DIETARY CHANGES AND POOR REPRODUCTIVE PERFORMANCE IN GLAUCOUS-WINGED GULLS

EDWARD C. MURPHY, ROBERT H. DAY,[1] KAREN L. OAKLEY,[2] AND A. ANNE HOOVER

Institute of Arctic Biology, Division of Life Sciences, University of Alaska, Fairbanks, Alaska 99701 USA

ABSTRACT.—The breeding phenology of Glaucous-winged Gulls (*Larus glaucescens*) on Squab Island, Aialik Bay, Alaska in 1979 was identical to that in 1980, but clutch sizes and later reproductive performance differed markedly. In 1979, clutch sizes were small, but chick growth rates and survivorship were high. In contrast, clutch sizes were large in 1980, but chick growth rates were slow, and chick survivorship was extremely low. The different patterns of reproductive success appear to be related primarily to annual differences in foods utilized by adults. When adults fed primarily on blue mussels (*Mytilus edulis*), reproductive performance suffered, i.e. at the time of egg laying in 1979 and during the chick period in 1980. A switch to mussels from other prey types thus probably indicates a lack of availability of more suitable or preferred foods. Reproductive success at this colony appears to be strongly food limited; the timing of such limitation is not confined to a particular stage of reproduction. *Received 4 January 1982, resubmitted 6 September 1983, accepted 23 February 1984.*

MOST studies of the breeding success of *Larus* gulls have focused on colonies where a substantial portion of the diet comes from the scavenging of human refuse (e.g. Paynter 1949, Vermeer 1963, Brown 1967, Haycock and Threlfall 1975). Kadlec and Drury (1968) concluded that the availability of human refuse is a major factor in the disparate levels of reproductive success among colonies of Herring Gulls (*L. argentatus*) in New England (also see Spaans 1971, Hunt 1972, Sibly and McCleary 1983). In contrast, Ward (1973) documented faster rates of chick growth and higher fledging success at two colonies of Glaucous-winged Gulls (*L. glaucescens*) where refuse was not available than at a third colony where refuse was a major component of the diet. Furthermore, Pierotti (1979, also see Pierotti and Annett MS) found intracolony differences in the diets of Herring Gulls; those specializing on refuse had lower reproductive success than did specialists on natural foods.

In the first studies of Glaucous-winged Gulls in Alaska, Patten (see Patten and Patten 1983) documented moderate reproductive success at one colony (Egg Island) where the breeding adults include garbage and fisheries offal in their diet, foods that are typical of most *Larus* gull colonies. Patten (1974) found high levels of reproductive success, averaging 1.8 chicks fledged per nest, at a colony in Glacier Bay, which has been deglaciated recently and where refuse is not included in the diet. Here we report the results of a 2-yr study of the breeding biology and food habits at another Alaskan colony of Glaucous-winged Gulls in a glaciated fjord in which breeding adults do not exploit garbage at the present time. We examine both the variability in reproductive success between years and the relationship between the level of reproductive success and foods brought back to the colony by foraging adults.

STUDY AREA

Squab Island (59°56'N, 149°43'W) is approximately 50 m wide by 300 m long. It is located at the north, or upper, end of Aialik Bay, approximately 25 km southwest of the town of Seward, Alaska (Fig. 1). Aialik Bay is a heavily-glaciated fjord; ice calved from Aialik Glacier, a tidewater glacier 2 km from Squab Island, frequently covers much of the upper bay during the summer. Tidal fluctuations are marked: maximum tidal range during the period we were in the field was 5 m, and average tidal range was about 4 m.

The maximum elevation of Squab Island is about

[1] Present address: Institute of Marine Science, 200 O'Neill Building, University of Alaska, Fairbanks, Alaska 99701 USA.

[2] Present address: 3605 Arctic Boulevard, #815, Anchorage, Alaska 99503 USA.

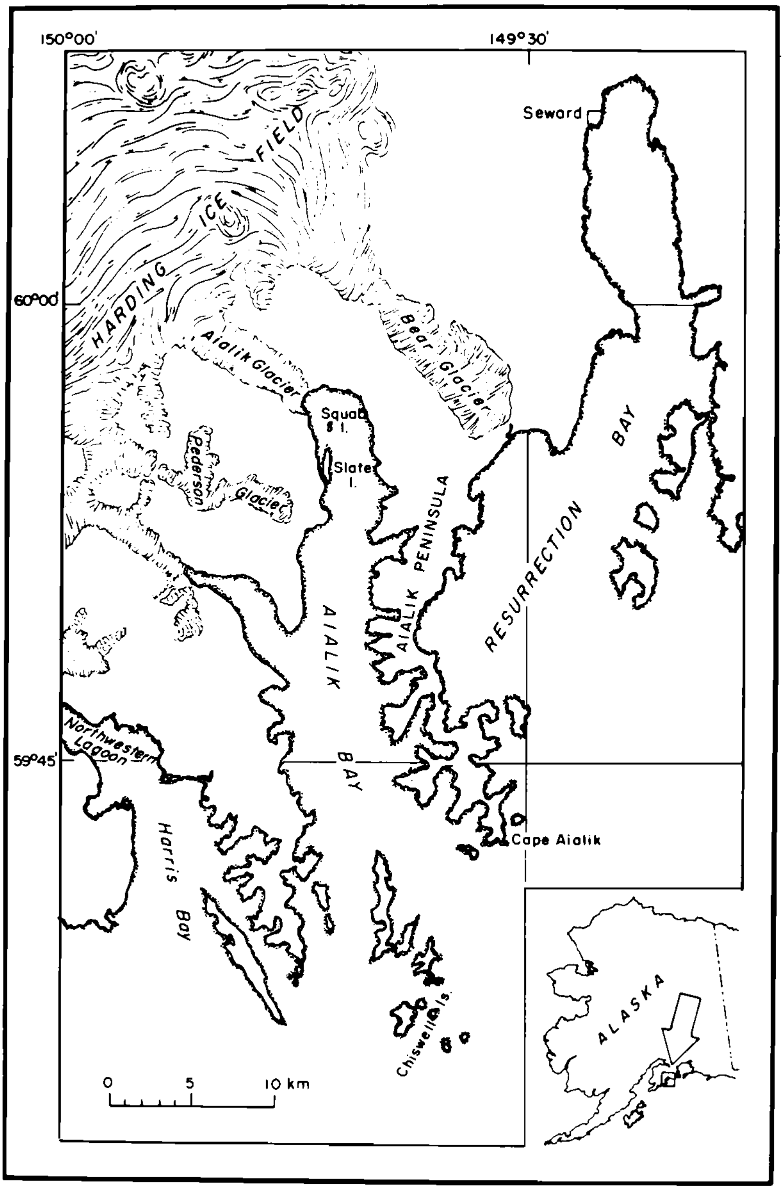

Fig. 1. Map of the study area, Squab Island, and vicinity.

40 m above mean lower low water. Inaccessible cliffs form the west side of the island, and steep slopes characterize the eastern shore. Neither high and flat nor low and steep portions are vegetated. Umbels (principally *Heracleum lanatum* and *Angelica lucida*), grasses (particularly *Elymus arenarius mollis*), and sedges (*Carex* spp.) dominate the vegetation, which is particularly lush on the lower, flatter portions of the island. In late May, when the gulls begin to nest, relatively little of the current year's vegetative growth has occurred; it is well developed, however, long before the time of fledging of chicks (late July and early August). Other seabirds breeding in upper Aialik Bay include American Black Oystercatchers (*Haematopus bachmani*), Mew Gulls (*Larus canus*), Arctic Terns (*Sterna paradisaea*), Pigeon Guillemots (*Cepphus columba*), Marbled and Kittlitz's murrelets (*Brachyramphus marmoratus* and *B. brevirostris*), and Horned Puffins (*Fratercula corniculata*).

Methods and Materials

Field routines.—Field crews first visited Squab Island on 18 May in 1979 and on 21 May in 1980, both shortly before egg laying. Thereafter in both years, visits to the island occurred one to several days apart until the chicks had fledged. Data collection ended on 12 August 1979 and 19 August 1980. In 1981, field crews visited the island between 22 May and 10 June, gathering data on clutch sizes on parts of the island.

When we located a nest, we placed a numbered flag 1.0–1.5 m away to mark its location. We defined an active nest as one known to contain at least one egg, at least temporarily, and here we consider only active nests. Nest scrapes or partially built nests were not marked or studied. Once all active nests were found, we measured the distance to the nearest active nest.

Any eggs present when a nest was first located were marked with a waterproof marking pen; new eggs were marked when found on subsequent visits. Dates of clutch initiation and clutch completion were recorded, when known. Egg losses were noted and hatching dates were recorded, if known. Upon hatching, chicks were temporarily identified with a numbered band made of masking tape. This band was removed once a chick was sufficiently large to retain a permanent U.S. Fish and Wildlife Service numbered metal band (Permit #20529). Each time we captured a chick, we weighed it (to the nearest gram) and measured its diagonal tarsus length (to the nearest 0.1 mm). Chicks later found dead were eliminated from all analyses of growth rates. For each active nest, clutch size, number of eggs known to hatch, and number of chicks known to fledge were recorded. These values are not free of bias, but any inaccuracies apply equally to both years (Murphy and Hoover MS). If an egg was laid and disappeared between successive visits, we would have underestimated clutch size. Likewise, if an egg hatched after a visit, we would have erroneously recorded the discrepancy as an egg loss rather than as chick loss.

We visited nests repeatedly to ascertain the numbers of chicks present. If chicks consistently moved into dense foliage before they were sighted and could not be seen, we would have recorded their absence as mortality. Because nests with chicks showed obvious signs of occupancy, however, it is unlikely that we erroneously recorded a nest failure if one or more chicks were alive but escaped our detection. Any dead chicks found were removed from the island; not many were found dead, however. Thus, our estimates of clutch size, hatching success, and fledging success represent minimum values.

Several studies have shown that human disturbance can adversely affect the reproductive performance of *Larus* gulls (e.g. Gillett et al. 1975; Fetterolf 1983; but see Pierotti 1979, 1982). Likewise, our activities in the colony may have affected the gulls. Our activity schedules were equivalent in both years, however, and, therefore, any differences between years in reproductive success cannot be due to our activities.

We obtained data on food habits opportunistically from (1) pellets of adults near the nests, (2) items that chicks regurgitated while they were being handled, and (3) observations of adults bringing items back to the nest. To examine the data on food habits before the hatching of the eggs, we first scored abundances of various food types in castings on a scale ranging from 0 (absent), through 1 (observed rarely), 2 (present, but of secondary importance), 3 (prevalent, but of shared primary importance), 4 (predominant), to 5 (only item) for each 5-day period. Once hatching began, we determined presence or absence of various food types in material regurgitated by chicks and then computed percentage abundance from samples collected within each 5-day period.

Data analysis.—Frequency distributions of most interval-scale reproductive variables departed significantly from a normal distribution. Distributions of nearest-neighbor distance and clutch-initiation date were skewed to the right and could be normalized by transformation to common log values. Therefore, for these variables, comparisons between years were made using log-transformed values. Analyses of differences in clutch size, hatching success, and fledging success between years were conducted by means of the modification of the Kruskal-Wallis Test outlined by Conover (1980) for contingency tables with one ordinal variable and one grouping variable.

RESULTS

Nest densities.—We found 234 active nests in 1979. Steep cliffs where there were few nests were not surveyed in 1979; the estimated total in 1979 was 280 nests. In contrast, there were 581 active nests in 1980, representing more than a doubling of estimated active nests between years.

Distance to the nearest active nest provides an inverse index of nest density. Distances to the nearest active nests were similar in both years (Table 1, $t = 0.231$, $v = 796$, $0.5 < P < 0.9$), indicating far more extensive use of the entire island for nesting in 1980 than in 1979. In 1979, territories were established and nest scrapes were observed in areas where no active nests were found later that year, suggesting that nesting attempts failed before or during egg laying in many areas of the island.

We used Harper's (1971) technique of estimating the area of a nesting territory by calculating it as a circle with a radius one-half of the distance to the nearest active nest. The 2-yr mean territory size for Squab Island was 11.4 m^2.

Breeding phenology.—Initiation dates of

TABLE 1. Summary of reproductive data for the Glaucous-winged Gull colony on Squab Island, Alaska, 1979–1980.

Attribute	Year	
	1979	1980
Distance to nearest active nest (m)	3.5 ± 2.3 (232)[a]	3.3 ± 1.6 (566)
Date of clutch initiation	2 June ± 6.0 days (125)	31 May ± 5.3 days (397)
Clutch size	2.06 ± 0.78 (229)	2.59 ± 0.63 (568)
Number hatching/clutch	1.03 ± 1.11 (232)	1.09 ± 1.24 (572)
Hatching success	50%	42%
Number fledging/clutch	0.95 ± 1.09 (190)	0.26 ± 0.58 (567)
Fledging success	92%	24%
Breeding success	46%	10%

[a] Mean ± standard deviation (sample size).

clutches were equivalent in both years (Table 1; $t = 1.420$, $v = 520$, $0.1 < P < 0.2$). The degree of asynchrony, as reflected by the standard deviation, was also similar in both years, and the ranges in dates clutches were initiated were virtually identical in both years (1979: 23 May–20 June; 1980: 21 May–21 June).

In 1979, hatching peaked on 1 July (SD = 4.86 days; range = 21 June–16 July; $n = 105$); in 1980, the mean date of hatching was 27 June (SD = 3.80 days; range = 20 June–13 July; $n = 96$). The difference between years is highly significant ($t = 5.096$; $v = 199$; $P < 0.001$). Earlier hatching in 1980 seems inconsistent with our observation that initiation dates of clutches were similar in both years. Hatching success, however, was higher in earlier clutches than in later clutches in 1980 but had no relationship with initiation date in 1979 (Murphy and Hoover MS). Thus, the 1980 sample of eggs with known hatching dates was derived primarily from the larger, early clutches, and the estimated mean date of hatching was therefore earlier than in 1979 (see Murphy and Hoover MS).

Reproductive success.—We omitted clutches of four eggs from the statistical analyses, because they were rare and possibly represented the efforts of two females. Glaucous-winged Gulls, like other larids, develop only three brood patches, and each brood patch is of sufficient area to cover only one egg (Drent 1970). Clutch sizes were lowest in 1979, averaging 2.1 eggs; in 1980, clutch sizes averaged 2.6 eggs (Table 1). As noted earlier, field personnel were on the island briefly during egg laying in 1981. In that year, the mean clutch size was 2.8 eggs (SD = 0.48, $n = 117$). The differences among years were highly significant (Kruskal-Wallis Test for Contingency Tables, $H = 123.761$, $v = 2$, $P < 0.001$); results of the multiple-comparisons procedure (Conover 1980) indicate that clutch size in each year was significantly ($P < 0.05$) different from that in either of the other two years.

Hatching success was poor on Squab Island in both 1979 and 1980; fewer than half of the eggs laid hatched (Table 1). In 1979, 52% of the clutches were successfully incubated, i.e. hatched at least one egg; in 1980, only 48% of the clutches were successfully incubated. The 1979 mean of 1.03 eggs hatching/clutch was similar to the 1980 mean of 1.09 ($H = 0.016$, $v = 1$, $0.5 < P < 0.9$), even though clutch sizes were significantly smaller in 1979.

Fledging success (number of chicks fledged/number of eggs hatched) was much higher in 1979 than in 1980 (Table 1). The gulls fledged 0.95 chicks/active nest in 1979 but only 0.25 chicks/active nest in 1980. This difference is highly significant ($H = 80.266$, $v = 1$, $P < 0.001$). The 1980 estimate of 0.25 chicks fledged/clutch is by far the lowest yet reported for the species.

Breeding success (number of chicks fledged/number of eggs laid) was 0.46 in 1979 and only 0.10 in 1980. Thus, clutch sizes were relatively small and hatching success was moderate in 1979, but survival during the chick period was high. In contrast, clutch sizes in 1980 were relatively large, but hatching success and chick survival were poor.

Growth rates of chicks.—We recorded both weight and tarsal length of chicks when we could capture them. Because weather prevented daily visits to the island during the peak of hatching in 1979, hatching dates were known for relatively few of the chicks. In 1980, observers visited particular nests on a daily basis

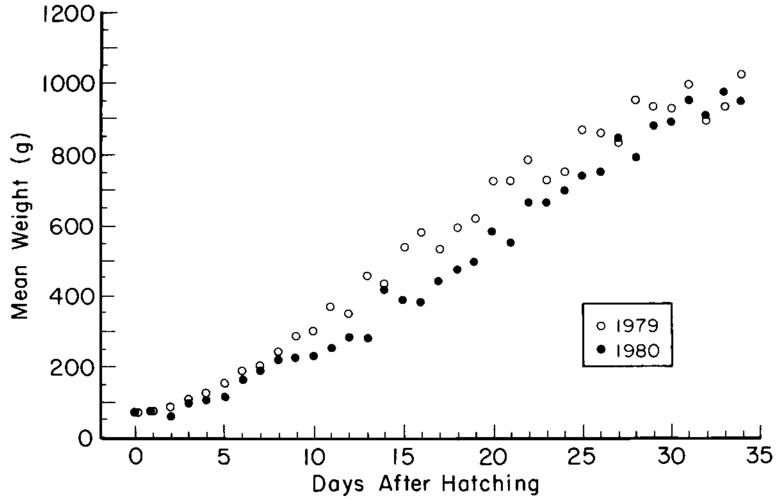

Fig. 2. Relationship between age and mean weight of chicks. Age-specific means, standard deviations, and sample sizes are reported in Murphy and Hoover (MS).

during the several-day period when eggs were most likely to hatch in those nests; because chick mortality rates were high in 1980, however, sample sizes of known-age chicks were again rather small.

Weight gain was more rapid in 1979 than in 1980 (Fig. 2); detailed data on weight gain and tarsus growth are reported elsewhere (Murphy and Hoover MS). Between hatching and 4 weeks of age, the 1980 mean weights exceeded the 1979 means on only two days, the day of hatching and day 27. Based on two-sample *t*-tests, average weights were significantly ($P < 0.05$) greater in 1979 than in 1980 on 17 of the first 29 days of life. In the fifth week of life, weights in 1980 increased more rapidly than in 1979, when weights were already reaching a plateau of about 1,000 g. Thus, near the end of the chick period, peak weights of chicks were comparable in both years.

Tarsal lengths were initially similar in 1979 and 1980 and again coincided at 4–5 weeks of age (Fig. 3). On 12 of 14 days in weeks 2 and 3 of age, however, the 1979 values were significantly ($P < 0.05$) higher than the 1980 values. Thus, chick survival was poor in 1980, and those chicks that did survive to fledging not only gained weight slowly but also experienced slow skeletal growth.

Food habits.—We observed the gulls to determine whether or not they were relying on human refuse for food during the breeding season. Both flight directions to and from the island and general observations throughout both summers indicated that the gulls did not commute to Seward (the nearest human community) while foraging during the breeding season; hence, the birds fed entirely within Aialik Bay. We believe that the high range of mountains separating Aialik Bay from Resurrection Bay prevented this overland flight.

Figure 4 summarizes our information on food habits. In 1979, blue mussels (*Mytilus edulis*) were the predominant food item before egg laying and remained important throughout the egg-laying period. During the times mussels were prevalent in castings, we observed adults feeding along rocky shorelines and on cobble beaches in upper Aialik Bay during low tides, and Squab Island was covered with regurgitated shells. We recovered one adult that had been killed by a Bald Eagle (*Haliaeetus leucocephalus*) on 5 June 1979 and that had approximately 150 intact mussels in its stomach; the mean length of a sample of these mussels was 14.6 mm (SD = 4.7 mm; $n = 59$; range = 6.4–25.6 mm). Based on age-length relationships reported by Feder et al. (1983) at Port Valdez, Alaska, these mussels probably averaged 2 yr of age and probably ranged from 1 to 3 yr of age. In 1980, mussels did not become a predominant item in the diet until the time of hatching but were prevalent in the 3 weeks following the initiation of hatching. Crabs (Crustacea: Decapoda,

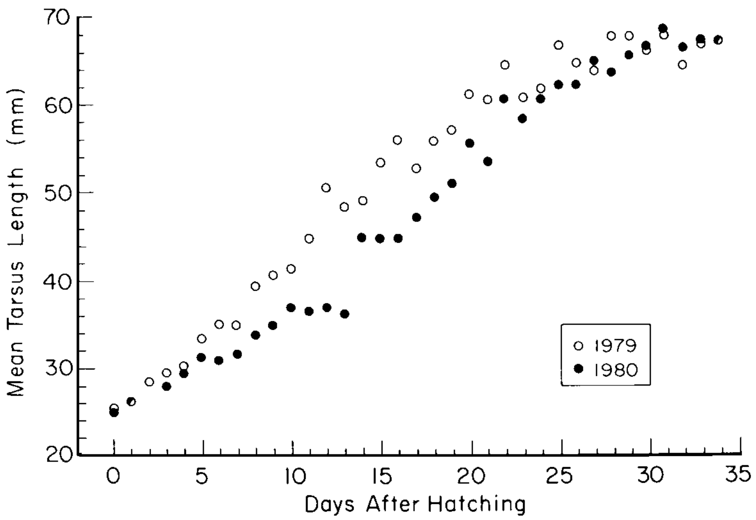

Fig. 3. Relationship between age and mean tarsal length of chicks. Age-specific means, standard deviations, and sample size are reported in Murphy and Hoover (MS).

Brachyura) occurred in the diet when mussels were prevalent and also appeared to be difficult to digest. Sea stars (Echinodermata: Asteroidea) occurred infrequently in the diet.

We observed algae in castings only briefly during the latter half of the egg-laying period in 1979 and found none in castings in 1980. Algae occurred in such high quantities that it appeared to us that the gulls were feeding directly on them rather than ingesting them incidentally.

Blood-soaked lanugo pelage from harbor seal (*Phoca vitulina*) pups was common during the seal-pupping period in both 1979 and 1980 (late May–early June; Hoover 1983). Regurgitated lanugo pellets were commonly seen throughout Squab Island when pupping on nearby ice-floes peaked. Although the gulls relied heavily on the afterbirths of harbor seals, Bald Eagles consistently displaced them from placentas in 1979; such displacements seemed relatively rare in 1980. Thus, the gulls apparently had less access to this food source during egg laying in 1979 than in 1980.

In 1979, fishes (e.g. walleye pollock, *Theragra chalcogramma*; cods, Gadidae; salmon, *Oncorhynchus* spp.; sand lance, *Ammodytes hexapterus*; and smelts, Osmeridae) became prevalent in the diet only when hatching began. In contrast, fishes were the dominant item in castings in 1980 during the early egg-laying period but occurred infrequently thereafter until about 3 weeks after hatching commenced. Euphausiids (Crustacea: Euphausiacea), shrimp (Crustacea: Decapoda, *Pandalus* spp.), and mysids (Crustacea: Mysidacea) were not observed in the diet in either year until hatching had begun; these foods were major items in the diet only during part of the chick period in 1979.

In 1980, three Pigeon Guillemot skulls were found near gull nests. Pigeon Guillemots nest in small numbers on Slate Island (see Fig. 1) and are numerous in Aialik Bay (Bailey 1977).

Discussion

Relatively few territorial pairs successfully built nests and laid eggs in 1979. Our qualitative observations indicated high levels of interference among nesting adults at that time, and intraspecific predation on eggs was observed. Thus, many territorial pairs in portions of the colony abandoned their breeding attempts quite early in 1979, and the difference in numbers of active nests between years reflects a large-scale failure at the nest-building stage in 1979.

Estimated territory sizes were equivalent in both years, averaging 11.4 m^2, and were smaller than those estimated at three other Glaucous-winged Gull colonies in Alaska (Patten and Patten 1983). Hunt and Hunt (1976) reported a

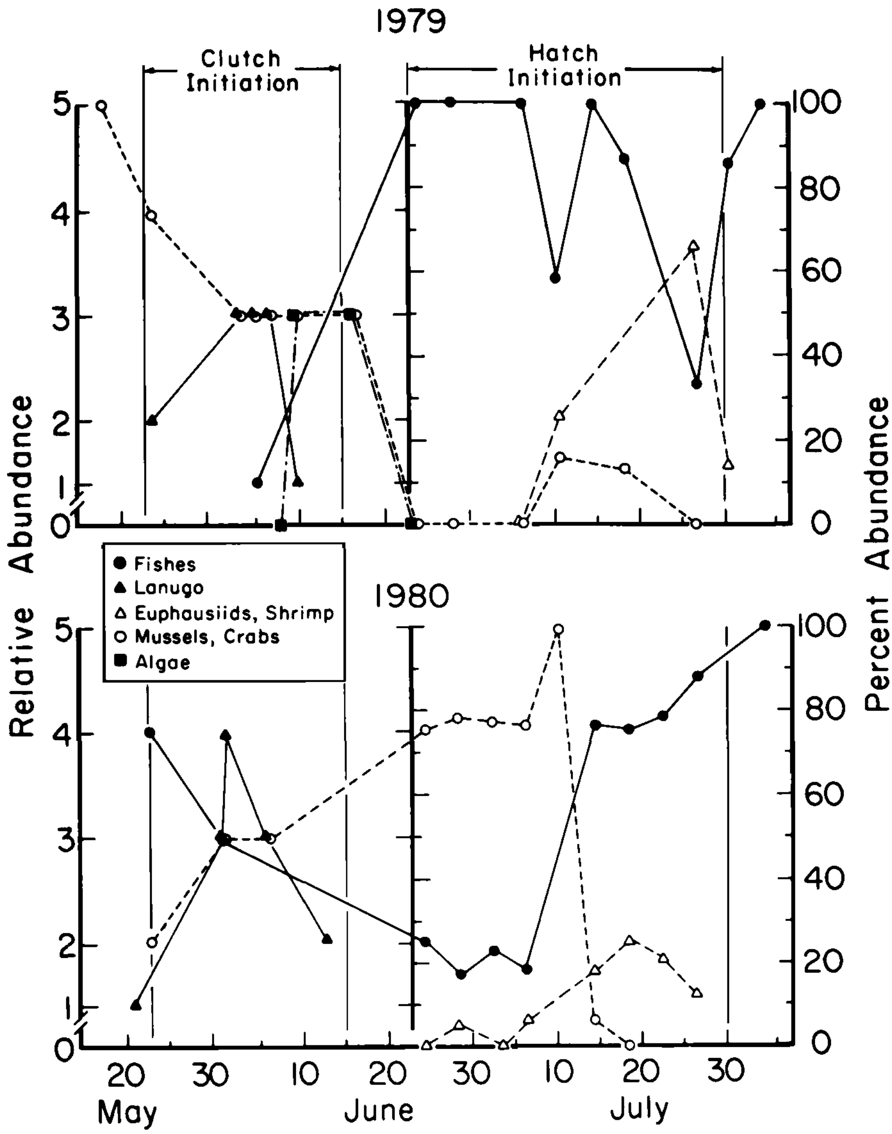

Fig. 4. Food habits of gulls nesting on Squab Island. Categories of relative abundance are summarized in the text and were determined qualitatively during visits to the colony before chicks hatched in both years. Values of percentage abundance, determined once hatching began, are based on an examination of 57 identifiable food items in 1979 and 132 items in 1980.

2-yr mean of 14.6 m^2 for Glaucous-winged Gulls on Mandarte Island, British Columbia, based on mapping of territorial boundaries. Our somewhat smaller value of 11.4 m^2 is based on Harper's (1971) method, which provides only a minimum estimate of territory size, because it is based on the estimated distance to the nearest boundary of the territory. Consequently, the average territory size on Squab Island during this study was probably similar to that on Mandarte Island but was smaller than that reported for other colonies in Alaska.

The average clutch size on Squab Island in 1979 was much smaller than has been found for Glaucous-winged Gulls anywhere else (e.g. Vermeer 1963, Moe and Day 1979, Patten and Patten 1983, Day and G. V. Byrd unpubl. data). In contrast, the 1981 mean clutch of 2.8 eggs was equal to the highest values reported for other populations. Thus, the variation in clutch size among years at Squab Island during this study was high and could indicate substantial annual variation in foraging conditions at the time of egg laying.

Hatching success at Squab Island was low in both years, and fledging success was exceptionally low in 1980. Breeding success in 1979 was equivalent to values reported for Egg Island, Alaska (Patten and Patten 1983) and for the 1961 values for Mandarte Island (Vermeer 1963); it was lower than all of the other values reported by Patten and Patten (1983) for other colonies in Alaska and the 1962 value for Mandarte Island (Vermeer 1963). The 1980 value for breeding success at Squab Island is by far the lowest yet reported for the species. Thus, clutch size was exceptionally small at Squab Island in 1979, and fledging success was extremely poor there in 1980.

Our findings of poor reproductive success in Aialik Bay, a glaciated fjord, contrast with those of excellent success in recently deglaciated areas of Glacier Bay (Patten and Patten 1983). Glaucous-winged and Herring gulls in Glacier Bay feed on a wide array of intertidal taxa and plunge-dive for small fishes, but Patten and Patten (1983) provide no quantitative estimates of the relative contribution of various food types to the diet.

The variation in diet between the 1979 and 1980 nesting seasons provides a plausible explanation for the variation between years in reproductive success. Depending on tidal conditions, mussels were readily available daily throughout the breeding season in both years. In each year, periods of poor reproductive performance coincided with the predominance of mussels in the diet. In 1979, when mussels were used heavily during egg laying, relatively few adults laid eggs and hatched them successfully; intraspecific predatory attempts on eggs appeared to be intense, and average clutch size was small. In 1980, mussels became prevalent in the diet once hatching began and were used extensively during the first several weeks of the chick period. Coincidentally, chick mortality rates were high, intraspecific predation on chicks was frequent, and growth (weight and tarsus) rates of the surviving chicks were slow.

A predominance of fishes coincided with high survivorship and rapid growth of chicks during the chick period in 1979 and with large clutches at the time of egg laying in 1980. Thus, an abundance of fish (and to a lesser extent, euphausiids and shrimp) appears to have important positive effects on the reproductive output of Glaucous-winged Gulls nesting on Squab Island (also see Lock 1973). Afterbirths and blood-soaked lanugo of harbor seals are probably also important during egg laying, and the similarities in egg-laying phenology between years may be related to marked similarities in phenology of seal pupping between years (Hoover 1983).

Our conclusion that blue mussels are avoided by Glaucous-winged Gulls when neritic fishes and invertebrates are available is in accord with studies of the food habits of Glaucous-winged Gulls elsewhere in Alaska. Trapp (1979) noted only low incidences of mussels in regurgitated pellets at two colonies in the western Aleutian Islands where mussels are abundant. Furthermore, mussels are of low caloric value compared with other intertidal prey (Altman and Ditmer 1968) and are avoided by Glaucous-winged Gulls that are foraging in intertidal zones (Irons 1982). Irons (1982) showed that small mussels are preferred over large mussels in the Aleutian Islands and suggested that the sturdy valves of mussels, which must be crushed in the gizzard, represent a high cost of digestion to gulls, compared with other intertidal prey.

Studies of *Larus* gulls elsewhere demonstrate that mussels are routinely incorporated into the diet and have no apparent adverse effect on reproductive success (Haycock and Threlfall 1975; Vermeer 1982). In contrast to the results of our study, mussels never predominated in the diet in these studies. Pierotti and Annett (MS), however, demonstrated that adults specializing on mussels had the highest reproductive success, those specializing on Leach's Storm-Petrels (*Oceanodroma leucorhoa*) had intermediate success, and those specializing on garbage had the lowest success in a colony of Herring Gulls in Newfoundland. We can provide no explanation for these discrepancies other than the observation that mussels at high latitudes grow more slowly than do those at temperate latitudes and are much more "obese" (Vermeij 1978); thus, their shells may be much thicker and more difficult for gulls to crush. Consequently, mussels in Alaska may be more difficult to digest than mussels near colonies at temperate latitudes, which would explain our results and Iron's (1982) findings of avoidance of mussels.

Most previous studies have postulated subtle (e.g. Brown 1967, Hunt 1972) to moderate (Pierotti 1979, 1982) influences of food availability on egg and chick survival. Our findings of early abandonment of nesting attempts and small clutch sizes in 1979 and poor chick survival and slow weight and skeletal growth of surviving chicks in 1980 suggest that reproduction is profoundly food limited at the Squab Island colony, as Lock (1973) postulated for gulls on Sable Island, Nova Scotia. The degree to which food limits reproductive output undoubtedly varies geographically, depending on the proximity of breeding colonies to suitable and preferred food supplies.

Summarizing earlier studies of the determination of clutch size in precocial birds, Winkler and Walters (1983: 55) suggested that "food supply during egg-laying may be a good predictor of food supply during brood rearing, and it may thus be used as a cue to adjust clutch size to future conditions." In our study, conditions during egg laying certainly were not linked to conditions when young would be in the nest. Large clutches were coupled with poor survivorship and slow growth rates of chicks in 1980; in 1979 clutch sizes were small, but, subsequently, chick survivorship and growth rates were high. Thus, food apparently acted temporarily and unpredictably as a proximate constraint on reproductive performance in our study.

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