THE OCEANIC DISTRIBUTION OF THE LAYSAN ALBATROSS, *DIOMEDEA IMMUTABILIS*

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THE purpose of this paper is to portray the oceanic distribution of the Laysan Albatross (*Diomedea immutabilis*) as indicated by records in the literature and by recoveries of birds banded by us. An attempt is also made to understand the reasons for the general distribution, as well as for changes associated with season and age.

The distribution of breeding colonies has been reviewed by Rice and Kenyon (1962), but no one has yet attempted an analysis of the pelagic range of the species. Present knowledge of the range is based upon incidental sightings at sea and recoveries of a few banded birds. Several publications list Laysan Albatrosses observed during transects of the North Pacific Ocean (for example, Clark, 1946; Hamilton, 1958; and Cogswell, 1946), and there are regional surveys as by Sanger (1965) off the coasts of Oregon and Washington, by Kuroda (1955) in the northwest Pacific Ocean, and by King (1970) near the eastern end of the Hawaiian Islands.

METHODS

Data used in the analysis consisted of 109 recoveries of birds we banded, 53 published records of birds banded by others, and 113 sight records. Of the 109 recoveries, 64 birds were less than 3 years of age, 23 were 3 to 7 years old, and 22 were adults, including 19 known breeders. No significance can be attached to the relative numbers of the different age classes; we banded several times as many young as juveniles or adults. The sightings date from 1897 (Kaeding, 1905), but most are since 1945. Sight records prior to 1897 were not included because of possible confusion between records of the Laysan and the Short-tailed Albatross (*D. albatrus*) prior to that date. Attempts have been made to verify all records and to eliminate questionable sightings, but data collected over such a long period and by so many different persons are subject to some error. Gathering of data over three-fourths of a century does have one advantage; it tends to smooth out annual vagaries such as Ingham (1959) and Tickell and Scotland (1961) noted in the annual patterns of dispersal of Giant Petrels (*Macronectes giganteus*).

The paucity of verified records (276) spread over the millions of square miles of the North Pacific Ocean is troublesome and in several instances makes impossible more than tentative statements. The problem is ameliorated, however, by multiple records in certain regions. Another question is whether our data reflect the distribution of albatrosses or of persons recapturing albatrosses. A minimum of 69 per cent and a maximum of 89 per cent of the recaptures were made by Japanese tuna fishermen; 9 per cent were taken as scientific specimens. The uncertainty in actual figures arises because the codes used by the U.S. Fish and Wildlife Service to indicate the method of recovery are not mutually exclusive.

This possible confusion as to the distribution being indicated is perhaps immaterial, for we can assume that most tuna fishermen are where tuna are or where tuna can be expected. The evidence also indicates a probable similarity in the distribution of tuna and albatrosses in the North Pacific because both derive a large proportion of their food from squid. Our studies on Midway indicate that at least 90 per cent of the Laysan's diet consists of squid. Nakamura (1965) reported that the main molluscan food item of skipjack tuna (*Katsuwonas pelamis*) in 1957–59 was squid. Waldron and King (1963) found that in Hawaiian waters squid constituted 35 to 83 per cent of the food items of: skipjack tuna; yellow fin tuna (*Neothunnus macropterus*); and bigeye tuna (*Parathunnus sibi*).

In analyzing the variation in oceanic distribution with age, three categories were established: young birds (to 3 years of age); juveniles (3–7 years); and adults (7 plus years). Separation into these classes is based upon differences in behavior. Until they are three or more years old, the young Laysans are at sea and seldom return to the breeding colony (Fisher and Fisher, 1969). Between three and seven years the juveniles establish patterns of return, territories, and pairs. They visit the breeding colony at intervals between January and June. After the age of seven, the birds can be expected to be breeders, or within a year of breeding. They tend to return to the colony initially between November and February. Such differences in the relationship between albatrosses of different ages and the breeding grounds may affect oceanic distribution despite the remarkable flight powers of the albatross.

All oceanic records in the immediate vicinity of the Hawaiian Island breeding colonies were omitted. Records associated with these colonies add nothing to our knowledge of oceanic distribution, and their inclusion in analyses of latitudinal and longitudinal movements or even of distribution introduces a bias. Breeding albatrosses are of necessity restricted in their oceanic travels, although perhaps less than many other species.

Sea-surface temperatures are 20-year means (1947–66) furnished by R. A. Schwartlose of Scripps Institution of Oceanography.

RESULTS

All 276 records reported here lie within the limits of 8 to 59° N lat. and 132° E to 116° W long. Published reports of occurrences within these limits include: 1) 25 sightings off Japan made by Kuroda (1955). Macdonald and Lawford (1954) and Wilhoft (1961) reported incidental sightings in the western and central Pacific area, as did Clark (1946), Dixon and Starrett (1952) and Hamilton (1958); 2) 11 sightings around the Aleutian Islands made by Kenyon (1961), Kuroda (1955), Macdonald and Lawford (1954), and Murie (1959); 3) Sight records off the west coast of North America by Sanger (1965), Love (1958), Willet (1913), Stager (1958), Thompson (1951), McHugh (1950), Kenyon (1950), Fredrich (1961), Holmes (1964), Kaeding (1905), and Yocum (1947); and 4) Occurrences around the Hawaiian Islands and other eastern North Pacific islands were recorded by Fisher (1948), Munro (1945, 1946), Hanson (1959), Jensen (1949), Cogswell (1946), Eastman and Eastman (1958), and Thompson (1951).

Few Laysan Albatrosses have been found south of approximately 28° N, except around the breeding colonies which are essentially between 28 and 22° N. According to Amerson (1969), Laysans are "accidental on islands in the

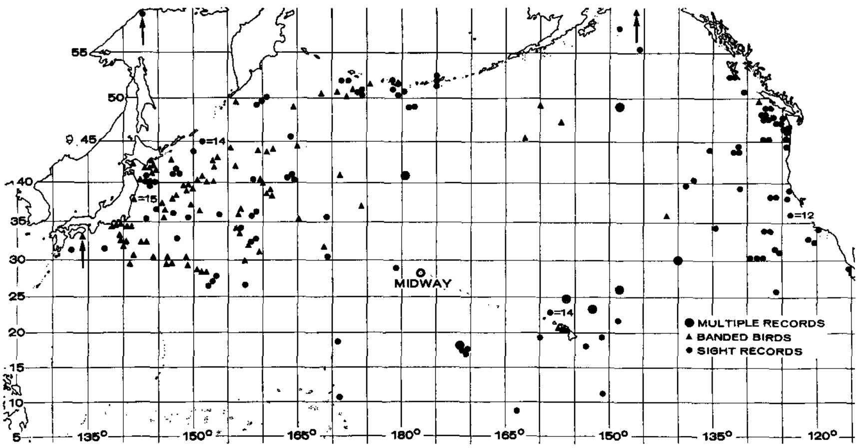

FIG. 1. Records of Laysan Albatrosses in the North Pacific Ocean: sight records and banded birds more than 3 years of age.

northern Marshalls [approx. 13° N] probably at-sea-visitor." However, he reported a Laysan Albatross at Mejit Island in the Marshalls, 10° 17′ N and 172° 52′ E. And there is the lone record at 8°. Dixon and Starrett (1952) stated that Laysans are "Noted south of 30th parallel only to eastward of Wake Island." Baker (1951) in his review of Micronesian ornithology reported no records of Laysan Albatrosses in the Micronesian Islands.

The plot of all the sightings of birds of unknown age and of recaptures of our banded birds more than three years of age (Fig. 1) indicates that the primary oceanic range of the Laysan Albatross lies between 28 and 52° N and

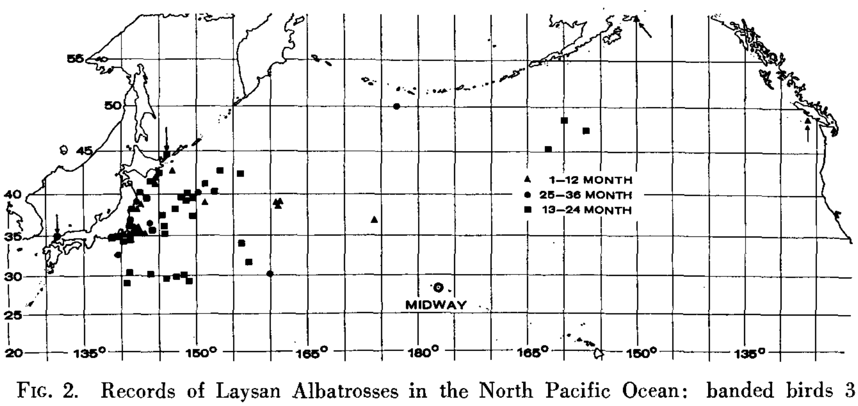

FIG. 2. Records of Laysan Albatrosses in the North Pacific Ocean: banded birds 3 or fewer years of age.

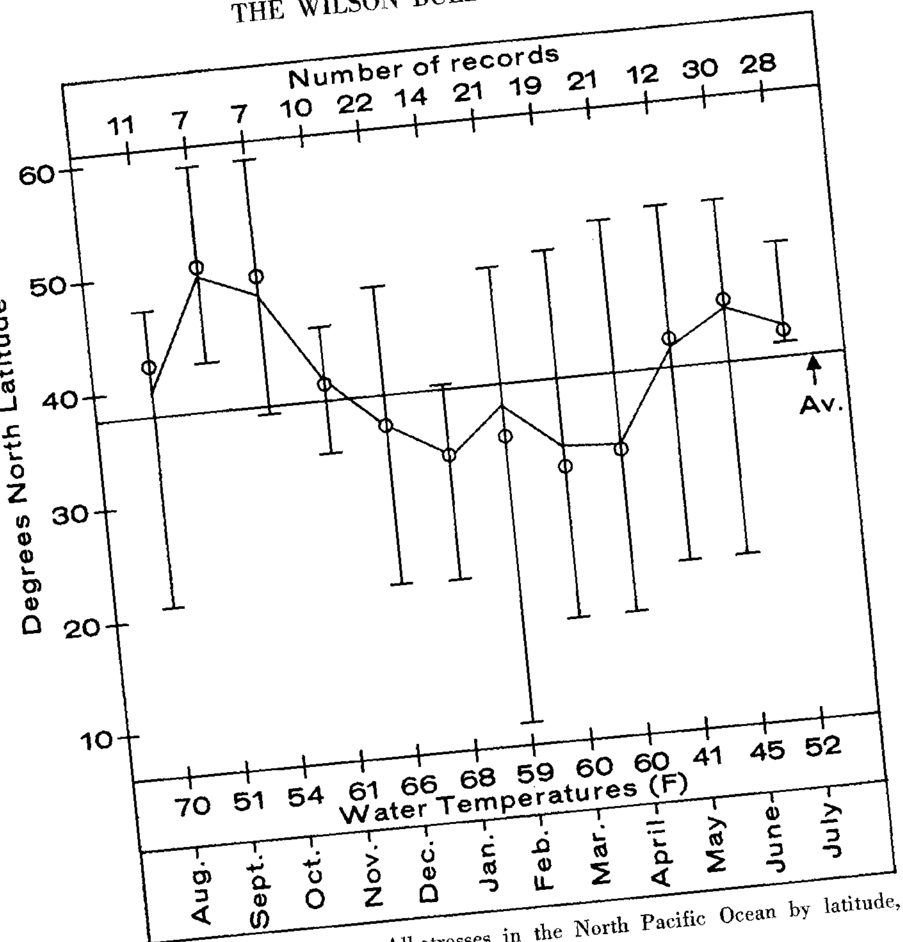

FIG. 3. Distribution of Laysan Albatrosses in the North Pacific Ocean by latitude, month and surface water temperature: birds of all ages.

between 140° E and 120° W. This area includes 83 per cent of all records. Within this general range are four areas of concentration: 1) east of Japan and the Kurile Islands; 2) south of the western Aleutians; 3) off the west coasts of British Columbia and the United States; and 4) at sea around the eastern end of the Hawaiian Islands.

Certain regions contiguous to the general range have few or no instances of sightings or recaptures of Laysans: 1) the Sea of Okhotsk and the Sea of Japan; 2) the Bering Sea; 3) west of lower California; and 4) a vast circle of ocean between the eastern Aleutians and the Hawaiian Islands, centering at 40° N and 170° W. The only evidence of Laysan Albatrosses in the seas west of Japan consists of the recovery of a banded bird off the southwest coast

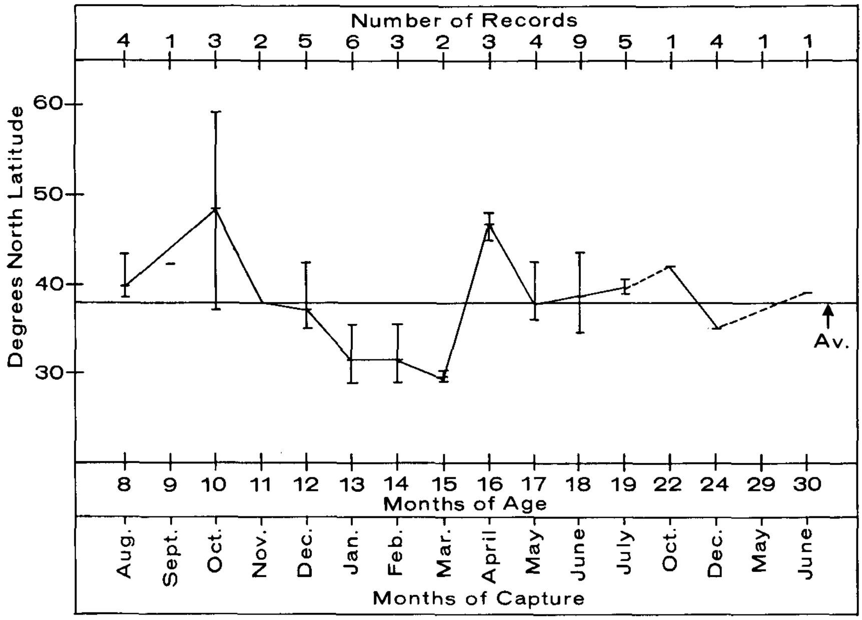

FIG. 4. Distribution of Laysan Albatrosses in the North Pacific Ocean by latitude, month and age: banded birds less than 3 years of age.

of Japan and another off the city of Okhotsk. Dement'ev et al. (1951) reported that the Laysan is a casual straggler "in Russia" but listed as evidence only one Laysan obtained in Kamchatkan waters. Kenyon (1950) reported no certain records in the Bering Sea, and Arnold (1948) and Kuroda (1955) saw no Laysans north of the Aleutians.

Records of birds three or fewer years of age are concentrated (87 per cent) in an area east of Japan and roughly bounded by 30 to 45° N and 140 to 160° E (Fig. 2). With only two exceptions, all birds recaptured at a year or less of age have been between 35 and 45° N and 140 and 175° E.

Seventy-two per cent of the 3- to 7-year-old birds recaptured (23) were in this area, and 17 per cent were nearby. One bird in the Aleutians and one in Hawaiian waters represented the records most distant from the concentration.

Although the 22 banded adults were recaptured in widely separated places, two-thirds were in this same area east of Japan.

The mean latitude of all recaptures or sightings is 38° N. The monthly mean latitude of these records and the 20-year means of sea-surface temperatures at these mean latitudes are shown in Figure 3. From May through November the albatrosses are most frequently north of 40° N and in temperatures of 41 to

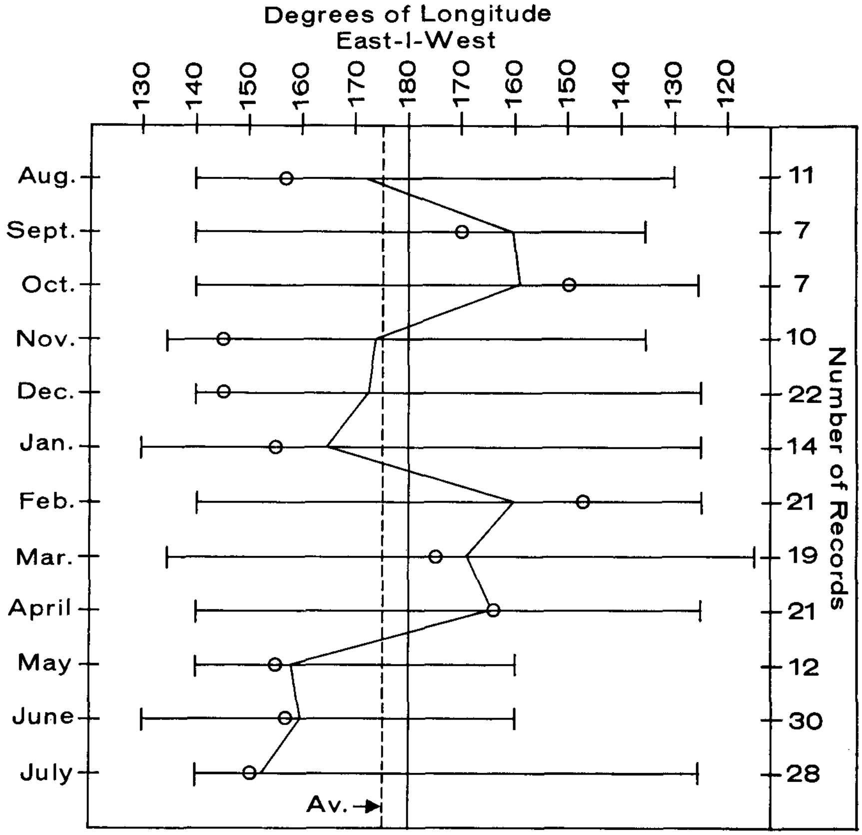

FIG. 5. Distribution of Laysan Albatrosses in the North Pacific Ocean by longitude and month: birds of all ages.

61° F (except in August). From December into April the majority of the albatrosses are south of 35° N and in water temperatures of 59 to 68° F.

Albatrosses less than three years of age exhibit essentially the same seasonal shift in latitude (Fig. 4). However, in their first 12 months (excluding, of course, approximately 5 months in the natal colony) the young birds are found mostly north of 38° N. Although they are south of this during the winter months at the beginning of their second year, none have been retaken below 30° N. They shift north a full month ahead of the older birds (March versus April, Figs. 3 and 4, respectively).

When the recaptures and sightings of all albatrosses are plotted by month and mean longitude (Fig. 5), the average longitude of occurrence appears to be 176° E. Seasonal shifts are apparent. From May through August and from

November through January the majority of albatrosses are found between 150 and 160° E; from February to April and from September–October most are found between 155 and 175° W.

DISCUSSION

General Considerations.—The Laysan Albatross ranges in significant numbers over most of the North Pacific Ocean north of 28° N and exclusive of the contiguous seas to the west and north. Continental land to the northwest, east, and northeast is an obvious barrier to this pelagic species. Islands to the north and west may function similarly, as is discussed later. But no land masses, even intermittent ones, delimit the southern extent of the range.

It is suggested that food is the most important single factor in determining the southern limits of the range and the relative abundance of Laysan Albatrosses within the range. Such a positive correlation between the occurrence of oceanic birds and their food supply is not new, of course. Kurochkin (1963), for example, regarded food as a primary determinant of distribution for many species including several procellariiform species. Voous (1965) stated that the distribution of many antarctic birds corresponded with the distribution of surface plankton. The papers of Jameson (1961) and of Gibson and Sefton (1959) on the Wandering Albatross (*D. exulans*), of Thompson (1951) on the Black-footed Albatross (*D. nigripes*) and of J. Fisher (1952), Salomonsen (1965), and Brown (1970) on the Fulmar (*Fulmarus glacialis*) also emphasized the importance of plankton.

With these views in mind, and recognizing that Midway Laysans obtain 90 per cent of their food from plankton-feeding squid whose distribution is less known than that of plankton, it is logical to relate the occurrences of plankton and these albatrosses.

Four factors directly and indirectly affect the volume of plankton in an area—nutrients, water movements, water temperature, and water salinity. Water movements, as in currents, convergences of currents, and upwellings, affect available nutrients, temperature, and salinity. Any type of turbulence that mixes deep and surface layers of the sea increases the availability of nutrients in the surface layers and lowers temperatures, and both actions are basically favorable to the growth of plankton. It is also established (Marr, 1956, for example) that the larger euphausids upon which both squid and albatrosses feed occur primarily in the near-surface, eutrophic waters and are virtually limited to cold currents. Thus, Laysans, plankton, squid, certain temperatures, and turbulence should coincide in their distribution. The available data support this view.

Laysan Albatrosses occur most frequently and in larger numbers where water temperatures range from 40 to 65° F (King, 1970, said below 72° F),

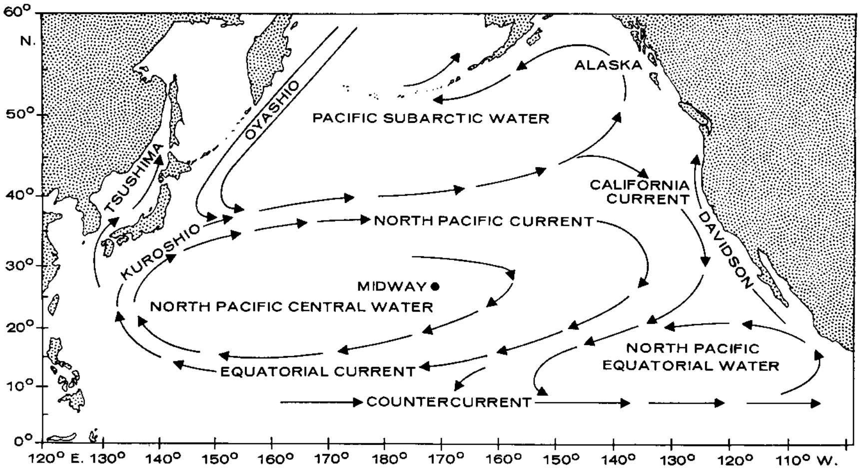

FIG. 6. Major water masses and currents in the North Pacific Ocean.

although the temperature variance over their general range is 36 to 84° F. And this temperature zone of preference coincides with the zone of highest plankton productivity—between 28 and 35° N (King and Iversen, 1962). In this zone, the south edge of the North Pacific Current, they obtained approximately 14,500 organisms per hour of trawling. North of 35° and in the Aleutian area the catch was 9,500 per hour. Between 28 and 5° N (Hawaiian and North Equatorial waters) King and Iversen reported less than 500 organisms per hour.

Therefore, the southern limit of the range of the Laysan Albatross appears to be formed by a major drop in the abundance of food organisms. Temperature may be the primary factor, but salinity may also be significant as Sanger (1970) suggested for the offshore waters west of North America. King (1970:96) stated that albatrosses "... tended to be most numerous over high-salinity water. . . ." but later ". . . it appears unlikely that surface salinity is a significant limiting factor in the distribution of sea birds in the study area." However, Seckel and Yong (1970:191) noted that "Hawaii is located in the vicinity of a relatively high salinity gradient that delineates the boundary of the North Pacific Central Water." The southern limit of the range of the Laysan thus appears to coincide with major, though gradual, changes in temperature and salinity. The limit can also be identified as the northern edges of the westward-trending Equatorial Current west of the Hawaiian Islands and of the North Pacific Equatorial Water between Hawaii and Central America (Fig. 6).

The correlation of turbulence and records of Laysan Albatrosses, mentioned earlier, is discussed in connection with the four major concentrations of birds (p. 15–18).

Extralimital areas.—The few records west of Japan and the Kuriles, north of the Aleutians, and west of Lower California, despite the presence of numerous fishing boats (Ommaney, 1963) which have been the main source of records elsewhere, support the hypothesis that these areas are indeed outside the regular range of the species.

The Japanese, Kurile, and Aleutian islands may form partial barriers to the seas behind them, since these albatrosses do not normally approach land other than that of the breeding grounds. Even more significant is the fact that to reach these outer, fringe areas an albatross would have to pass through or over rich seas which are presumably attractive feeding grounds for the species. It is probable that the Tsushima Current just west of the Japanese islands, with its warmth and its low productivity (Sorokin and Koblentz-Mishke, 1958), is a major deterrent to the Laysan Albatross. The warm North Pacific Equatorial Water west of Lower California may be a similar factor.

The Central North Pacific area, in the south edge of and just south of the Pacific Subarctic Water (Fig. 6), also lacks significant numbers of records. Less than 10 per cent are from this several-million-square-mile region which is devoid of strong currents, turbulences or upwellings and which is lower in plankton productivity than the regions to the north or south (King and Iversen, 1962). The occasional records within this vast expanse of sea are in either the fringes of the Aleutian Current or the eastward extension of the North Pacific Current, and the birds may be assumed to be vagrants from the richer areas near the source of these currents. However, the scarcity of records may reflect the lesser human use of this region, despite our earlier discounting of this possibility for other parts of the North Pacific.

Areas of concentration.—Four major concentrations of albatrosses are evident on Figure 1: 1) east of Japan; 2) south of the western Aleutians; 3) west of North America; and 4) around the larger, eastern islands of Hawaii.

There are reasons for the Laysan Albatrosses to be numerous in each of these areas. In each instance the conditions within the region of the concentration are generally constant from year to year within a certain range of coordinates. Bourne (1967:141) has noted that seabirds ". . . are normally restricted to very limited sea-areas by strict preferences for certain types and temperatures of surface water. . . ." Bailey (1968) noted this same phenomenon among seabirds in the western Indian Ocean. The Laysans apparently respond to permanently profitable foraging areas and do not utilize intermittent, locally enriched seas. The first reason may be the time and space lag between surface enrichment and the resulting production of suitable food. Secondly, the exigencies of amount of food, of time, and of distance probably make it impossible for the Laysans to rely on spotty food resources during such critical times of the year as the immediate pre-egg stage and the chick-feeding period (Fisher, 1967). And last, species in which each member is so closely restricted to its own island and natal colony for breeding (Fisher, 1971*b*) might be expected to be similarly related to its feeding areas.

The major concentration of records is east of Japan where the cold waters of the Oyashio Current collide with the warmer waters of the Kuroshio Current (Fig. 6). The resulting turbulence and many eddies occur between 35 to 40° N and 140 to 160° E (Seckel, 1970) and subside into the North Pacific Current still farther east. This region has been identified by Koblentz-Mishke (1965, Fig. 2) as having the greatest primary production in the North Pacific Ocean. More than a third (36 per cent) of the records are within the longitudinal limits of the turbulence and 30 to 45° N. Nearly half (45 per cent) are here, if sightings and recaptures on the immediate fringes of the region are included. Kuroda (1955) said of the Laysan in the northwest Pacific "This species was most plentiful 180–200 miles eastsoutheast of Shinshiru Island, where we saw 14 birds in one day." This is within the area of turbulence. Because of the turbulence and the consequent abundance of nutrients, plankton and squid occur year-round, with only minor seasonal changes, and the albatrosses find a plentiful food supply which they exploit constantly.

Although the second area of concentration, the western Aleutian region, includes only 7 per cent of the records, we believe the Laysan Albatross uses this area more extensively than the data may indicate. One reason is that Laysans tend to move into cooler waters during the summer months where plankton and presumably squid, are seasonally more abundant (King and Iversen, 1962). Another is that the Aleutian Current courses northeastward through the islands while the Oyashio comes southward in the western part of this region. Such flows may produce major eddies and turbulence and rich waters around islands (Wyrtki, 1967), as has been demonstrated behind the islands of Johnston and Hawaii (Manar, 1969). Larrance (1971) has noted the higher primary productivity in Aleutian coastal waters, as compared to areas to the south. Bourne (1963:836) also noted the higher productivity of seas around islands. The Aleutian region thus has all the features of a major seasonal feeding ground.

Along the west coast of North America (120–140° W and 30–50° N) is the third concentration (25 per cent of the records). Only two of our banded Midway birds have been found here. Few of these North American records are inshore, and winter reports are negligible. It appears that the Davidson Current, which in winter flows north along the coast to about 48° N, rather than the continental shoreline, forms the eastern boundary of the Laysan range in these latitudes. The Davidson and the various northward extensions of the North Pacific Equatorial Water are probably responsible for the absence of Laysan Albatrosses in the area south of 30° N and east of 145° W. The warmth of this water and its low oxygen and salinity are not typical of waters frequented by albatrosses.

Considering the amount of ship traffic, the number of scientific voyages, and the number of persons involved here in the past 75 years, it is apparent that this is a lesser concentration of Laysan Albatrosses than occurs east of Japan. Although these offshore waters are reportedly rich and upwellings are prevalent from March through July (Sverdrup et al., 1942), there are a number of reasons why albatrosses may occur here less frequently. 1) The richness of these waters, as in the Aleutians, may be only seasonal and also considerably less because of the admixture of warmer, southern waters. 2) It has been suggested that Laysans avoid waters of low salinity, as found at least off Oregon (for example, Sanger, 1970). 3) Prevailing winds and water currents are not as advantageous for movement to and from this area as to the waters off Japan, and the distances are greater. 4) Another possibility about which we known little is that Laysan Albatrosses breeding on different islands may go to different parts of the ocean. Tickell found some indication of this segregation in young *D. melanophris* (1967) and in *D. exulans* and *D. epomophora* (1968). Our data indicate that Midway birds are for the most part (90 per cent) recaptured west of 180°. However, nearly half of all known oceanic records of Laysans (117 of 276) are east of the date line. This could be an indication that Laysan Albatrosses breeding in the western end of the Hawaiian Chain move northwest to sea and the Japanese or Aleutian concentrations and that albatrosses breeding farther to the east move into either the Hawaiian or North American concentrations referred to earlier. However, the picture is clouded by the fact that virtually all Laysans now breed east of 180°. 5) There is still another explanation for the lesser number of recaptures and sightings off the North American coast. At least 61, and perhaps 85 per cent since reporting techniques vary, of the recaptures were made by fishermen. The Japanese tuna fishermen of the western and central Pacific are predominantly surface fishermen of the open sea, and they recapture albatrosses on their long-line sets of tuna hooks or in their surround nets. Fishing in the far northeastern North Pacific, aside from a minor component of surface trolling for sport fishes, is closer inshore and directed more toward deeper dwelling fishes. Hence we should not expect as many albatross recaptures in these waters as in the Japanese area, even though the number of birds and fishermen were the same as in the western Pacific.

Nevertheless, a significant number of Laysan Albatrosses have been recorded in the cool offshore waters of North America, waters formed by the California Current or the lower limits of the Aleutian Current.

Ten per cent of our Laysan records are from the fourth area, the vicinity of the five large, easternmost islands of the Hawaiian Chain, all of which are east and south of the primary sea range indicated earlier. Several factors, some factors unique, some perhaps common to other concentrations, may influence the number of birds observed here. This concentration is no more than 800 miles from the breeding grounds, compared to 2,000 miles for the Japanese concentration, 1,200 for the Aleutian area, and the nearly 3,000 miles between the American concentration and the breeding grounds. There are major water eddies, turbulence and subsequent rich waters in the lee of these large Hawaiian islands (Manar, 1969), which may provide adequate feeding grounds in the otherwise generally unproductive Hawaiian waters (King and Iversen, 1962). A large fleet of sportfishing boats and an active Audubon Society probably increased greatly the number of sight records. But the concentration of Laysan Albatrosses appears to be factual, and the primary reason may be that the North Pacific Current, which turns southward at about this longitude (Fig. 8), brings cooler, more productive water and Laysan Albatrosses with it. And the prevailing northeast trade winds, moving essentially parallel to this current, may further influence albatrosses to move southward into this region.

Because of this Hawaiian concentration it is necessary to extend the primary oceanic range of the Laysan south to 20° in the region of 155° W long.

Distribution by age.—Eighty-seven per cent of the 64 young birds were recovered in and around the Oyashio-Kuroshio turbulence east of Japan. The 13 per cent retaken outside this area are considered to be exceptions. Other than the two occurrences west of Japan, the sites of recapture are ones to which inexperienced birds may well have been transported by ocean currents (Figs. 2, 6).

The offshore waters of Japan constitute a nursery area, at least for Midway birds, in which the young remain until they begin their annual visits to the breeding colonies (Fisher and Fisher, 1969). Tickell (1967) reported similar concentrations of *D. melanophris* in their first 3 years of age. While adults are commonly recaptured on both sides of the Atlantic, Falkland Islands young go to the western Atlantic and South Georgia young move into the eastern Atlantic. Within a few months of fledging, Fulmars from West Greenland and St. Kilda go to the Newfoundland Banks (J. Fisher, 1952:325; J. Fisher and Lockley, 1954:138). And Robertson has suggested recently (1969) that young Atlantic Sooty Terns (*Sterna fuscata*) may congregate in the Gulf of Guinea in Africa while those of the Pacific assemble in the central Philippines. It seems probable that as we learn more of the oceanic distribution of seabirds of different ages we shall discover that many species exhibit at least a partial segregation by age which reduces intraspecific competition.

Factors other than the richness of these Japanese waters are important in attracting young Midway Laysans. The area is closer to Midway than is any other known and abundant food source, and it is more easily reached by inexperienced birds with relatively poor powers of flight. As the young bird leaves Midway it is subjected to westward trending water currents (Fig. 6) and generally consistent winds from the east-northeast sector (U.S. Naval Oceanog. Office, 1966). As it rests or feeds on the water it is carried west by south; its weak flight is greatly affected by the wind, and the bird in the air also drifts southwest. Should it drift too far to the south, another factor increases the rate of its westward trend—the westerly flow of the Equatorial Current. One might compare this latter current to a drift fence along which the young birds move until they reach the Kuroshio Current which then moves them north to the nursery area. Conditions in these critical months of July–September may be particularly advantageous to these birds. King and Hida (1957) obtained their largest plankton catches then and reported that surface catches at night were 1.5 times as large as in daytime. These data may mean that not only are the squid attracted to the abundant food, they are attracted presumably in greater numbers to the surface and at night. This, of course, means greater accessibility for the initial foraging efforts of the young birds. The abundant supply and greater availability of suitable food organisms to inexperienced birds could be expected to hold the birds there until initial sexual development stimulates them into migratory patterns.

The 23 juveniles were recaptured at sites more widespread than those of young birds, but 72 per cent were taken in the rectangle described as the nursery area. An additional 17 per cent were retaken nearby. Thus even juveniles, most of which have already made one or more trips to the Midway breeding colonies, return to the offshore waters of Japan.

The 22 adults were widely scattered at the time of recapture, but 68 per cent were secured off Japan. One was recovered off California, one in the Hawaiian area, and four in the Aleutians. Since 19 of these adults were known to have bred on Midway, it is plausible to suggest that a majority of Midway's breeders return at times to feed in this area. It is unfortunate that we did not know the current breeding status of each of these adults, for then we might know whether they move between the breeding colony and this area during the nesting season. Other studies in progress show that Midway adults feeding chicks may fly east and north at least 1500 miles.

It is evident that Midway birds of all ages feed in the turbulent convergence of currents east of Japan, that a high percentage remain there for the first three years of life, that juveniles return there as they initiate periodic visits to the breeding colony between the ages of 3 and 7 years, and that many of Midway's breeding Laysan Albatrosses feed there at least from time to time.

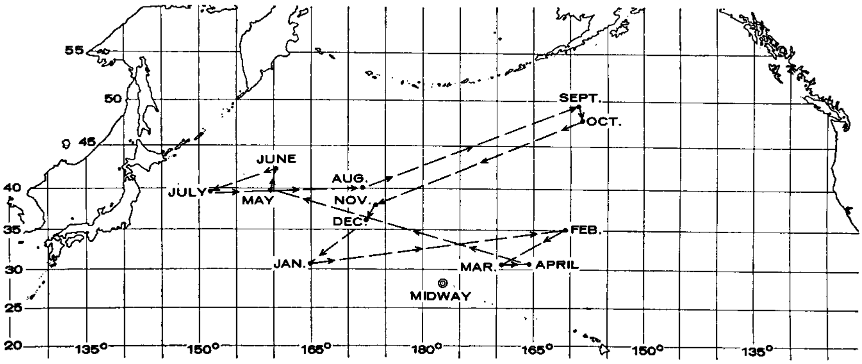

FIG. 7. Distribution of Laysan Albatrosses in the North Pacific Ocean by latitude, longitude and month: mean locations of birds of all ages.

Seasonal distribution.—Figure 5 illustrates the occurrence of four periods of longitudinal shift: eastward (into west longitude) in January and August and westward in April and November. In Figure 3 three latitudinal shifts are shown: northward in April–May and August–September and southward in October–December. Figure 7 is an attempt to portray graphically the combined results of the longitudinal and latitudinal shifts for birds of all ages. We believe the directions of movement are accurately shown, but the extent of the shifts is probably unduly influenced by the use of averages including extreme records.

Starting in August, the first month of the year in which no Laysans are involved with reproduction, there is a shift in concentration toward the northeast along the North Pacific Current and perhaps into Pacific Subarctic Water. This continues until October. The birds move from water near 70° F into 50-degree and presumably more productive water. In November the birds are back in the central reaches of the North Pacific Current where the sea-surface temperatures are now in the low 60s. In December and January the albatrosses are near 30–35° N and 170° E where temperatures gradually climb into the upper 60s. The birds then move eastward, with no change in latitude, to 165° W where water temperatures are 60° or below. The birds are probably in the same water as in December–January, water that has cooled as it moved eastward in the southern fringe of the North Pacific Current. In April the move is west and north to the 40–50° F waters east of Japan, waters brought to this temperature by the cold waters of the Oyashio Current. The albatrosses remain until late July. In all the above statements we are referring to "average moves," not necessarily to movements of the entire populations.

It might be suggested that Figure 7 reflects at least in part the movements to and from the breeding grounds. And one might justifiably speculate, on the

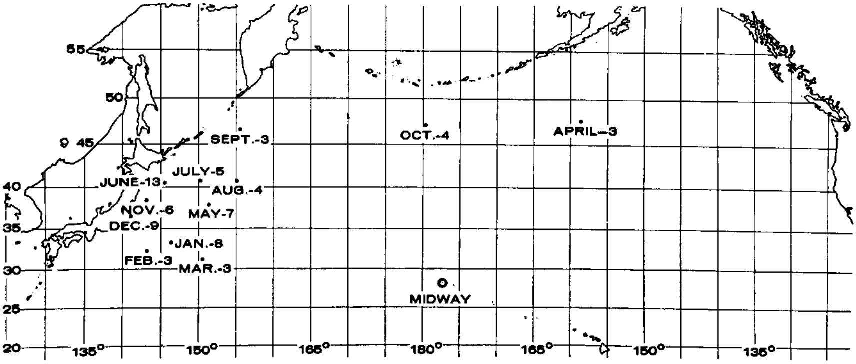

FIG. 8. Distribution of Laysan Albatrosses in the North Pacific Ocean: mean location of birds 4 or fewer years of age.

basis of this study and published information on the biology of the Laysan Albatross, that: 1) virtually all of the birds less than 3 years of age are in the May–July plotting; 2) the August to November roundtrip is made mostly by breeders, along with some older juveniles; and 3) the December to May plotting consists primarily of breeders, with 3- to 7-year-olds contributing to the March to May portion (Fisher and Fisher, 1969). It is perhaps equally logical, with regard to the December–May period, to suggest that incubating birds (November–January) with their longer periods of relief from nest duties (8–20 days, Fisher, 1971*a*) can subsist in less productive areas. But when the food requirements of the chick are added to those of the foraging parents and when the total time for travel and foraging between chick feedings averages 2 days (February–April) the adults shift eastward to presumably better food sources. Also during this time, nestling mortality has released additional parents and the chicks are fed smaller amounts and less frequently, as evidenced by the fact that their weight declines after May (Fisher, 1967). These factors may permit failed or even current breeders to move northwest in April and May.

However, we believe that the movements of breeding birds are not significantly involved in the conclusions to be reached from study of Figure 7. First, the Laysans four or fewer years of age show the same directional shifting (Fig. 8), and most of these are not yet making their periodic visits to the natal colonies. Second, only 37 per cent of the banded portion of the sample is of an age to visit the colony or to breed. And third, Laysan Albatrosses in short periods of time are capable of traversing distances greater than those involved in the latitudinal shifts. Kenyon and Rice (1958), for example, showed that Laysans removed from eggs or young chicks home at the rate of nearly 200 miles per day.

Furthermore, evidence from the literature, though scanty, tends to support the concept of these movements and concentrations. King (1970:9) in recording Laysan Albatrosses at sea east of the Hawaiian Islands and between 10 and 25° N and 148 and 150° W, gave their status as "Uncommon visitor February–April, rare or absent May–January." He also noted that the decline in numbers in April was accompanied by ". . . a contraction of range to the northern end of the study area."

Amerson (1969:293) wrote of the Laysan "Found at sea normally south to 15° N in the Central Pacific during the *breeding seasons*. . . ." [italics mine], thus indicating his belief in a seasonal shift. However, his reasons were not stated, and we now know that Laysans seldom penetrate this far south.

The northward movement of the albatrosses in summer may well be related to the seasonal northward advection of southern water into the latitudes of the Hawaiian Islands (Seckel and Yong, 1970). This advection brings warm water of lower salinity into the southern part of the albatross range.

The observations of McHugh (1950), Holmes (1964), and Sanger (1970) that Laysan Albatrosses were more abundant off the North American coast "in winter" lends some strength to our view of eastward shifts in February and March.

Hamilton's observations (1958) during a June transit west to east and between 35 and 48° N tend to substantiate the midsummer concentration around the 40th parallel.

Austin and Kuroda (1954) believed that the Laysan was a regular visitor off the Pacific coasts of Honshu and Hokkaido from early spring to late autumn, and Kuroda (1957) said that it arrives off Japan in March. We presume he meant greater numbers were present there at that time. It is probable that this influx is of young birds which we think move north in March (Fig. 4). He further wrote (p. 448) of a "post-breeding movement northward in spring." This may correspond to the April shift or perhaps the greater occurrence off Japan in July. He indicated this was a movement with the northward trend of the warm Bonin Island Air Mass. We regard it as a seasonal movement away from the increasingly warm waters of the Kuroshio Current. The average water temperatures in July drop from 81° F at 30° N to 53° F at 45° N in these longitudes, and Kuroda had earlier (1955) stated that the Laysan ". . . seems to avoid water above 13° C." In 1960 he indicated that the Laysans congregated off the Kuriles in June and July at sea temperatures slightly above 40° F, which is in basic agreement with the data in Figure 3. He did not find many Laysans in either the colder or warmer waters of this region. Szijj (1967) noted that albatrosses in southern seas were most numerous at water temperatures between 6 and 13° C.

The implication is that Laysans seek out these temperatures, for one reason or another, probably food. It is probable that the Laysan adult, like the Fulmar (J. Fisher, 1952:325; Brown, 1970; and Salomonsen, 1965), regularly moves to a food source that is adequate, accessible and predictable on a time and place basis. This seasonal phenomenon is also reported for the Wandering Albatross (Tickell, 1968; Gibson and Sefton, 1959, 1960; and Jameson, 1961). Dixon (1933) and Tickell and Gibson (1968) believed that Wanderers, especially those of pre-breeding age, had a regular migratory path between South Georgia and the sea off New South Wales. And Gibson (1963: 216) has said of the Wanderer: ". . . when free from breeding commitments at their home islands, these birds returned regularly to an assured natural food supply, contrary to the generally held conception of a free-ranging ocean wanderer unbound by conventional migrations." The Royal Albatross regularly moves between Campbell Island and South America (Dixon, 1933; Tickell, 1968). Falla (1963) noted that "several albatrosses" breeding in the Subantarctic moved into colder waters in late summer, a shift perhaps comparable to the September–October move of Laysans.

Our data (Fig. 7) do not support Bourne's view (1967) that seabirds tend to move clockwise around anticyclonic stationaries in the middle latitudes of the Northern Hemisphere.

SUMMARY

All 276 oceanic records of Laysan Albatrosses are within the limits of 8 to 59° N and 132° E to 116° W in the North Pacific Ocean. The primary range, however, is between 28 and 52° N and 140° E–120° W.

The northern boundary of their distribution is the Aleutian Islands and the relatively non-productive waters of the Bering Sea. The Kurile and Japanese islands, along with the warm Tsushima Current, constitute a western barrier. The North American continent with its warm inshore Davidson Current forms the eastern limit. The southern border is marked by warm equatorial waters of low salinity and low productivity.

Within these limits Laysan Albatrosses tend to congregate in four regions: 1) east of Japan (35–40° N and 140–160° E); 2) south of the western Aleutians (50° N and 165° E–175° W); 3) off the west coast of North America (30–50° N and 120–135° W); and 4) near the large, eastern islands of Hawaii (20° N and 150—160° W).

The Japanese region serves as a nursery foraging area for birds fewer than 4 years of age; seldom are they recaptured elsewhere. However, older juveniles and adults from Midway also return there to feed.

There is evidence of seasonal shifts in concentrations; the birds move east in January and August, west in April and November; they move north in April–May and in August–September, south in October–December. In general these movements are associated with changes in surface water temperatures.

Laysan Albatrosses tend to be associated with turbulent seas, eddies and currents; the birds most frequently are in water temperatures of 40 to 65° F. Such waters are generally most productive, and it is suggested that food is the primary determinant of the Laysan's distribution.

ACKNOWLEDGMENTS

It is impossible to thank individually the many persons who have so obviously contributed to this study, but our appreciation is no less sincere. We do want to note particularly the contributions of the unknown men of the Japanese tuna fleet, for without their cooperation in recapturing significant numbers of albatrosses at sea this study would have been impossible.

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Unfortunately, we did not know of the significant report by V. P. Shuntov (Zool. Zhurnal, 47:1054–1064, 1968) until after our paper was in press. His study of the distribution of the Laysan Albatross, based on approximately 800 records obtained at sea over a 10-year period, is in nearly complete agreement with ours in relation to basic distribution and its correlation with land masses, oceanic currents and primary productivity, to major areas of concentration, to temperature preferences, and to seasonal movements. The major difference is that Shuntov found a summer and fall penetration of the western and southern parts of the Bering Sea by significant numbers of Laysans and lesser numbers throughout the Sea of Okhotsk in these seasons. We thank Dr. Isaac Shechmeister of Southern Illinois University for translating this article for us.

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