	(6)	(9)	(179)
Range	71-86	71-89	73-85	74.5-85.9	77-78	81-84	71-89
Mean w/SE	79.17 ± .45	79.95 ± .51	79.00 ± .71	78.57 ± .68	77.67 ± .21	82.44 ± .34	79.45 ± .27
SD	3.51	4.15	3.17	2.90	.52	1.01	3.63
CULMEN	(56)	(59)	(24)	(23)	(14)	(17)	(193)
Range	14.20-16.70	14.00-16.60	14.00-16.10	14.20-15.50	14.40-16.20	13.50-16.00	13.50-16.70
Mean w/SE	15.43 ± .08	15.44 ± .08	15.03 ± .11	14.87 ± .08	15.21 ± .14	14.99 ± .14	15.26 ± .04
SD	.59	.65	.52	.40	.54	.58	.61
TARSUS	(61)	(64)	(21)	(18)	(6)	(9)	(179)
Range	20.00-25.00	20.00-25.10	21.50-24.40	22.00-24.00	21.50-22.70	21.00-22.80	20.00-25.10
Mean w/SE	22.81 ± .13	22.70 ± .16	22.69 ± .16	22.94 ± .12	22.07 ± .20	22.28 ± .19	22.72 ± .08
SD	1.03	1.26	.75	.53	.50	.58	1.03
WEIGHT	(53)	(56)			(6)	(9)	(124)
Range	32.00-52.00	29.00-53.00			34.00-38.00	32.00-37.00	29.00-53.00
Mean w/SE	40.93 ± .65	40.13 ± .67			36.33 ± .76	34.11 ± .51	39.85 ± .45
SD	4.91	5.03			1.86	1.54	5.04

TABLE D.—*Oceanodroma leucorhoa chapmani*

Characters and measurements	San Benitos (breeding)		Total
	males	females	
WING	(45)	(40)	(85)
Range	140-150	144-153	140-153
Mean w/SE	145.44 ± .37	148.28 ± .39	146.78 ± .31
SD	2.48	2.44	2.83
TAIL	(39)	(39)	(78)
Range	74-82	74-85	74-85
Mean w/SE	77.33 ± .37	78.62 ± .38	77.97 ± .27
SD	2.29	2.36	2.40
CULMEN	(45)	(41)	(86)
Range	14.00-16.00	14.50-16.50	14.00-16.50
Mean w/SE	15.16 ± .08	15.47 ± .07	15.31 ± .06
SD	.57	.48	.55
TARSUS	(40)	(39)	(79)
Range	20.00-23.50	20.00-24.00	20.00-24.00
Mean w/SE	21.73 ± .11	22.23 ± .13	21.97 ± .09
SD	.72	.80	.80
WEIGHT	(39)	(39)	(78)
Range	29.00-39.00	30.00-42.00	29.00-42.00
Mean w/SE	33.97 ± .35	35.59 ± .46	34.78 ± .30
SD	2.18	2.90	2.68

TABLE E.—*Oceanodroma leucorhoa socorroensis*

Characters and measurements	Eastern Pacific (at sea)		Guadalupe I. (summer breeding)		Guadalupe I. (winter breeding) "kaedingi"		Total
	males	females	males	females	males	females	
WING	(20)	(26)	(68)	(49)	(22)	(20)	(205)
Range	131-150	134-153	134-146	136-150	140-150	140-147	131-153
Mean w/SE	142.05 ± .92	142.46 ± .77	141.07 ± .33	142.71 ± .46	144.68 ± .59	143.70 ± .72	142.38 ± .23
SD	4.12	3.90	2.73	3.22	2.75	2.34	3.31
TAIL	(20)	(28)	(44)	(38)	(18)	(17)	(165)
Range	67-81	68-81	68-79	68-80	70-82	73-84	67-84
Mean w/SE	73.05 ± .92	74.43 ± .58	73.73 ± .42	74.29 ± .48	77.72 ± .75	78.24 ± .67	74.79 ± .27
SD	4.14	3.05	2.81	2.98	3.20	2.77	3.51
CULMEN	(21)	(26)	(45)	(39)	(18)	(17)	(166)
Range	13.00-15.20	12.90-15.00	13.00-15.50	13.30-15.50	13.50-15.90	14.00-15.60	12.90-15.90
Mean w/SE	14.02 ± .12	13.88 ± .11	14.20 ± .11	14.08 ± .09	14.82 ± .13	14.82 ± .11	14.23 ± .05
SD	.54	.54	.74	.56	.56	.43	.67
TARSUS	(22)	(28)	(45)	(38)	(18)	(17)	(168)
Range	18.30-22.10	18.80-21.90	19.00-22.80	19.00-22.30	21.00-23.00	20.90-23.50	18.30-23.50
Mean w/SE	20.52 ± .19	20.40 ± .15	20.52 ± .13	20.23 ± .13	22.09 ± .15	22.02 ± .15	20.75 ± .08
SD	.90	.77	.89	.81	.62	.60	1.04
WEIGHT	(14)	(16)	(66)	(45)	(7)	(4)	(152)
Range	25.20-40.00	28.0-42.0	24.00-44.00	22.40-42.10	22.80-43.80	22.40-37.50	22.40-44.00
Mean w/SE	32.71 ± 1.13	33.32 ± .97	31.41 ± .43	32.29 ± .56	32.70 ± 3.52	29.80 ± 3.56	31.71 ± .34
SD	4.23	3.89	3.46	3.76	9.32	7.12	4.16

Red-tailed Tropicbird (*Phaethon rubricauda*)*

Patrick J. Gould, Warren B. King, and Gerald A. Sanger

Introduction

The material contained in this report is a summary of all at-sea observations of Red-tailed Tropicbirds (*Phaethon rubricauda*) gathered by the Pacific Ocean Biological Survey Program (POBSP) in the central and eastern Pacific Ocean. Humphrey (1965) has given a general summary of the objectives of this program, while Gould (pp. 1-5, herein) has summarized the areas surveyed, the methods and materials used in obtaining and analyzing the data, and has acknowledged all personnel who have taken part in the gathering of the data. The reader is referred to the latter paper for a more complete account of these activities. Literature records and data obtained from POBSP island surveys are included as general background information.

Pelagic observations began in August 1963 and continued through November 1968. During this time over 2200 Red-tailed Tropicbirds were recorded during 2968 days (over 21,500 hours) and more than 208,000 miles of diurnal observations.

SUMMARY OF PUBLISHED PELAGIC DISTRIBUTION.—Red-tailed Tropicbirds are typically wide ranging, solitary, and highly pelagic seabirds. Individuals have been recorded from 39°N to almost 38°S, and from about 300 miles off the western American coasts (extreme southern California to Chile) to southeastern Australia, Formosa, and Honshu, Japan. Population estimates for the central Pacific

islands visited by the POBSP indicate total numbers in that area to be in excess of 31,000 birds (Table 33).

The appendix table summarizes significant published pelagic observations. Only birds specifically noted as *Phaethon rubricauda* are included in this list. A number of sightings of "tropicbirds" or "*Phaethon* sp." are omitted, as are those suggesting any uncertainty in identification. Despite these precautions, it is possible that some of the included sight records were in error since immature Red-tailed Tropicbirds resemble Red-billed Tropicbirds (*Phaethon aethereus*).

In general, Red-tailed Tropicbird sightings are widely scattered across the tropical and subtropical Pacific. Birds have been seen in higher latitudes in the far western Pacific than in the far eastern Pacific. Austin and Kuroda (1953:315) list six specimen records for Honshu, Japan, the northernmost from 39°N, 142°E. In the southern hemisphere, Hindwood (1955) lists several records from New South Wales (ca. 28°S to 30°S), and the adjacent ocean. Falla, et al. (1967:59-60) speculate that this species may penetrate the Tasman Sea. Peter Harper (pers. comm.) confirms this with a sighting of two birds at 42°S. In contrast, the highest eastern Pacific latitude sightings recorded are at Guadalupe Island, ca. 29°N (Kaeding, 1905) and 12°S (Bourne and Radford, 1961:22). The POBSP records extend the known range of the species in the eastern Pacific to 31°N and to 24°S.

BREEDING PHENOLOGY.—The breeding cycle of individual Red-tailed Tropicbirds in the central Pacific is annual, but the cycles for any given population may be extended or irregular. On most islands, birds have been recorded at some stage of breeding activity during all months. In the northwestern Hawaiian Islands breeding activity begins in late

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TABLE 33.—Recent maximum population estimates¹ of Red-tailed Tropicbirds for central Pacific islands visited by the POBSP

Location	Number
HAWAIIAN ISLANDS	
Kure	2,500
Midway	7,500
Pearl and Hermes Reef	165
Lisianski	3,000
Laysan	4,000
Gardner Pinnacles	50
French Frigate Shoals ²	225
Necker	200
Nihoa	500
Kaula	common
Lehua	500
WAKE ATOLL	20
JOHNSTON ATOLL	110
MARSHALL ISLANDS	
Taongi	525
Bikar	125
Eniwetok	150
Taka	25
Jemo	3
Erikub	1
LINE ISLANDS	
Palmyra	20
Christmas	8,000
Jarvis	2,000
Malden	40
Starbuck	10
PHOENIX ISLANDS	
Canton	10
Enderbury	1,000
McKean	500
Birnie	50
Phoenix	175
Hull	3
Sidney	4
Gardner	4
HOWLAND	130
BAKER	20

¹ High count for one day of breeding and displaying adults.

² Includes breeding and displaying adults and chicks.

March when a few eggs are laid, but May and June appear to be the principal months of egg-laying. Chicks have been recorded in all months but are most common in July and August. Maximum numbers of adults have been recorded between April

and September; numbers then diminish rapidly to a low in December and January.

On Johnston Atoll, the population follows the same breeding pattern except that it is about one or two months ahead of the Northwest Chain. The egg-laying peak is in late March, and chicks are present from late April through August. The maximum population occurs in May, and numbers diminish after July.

In the Phoenix and Line groups the breeding cycle is similar to that of the Leewards but may be somewhat later. On some islands egg-laying peaks are decidedly variable. The breeding cycle of birds in the Marshall and Gilbert islands has not been documented. On Wake Island breeding occurs mainly from March through July or August.

Behavior

Definitions of special terms used in this section are as follows: a "sighting" refers to one or more birds observed together and acting as a unit; a "flock" is considered to be the association of five or more individuals; a "mixed" flock or sighting is one that contains more than one species; a "pure" flock or sighting is one that contains only one species. "BPS (birds per sighting)" is a good index of the gregariousness or flocking tendency of a species. In this section all data, except when specifically stated otherwise, were collected under the following conditions: (1) at sea (including areas immediately offshore), (2) within about one mile of the ship, (3) in the central Pacific, (4) from 1964 through 1966. Within these parameters 1574 Red-tailed Tropicbirds and 1323 Red-tailed Tropicbird sightings were recorded (Table 34).

Red-tailed Tropicbirds are among the most solitary of seabirds. Of all individuals seen, 73.2 percent (87.2 percent of all sightings) were alone. The BPS ratio was 1.19 (Table 34) as compared with Sooty Terns (*Sterna fuscata*) and Wedge-tailed Shearwaters (*Puffinus pacificus*) which had BPS ratios of 12.79 and 4.56, respectively (derived from Tables 2 and 17). Further, only 4.5 percent of all individuals (4.4 percent of all sightings) were associated with other seabirds. Table 35 gives the frequency with which Red-tailed Tropicbirds were associated with other species of seabirds. The infrequency of such associations can best be explained by tropicbird

TABLE 34.—Frequency of Red-tailed Tropicbirds in the central Pacific Ocean, 1964–1966

Birds per sighting	Sightings (No.)	Total sightings (%)	Birds (No.)	Total birds (%)
1	1153	87.2	1153	73.2
2	118	8.9	236	15.0
3	37	2.8	111	7.0
4	7	0.5	28	1.8
5	4	0.3	20	1.3
6	2	0.15	12	0.8
7	2	0.15	14	0.9
Total	1323		1574	

(mean number of birds per sighting: 1.19)

behavioral patterns, particularly those connected with feeding.

Red-tailed Tropicbirds are regularly attracted to ships, which they often follow for ten or fifteen minutes and occasionally for an hour or more. This, in itself, would decrease the chances of observing them in association with other species, since most other species are not ship followers. The major attraction of the ship is apparently the flying fish scattered by its approach. Tropicbirds circle above or behind the ship at estimated heights aver-

TABLE 35.—Frequency of Red-tailed Tropicbird sightings associated with other seabirds, 1964–1966

Seabird species	Sightings (No.)	Sightings (%)
<i>Sterna fuscata</i>	32	2.4
<i>Puffinus pacificus</i>	24	1.8
<i>Phaethon lepturus</i>	14	1.1
<i>Pterodroma externa</i>	11	0.8
<i>Pterodroma nigripennis</i>	10	0.8
<i>Fregata species</i>	9	0.7
<i>Anous stolidus</i>	5	0.4
<i>Bulweria bulwerii</i>	5	0.4
<i>Gygis alba</i>	4	0.3
<i>Sula dactylatra</i>	4	0.3
<i>Sula sula</i>	3	0.2
<i>Oceanodroma leucorhoa</i>	3	0.2
<i>Puffinus griseus</i>	2	0.2
<i>Puffinus puffinus</i>	2	0.2
<i>Puffinus nativitatis</i>	2	0.2
<i>Pterodroma alba</i>	1	0.1
<i>Pterodroma neglecta</i>	1	0.1
<i>Sterna lunata</i>	1	0.1
<i>Catharacta skua</i>	1	0.1
<i>Stercorarius pomarinus</i>	1	0.1

aging 40 meters ($n = 307$ sightings, range 3 to ca. 250 m). While circling, their heads are held downward, bill pointing toward the water. When a fish is spotted they half-fold their wings and drop to the water in a controlled dive, often changing direction to compensate for movement of the fish. In 17 recorded instances diving heights ranged from 10 to 50 meters (average of 25 m).

Unlike the feeding behavior of most seabirds in our study area, all Red-tailed feeding was accomplished only by the "plunge to surface" and "direct to prey air dive" methods described by Ashmole and Ashmole (1967:70–71). We have one record of possible "contact dipping" (see below), but in this instance the bird may have lost sight of the fish and pulled out of the dive before hitting the water since it was not noted to have captured a fish. The following examples are taken directly from POBSP field notes:

CONTACT DIPPING?

15 August, 1964. 1818 Hours. Anonymous. "... another dive from 100 feet just skimmed surface of water."

PLUNGE TO SURFACE

09 January 1965. 0715 Hours. Warren King. "2 birds. Birds were feeding, dropping into water from 40 feet or so, breaking their fall slightly with their wings and steering as well. Did not appear to go below surface. Wings somewhat extended a split second after impact keeping birds on surface."

DIRECT TO PREY AIR DIVE

07 February 1964. 0844 Hours. Patrick Gould. "1 bird made at least 6–10 dives, 2 from at least 100 feet up. Bird half closed its wings, steering with wings, did not break fall, completely submerged in water with great splash,

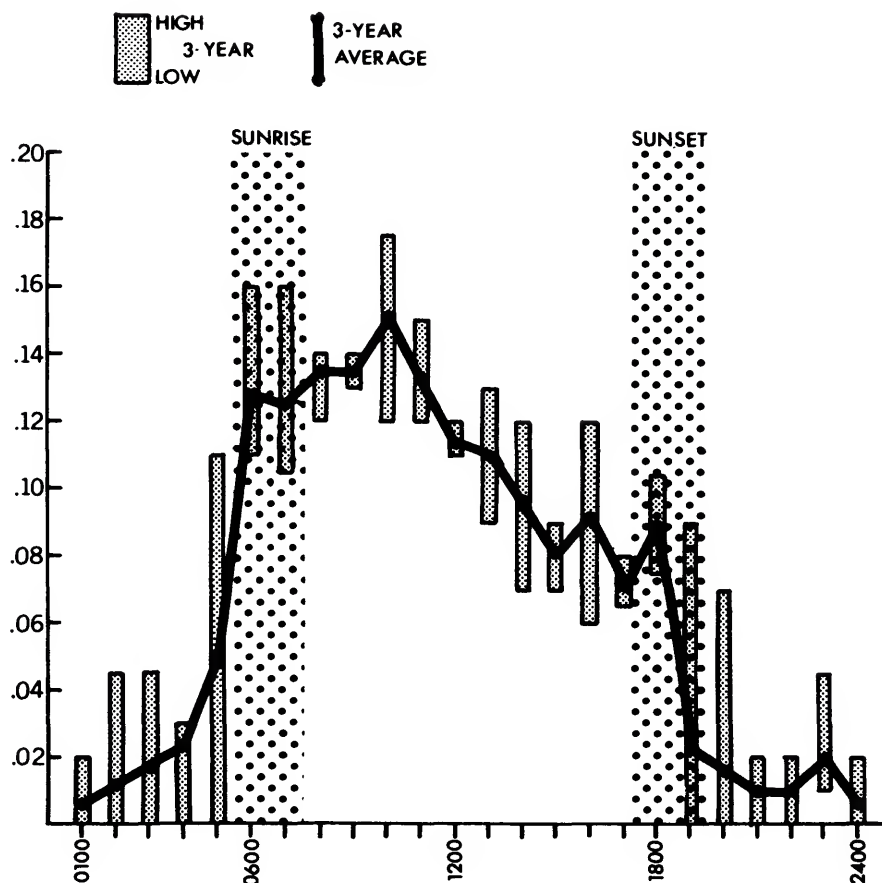


FIGURE 126.—Hourly densities of Red-tailed Tropicbirds in the central Pacific, 1964–1966. Number of hours of observation per time period ranged from 183.7 at 0400 to 1151.6 at 1500. Total hours of observation equal 15,962.0.

but did not remain in water for longer than 2 seconds. A series of shorter dives were also made. One bird, after starting its dive, altered its direction to more of an incline and spiraled down, evidently keeping the fish in sight at all times. It was noted to check itself in mid-dive several times but this appeared to be due to movement of prey rather than trying to reduce speed."

The above feeding habits are probably incompatible with the feeding habits of other species in mixed flocks where the birds are concentrated and swirling in circles over the food. A diving bird would not be able to keep a fish in sight or avoid swirling birds. Although boobies (*Sula*) use the "direct to prey air dive" when by themselves, they apparently always switch to "dipping" or "surface

dive" when in mixed flocks. Tropicbirds are apparently not as versatile as boobies, and, even when attracted to mixed feeding flocks, generally remain on the periphery.

Red-tailed Tropicbirds have been recorded at all hours of the day but are most commonly observed in the morning. Peak numbers occurred around 1000 hours (Figure 126). Nocturnal density figures are low due to the difficulty in seeing and identifying single birds at night. Most birds were active, but 14.2 percent of all individuals recorded were sitting on the water. Many of the birds were apparently roosting on the water and were flushed by the approaching ship.

TABLE 36.—Measurements (in mm) of Red-tailed Tropicbirds from the central Pacific

Area and source	Sample size	Range	Mean	Standard error
Wing length				
Laysan (Stager, 1964)	7	307-322	313	-
Northwestern Hawaiian Islands and Johnston Atoll (POBSP)	22	301-329	316	1.5
At sea, N of 10°N (POBSP)	79	287-343	316	1.4
At sea, 4°N-10°N (POBSP)	12	307-344	320	3.4
At sea, S of 4°N (POBSP)	18	315-350	329	2.5
Line and Phoenix (POBSP)	21	310-345	334	2.1
Marquesas, Tuamotus, Society, etc. (Stager, 1964)	7	320-344	330	-
Exposed culmen				
Laysan (Stager, 1964)	7	58-63	61	-
Northwestern Hawaiian Islands and Johnston Atoll (POBSP)	21	50-66	61	0.6
At sea, N of 10°N (POBSP)	77	57-69	62	1.0
At sea, 4°N-10°N (POBSP)	12	59-65	62	0.6
At sea, S of 4°N (POBSP)	17	61-67	63	0.4
Line and Phoenix (POBSP)	21	59-68	63	0.6
Marquesas, Tuamotus, Society, etc. (Stager, 1964)	7	62-70	66	-

Specimen Records

Two races have been recognized in the central Pacific. *Phaethon rubricauda rothschildi* (Mathews) breeds on the northern islands, including Johnston Atoll, Wake, and the northwestern Hawaiian Islands. A larger form, *P. r. melanorhynchos* Gmelin breeds on islands farther south, including the Marquesas, Line, Phoenix, Tuamotu, and Society islands. Wing length and exposed culmen are the major distinguishing criteria. These races appear to represent parts of a broken cline of increasing size from north to south. Our measurements (Table 36) show that birds from northern islands (Johnston Atoll and the northwestern Hawaiians) have shorter average wing and exposed culmen lengths than birds from Line and Phoenix islands. These in turn apparently have shorter average exposed culmens (Stager, 1964) than birds from farther south and east (Marquesas, Tuamotus, and Society islands).

Specimens have been taken at sea in every month of the year and along all commonly used POBSP cruise tracks. Greatest numbers were collected from June through November, the period, also, when

the greatest number of sightings was recorded. Specimens collected at sea in the central Pacific were divided into three groups for analysis: (1) those collected north of 10°N, (2) those collected between 10°N and 4°N, and (3) those collected south of 4°N (Table 37). Birds collected north of 10°N agree in mensural characteristics with those of the northwestern Hawaiian population. Birds collected south of 4°N are larger than those from the northwestern Hawaiian population areas but slightly smaller than birds from the southern islands. Birds collected in the intermediate zone are intermediate in their measurements, but fall closer to the northern population.

Eighteen specimens (all but three either immature or subadult) were collected at sea in the eastern Pacific (Table 37). These show the same tendency for larger birds to be found in southern latitudes, and smaller birds to be found in northern latitudes. Two specimens in the United States National Museum (USNM 212164, 212165), collected at 10°N, 130°W, conform in size, as expected, to the population from the northwestern Hawaiian Islands.

Exceptions to the above pattern do occur. Seven

TABLE 37.—Measurements (in mm) of POBSP specimens from the eastern Pacific, latitudes south to north (SA=subadult, IM=immature, AD=adult)

Area	Date	Age	Sex	Wing length	Exposed culmen
24°14'S, 75°27'W	22 Apr 65	SA	♀	330	68
24°14'S, 75°27'W	22 Apr 65	SA	♀	320 (worn)	66
24°14'S, 75°27'W	22 Apr 65	SA	♂	314	69
23°45'S, 75°45'W	22 Apr 65	SA	♂	332	68
23°45'S, 75°45'W	22 Apr 65	SA	♀	329	64
23°45'S, 75°45'W	22 Apr 65	SA	♂	312	68
17°02'S, 106°46'W	15 Mar 68	IM	♀	321	68
16°34'S, 107°01'W	15 Mar 68	AD	♀	334	68
14°08'S, 108°26'W	16 Mar 68	IM	♀	332	66
14°00'S, 104°58'W	4 Mar 67	SA	♀	344	63
13°21'S, 108°53'W	16 Mar 68	IM	♀	339	70
9°57'S, 112°23'W	23 Aug 67	SA	♀	323	65
2°31'S, 118°50'W	27 Feb 68	AD	♀	321	63
1°05'N, 111°51'W	21 Mar 68	IM	♀	334	64
8°08'N, 112°11'W	3 Nov 67	SA	♀	318	63
8°08'N, 112°11'W	3 Nov 67	SA	♀	322	61
13°41'N, 112°20'W	11 Feb 67	SA	♂	328	62
31°39'N, 123°22'W	13 Feb 67	AD	♀	310	59*

* Banded on Kure Atoll.

TABLE 38.—At-sea recoveries of banded Red-tailed Tropicbirds (AD=adult, SA=subadult, L=local, N=nestling)

Banding			Recovery				Elapsed	
Location	Date	Age	Location	Date	Age	Sex	Months	Miles
Kure	14 Oct 64	L	31°39'N, 123°22'W	13 Feb 67	AD	♀	28.0	3,300
Kure	1 Apr 64	AD	4°40'N, 154°20'W	30 Nov 67	?	?	8.0	2,000
Kure	15 Oct 64	N	38°30'N, 178°30'W	28 Apr 70	?	?	66.4	600
Midway	14 Feb 64	AD	125 mi SW Midway	10 Jul 64	AD	?	6.9	125
Midway	27 Jul 65	AD	33°02'N, 154°34'W	15 Nov 66	AD	?	15.6	1,290
Laysan	10 Sep 67	AD	15°00'N, 117°30'W	27 Feb 68	?	?	5.6	3,100
Christmas	21 Nov 64	N	1°57'N, 177°26'W	17 Sep 66	AD	♀	21.9	1,200
Jarvis	15 Nov 64	N	0°22'S, 178°38'W	15 Oct 66	AD	♀	23.0	1,060
Jarvis	16 Nov 64	N	1°17'N, 177°44'W	10 Dec 66	AD	♂	25.1	1,060
Jarvis	15 Nov 64	N	0°38'N, 176°35'W	7 Feb 66	SA	♂	14.7	975
Enderbury	2 Oct 65	N	7°30'S, 170°49'W	1 Dec 66	SA	♂	14.0	270

exceptionally large birds (wing=335–342 mm, exposed culmen=64–69 mm) were collected north of 10°N and are referable to *P. r. melanorhynchos*. The northernmost location was at 17°52'N, 166°20'W. Two each were taken in April and September and three in November. Conversely, two exceptionally small birds (wing=315–319 mm, exposed culmen=62–62 mm) have been taken south of 4°N and are referable to *P. r. rothschildi*. The southernmost location was at 00°21'S, 178°38'W. One each was collected in April and October.

There is no way of proving the island of origin

of a bird collected at sea unless it was banded as a nestling. It is reasonable, however, to assume that most birds collected north of 10°N originated on northern islands because of the agreement in measurements between island and at-sea specimens. On the same basis we can assume that the birds collected south of 4°N most likely originated on the southern islands. It thus appears that Red-tailed Tropicbirds, especially young, disperse widely at sea, but tend to remain within the latitudinal range of their respective populations.

Six specimens, assigned by us to *P. r. melano-*

rhynchos and collected off northern Chile (three at 23°45'S, and three at 24°15'S), represent a considerable extended range to the southeast for this species. One bird, originally banded as a local on Green Island, Kure Atoll, and collected off northern Baja California (31°39'N, 123°22'W), represents a northeast range extension. Its measurements conform to the *P. r. rothschildi* population.

Eleven banded birds have been recovered at sea (Table 38). Although the sample size is small, these recoveries support the preceding arguments that birds disperse widely but tend to remain within the latitudinal boundaries of their respective populations. The Kure bird recovered at 04°40'N appears to be an exception; however, this latitude is approximately at the southern border of the Equatorial Countercurrent, which is the dividing line between several northern and southern seabird distribution patterns.

Molt

Molt in Red-tailed Tropicbirds appears to take place nearly continuously except when individuals are within a breeding cycle. Not one individual of 57 adult birds collected on many islands of the central Pacific, including the Hawaiian, Line, Phoenix, and Marshall groups and Johnston and Howland islands, was molting remiges or rectrices, although several birds showed light body contour feather molt.

The juvenal appearance, characterized by heavy black vermiculations over the entire dorsal surface, a black suffusion spreading into the vanes, both dorsally and ventrally, from the black dorsal shafts of the larger primaries, excluding the outermost, short, white central rectrices and a blackish bill, changes within 15 months, probably starting with a complete annual molt, to a distinctive subadult form which probably persists (on the basis of two specimens, 15 and 16 months, respectively) well into the second year, when it is gradually replaced by the typical adult form. Subadults have white backs and rumps, flecked with black, but the vermiculations on head and nape remain. The primary vanes become entirely white, the shafts remaining black dorsally. The central rectrices elongate, although not to the extent of adults, and get the first hint of reddish pigment. The bill becomes

increasingly yellow, excluding the base which remains dark. Between 15 or 16 months and 23 months all black spots have disappeared from the dorsal surface except the central portion of the vanes of the longest secondaries which remain black in all age classes. The black vermiculations of head and nape remain only at the bases of feathers of this area and are masked by white, which condition persists in adult birds. The central rectrices are red but possibly not as long as those of breeding birds. It may be possible to distinguish some third year birds from older birds by their orange rather than red bills (the nares remain dark even in breeding birds) and by the retention of black spots in a few dorsal secondary coverts, often well hidden. Otherwise, they are indistinguishable from breeding birds. Our sample in this age class is four birds, 23, 24, 26, and 29 months. Most do not breed until at least four years, possibly older. Thus, there is a period of at least one year when birds have adult appearance but do not breed.

Because the breeding cycles of populations are not precisely synchronized, but extend in some cases nearly year-round, and because there is evidently some mixing at sea of populations from the southern and northern hemispheres, some of the birds collected in any given month at sea are undergoing flight feather molt. In only 4 months (June, August, September, and December) were more than one-half of adults taken at sea not molting remiges and rectrices. Subadult and immature birds (those with at least some black vermiculations on their backs) molt almost continuously. Only 5 of 54 immature or subadult birds (9.3 percent) were molting neither remiges nor rectrices, whereas 27 of 81 adults (32.5 percent) had no rectrix or remex molt. All 18 birds collected in the eastern Pacific (Table 37), 3 adults and 15 subadults or immatures, were undergoing molt of flight feathers.

The pink flush that appears in the plumage of some adult birds is evidently not tied directly to breeding. Eight of 81 (9.9 percent) adult birds taken at sea had a pink flush; only 2 of these were not molting flight feathers.

REMEX MOLT.—Remex molt proceeds outward from the carpal joint toward the outermost primary, and inward along the secondaries toward the body. Secondary molt will not be considered further here. Primary molt can occur at one locus, or at 2 or 3 loci simultaneously.

<i>number of loci</i>	<i>number of specimens</i>	<i>percent of total specimens</i>
0 (no molt)	34	25.2
1	52	38.5
2	41	30.4
3	8	5.9
	135	100.0

Because the innermost primaries were often difficult to identify on the specimens, and, therefore, molt of Remiges 1 or 2 might have been overlooked, some specimens recorded molting at 1 or 2 loci might have been molting actually at 2 or 3 loci. Of those birds molting at 2 or 3 loci, the mean number of feathers between loci was 3.3 (range 0-6). Remex molt is usually symmetrical.

<i>number of feathers between loci</i>	<i>number of occurrences</i>
0	6
1	2
2	8
3	13
4	13
5	13
6	2

RECTRIX MOLT.—Red-tailed Tropicbirds usually have 14 rectrices, including the two red elongate central feathers, although 9 of 135 specimens taken at sea (6.7 percent) had 16 rectrices, one apparently had only 12 and 2 seemed to have 15.

Growth and replacement of the two central rectrices is apparently continuous. Even among breeding birds, otherwise not molting, one of the central rectrices is usually shorter than the other and is growing. Because molt of the central rectrices is evidently not part of the normal molt cycle, it will not be considered further here.

Rectrix molt is usually completed before remex molt. Of 40 adults and 26 subadults or immatures

<i>number of loci</i>	<i>number of specimens*</i>	<i>percent of total specimens</i>
0 (no molt)	150	56.1
1	83	30.9
2	34	12.6
3	1	.2
4	1	.2
	269 ^b	100.0

* Each side is considered independently because rectrix molt is frequently asymmetrical.

^b The rectrices on one side of one specimen had been damaged to the extent that molt determination was impossible.

that were not molting rectrices, 13 adults and 21 subadults or immatures had not yet finished remex molt. Only one adult and one immature of 135 specimens had completed remex molt but not rectrix molt. Rectrix molt usually proceeds from one or two loci (see bottom of column 1).

Of those birds molting at two or more loci, the mean number of feathers between loci was 2.1 (range 0-4).

<i>number of feathers between loci</i>	<i>number of occurrences</i>
0	3
1	9
2	14
3	8
4	5

It was not possible to determine the sequence of rectrix molt, nor was there any obvious correlation between the stages of remex and rectrix molt.

Distribution and Abundance

Figures 130-141 summarize the observations of Red-tailed Tropicbirds made by POBSP in the central and eastern Pacific between 1963 and 1968. Data from January (Figure 130), for example, are taken from all years in which observations were made that month. Each day's observations are expressed in terms of birds per mile of observation, and are located on the maps at the position of the ship at noon (open circles). Areas of equal density were contoured to show relative abundance in different parts of the ocean and in different months. Where single line oceanic transects prevented accurate contouring, contours were extended an arbitrary distance on either side of the cruise track, just enough to indicate the densities encountered along the track.

An annual pattern of pelagic occurrence is evident in the monthly distribution maps. In order to examine this pattern more closely, the absolute density of Red-tailed Tropicbirds (birds per 100 mi²) was determined for each month, for each of four broad latitudinal bands between 30°N and 20°S (20°-30°N, 10°-20°N, 0°-10°N, 0°-20°S).

CENTRAL PACIFIC.—The Red-tailed Tropicbird was present throughout the pelagic central Pacific during all months. Abundance in the region was generally low in late winter and spring and high in summer and fall (Figure 127a). As is the case with

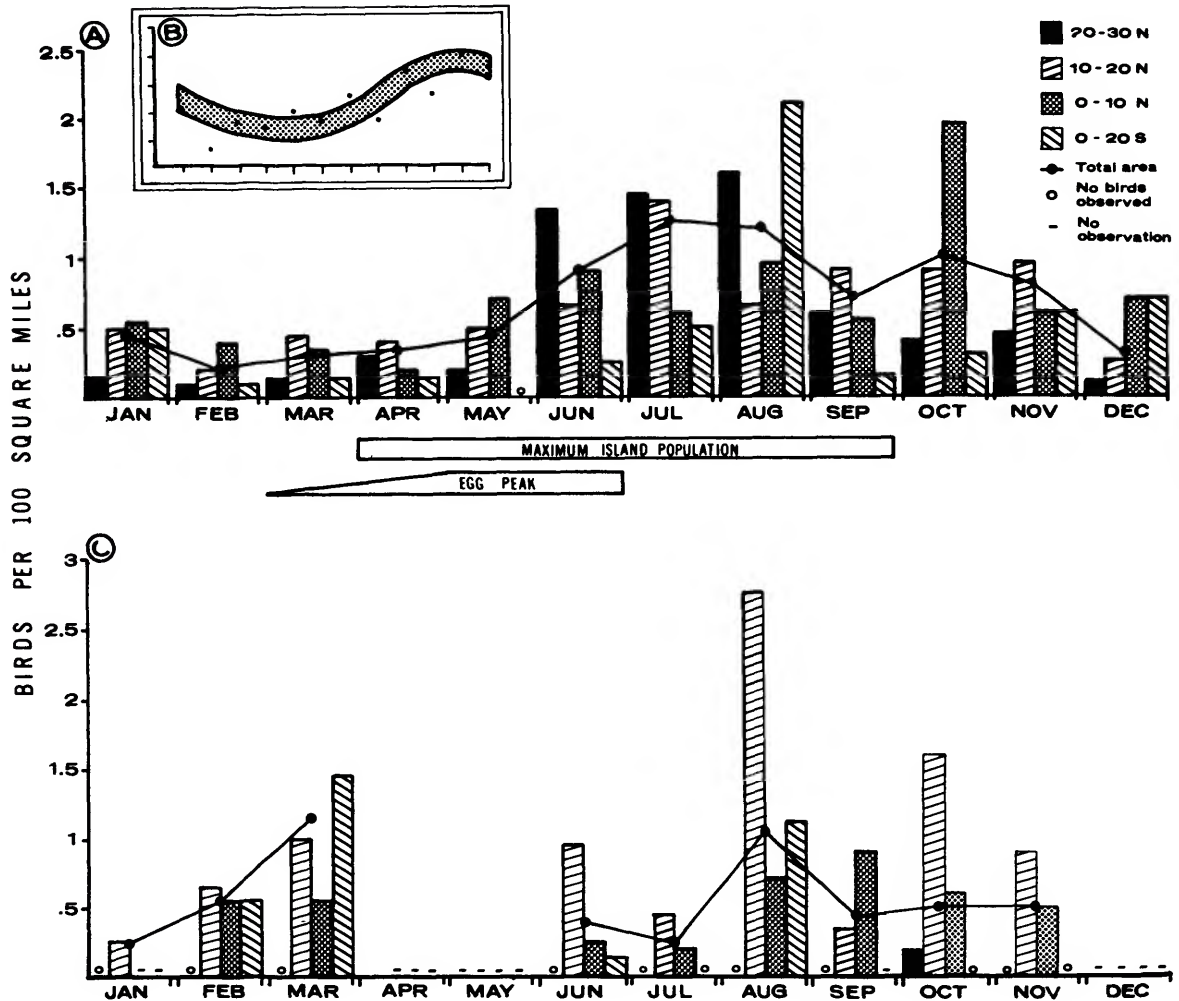


FIGURE 127.—Absolute density of Red-tailed Tropicbirds (birds per 100 square miles) in 10° wide latitudinal zones: A,B, in the central Pacific; C, in the eastern Pacific.

most other seabirds, the pelagic distribution of Red-tailed Tropicbirds is greatly affected by the breeding cycle. Adults tend to remain near breeding islands while breeding, particularly in the early stages (i.e., egg-laying and incubation). This was reflected in the differences in abundance observed between the latitudinal bands of 20°N to 30°N and 10°N to 20°N (Figure 127a). The former area encompasses the major breeding islands, and most cruises within this area remained relatively close to land. In contrast, the latter area includes only one

small breeding location (Johnston Atoll), and most cruises within the area were far from land. The only months when densities in the 20°N to 30°N area were greater than those of 10°N to 20°N were in June through August, when peak numbers occurred on the breeding islands. In the 10°N to 20°N zone, densities were relatively high from September through November; the July peak can be explained by one day of observation near Johnston Atoll, when density was high (.18 birds per mile). Figure 127b shows a typical annual cycle

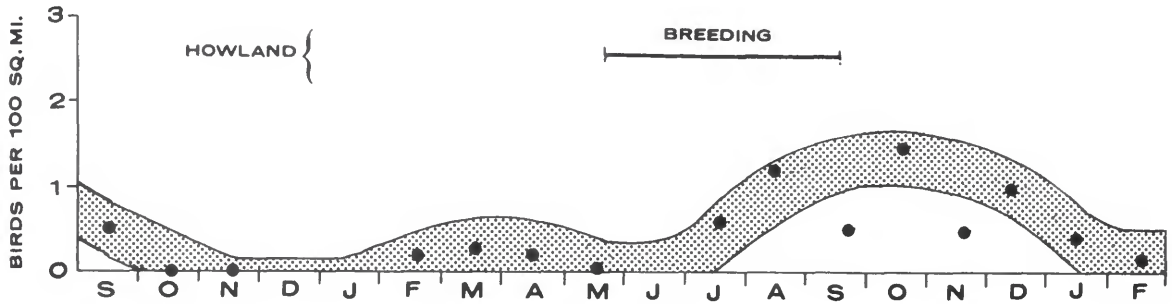


FIGURE 128.—Diurnal abundance of Red-tailed Tropicbirds in a pelagic area near Howland Island.

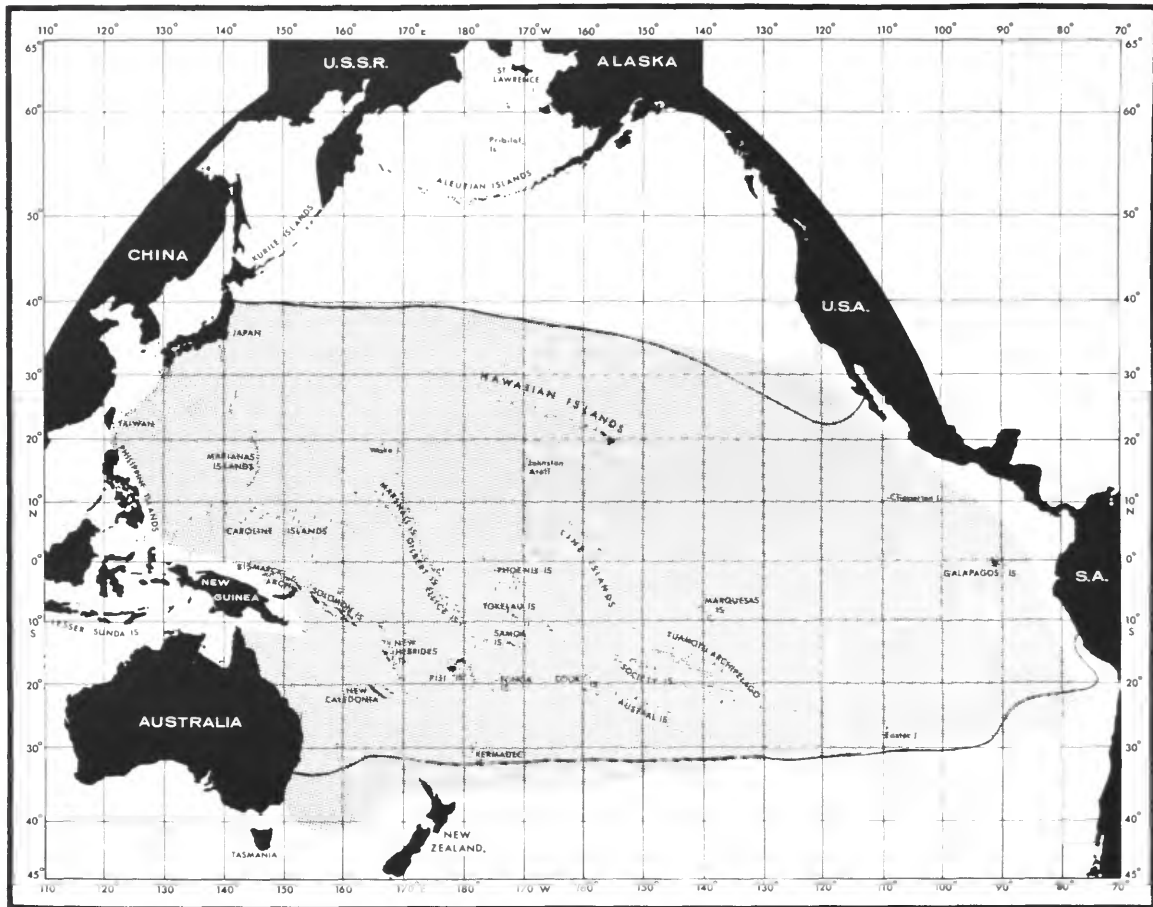


FIGURE 129.—Range of the Red-tailed Tropicbird (*Phaethon rubricauda*) in the Pacific Ocean. Dark lines indicate the location of the 22°C isotherm in summer (after Muromtzev, 1958).

for a relatively small pelagic study area, 50 miles off Johnston Atoll.

The absolute density (birds per 100 mi²) of the species was calculated for a pelagic area near Howland Island for the period September 1965 through February 1967 (Figure 128). Peak numbers (1.9 birds/100 mi²) occurred in October 1966, immediately following the Howland Island breeding season. Relatively high numbers (1.2 birds/100 mi²) also occurred in August 1966, during the breeding season.

EASTERN PACIFIC.—Although our data are incomplete for the eastern Pacific, the species was present each month observations were made. Observations were made in all months except April, May, and December (Figure 127c).

WESTERN PACIFIC.—The Red-tailed Tropicbird apparently occurs in the southwestern Pacific more commonly during the southern summer than during other seasons. Of the 24 records from the southwestern Pacific in the appendix for which there are definite dates, 18 were from October through March. Sorensen (1964) states that this species occurs year-round in the Kermadec Islands, but most abundantly from October through May.

Environmental Factors

It was noted that this species ranges to higher latitudes in the western Pacific than in the eastern Pacific (see Appendix). This is probably explained by the fact that the Kuroshio and East Australian Currents carry relatively warm water to relatively high latitudes in the western Pacific.

The range of this species, as indicated in Figure 129, generally parallels the summer surface water isotherms of ca. 22°C in both the north and south Pacific (Muromtzev, 1958, figs. 111, 112). Similarly, the distribution of surface salinity in the Pacific Ocean (Muromtzev, 1958, fig. 134) suggests that the species does not range into waters with salinities less than 33.5–34.0‰ in the northern hemisphere and less than 35.0‰ in the southern hemisphere. Its range appears limited to the waters between the bounds of the north and south subtropical convergences.

It is apparent from the preceding documentation of the northern and southern subspecies that trans-equatorial movements are minimal. It seems possible that the rich equatorial current region,

especially the countercurrent, acts as a restraint to bihemispheric movement of the subspecies, i.e., because of the increased abundance of food in the equatorial region, birds flying north from the south Pacific would have no reason to continue northward beyond the equatorial current region, and the same would apply to northern birds flying south. The pattern of distribution noted in the February map (Figure 131) may possibly be explained by this.

Discussion

The Red-tailed Tropicbird has an extremely wide pelagic range, which includes virtually all of the tropical and subtropical Pacific. It generally ranges to higher latitudes in the western Pacific (30°–35°N) than in the eastern Pacific (20°–25°N). Although there is little direct supporting evidence, it seems probable that most of the population stays within latitudes of less than ca. 30° in both hemispheres, but that individual birds occasionally wander to higher latitudes, or are carried there by storms.

It is apparent from our specimen data that a strong tendency exists for birds breeding on southern islands to remain in more southern latitudes, although they may disperse widely within these areas. Racial mixing in pelagic areas, however, does occur and individuals may be found far north or south of the usual range of their respective populations.

The distribution and abundance of Red-tailed Tropicbirds in the central Pacific appears to be generally correlated with the breeding season. The period (June through August) of maximum abundance and closest proximity to land in the northern part of their range corresponds to the breeding season in the Hawaiian Islands. Minimum abundance is found immediately following the dispersal of fledged young from the breeding grounds, and birds are absent from the vicinity of the islands the rest of the year. Peak abundance occurred at sea near Howland Island immediately following the breeding season.

Although our data from the eastern tropical Pacific do not cover all months, there appear to be peaks in abundance in both winter (February) and summer (August). The winter peak possibly contains some central Pacific breeders; the pelagic oc-

currence of the species in the central Pacific is at a low ebb at this time. Our data suggest that pre-breeders are more likely to visit the eastern Pacific than breeding age birds. Birds were seen each

month that POBSP cruises were conducted, these being all months except April, May, and December. Thus, it seems quite probable that the species occurs in the eastern tropical Pacific year-round.

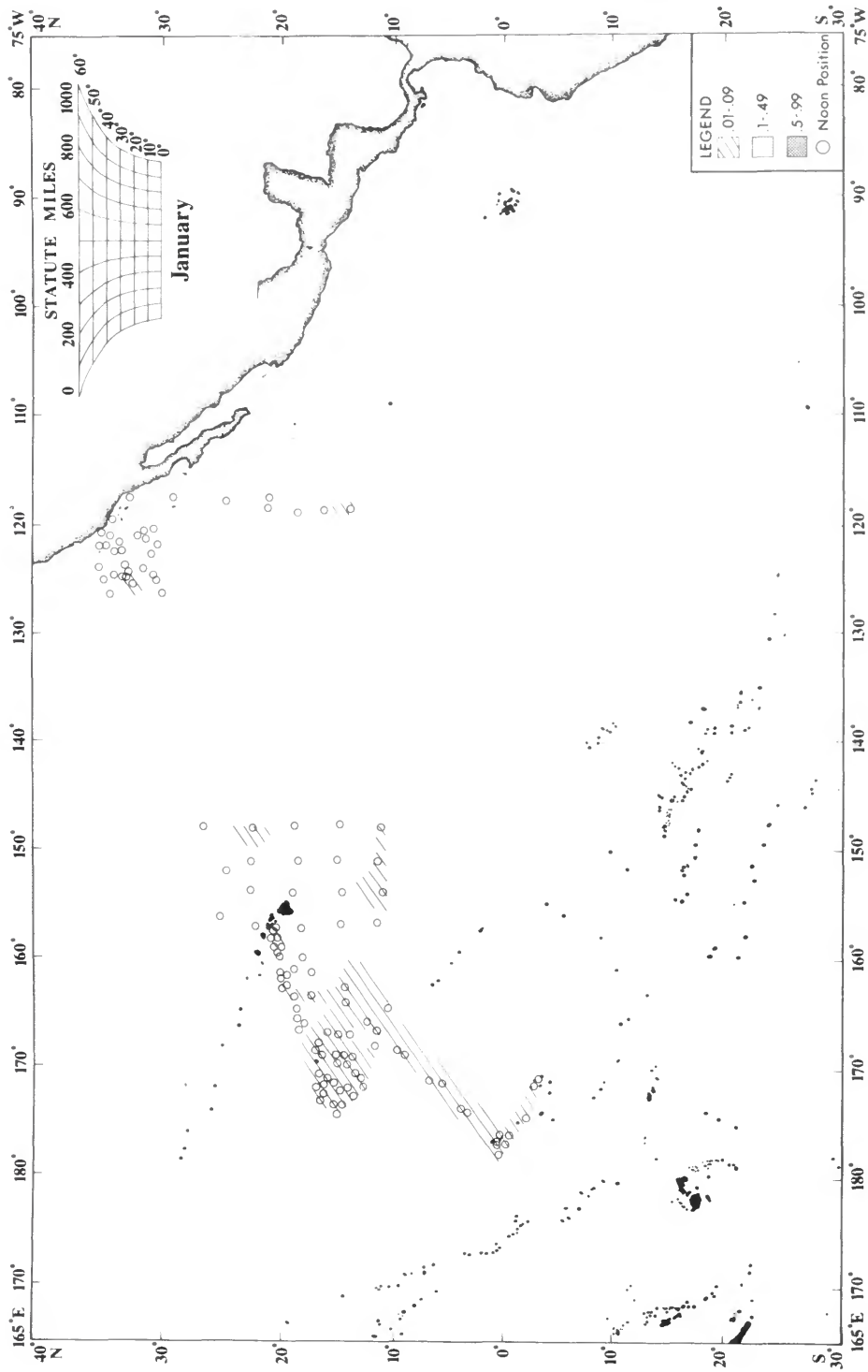


FIGURE 130.—Daily density (APM) of Red-tailed Tropicbirds in the central and eastern Pacific based on POSSP observations in January 1963-1968.

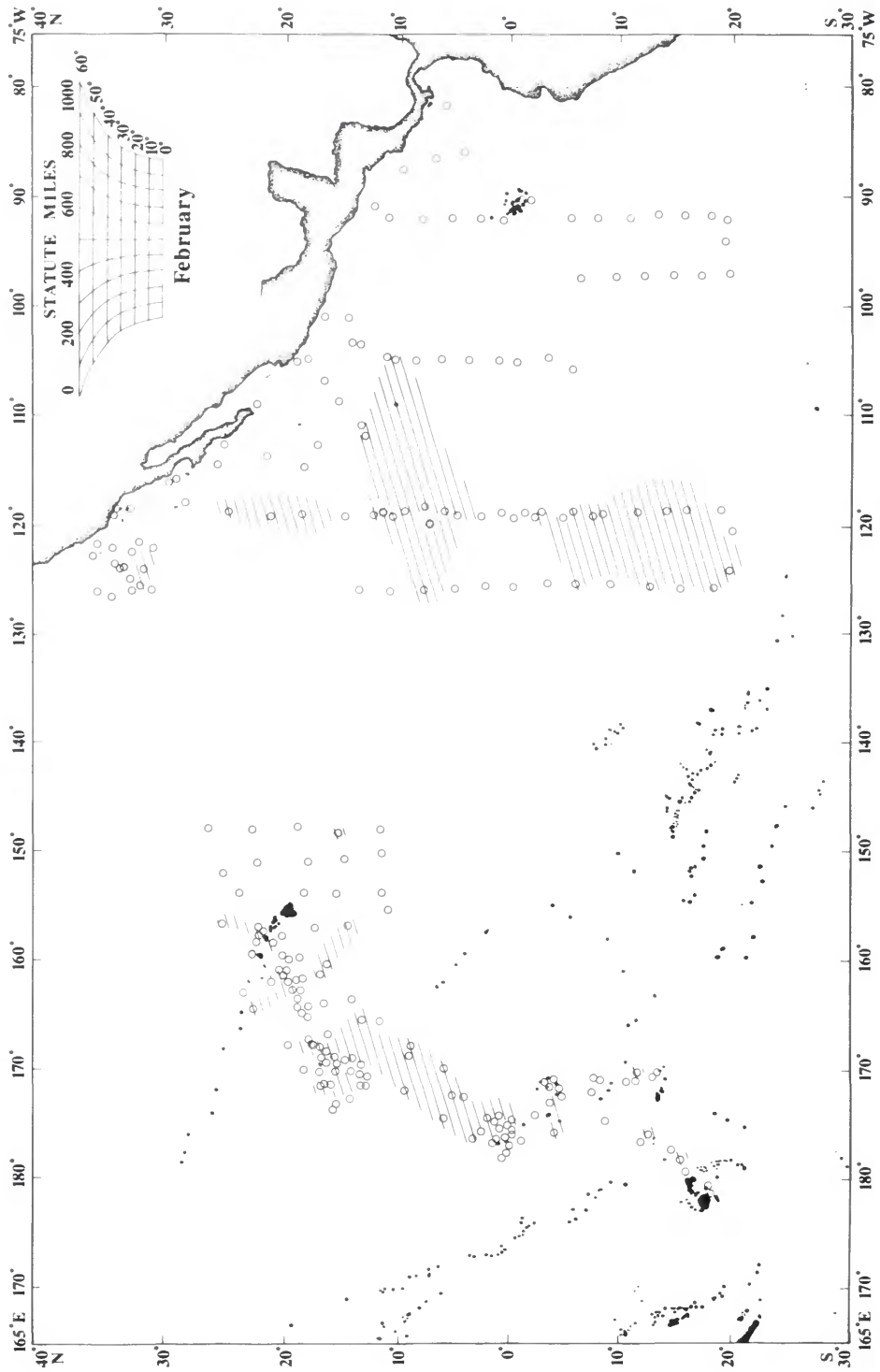


FIGURE 131.—Daily density (BPM) of Red-tailed Tropicbirds in the central and eastern Pacific based on ROASP observations in February 1968-1968.

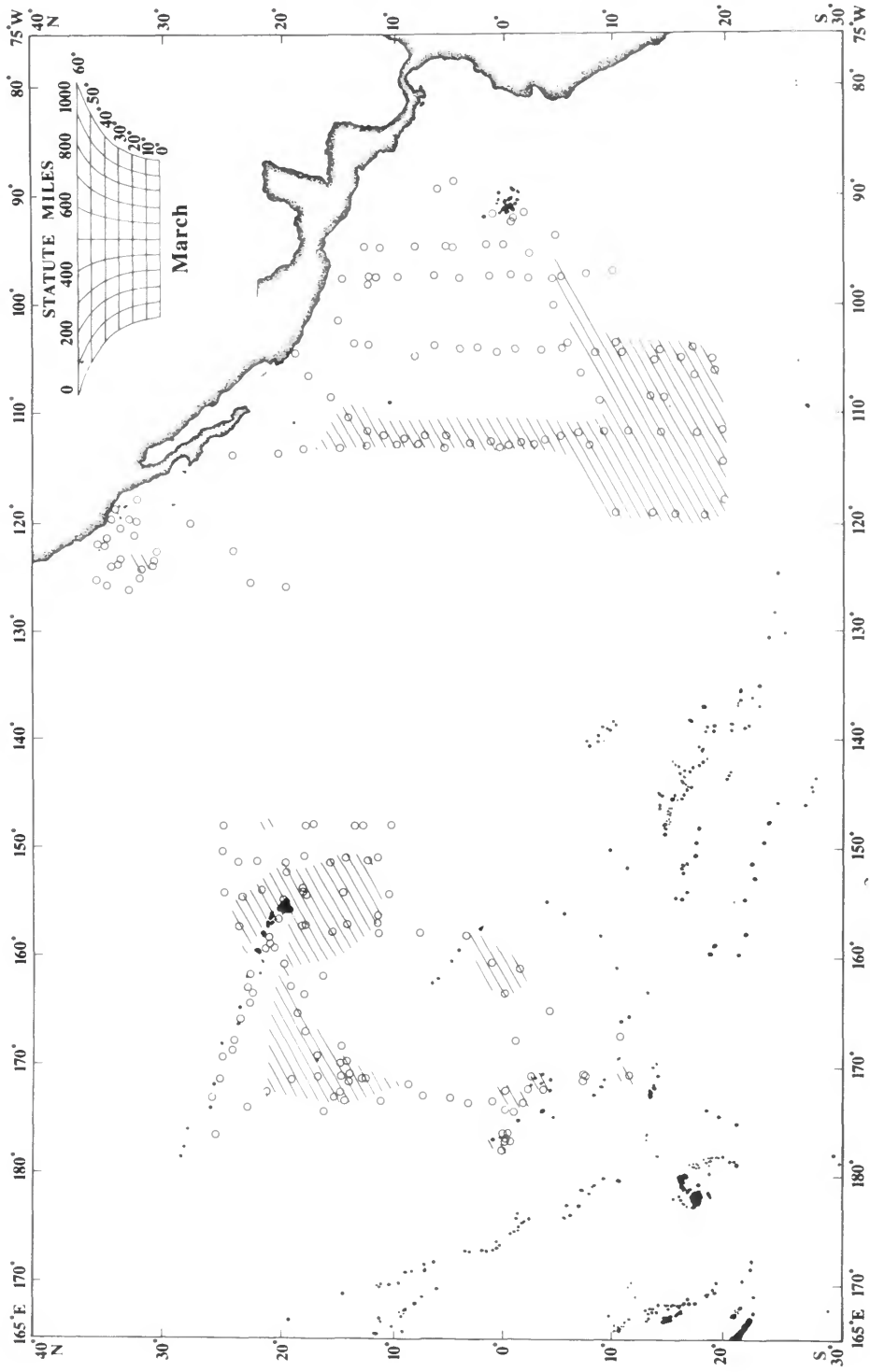


FIGURE 132.—Daily density (birds per square mile) of Red-tailed Tropicbirds in the central and eastern Pacific based on rookery observations in March 1963-1968.

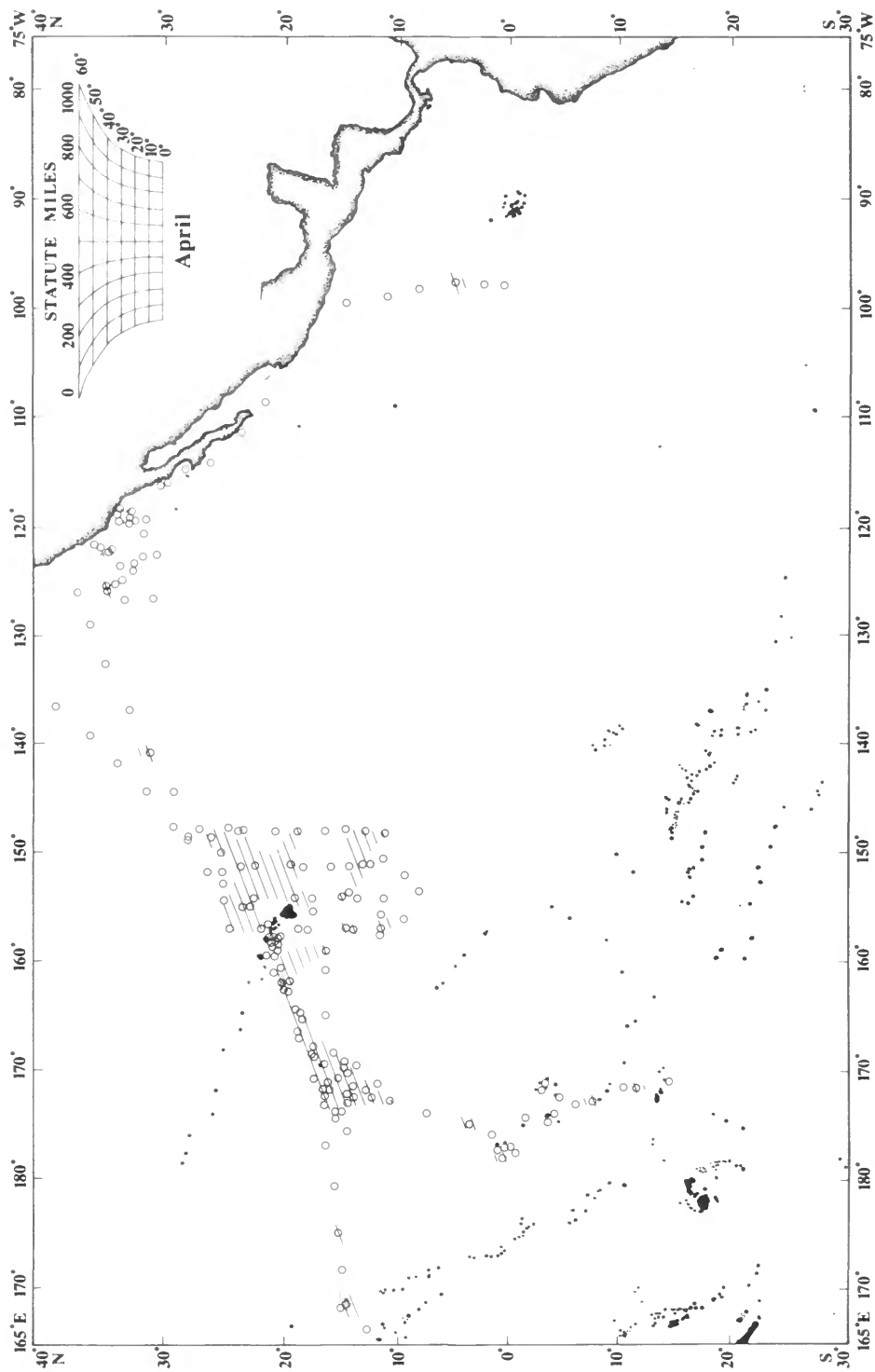


FIGURE 133.—Daily density (BPM) of Red-tailed Tropicbirds in the central and eastern Pacific based on rostr observations in April 1968-1968.

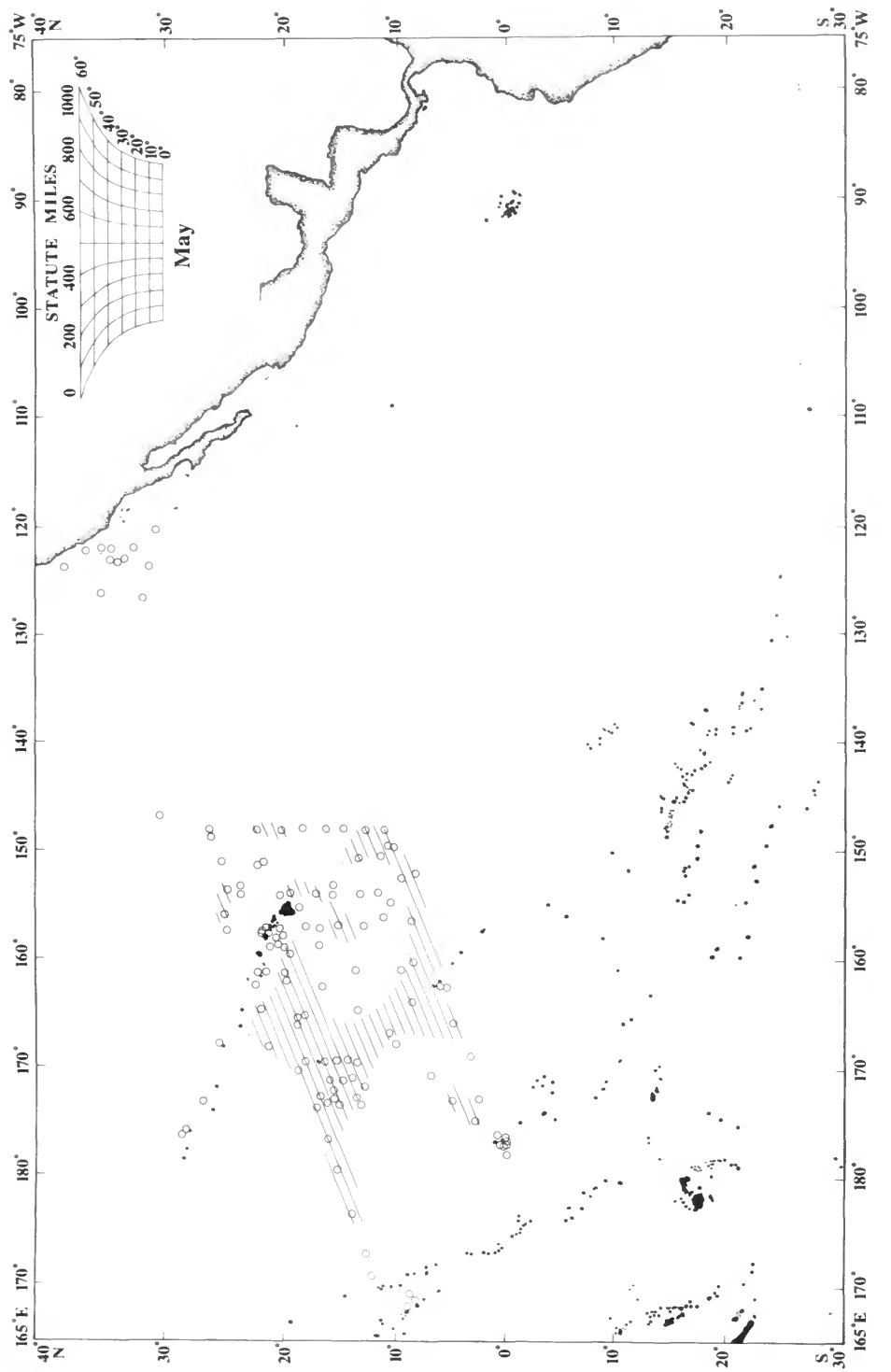


FIGURE 134.—Daily density (APM) of Red-tailed Tropicbirds in the central and eastern Pacific based on rossi observations in May 1963-1968.

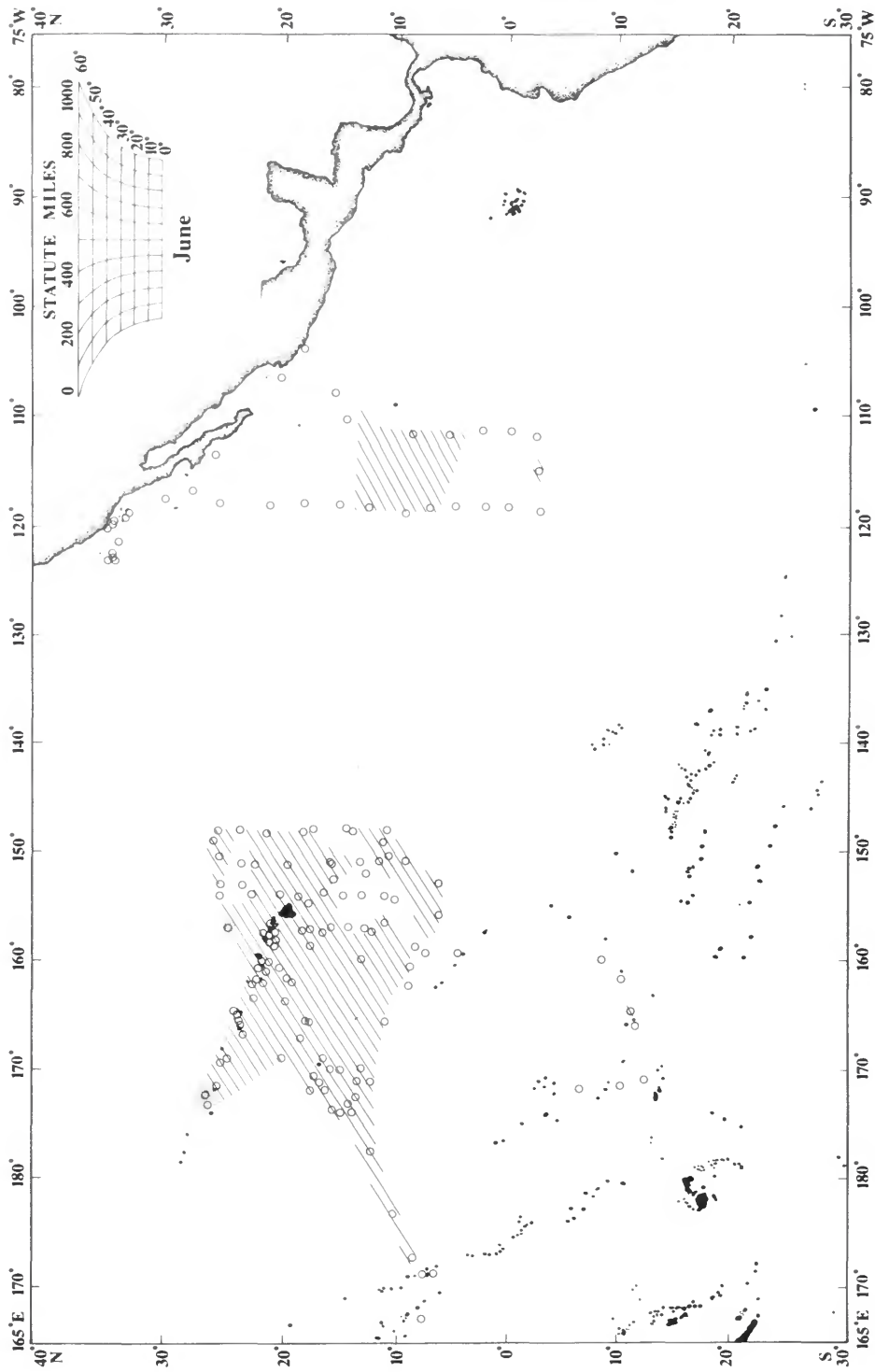


FIGURE 135.—Daily density (bpm) of Red-tailed Tropicbirds in the central and eastern Pacific based on robs observations in June 1963-1968.

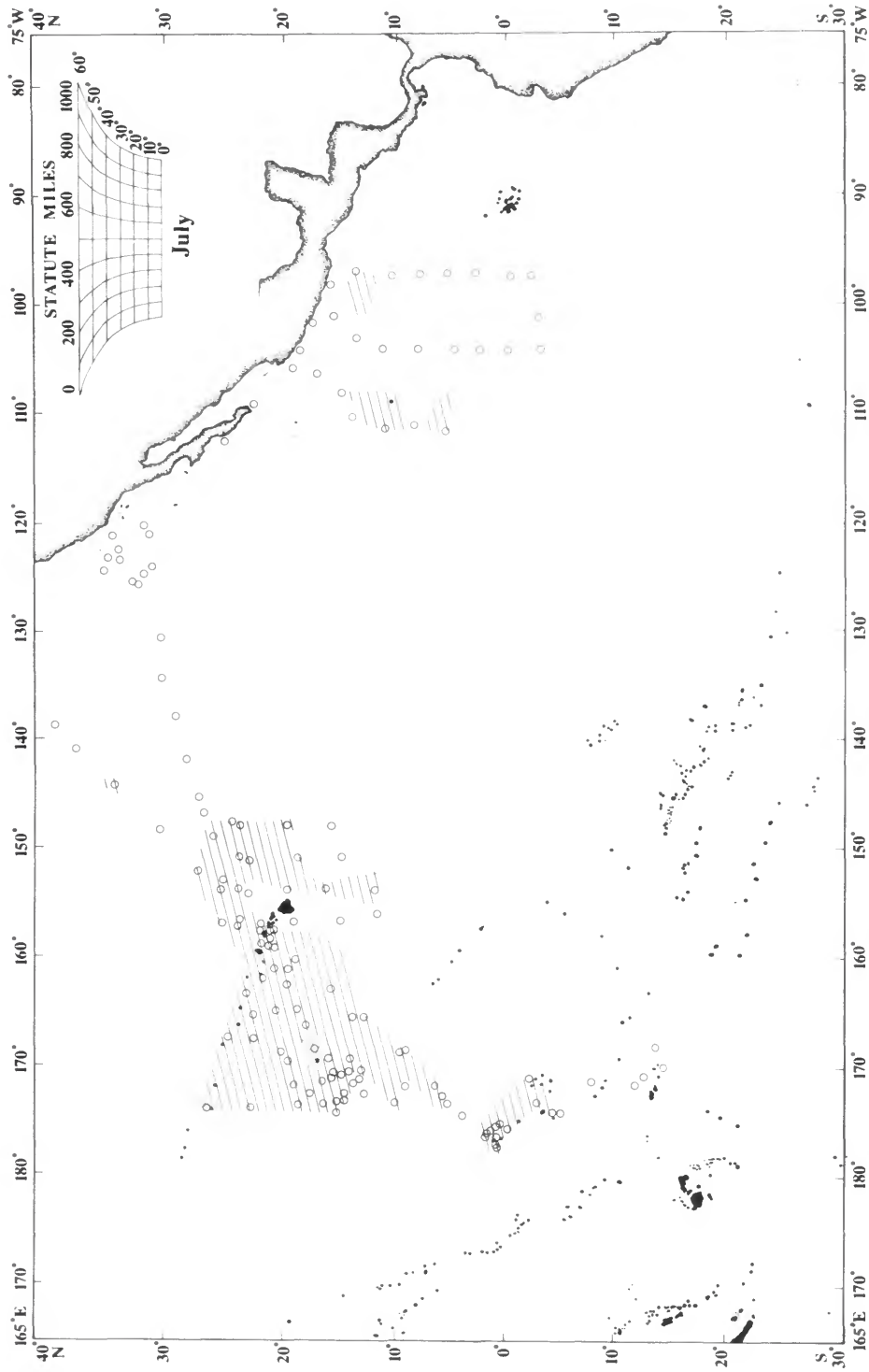


FIGURE 136.—Daily density (BPM) of Red-tailed Tropicbirds in the central and eastern Pacific based on possr observations in July 1963-1968.

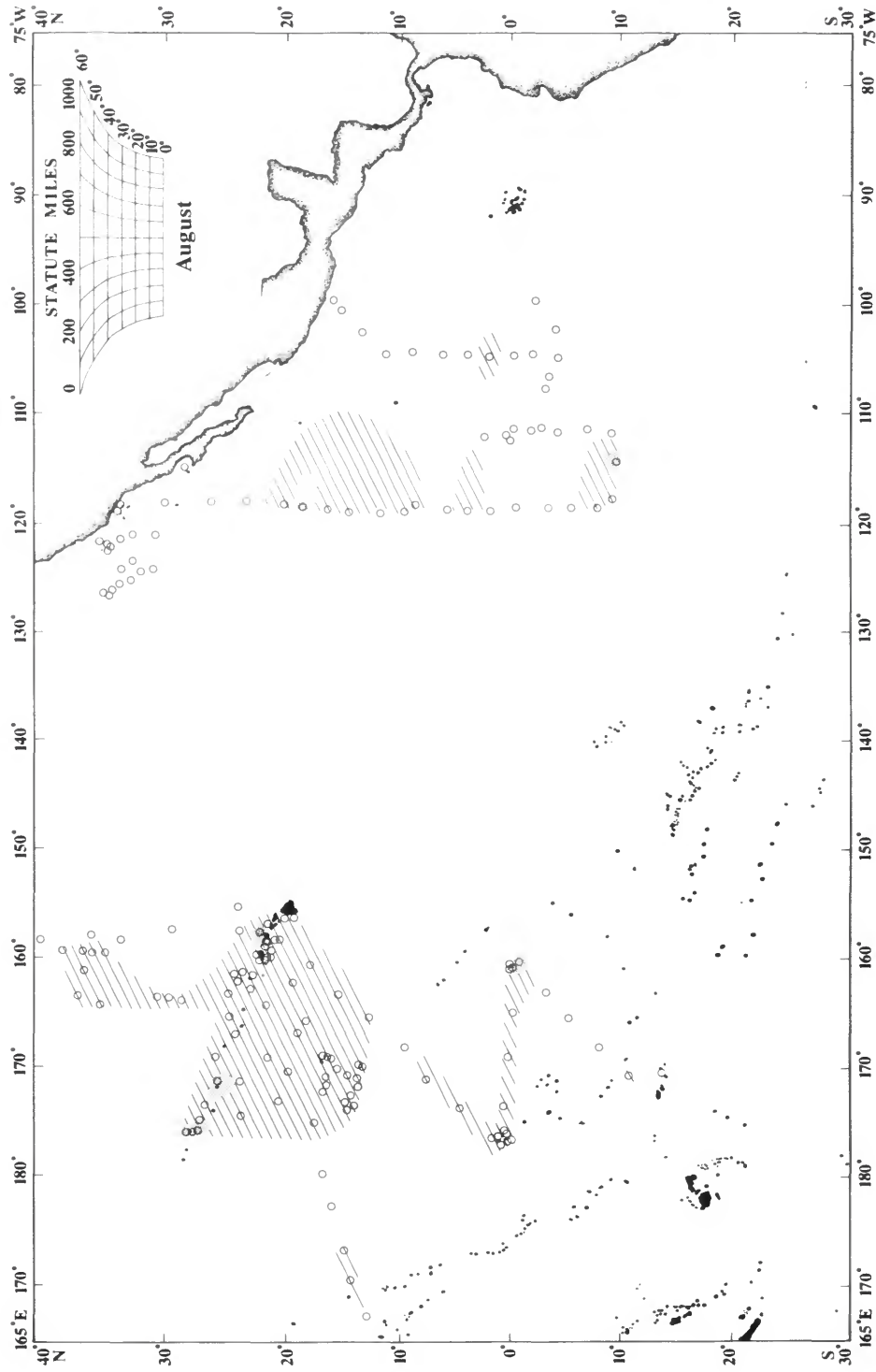


FIGURE 137.—Daily density (birds per square mile) of Red-tailed Tropicbirds in the central and eastern Pacific based on rookery observations in August 1963-1968.

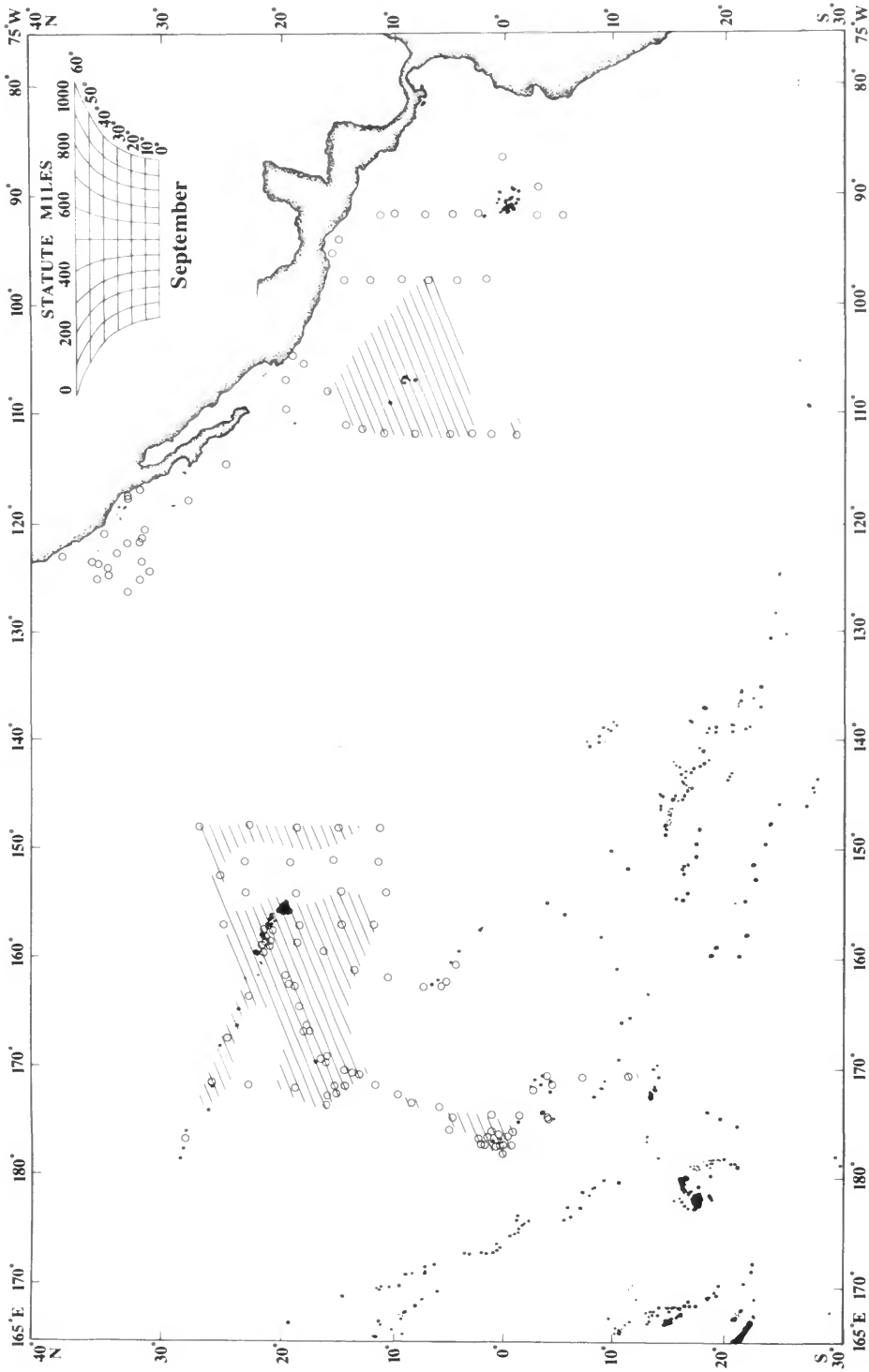


FIGURE 138.—Daily density (APM) of Red-tailed Tropicbirds in the central and eastern Pacific based on BOSSP observations in September 1968-1968.

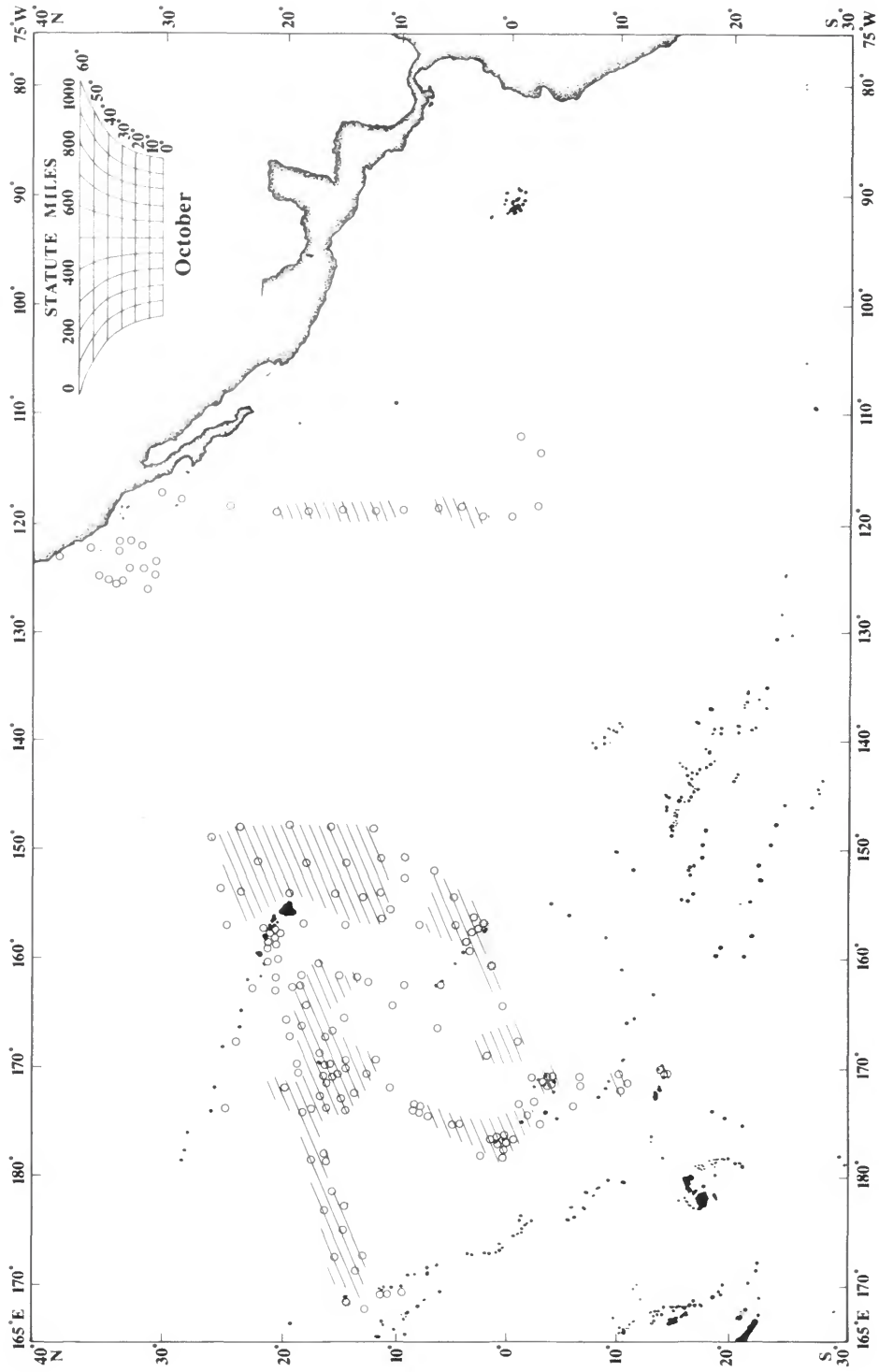


FIGURE 130.—Daily density (SPM) of Red-tailed Tropicbirds in the central and eastern Pacific based on 10BSP observations in October 1963-1968.

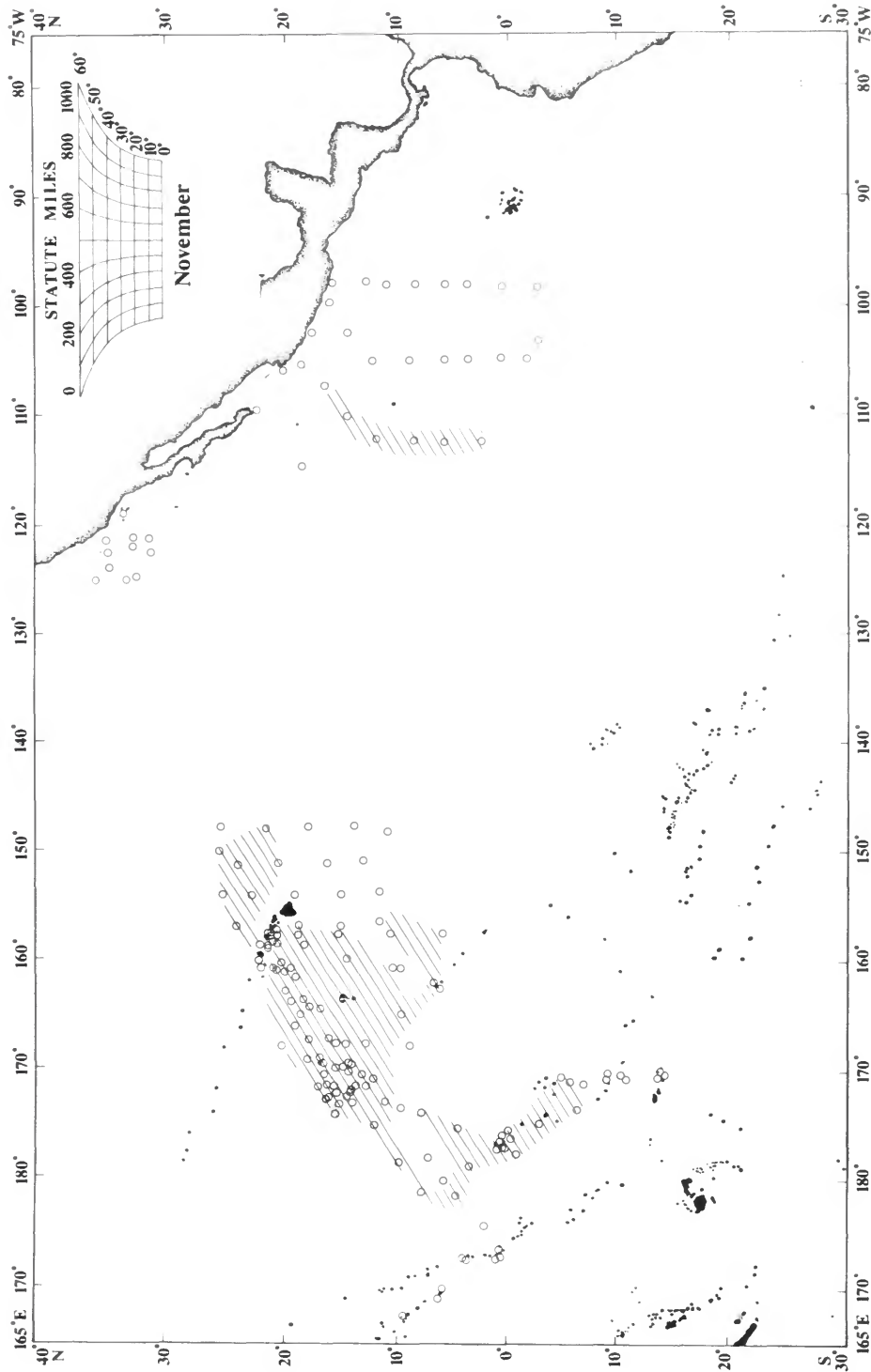


FIGURE 140.—Daily density (APM) of Red-tailed Tropicbirds in the central and eastern Pacific based on 10858 observations in November 1963-1968.

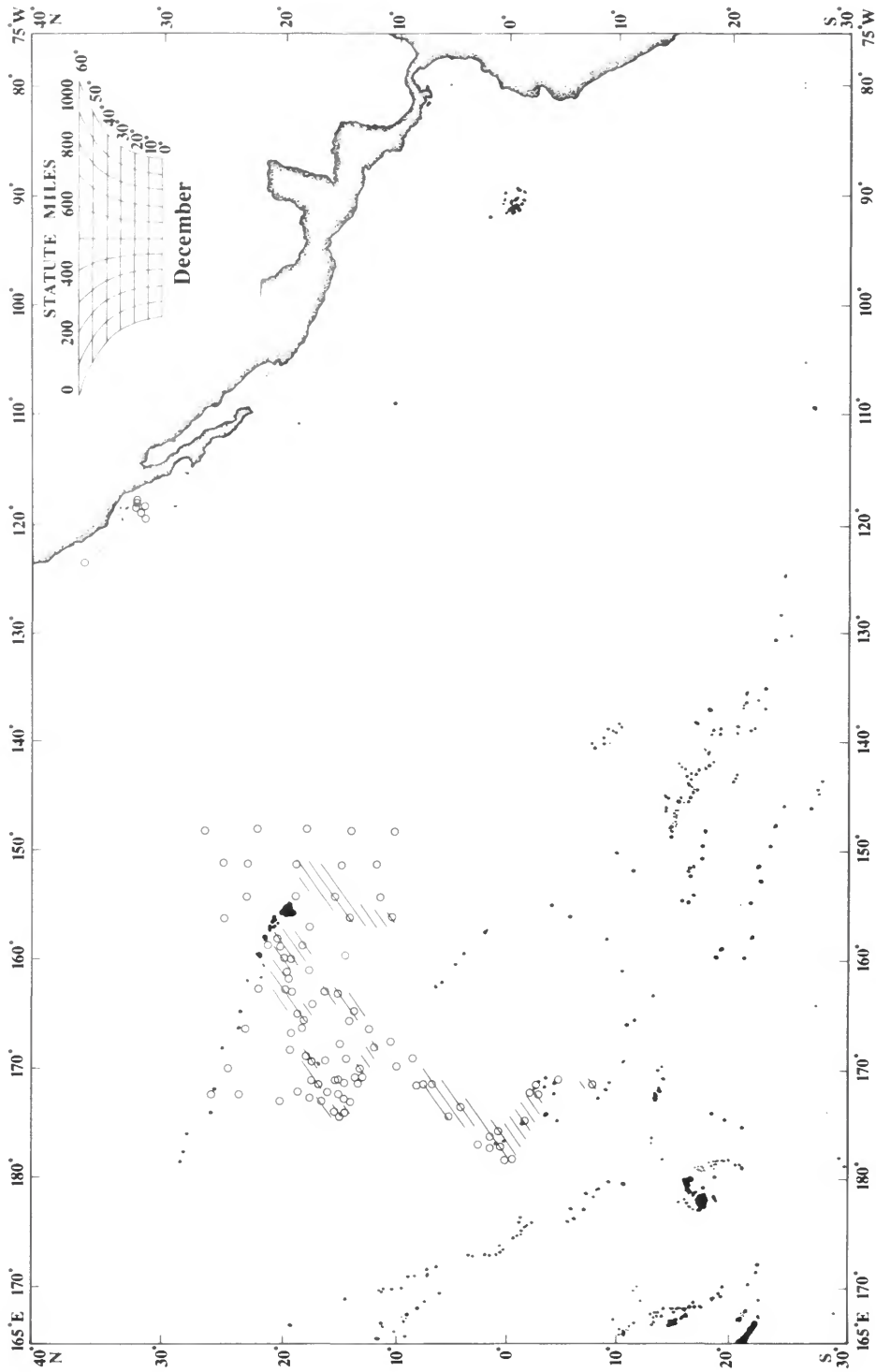


FIGURE 141.—Daily density (SPM) of Red-tailed Tropicbirds in the central and eastern Pacific based on ROBSF observations in December 1968-1968.

Appendix

Summary of published data on Red-tailed Tropicbird distribution

Location	Date	Remarks	Source
EAST-CENTRAL PACIFIC			
30°N, 132°W	no date	seen continuously around ship	Mörzer Bruyns, 1965:63
Guadalupe I., Mexico	23 Jul 1897	1 specimen	Kaeding, 1905:109
Clipperton I., Mexico	19 Aug 1958	1 specimen (adult ♂)	Stager, 1964:360
8°N, 119°W to Manzanilla, Mexico	1-19 Oct 1955	infrequent	King and Pyle, 1957:36
Manzanilla, Mexico to 9°S, 120°W to ca. 5°N, 139°W	24 Oct-20 Nov 1955	singles and pairs frequently seen	" " " "
6°N, 82°W	2 Jan 1963	1	Morris <i>in</i> Bourne, 1965:29
0°26'N, 98°36'W	22 Nov 1957	1	Gibson, 1960:16
0°07'N, 87°50'W	2 Apr 1950	1	Laird, 1951:177
1°10'S, 100°37'W	28 Feb 1947	1	Fleming, 1950:172
3°58'S, 91°15'W	1 Apr 1950	1	Laird, 1951:177
4°02'S, 110°31'W	22 Nov 1957	3	Gibson, 1960:16
5°15'S, 113°W	10 Nov 1960	1, possibly 4 others	Simple <i>in</i> Bourne and Radford, 1962:21
8°03'S, 133°36'W	30 Sep 1928	6 in 3 sightings	Jespersen, 1933:216
SOUTHEAST PACIFIC			
12°S, 100°W	25 Apr 1960	1 on board ship	Harrison <i>in</i> Bourne and Radford, 1961:21
Easter I.	Dec 1968	fair numbers, breeding	Johnson, et al., 1970:535-536
CENTRAL PACIFIC			
30°N, 150°W	26 Jul 1959	1 seen close for 1½ hrs.	Agnew <i>in</i> Bourne and Radford, 1961:22
27°19'N, 172°25'W	24 Aug 1960	6	Wilhoft, 1961:261
22°N, 165°W	28 Apr 1945	3	Cogswell, 1946a:48
17°44'N, 159°56'W	20 Jul 1959	1	Wilhoft, 1961:261
7°N, 166°W	4 Nov 1960	1	Mörzer Bruyns, 1965:63
7°46'S, 167°16'W	31 Oct 1928	1	Jespersen, 1933:216
8°40'S, 136°54'W	1 Oct 1928	1	" " "
Nuku Hiva, Marquesas	2 Oct 1928	a few	" " "
Near Marquesas	Dec 1955	none	King and Pyle, 1957:36
SOUTH-CENTRAL PACIFIC			
13°37'S, 177°18'W	24 Jul 1959	1	Wilhoft, 1961:261
Near Suva, Fiji	31 May 1959	1	Peakall, 1960:201
27°06'S, 177°41'E	13 Dec 1928	1	Jespersen, 1933:216
28°18'S, 177°01'E	9 Dec 1928	3 in 2 sightings	" " "
29°12'S, 178°28'E	11 Dec 1928	1	" " "
Kermadec I.	all year	most from Oct to May	Sorensen, 1964:73
NORTHWEST PACIFIC			
Honshu, Japan	May 1907; 1885; 20 Nov 1934;	4 records are for spent, "probably storm-driven birds"	Austin and Kuroda, 1953:315

Summary of published data on Red-tailed Tropicbird distribution—Continued

Location	Date	Remarks	Source
	1917; 30 Mar 1951; no date		
Linschoten I.	14 Aug 1906	1 observed, may be more common than supposed	Clark, 1910:42
WEST-CENTRAL PACIFIC			
West Pacific	no date	4 widely scattered sightings	MacDonald and Lawford, 1954:22
Western tropical Pacific	Aug 1945–Mar 1946	6 sightings from 66 to 195 mi from land	Dixon and Starrett, 1952:270
Taiwan	21 May 1937	1 offshore	Hachisuka and Udagawa, 1951b:124
25°26'N, 124°18'E	30 May 1929	1	Jespersen, 1933:216
19°09'N, 120°05'E	22 May 1929	1	" " "
15°N, 160°W–1°S, 148°W	4–5 Dec 1955	singles and pairs frequently seen	King and Pyle, 1957:36
10°N, 150°–120°W	1–19 Oct 1955	infrequently seen	" " " "
Mariana and Caroline I.	no date	uncommon throughout most of Micronesia, may be a resident only in the northern Marianas	Baker, 1951:71
Palau I.	28 Oct 1960	1	Mörzer Bruyns, 1965:63
SOUTHWEST PACIFIC			
Thursday I.	18 Mar 1929	1	Jespersen, 1933:216
15°30'S, 159°45'E	Jun 1951	1	MacDonald and Lawford, 1954:22
17°57'S, 169°52'E	10 Dec 1957	2 approached from direction of New Hebrides	Gibson, 1960:18
23°28'S, 127°31'W	9 Jul 1948	3 birds in 2 sightings	Fleming, 1950:175
24°40'S, 164°W	11 Mar 1947	1	Fleming, 1950:172
25°13'S, 130°28'W	2 Dec 1948	several off Pitcairn I.	Fleming, 1950:181
26°16'S, 161°24'E	19 Dec 1957	1	Gibson, 1960:18
26°15'S, 176°56'W	14 Mar 1947	1	Fleming, 1950:172
28°20'S, 140°45'W	29 May 1955	no details	King in Bourne, 1964:28
30°55'S, 155°17'E	20 Dec 1957	1	" " " "
32°11'S, 155°07'E	24 Feb 1929	1	Jespersen, 1933:216
33°25'S, 162°45'E	27 Jan 1929	2	" " "
33°27'S, 157°10'E	29 Jan 1929	3	" " "
33°30'S, 165°53'E	26 Jan 1929	1	" " "
New Zealand	1877, 1936, 1942	only 3 records	Oliver, 1955:195
Northern New South Wales, Australia	17 Jun 1945	hurricane-driven bird, 120 mi from coast, at altitude of over 1000 ft	Hindwood, 1947:57
Port Kembla, N.S.W., Australia	13 Nov 1955	1	Gibson and Sefton, 1956:198
coastal N.S.W.	12 Jan 1955	bird found dead	Hindwood, 1955:160
Tasman Sea	no date	may penetrate area as far as 38°S	Falla, et al., 1967:59–60
18°16'S, 151°21'W	18 Oct 1928	1	Jespersen, 1933:216
9°53'S, 161°28'W	24 Oct 1928	2 in 2 sightings	" " "
20°57'S, 158°58'W	21 Oct 1928	a few	" " "

Recoveries of Banded Laysan Albatrosses (*Diomedea immutabilis*) and Black-footed Albatrosses (*D. nigripes*)*

Chandler S. Robbins and Dale W. Rice

Introduction

This paper summarizes the distribution of at-sea recovery records of banded Laysan Albatrosses (*Diomedea immutabilis*) and Black-footed Albatrosses (*D. nigripes*). Both species now nest primarily in the leeward Hawaiian Islands, and both roam over the north Pacific Ocean, covering essentially the entire area from Japan to the continental United States and from the vicinity of the Aleutian Islands south to about 20°N. Maps showing the breeding sites and the total marine range for both species (prepared by E. M. Reilly, Jr.) have been published in Volume 1 of the *Handbook of North American Birds* (Palmer, 1962). Although these maps indicate the known limits of occurrence, they do not attempt to show concentration areas, seasonal changes in distribution or abundance, or differences in distribution of the various age classes.

More than two dozen papers have been published summarizing observations at sea of one or both species of albatross in various parts of the north Pacific Ocean—primarily along the American and Japanese coasts and along the main trans-Pacific shipping lines. Unfortunately, these publications have been limited both geographically and seasonally and only two papers (Shuntov, 1968; Fisher and Fisher, 1972) have come close to bracketing the entire range of either species.

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*Paper Number 101, Pacific Ocean Biological Survey Program, Smithsonian Institution, Washington, D.C. 20560.

Shuntov (1968) gave summer and winter maps for each species, showing concentration areas, normal range, and the area within which each species is rare. Fisher and Fisher (1972) summarized the geographic occurrence at sea of Laysan Albatrosses based on a combination of 109 recoveries of birds they had banded, 53 published records of birds banded by others, and 113 sight records. They pointed out four regions in which Laysan Albatrosses tend to congregate. They described seasonal shifts in concentrations, and they attempted to explain distribution and movements in relation to turbulences, eddies and currents, water temperatures, and food supply. Our findings, based on a much larger sample of banded birds, both Laysan and Black-footed Albatrosses, show a more orderly distribution pattern, both for adults and for the various age classes of subadult birds.

ADVANTAGES OF USING BANDING RECOVERIES.—The use of recoveries of banded birds as a means of showing geographic range at various seasons and for various age groups has several distinct advantages over compiling published data from sight observations. The age of the great majority of banded birds is known, permitting mapping of distribution and relative abundance by age group. Except for a very short period in the first season at sea, there is no way to distinguish birds of the year from older birds by means of sight observations. Recovery records are accumulated over many years, thanks to the long life span and the long period over which both species have been banded in good numbers. This prevents abnormalities of weather, human activities, or bird distribution from unduly affecting the total picture. All portions of the oceanic range are included in the re-

covery reports, even though there is geographic and probably seasonal variation in intensity of recapture effort. For a comparative study of the distribution of these two species, the use of banding recoveries offers a fairly uniform means of sampling populations throughout the area in which both species range.

LIMITATIONS OF BANDING RECOVERIES.—The principal biases involved in using banding recovery data relate to geographical differences in human contact with the birds and in reporting rate. Since most of the at-sea recoveries of banded albatrosses have come from fishing vessels, the recoveries are concentrated in those locations that are most heavily used for fishing—especially longline tuna sets. Variation from month to month and from year to year in fishing activity also greatly influences human contact with albatrosses. Unfortunately, accurate figures on relative fishing effort throughout the north Pacific are not available on a monthly basis, year by year. If they were, this would permit mapping recoveries per unit of fishing effort and result in a more meaningful analysis of albatross distribution than is presently possible. Nevertheless, Japanese longline fishing effort is well distributed over most of the north Pacific as shown by Rothschild and Uchida (1968:21), and as reflected in the recovery records that have been obtained. Changes in geographic concentrations of albatrosses may very well be related to similar changes in distribution and abundance of the commercial fishery resource, so the centers of concentration of the birds may actually be localized in the areas where the greatest fishing activity takes place. Shuntov (1968:1064) concluded that “albatrosses are most numerous in waters with an increased biological productivity.”

Banding recoveries generally cannot be used to describe the extreme geographical limits of a bird's range, because only a small percentage of the birds banded are recovered. Thus the areas where a species is common are much better represented by recovery records than are the marginal portions of the range. This paper, therefore, deals primarily with seasonal changes in the centers of populations of the various age groups rather than with records of individual birds.

The Black-footed Albatross has a more varied diet than the Laysan, is more readily attracted to fishing vessels (and other boats) and so is much

more likely to be captured at sea. Thus, recovery rates cannot be used to compare abundance of one species with the other in any region of interest. Differences in the ratio of Laysan to Black-foot recoveries from one part of the range to another, however, can be used to show geographic differences in relative abundance. Furthermore, differences in the distribution of the various age classes can readily be detected, since it is unlikely that there are any geographical biases that would favor selective capture of one age class over another. Birds in their first three or four years, especially Laysan Albatrosses, appear to be more susceptible to capture than fully adult birds, but this holds true in all parts of their range. The recovery rate for Laysan Albatrosses reached a strong peak in their second summer, while the highest recovery rate for Black-footed Albatrosses occurred in their third summer.

BANDING HISTORY.—The first Laysan Albatrosses were banded by F. C. Hadden at Midway Atoll in 1937, and the first Black-footed Albatrosses, by George C. Munro at the same location in 1940. Banding continued on a small scale through 1952, largely under the auspices of George Munro and the Hawaii Audubon Society, with several hundred albatrosses banded at Midway in most years. Some 335 adults were banded by Johnson Neff and Philip A. DuMont of the U.S. Bureau of Sport Fisheries and Wildlife in 1954.

The great majority of the banding of both species was done during the period 1956–1969. During 1956–1967, the U.S. Bureau of Sport Fisheries and Wildlife, at the request of the U.S. Navy, conducted studies on albatrosses on Midway and some of the other leeward Hawaiian Islands to obtain information on albatross biology and habits that could be used in reducing the hazard of birds to aircraft at Midway. And during the period 1963–1969, the Pacific Ocean Biological Survey Program of the Smithsonian Institution included an extensive banding program on all the major nesting islands of the Laysan and Black-footed Albatrosses.

Nearly all of the banded birds were tagged in their nesting colonies in the leeward Hawaiian Islands, but four of them were captured and banded at sea, and one was banded on Torishima Island, Japan. The great majority were banded on the Midway Islands (28°13'N, 177°20'W), but there are also a few recoveries from albatrosses banded at

TABLE 39.—*Manner of recovery of Laysan and Black-footed Albatrosses*

Action	Laysan Albatross				Black-footed Albatross			
	Young	Adult	Total	Percent	Young	Adult	Total	Percent
Shot	11	17	28	11.2	19	18	37	13.1
Caught on fish hook or net	121	22	143	57.4	68	72	140	49.5
Caught and released with band	6	2	8	3.2	3	17	20	7.1
Caught by hand	6	3	9	3.6	9	4	13	4.6
No information	22	12	34	13.7	7	16	23	8.1
Found dead	22	2	24	9.6	19	19	38	13.4
Miscellaneous	2	1	3	1.2	6	6	12	4.2
Total	190	59	249	99.9	131	152	283	100.0

Kure Atoll, about 90 miles west of Midway, and 68 from birds banded on islands in the Hawaiian Islands National Wildlife Refuge (French Frigate Shoals, Laysan, Lisianski, and Pearl and Hermes Reef), between Midway and the main Hawaiian Islands. The nesting islands on which the recovered albatrosses were banded extend in nearly a straight line from 23°40'N, 166°10'W to 28°20'N, 178°10'W, a distance of about 1000 nautical miles.

SOURCE OF DATA.—The recovery records on which this paper is based are from the files of the Bird Banding Laboratory of the U. S. Bureau of Sport Fisheries and Wildlife at the Office of Migratory Bird Management in Laurel, Maryland.

Although the great majority (73%) of the birds discussed in this paper were banded by the authors (54%), and by *POBSP* personnel (19%), 76 of the recoveries are from birds banded by H. I. Fisher and assistants (Fisher and Fisher, 1972), 37 were banded by R. R. Sheehan, 28 by E. Kridler, 21 are from bandings by George Munro and his collaborators of the Hawaii Audubon Society, and from 1 to 8 each are from bandings by 13 other individuals. This analysis includes recovery records processed through August 1972.

Summarized herein are 324 recoveries of Laysan Albatrosses from 165,890 birds banded from 1937 through 1969, and 399 recoveries of Black-footed Albatrosses from 48,727 birds banded from 1940 through 1969. Since tens of thousands of birds from these banded samples are still alive, including some individuals from nearly all years of banding, the figures given here cannot be used to compute final recovery rates.

Although most of the banding recovery records specified the date and the latitude and longitude of recapture, some oceanic records had to be omitted because of insufficient data. Also omitted were all recaptures on the various nesting islands.

MANNER OF RECAPTURE.—The principal means of recovery of banded albatrosses at sea is by fishermen who capture the birds on baited hooks or in nets. The large majority are taken on longline tuna gear; a typical set (Rothschild and Uchida, 1968) contains 2000 hooks on 120 kilometers of line. As shown in Table 39, more than 50 percent of a sample of more than 500 recoveries received for each species were reportedly obtained by this means. Many of the birds listed in other categories, e.g., found dead, caught by hand, caught and released with band, and no information, probably also were taken on fish hooks or in nets. It is apparent from Table 39 that both species are equally susceptible to being recovered in the various manners listed. Thus, although the Black-footed Albatross more frequently comes in contact with man through its habit of following ships, there is no apparent bias in favor of one species or the other being taken by fishing gear rather than by other means.

Both adult and young Black-footed Albatrosses appear to be equally susceptible to being recovered by each of the listed categories, with the possible exception of the first. The manner of recovery of young Laysan Albatrosses is very similar to that of Black-footed Albatrosses. Adult Laysans, however, are much less frequently reported as captured in

nets or on hooks, and a higher proportion of these birds were obtained by shooting.

Figure 142 shows the monthly distribution of recoveries at sea of the Laysan and Black-footed Albatrosses combined, according to manner of recovery. The top line shows all birds caught on fish hooks or in nets. The bottom solid line shows the recoveries of birds that were shot, and the dashed line shows birds recovered by all other means.

It is apparent from Figure 142 that fishermen encounter albatrosses most frequently in the months of May, June, July, and August, and least frequently in September, October, and November. The largest numbers obtained through shooting were in May, June, September, and October; and almost none were shot in December, January, and February. The seasonal distribution of birds obtained by other methods so closely parallels the graph for birds that were caught on fish hooks that the fishing industry probably accounts for most of the birds reported by "other" means.

ACKNOWLEDGMENTS.—We wish to thank Eugene Kridler of the U.S. Bureau of Sport Fisheries and Wildlife for his cooperation not only on the Midway studies, but also for making available his banding recoveries from the Hawaiian Islands National Wildlife Refuge (French Frigate Shoals, Lisianski, and Pearl and Hermes Reef). Other Bureau collaborators who contributed materially to the banding of these albatrosses were Karl W. Kenyon, Dr. John W. Aldrich, Cdr. E. P. Wilson, Edward J. O'Neill, Dr. Paul A. Stewart, Norman E. Holgersen, John Waters, Willis C. Royall, Jr., Johnson Neff, and Philip A. DuMont.

Navy and Coast Guard personnel not only provided the necessary logistical support, but also assisted in many other ways. Cdr. Glenn Wilson, Lt. Ralph Stockstad, James L. Priest, Lt. Kenneth C. Balcomb, and Marvin L. Cunningham banded albatross chicks in our study plots in years when we were not present at the proper season.

Mrs. Blanche A. Pedley of the Hawaii Audubon Society went to considerable effort to supply banding data from the Society's files in order to complete the official records of birds banded by George Munro and Miss Grenville Hatch.

Personnel from the Pacific Ocean Biological Survey Program of the Smithsonian Institution under the direction of Dr. Philip S. Humphrey conducted intensive banding during the period 1963–1969 and

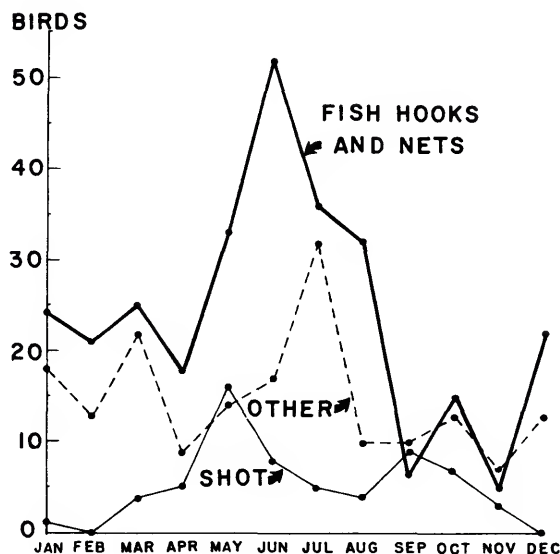


FIGURE 142.—Manner of recovery of banded Laysan and Black-footed Albatrosses at sea.

also cooperated closely with us in many ways. One hundred thirty-nine recoveries used in this report were from birds banded by them.

We are indebted to Harvey I. Fisher for checking nesting albatrosses on our study plots at times when we could not be on Midway, and for the use of recoveries of birds banded by him and included in his publication (Fisher and Fisher, 1972).

We also acknowledge with thanks the following banders, each of whom contributed one or more recovery records to this study: Fred C. Hadden, Richard C. Harlow, J. H. Scarlett, R. Sheehan, Eric E. Smith, Yamashina Institute for Ornithology, and Dr. C. F. Yocom.

We appreciate the fine international cooperation of Dr. Y. Yamashina of the Yamashina Institute for Ornithology and Dr. Tatsuo Udagawa, both of Tokyo and of A. Vinokurov and T. Shevareva of the Centre of Ringing in Moscow. Through their efficient processing and reporting recovery information, actual dates and exact positions of nearly all western Pacific recaptures were made available.

We thank Brian Sharp and Jay M. Sheppard of the Bird Banding Laboratory for providing copies of banding recovery records, and Rosemary O'Loughlin and Nancy Mullis for assistance in

locating some original recovery letters for confirmation of locations and dates. Danny Bystrak prepared the final maps.

We also thank Mr. Warren King, Mrs. Herbert Church, and Mr. Gerald Sanger of the Smithsonian Institution's POBSP for their many helpful suggestions regarding this manuscript.

General Patterns of Distribution

The following summary of the nesting cycle of both species is condensed from Rice and Kenyon (1962b:564-566). The nesting birds arrive on the islands in the latter half of October (Black-footed Albatross) and first half of November (Laysan Albatross). Egg-laying occurs primarily in the latter half of November (Black-footed) and from November 20 to January 5 (Laysan), and incubation requires about 65 days. Early in the incubation period the female, and then the male, is away at sea for about three weeks at a time. As incubation progresses, each mate's turn on the egg becomes progressively shorter as does the distance they can travel from the island. For the first 12 to 24 days after hatching, the chick of each species is attended by a parent, the male and female changing place at intervals of about two days. Both parents then leave the chick and forage independently; a parent returns to feed the chick at an average interval of one and one-half days to two days. Departure from the island of both young and adults of both species takes place primarily in June but departure of the Laysan continues into July.

Our studies with both species, and those by Fisher and Fisher (1969) on the Laysan Albatross, have shown that one-year-old birds do not return to the nesting islands, but remain continuously at sea. By the end of their second winter at sea, a very few individuals of each species return to their natal islands in April. With increasing age these nonnesting birds return to their islands in larger numbers, and earlier and earlier in the season (largely in March for the 3- and 4-year-olds and as early as February or January for the older birds).

In order to determine the distribution patterns of the albatrosses during the periods they are away from the nesting islands, recoveries for each species were plotted on a monthly basis for birds in their first, second, third, and fourth years at sea and for adults. First-year recoveries were of birds from time

of fledging until the following May.

Recoveries of Laysan Albatrosses occurred largely during the period December through July, with a peak of adult birds (40%) in May and June and a peak of young birds (31% of the year's recoveries) in June of the year after fledging.

Recovery records of the Black-footed Albatross at sea are strongly clustered around the months of March through August. Half (50%) the recoveries of birds in their second, third, and fourth years of life were reported in June and July, and the peak of reporting of adult recoveries (45%) was in the months of March, June, and July. The fewest recoveries for both young and adults were obtained in the months of November and December.

LAYSAN ALBATROSS.—Banding recoveries (Figure 143) indicate that young Laysan Albatrosses spend their first summer primarily between 40°N and 45°N and that they range all the way from Japan east to at least 172°W. More than half of the recoveries of Laysan Albatrosses during their first summer (summer of fledging) came from within 300 miles of the east coast of northern Japan. One bird (band number 767-77884, banded as a chick by Robbins on 30 March 1965, at Sand Island, Midway) was found dead on 11 September 1965, on San Cristobal Island (10°15'S, 161°16'E), furnishing the first record for the British Solomon Islands. This is the only Laysan Albatross recovery from south of the equator. Comparison of Figures 143 and 147 shows that the distribution of young Laysan Albatrosses during their first summer is quite different from the distribution of adults during the same months. Half of the recoveries of adults came from north of 45°N, while only two birds in their first summer were recovered north of 45°N.

Laysan Albatrosses tend to be more widely scattered in their first four or five winters (December through March), than at a later age. Four of the 43 first-winter recoveries (Figure 143) were from east of the 180th meridian, as were 6 of the 17 third-winter recoveries (Figure 145). In contrast, there was only one winter recovery east of the 180th meridian for birds in their sixth winter or older, even though the entire chain of nesting islands is situated east of the 180th meridian. As was true in the summer months, the records for the first winter were concentrated off the coast of Japan, with half of the recoveries coming from within 600 miles of Japanese shores.

Recoveries during the second summer (Figure 144) were concentrated off the east coast of northern Japan, and it appears that birds of this age stay much closer to shore than either first-year birds or birds older than three years. All of the 55 recoveries of birds in their second summer occurred west of 160°E.

Recoveries for the second winter at sea (Figure 144) were few in number (13), but they also were all from west of 160°E. There was more overlap between the summer and winter range of birds in their second calendar year of life than in other years.

Third-year recoveries (Figure 145) were similar to second-year recoveries except that the birds appeared to scatter farther out to sea and were not so concentrated near the Japanese coast. This was especially true of birds in their third winter at sea, because they ranged all the way east to 134°W.

Fourth- and fifth-year birds (Figure 146) tended to range farther northeast in summer than did younger birds during the same months. The summer season distribution of adults was still farther to the northeast, with half of the birds north of 48°N and with the heaviest concentration off the western Aleutian Islands.

As shown in Figure 147, at-sea recoveries of adult Laysan Albatrosses lay almost entirely (90%) west of the 180th meridian. The recoveries indicate very little overlap between summer and winter range. During the summer (May through 5 October), all but five of the recoveries came from north of 40°N; while during the winter months (December through March), all except two recoveries were from south of 40°N. The summer recoveries were fairly uniformly distributed between northern Japan and the Aleutian Islands, except for a concentration of records from the immediate vicinity of the Aleutians. The winter recoveries of adults were all from the area between Japan and their breeding islands in the leeward Hawaiian chain. In addition to the summer and winter recoveries, there were widely scattered recoveries for the intervening months of April, October, and November.

BLACK-FOOTED ALBATROSS.—After leaving their nesting islands in June and early July, young Black-footed Albatrosses scatter both eastward and westward to within a few hundred miles of the coasts of North America and Japan. All of the nine first-

summer recoveries fell between 35°N and 45°N (Figure 143).

In the first winter, the birds shift southward. Nine of the 14 recoveries were between 30°N and 35°N, and the recoveries appeared to be slightly more clustered than they were during the summer season. One concentration was half way between Japan and Midway; the other was close to the shores of California and Baja California. There was only one first-winter recovery in the vicinity of the Hawaiian chain. The banding recoveries indicate a strong eastward shift in the population by the second summer (Figure 144). All but 5 of the 31 recoveries came from the eastern half of the north Pacific and half of these came from within about 200 miles of Canada and the United States (exclusive of Alaska). The principal concentration of coastal recoveries of birds in their second summer extends from 30°N to 47°N (13 out of 15 recoveries from south of Alaska).

Recoveries of birds taken in their second and third winters (Figures 144, 145) suggest a shift toward the central Pacific. The total numbers involved, however, are admittedly very small (14 birds in their first winter, 6 in their second, and 8 in their third).

A decided northward trend in summer distribution with increasing age is indicated. The heaviest single concentration in the third summer (Figure 145) was along the United States coast between 40°N and 51°N; 24 recoveries were reported from here as compared with 4 farther south and 1 farther north along the coast.

By the fourth summer (Figure 146), only 7 of the 15 coastal recoveries were in the 40°N to 48°N range; one was farther south, and 8 farther north off Canadian and Alaskan shores.

The Black-footed Albatross has a greater distributional range than the Laysan both in latitude and in longitude. It tends to winter farther south than the Laysan and to be concentrated in winter in the central portion of the north Pacific Ocean. Recoveries of adults (Figure 148) within 1000 miles of the Japanese coast in winter were just about equal to the number within the same distance of the North American coast at this season.

Summer recovery records of banded adults also were quite uniformly distributed throughout the north Pacific Ocean, except for concentrations within 200 miles of the coasts of Japan, Alaska,

British Columbia, Washington, and Oregon. The numbers of recoveries of adult birds east and west of the 180th meridian were similar.

The separation of summer and winter records is nearly as clear cut as for the Laysan Albatross. There were only three summer recoveries of adult Black-footed Albatrosses south of 30°N, and except for five recoveries close to the California coast, there were only two winter recoveries north of 35°N. The "winter" bird recovered at 50°N was taken on 25 March 1966 and was actually an early spring migrant. The other "winter" bird, at 37°N, was taken on 9 December 1950 and could well have been a late migrant.

A similar comparison may be drawn for birds in their first four years. There was only one summer recovery (out of 20) south of 35°N in the western Pacific, and only six (out of 86) in the eastern Pacific. There was only one winter record north of 40°N.

Concentration Areas

LAYSAN ALBATROSS.—Shuntov (1968) showed two concentration areas for the Laysan Albatross in summer, as depicted in our Figure 149, and three in winter (Figure 150). The banding recoveries show the same summer concentration area extending east from northern Japan; this is occupied primarily by young birds near shore and older ones farther to the northeast. The concentration that Shuntov pictures in his winter map along the south edge of the western Aleutian Islands is a major feeding area for adult Laysan Albatrosses in summer. There are no winter banding recoveries from the vicinity of the Aleutians. There are relatively few recoveries for Shuntov's concentration zone between Kamchatka and the western Aleutians, but several from a small concentration of adult birds off the south tip of Kamchatka. Figures 87, 88, 89 show the principal concentration area of Laysan Albatrosses in July, August, and September, a period in which sampling effort is low and only 16 banding recoveries of adults are available. First- and second-year birds summer to the south of this concentration area.

The winter banding recoveries are strongly clustered between Japan and the nesting islands. This zone includes Shuntov's western concentration and the southern half of the large one south of Kamchatka. A large concentration of wintering first-

year birds occurs southeast of Japan as a southward extension of his westernmost concentration.

Fisher and Fisher (1972) reported the concentration areas off Japan and the western Aleutians as well as two others which neither Shuntov (1968, figs. 4, 6), Sanger (p. 134 ff, herein), nor we consider important: one off the west coast of British Columbia and the United States (from which there are only four banding recoveries), and one around the eastern end of the Hawaiian Islands (two recoveries). These surely must be of minor importance as compared with the concentrations reported by Shuntov (1968).

BLACK-FOOTED ALBATROSS.—The summer banding recoveries may exaggerate the importance of the coastal waters as concentration areas for Black-footed Albatrosses, but these recoveries are in close agreement with Figures 73, 74, and 75. Shuntov's (1968) summer distribution map (Figure 151) shows major concentrations along the 40th parallel west of Midway and through much of the eastern Pacific. The banding records do not detect these areas as being of any special significance, but show heavy concentration zones only in the offshore area from the Aleutians to northern California as mapped by Shuntov. Banded birds also were concentrated off the coast of northern Japan in an area not considered especially important by Shuntov. Quite possibly the large concentrations along and to the south of the 40th parallel are under-sampled by banding recoveries, because no more birds have been reported from there than from farther north.

The winter banding recoveries match well with that part of Shuntov's map (Figure 152) that lies south of 40°N. By including November records in his winter map, Shuntov included a considerable area north of 40°N that we do not consider as winter range. Otherwise, the principal differences are a greater spread of banding recoveries to the west of Midway, extending fully halfway to Japan, fewer recoveries northeast of the Hawaiian chain, and fewer along the south side of the chain.

Statistical Analysis of Geographic Range

The recovery records of each species were grouped by months and by age of the birds, and the mean, standard deviation, and standard error were computed to determine which of the apparent

TABLE 40.—Mean position, standard deviation, and sample size of Laysan Albatross band recoveries by age and month (positions based on fewer than five records are in parentheses)

Month	Year at sea				
	1	2	3	4 and 5	6+
May	—	38.54°N-148.03°E 3.95 5.04 11	42.36°N-156.56°E 6.45 17.13 5	44.64°N-166.10°E 6.52 9.57 5	45.93°N-171.68°E 6.24 19.36 22
Jun	—	41.05°N-147.16°E 3.17 5.72 24	(39.43°N-144.80°E) 0.78 2.13 3	43.39°N-164.31°E 3.42 30.72 8	47.89°N-168.43°E 5.01 8.11 18
Jul	(42.3°N-172.3°W) — —	39.88°N-147.67°E 2.59 4.41 17	(43.17°N-151.40°E) 1.26 7.29 3	— — —	45.90°N-174.70°E 4.29 35.92 5
Aug	42.18°N-151.91°E 2.95 7.86 15	(39.55°N-147.00°E) 5.30 4.67 2	— — —	(42.7°N-144.0°E) — — 1	45.39°N-150.49°E 4.99 11.42 8
Sep	44.60°N-147.54°E 5.34 6.35 5	(45.35°N-149.25°E) 1.20 3.61 2	(46.45°N-165.10°E) 5.30 17.11 2	(46.0°N-151.8°E) — — 1	(47.10°N-176.33°E) 10.67 33.90 3
Oct	43.95°N-170.89°E 7.13 33.60 8	41.32°N-144.78°E 1.21 3.33 6	— — —	(34.17°N-151.00°E) 11.26 6.38 3	(47.55°N-172.80°E) 7.36 29.18 4
Nov	(39.83°N-143.87°E) 4.54 3.65 3	(40.05°N-146.50°E) 1.06 4.95 2	(33.0°N-139.4°E) — — 1	(42.60°N-152.13°E) 4.68 1.40 3	(37.52°N-160.30°E) 5.05 15.51 4
Dec	36.64°N-144.97°E 2.58 5.95 10	35.94°N-146.43°E 1.65 6.57 9	(36.82°N-147.02°E) 1.35 3.10 4	(35.85°N-147.25°E) 0.21 8.41 2	36.76°N-160.18°E 4.45 13.31 5
Jan	32.23°N-149.91°E 2.30 7.53 13	(32.90°N-142.50°E) 5.52 2.12 2	33.18°N-158.17°E 3.33 23.34 6	— — —	35.36°N-145.12°E 2.33 9.67 8
Feb	32.38°N-159.94°E 3.96 23.51 13	(33.5°N-135.7°E) — — 1	(32.30°N-170.35°W) 1.73 30.71 4	(30.17°N-159.70°E) 2.52 26.34 3	29.82°N-157.10°E 1.00 12.14 6
Mar	29.29°N-150.83°E 3.12 15.07 7	(30.0°N-160.0°E) — — 1	(32.40°N-147.20°W) 2.52 13.37 3	(30.10°N-158.20°E) 5.37 19.09 4	33.46°N-157.66°E 5.82 21.68 10
Apr	(48.45°N-156.38°W) 1.59 27.50 4	(49.0°N-145.0°E) — — 1	(24.7°N-171.0°W) — — 1	(32.10°N-154.02°E) 6.62 26.54 4	40.00°N-176.60°E 10.98 24.06 8

differences in distribution were merely the result of small sample size and which differences were statistically significant. Although the sampling technique (recoveries of banded birds) was far from ideal from the statistical point of view, it was conducted the same way for all age groups of both species, and should provide a valid means of portraying differences in distribution as a function of age and season.

When broken down by years of age, many sample sizes for a given month are of ten or fewer individuals (Tables 40, 41). Starting with these small samples for each age and each month, comparisons

were made with adjacent months and adjacent years. Whenever the distribution was found to be similar, other months or other years were included to provide larger samples. These larger samples in turn gave more critical comparisons between other years and other seasons.

The largest sample for each species (with the exception of a few individual months) was the birds of breeding age. This sample of adults, therefore, was used for comparison with birds of the younger age groups.

LAYSAN ALBATROSS.—Adult Laysan Albatrosses were significantly farther north ($p < .05$) during

TABLE 41.—Mean position, standard deviation, and sample size of Black-footed Albatross band recoveries by age and month (positions based on fewer than five records are in parentheses)

Month	Year at sea			
	1	2	3, 4, and 5	6+
May	-	(36.2°N-141.0°E) - -	46.51°N-147.95°W 8.87 30.07	41.07°N-157.11°W 9.51 33.13
Jun	-	1 40.08°N-127.92°W 6.58 9.77	15 45.15°N-132.34°W 7.18 20.83	26 43.15°N-164.79°W 6.31 40.14
Jul	(39.5°N-177.7°W) - -	8 38.09°N-135.51°W 4.89 22.04	21 45.05°N-134.06°W 5.87 22.96	34 44.67°N-153.37°W 5.51 37.05
Aug	1 40.40°N-157.90°E 1.56 11.10	10 47.01°N-172.19°W 12.18 34.95	31 46.89°N-160.80°W 6.38 43.11	42 46.66°N-162.46°W 5.63 34.58
Sep	5 (40.77°N-165.53°W) 2.35 31.12	8 (48.68°N-138.85°W) 6.92 20.18	8 48.94°N-147.32°W 4.89 32.22	25 48.97°N-166.32°W 7.62 31.80
Oct	3 (39.40°N-167.25°E) 2.26 15.20	4 (40.2°N-150.8°E) - -	8 43.42°N-169.28°E 8.93 32.36	9 41.16°N-149.94°W 10.56 28.67
Nov	2 (35.2°N-171.7°E) - -	1 (35.2°N-171.7°E) - -	5 (48.4°N-125.0°W) - -	12 (29.18°N-172.70°W) 8.95 17.71
Dec	1 (33.30°N-157.43°E) 1.50 16.90	1 (32.30°N-174.40°W) 0.71 22.06	1 -	4 32.62°N-179.77°E 4.18 13.28
Jan	3 (31.73°N-176.73°W) 1.55 47.23	2 -	5 31.30°N-159.08°W 7.71 22.87	6 30.63°N-173.31°E 2.66 15.76
Feb	3 (36.8°N-124.0°W) - -	2 (31.75°N-150.00°W) 2.47 0.71	5 (29.4°N-156.4°W) - -	14 29.91°N-178.84°W 5.08 23.65
Mar	1 29.46°N-158.60°W 4.96 37.82	2 (27.75°N-170.80°E) 6.01 2.83	1 33.14°N-176.00°W 3.98 42.14	13 30.31°N-174.90°W 6.58 29.65
Apr	7 (40.20°N-135.77°W) 6.93 20.07	2 (31.3°N-166.0°E) - -	5 (26.5°N-175.5°W) - -	28 36.08°N-152.40°W 7.92 35.30
	3	1	1	16

the months of May through August than from December through March. The 3- to 5-year-old birds were significantly farther north from May through November than from December through April. Birds in their second year were significantly farther north from June through November than from December through March.

The only statistically significant latitudinal difference among age classes of the Laysan Albatrosses occurred in the month of May when adults were farther north than birds in their second year of life. There was a consistent trend, however, for birds in their second year to be farther south than birds in

their third to fifth years, and for these in turn to be farther south than the adults. This trend was noted in the months of January, February, March, May, June, and December. Sample sizes for one or more of the age groups were insufficient to show any trend for July, August, and November. Only in the principal migration months of April, September, and October did one of the three age classes not conform to this general observation. This is in marked contrast to the Black-footed Albatross, in which there was not a single month when the mean position in latitude increased progressively within these three age categories.

BLACK-FOOTED ALBATROSS.—Adult Black-footed Albatrosses were significantly farther north ($p < .05$) from May through October than they were in January through March, and significantly farther north from June through September than from November through April. Birds in their third and fourth years were significantly farther north from May through July and September and October than they were in February and March, and birds in their second year were found significantly farther north from June through October than in January and March. There were too few records for many of the other months. All age classes showed a high degree of variability in latitude during the northward migration in the month of April, and to a lesser extent during the southward migration in October and November (when the small sample size also made it difficult to draw conclusions).

The only significant differences in latitude for different age classes in the Black-footed Albatrosses were between first-year and adult birds in the months of July, August, and September and between second-year and adult birds in the month of July. In each of these cases the younger birds were distributed significantly farther south ($p < .05$) than adults.

The small number of significant differences found does not mean that there are not differences in distribution, but only that with the present small sample sizes no other differences could be confirmed as statistically significant.

Black-footed Albatrosses in their first year at sea stayed significantly farther toward the western Pacific in July and August than did birds in any older age group.

No significant differences in longitude were found between the 2-year-old and the 3- and 4-year-old birds.

Significant differences in longitude were found between adults (6 years and more) and 3- and 4-year birds for the months of February, June, and July. In each case, the adult birds were found farther west than the 3- and 4-year-olds.

In the Black-footed Albatross, birds in their third to fourth year occur, on the average, farther north than the adults in the months of January, February, April, May, June, July, September, October, and November. Only in March and August were the adults farther north (insufficient data for December).

Comparison of Distribution of Laysan and Black-footed Albatrosses

Despite the geographical and temporal biases inherent in the way in which albatrosses are recovered and reported, there are certain comparisons that can be drawn between the ranges of the two species (as long as both species are recovered in the same general fashion). The most striking difference between the recovery patterns of the Laysan and Black-footed Albatrosses is the very heavy concentration of Laysan Albatross records within 1000 miles of the Japanese coast as compared with the more uniform distribution of Black-footed Albatross records throughout the north Pacific Ocean. Both species demonstrate a strong tendency to wander both to the east and the west in their first eight to ten months at sea. By the end of the first winter, the two species begin to separate into distinct patterns. The Laysan Albatross moves strongly toward the Japanese coast and the Black-footed Albatross shows a less pronounced tendency in the opposite direction.

Using the 180th meridian as the dividing line, 90 percent of the Laysans recovered spent their first winter in the west and 50 percent of the Black-footed Albatrosses spent their first winter in the east. From the second year on, more than 90 percent of the Laysan recoveries (all seasons) came from the western half of the Pacific Ocean, and a similar percentage of the Black-foots in their second, third, and fourth summers came from the eastern half.

By the time the albatrosses reach breeding age (generally 7 or more years of age for the Laysan and 5 or more for the Black-footed), the geographic separation during the summer months dissolves, but the pelagic distribution patterns during the winter (the breeding season) remain fairly distinct. Although both species nest on the same islands, and in about the same relative abundance even at both ends of their breeding range, the great majority of winter recoveries of Laysans were from west of 160°E, while most recoveries of Black-foots were from east of this line. Nearly all winter recoveries of Laysans were from north of 30°N, whereas more than half of the winter recaptures of Black-foots were south of 30°N. Both species are well distributed west of the 180th meridian in the summer months, but nearly all of the summer recoveries

from east of the 180th meridian were of Black-footed Albatrosses.

Comparative distribution of the two species at sea throughout the year is summarized in Figures 153 through 164 where the hatching covers the area represented by one standard deviation from the mean latitude and longitude of all banding recoveries for the month. This is the range within which two-thirds of the population is to be expected. On each map, the range of the Laysan Albatross is centered to the left of that of the Black-footed Albatross. The maps show dramatically those months in which one or both species is confined to a relatively small area as compared with those months when records are scattered over a large portion of the north Pacific Ocean.

Maps for birds in their first summer and autumn at sea were prepared by combining two months in order to increase the sample size. Thus, Figure 165 shows combined records for the months of July and August, and Figure 166 shows September and October. The November (Figure 167) and December (Figure 168) maps are based on Laysan Albatrosses in their first, second, third, and fourth years, and Black-footed Albatrosses in their first and second years, because there was no apparent difference between years and because the samples were very small.

Mean recovery positions of adults of each species are summarized by two-month periods (each month weighted equally) in Figure 169. The large dots indicate positions based on 10 or more recoveries for each month; the small dots are based on fewer than ten in one or both months. Note the similarity between the patterns for the two species, even though separated by 30° of longitude. A similar chart for Laysan Albatrosses published by Fisher and Fisher (1972), apparently was based on a mixture of banding recoveries (birds of all ages) and sight observations. Their sample would seem too small to be representative.

Recovery positions of adults of the two species were compared statistically on both a monthly and seasonal basis by means of the "t" test. The winter (December through March) distribution of adult Laysan Albatrosses was significantly different ($p < .05$ for latitude, $p < .01$ for longitude) from that of adult Black-footed Albatrosses for the same period; mean positions were 34.3°N, 153.3°E for the Laysan ($n=29$) and 30.3°N, 178.5°W for the

Black-footed ($n=53$). Recovery positions in early summer (May through July) also differed significantly ($p < .05$ for latitude, $p < .01$ for longitude); mean positions were 47.3°N, 167.5°E for the Laysan ($n=45$) and 43.5°N, 164.9°W for the Black-footed ($n=84$).

No difference could be detected between the distribution of recoveries from birds banded at Midway and Kure, at the west end of the leeward Hawaiian chain, and birds banded farther east at Pearl and Hermes Reef, Lisianski, Laysan, and French Frigate Shoals.

Discussion

The Laysan and Black-footed Albatrosses together utilize almost the entire Pacific Ocean north of the tropics. Their distribution is limited by the land masses of Japan, and the Asian and North American continents, and by a line that follows the continental shelf in the Bering Sea. Cone (1964: 83) has shown that albatrosses are incapable of sustained flight in calm air, so they could not survive long in equatorial waters of the central Pacific.

Although Laysan and Black-footed Albatrosses nest on the same islands, and although there is almost complete overlap in their total oceanic ranges, each species has its own distinctive distribution pattern within its range, with significantly different centers of population, month by month.

The pelagic ranges of the adults of both species most closely coincide in February, when they are making the shortest and most frequent foraging trips to provide food for the newly hatched young. Ranges expand in March as trips become longer and as chick mortality relieves some of the adults from "domestic" duties. Northward migration of the nonbreeding adults in April and May gives a wide distribution pattern, which contracts on the summer feeding areas in June. The northward migration in June and July of the adults at the close of the breeding season is hardly sampled by the banding recoveries; it probably takes place rapidly and through waters that are not being heavily used by the fishing fleets.

The greatest northward penetration occurs in September. The southward movement takes place gradually during October and November, and by December both species are within commuting range of their nesting islands.

Young birds of both species during their first summer and fall remain largely south of the range of the adults at those seasons. In the first winter, young Laysans remain closer to Japan than do the adults. In their next four summers (Table 40, Figure 170), the average population center shifts gradually east-northeast from Japanese waters to the adult summering area in waters south of the Aleutian Islands. There is also a tendency to move slightly northward as each summer progresses.

It is not until January, February, and March of the third winter at sea that there is a strong movement away from Japanese waters. This coincides with the first return of many of these birds to their natal islands in the month of March.

We have no explanation for the tendency of young Black-footed Albatrosses to fly toward Japan when they first leave their natal islands. Most of

these young birds seem to favor waters west of the 180th meridian through their first summer and fall, though they spend subsequent summers and winters in the eastern half of the Pacific. The central Pacific, which is the major wintering area of adult Black-footed Albatrosses, is relatively clear of first-winter birds.

In their second through fifth summers, Black-footed Albatrosses remain closer to the Pacific coast of the United States and Canada than do the adults; and as each summer progresses they shift gradually northward (Table 41).

In October and November, the majority of the band recoveries of subadult Black-footed Albatrosses of all ages come from the *western* Pacific (west of the 180th meridian). Recovery records are too few to permit comparison of winter ranges of the various age groups.

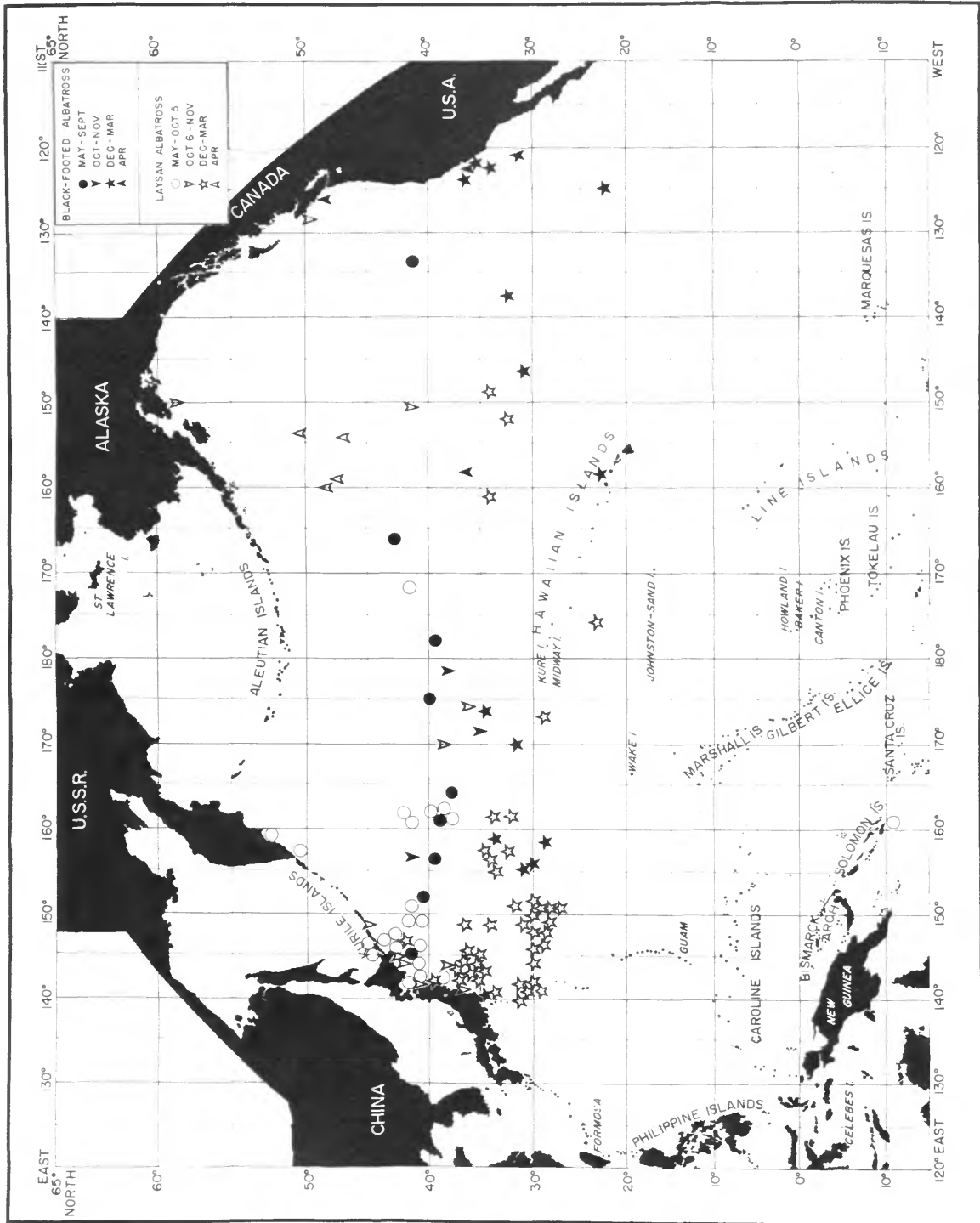


FIGURE 143.—Recoveries of albatrosses in their first 10 months at sea, July through April.

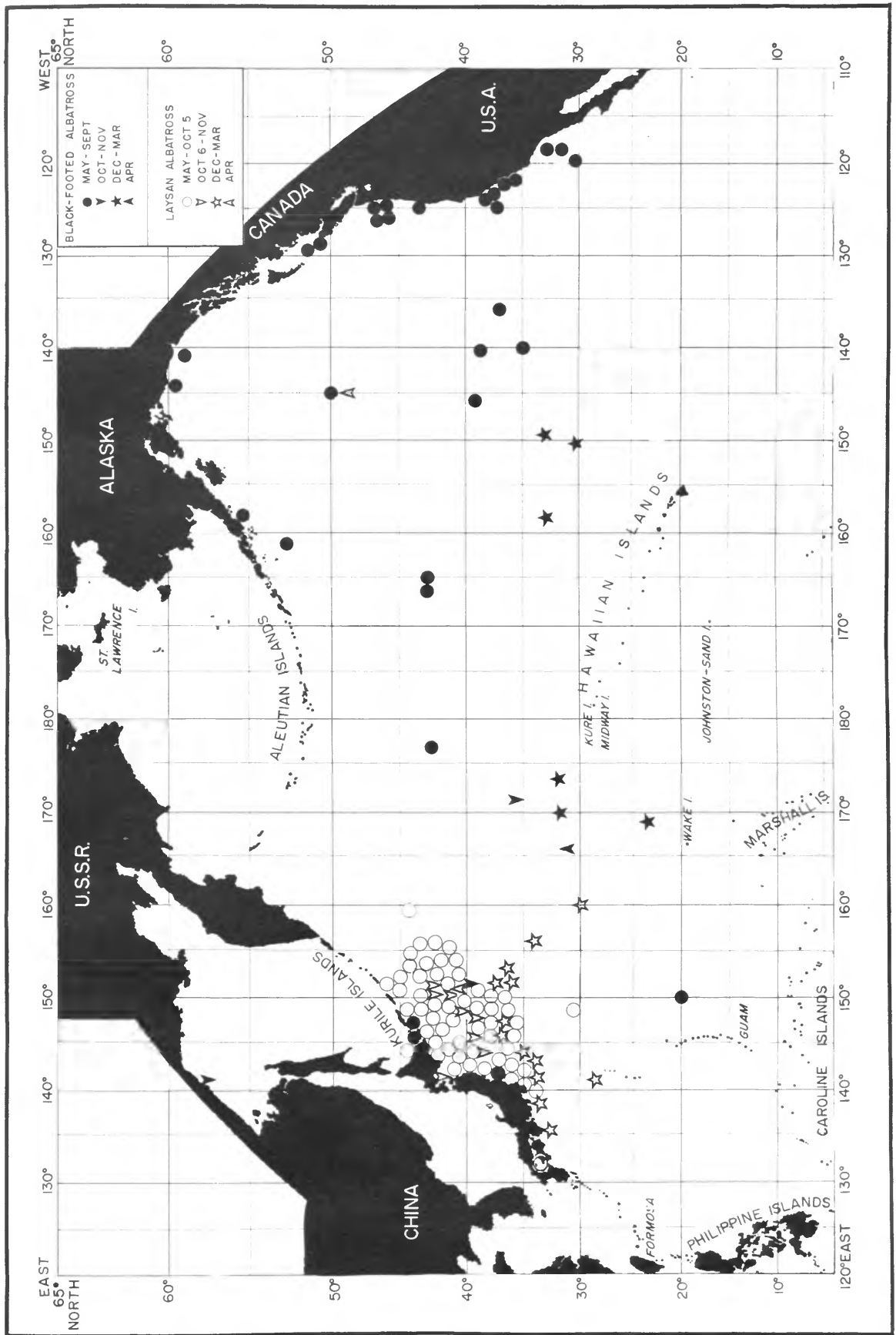


Figure 144.—Recoveries of albatrosses in their second year at sea, May through April.

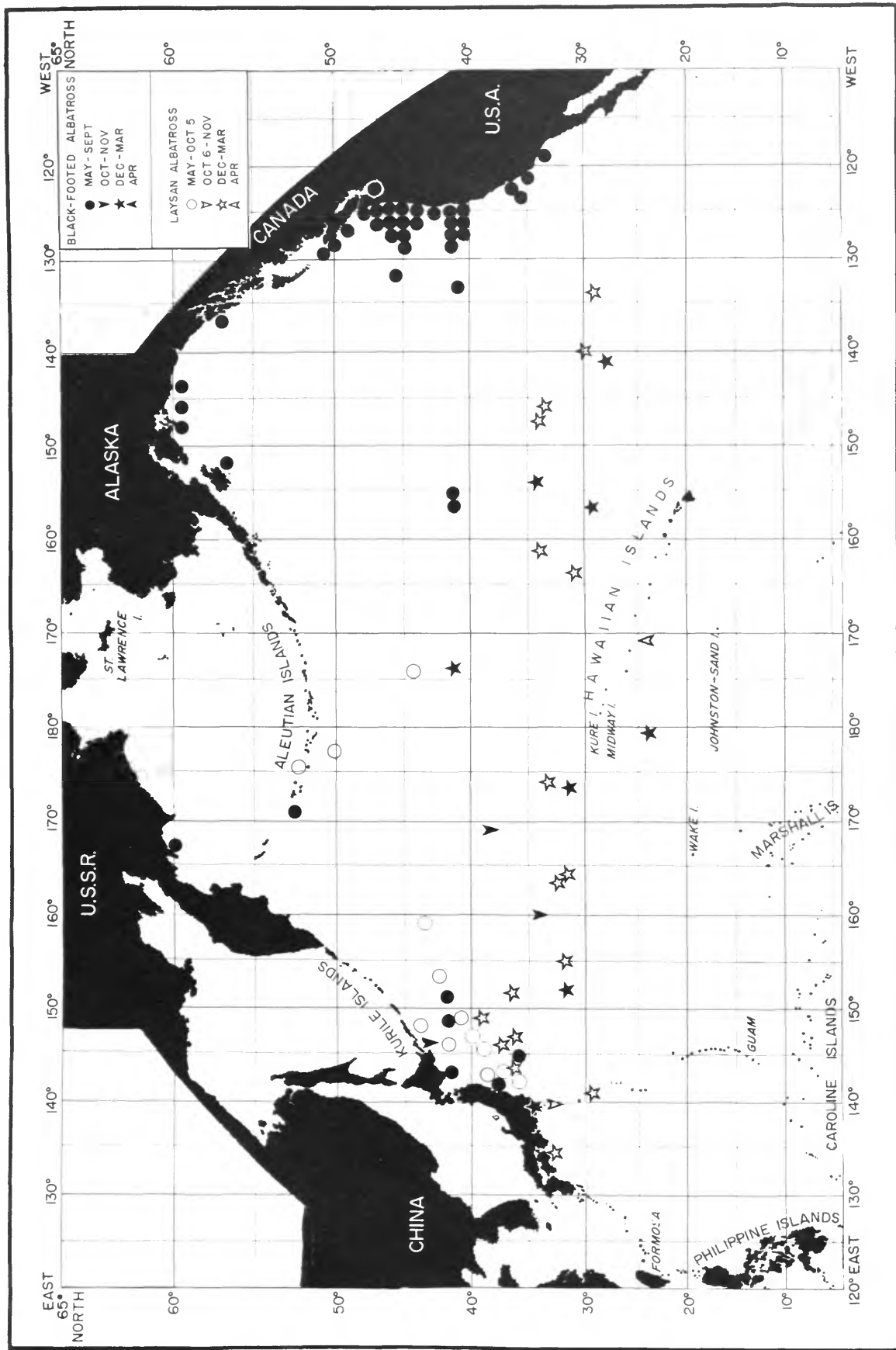


FIGURE 145.—Recoveries of albatrosses in their third year at sea, May through April.

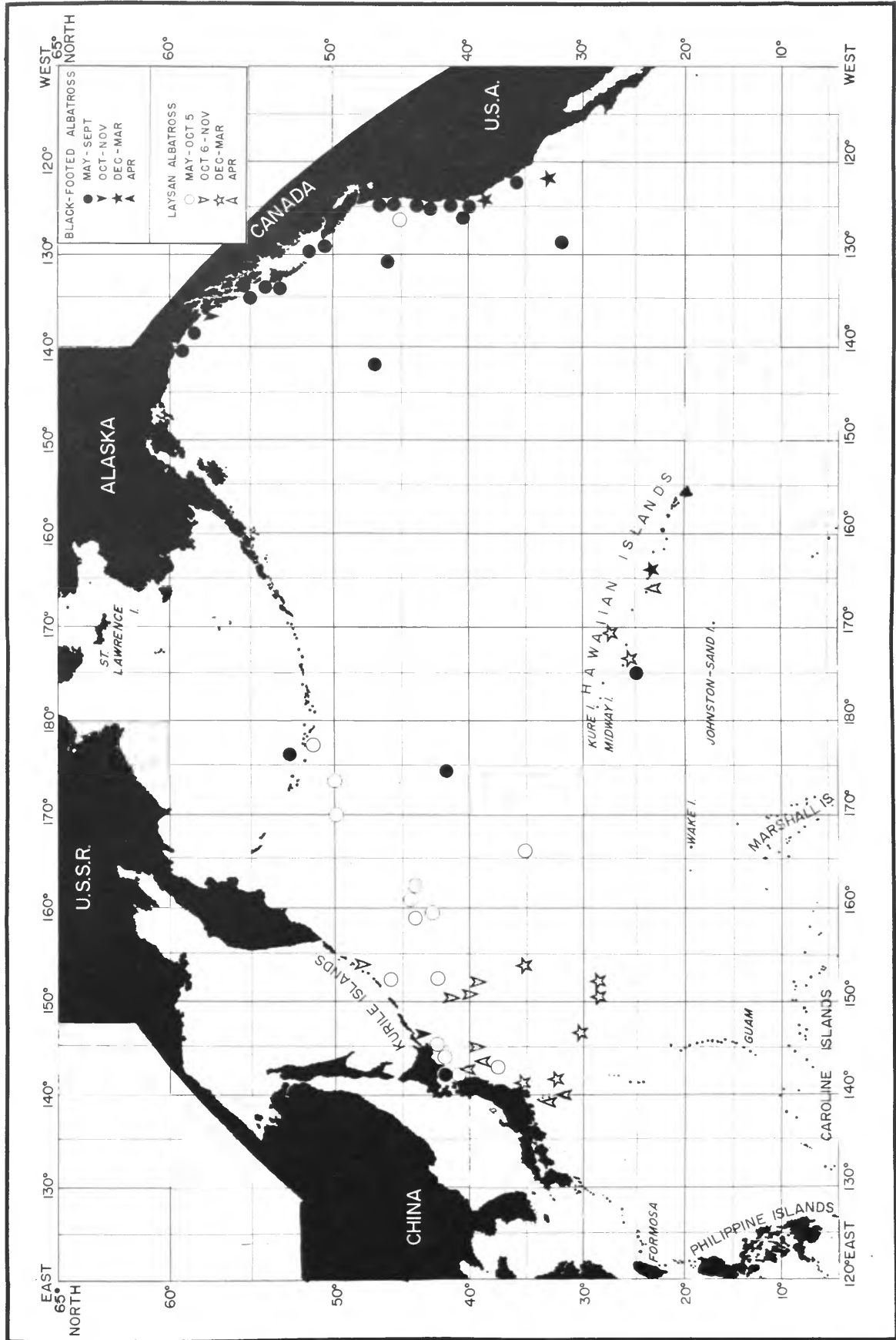


FIGURE 146.—Recoveries at sea of Black-footed Albatrosses in their fourth year and of Laysan Albatrosses in their fourth and fifth years.

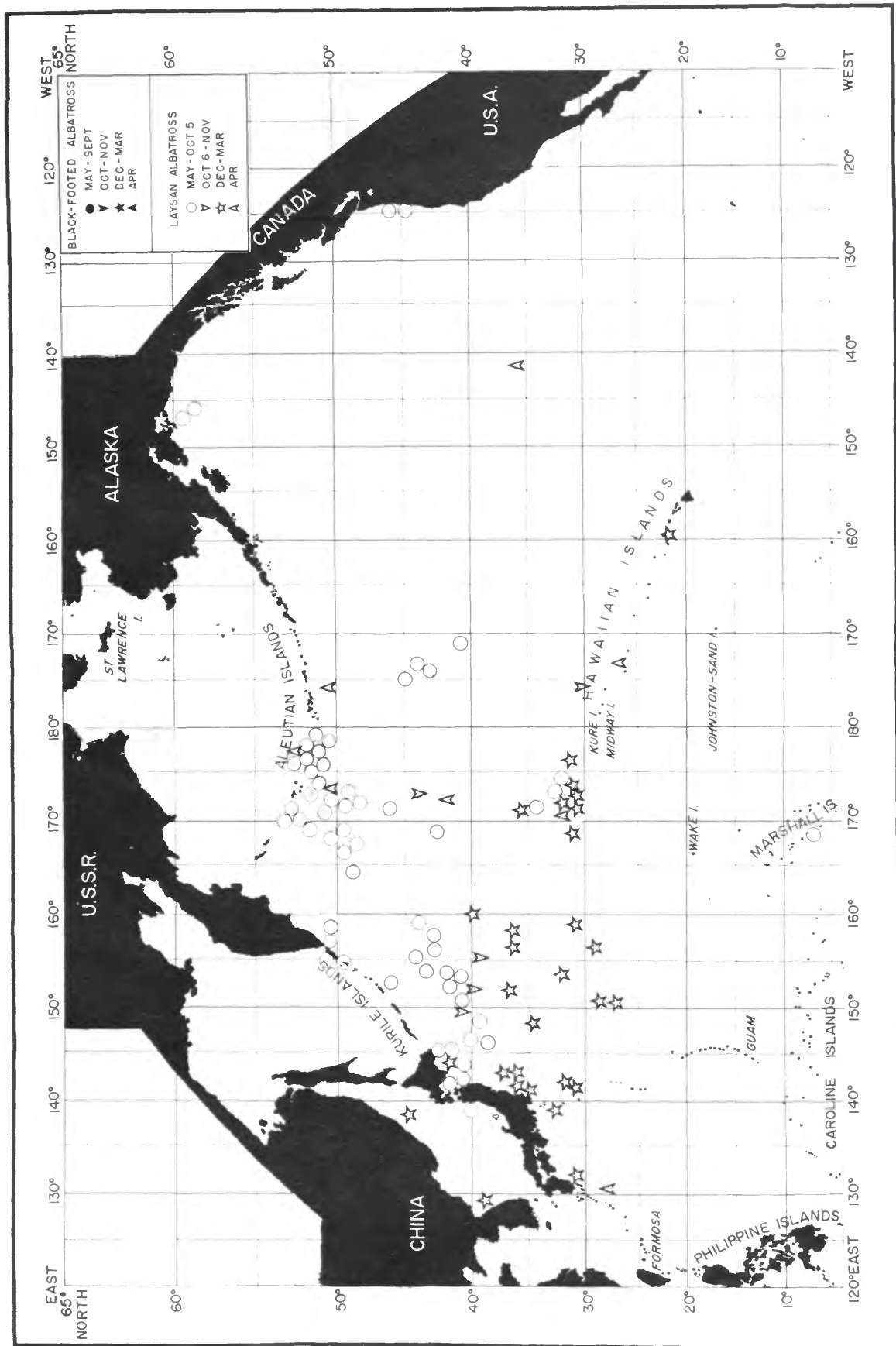


FIGURE 147.—Recoveries at sea of adult Laysan Albatrosses.

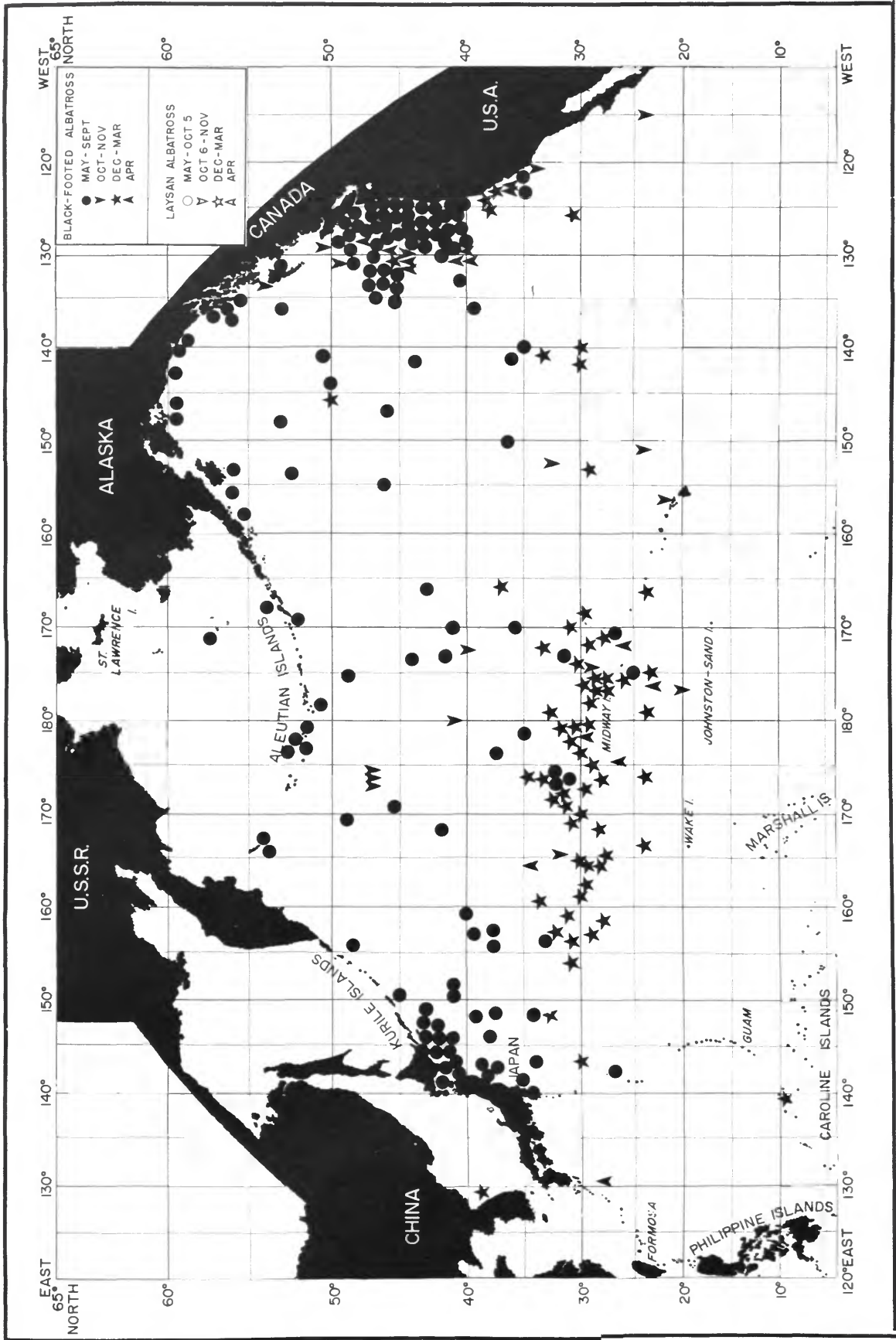


FIGURE 148.—Recoveries at sea of adult Black-footed Albatrosses.

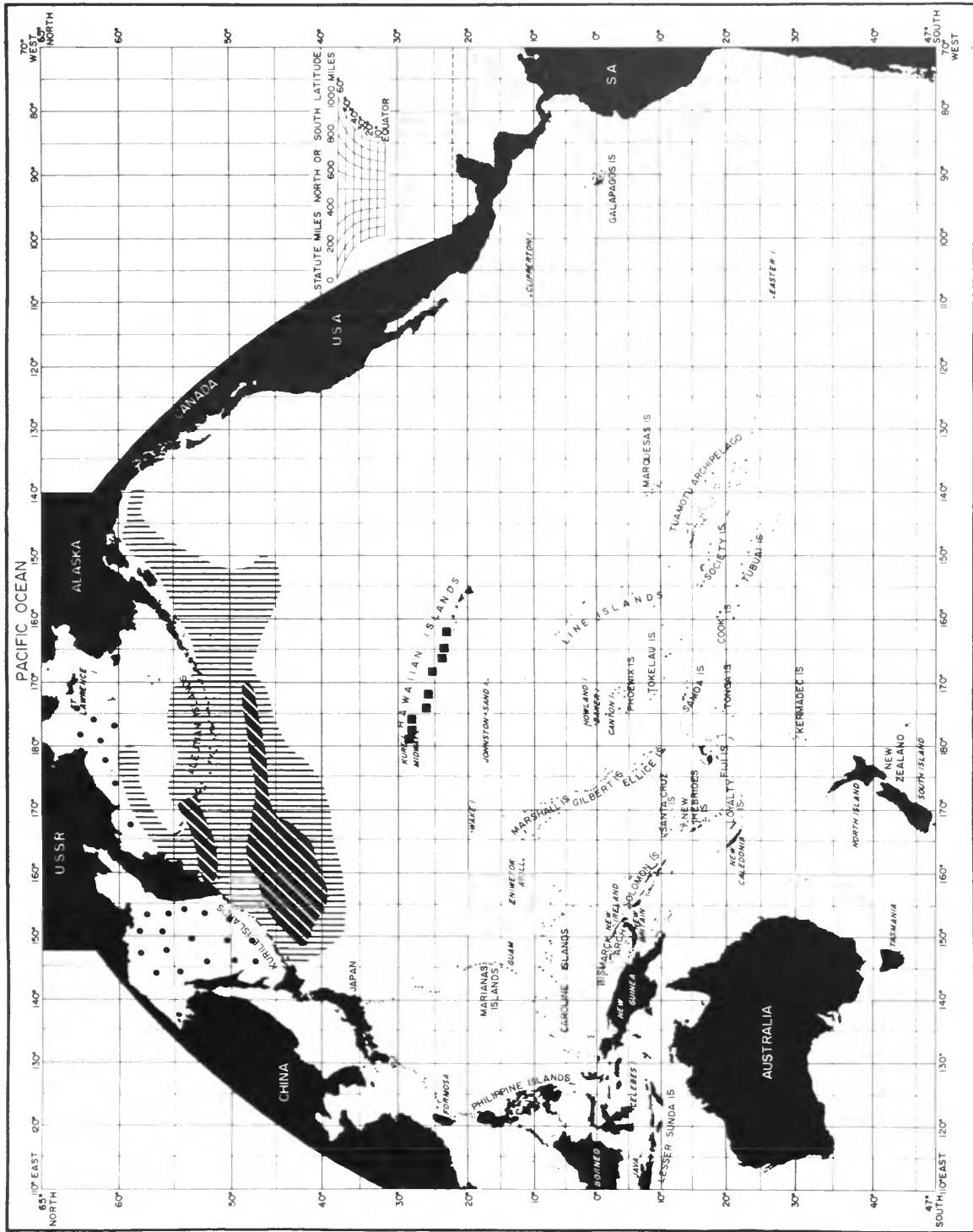


FIGURE 149.—Summer (May-September) distribution of Laysan Albatrosses, after Shuntov, 1968. (Concentration areas are indicated by heavy shading, remainder of regular range by vertical lines, areas of rare occurrence by dots; nesting islands are shown as black squares.)

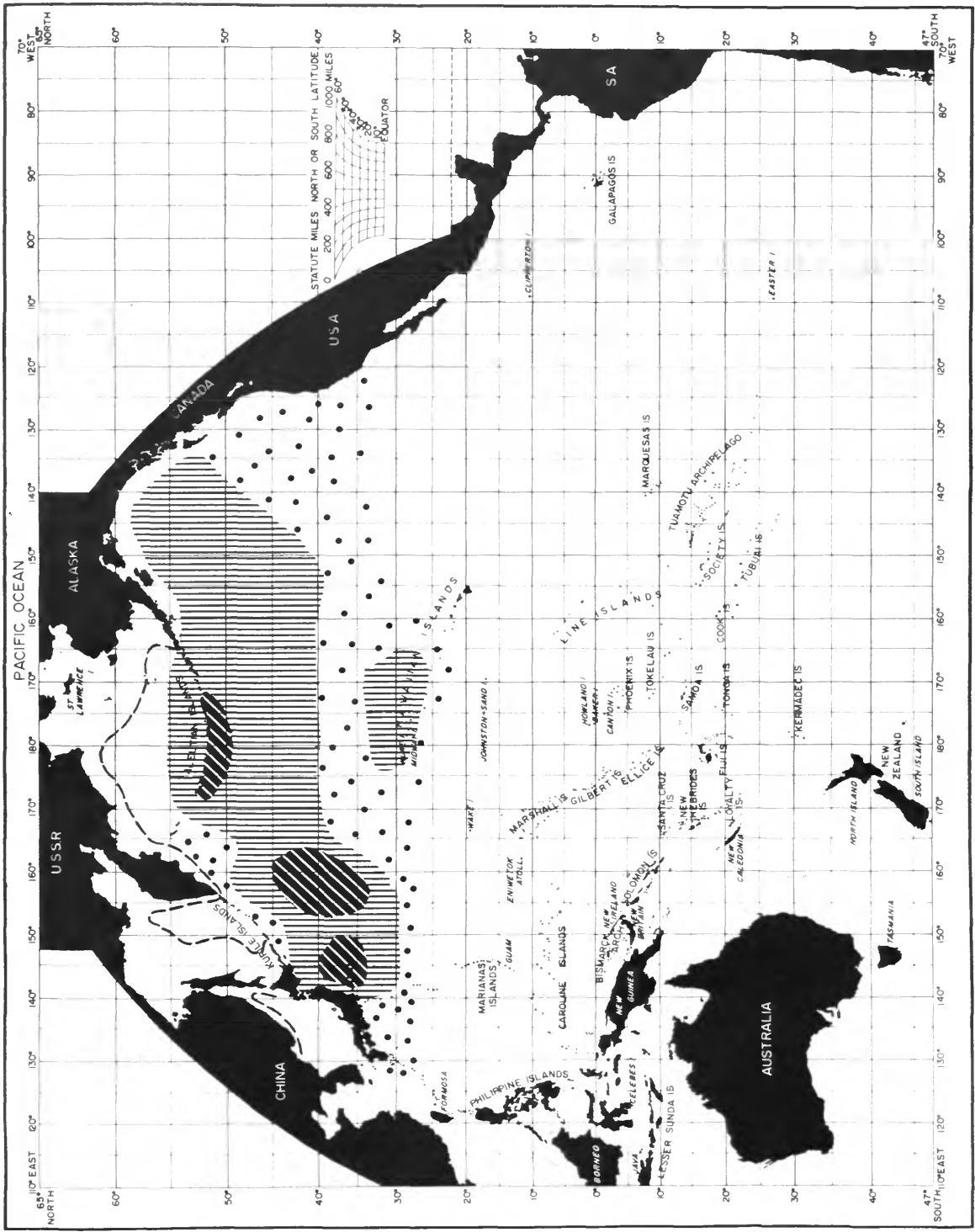


FIGURE 150.—Winter (November–March) distribution of Laysan Albatrosses, after Shuntov, 1968. (The February limit of sea ice is indicated by a dashed line, other symbols as in Figure 149.)

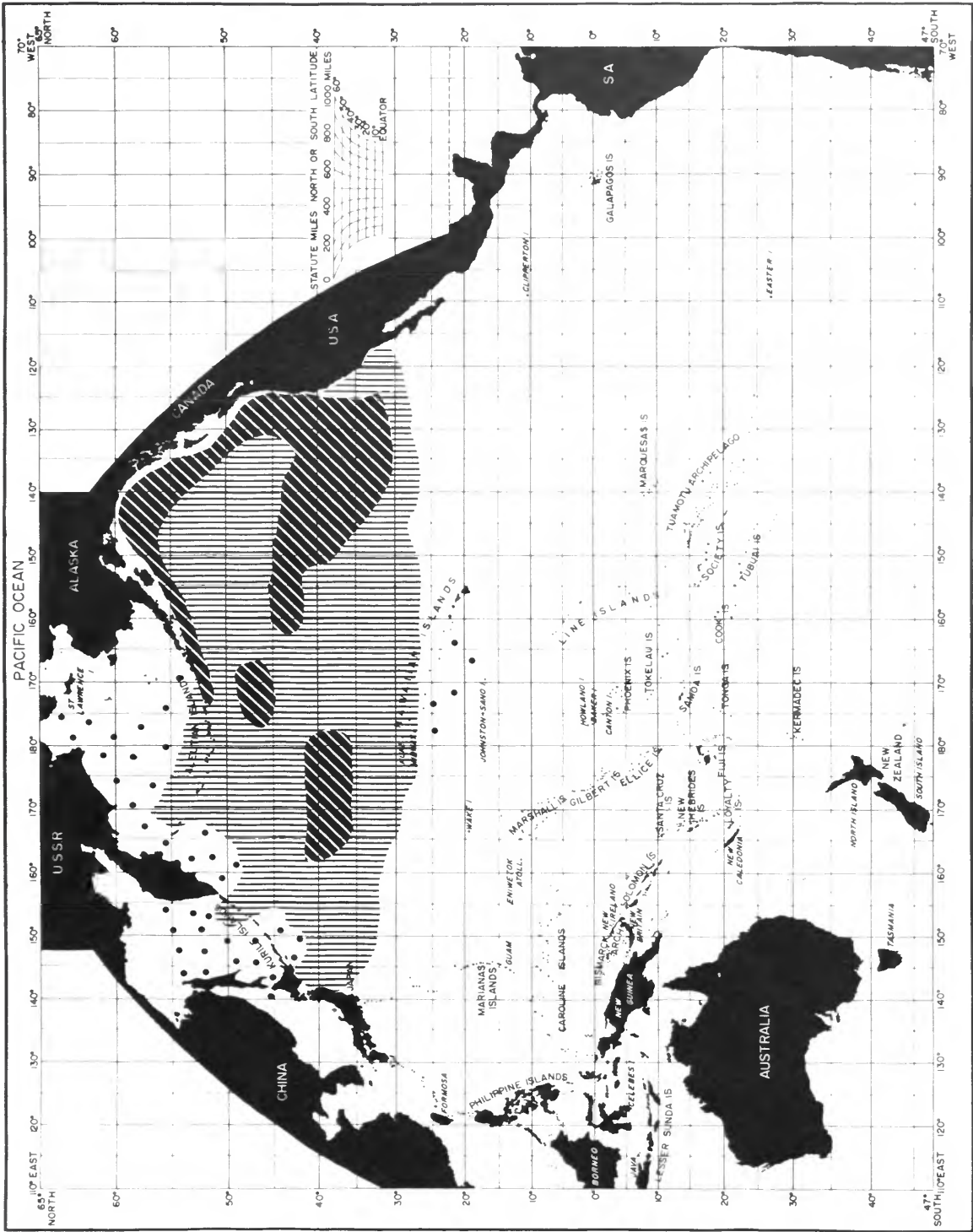


FIGURE 151.—Summer distribution of Black-footed Albatrosses, after Shuntov, 1968. (Symbols as in Figure 149.)

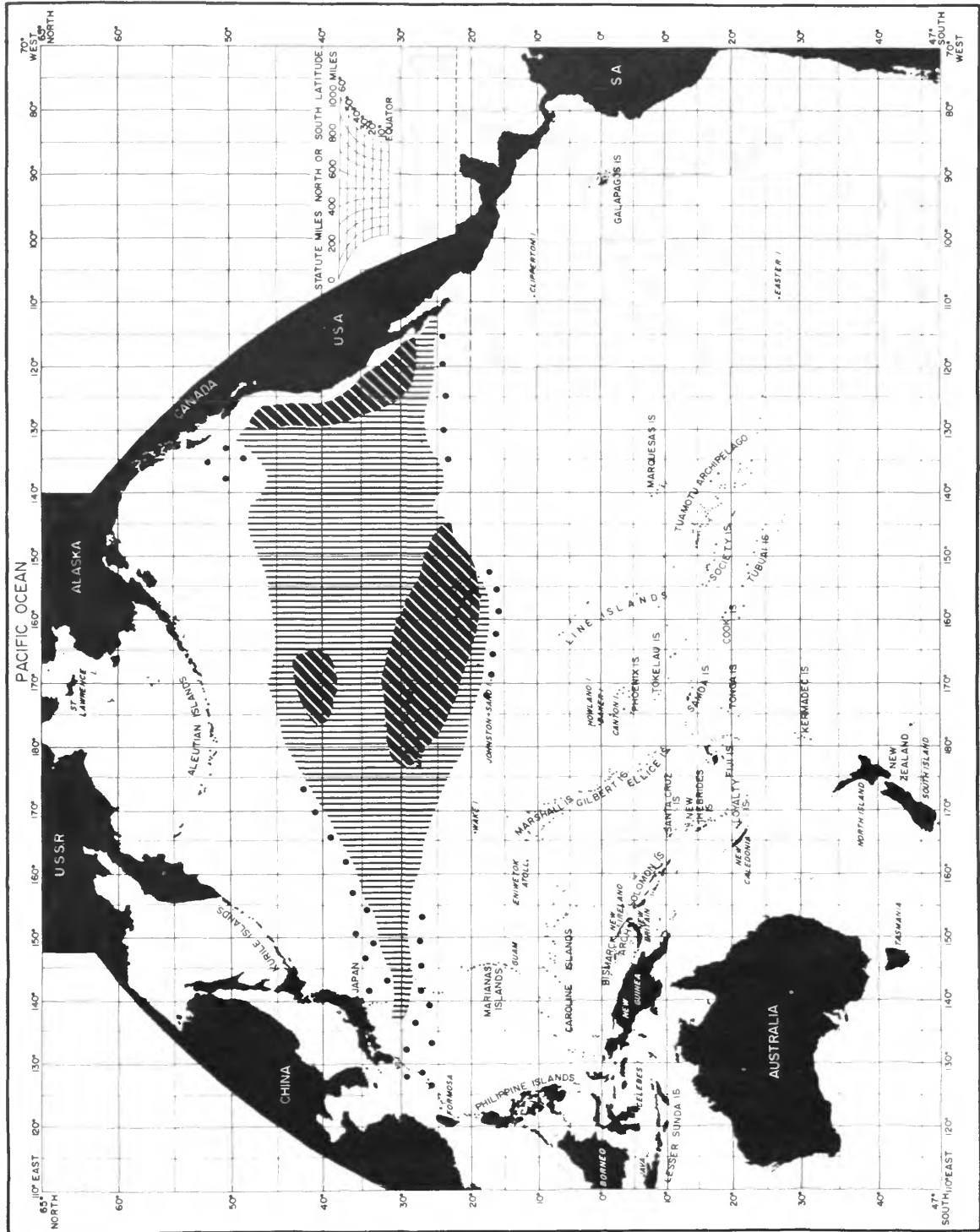


FIGURE 152.—Winter distribution of Black-footed Albatrosses, after Shuntov, 1968. (Symbols as in Figure 149.)

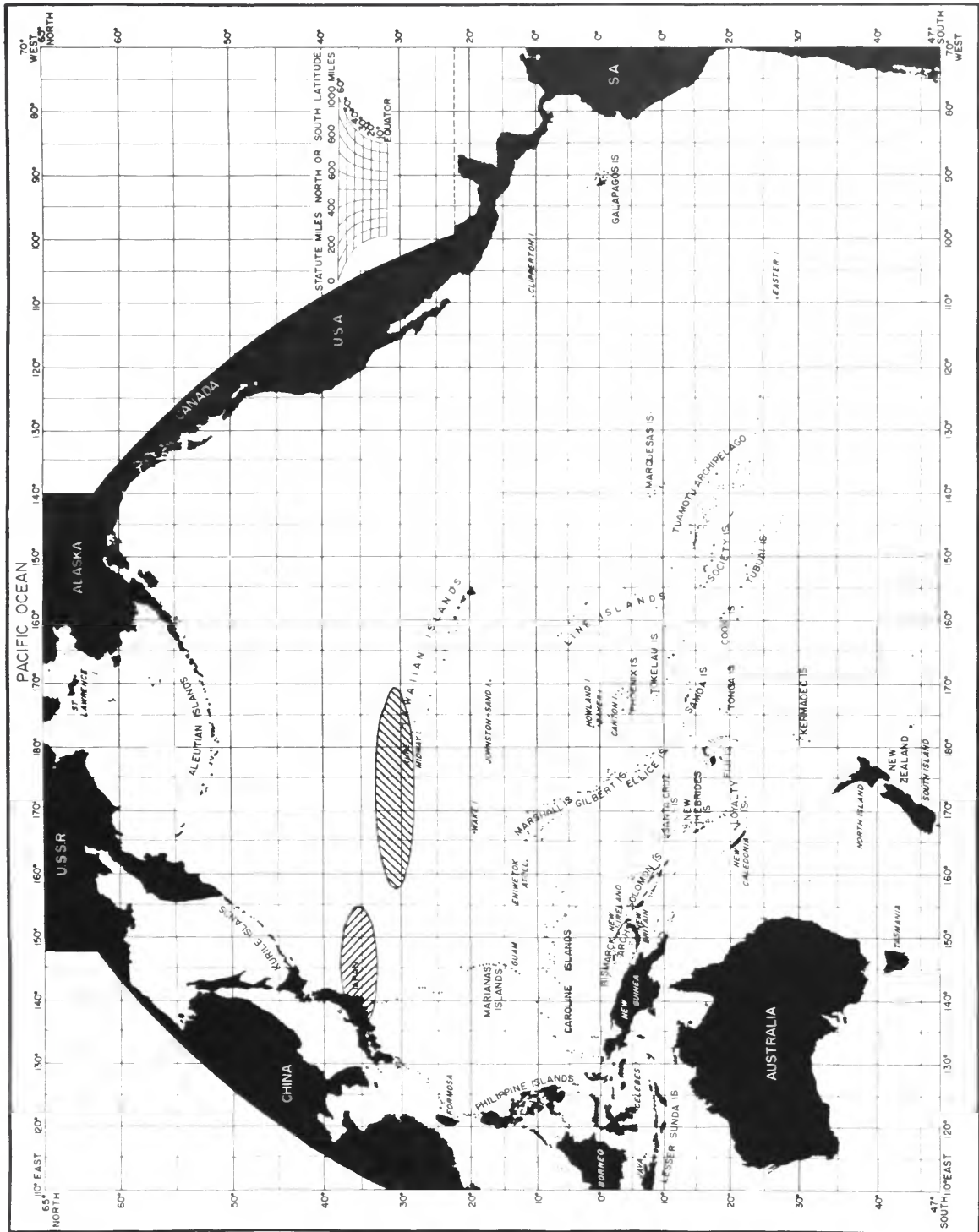


FIGURE 153.—Comparative January distribution of adult Laysan (left) and Black-footed Albatrosses. (Shaded areas enclose one standard deviation from the mean latitude and longitude of all pelagic band recovery locations.)

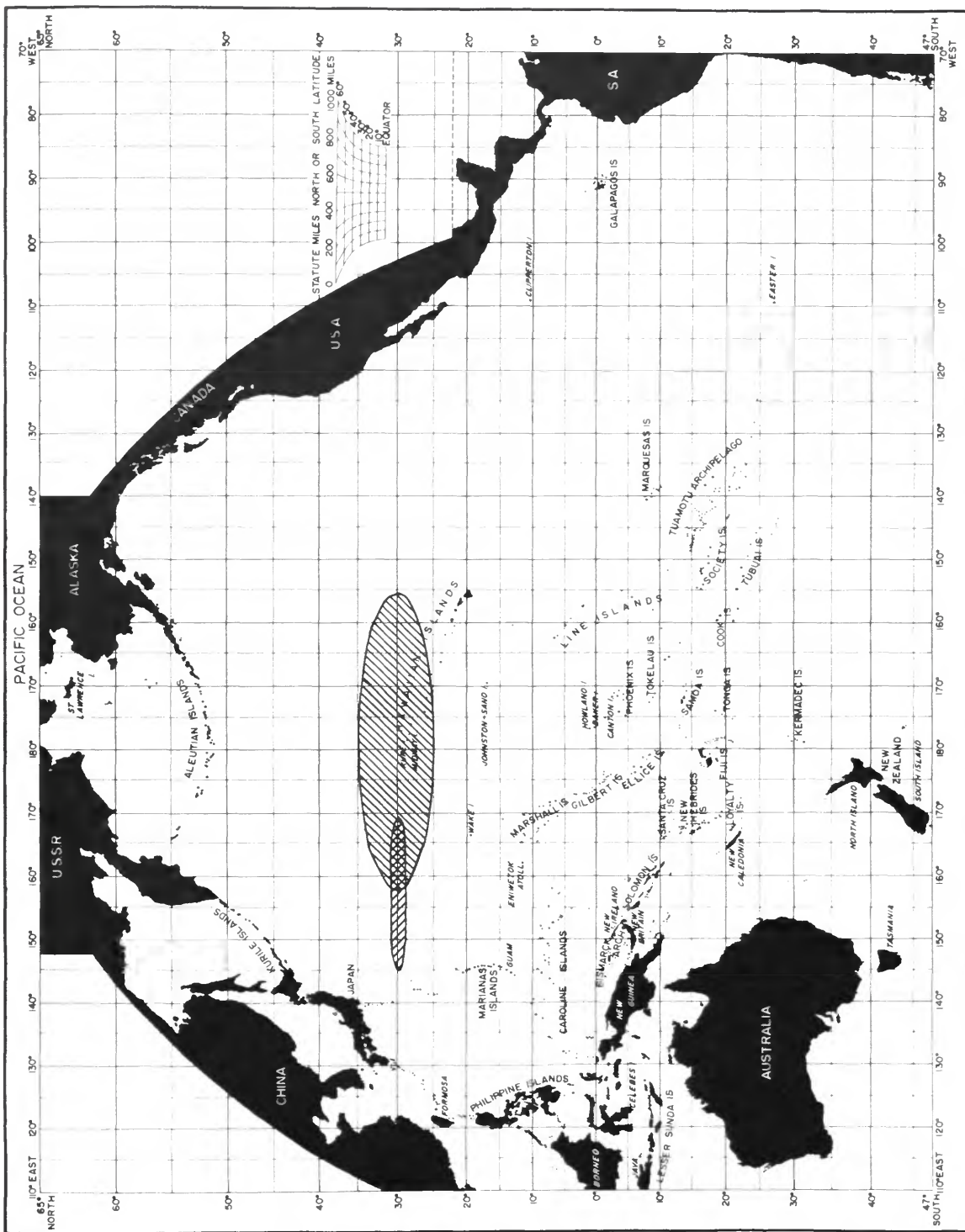


FIGURE 154.—Comparative February distribution of adult Laysan (left) and Black-footed Albatrosses. (For explanation see Figure 153.)

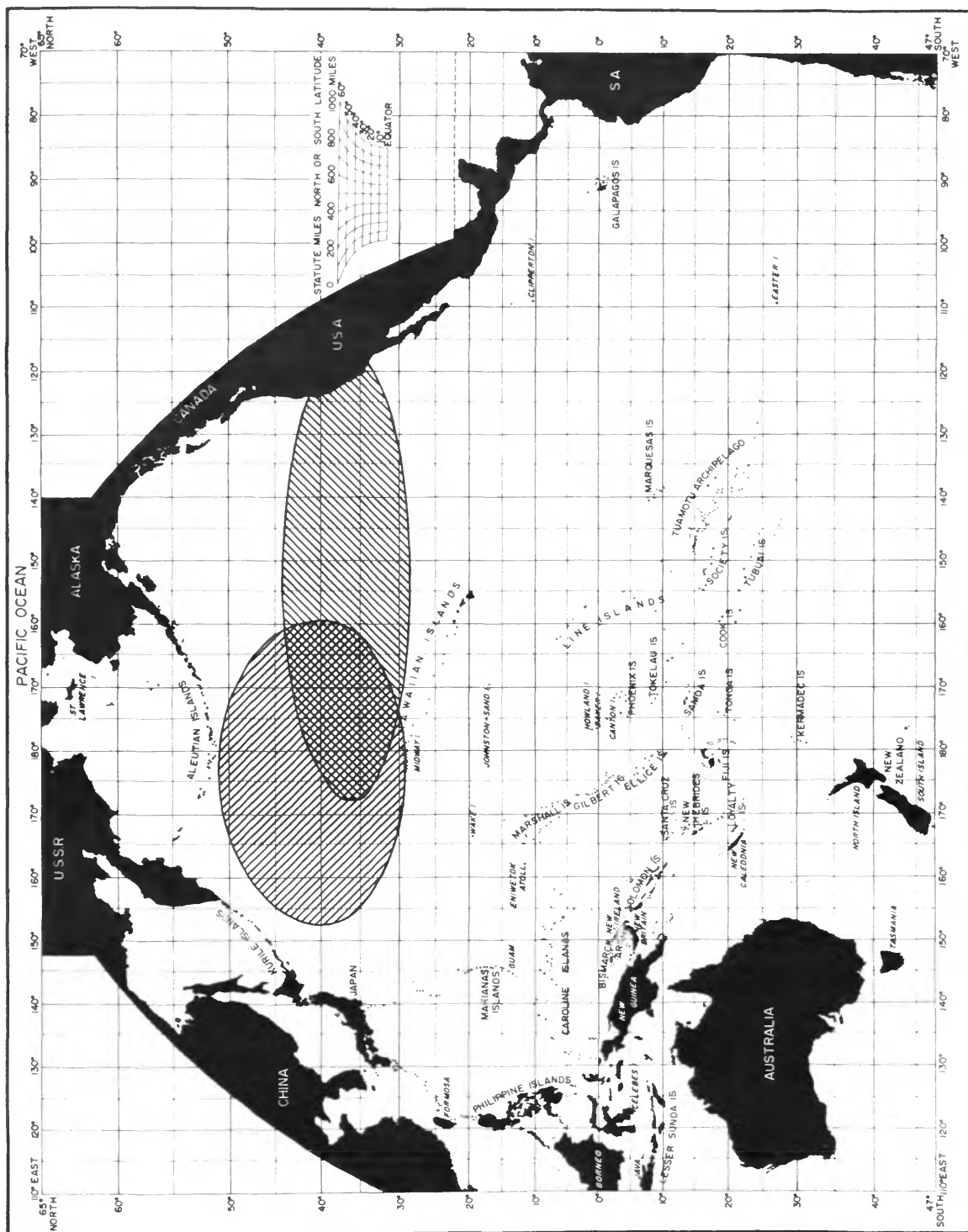


FIGURE 156.—Comparative April distribution of adult Laysan (left) and Black-footed Albatrosses. (For explanation see Figure 155.)

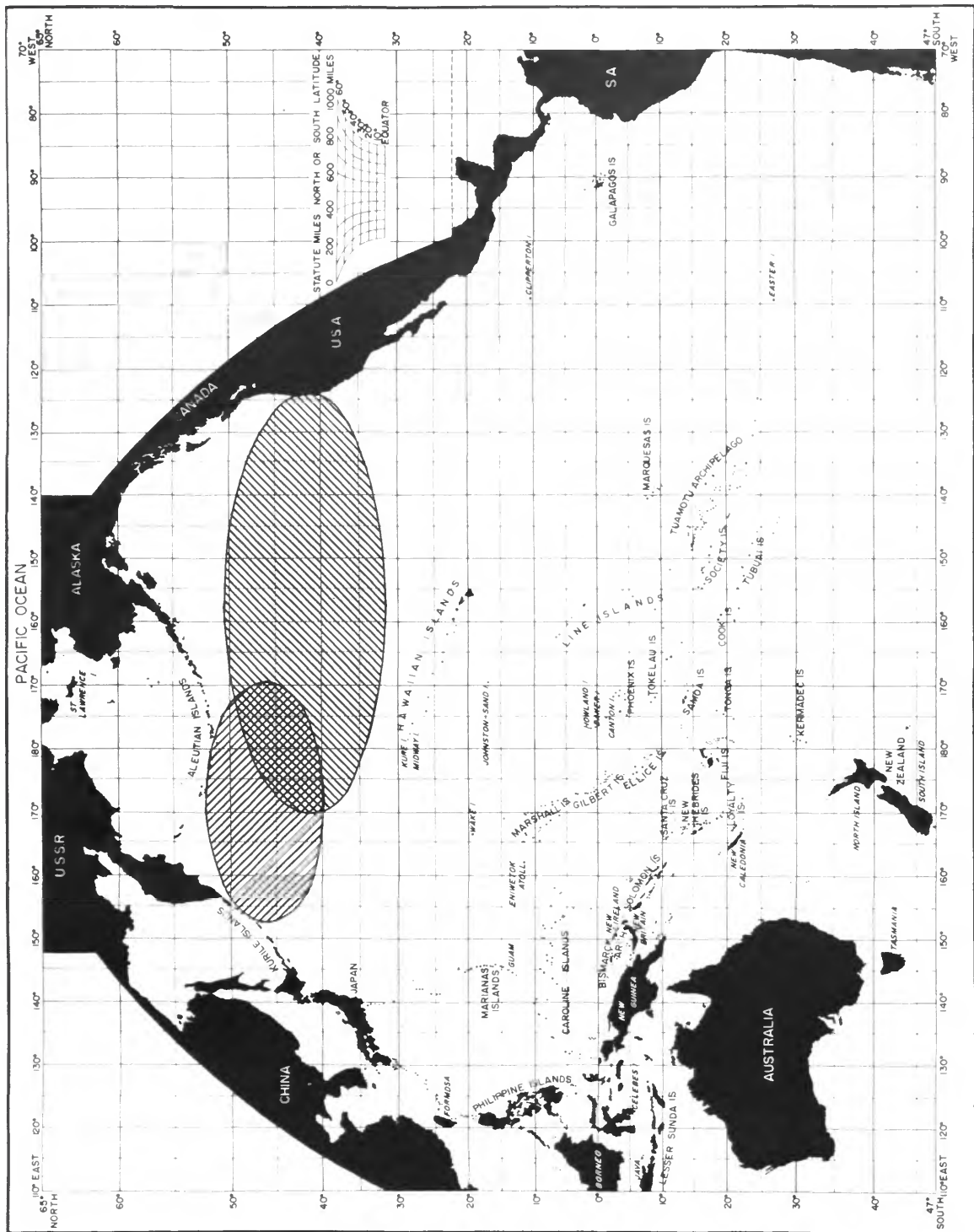


FIGURE 157.—Comparative May distribution of adult Laysan (left) and Black-footed Albatrosses. (For explanation see Figure 153.)

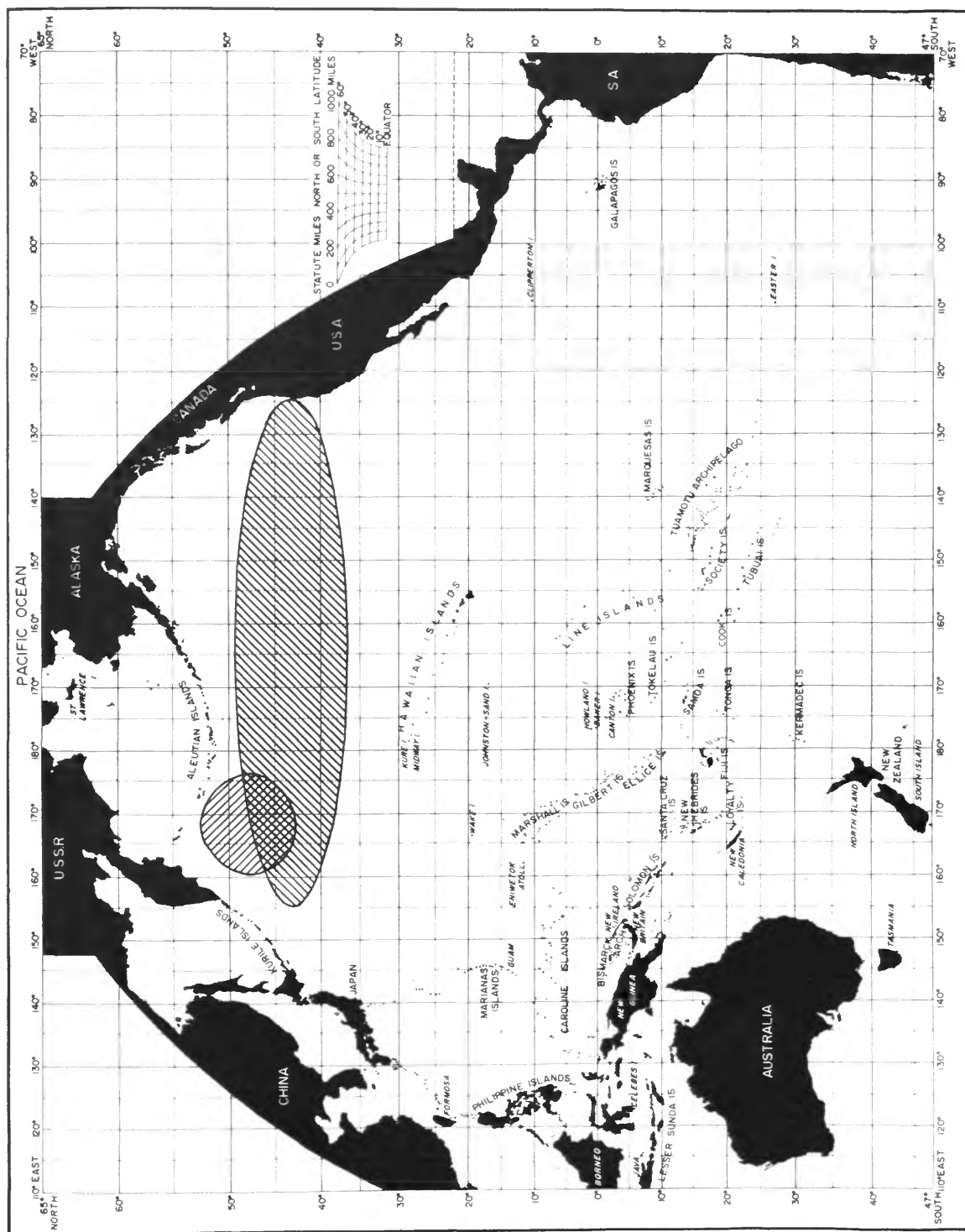


FIGURE 158.—Comparative June distribution of adult Laysan (left) and Black-footed Albatrosses. (For explanation see Figure 155.)

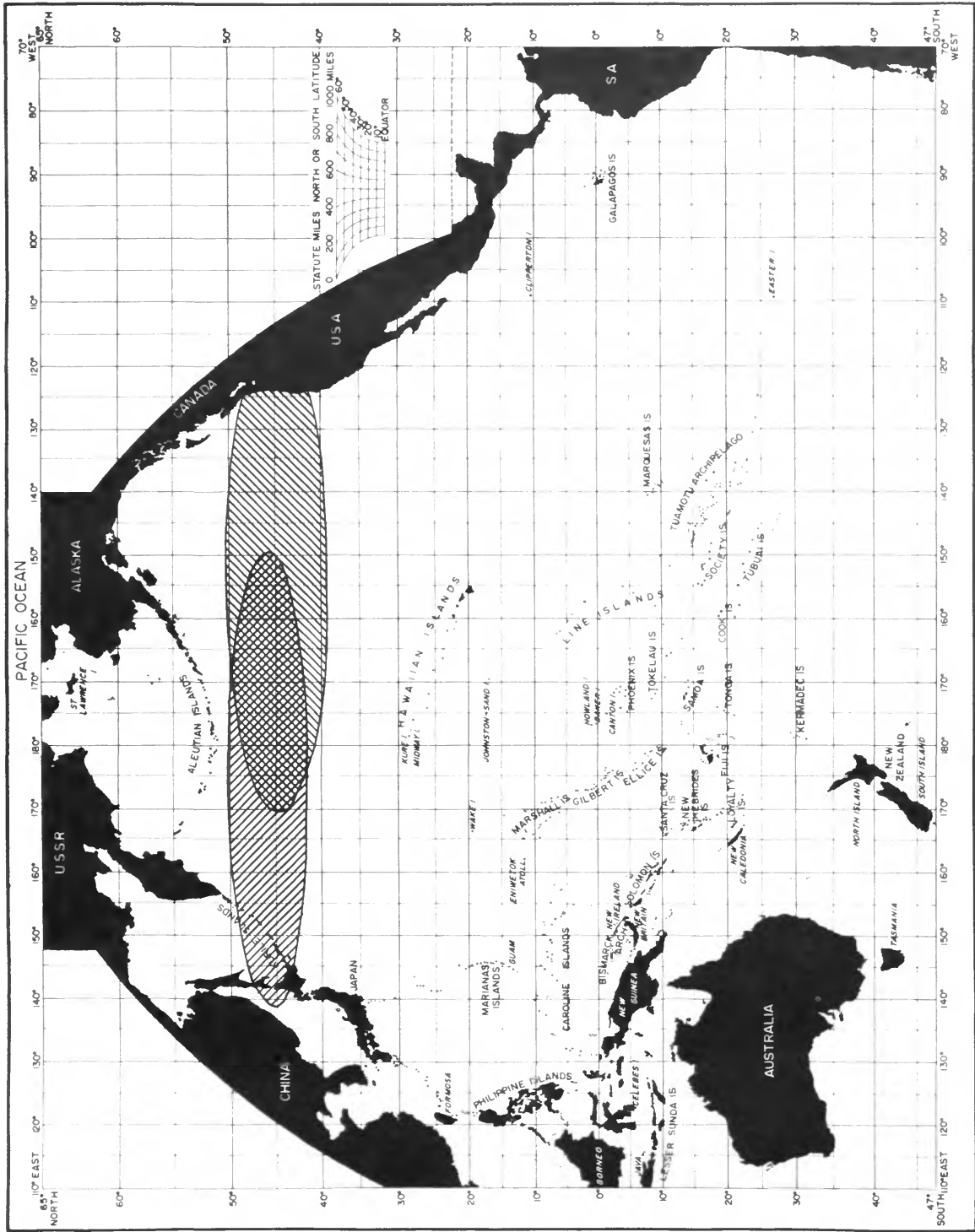


FIGURE 159.—Comparative July distribution of adult Laysan (left) and Black-footed Albatrosses. (For explanation see Figure 155.)

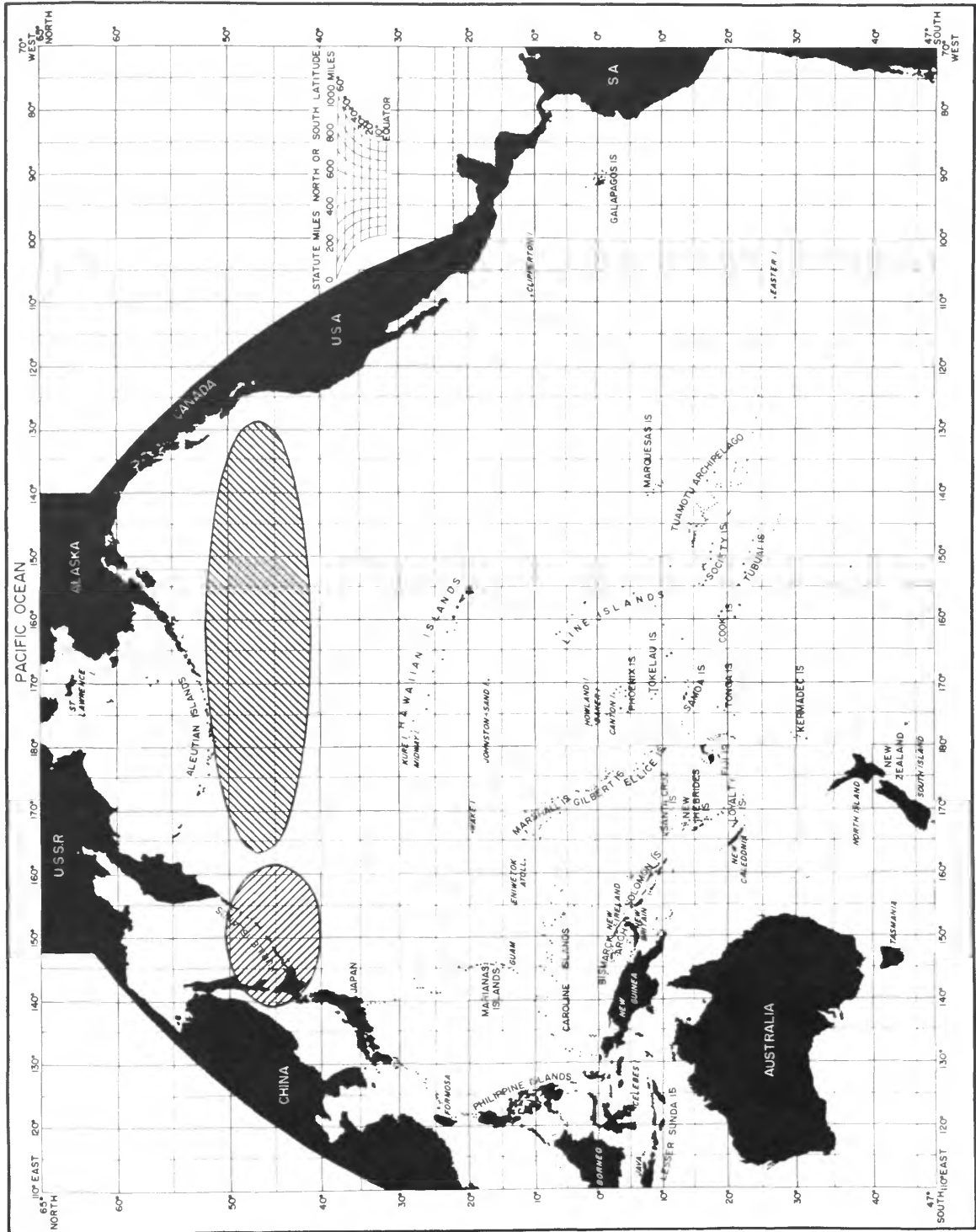


FIGURE 160.—Comparative August distribution of adult Laysan (left) and Black-footed Albatrosses. (For explanation see Figure 153.)

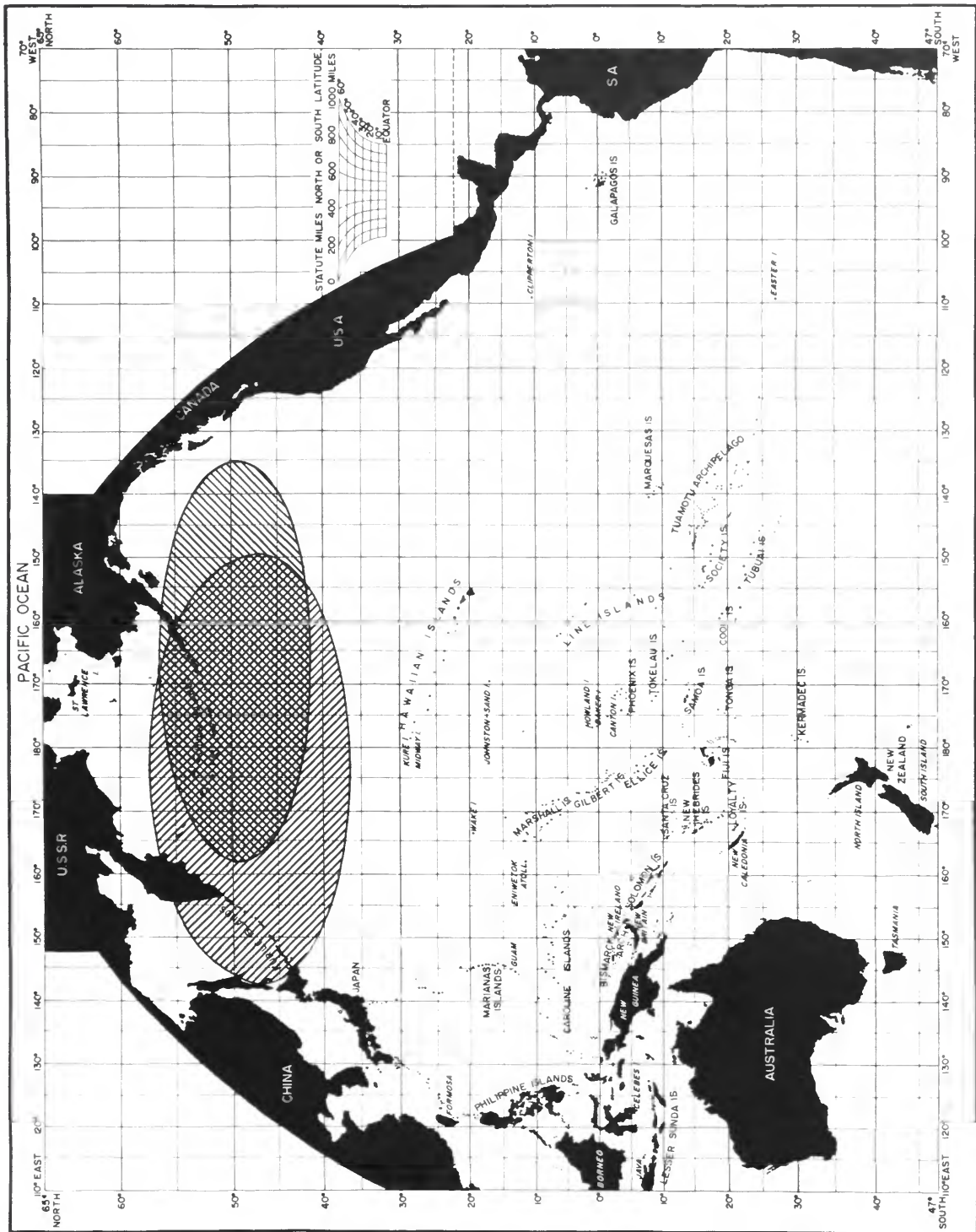


FIGURE 161.—Comparative September distribution of adult Laysan (left) and Black-footed Albatrosses. (For explanation see Figure 155.)

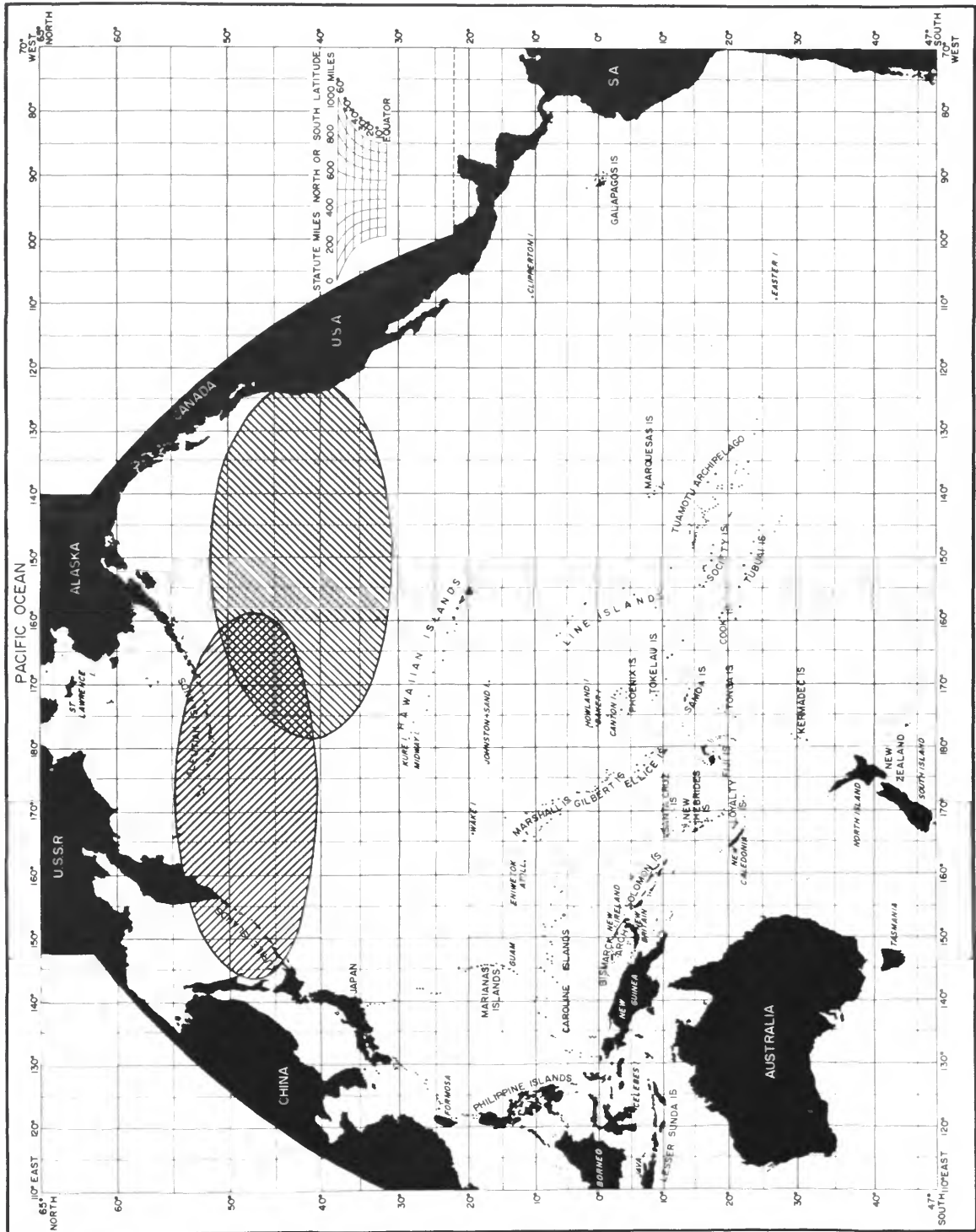


Figure 162.—Comparative October distribution of adult Laysan (left) and Black-footed Albatrosses. (For explanation see Figure 158.)

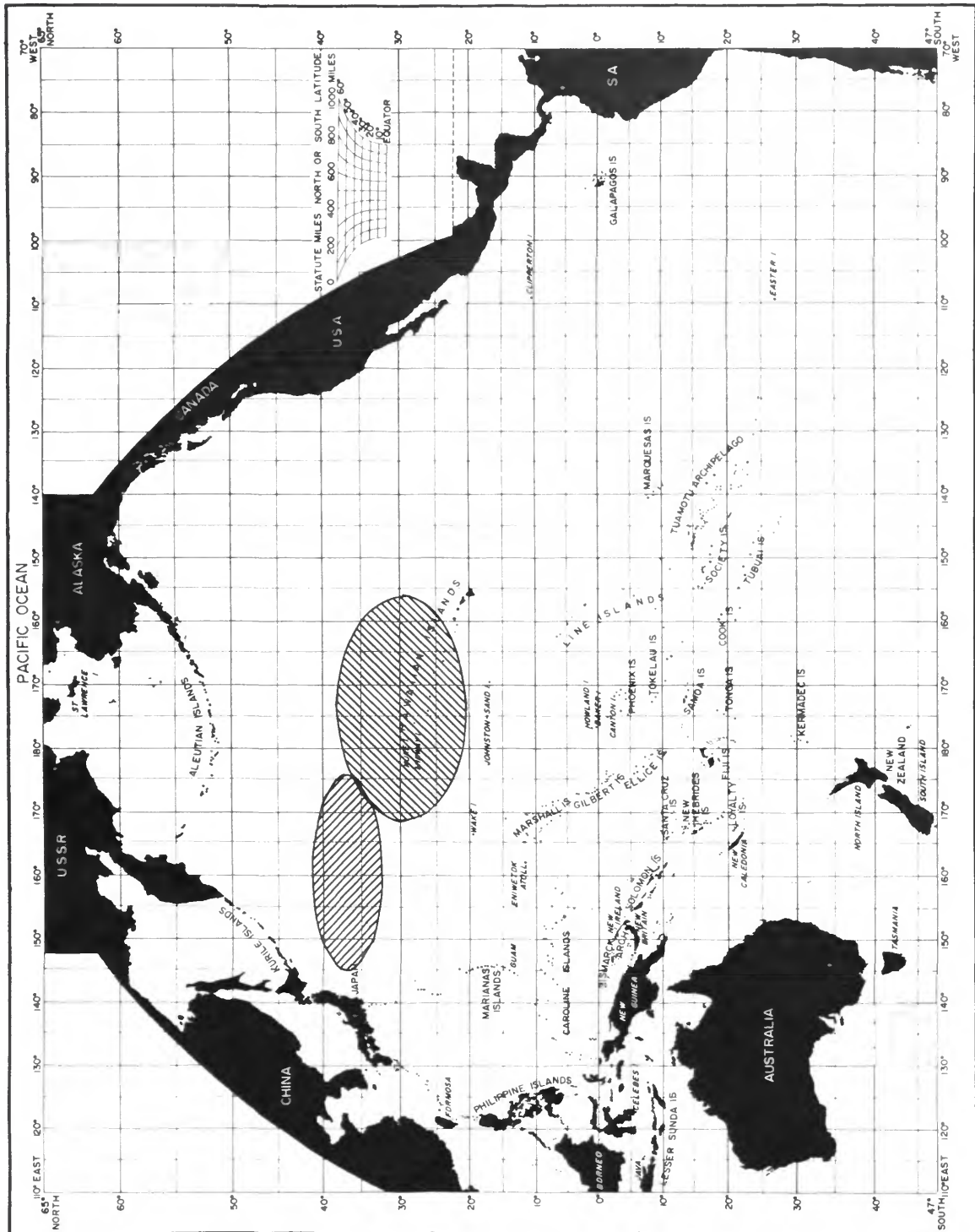


FIGURE 168.—Comparative November distribution of adult Laysan (left) and Black-footed Albatrosses. (For explanation see Figure 159.)

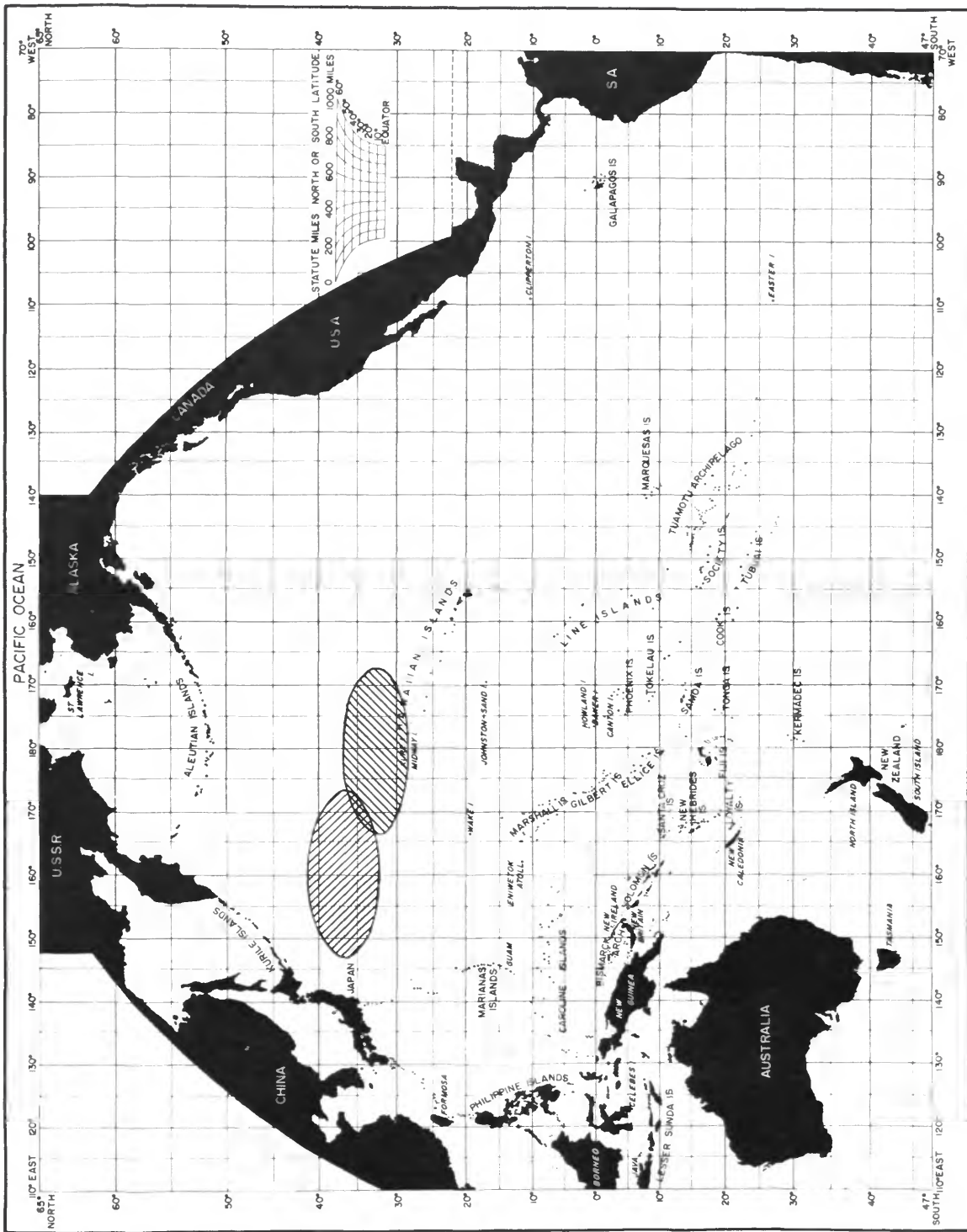


FIGURE 164.—Comparative December distribution of adult Laysan (left) and Black-footed Albatrosses. (For explanation see Figure 155.)

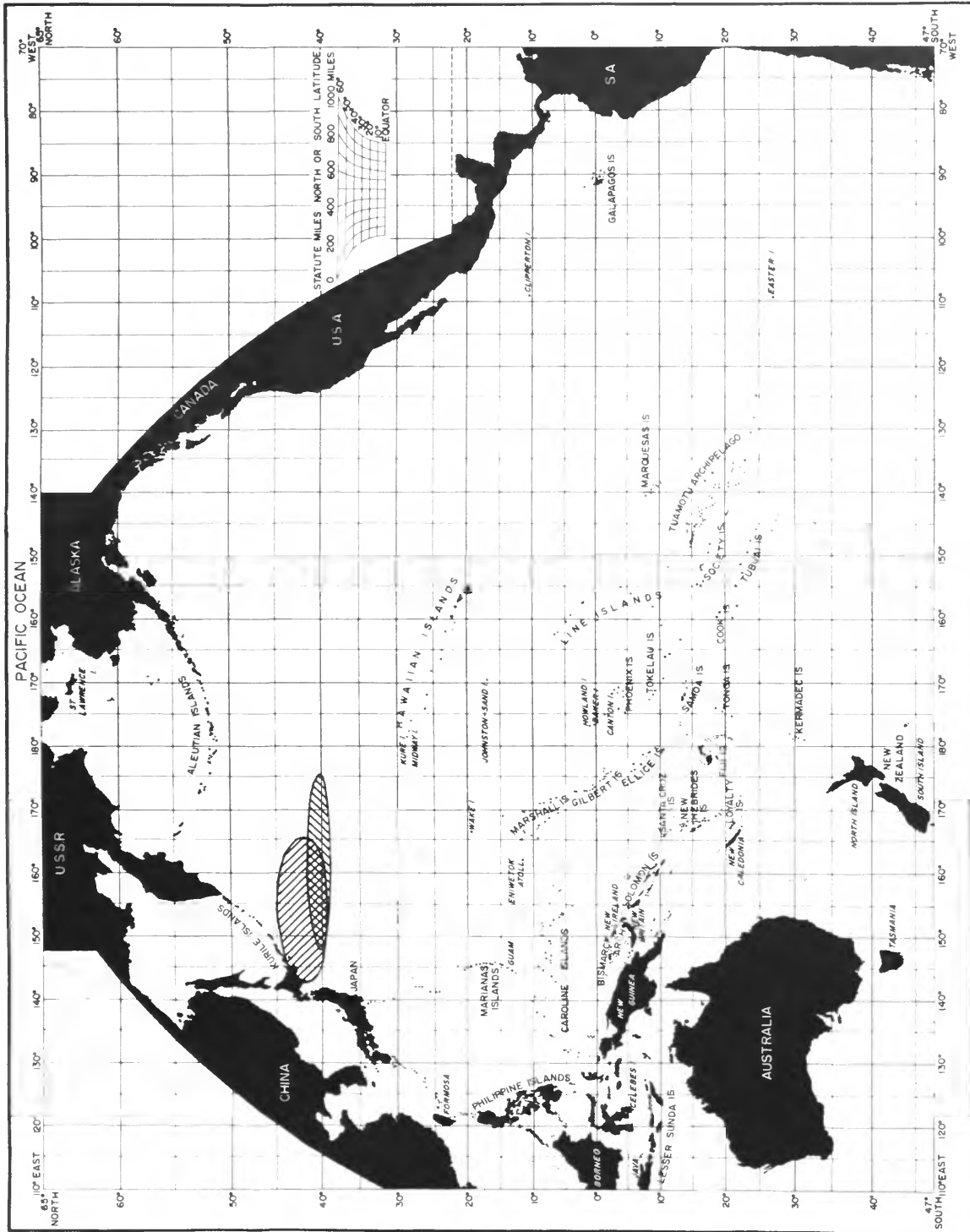


FIGURE 165.—Comparative July–August distribution of young Laysan (left) and Black-footed Albatrosses in their first months at sea. (For explanation see Figure 153.)

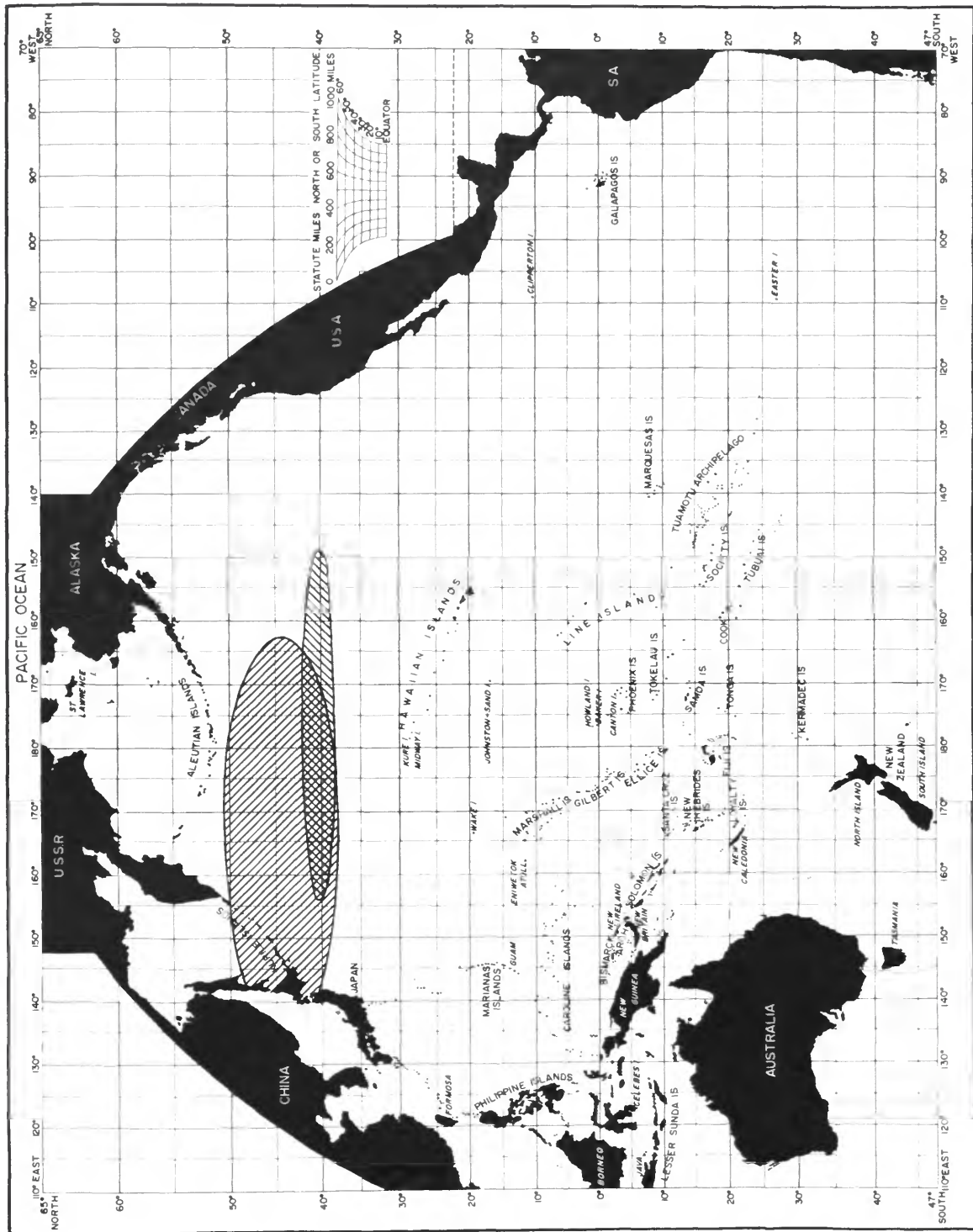


FIGURE 166.—Comparative September–October distribution of young Laysan (left) and Black-footed Albatrosses in their first season at sea. (For explanation see Figure 155.)

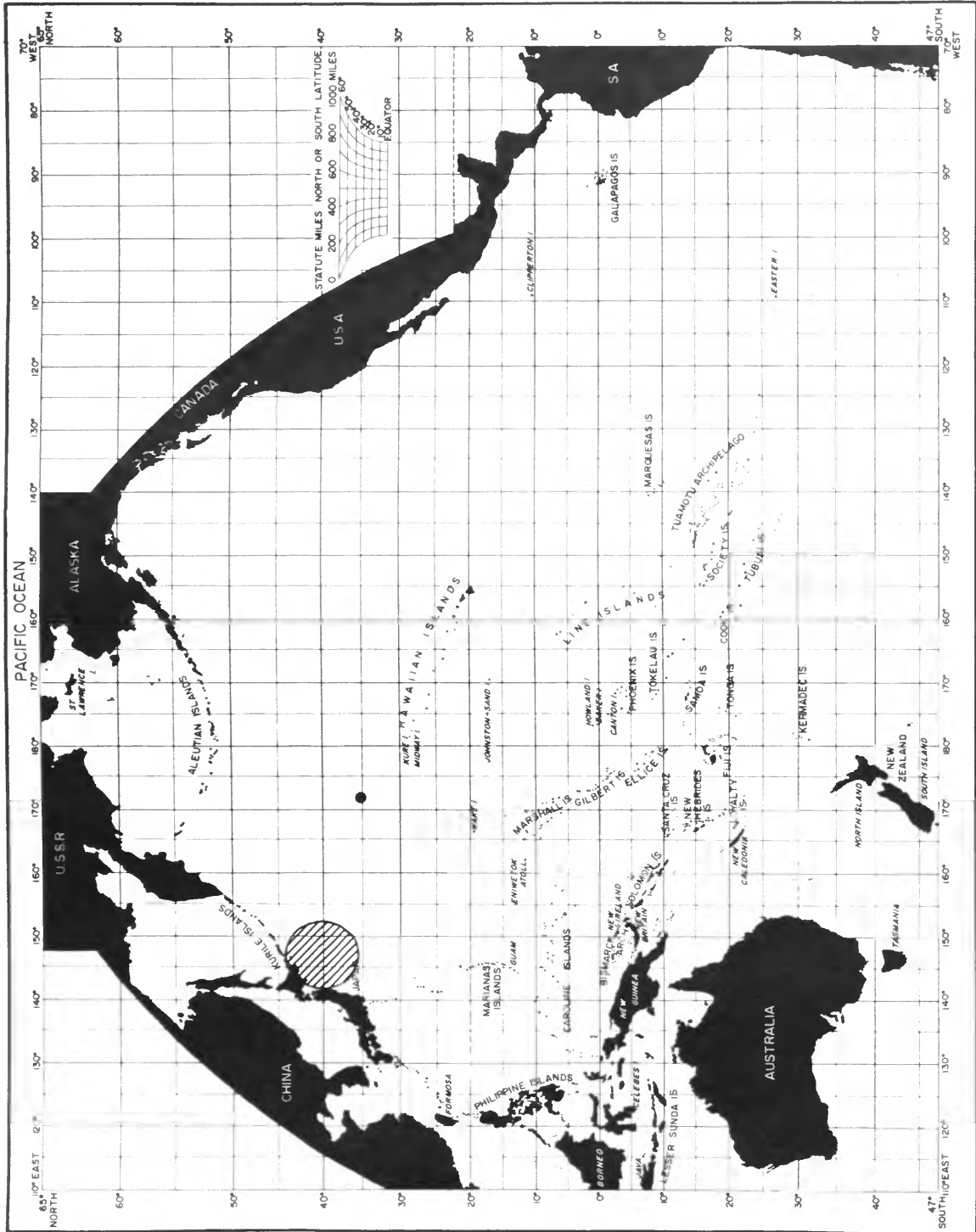


FIGURE 167.—Comparative November distribution of young Laysan Albatrosses (left) in their first four Novembers at sea and of young Black-footed Albatrosses in their first two Novembers at sea. There have been no pelagic recoveries of banded Black-footed Albatrosses in their third and fourth Novembers.

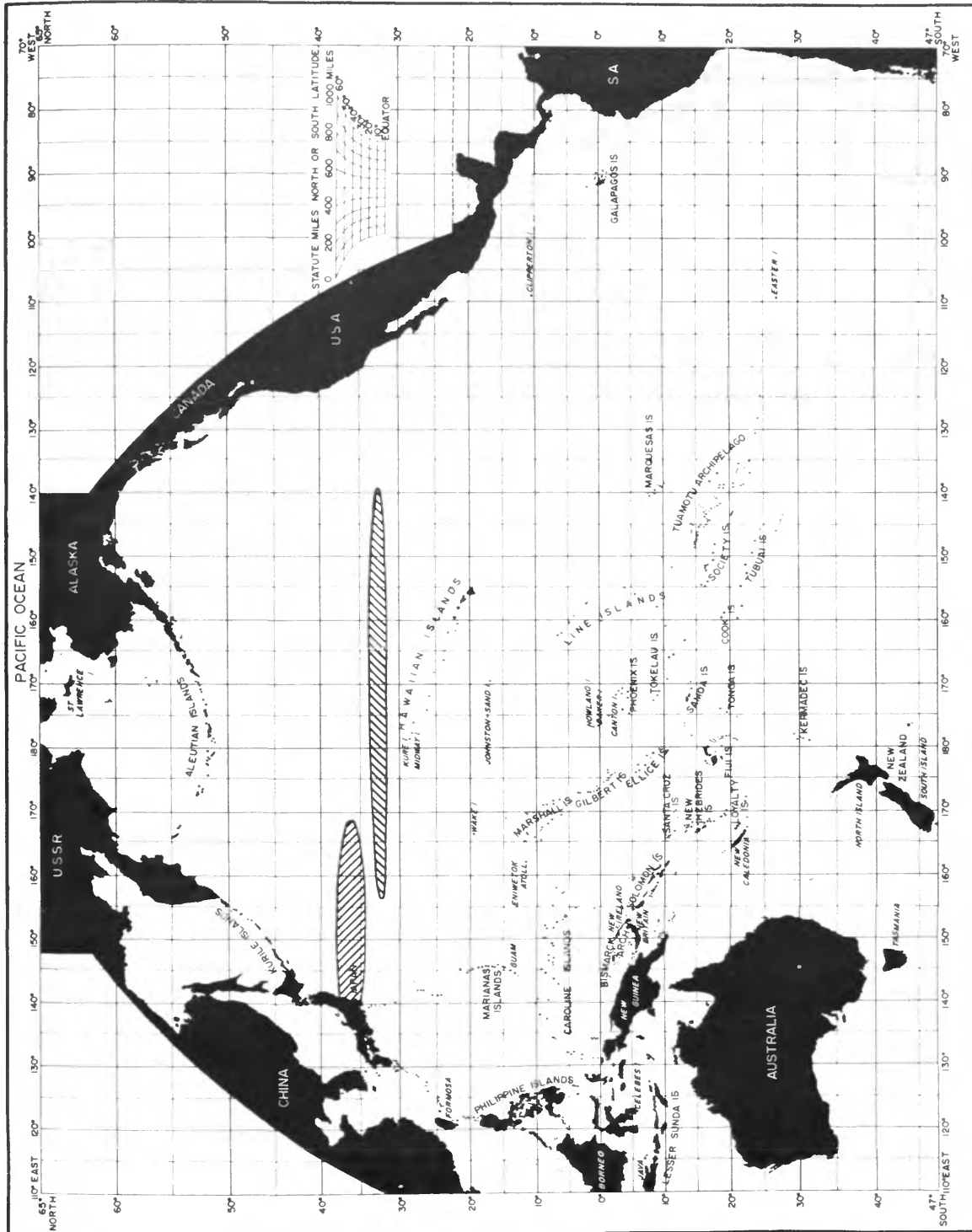


FIGURE 168.—Comparative December distribution of young Laysan Albatrosses (left) in their first four Decembers at sea and of young Black-footed Albatrosses in their first two Decembers at sea. (For explanation see Figure 155.)

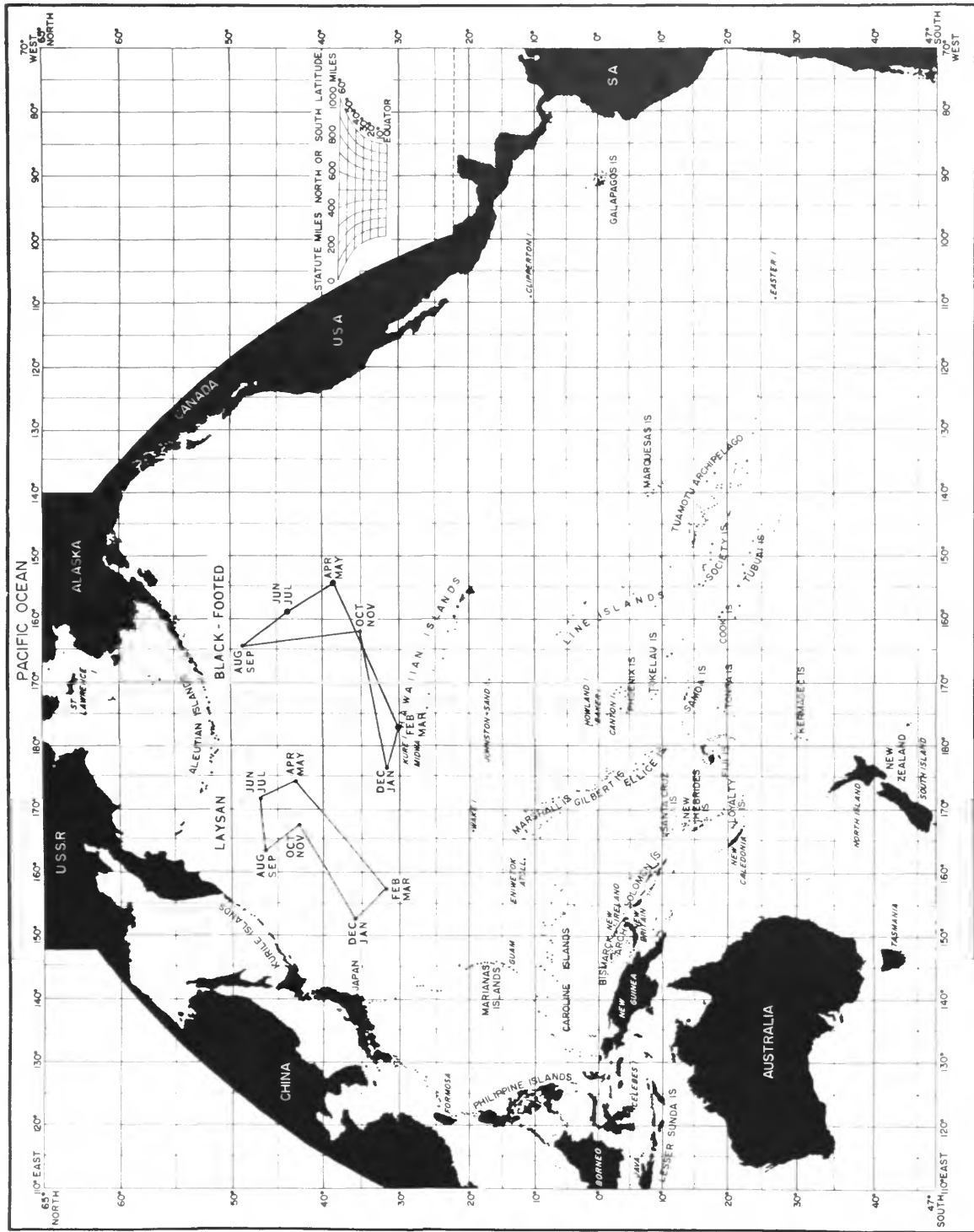


FIGURE 169.—Mean bi-monthly positions of banded albatrosses recovered at sea in the north Pacific.

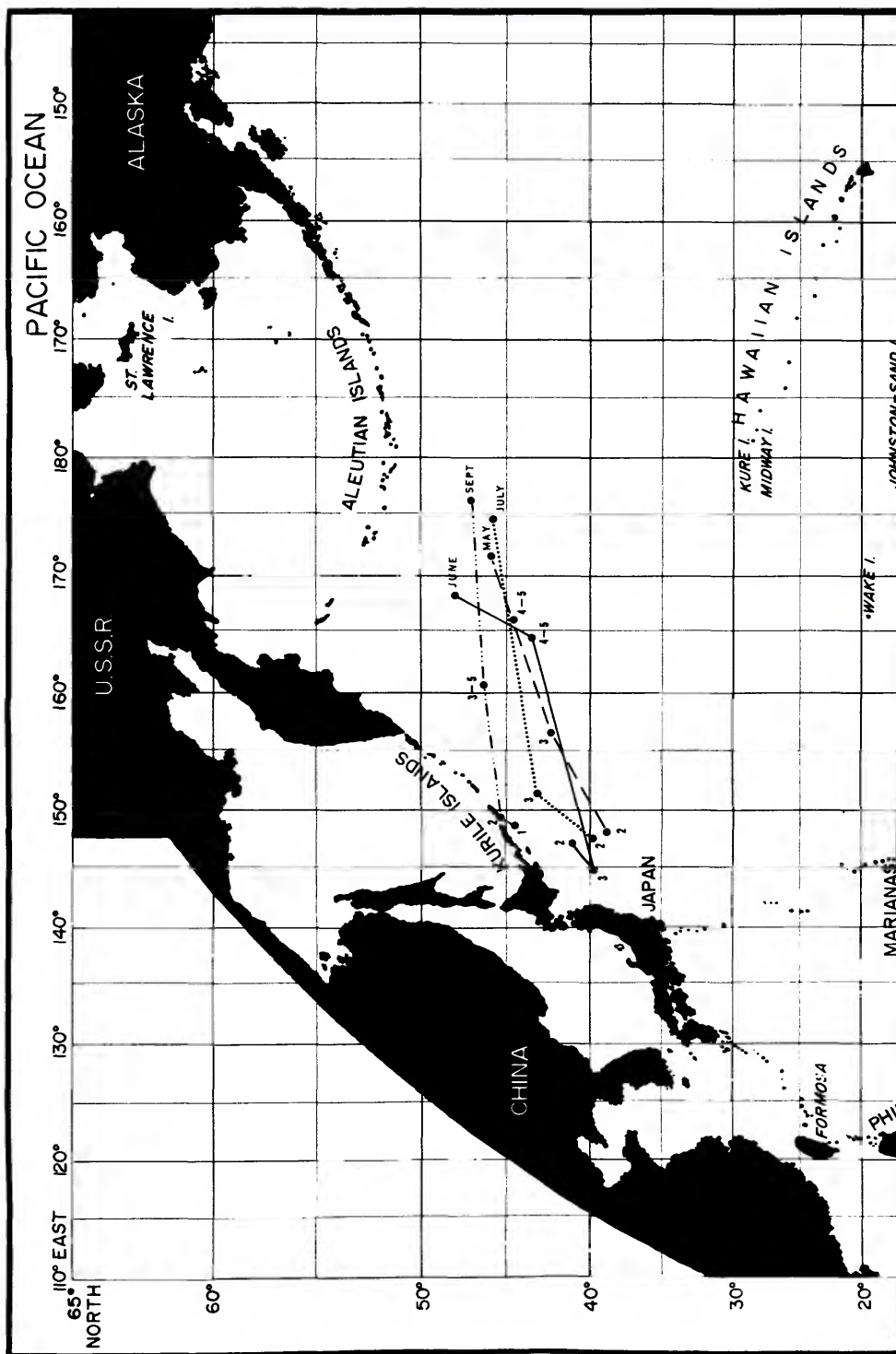


FIGURE 170.—Mean monthly positions of Laysan Albatrosses in summer, by age. The month labels identify the mean positions of adults. Numbers designate the first, second, etc. summer of life. August recoveries (not plotted) of all age classes are concentrated near 150°E.

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