

HABITAT PARTITIONING BY FORAGING GULLS IN MAINE AND NORTHWESTERN EUROPE

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GULLS (Family Laridae) are generalized foragers that utilize many kinds of food items ranging in size from insects to the carcasses of whales. They forage in the air, on foot in fields and the intertidal zone, and by swimming and diving for underwater prey. Although species and individual gulls may show considerable specialization in foraging techniques and food preferences, most species of gulls forage at least occasionally over a large range of available habitats and use a wide variety of feeding techniques.

Generally no more than two or three species of gulls breed sympatrically. Such species are usually separated by marked differences in size; this in the case in Maine, where three species breed: the Great Black-backed Gull (*Larus marinus*, length ca. 71 cm), the Herring Gull (*L. argentatus*, ca. 56 cm), and the Laughing Gull (*L. atricilla*, ca. 33 cm). In certain parts of northwestern Europe (Scotland, Norway) up to six species of gulls may be found breeding in the same region. These species fall into three general size classifications: 1) Large, Great Black-backed Gull; 2) medium, Herring Gull and Lesser Black-backed Gull (*L. fuscus*, ca. 53 cm); and 3) small, Mew Gull (*L. canus*, ca. 41 cm), Black-headed Gull (*L. ridibundus*, ca. 37 cm), and Kittiwake (*Rissa tridactyla*, ca. 41 cm). The similarity in size of several of the sympatric species in Europe contrasts with the marked differences between the Maine gulls.

The comparison of partitioning of foraging habitats by gulls in Maine and northwestern Europe is of interest not only because of the different number of species present in the two areas, but also because the two regions have similar intertidal environments (see Stevenson and Stevenson 1949). Most studies of habitat partitioning to date have dealt with species more specialized in habitat and food preferences than gulls (MacArthur 1958, wood warblers; Recher 1966, shorebirds; Cody 1968, grassland birds; Schoener 1968, *Anolis* lizards). The question the present study investigates is whether the packing of additional generalized species into similar geographical areas will result in an increased specialization in habitat use or feeding methods, or in an expansion into the use of other resources.

METHODS

We studied foraging gulls by censusing those visible from coastal roads. In Maine (see Figure 1) we surveyed the shoreline between Belfast, Waldo County,

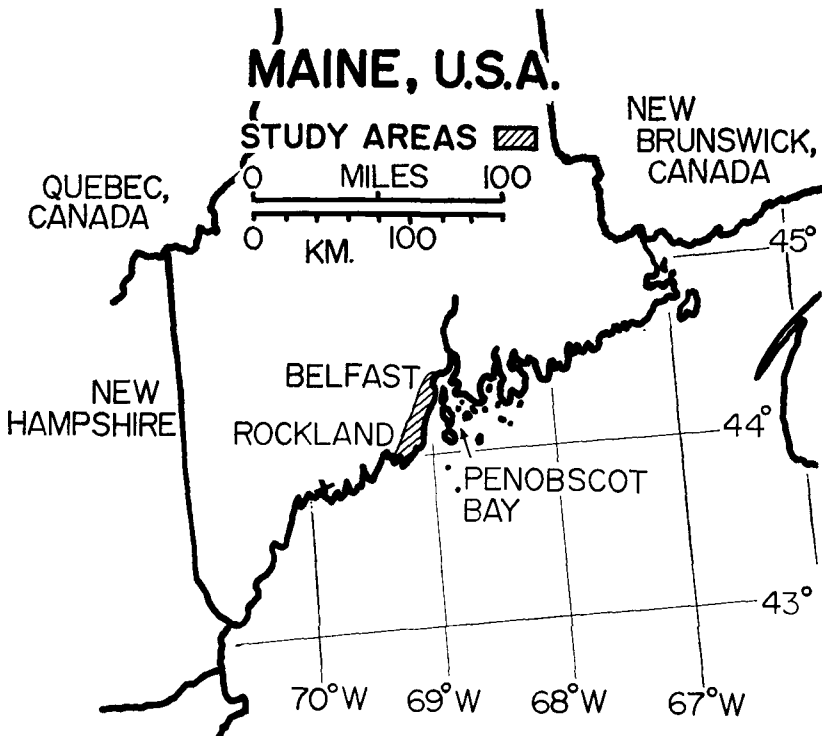


Figure 1. Field sites, Maine.

and Port Clyde, Knox County, periodically during the breeding seasons of 1967–1969 and recorded the species, activity, and foraging substrate for all gulls seen.

In Scotland and Norway (Figures 2 and 3), we used the same census methods during July and August of 1970. In Scotland we surveyed several areas repeatedly over 2- or 3-day periods: St. Andrews (3 tide cycles), Ythan Estuary (3 tide cycles), Orkney Mainland (6 tide cycles), Kyle of Lochalsh (4 tide cycles), and the area around Loch Moidart (3 tide cycles). In Norway we visited most areas only once.

Except for those studies designed to examine the effect of tide level on foraging activity, all surveys in Maine were conducted within 2 hours of low water. In Scotland most observations were made within 2 hours of low water except those made while driving between study areas. In Norway the timing of all observations to coincide with low tide was impossible, but we visited places where mud flats existed as near low tide as possible.

Data for the analysis of partitioning of the intertidal substrate by changes in the tide level were gathered by making repeated observations of foraging gulls at a given location from high until low tide. The division into three tide levels was based on the time elapsed from the time of high tide.

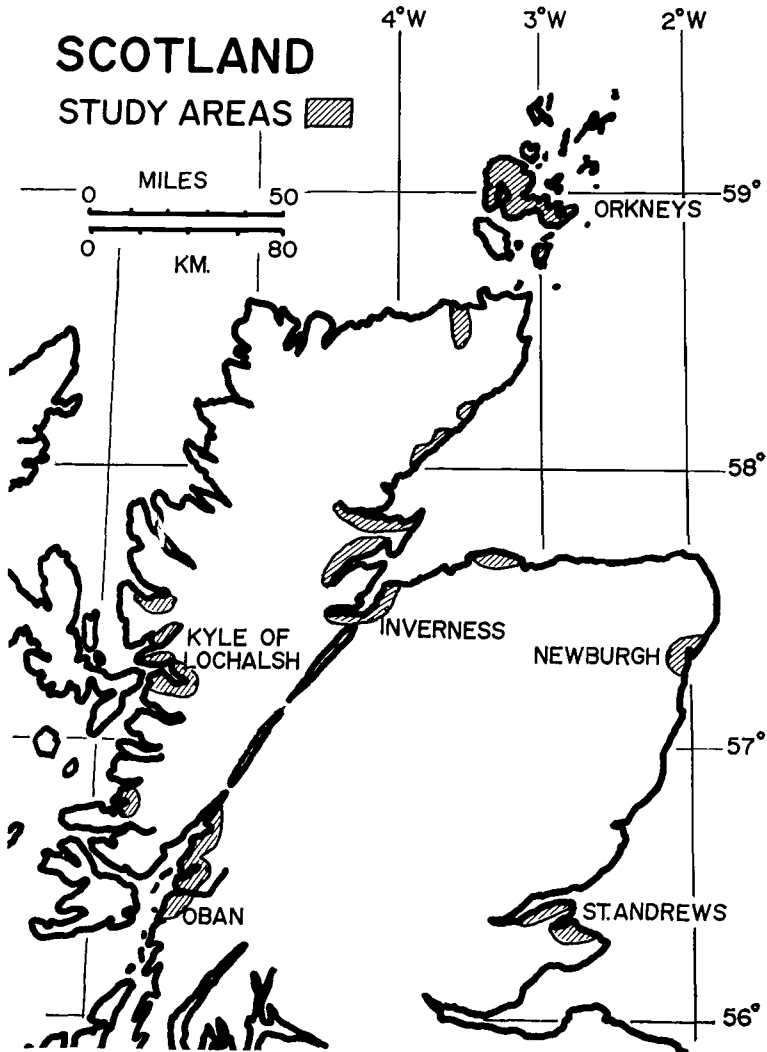


Figure 2. Field sites, Scotland.

Foraging substrates were classified according to the following criteria:

1. Mud. In these areas particle size was smaller than approximately 3 mm in diameter. While this category includes what is normally thought of as clay or mud, it also includes coarse sand and small pebble beaches.

2. Mussels. These were areas where at least one-half the surface was covered with clumps of mussels (*Mytilus* sp. or *Modiolus* sp.). Birds foraging on this substrate may have been gathering either the mussels themselves or other organisms found among the mussels.

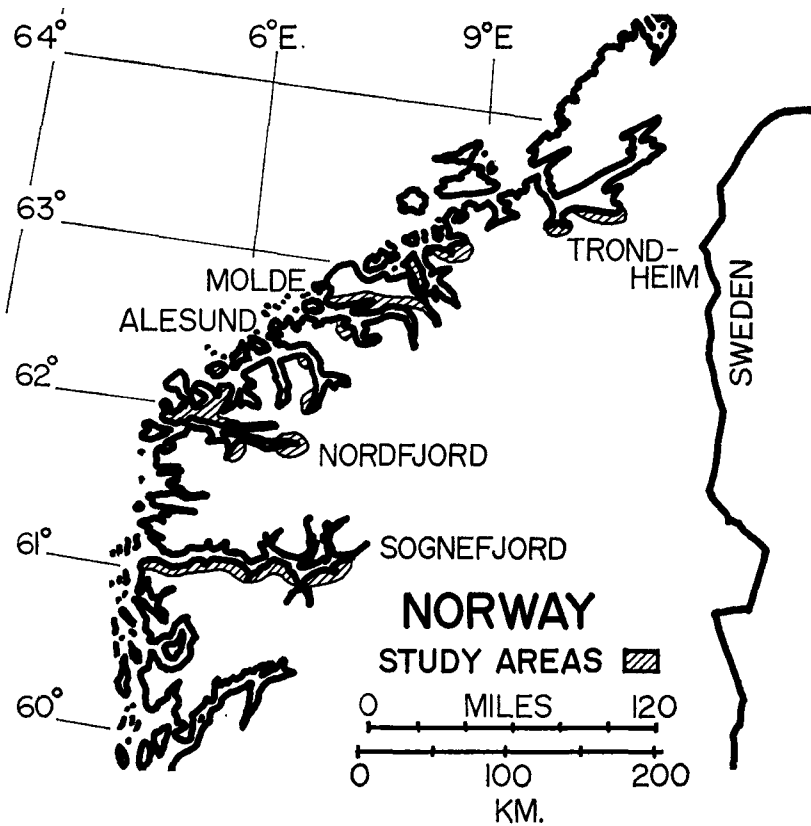


Figure 3. Field sites, Norway.

3. Rock. This category included all substrates with an average particle size greater than approximately 1 cm, from cobble beaches to large boulders and exposed ledges. In some instances the rocks were covered with algae.

4. Water. Included as feeding on this category were birds on the water's surface and those flying up from the surface in order to plunge-dive after submerged prey.

5. Air. All birds foraging from the air (hawking for insects or dipping for objects at or below the surface of the water) were classified as using this substrate, with the exception of the plunge-diving mentioned above.

6. Fields. This substrate includes both natural fields with low vegetation and cultivated lands with or without a covering of vegetation.

7. Dumps. These are terrestrial solid-waste-disposal grounds. No differentiation as to types of management (cut and fill, burning, etc.) was made.

8. Effluent. This category refers primarily to the liquid wastes discharged from sewers and fish processing plants. The discharge outlets were either subsurface or intertidal, and their amounts of solid material varied.

The survey data were analyzed for gull species diversity on each substrate, feeding

TABLE 1
NUMBER OF GULLS COUNTED IN COASTAL SURVEYS

| | Maine | Eastern Scotland | Orkneys | Western Scotland | Norway | Total |
|-------------------------|--------|---------------------|---------|---------------------|--------|--------|
| <i>Larus marinus</i> | | | | | | |
| Total | 1,526 | 394 | 557 | 97 | 348 | 2,922 |
| % feeding | 47.5 | 14.0 | 3.1 | 16.5 | 14.7 | 29.5 |
| <i>L. fuscus</i> | | | | | | |
| Total | — | 4 | 16 | 32 | 91 | 143 |
| % feeding | — | 100.0 | 6.3 | 21.9 | 32.9 | 29.4 |
| <i>L. argentatus</i> | | | | | | |
| Total | 19,412 | 5,260 | 1,683 | 1,471 | 2,125 | 29,951 |
| % feeding | 56.1 | 21.9 | 14.4 | 27.1 | 27.3 | 43.9 |
| <i>L. canus</i> | | | | | | |
| Total | — | 298 | 2,693 | 419 | 1,767 | 5,177 |
| % feeding | — | 82.5 | 49.6 | 41.1 | 50.9 | 51.0 |
| <i>L. ridibundus</i> | | | | | | |
| Total | — | 3,435 | 929 | 621 | 175 | 5,160 |
| % feeding | — | 66.7 | 49.0 | 59.1 | 67.4 | 62.6 |
| <i>L. atricilla</i> | | | | | | |
| Total | 228 | — | — | — | — | — |
| % feeding | 94.3 | — | — | — | — | — |
| <i>Rissa tridactyla</i> | | | | | | |
| Total | — | 1,181 | 264 | 0 | 578 | 2,023 |
| % feeding | — | 0.8 | 0.8 | — | 3.5 | 1.5 |
| TOTAL | 21,166 | 10,572 | 6,142 | 2,640 | 5,084 | 45,604 |

substrate diversity of each gull species, and the average foraging habitat overlap between gull species in each area.

Species diversity (SD) indices were calculated using the formula

$$SD = \sum_i P_i \ln P_i \quad \text{Equation 1}$$

where P_i is the proportion of all gulls seen on a given substrate that belong to the i^{th} species. Habitat diversity (HD) indices were obtained using the same formula where P_i is the proportion of the species in question on the i^{th} substrate.

Substrate overlap between species was measured by the formula

$$D = 1 - \frac{1}{2} \sum_{i=1}^n |P_{x, i} - P_{y, i}| \quad \text{Equation 2}$$

where $P_{x, i}$ and $P_{y, i}$ are the frequencies for species x and y respectively, for the i^{th} category (Schoener 1968).

RESULTS

Field work during three breeding seasons in Maine and 5 weeks during July and August in northwestern Europe yielded a total of 45,604 gulls counted from 24 and 26 days of surveying respectively (Table 1).

TABLE 2
PERCENTAGE USE OF SUBSTRATES BY FORAGING GULLS

| | Dumps | Efflu- ent | Mud | Mus- sels | Rock | Water | Air | Fields | Total number feeding (100%) |
|-------------------------|-------|---------------|------|--------------|------|-------|------|--------|--------------------------------------|
| Maine | | | | | | | | | |
| <i>Larus marinus</i> | 45.2 | 25.9 | 10.3 | 6.9 | 7.7 | 3.9 | 0.0 | 0.0 | 735 |
| <i>L. argentatus</i> | 30.8 | 19.7 | 26.6 | 12.9 | 5.2 | 4.3 | 0.4 | 0.0 | 10,791 |
| <i>L. atricilla</i> | 0.0 | 0.9 | 69.3 | 4.2 | 0.0 | 3.3 | 22.3 | 0.0 | 215 |
| Northwestern Europe | | | | | | | | | |
| <i>L. marinus</i> | 32.9 | 32.1 | 16.8 | 0.0 | 2.9 | 15.3 | 0.0 | 0.0 | 137 |
| <i>L. fuscus</i> | 4.8 | 64.3 | 0.0 | 0.0 | 0.0 | 14.3 | 11.9 | 4.8 | 42 |
| <i>L. argentatus</i> | 24.1 | 24.1 | 12.9 | 13.1 | 11.9 | 12.7 | 0.8 | 0.5 | 2,373 |
| <i>L. canus</i> | 0.3 | 1.6 | 6.5 | 0.2 | 0.6 | 15.2 | 0.9 | 74.6 | 2,642 |
| <i>L. ridibundus</i> | 0.1 | 8.1 | 62.3 | 0.1 | 2.8 | 11.8 | 3.4 | 11.5 | 3,232 |
| <i>Rissa tridactyla</i> | 0.0 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 31 |

Although the relative areas of each of the substrates was not established, it is clear from Tables 2 and 3 that gulls segregated their foraging grounds by selecting different habitats. Table 2 shows that certain substrates were preferred by some species and avoided by others, while Table 3 shows that the percentage composition of species on each substrate varied from the percentage that each species contributed to the total feeding population.

Striking differences in the usage of certain substrates were found between the areas studied in Maine and Europe. No gulls were recorded foraging in fields during surveys in Maine, although they occasionally do so in Maine and elsewhere in the eastern United States. In contrast, fields in Europe were a major foraging substrate for Mew Gulls and to a lesser extent for Black-headed Gulls.

In Maine Herring Gulls were the principal users of mud flats (Table 3), but in Europe they were disproportionately scarce on this substrate. While Herring Gulls may exploit intertidal flats in other regions (Holland (Spaans 1971) and southern England (Harris 1965)), they appeared to have been replaced on the mud flats of Scotland and Norway by the Black-headed Gull.

In Maine foraging activity on the water was dominated by Herring Gulls (Table 3), while in Europe Herring Gulls shared this substrate with large numbers of Black-headed and Mew Gulls. In aerial foraging Herring Gulls played a less significant role in Europe than in Maine.

The foraging behavior of the Great Black-backed Gull in Europe was very similar to its behavior in Maine. In both places many were seen eating carrion, ranging from fish to seal carcasses. These birds were recorded as feeding on the substrate they were standing on, which included

TABLE 3
PERCENTAGE COMPOSITION OF FORAGING GULLS ON EACH SUBSTRATE

| | Dumps | Efflu- ent | Mud | Mus- sels | Rock | Water | Air | Fields | % of all feeding gulls |
|-------------------------|-------|---------------|-------|--------------|-------|-------|-------|--------|------------------------------|
| Maine | | | | | | | | | |
| <i>Larus marinus</i> | 9.0 | 8.1 | 2.4 | 3.4 | 9.1 | 5.6 | 0.0 | 0.0 | 6.18 |
| <i>L. argentatus</i> | 91.0 | 91.8 | 92.8 | 95.9 | 90.9 | 93.0 | 47.3 | 0.0 | 91.99 |
| <i>L. atricilla</i> | 0.0 | 0.1 | 4.8 | 0.6 | 0.0 | 1.4 | 52.7 | 0.0 | 1.83 |
| TOTAL | 100.0 | 100.0 | 100.0 | 99.9 | 100.0 | 100.0 | 100.0 | 0.0 | 100.0 |
| Northwestern Europe | | | | | | | | | |
| <i>L. marinus</i> | 6.8 | 4.5 | 0.9 | 0.0 | 1.0 | 1.9 | 0.0 | 0.0 | 1.14 |
| <i>L. fuscus</i> | 0.3 | 2.8 | 0.0 | 0.0 | 0.0 | 0.5 | 3.2 | 0.1 | 1.48 |
| <i>L. argentatus</i> | 90.6 | 58.4 | 12.2 | 97.5 | 71.9 | 27.1 | 12.0 | 0.5 | 27.77 |
| <i>L. canus</i> | 1.4 | 4.3 | 6.9 | 1.9 | 4.1 | 36.2 | 15.2 | 83.7 | 31.34 |
| <i>L. ridibundus</i> | 0.8 | 26.8 | 80.0 | 0.6 | 23.0 | 34.3 | 69.6 | 15.7 | 37.74 |
| <i>Rissa tridactyla</i> | 0.0 | 3.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.13 |
| TOTAL | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |

nearly all Great Black-backs on mud in Europe and small percentages on mud, mussels, and rock in Maine. Very few Great Black-backed Gulls were seen foraging in the intertidal zone on either continent, and clearly this is not an important feeding habitat for them (Harris 1965, Hunt MS).

For the two medium-sized gulls in Europe, the Lesser Black-backed and Herring Gulls, some habitat segregation was apparent. The Herring Gull was the littoral feeder, and the Lesser Black-backed Gull foraged more at sea or inland (Harris 1965). Our limited data on the Lesser Black-backed Gull tend to confirm this. Of 114 gulls recorded feeding behind ferry boats in Norway, 75% were Lesser Black-backed Gulls. While these results were not combined with the land-based surveys, they account for 74% of all feeding Lesser Black-backed Gulls seen in Norway.

Habitat segregation is more apparent in the three small gulls. The Mew Gull makes extensive use of fields as well as some intertidal foraging, the Black-headed Gull concentrates on the intertidal, and the Kittiwake, while occasionally using the intertidal (Alexander 1937) concentrates its foraging efforts at sea.

In Maine all three species of gulls overlapped extensively in the natural foraging grounds utilized. Where different species used the same substrate in Europe, generally the overlapping species were of different size classes. Interactions between size classes appear to have had some effect in determining which species would utilize each habitat. Small gulls in Europe chiefly occupied and often dominated those environments in which food items were generally small and evenly dispersed (e.g. air, water, mud). In contrast the large species generally dominated the more

TABLE 4
SPECIES DIVERSITY (SD) ON EACH HABITAT

| | Maine | Europe | Eastern Scotland | Orkneys | Western Scotland | Norway |
|----------|-------|--------|---------------------|---------|---------------------|--------|
| Dumps | 0.30 | 0.39 | 0.31 | 0.33 | 0.40 | 0.98 |
| Effluent | 0.29 | 1.15 | 1.07 | 0.99 | 1.19 | 0.88 |
| Air | 0.70 | 0.90 | 0.08 | 0.25 | 0.0 | 1.20 |
| Water | 0.29 | 1.19 | 0.51 | 0.75 | 0.85 | 1.02 |
| Rock | 0.31 | 0.75 | 0.77 | 0.39 | 0.72 | 0.89 |
| Mussels | 0.19 | 0.13 | 0.10 | — | — | 0.0 |
| Mud | 0.31 | 0.65 | 0.43 | 0.73 | 1.00 | 1.24 |
| Fields | 0.0 | 0.46 | 0.75 | 0.35 | 0.58 | 0.05 |

clumped sources of food (e.g. dumps, effluent, rocky coasts). The smaller gulls that utilized these substrates in the presence of the larger species were usually found in relatively small numbers and often foraged in the less productive areas. This was also seen in the use of mussel beds in both Maine and Europe on which smaller gulls did not attempt to feed in numbers until most of the Herring Gulls had finished feeding.

Few gulls anywhere fed in the intertidal zone when the tide was

TABLE 5
FEEDING HABITAT DIVERSITY (HD) FOR EACH SPECIES

| | Maine | Europe | Eastern Scotland | Orkneys | Western Scotland | Norway |
|---------------------------------|-------|--------|---------------------|---------|---------------------|--------|
| <i>Larus marinus</i> | | | | | | |
| Natural substrates ¹ | 1.35 | 0.92 | 0.80 | 0.69 | 0.96 | 0.67 |
| All substrates | 1.45 | 1.42 | 0.90 | 0.72 | 1.42 | 1.26 |
| <i>L. fuscus</i> | | | | | | |
| Natural substrates ¹ | — | 1.01 | — | — | — | 0.69 |
| All substrates | — | 1.11 | 1.04 | — | 0.41 | 0.91 |
| <i>L. argentatus</i> | | | | | | |
| Natural substrates ¹ | 1.17 | 1.48 | 1.04 | 1.07 | 0.99 | 1.16 |
| All substrates | 1.61 | 1.80 | 1.46 | 1.01 | 1.53 | 1.43 |
| <i>L. canus</i> | | | | | | |
| Natural substrates ¹ | — | 0.74 | 0.55 | 0.18 | 0.87 | 1.04 |
| All substrates | — | 0.86 | 0.61 | 0.23 | 1.21 | 1.11 |
| <i>L. ridibundus</i> | | | | | | |
| Natural substrates ¹ | — | 1.02 | 0.80 | 1.20 | 1.39 | 0.91 |
| All substrates | — | 1.23 | 0.90 | 1.45 | 1.55 | 1.02 |
| <i>L. atricilla</i> | | | | | | |
| Natural substrates ¹ | 0.83 | — | — | — | — | — |
| All substrates | 1.04 | — | — | — | — | — |
| <i>Rissa tridactyla</i> | | | | | | |
| Natural substrates ¹ | — | 0.0 | 0.0 | — | — | — |
| All substrates | — | 0.0 | 0.0 | — | — | 0.0 |

¹ Excluding fields.

TABLE 6
AVERAGE PERCENT OVERLAP OF FEEDING HABITATS

| | Natural substrates excluding fields | Natural substrates and fields | Natural substrates, dumps, and effluent | Natural substrates, fields, dumps, and effluent |
|------------------|--|--|--|--|
| Maine | 61.52 | — | 43.66 | — |
| Eastern Scotland | 65.88 | 31.94 | 30.33 | 22.76 |
| Orkneys | 31.98 | 28.81 | 55.17 | 44.87 |
| Western Scotland | 76.39 | 50.90 | 55.89 | 41.58 |
| Norway | 65.90 | 59.49 | 43.96 | 42.75 |
| All Europe | 49.46 | 37.77 | 38.47 | 33.89 |

high. Comparisons of the utilization of the intertidal zone by foraging gulls at one-half tide and low tide revealed different patterns in Maine and Scotland. In Maine the number of foraging gulls of all species increased as the tide dropped, but the numbers of Laughing Gulls increased in proportion to the Herring and Great Black-backed Gulls. This increase in Laughing Gulls was probably related to the exposure of their preferred foraging areas on mud flats. In Scotland the absolute number of Black-headed and Mew Gulls decreased between midtide and low tide, while the Herring and Great Black-backed Gulls decreased in number in eastern Scotland and increased in western Scotland between midtide and low water. The significance of the differences in these changes in numbers is not known.

Substrate utilization changed between midtide and low water in all study areas. In Maine Herring Gulls shifted to mud from other substrates as the tide dropped. Great Black-backed and Laughing Gulls moved to both mud and mussels. On the east coast of Scotland Herring Gulls went from mussels to both mud and rock as the tide dropped, while the Great Black-backed Gull showed increased foraging only on mud. Both Mew Gulls and Black-headed Gulls increased their foraging activity on mussels as the larger Herring Gulls moved away, and the Black-headed Gull also increased its foraging on the water. On the west coast of Scotland the patterns of habitat utilization were not comparable with the other areas as no mussel beds were seen.

Species diversity (Table 4) on the various substrate types in all regions of Europe was greater than in Maine, although the differences were significant only between Maine and the Orkneys and between Maine and Norway ($P < 0.05$). Species diversity indices in Maine were uniformly low, except that for air, while in each of the subareas studied in Europe, the value of the diversity indices fluctuated widely from one substrate to another.

Indices for the diversity of habitats used by gulls in each region

(Table 5) showed a slight trend towards lower values in European areas than in Maine, but the difference was significant only between Maine and eastern Scotland ($P = 0.036$, Mann-Whitney U Test, Siegel 1956).

Overlap (Table 6) decreased in Europe as fields were added to the available natural foraging areas. With the exception of the Orkneys, overlap was further decreased in both Maine and Europe as dumps and effluent were added to the range of substrates utilized. The combination of natural substrates plus fields and man's refuse yielded a still lower value for overlap in Europe.

DISCUSSION

Gulls are opportunists and may shift their foraging patterns radically to take advantage of short-term fluctuations in food supply (Ingolfson 1967, Hunt MS). We believe our surveys were conducted over a sufficiently long period in Maine and wide enough geographic range in Europe to eliminate distortion by this possibility for bias.

Our results show that in northwestern Europe six species of gulls have not been packed into a habitat equivalent to that which supports only three species of gulls in Maine. Instead, two of the European species, the Kittiwake and the Mew Gull, occupy niches for which no specialists exist in Maine, the open sea and inland fields. These two species appear to have no ecological counterparts in Maine.

A comparison of the degree of specialization in habitat preferences between gulls in Maine and Europe is instructive. When all gull species were considered, no statistically significant differences were found in niche breadth between the gulls studied in Europe and those in Maine (Table 5). Herring Gulls on both sides of the Atlantic had similar foraging habitat diversity indices, as did the Laughing Gull and its apparent ecological counterpart, the Black-headed Gull (Tables 2 and 5). Although the Great Black-backed Gull in Europe appears to have a more restricted niche breadth than in Maine (Table 5), observations of feeding behavior indicate that this species occupies essentially the same niche in both places. These similarities, in addition to the high species diversity indices on European intertidal substrate types, indicate that the additional species in Europe are not coexisting through an increase in habitat specialization within the intertidal zone.

The coexistence of European gulls appears to be maintained through two possible means: (1) the addition of two more niches discussed above, and (2) the use of superabundant food supplies available from man, which allows greater overlap on natural foods than would be expected if natural foods were the only resource available. By foraging on man's waste gulls reduce their overall foraging overlap because waste is par-

tioned in addition to natural foods. Without the large quantities of food available from dumps, sewers, and fishing operations, gull populations would be forced to compete for limited natural resources. Under these circumstances it is possible either that competitive interactions would result in the eventual reduction of overlap and an increase in specialization in the use of natural resources, or that fewer species would continue to coexist.

MacArthur and Levins (1967) have demonstrated a theoretical limit to species overlap of 0.54 with reference to similarities in the alphas of the Gause competition equations. Although from the information available it is not possible to calculate the alphas of the gulls studied, calculations of overlap in habitat utilization (Equation 2) showed that values in excess of 0.60 were found when only natural substrates were considered. The drop in overlap to below 0.54 when fields and sources of waste were included (Table 6) is suggestive of the importance of man's refuse in reducing competition. The differences in measuring overlap preclude this being used as an adequate field test of MacArthur and Levins' model.

Our studies suggest that the size of sympatric species is important in two ways: (1) gulls of different sizes may be able to utilize foods of different sizes in the same substrate, and (2) through aggressive interactions larger gulls may dominate smaller gulls in areas where food may be most efficiently obtained (see Drury and Smith 1968). Evidence for such aggressive interactions between large and small species has been obtained by one of us (GLH) for Herring and Ring-billed Gulls (*L. delawarensis*) in the southeastern United States (unpublished field notes) and by Moyle (1966) for Glaucous-winged Gulls (*L. glaucescens*), Mew Gulls, and Bonaparte's Gulls (*L. philadelphia*) on Alaskan salmon streams.

European gulls do exhibit certain shifts in foraging strategies that appear to be related to the large number of interacting species. Among these are notably the Herring Gull's decreasing use of mud and water as foraging substrates, presumably a response to competition from the smaller Black-headed and Mew Gulls that may forage more efficiently on the small, scattered food items in these areas. The extensive use of fields by the Mew Gull in Europe may also be a response to competitive interactions. In California, where other populations of this species occur in winter, the Mew Gull has no competitor equivalent to the Black-headed Gull. Grinnell and Miller (1944) state that in California *L. canus* is "typically [found on the] outer shore-line and adjacent ocean waters." Ingolfson's (1967) work makes it clear that many species of gulls are highly adaptable in their foraging habits, and it is not surprising that local populations may show considerable variation in foraging under different local conditions.

Finally, it is of interest to compare our findings about gulls with those of Lack (1969) who studied tits (Paridae) in Europe and North America. With tits, six species coexist over a wide expanse in Europe; in middle North America rarely are more than two species ever sympatric. Lack has found that while European tits show both behavioral and morphological traits that would permit sympatry, such adaptations are not found in North American tits. Lack concludes from this that North American tits are in an earlier stage of their evolution, and have not had time to evolve the adaptations necessary to allow coexistence of large species groups. The pattern of distribution of gull species in Europe and North America is similar to that in tits. Throughout North America sympatry in gulls is generally limited to two or rarely three species, the members of each species pair differing considerably in size. In Europe, from four to six species of gulls can be found breeding in a single region (Voous 1960). Within these European species assemblages are both behavioral and morphological adaptations that permit partitioning of foraging habitats and food resources. The increase in foraging habitat specialization of European gulls as compared with gulls in Maine appears to be less than what might have been predicted on the basis of Lack's observations on tits. The relatively short history of sympatry for some of the European gulls reported by Mayr (1963) may be responsible for this.

ACKNOWLEDGMENTS

Financial support for the work in Scotland and Norway was provided by the Frank M. Chapman Memorial Fund, American Museum of Natural History. The work in Maine was funded by the Biological Laboratories of Harvard University, a Richmond Fellowship from Harvard University, National Institutes of Health Pre-Doctoral Fellowships (numbers 8-FI-GM-31, 846-01A1 and 5-FI-GM-31, 864-02) and grant numbers GB 7346 and GB 8620 from the National Science Foundation, Reed C. Rollins, Harvard University, Principal Investigator.

We wish to thank G. M. Dunnet and the staff and students at Culterty Field Station, Newburgh, Scotland, for their help and advice on aspects of the field work in Scotland. The manuscript has benefited from critical reading by Martin L. Cody and Thomas W. Schoener.

SUMMARY

Comparisons were made of the partitioning of foraging habitats by three species of gulls in Maine (*Larus marinus*, *L. argentatus*, and *L. atricilla*) and six species in Scotland and Norway (*L. marinus*, *L. fuscus*, *L. argentatus*, *L. ridibundus*, *L. canus*, and *Rissa tridactyla*). Feeding habitat diversity was found to be generally similar in Maine and Europe, although species diversity within each foraging habitat was greater in two areas studied in Europe. The data support the notion that gulls in Europe have remained generalists and that packing of new species into

areas of sympatry has been accomplished by adding new niches (fields and feeding at sea). It is suggested that the availability of waste has reduced selective pressure for greater specialization within natural areas by providing an alternative food resource.

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