POST-BREEDING MOVEMENTS AND MORTALITY IN THE WESTERN GULL, *LARUS OCCIDENTALIS*

MALCOLM C. COULTER[1]
Point Reyes Bird Observatory
Box 321
Bolinas, California 94924

Many species of birds move away from their breeding areas during the nonbreeding season. This movement may involve long or short distances; it may be migratory or random. In some species the pattern differs among breeding populations. Populations of the Fox Sparrow (*Passerella iliaca*) that breed in different localities also migrate to different localities (Swarth 1920). The Great Cormorant (*Phalacrocorax carbo*), although nonmigratory, shows post-breeding, colony-specific dispersal tendencies (Coulson and Brazendale 1968). These differences also have been shown in some colonial birds whose colonial habit conveniently divides them into discrete, locally concentrated populations. For example, Eaton (1933, 1934a, b) discussed the differences among different colonies of Herring Gulls (*Larus argentatus*). Herring Gulls also show age-specific dispersal patterns (Eaton 1933). Young birds from New England frequently winter along the Gulf of Mexico while adults remain near the breeding area.

The Western Gull (*L. occidentalis*) which nests colonially, also offers a unique opportunity to study geographic and age-related differences in patterns of movement. Woodbury and Knight (1951) and Devillers et al. (1971) have suggested the existence of geographic differences in post-breeding movements. The breeding range of this gull (A.O.U. Check-list 1957) extends from southern British Columbia south to the tip of Baja California and into the Gulf of California. It is the only gull that breeds along this coast, its range slightly overlapping that of the Glaucous-winged Gull (*L. glaucescens*) in the north and that of the Heermann's Gull (*L. heermanni*) in the Gulf of California. It rarely wanders inland, and then only along large rivers (Devillers et al. 1971), and it does not wander far from land (Sanger 1973). It is found along a narrow, coastal band which runs largely north–south.

Since the late 1920s, Western Gulls have been banded along the West Coast of the United States and northern México. Ferris (1940) reported on birds he banded on Haystack Rock, Oregon, from 1930 to 1937. Woodbury and Knight (1951) reported on results of later banding done by Ferris and compared them with results of banding on Los Coronados Islands, México, between 1938 and 1940. Since 1940, there has been much additional banding on the Channel Islands and on the Farallon Islands off California. Enough data are now available to allow for geographic and age comparisons of the birds' movements.

METHODS

The U.S. Fish and Wildlife Service Bird Banding Laboratory provided information on all Western Gull banding recoveries through 1968. The Point Reyes Bird Observatory provided records of birds banded on the Farallon Islands by their personnel through 1971 and of color-banded birds sighted in 1971. I disregarded recoveries of all birds banded outside the breeding season or banded in other than a breeding colony. Because I was interested in movements during the nonbreeding season when the populations are absent from the breeding sites, I analyzed only the returns from September through March.

I considered three localities: Haystack Rock, Oregon, Farallon Islands, California, and the Channel Islands, southern California and northern México. The first two maintain single breeding colonies. The last includes a number of closely situated islands; data from these were combined to increase sample size. Table 1 lists the number of recoveries for each breeding area.

Most recoveries were from the United States. The lack of recoveries from Canada and México probably is due to the sparseness of human populations north of Vancouver Island and over most of Baja California. My results, therefore, are based largely on movements along the coast of the United States.

Unless otherwise specified, the statistical test used was a Mann-Whitney U Test.

RECOVERIES

The geographic distribution of recoveries is shown in figure 1. Most recoveries occurred along the coast or very close to it. Exceptions were the few birds which wandered into Puget Sound and along the Straits of Georgia (essentially protected areas of ocean), those that wandered up the Columbia River, and those found in San Francisco Bay. This last site must be an important wintering area because

[1] Present address: Biology Department, University of Pennsylvania, Philadelphia, Pennsylvania 19174.

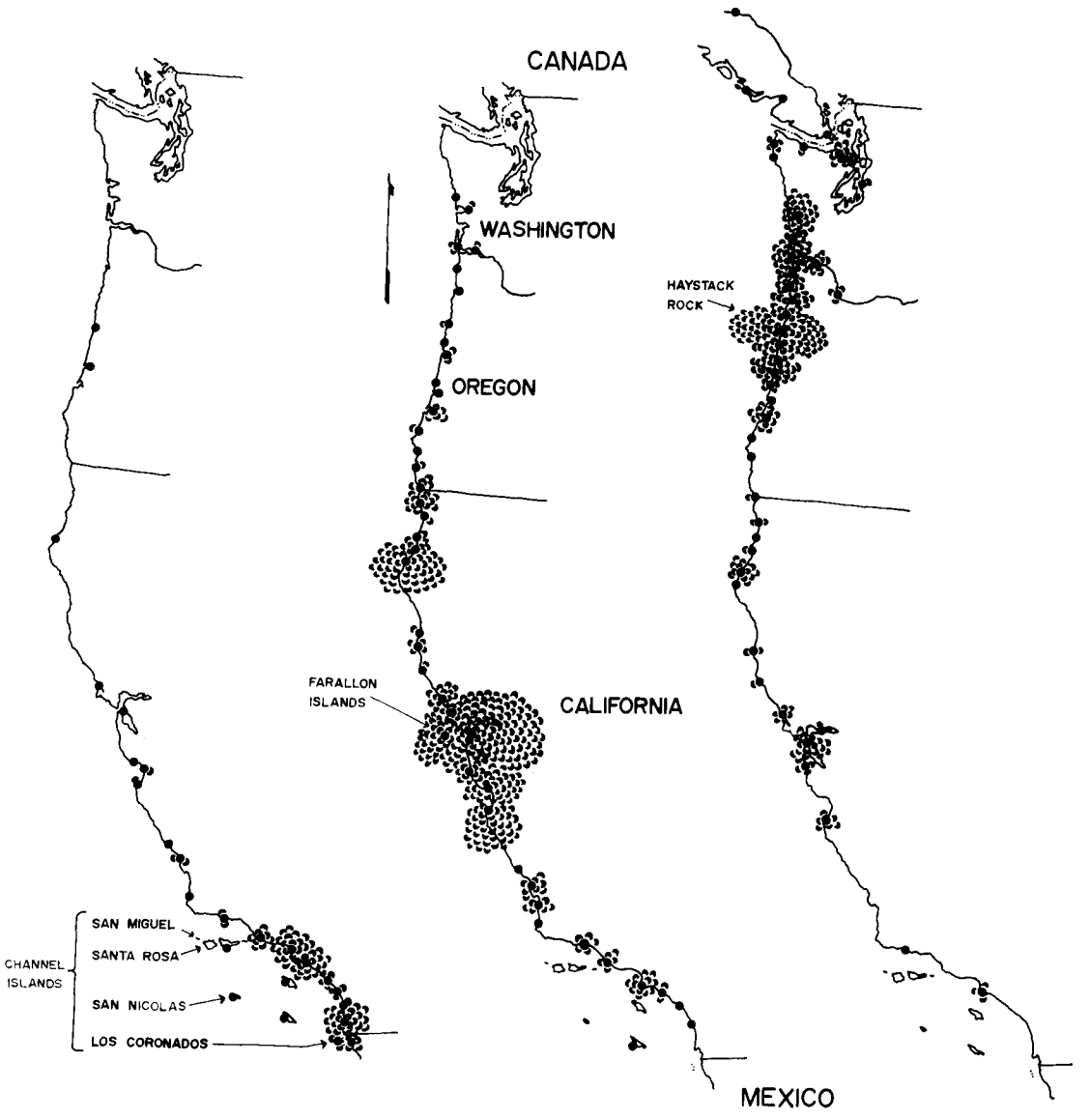


FIGURE 1. Locations of Western Gull banding recoveries according to breeding locality. Localities from left to right are Channel Islands, Farallon Islands, and Haystack Rock. Individual colonies are indicated by arrows. Each dot represents one recovery.

a great number of recoveries of both Farallon Island and Haystack Rock birds were from the Bay area. The concentration probably reflects to some degree the numbers of people in the area, but because the number of recoveries is much higher than that in adjoining areas, it also must be due to protection from winter storms and abundant food in the form of garbage and other human wastes. Fewer recoveries were recorded from similar but smaller protected areas such as Humboldt Bay, the mouth of the Columbia River, and the bays along the Oregon and Washington coasts. Recoveries also were most numerous around cities. It is impossible at present to separate the effects of protection from ocean weather and food availability from the bias of human concentrations.

Channel Islands. The Channel Island recoveries were largely from southern California reflecting little tendency among the birds to disperse. The average distance of winter recoveries from the breeding colonies was 193 km. Many birds were recovered around San Diego (largely birds from nearby Los Coronados) and Los Angeles. No significant differences were found in dispersal pattern between age groups (one-tailed, $P > 0.1$).

The birds showed a slight tendency to move south rather than north. Because of the strong

TABLE 1. Numbers of banding recoveries of the Western Gull between September and March, listed by breeding colony.

Location	Banding dates	No. of recoveries
CHANNEL ISLANDS		127
Los Coronados Islands	1928, 1938–1940, 1965–1966	79
San Nicolas Island	1968	10
Santa Rosa Island	1956, 1961–1962, 1965	27
San Miguel Island	1956, 1961–1962	11
FARALLON ISLANDS	1933, 1945–1946, 1958, 1960–1961, 1965, 1967–1971	409[a]
HAYSTACK ROCK	1930–1940	368

[a] This figure includes 321 banding recoveries and 88 sight records of birds color-banded in 1971.

bias from sparse human occupation of Baja California, I eliminated the Coronados recoveries from the analysis of directional tendency. For the other colonies the ratio of numbers of birds found north to numbers found south of the breeding colony was 0.70. This is not significantly different from 1.00, indicating no directional preference (t-test, $P > 0.1$). The lack of significance may be due to small sample size ($N = 17$).

Farallon Islands. Farallon birds dispersed along the coast tending to move farther than the Channel Island birds. Winter recoveries averaged 229 km. One-third of all Farallon recoveries were from the San Francisco area. Again, age groups did not differ significantly in dispersal pattern (one-tailed, $P > 0.1$).

The ratio of birds moving north to those moving south was 0.64, close to that for the Channel Island birds. The Farallon ratio was significantly different from 1.00 (t-test, $P < 0.02$).

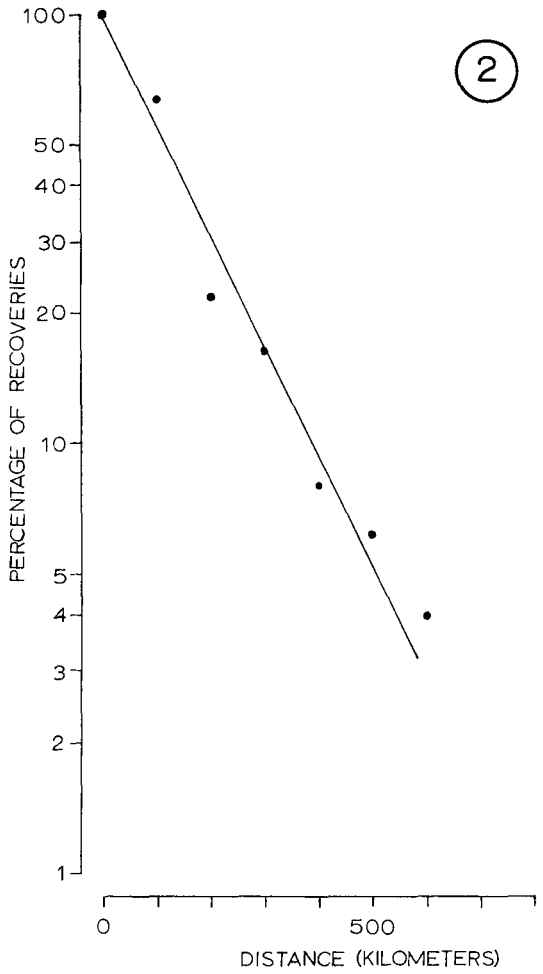
Haystack Rock. The Oregon recoveries were scattered mainly along the coasts of Oregon and Washington, with a small concentration in San Francisco Bay. The average distance from the breeding colony was 341 km, larger than that for the other two areas. However, large differences in dispersal distance were found between age groups. Recoveries of first-year birds averaged 396 km. Those of birds over two years old averaged 227 km. Thus, younger birds moved much farther than birds from more southern colonies. Older birds moved about the same distance as those from the Farallon Islands. The dispersal pattern of the second-year birds did not differ significantly from those of the younger or older birds, but the difference in dispersal patterns between the first and older than second-year birds was highly significant (one-tailed, $P < 0.001$).

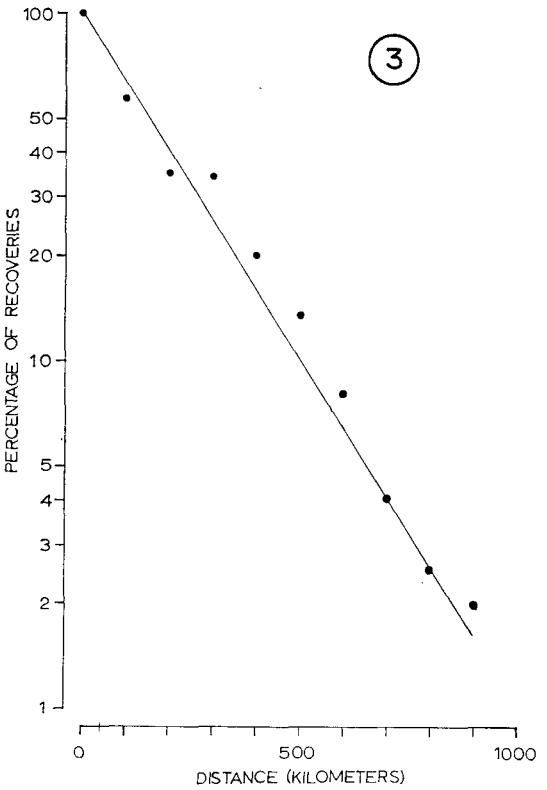
The birds showed a tendency to move south. The ratio of northern to southern recoveries was 0.73. This was significantly different from 1.00 (t-test, $P < 0.02$).

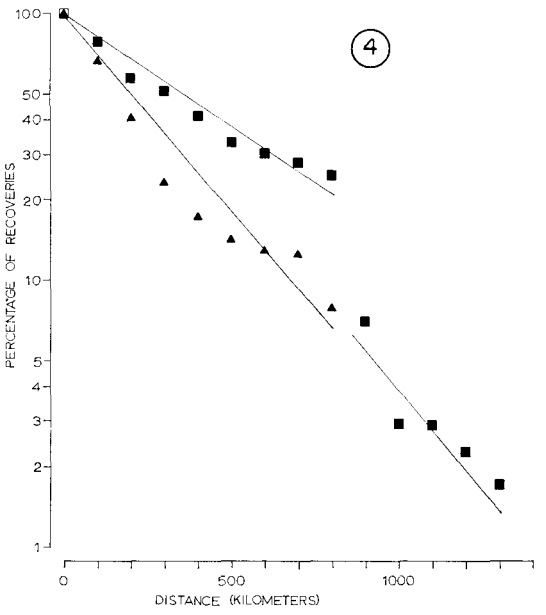
Trends. The three populations of Western Gull exhibited a cline in dispersal tendency; northern birds dispersed farthest during the nonbreeding season; southern birds moved least. This cline is even more dramatic if we consider the yellow-legged Western Gulls from the Gulf of California which apparently are quite sedentary (Devillers et al. 1971). The movement patterns for both the Channel Island and the Farallon Island birds were significantly different from that of the younger Haystack Rock birds (two-tailed, $P < 0.01$ in both cases). The older Haystack Rock birds showed a pattern similar to that of the Farallon birds, and neither differed significantly from the Channel Island pattern (two-tailed, $P > 0.1$) though the Channel Island birds moved a shorter average distance. The birds from all areas showed a slightly greater tendency to move south rather than north. The overall ratio was 0.70 which differed significantly from 1.00, the ratio for no directional preference (t-test, $P < 0.001$).

DISPERSAL VERSUS MIGRATION

Coulson and Brazendale (1968) discussed the distinction between migration and random dispersal. In the case of random dispersal, it should be possible to describe the smaller numbers of recoveries at progressively greater distances from the breeding colony by a simple mathematical relationship. Once the mathematical relationship is determined, one should be able to predict the distance of the more extensive movements from a knowledge of those nearer the natal area. This would be impossible in the case of a true migration because there is no means of predicting the ex-







FIGURES 2–4. Distribution of winter banding recoveries away from breeding colonies. See text for explanation. Figure 2: Channel Islands; Figure 3: Farallon Islands; Figure 4: Haystack Rock. (■): first-year birds; (▲): older than second-year birds; (●): birds of all ages.

tent and position of the wintering area from the more local recoveries.

I distinguished migration from random dispersal in the Western Gull using the methods of Coulson and Brazendale (1968). The recoveries were grouped according to 100-km zones away from the nesting colony. The percentage of birds recovered in each zone plus the percentage of birds recovered at greater distances was plotted on semilog graph paper against 100-km zones. For example, the percentage of recoveries at distances greater than 100 km was plotted as a single dot at 100 km; similarly, recoveries from 200 km or farther were plotted at 200 km. The difference between the points at 100 and 200 km represents the percentage of recoveries from the zone between 100 and 200 km from the nesting area. Semilog paper was used so that the steepness of the curve would be directly related to the proportion of birds reaching a given zone which remain in that zone. A linear relationship would imply that a constant proportion of the birds which enter a zone remain within it irrespective of the distance from the colony. This relationship can be expressed as $p_j = r^j$ where j is the number of zones from the colony, p_j is the proportion of birds moving beyond the outer limit of zone j, and r is a constant for each colony and is the proportion of birds entering each zone which move beyond.

The results are summarized in figures 2 to 4. The points in the Channel Island and Farallon Island graphs are nearly linearly arranged, implying random dispersal rather than migration. The values of r with their standard errors for the three areas are: 0.404 ± 0.1010 for the Channel Islands; 0.595 ± 0.7640 for the Farallon Islands; and 0.706 ± 0.0751 for Haystack Rock. Again, we see the greater tendency for the northern birds to disperse farther.

The results for the Channel Island birds, biased by the lack of Mexican recoveries, are based primarily on recoveries from north of the breeding colonies. There is no way at present to eliminate this bias in order to analyze differences in north-south dispersal tendency. These data were analyzed for the Farallon birds which showed no differences in northern against southern dispersal tendencies (two-tailed, $P > 0.45$).

The Haystack Rock graph (fig. 4) is quite different. Because age-related differences in movement were large, I considered only first-year and older than second-year birds and graphed these separately. (I did not graph the second-year birds because I was interested in the two extremes, and the second-year birds showed intermediate tendencies. Also, the sample size was quite small.) Both plots are roughly linear. The plot for the first-year birds has a break at about 800 km after which the slope is steeper. It is interesting to note that the steep plot for the younger birds seems to be a continuation of the plot for the older birds. The values of r with their standard errors are 0.844 ± 0.0742 for the first-year birds up to 800 km, 0.593 ± 0.1755 for the first-year birds beyond 900 km, and 0.655 ± 0.0894 for birds older than two years. The graph for the older birds and for the younger birds beyond 900 km indicates dispersive movements. However, the break in the younger birds' graph may indicate migration. First-year birds may be migratory as are New England first-year Herring Gulls (Eaton 1933). Alternatively, the break and the continuing linear section may indicate either the occurrence of both migratory and dispersive birds among the first-year gulls, or migration to a wintering area about 800 km from the breeding colony and dispersal from the wintering area. Another explanation is equally likely. The distance to the break is the same as the distance to San Francisco Bay. (The northern component, extending only to about 480 km, does not influence the position of the break.) Because the Bay is large, well protected, and offers a good food supply, it may attract birds which might otherwise disperse much farther. Finally, the number of recoveries from this area (21) may be a result of human bias, for it represents only about 8% of all Haystack Rock recoveries.

Although it is unclear whether the young birds from the northern colony migrate or disperse randomly, the older birds from the northern colony and the birds from the southern areas appear to disperse randomly.

MORTALITY

Banding recoveries reveal a good deal about mortality and often have been used to calculate mortality rates. For seabirds, however, calculated mortality rates may be unreliable due to the rarity of human presence for effecting recoveries at sea. Recoveries can be used with more reliability to indicate the timing of mortality. I analyzed the Western Gull data to determine seasonal variation in mortality (fig. 5). First-year birds and older than first-year birds were analyzed separately. Young birds have a much higher death rate than adults. This is heaviest shortly after the breeding season. Adult mortality among

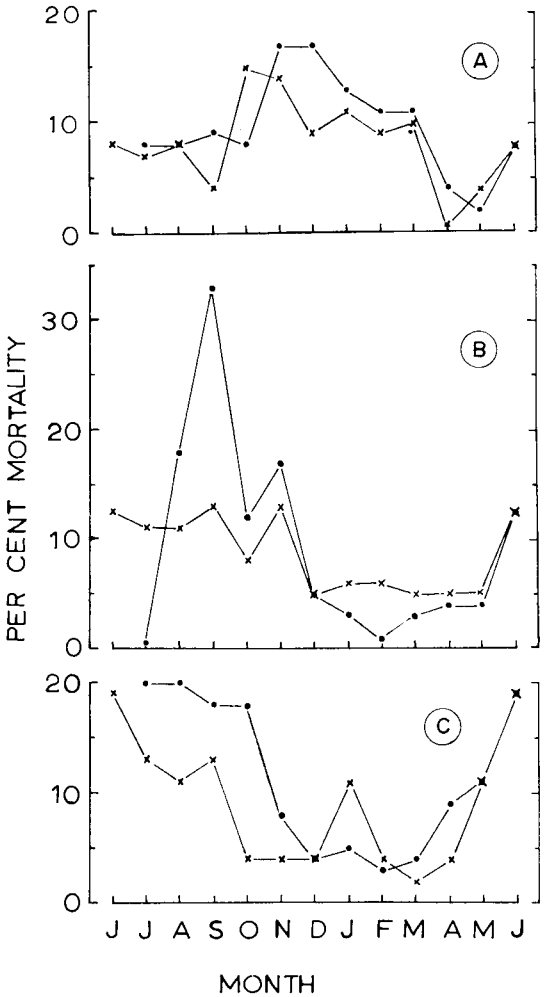


FIGURE 5. Proportional monthly mortality of Western Gulls from different areas. A: Haystack Rock; B: Farallon Islands; C: Channel Islands. (–•–): first-year birds; (–x–): older than first-year birds.

Channel Island and Farallon Island birds is greatest from June to September, i.e., from the middle of the breeding season through a period shortly after its termination. Mortality in Haystack Rock birds occurs largely during the winter from October to March.

DISCUSSION

Seasonal variations in the environment affect the number of animals that can be supported. Van Tets (1968) discussed the implications of seasonal variation in mortality rates of six gull species. I will extend his ideas to seasonal movements of the Western Gull.

Western Gulls are coastal and eat largely seafood. I have observed adults feeding fish, squid, and shrimp to chicks on the Farallon Islands. Like most gulls, however, they will eat anything available. With the increase in human population, the birds have turned to garbage in areas where this is readily available.

Western Gulls breed in colonies ranging in size from a few birds to many thousands. All colonies considered here consisted of at least five hundred individuals, and the Farallon colony consisted of about twenty thousand birds. During the early part of the breeding season, only adults are found around the breeding colony. With the hatching, growth, and fledging of chicks, demand on the environment increases. The situation may be aggravated by large numbers of Sooty Shearwaters (*Puffinus griseus*) which pass along the coast at this time and appear to compete with Western Gulls for food. One would expect high mortality among adults and juveniles late in the breeding season and shortly thereafter. This is true for both the Channel Island and Farallon Island birds in which mortality is highest in the breeding season. One would expect this pressure to affect emigration rate as well. Birds from all colonies move away after the breeding season.

At the same time, food supply decreases due to changes in ocean currents (Sverdrup et al. 1942). During the summer, the ocean currents are associated with large upwellings and high ocean productivity. In the autumn, currents change and the upwellings cease, resulting in lower productivity. However, the change is not equally great all along the coast. During the summer, ocean productivity, inversely related to water temperature, is greater in the north (Reid 1962) while in the winter, it is nearly the same along the whole coast (Lasker 1970). The change is greater toward the north. Yet much more important, physical feeding conditions are worse in the north: days are shorter and severe winter storms are more frequent. Feeding conditions appear worse, and the carrying capacity appears to decrease northward.

One would expect bird movements to result in fewer birds in the areas of lower carrying capacity. Among the Channel Islands, where feeding conditions are best, dispersal occurs over short distances. Farallon birds are in a slightly more critical food situation. While birds are able to find refuge in San Francisco Bay, the feeding conditions off the northern California coast are poorer than they are farther south. Farallon birds move farther than Channel Island birds.

The feeding situation for the Haystack Rock birds appears even more severe. They are probably similarly subject to a high mortality

shortly after the fledging period, but on a relative scale winter mortality is greater. This is indicated by a recovery rate of first-year Haystack Rock birds which is nearly twice that of the southern areas. A similar increase of winter mortality exists in Glaucous-winged Gulls farther up the coast (van Tets 1968). The bad winter feeding conditions off the Oregon coast are the likely cause. Pressure to spread out, away from the breeding colony, exists. Young birds, which probably are not as efficient feeders as adults, are under greater pressure. The youngest birds disperse quite far. With the disappearance of young birds, demand on the environment is reduced as is pressure for dispersal. Adult birds which are more efficient feeders do not move as far.

SUMMARY

Banding recoveries of Western Gulls from different colonies along the Pacific Coast of the United States were analyzed. Birds from the southern colonies were shown to have dispersive rather than migratory movements during the nonbreeding season. There is a cline in dispersal tendency. Birds from the northern colonies move farther than those from the southern colonies. Birds from Haystack Rock, the northernmost colony studied, show age-specific dispersal tendencies, the younger birds moving farther. Mortality for the southern colonies is heaviest shortly after the breeding season; mortality for Haystack Rock birds is heaviest during the winter. These findings are related to increased demand on the environment and decreased carrying capacity of the environment at the end of the breeding season and during the winter.

ACKNOWLEDGMENTS

I am grateful to the U.S. Fish and Wildlife Service Bird Banding Laboratory for providing me with records of Western Gull banding recoveries. The Point Reyes Bird Observatory generously allowed me access to their records. Lauress Wise II helped me with analysis. M. G. Bulmer offered helpful suggestions on statistics. I am particularly grateful to my colleagues at the Edward Grey Institute for helpful and stimulating discussions, particularly Luc Schifferli and Martin Garnett. E. K. Dunn, M. Garnett, C. M. Perrins, John Smail, and D. Ainley read eariler drafts of this paper and made pertinent comments. I am also indebted to M. Mullin and G. C. Anderson for suggesting references on ocean productivity. Etsu Hirai helped with the typing. This is contribution number 50 of the Point Reyes Bird Observatory.

LITERATURE CITED

American Ornithologists' Union. 1957. Checklist of North American Birds. Fifth ed., Baltimore, Md.

Coulson, J. C., and M. G. Brazendale. 1968. Movements of cormorants ringed in the British Isles and evidence of colony-specific dispersal. Brit. Birds 61:1–21.

Devillers, P., G. McCaskie, and J. R. Jehl, Jr. 1971. The distribution of certain large gulls (*Larus*) in southern California and Baja California. California Birds 2:11–26.

Eaton, R. J. 1933. The migratory movements of certain colonies of Herring Gulls (*Larus argentatus smithsonianus* Coues) in eastern North America. Bird-Banding 4:165–176.

Eaton, R. J. 1934a. The migratory movements of certain colonies of Herring Gulls in eastern North America. Part II. Bird-Banding 5:1–19.

Eaton, R. J. 1934b. The migratory movements of certain colonies of Herring Gulls in eastern North America. Part III. Bird-Banding 5:70–84.

Ferris, R. 1940. Eight years of banding Western Gulls. Condor 42:189–197.

Lasker, F. 1970. Utilization of zooplankton energy by a Pacific sardine population in the California Current, p. 265–284. *In* J. H. Steele [ed.]. Marine food chains. Oliver and Boyd, Edinburgh.

Reid, J. L. 1962. On circulation, phosphate-phosphorous content and zooplankton volumes in the upper part of the Pacific Ocean. Limnol. Oceanogr. 7:287–306.

Sanger, G. A. 1973. Pelagic records of Glaucous-winged and Herring Gulls in the North Pacific Ocean. Auk 90:384–393.

Sverdrup, H. U., M. W. Johnson, and R. H. Fleming. 1942. The oceans. Prentice-Hall, New York.

Swarth, H. S. 1920. Revision of the avian genus *Passerella*, with special reference to the distribution and migration of the races in California. Univ. California Publ. Zool. 21:75–224.

Van Tets, G. F. 1968. Seasonal fluctuations in the mortality rates of three northern- and three southern-hemisphere gulls. C. S. I. R. O. Wildl. Res. 13:1–9.

Woodbury, A. M., and K. Knight. 1951. Results of the Pacific gull color-banding project. Condor 53:57–77.

Accepted for publication 13 November 1973.