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THE ECOLOGY OF SEABIRD FEEDING FLOCKS IN ALASKA

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ABSTRACT.—Seabirds commonly gather into mixed-species flocks to feed on fish schools and other concentrations of prey. We group Alaskan and Washington seabird feeding flocks into three types on the bases of flock size and longevity and the nature of the food source. Small, short-lived flocks over tightly clumped prey are called Type I; larger (5,000+ individuals), longer-lasting flocks over less tightly clumped and less reactive prey are called Type II; Type III flocks form where zooplankton and other organisms are concentrated by downwelling. Birds participating in the flocks are assigned to four functional groups (some species fit into two groups): *catalysts* (larids and shearwaters) are highly visible birds that other birds watch and follow to food sources; *divers* (alcids, loons, cormorants) exploit the food sources underwater by pursuit diving; *kleptoparasites* (jaegers and gulls) steal food from other flock members; and *suppressors* (shearwaters and cormorants) interfere behaviorally with the feeding of other flock members by reducing the effective prey availability.

Most flocks occurred within a few kilometers of shore. Type I flocks on the Washington coast averaged larger, lasted longer, and contained more species than Alaskan Type I flocks. The Washington and Alaska flocks contained about the same number of locally breeding species, but the Washington flocks also contained several migrant species that breed elsewhere in North America. Both contained shearwaters, migrants from the southern hemisphere, but the shearwaters were much more important in the Alaskan flocks.

Black-legged Kittiwakes and shearwaters (catalysts) initiated most Alaskan flocks and were important in the development of flocks initiated by other birds. Once a flock was initiated, it grew until the food source became unavailable or until the local pool of prospective flock members was exhausted. The divers were able to discriminate from considerable distances between kittiwakes feeding on single fish and kittiwakes feeding on fish schools and approached only the latter. The various species tended to occupy characteristic positions within Type I flocks. Gulls and kittiwakes were central, and the various divers took peripheral positions. Kleptoparasitism by jaegers did not appear to influence Type I flock organization. Shearwaters, the most important suppressors, sometimes pursuit-plunged into fish schools and euphausiid shoals in such numbers that the prey concentrations were drastically reduced, scattered, or driven downward in seconds, and other birds were then unable to feed.

Type II flocks were divisible into two groups, one consisting largely of kittiwakes and shearwaters and feeding on capelin, and the other dominated by shearwaters and feeding on pelagic crustaceans. Kleptoparasitism by Pomarine Jaegers in the capelin-based Type II flocks was frequent and differed from the kleptoparasitism of solitary birds in that the jaegers preferentially attacked birds carrying fish in their bills. Suppression appeared unimportant in capelin-based Type II flocks but probably kept alcids and gulls from joining the crustacean-based flocks. In some island groups Type III flocks occurred daily. They were less regular in structure and composition than Type I or Type II flocks.

Kleptoparasitism by gulls and kittiwakes tended to keep puffins and other alcids on the edges of the flocks. The alcids' underwater approaches to the fish schools from the sides may have tended to keep the schools compact and near the surface. It has been hypothesized that the antipredator function of schooling by baitfish involves predator satiation and the difficulty of locating schools. Schooling does not function as a deterrent to aerial predators in the same way that it does to swimming ones, however. Either birds are less important as predators, or schooling confers a different advantage in escaping aerial predation. Apparently, fish schools can escape rather quickly from bird flocks by descending away from the surface out of visual contact. *Received 8 January 1980, accepted 12 February 1981.*

FISH-EATING and other seabirds in most of the world's oceans exploit fish schools and other clumped food sources in multispecies flocks. These flocks often include several species that feed differently (Gould 1971, Scott 1973, Sealy 1973) but sometimes in a complementary manner. If indeed the birds use complementary tactics when feeding together, the assemblages may be tightly interacting, coevolved systems. We studied the avian communities of the temperate and subarctic northeast Pacific Ocean to discern how intense, consistent, and obligatory such feeding interactions are. We surveyed the geographic and hydrographic distributions of flocks in our study areas and characterized them by structure, species composition, and food resources.

We use "feeding flock" differently from previous authors (reviewed by Morse 1970, 1977). Morse (1970: 119) defined a flock as "any group of two or more birds, whose formation depends upon positive responses by individuals to members of their own or other species" in contrast to an aggregation, which is "a group of individuals that is drawn together only by some extrinsic factor such as a localized food or water source." Although these definitions appear inclusive, the associations we studied fall between them. They form over, and ultimately in response to, localized fish schools or other prey concentrations, but the mechanism of formation entails a positive attraction of birds to other foraging birds. Feeding flocks are separable from the foraging flocks common among terrestrial insectivorous birds (Morse 1970). The latter search as a group for dispersed food, while birds involved in feeding flocks often search individually for clumped food resources, and the flock forms once a food source is located.

Foraging in mixed-species flocks of terrestrial birds may be adaptive because group foraging is more efficient (Murton 1971), because predator detection is more effective in groups (Hamilton 1971, Pulliam 1973, Vine 1973), or through a combination of the two (Morse 1970). Marine flocks appear to have no major antipredator function, as the larger marine birds are quite free of predation while at sea; therefore, we concentrated our efforts on foraging performance. The thrust of our analysis is to assess the effects of the various species on the stability, longevity, and efficiency of the flocks. This approach is justifiable under the assumption that, once a prey concentration is located, maximum benefit is derived by all of the participating birds if contact with the prey is maintained as long as possible, while individual capture rates remain high.

STUDY AREA AND METHODS

We conducted our studies in the Gulf of Alaska in 1975 and 1976, primarily during the summer. In early August 1975, flocks in Chiniak Bay and the waters just east of Woody Island, near the village of Kodiak, were studied intensively. Data also were collected during August at Sundstrom Island, several places in the Shumagin Islands, and in Unalaska Bay. We also observed Chiniak Bay flocks in late September 1975. Locations at which feeding-flock data were gathered in Alaska are shown in Fig. 1.

In extensive nearshore operations around Kodiak in May 1976, we demonstrated that feeding flocks were uncommon in that month. We conducted further, vessel-based studies in the nearshore waters around Kodiak Island, in the Semidi and Shumagin islands, and in Unalaska Bay in July and early

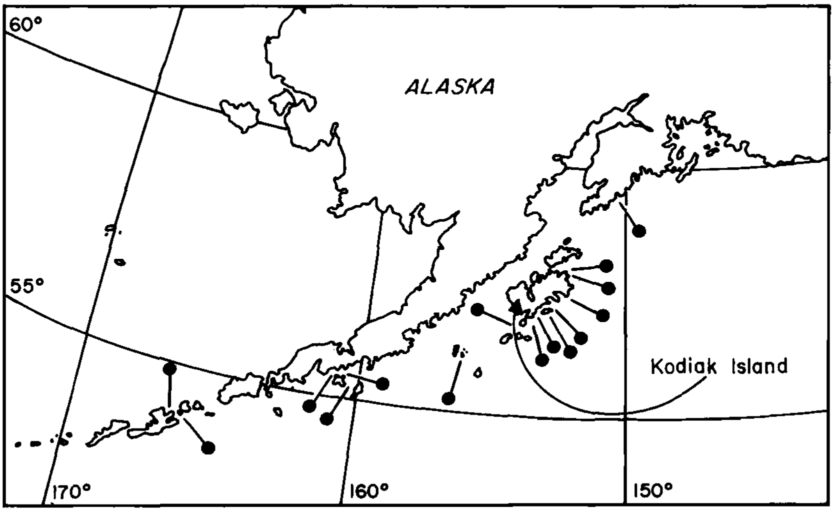

Fig. 1. Locations at which observations of marine-bird foraging flocks were made, 1975–1976.

August 1976. Intensive shore-based studies of flocks were made in August and September 1976 at Chowiet Island in the Semidi group, at Kodiak, and at East Unalga Island.

In addition, WH studied 65 flocks at Destruction Island, Washington in May–July 1974 and has observed flocks elsewhere along the Washington and Oregon coasts over several years.

We observed the flocks from the research vessels 'Surveyor' and 'Acona,' from smaller launches carried aboard those vessels, and from land at several sites overlooking areas of flock activity. The larger vessels were useful for determining the overall distribution of feeding flocks but usually were unsuitable for detailed observation. The smaller launches were used for detailed study in protected waters. Land-based work involved extensive observations of flocking in limited areas.

The 'Surveyor' is an 82-m vessel capable of 16 knots. We normally observed from the flying bridge, 15 m above the water. Her launches are 10-m craft with covered cabins and are capable of moving at about 8 knots. Normally, we sat on the foredeck or the cabin roof for flock observation, so our eye level was about 2 m above the water. The 'Acona' is a 27-m vessel capable of 10 knots. We made our observations from the fore and aft decks, where eye level was about 4 m above the waterline. We also made extensive use of a 5-m Boston Whaler, which was carried on the deck of the 'Acona.' All shipboard observations were made with 8× or 10× binoculars.

Land-based observations were made from points or headlands overlooking the ocean, often 20 m or more above sea level. A 20×–45× spotting scope was used as well as binoculars. All the Destruction Island flocks were observed from the island. On Kodiak, we made land-based observations from several points on the road system around the village of Kodiak. Most observations from Chowiet were made from the northwest point or in the coves on the north side of the island. Land-based observations at East Unalga were made from bluffs on the southwest and east sides of the island, overlooking the south end of Unalga Pass in the first instance, and Baby and Akutan passes in the second.

We recorded the time sequence of flock events and information on location, configuration, and composition. Environmental data collected included weather conditions and sea state. The behavioral data collected included descriptions of foraging methods and positions and patterns of arrival and departure. Flock initiations and observations of interactions (chases, displacements, kleptoparasitism, attraction) were stressed. In the analyses our flock observations are grouped into three catagories: all flocks recorded, all flocks where counts of individuals are available, and flocks actually seen being initiated.

The location information included the position of the flock relative to nearby landmarks, distance from the observer, and water depth (if determinable). The time sequences began with the initiation of the flock or the time we discovered it and included the times to the nearest second of all events noted in the flock. Observations of flock configuration and composition included estimates of flock size and shape and of the numbers and distribution of each species within the flock. If the flock as a whole was moving, its direction was recorded. For each species, we recorded arrivals and departures, vertical and horizontal position within and around the flock, feeding methods and rates, and interactions, especially between members of different species. The prey captured by flock members were identified when possible, usually in the bills of birds. Any marine mammals associated with flocks were noted and counted.

RESULTS

FLOCK TYPES

We recognized three principal flock types on the bases of flock size, longevity, and the nature of the food sources used.

Type I flocks are relatively small (usually <500, often <50 individuals) aggregations that form over fish schools or other highly clumped food sources. They form after the discovery of schools at or near the surface and end when the fish descend below contact with the birds. They are transient aggregations, usually lasting no more than a few minutes. Type I flocks were virtually limited to nearshore waters (220 of 221 observed in Alaska were within 5 km of shore). We spent extensive periods farther offshore in both summers, so this distribution does not reflect sampling bias. In Alaska and Washington, sandlance (*Ammodytes* sp.), herring (*Clupea harengus*), and various smelts (Osmeridae) probably were the most important baitfish exploited by Type I flocks, although in the absence of definitive diet studies the relative contributions of these and other fish species were unclear. Certainly these fish were the most important species carried to the nests of flocking birds at Destruction Island and at Chowiet [at Destruction Island, anchovies (*Engraulis mordax*) also were important].

In Alaska we collected data on 221 Type I flocks. We were able to get counts of each participating species in 155 flocks, and we observed the initiations of 112 flocks. At Destruction Island WH determined the composition of 52 flocks and observed 13 initiations.

Type II flocks are much larger (typically 5,000 to 50,000 or more individuals). They form over concentrations of prey that apparently do not act as cohesive units. Type II flocks feeding on capelin (*Mallotis villosus*) were regular in summer around Kodiak Island and elsewhere along the Alaska Peninsula. The capelin gathered into large spawning or post-spawning concentrations in fairly shallow water and remained for days or weeks. In the concentrations we observed, the fish tended on the average to be a meter or more apart, at least near the surface. The Type II flocks over these concentrations were present throughout the day and were present day after day. We were not able to tell whether they persisted through the night or re-formed each morning. We collected behavioral and compositional data from six Type II capelin-based flocks. Some of these flocks were studied for 2 or more consecutive days.

Other Type II flocks, dominated by shearwaters, fed on concentrations of euphausiids and perhaps other pelagic crustaceans. These prey swarmed to the surface in the evening and early morning, and the flocks usually were crepuscular or nocturnal. A few euphausiid species also swarm at the surface during the day (Brinton 1967), and occasionally we did observe the flocks during daytime.

The swarms we observed moved actively, and, as portions of them surfaced, thousands of shearwaters pursuit-plunged (see Appendix I for feeding-method terminology) into small areas, churning the water to froth. The shearwaters fed for very short periods (usually 20–60 s) in each location, suggesting that their activity decimated or dispersed the prey at those spots. Other (or re-formed) lobes of the swarm continued to surface, however, and the shearwaters moved about *en masse*, at times feeding for hours.

TABLE 1. Major functional groups of flock-feeding marine birds in the northeast Pacific Ocean. Scientific names are given in Tables 2, 3, and 6. Species are listed in decreasing order of importance.

Catalysts	Divers	Kleptoparasites	Suppressors
Black-legged Kittiwake	Horned Puffin	Pomarine Jaeger	Short-tailed Shearwater
Glaucous-winged Gull	Pelagic Cormorant	Parasitic Jaeger	Sooty Shearwater
Herring Gull	Red-faced Cormorant	Black-legged Kittiwake	
Mew Gull	Tufted Puffin	Glaucous-winged Gull	
Sooty Shearwater	Common Murre	Long-tailed Jaeger	
Short-tailed Shearwater	Rhinoceros Auklet		
	Thick-billed Murre		
	Double-crested Cormorant		

Type III flocks, or "rip flocks," formed where local water-mass discontinuities involving downwelling (rips) concentrated zooplankton and small fish. In Alaska, these rips are most common in island archipelagos and off headlands, where tidal currents flowing past the land meet and coalesce downstream from the obstructions. The duration of the flocks is thus limited by the tidal cycle. Type III flocks occurred daily in several places in the Semidi Islands and in the eastern Aleutians. We have little information on the prey obtained by rip flocks, but in the Semidi Islands murres carried small baitfish from the flocks, and puffins, which fed extensively but not exclusively in the rip flocks, predominantly carried juvenile *Ammodytes* to their burrows. Gould (1971: 16–25) and Ashmole (1971: 243) have described seabirds feeding at similar but much larger and more persistent hydrographic features in the tropical Pacific. Our observations of Type III flocks were made incidentally to studies of Type I and Type II flocks. Definitional problems (where and when does one flock end and the next start?) preclude our giving a count of Type III flocks studied.

FUNCTIONAL ROLES OF SPECIES IN FEEDING FLOCKS

We have grouped the species that participate in feeding flocks into four functional groups, *catalysts, divers, kleptoparasites,* and *suppressors* (Table 1). These groups are defined by their roles in flock organization, but the definitions correspond closely to the descriptions of different foraging tactics employed by the birds. The groups are not mutually exclusive, as some species perform different roles in different situations and are placed into two groups.

Catalysts are birds whose foraging and feeding behaviors are highly visible. The various flocking species watch the catalysts and use their feeding behaviors as indicators of the presence of food. Catalysts usually were the initiators of feeding flocks; even when contact with a fish school was made by a noncatalyst species, the arrival of a catalyst was necessary for rapid flock development. The most important catalysts in our study were gulls, especially Black-legged Kittiwakes and Glaucous-winged Gulls.[1] The shearwaters occasionally were used as fish location cues, primarily by kittiwakes and other shearwaters, so they may be considered to be catalysts.

Divers include birds that forage by pursuit-diving and pursuit-plunging. The larger Alcidae (auks) and the smaller cormorants were important divers in Alaskan feeding flocks. In addition, when small numbers of shearwaters joined the flocks,

[1] Scientific names of birds are given in Tables 2, 3, and 6.

TABLE 2. Species composition of Destruction Island flocks.

Species[a]	Number of flocks with species present (n = 52)	Number of individuals	Mean number/ flocks with species present	Mean number/ all flocks
Common Loon (*Gavia immer*)	8	13	1.6	0.3
Arctic Loon (*Gavia arctica*)	22	155	7.0	3.0
Red-throated Loon (*Gavia stellata*)	2	2	1.0	—
Sooty Shearwater (*Puffinus griseus*)	17	757	44.5	14.6
Brandt's Cormorant (*Phalacrocorax penicillatus*)	13	168	12.9	3.2
Pelagic Cormorant (*Phalacrocorax pelagicus*)	23	659	28.6	12.7
Cormorant spp.[b]	39	1,288	33.0	24.8
Large gulls[c]	52	3,527	67.8	67.8
Heermann's Gull (*Larus heermanni*)	7	492	70.3	9.5
Bonaparte's Gull (*Larus philadelphia*)	4	71	17.7	1.4
Black-legged Kittiwake (*Rissa tridactyla*)	2	6	3.0	0.1
Common Murre (*Uria aalge*)	37	1,045	28.2	20.1
Pigeon Guillemot (*Cepphus columba*)	2	2	1.0	—
Rhinoceros Auklet (*Cerorhinca monocerata*)	51	3,590	70.4	69.0
Tufted Puffin (*Lunda cirrhata*)	33	779	23.6	15.0

[a] The following species each occurred once: Sabine's Gull (*Xema sabini*), California Gull (*Larus californicus*), Double-crested Cormorant (*Phalacrocorax auritus*), Marbled Murrelet (*Brachyramphus marmoratus*), Buller's Shearwater (*Puffinus bulleri*), and Fork-tailed Storm-Petrel (*Oceanodroma furcata*).
[b] Cormorant spp. includes all the birds in the previous two rows, plus some unidentified cormorants, assumed to be one or the other of those species.
[c] Large gulls includes Western and Glaucous-winged gulls (*Larus occidentalis* and *L. glaucescens*) and their hybrids.

they functioned as divers. At Destruction Island, the nonbreeding loons and a large cormorant (*Phalacrocorax penicillatus*) also were important as divers.

Kleptoparasitism is the pirating of fish or other food from other birds. Jaegers exploited the flocks only in this manner, but gulls and kittiwakes (catalysts) also were facultative kleptoparasites. Although kittiwakes and gulls obtain most of their food in flocks by aerial and surface plunging, they also regularly attempt to rob each other and other birds.

Suppressors are species whose feeding sharply decreases the availability of prey to the other flock members. Sooty and Short-tailed shearwaters were the two important suppressors of the Alaskan flocks. Their noisy and disruptive feeding tactics (group pursuit-plunging) appeared to disperse or decimate the food sources and also may have interfered with the ability of the other birds to locate prey.

TABLE 3. Species composition of Alaskan Type I flocks.

Species[a]	Number of flocks with species present (n = 155)	Number of individuals	Mean number/ flocks with species present	Mean number/ all flocks
Shearwaters[b]	27	3,458	128.1	22.3
Fulmar (*Fulmarus glacialis*)	7	9	1.3	0.1
Cormorants[c]	43	1,649	38.3	10.6
Glaucous-winged Gull (*Larus glaucescens*)	54	1,526	30.1	9.8
Mew Gull (*Larus canus*)	2	11	5.5	0.1
Black-legged Kittiwake (*Rissa tridactyla*)	140	3,646	26.0	23.5
Murres[d]	10	53	5.3	0.3
Horned Puffin (*Fratercula corniculata*)	78	1,820	23.3	11.7
Tufted Puffin (*Lunda cirrhata*)	57	1,399	24.5	9.0

[a] The following species each occurred once: Fork-tailed Storm-Petrel (*Oceanodroma furcata*), Parasitic Jaeger (*Stercorarius parasiticus*), Red-legged Kittiwake (*Rissa brevirostris*), Pigeon Guillemot (*Cepphus columba*), Marbled Murrelet (*Brachyramphus marmoratus*), and Rhinoceros Auklet (*Cerorhinca monocerata*).
[b] Numbers are combined for Short-tailed and Sooty shearwaters (*Puffinus tenuirostris* and *P. griseus*).
[c] Numbers are combined for Red-faced and Pelagic cormorants (*Phalacrocorax urile* and *P. pelagicus*).
[d] Numbers are combined for Common and Thick-billed murres (*Uria aalge* and *U. lomvia*).

COMPOSITION, STRUCTURE, AND DYNAMICS OF FLOCKS

Type I flocks.—The species compositions of the Destruction Island and Alaskan Type I flocks are summarized in Tables 2 and 3. Twenty-one species occurred in Destruction Island flocks, although 10 of these were recorded fewer than five times. A maximum of 13 species was recorded from a single flock. Seven species nesting in the area made up the bulk of most flocks and, overall, accounted for 93% of the participating individuals. Large gulls (Western, Glaucous-winged, and their hybrids; see Hoffman et al. 1978) and Rhinoceros Auklets each accounted for 32% of the individuals, while the murres, puffins, and cormorants together accounted for 29%. Pigeon Guillemots were recorded twice and two other area residents, Marbled Murrelets and Fork-tailed Storm-Petrels, once each. The remaining 7% of the individuals were distributed among 11 species of migrants. Sooty Shearwaters accounted for the majority of these. Heermann's Gulls took part extensively when they were present but appeared at Destruction Island only in July, toward the end of the study period. Loons were regular participants but in low numbers. The others were rarely participants and appear to be of no functional importance to the flocks.

The composition of the Alaskan flocks was strikingly different. Although we gathered composition data on three times as many flocks and from a wide geographic area, only 18 species were recorded participating. Gulls accounted for 38% of the flock participants (27% kittiwakes, 11% Glaucous-winged Gulls). Cormorants were less regular and less common in the flocks than at Destruction Island. Most of the species were breeding in the study areas, but the two migrant shearwater species accounted for 25% of all individuals seen. Type I flocks in Alaska tended to be smaller and to have significantly fewer species than at Destruction Island. The mean

TABLE 4. Species roles in initiations of Type I feeding flocks in Alaskan waters.

Species	Number of flocks in which species occurred: All flocks (n = 221)	Number of flocks in which species occurred: Flocks seen being initiated (n = 112)	Species initiated flock formation: Number of flocks	Species initiated flock formation: Percentage all flocks	Species initiated flock formation: Percentage flocks with species present
Sooty Shearwater	18	3	1	0.9	33.3
Short-tailed Shearwater	32	27	9	8.0	33.3
Cormorants	74	31	2	1.8	6.5
Glaucous-winged Gull	81	23	2	1.8	8.7
Black-legged Kittiwake	204	101	85	75.9	84.2
Horned Puffin	112	52	7	6.3	13.5

number of species in the Alaskan flocks, 2.79 (range 1–6) differs significantly from the 5.54 (range 1–13) at Destruction Island (Student's t = 8.716, 103 df, $P < 0.001$).

The Alaskan flocks averaged 88.1 (range 2–995) individuals and the Destruction Island flocks 212.0 (range 4–590) individuals (t = 3.89, 207 df, $P < 0.001$). The difference in flock size may result largely from the greater mean duration of Destruction Island flocks ($\bar{x}$ = 819 vs 100 s at Chowiet; unpaired t, unequal variances = 5.46, $P < 0.001$) and partly from the fact that many of the Alaskan observations were taken in restricted bays and channels with relatively small bird populations.

The lower species richness of the Alaskan flocks results largely from the absence of Northern Hemisphere migrants. The segments of the nesting communities that eat midwater fish are of similar size, although, overall, the Alaskan seabird community is much richer. For example, 7 of at least 19 breeding seabird species in the Semidi Islands were regular foragers on midwater baitfish, while 7 of only 13 residents on the Washington coast used this resource. The presence of more plankton feeders in the Alaskan communities accounts for the increased community richness.

Type I flock initiations.—Typically a single individual or a small group of birds detected the fish school and began feeding. In most cases a catalyst located the school. Of 112 Alaskan Type I flock initiations we observed, 85 (76%) were by Black-legged Kittiwakes (Table 4). Five of seven initiations reported by Sealy (1973) in the Queen Charlotte Islands were also by (nonbreeding) kittiwakes.

We observed only two initiations by Glaucous-winged Gulls in Alaska, although they were present in 36% of the flocks. However, Glaucous-winged and Western gulls accounted for 10 of 13 flock initiations recorded on the Washington coast in 1974. In the presence of kittiwakes, Glaucous-winged Gulls seemed less active in searching for schools. When Alaskan flocks dispersed, kittiwakes normally left rather quickly and spread out into a wide-ranging search pattern. The Glaucous-winged Gulls usually sat on the water at the old flock site for several minutes or until a new flock began to form nearby.

Cormorants and Horned Puffins were the only divers observed to initiate flocks. When they discovered fish schools, flock development was slow until a catalyst arrived and began feeding. For example, at Chowiet Island on 8 August 1976, WH observed a flock that started with three Horned Puffins diving. Two Glaucous-winged Gulls joined them and sat on the water. After 20 s (presumably when the fish school approached the surface) the gulls began feeding, and within the next 20

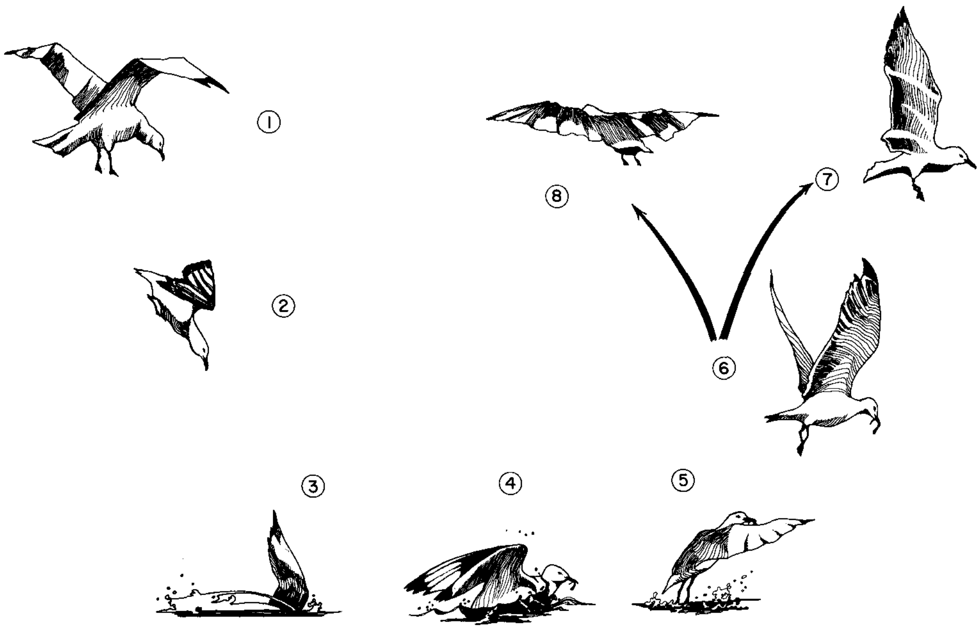

Fig. 2. Sequence of a typical feeding plunge of a Black-legged Kittiwake. The characteristics of steps 6–8 are used as food-location cues by other species participating in mixed-species feeding flocks.

s the flock grew to about 50 birds. The same morning several flocks initiated by kittiwakes were observed, and they each grew to 40–100 birds within the first 20 s.

The regular Type I participants responded in very specific ways to the behavior of Black-legged Kittiwakes. The response patterns demonstrated that the birds normally were able to distinguish searching kittiwakes from feeding kittiwakes, kittiwakes feeding on garbage from kittiwakes feeding on fish, and kittiwakes feeding on single fish from kittiwakes feeding on fish schools. When no flocks are active in an area, kittiwakes spread out and fly slowly 10–25 m above the water searching for food. Birds that circle, hover, or plunge attract other kittiwakes.

The responsiveness of the divers to feeding kittiwakes varied considerably from area to area and through the season. Observations (by WH and JAW) at Kodiak 26–29 August 1976 were of unusually selective birds, so they best illustrate the birds' discriminative capabilities. When a kittiwake plunged (Fig. 2, steps 1–3), other kittiwakes responded immediately, but the Horned Puffins and cormorants (both Pelagic and Red-faced) did not move until the first kittiwake left the water. If the kittiwake flew to continue searching (Fig. 2, step 7), the divers did not approach, but if it circled over the spot (step 8), they flew or dived to the spot (Table 5), and an active flock formed.

We also have observations of alcids using the direct flight of birds to a flock as a flock presence cue (Fig. 3). In one case at Destruction Island, WH observed gulls feeding on a fish school to the south of the island. Rhinoceros Auklets off the southwest end of the island took off from the water and flew to the flock. Other auklets flying past the northwest point of the island, and completely blocked from view of the flock, veered south around the island to follow the first auklets into the flock.

TABLE 5. Species' responses (percentage of observations) to behavioral cues of Black-legged Kittiwakes in feeding-flock formation.

Species	Response	Kittiwake behavior: Plunge and leave ($n = 54$)	Kittiwake behavior: Plunge and circle ($n = 26$)	Chi-square
Black-legged Kittiwake	Positive	94	100	0.36
	Negative	6	0	
Horned Puffin	Positive	0	73	47.80*[a]
	Negative	100	27	
Cormorants	Positive	2	88	58.63*
	Negative	98	12	

[a] * = $P < 0.0001$.

Common Murres and Horned Puffins similarly were observed to follow kittiwakes to a flock around the northwest point of Chowiet Island. Gould (1971) reports that similar responses to travelling birds extend the "drawing radius" of central Pacific flocks well beyond the distance that the flocks are actually visible.

Shearwaters used somewhat different cues in responding to birds locating prey concentrations. Our best data on shearwater flock initiations came from near East Unalga Island, in September 1976. When shearwaters were present in large numbers, they frequently streamed through feeding grounds in relatively dense lines (Fig. 4A) that were sometimes several kilometers in length. Stragglers spread out across the adjacent water. When a kittiwake or one of the stragglers plunged (Fig. 4B), apparently upon sighting a single prey or a prey concentration, nearby members of the line turned and approached. Others in the line followed (Fig. 4C). Clearly many of the birds responded by following their neighbors rather than by independently flying to the flock. When the submerged shearwaters emerged, the arriving birds passed on by (Fig. 4D), and eventually the birds that entered the feeding flock rejoined the line (Fig. 4E).

Flock development.—Once a Type I flock had been initiated, it developed following a fairly regular pattern. Gulls and kittiwakes flew in at 10–25 m altitude. In wind they swung around to join the flock at the downwind end, but in calm air they approached from all directions, and began searching as soon as they approached the flock. Alcids pursuit-plunged or landed and dived at the boundaries of the flock and swam in underwater. Nearby cormorants and alcids sometimes dived toward the flock. Shearwaters flew to the center of the flock and pursuit-plunged. The flock built until contact with the fish apparently was lost, or until all interested birds within sight had joined. Near colonies, some long-lived flocks reached "equilibrium" when the number of birds coming in was similar to the number returning to the colony with prey loads.

Type I flock structure.—Kittiwakes were mostly aerial and formed the bulk of the above-surface part of Alaskan flocks. In calm air they usually gathered into fairly circular groups, but in wind the flocks usually were elongated along the axis of the wind. Glaucous-winged and Western gulls played a similar role in the Destruction Island flocks but spent more time sitting on the water and surface-dipping (see Appendix I). Flocks often had one or more foci of intense gull activity, probably corresponding to spots where portions of the fish school were close to the surface.

Fig. 3. An example of social attraction of birds to a feeding focus not directly visible to them. The feeding flock at A is observed by birds at B, which fly to join it. Birds at C cannot see the flock but follow the birds flying from B.

These foci typically were short-lived in comparison to the duration of the flock as a whole.

Diving birds often were distributed in particular patterns around the flocks. In Alaska, puffins tended to dive and surface in a circle around the area of kittiwake activity. Cormorants dived and surfaced in the centers of the flocks, and actively joined the local foci of kittiwake feeding.

The Destruction Island flocks tended to have more complex organization. Most were distinctly elongated along the axis of the wind, and the birds were arranged

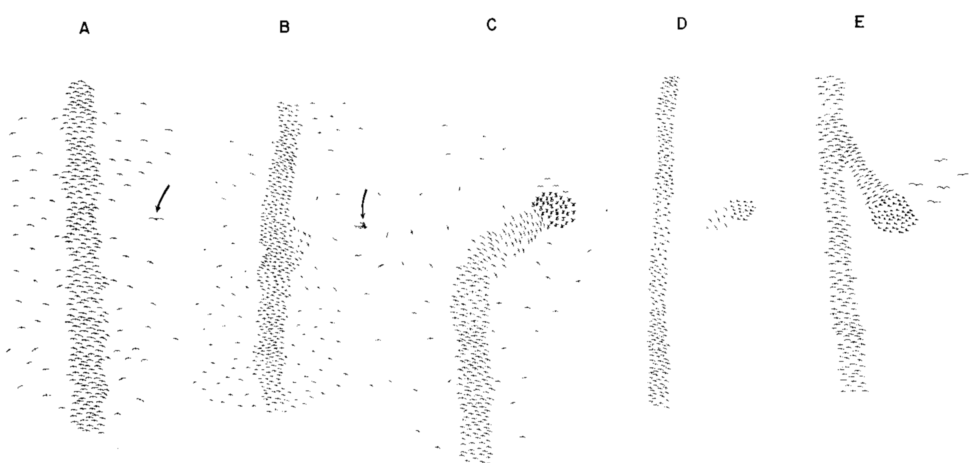

Fig. 4. Sequence of response of a single shearwater flock (moving toward the top of the figure) to a foraging kittiwake (arrow) that discovered food.

in a rather stereotyped pattern. Gulls stayed over the school, loons surfaced and dived at the upwind end of the flock, Rhinoceros Auklets and Tufted Puffins usually sat laterally to the gulls, and cormorants typically were located at the downwind end and in the interior of the flock. Many of the longer-lasting flocks moved considerable distances (always upwind) while remaining active. The loons appeared to lead the other birds, staying ahead of the general gull activity.

Type I flock breakup.—The kittiwakes and gulls generally lost contact with prey first, because they must maintain visual contact from the air or the water surface. When they lost contact, some of the kittiwakes sat on the water at the site, but most gradually dispersed outward in characteristic searching flight.

The Alaskan Glaucous-winged Gulls usually sat on the water after they lost contact and waited for the kittiwakes to locate the next school, but at Destruction Island the Glaucous-winged and Western gulls spread out and searched like kittiwakes. This difference is reflected in the initiation frequencies. Of the 112 initiations we saw in Alaska, Glaucous-winged Gulls accounted for only 6% (2 of 23) of initiations of flocks containing them. In contrast, at Destruction Island the large gulls initiated most (10 of 13) of the flocks. Usually the diving species made a few dives after the gulls lost contact, but soon lost contact themselves. When flocks were frequent, the divers did not search underwater for schools once they had lost them, but waited on the surface as the gulls searched for other schools. At times when flocks were less frequent, some of the divers dived for several minutes after surface contact was broken.

Kleptoparasitism in Type I flocks.—Kleptoparasitism is prevalent among gulls and is the predominant foraging method of jaegers at sea. We observed jaegers approaching flocks and attacking kittiwakes. The kittiwakes did not exhibit obvious escape maneuvers until attacks were initiated, and, even then, most of the birds in the flocks did not appear to react. The jaegers did not often enter large Type I flocks, but remained in the general area and attacked lone birds.

Our observations indicate that those jaegers that do enter the larger flocks have lower success at obtaining food (at least on a per-attack basis) than those that attack lone kittiwakes. For example, on the afternoon of 25 July 1976 we observed a large flock of kittiwakes feeding intermittently on capelin at Two-headed Island, off the south shore of Kodiak Island. One Parasitic Jaeger entered the flock and attacked several kittiwakes. At each attack, 3–5 kittiwakes followed the jaeger closely but did not interfere with either the jaeger or the chased kittiwake. In four consecutive attacks that occurred close to our vessel, the jaeger succeeded in forcing the kittiwake to regurgitate, but in each case the following kittiwakes beat the jaeger to the regurgitated food and swallowed it themselves.

Gulls (especially kittiwakes) opportunistically attempted to rob a variety of birds. Because the fish-eating alcids carry fish to their nests in their beaks, they are vulnerable to robbery (e.g. Grant 1971, Nettleship 1972). The puffins and Rhinoceros Auklets may be more vulnerable than the murres, because they carry several fish crossways in the bill rather than one lengthwise and largely inside the bill. On the water the alcids usually are successful at escaping robbery by diving, but occasionally one is robbed by a gull attacking just as the bird emerges from a dive. We did not observe any attempts at robbery of cormorants.

Suppression of Type I flocks.—The two species of shearwaters are very gregarious and regularly travel in flocks of several hundred to many thousand birds. In the North Pacific they are strictly nonbreeding migrants, although they are the most abundant Alaskan seabirds. They feed primarily by pursuit-plunging. Typically, a flock sat on the water or flew as a group until a bird (a shearwater or gull) discovered a school of fish or a shoal of euphausiids or other crustaceans at the surface. The entire flock then flew to the site and plunged into the water. If the flock was large, birds continued to fly in for as much as 20–30 s. Dive times were easily obtained for birds in these flocks, because the birds surfaced simultaneously (generally within a 5-s period). Birds arriving after a flock surfaced lit on the water. Few of the shearwaters ever made a second dive at a site. Instead, they sat on the water and waited for a new school to be located (or flew about searching for one). Normally they did not dive to search for schools, but dived at schools located visually.

On 22 September 1975 the area of outer Chiniak Bay, Kodiak, between Long Island and Middle Bay, contained about 5,000 Short-tailed Shearwaters, distributed in several discrete flocks of 500–800 birds each, 1,000–2,000 Common Murres, several hundred puffins of both species, and 800–1,000 Black-legged Kittiwakes. Apparently, all were feeding on juvenile fish [juvenile sandlance (*Ammodytes*) were schooling abundantly in the bay at that time]. Both the kittiwakes and the shearwaters frequently were locating fish schools, but each time a school was located, the nearest flock of shearwaters would fly into it within 10–25 s. The shearwaters rafted on the surface upon emerging and waited for the next school to be located or took off *en masse* to search aerially. We saw no attempts by the murres and puffins to join the flocks.

Type II flocks.—Table 6 summarizes the compositions of the six Alaskan Type II capelin-based flocks that we studied. These flocks were dominated by Sooty Shearwaters and Black-legged Kittiwakes, but 14 other species also occurred in them. Several of these species apparently were not feeding on the capelin and may have been just passing through. In Alaska, the alcids tended to avoid Type II flocks. WH has seen similar flocks off the Oregon and Washington coasts, apparently exploiting concentrations of northern anchovy (*Engraulis mordax*). Alcids occurred in these flocks much more frequently than in the Alaskan flocks. Northern sea lions (*Eumetopias jubata*) were present in three of the flocks and harbor seals (*Phocaena phocaena*) in two.

The Type II flocks that fed on crustaceans were composed almost entirely of shearwaters (for 10 flocks, mean = 64,500 shearwaters, range 800–300,000; counts of large flocks were made by counting 50 or 100 birds, then counting by 50s or 100s to 1,000, and then counting thousands). Smaller numbers of Black-legged Kittiwakes, Tufted Puffins, and occasionally other birds joined them, but we do not have accurate counts of these. Short-tailed Shearwaters appeared to be much more common than Sooty Shearwaters in these flocks, but we could not determine the actual ratios of the two. Hump-backed and finback whales (*Megaptera novaengliae* and *Balaenoptera physalis*) were present under some of the flocks.

We did not observe the initial steps in the formation of Type II flocks but have no reason to suspect fundamental differences from those of Type I flocks (except that shearwaters, which normally travel in large groups, may arrive in groups instead of singly). The Type II flocks had less structural complexity than the Type I flocks. Gulls and kittiwakes fed almost exclusively from the air. Shearwaters mingled among the gulls but fed by pursuit-plunging and pursuit-diving. We did not detect any trends in flock shape nor any tendencies for particular species to occupy peripheral positions.

Kleptoparasitism in Type II flocks.—Pomarine Jaegers regularly joined the Type

TABLE 6. Composition of Type II capelin-based feeding flocks observed in Alaskan waters.

Species	Number of flocks (n = 6)	Number of individuals	Mean number/ flocks with species present	Mean number/ all flocks
Sooty Shearwater	6	93,650	15,608	15,608
Manx Shearwater (*Puffinus puffinus*)	1	1	1	0.2
Fulmar	1	50	50	8.3
Fork-tailed Storm-Petrel	2	40	20	6.7
Cormorant	3	140	46.7	23.3
Northern Phalarope (*Lobipes lobatus*)	1	100	100	16.7
Parasitic Jaeger	4	7	1.8	1.2
Pomarine Jaeger (*Stercorarius pomarinus*)	6	238	39.7	39.7
Antarctic Skua (*Catharacta maccormicki*)	1	1	1	0.2
Glaucous-winged Gull	6	1,290	215	215
Black-legged Kittiwake	6	51,900	8,650	8,650
Arctic Tern (*Sterna paradisaea*)	1	3	3	0.5
Common Murre	1	100	100	16.7
Ancient Murrelet (*Synthliboramphus antiquus*)	1	20	20	3.3
Horned Puffin	3	140	46.7	23.3
Tufted Puffin	5	631	126.2	105.2

II capelin flocks but foraged by a "low stakes" method of kleptoparasitism. They patrolled through the busy areas of the flocks and preferentially attacked birds (kittiwakes and shearwaters) that surfaced with fish in their bills. If the victim dropped its fish, the jaeger retrieved it. Thus, by dropping the one most recently caught fish, the victim could protect its (often large) load of swallowed fish.

On 6 August 1975 at least 100 Pomarine Jaegers were present off Kodiak in a flock of about 10,000 Black-legged Kittiwakes and 40,000 Sooty Shearwaters. We were unable to detect any effects of their activity on the overall foraging behavior of the kittiwakes.

Kleptoparasitism by kittiwakes also was important in Type II flocks. Kittiwake piracy attempts on all birds increased when the frequency of fishing plunges decreased. When given a choice, kittiwakes apparently preferred to catch their own food (they are much better at it, with overall success rates around 60% for plunges, under 10% for piracy), but, when fish were not immediately available, they regularly tried to rob other birds. Kittiwake piracy attempts on each other were more frequent in Type II than in other flock types (we observed piracy attempt rates as high as 50/100 birds/h in Type II flocks—rates were hard to determine in Type I flocks but were much lower, ca. 10/100 birds/h).

Suppression in Type II flocks.—The Type II capelin-based flocks did not appear to be subject to suppression. In the crustacean-based flocks, however, the shearwaters wheel about in tremendous streams and plunge synchronously into the water. We have observed such flocks off Ugak Island (off Kodiak) on several occasions from mid-May through September, off Chirikof Island in September, in the eastern Aleutians throughout September, and irregularly elsewhere throughout the continental shelf areas of the Gulf of Alaska and the southern Bering Sea. Tufted Puffins were seen regularly in the vicinity of these flocks, but they dived independently and did not attempt to join the local foci of shearwater activity, so they may have been inhibited by the commotion of the flocks.

Composition, structure, and development of Type III flocks.—Type III flocks formed after slack tide, when rips began to form in the accelerating currents. We did not detect any particular patterns of development. Birds flew in and landed in the forming rip as singles or more frequently in groups. After 60–120 min flock size sometimes appeared to reach equilibrium, with the number of arrivals approximating the numbers returning to the colonies.

These flocks generally were dominated by alcids but sometimes contained large numbers of Fulmars, kittiwakes, and Glaucous-winged Gulls. We lack numerical composition data, because the flocks usually were observed at great distances, so that the alcids could be identified only in flight, and because they had less discrete boundaries than the other flock types. During August 1976 WH observed Type III flocks around Chowiet Island that contained tens of thousands of Tufted Puffins and Common Murres, thousands of Horned Puffins, Thick-billed Murres, and Fulmars, and smaller numbers of several small alcids. In September 1976, rips in Baby Pass off East Unalga Island contained flocks of at least eight species of alcids, including the rare Whiskered Auklet (*Aethia pygmaea*).

The rips that Type III flocks occupied were regular in occurrence. Thus, in the 2 weeks WH spent at East Unalga, rips formed in the southern end of Baby Pass, off the southeast corner of Egg Island, and in several other locations on each outgoing tide, as water rushed through the passes from the Bering Sea to the Pacific. On the incoming tides, rips extended north from Egg Island toward Unalaska, north from the Baby Islands into Akutan Pass, and into the Bering Sea, north of the passes. These rips were visible for several kilometers as disturbances on the ocean surface, so the birds might have flown to the area of a rip directly in response to its physical appearance or from memory. Within concentrations of birds along rips, however, gulls and kittiwakes clearly responded to each other in joining over local concentrations. The alcids were not observed moving along the rip in response to the gulls, but, when they first approached a rip, they apparently preferred to alight in places where other alcids were concentrated. Conspecifics tended to group together, but we did not detect any pattern in the dispersion of these groups within the flocks. We did not observe any particular effects of kleptoparasites or of suppressors on the Type III flock organization.

Discussion

Flock structure and organization.—Flock feeding is frequent in coastal areas of the northeastern Pacific through the nesting season, and breeding and nonbreeding individuals of several seabird species are regular participants in the flocks. The major flocking species exhibit complex and standardized behavior patterns in the flocks. Some of these species' behavior patterns tend to be complementary and indicate a degree of integration in the community. Our observations of the responses to catalysts in Type I flock formation (Fig. 2, Table 5) showed that the divers were strongly attuned to kittiwake foraging behavior. If we make one reasonable but unproved assumption about kittiwake behavior, these response patterns can be interpreted as having allowed the divers to determine from a distance which kittiwake plunges were likely to indicate the presence of a fish school. The assumption is that a foraging kittiwake will not abandon a school of visible baitfish to search for other fish. It follows from this assumption that, when a kittiwake makes a plunge but does not circle back, there is not a fish school visible beneath it and that, in the cases where we saw a kittiwake catch and swallow a single fish without circling back, it saw only the single fish. If this assumption is correct, then the divers' habit of joining only those kittiwakes that circled back saves them the energy of following kittiwakes that have not located fish schools. The behavior of other arriving kittiwakes supported this assumption. When the first bird left without circling, later arrivals did not plunge or circle, although they often did try to rob the first bird. When the first bird did circle back over the site, the other kittiwakes invariably circled and plunged, confirming that fish schools were present, and divers joined the flock.

The kleptoparasitic interactions provide more provocative evidence of community integration. We suspect that the characteristic arrangement of alcids on the periphery of the Alaskan Type I flocks is an adaptation to avoid kleptoparasitism. Because the alcids can escape robbery attempts by diving (unless they are attacked just as they emerge), obviously the safest places to emerge are on the fringes of the flock, out from under the gulls. Most of the attempts at kleptoparasitism of puffins that we observed occurred when puffins emerged directly under the flock of kittiwakes. These attacks occurred at times when the kittiwakes were circling but doing little or no plunging, which suggests that puffins swimming underwater may have difficulty seeing birds flying above them but may have much less difficulty detecting areas where kittiwakes are actively plunging and disrupting the surface.

This reaction of the alcids to kleptoparasitism may be very important to the overall performance of the flocks. Because the alcids dived on the fringes of the flock and presumably approached the fish schools from the sides or from beneath in the concentrated Type I flocks, they may have had the effect of concentrating the school or of delaying its descent out of contact with the flock. If this is so, then the divers' positioning may contribute significantly to the length of time the fish school is available to the flock. Thus, an aggressive, proximately destabilizing behavior (kleptoparasitism) may have the incidental effect of forcing the alcids to forage in a manner that probably stabilizes the flock and increases food availability to all the birds (but especially to the gulls).

The mutualistic role of kleptoparasitism in flock organization appears to be a purely incidental result of aggressive behavior by the kittiwakes and gulls. These birds attempt to rob each other and other birds in a wide variety of situations, both within and outside of flocks. We saw them attempt to rob only those species that regularly held fish crossways in their bills. If attempted robberies were in fact aggressive attempts to force the divers to position themselves laterally to the schools, we would expect gulls to attack murres and cormorants as well. Instead, we saw only attacks directed at those species that were vulnerable to robbery per se.

Our observations also showed that community integration was not complete, that interference among species could limit species participation and/or success in flock feeding. Flock suppression is the most obvious example of species interference, but we found evidence indicating two more subtle examples as well. The first involved the activities of cormorants in Type I flocks. The cormorants tended to move to the centers of the flocks and to plunge there. Because they normally swallowed their prey under water, they were relatively invulnerable to gull kleptoparasitism. This foraging location is likely to have a destabilizing and shortening effect on the flocks by causing maximum disruption of the fish schools, but such destabilization would be difficult to demonstrate. Our Type I flocks with cormorants were not noticeably shorter in duration than flocks without cormorants, but, as we had no control over other variables affecting fish-school movements, the data are inconclusive.

The other example of possible interference involves the possible exclusion of alcids from Type II flocks by gull and kittiwake kleptoparasitism. We observed several Type II flocks in an area (near Chiniak Bay, Kodiak) where puffins were common and were readily taking part in Type I flocks, but few of the puffins joined the Type II flocks, and most of those that did were subadults. Because the flocks are very large (sometimes more than a kilometer in diameter), puffins cannot swim in under water from the edges and thus are continuously vulnerable to kleptoparasitism. In all flocks, kittiwake piracy attempts on all birds increased when the frequency of fishing plunges decreased. When given a choice, kittiwakes apparently prefer to catch their own food, but, when fish are not immediately available, they regularly try to rob other birds. Because the fish under Type II flocks are relatively dispersed, kittiwake piracy attempts on each other are more frequent than in other flocks. Murres and cormorants are less vulnerable to the kittiwakes, and both participated in Type II flocks, but neither was common in the areas in which we observed Type II flocks.

Suppression was the most obvious and probably the most important type of interspecies interference. The combined activity of 500 or more birds simultaneously diving into a dense fish school must result in dispersing the school, driving it deeper into the water column, or decimating it. When flocks of shearwaters were feeding in an area in this way, they clearly prevented the normal development of Type I flocks. Some kittiwakes joined the shearwater flocks, but typically they foraged for only 5–10 s on a given school before the school was unavailable to them. Puffins and murres in the area did not attempt to join the massed attacks, but instead they dived solitarily or in small groups throughout the area.

The complementarity of the feeding behavior of catalyst and diving species in Type I flocks appears to be mutually beneficial. Given the apparent mutualism, we must consider the possibility that the birds' behavior and perhaps morphology have coevolved to effect a more efficient mutualistic system. If this were the case, the traits that we would expect to be modified would be the behavior and color of the catalyst species. Our observations suggest, however, that any such modification is minor. Aerial plunging is inevitably a highly conspicuous method of foraging, so birds that forage in this manner will, almost by definition, be highly visible. The possibility that the plumage patterns of catalysts are selected to maximize visibility is more difficult to evaluate. Gould (1971) found a strong correlation between plumage patterns (white wing linings contrasting with dark mantle) that were highly visible in flocks and flock participation in the central Pacific; he explained this in terms of social mimicry (Moynihan 1960, 1968). Simmons (1972) also suggested that white or black-and-white plumage in seabirds has often evolved to aid in group formation for feeding. While we have demonstrated a potential benefit to the catalysts from attracting other birds in our area, it seems unlikely that this benefit is sufficiently general to account, by itself, for the prevalence of white plumage in flock-feeding seabirds, especially as it also occurs in seabird communities that lack pursuit-diving species. As Simmons and others have noted, birds presenting white ventral and anterior aspects should be much less visible to submerged prey and thus should be more successful than darker birds at this form of feeding. Because these two potential selective forces apparently operate in the same direction, separating their effects would be extraordinarily difficult.

Interactions of the feeding birds and their prey.—The hypothesis that schooling of fishes is an antipredator adaptation figures prominantly in discussions of the functions of schooling (e.g. Brock and Riffenburg 1960, Clarke et al. 1967). Brock and Riffenburg developed a geometrical proof demonstrating that an aquatic predator should have greater difficulty finding tightly clustered prey than dispersed prey and that, when it does find a school, it can only eat a small portion before becoming satiated. This may be an effective strategy against aquatic predators, especially those that forage alone, but birds probably forage more successfully on schooled than dispersed prey. Because many birds may respond to the discovery of a school, the geometric advantages of prey aggregation are largely circumvented. Our observations demonstrate that schooling does not interfere with the birds' ability to select and capture individual prey; we have recorded 70–100% success rates by kittiwakes and Glaucous-winged Gulls feeding in flocks. Simmons (1972) described schools of larger fish in the tropical Atlantic that packed together very tightly and apparently were not attacked by birds, but we have no evidence that the Alaskan baitfish achieved this degree of packing. The persistence of schooling in the presence of abundant flock-feeding birds suggests that birds are less important as predators than large fish and predatory marine mammals, or, alternatively, that schooling confers some different advantage in escaping avian predation.

Above we noted that the divers generally quit diving shortly after the catalyst species ceased feeding on each fish school. This suggests that deep fish schools can escape rather quickly from the divers. The birds can no longer watch each other to relocate the school once it is too deep to be visible from the surface, so the fish need not lose all of the divers at once.

We also observed that the longer-lasting flocks at Destruction Island uniformly tended to move upwind. This consistent upwind direction of movement and the equally consistent orientation of the flocks on the axis of the wind suggest that the fish schools orient in some way to the wind. Perhaps the fish orient to the water movements within the wind-generated surface waves. A more interesting, but perhaps less likely, possibility is that the birds, by consistently approaching the schools from downwind, are actually driving the fish upwind.

Concluding comments.—The features of apparent community organization and complementarity of roles in mixed-species marine-bird feeding flocks suggest some hypotheses that should be explored through further research. Our observations lead to the prediction that the feeding success of all the flock-feeding species should be greatest where catalyst numbers are adequate—where there are few catalysts present, at least some of the flock-feeding species might experience difficulties in locating food. From this we might expect that populations of the normally flocking species should increase more rapidly when catalysts are present in at least moderate numbers than when their densities are low. This suggests that reductions in populations of catalyst species might have far-reaching impacts upon such systems. As we have suggested that the catalyst species derive benefit from the participation of divers in feeding flocks, we also might expect catalysts to have somewhat greater foraging success in areas populated by moderate numbers of diving species in comparison to areas with few divers. Finally, if species whose role in feeding flocks is disruptive (e.g. shearwaters, cormorants) are abundant, their activities might have a major effect on the population dynamics of other species that normally associate with feeding flocks.

These suggestions, and our observations of northwestern Pacific mixed-species flocks reported here, indicate that the marine-bird assemblages occurring in such areas have complex sorts of interrelationships, involving varying degrees of interdependence. As these birds may play a major role in the trophic dynamics of marine ecosystems (Wiens and Scott 1975, Furness 1978), their patterns of feeding and their associations obviously merit close study.

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APPENDIX I. Feeding methods used in north Pacific feeding flocks. All except those marked by an asterisk are from Ashmole (1971).

Aerial piracy	One bird chases another in the air and attempts to rob it.
*Aerial plunging	Bird plunges from air for a fish near the surface.
Pursuit-plunging	Bird plunges from air and swims under water.
*Surface-plunging	Bird plunges from sitting position on surface; submerges most of its body.
*Hop-plunging	Bird sitting on the water jumps into air then plunges.
Pursuit-diving	Bird dives from surface, swims under water.