MARINE BIRDS FEED AT GRAY WHALE MUD PLUMES IN THE BERING SEA

BRYAN S. OBST1 and GEORGE L. HUNT JR.2
1Department of Biology, University of California, Los Angeles, California 90024 USA, and
2Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717 USA

ABSTRACT.—Gray whales (Eschrichtius robustus) feeding in the northern Bering Sea produce prey-rich mud plumes that provide ephemeral foraging opportunities for seabirds. Approximately 67% of all gray whales were attended by birds. In four whale-associating bird species (Northern Fulmar, Fulmarus glacialis; Red Phalarope, Phalaropus fulicaria; Black-legged Kittiwake, Rissa tridactyla; and Thick-billed Murre, Uria lomvia), from 17 to 87% of all individuals that we observed on the water or foraging were in the whales’ mud plumes. The combined density of these same four species was strongly correlated with whale density over a broad range of spatial scales. The whale-associating seabirds exhibited species-specific patterns of foraging behavior at plumes, including differences in mean group size, mean residence time, and patterns of movement between plumes. Birds tended to form larger groups and to form more mixed-species flocks in association with whales. The association of marine birds with gray whales in the Bering Sea provides a model system for examining seabird interactions at fine-scale oceanographic patches and demonstrates the importance of these patches in shaping patterns of seabird distribution and behavior. Received 12 February 1988, accepted 11 April 1990.

LITTLE information is available on the ways in which patterns of distribution and behavior of marine birds are influenced by patterns of patchiness in the ocean at scales of 1–100 m (i.e. fine-scale patches). This is unfortunate, because interactions of foraging seabirds with their prey are bound to occur at relatively small scales (Brown et al. 1979, Brown 1980, Hunt et al. 1985, Obst 1985, Safina and Burger 1985, Heinemann et al. 1989, Piatt in press). Attempts to understand the ways in which birds respond to oceanographic events at larger scales must incorporate information on how individual seabirds make decisions regarding where they will spend their time. Fine-scale patterns are notoriously resistant to study in pelagic systems, because of the difficulties associated with systematically locating and quantifying small, ephemeral patches. These difficulties are compounded by the difficulties presented in tracking and observing the behavior of individual seabirds in the open ocean.

Gray whales (Eschrichtius robustus) are plentiful on their summer foraging grounds in the northern Bering Sea. They are unique among large cetaceans in that they are specialized as bottom foragers (Evans 1982, Jones et al. 1984). The whales slurp deep furrows in the sea floor (Oliver et al. 1983, 1984) and strain the sediments through their baleen to remove benthic amphipods, their major food (Rice and Wolman 1971, Nerini 1984). Recent estimates have placed the turnover of sediments by gray whales in the Bering Sea at ca. 109 m3 per summer (Johnson and Nelson 1984). Much of this sediment is carried to surface waters as the whales surface to breathe, which creates large muddy plumes in their wakes (Rugh and Fraker 1981). Large numbers of whole and damaged benthic invertebrates are included in these plumes, some of which may remain at the surface for several minutes after a whale has surfaced (Fig. 1).

In a series of aerial surveys in the northern Bering Sea, Harrison (1979) detected seabirds of several species that apparently feed in muddy patches left by gray whales. He suggested that foraging in association with gray whales may be important for Bering Sea birds. Foraging associations between seabirds and cetaceans are common throughout the world’s oceans (see Evans 1982 and Burger 1988 for recent reviews). During three field seasons (1983–1985) of oceanographic cruises in the Bering Sea, we were impressed by the widespread associations between birds and gray whales throughout the Chirikov Basin. In 1985, we studied the association of seabirds with gray whale mud plumes as a model system of the influence of ephem-
eral, fine-scale patches on the species-specific foraging behavior and distribution of marine birds at sea.

METHODS

Our study was conducted aboard the 'Alpha Helix' between 28 July and 4 August, 1985, in the Chirikov Basin to the west and southwest of King Island (Fig. 2). On a series of six shipboard transects (cumulative 300 transect miles), the number of birds of each species that occurred within a 90-degree arc 300 m ahead and to one side of the ship was recorded on a portable microcomputer, along with the the birds' behavior when first observed, size of flocks, weather and viewing conditions, and the ship's speed and position (Updegraff and Hunt 1985). The presence, absence, and estimated numbers of gray whales along the transect lines were also noted, as were any observed associations between seabirds and whales or whale plumes.

To observe the behavior of seabirds associated with gray whales, we also stopped the ship within 300-500 m of foraging whales and bird associates. This distance allowed us to view the animals' activities without disturbing them. With three to six observers simultaneously on the bridge, we monitored the diving behavior of the whales, the arrival and departure of birds from the whale-generated mud plumes, and the duration of foraging activities of the birds at the plumes. Observations were recorded onto a cassette tape recorder. The tape was allowed to run continuously throughout an observation period, which lasted up to 60 min for a single whale. We subsequently transcribed the tapes, and determined the temporal course of events.

To determine what the birds ate, we collected birds seen feeding at plumes. We shot birds from the ship's bow or from a small launch and retrieved them from the sea surface by net. We collected 28 birds at whale slicks to the west of King Island on 29 July (n = 12) and 30 July (n = 16), 1985. Stomachs were either removed immediately or first flushed with ethanol to inhibit further digestion of prey and dissected 1-2 hours later. The size, number, and species of recognizable prey items were recorded for each stomach.

RESULTS

SEABIRD-WHALE ASSOCIATIONS

Gray whales were abundant in the study area. One or more gray whales were recorded in 39% (77/195) of our 10-min transect segments. Seabird-gray whale associations were also common during our study. Of 95 whales or whale groups seen within 500 m of the ship (i.e. whale events) along a cruise track from King Island to St. Lawrence Island, 63 (66%) had associated birds. Northern Fulmars (Fulmarus glacialis), Red Phalaropes (Phalaropus fulicaria), Black-legged Kittiwakes (Rissa tridactyla), and Thick-billed Murres (Uria lomvia) were observed at 48%, 28%, 23%, and 12% of all whale events, respectively. The percentages of all individuals recorded on the water and observed in association with whale events ranged from 17% (Thick-billed Murres) to 87% (Red Phalaropes and Black-legged Kittiwakes) (Table 1). For these four species, combined bird density averaged 3.5 times greater in transect segments in which gray whales were present than in those in which whales were absent (Table 1).

Other less common surface-feeding species (Sabine's Gull, Xema sabini; Glaucous Gull, Larus hyperboreus; Herring Gull, L. argentatus; Pomarine Jaeger, Stercorarius pomarinus; Parasitic Jaeger, S. parasiticus; and Long-tailed Jaeger, S. longicaudus) were observed with whales at least once during the study. Several species of pursuit-diving alcids were recorded regularly during transects but were never observed feeding in association with whales. They included Least Auklet (Aethia pusilla), Crested Auklet (A. cristatella), Parakeet Auklet (Cyclorrhynchus psittacula), Tufted Puffin (Fratercula cirrhata), and Common Murre (Uria aalge).

Correlations between bird and whale densities.—For the common, whale-associating species, the density of birds observed either feeding or on the water was strongly correlated with the number of whales in a transect segment. Such correlations were observed at a variety of measurement scales (segment lengths), ranging from
approximately 1.5 nautical miles (10 min of transect time) to 10 nautical miles (see Table 2). Correlation coefficients changed little with measurement scale either within individual transect lines (maximum $r$ between 0.73 and 0.89) or for all transects pooled ($r$ between 0.33 and 0.37; Table 2). Correlation coefficients were generally higher when only transect segments along a single transect line were considered than when data from all six transects were pooled. This decrease in correlation reflects a loss of information in the pooled data, which is inevitable because of temporal variation in numbers of birds and whales encountered.

By comparison, the density of Least Auklets—an abundant species that we never saw feeding in whale plumes—was not significantly correlated with whale density at any measurement scale. In fact, correlation coefficients were uniformly negative ($r$ between $-0.27$ and $-0.12$) for all six transect lines.

Flock composition.—For each of the four common whale-associating species, the mean number of birds seen to feed or on the water was greater among whale-associating flocks than among those apart from whale events (Table 1). This was true whether the number of each species was considered separately (whale-associating flocks were 1.8-2.4 times larger) or the numbers of all four species were combined (whale-associating flocks 5.7 times larger).

Multispecies flocks were common at whale

---

Fig. 2. Location of seabird transect lines in relation to the principal feeding grounds of the gray whale in the Chirikov Basin, northern Bering Sea. Boundaries of the whale feeding grounds are taken from Johnson and Nelson (1984: 1150), and the rough limits of the Ampeliscid benthic community are drawn after Nerini (1984: 423).
TABLE 1. The importance of gray whale mud plumes as foraging sites for Bering Sea birds. Numbers refer only to birds observed feeding or on the water during transects. Differences between means (two-tailed Student's t-test) are significant at * = P < 0.05, ** = P < 0.01, and *** = P < 0.001; sample sizes are in parentheses.

| Species          | Away from plumes (n) | At plumes (%) | With whales (f ± SE) | Without whales (f ± SE) | Ratio   | Birds per flock |
|------------------|----------------------|---------------|----------------------|-------------------------|---------|-----------------|
|                  |                      | At plumes (n) |                      |                         |         |                 |
| Northern Fulmar  | 157                  | 190           | 55                   | 2.68 ± 0.69             | 0.81 ± 0.16 | 3.3***         | 3.91 ± 0.55 (46) | 1.78 ± 0.25 (87) | 2.2*** |
| Red Phalarope    | 80                   | 505           | 87                   | 5.17 ± 1.50             | 1.17 ± 0.51 | 4.4**          | 19.28 ± 3.25 (35) | 7.69 ± 2.94 (9)   | 2.4*   |
| Black-legged Kittiwake | 23       | 155           | 87                   | 1.72 ± 0.56             | 0.18 ± 0.06  | 9.6***         | 4.05 ± 1.02 (37)  | 1.72 ± 0.30 (18)  | 2.4*   |
| Thick-billed Murre | 271             | 56            | 17                   | 1.59 ± 0.26             | 1.00 ± 0.15 | 1.6            | 2.08 ± 0.48 (24)  | 1.22 ± 0.04 (176) | 1.7*** |
| Species combined | 531                  | 906           | 63                   | 11.16 ± 1.92            | 3.16 ± 0.68 | 3.5***         | 9.83 ± 1.44 (90)  | 1.74 ± 0.18 (289) | 5.7*** |

* Sample sizes are 112 transects with whales present, 81 transects without whales.

behaviors and prey capture. As a whale surfaced, kittiwakes would lift and resettled directly above it, dipping and picking in the forming plume. When the whale swam at the surface, usually making several “blows” events. Groups of whale-associating birds comprised from one to six species. Mixed-species flocks accounted for 48% (29/61) of all whale-associating groups. In contrast, only 2 of 67 flocks that fed or were on the water apart from whales comprised more than one species. At plumes, the frequency of flocks encountered declined as species' diversity increased. Mono-specific flocks were most common, and two-, three-, and four-species assemblages were progressively rarer. The observed frequency distribution was not significantly different from that predicted by a binomial expansion based upon the independent probability that each species was present or absent at a given whale event (P > 0.25). Similarly, among the four common whale-associating species, there was no statistically significant tendency for any pair of species to co-occur in a flock more often than one would predict by chance association alone (P > 0.25).

BEHAVIOR AT MUD PLUMES

The foraging behaviors of the individual species feeding at mud plumes varied markedly. We observed differences in the timing of arrival at the plumes, the length of time birds remained at a given plume, and methods of prey capture while they fed.

Black-legged Kittiwakes.—Black-legged Kittiwakes were the most active of the whale-associating species. As a whale surfaced, kittiwakes in the area flew rapidly to the whale and hovered directly above it, dipping and picking in the forming plume. When the whale swam at the surface, usually making several “blows” along the way, kittiwakes would lift and resettled directly above it, dipping and picking in the forming plume. When the whale swam at the surface, usually making several “blows” along the way, kittiwakes would lift and resettled directly above it, dipping and picking in the forming plume. When the whale swam at the surface, usually making several “blows”
The behavior of the kittiwakes was synchronized with the behavior of the whales (Fig. 4). Discrete flocks of kittiwakes followed individual gray whales for periods of at least one hour. The flocks spent much of the time resting on the water, waiting for the whale to surface from a feeding dive. Flocks took wing immediately after the whale blew (perhaps first alerted by its sound), flew to it, and fed vigorously while it was at the surface and producing a fresh plume. When the whale submerged for another feeding dive (throwing its fluke up as it dived), the kittiwakes again settled on the water. The rate of surface-pecking declined rapidly, and the birds then waited for the next fresh plume.

The periodicity of the birds' feeding cycle varied with the periodicity of an individual whale's diving cycles. Comparison of the diving rhythms of two gray whales and their attendant kittiwake flocks indicates that the birds remained longer at the plumes of the whale with longer foraging dives. These birds did not spend significantly more time actually feeding at the plumes that were produced (Table 3). The birds with the longer-diving whale spent extra time resting on the water, ostensibly waiting for the whale's next blow.

Red Phalaropes.—Like kittiwakes, phalaropes typically arrived as plumes formed when a whale surfaced. Unlike kittiwakes, however, phalaropes never fed while flying. All phalaropes fed while they swam at the plume. Oc-
TABLE 3. Comparison of the diving behavior of two gray whales (A and B) and the behavior of their two attendant Black-legged Kittiwake flocks. Times (s) are $\bar{x} \pm SE (n)$. Significant differences between means (two-tailed $t$-test) for the two whales and for the two kittiwake flocks are indicated by $^* = P < 0.05$, $^{**} = P < 0.01$, and NS = not significant.

|                      | Whale A          | Whale B          | Ratio A : B |
|----------------------|------------------|------------------|-------------|
| **Gray Whales**      |                  |                  |             |
| At surface           | 93.0 $\pm$ 6.8 (5) | 68.8 $\pm$ 5.4 (8) | 1.35$^*$    |
| Under water          | 411.6 $\pm$ 23.2 (5) | 211.1 $\pm$ 6.9 (7) | 1.95$^{**}$ |
| Total cycle          | 504.6 $\pm$ 40.5 (5) | 279.9 $\pm$ 20.0 (7) | 1.80$^{**}$ |
| **Black-legged Kittiwakes** |            |                  |             |
| In air               | 93.4 $\pm$ 13.1 (5) | 52.2 $\pm$ 6.7 (7) | 1.79$^*$    |
| On water             | 332.2 $\pm$ 30.4 (5) | 199.5 $\pm$ 15.6 (6) | 1.66$^{**}$ |
| Feeding (whole flock)| 94.3 $\pm$ 10.8 (4) | 106.4 $\pm$ 13.7 (6) | 0.89 (NS)   |

casional birds spun and dabbed in typical phalarope fashion, but the vast majority simply swam and picked at the surface. As they arrived, flocks of phalaropes usually settled on the freshest part of the plume, but unlike kittiwakes, they did not follow the whale if it repeatedly surfaced. Often, members of the flock spread out by swimming “up-plume” toward the newer portions. The time devoted to a given plume was more variable—and averaged longer—than in kittiwakes (16.80 $\pm$ 6.8 min, $n$ = 6 flocks; Fig. 2). Moreover, feeding continued in the flock during its entire attendance at a plume, although feeding was always most vigorous upon arrival. We never observed phalaropes landing or attempting to feed on the backs of the whales, as reported elsewhere (Kumlien 1878).

The amount of time Red Phalaropes spent feeding at a given plume exceeded, on average, the period of a whale’s dive cycle. Phalaropes rarely moved along with an individual whale. They abandoned plumes by suddenly taking wing and wheeling in tight flocks at heights of 2-50 m. These flocks circled, apparently until they spotted a surfacing whale; then they rapidly settled behind it on the new plume. Among whale-associating species, Red Phalaropes occurred in the largest groups (Table 1). Flocks tended to fragment while the birds fed at plumes, but formed again during the apparent search flights. Phalarope densities were highest in transects with whale groups rather than with isolated whales, and their “whale-hopping” behavior is probably facilitated by their selection of waters with whale groups.

Northern Fulmars.—The behavior of Northern Fulmars at whale plumes was distinctive in several ways. On average, fulmars invested the longest time at a given plume, often >30 min (Fig. 3). In fact, their persistence at plumes usually outlived our patience for monitoring their activities. Although fulmars often occurred in small groups at mud plumes (Table 1), they were distinctly less flock-oriented than kittiwakes or phalaropes. Individual fulmars arrived at and departed from plumes throughout our observation periods. Some fulmars first arrived long after other species had stopped feeding. There was surprisingly little coordination between fulmar activities and whale movements. Fulmars seldom pursued surfacing whales closely, and often settled in older parts of plumes, even as fresh material was being released by a whale.

Northern Fulmars fed by settling on the surface of a plume, paddling slowly, and pecking at the surface film. Rates of pecking remained high throughout the fulmars’ residence at a plume ($\bar{x}$ = 75 pecks/min, $SE = 11$, $n$ = 4). In contrast, feeding activity of kittiwakes and phalaropes was initially intense, but waned gradually.

Thick-billed Murres.—Among the four most common whale-associating species, Thick-billed Murres were the only pursuit divers. They were irregular visitors at whale plumes; only 17% of all murres seen on the water were conspicuously associated with whales (Table 1). Yet, those murres we observed with whales were clearly keyed in to a whale’s presence.

Most often, Thick-billed Murres flew to a surfacing whale, hovered briefly with rapid wing beats, then dropped into the water directly behind or in front of the traveling whale. The murres immediately dove upon hitting the water, and presumably fed in the rapidly settling sediment. In other cases, individual murres...
Fig. 5. The length of prey (amphipods) taken from the stomachs of seabird species collected while they fed at gray whale mud plumes as a function of body mass. In general, the average size of the largest prey items increased with the size of the predator, and the majority of large (>10 mm) prey items were found in the largest bird species. Abbreviations: RP = Red Phalarope; BLK = Black-legged Kittiwake; NF = Northern Fulmar; TBM = Thick-billed Murre. Sample size is 7 for each bird species.

Stomach Contents

We collected 28 birds as they fed at whale plumes, 7 individuals of each of the four common whale-associating species. A detailed analysis of the stomach contents of these birds and their relationship to the underlying benthic communities will be presented elsewhere (N. Harrison and J. Grebmeier in prep.). We will summarize briefly these data. Stomachs of the whale-associating birds contained almost exclusively benthic crustaceans. Most important were tube-dwelling Ampelisca amphipods (Table 4), a major food of the gray whale and an infaunal form not normally present in surface waters (Rice and Wolman 1971, Nerini 1984). In general, there was a broad overlap in the species and sizes of prey taken by the birds, particularly among the surface feeders. There was a trend for mean prey size to increase with the body size of the predator among the four common whale associates (Fig. 5). In particular, Red Phalaropes took only small amphipods (of the 10 largest items, \( \bar{x} = 2.9 \) mm), while Thick-billed Murres took most (70%) of the items larger than 1 cm (Ampelisca macrocephala, Lembos spp.) present in the 28 birds. Net tows through fresh mud plumes suggest that large amphipods settle most rapidly (Harrison and Grebmeier in prep.) and may therefore be most available to the diving murres. Prey items from Black-legged Kittiwakes and Northern Fulmars were similar in size and species, despite the birds’ markedly different behaviors at plumes.

Discussion

Distribution of birds.—Because of the difficulties in systematically locating and quantifying small-scale patches of prey in the open ocean, few investigators have examined the importance of such patchiness in shaping patterns of seabird distribution and behavior. Previous studies have focused on two types of patches: (1) subsurface prey patches located by SONAR, which usually lack a conspicuous surface expression (Woodby 1984, Obst 1985, Safina and Burger 1985, Schneider and Piatt 1986, Hunt et al. MS); and (2) conspicuous surface phenomena, presumed to be correlated with increased prey availability (Brown 1980, Au and Pitman 1986, Haney 1986). Correlations between sea-
Table 5. Summary of studies that analyze effect of small-scale prey patches on the distribution of seabirds.

| Source                        | Patch type          | How identified | Scale | Bird-density increase in transects with prey patch? | Corr. with patch number or size | $r$ |
|-------------------------------|---------------------|----------------|-------|-----------------------------------------------------|---------------------------------|-----|
| This study                    | Gray whale plumes   | Visual         | 1.5-10 NM | Yes (3.1)                                           | <0.001                           | Yes | 0.1-0.8 |
| Schneider and Platt 1986      | Fish schools        | Acoustic       | 0.25-15 km | ?                                                   | Yes 0.1-0.9                      |     |
| Safina and Burger 1985        | Fish schools        | Acoustic       | Variable | ?                                                   | No (NS)                          |     |
| Obst 1985                     | Krill schools       | Acoustic       | 10 min (1-2 NM) | Yes (2.6)                                   | <0.001                           | No  | (NS)    |
| Heinemann et al. MS           | Krill schools       | Acoustic       | Yes     | ?                                                   | No (NS)                          |     |
| Haney 1986                    | Sargassum reef      | Visual         | 15 min (6-10 NM) | Yes                                           | ?                                |     |
| Woodby 1984                   | Fish schools        | Acoustic       | 10-15 min | No                                                   | NS                               |     |
|                               | Zooplankton         | Acoustic       | 22-5.6 km | Yes (1-1.8)                                         | <0.05                            |     |

* All subsurface except whale plumes and Sargassum reef.

1 Visual = visually at surface, and Acoustic = acoustically, using echo-sounding methods.

2 NM = nautical mile.

Despite the co-occurrence of the birds and whales throughout large areas of the transects, the diets of nonwhale-associating alcids in the Chirikov Basin vary, and they range from diets made up primarily of planktonic crustaceans (Least and Crested auklets) to diets dominated by fish (puffins and the Common Murre; Harrison 1987). None of these species is known to eat substantial quantities of the benthic amphipods that dominated the diets of the whale-associating species. If numbers of all alcids were included in our analyses, correlations between seabird densities and whale densities would certainly have been poorer. This points to the need to use information obtained from behavioral observations of patch use and analyses of stomach contents in distributional studies.

Least Auklets showed negative correlations with whales on all transects, which suggests a tendency to prefer different habitats for foraging. In sharp contrast to our findings, Harrison (1979) reported that small auklets (including Least Auklets) were numerically dominant among the species he observed at mud patches. Kittiwakes and fulmars were comparatively rare. It is difficult to interpret these discrepancies, but the complete absence of auklets from all whale events that we observed suggests a large annual or seasonal difference in the foraging behavior of these birds. Alternatively, Harrison’s aerial observations may not have permitted him to distinguish individuals that...
happened to be near whale plumes from those that actively entered and fed in them.

**Behavior of birds at plumes.**—Most studies of seabird behavior at fine-scale patches have suffered from a dearth of information regarding the size, composition, and distribution of the prey patches. In fact, many studies have used the characteristics of the seabird flocks themselves (e.g. size, density, and fixity) to infer characteristics of prey patchiness (e.g. presence/absence, location, size, density, and movement of patches) (Hulsman 1978; Hoffman et al. 1981; Duffy 1983, 1986). This approach may lead to a certain circularity, when differences in predator behavior—first assumed to reflect differences in prey patches—are later offered as evidence for behavioral adaptation (resource partitioning, mutualism) to the varying patch types (Duffy 1983, 1986).

We found that the behavior of the four primary whale-associating bird species varied markedly and consistently from one another at similar patches. That is, a single oceanographic event represented four separate kinds of patches to the birds. For kittiwakes, it represents a highly ephemeral but regularly recurring patch; for phalaropes, clustered patches of intermediate duration; for fulmars, a stable, isolated patch; and for the murres, a subsurface patch of denser-than-background prey. The disparate foraging abilities of these species appeared to define the characteristics of each patch. Kittiwakes are aerial foragers (Hoffman et al. 1981) whose buoyant flight and hovering ability allow them to effectively track resources through time and space. In contrast, fulmars are specialized for sustained, soaring flight, and appear to invest more time in a given patch once they have interrupted their aerial progress by settling. Red Phalaropes are intermediate in their behavior. They invest considerable time and effort in the search for productive patches, and utilize them extensively once they have settled. Thick-billed Murres appear to use their pursuit-diving ability to track settling patches in the vertical plane. Although the foraging behaviors differed, there was a high degree of overlap in type and size of prey that the three surface-feeding species took from whale plumes (Table 4; Fig. 5). We suggest that seabird ecologists must be cautious in interpreting the existence of differing foraging behaviors among species as evidence that they avoid competition by the use of different resources (e.g. Sealy 1973, Hoffman et al. 1981, Duffy 1986).

**Flock composition.**—Mixed-species flocks are widespread among seabirds and may account for the majority of feeding assemblages in many communities. Previous descriptions of mixed-species seabird flocks have emphasized functional roles of the constituent members, especially the tendency of certain nuclear species to initiate flocks, and the tendency for other kleptoparasitic and “suppressor” species to disrupt them (Sealy 1973, Hoffman et al. 1981, Duffy 1986). Such roles were conspicuously absent among the whale plume flocks. The regular interspecific associations that one might expect if certain species were acting as resource guides or catalysts to flock formation were absent. In particular, Black-legged Kittiwakes (identified as catalysts in other systems; Sealy 1973, Hoffman et al. 1981) were not regularly first to arrive at whale plumes, and they did not contribute to multispecies flocks more often than their general abundance would predict. We observed no kleptoparasitism or flock suppression.

We believe that the absence of functional roles among species sharing gray whale mud plumes is attributable to the characteristics of the patch. Compared with fish shoals or plankton swarms, whale events are highly conspicuous (even at large distances), large relative to the flock size, rich in easily captured prey, and ephemeral but recurring and potentially predictable. Equal access to information regarding the appearance of a patch may mitigate the usual reliance on mobile species as guides. Because prey is briefly but regularly abundant, competition for individual items may be minimized. The dynamics and the plasticity of interspecific behavior as a function of patch characteristics (size, quality, duration) warrant further attention by marine ornithologists.

**Gray whales and Bering Sea bird ecology.**—Associations between seabirds and gray whales account for the majority of observations of feeding birds of at least three species (Table 2). Whale-generated food may be important ecologically. Nearby King and St. Lawrence islands support large colonies of breeding seabirds, including Black-legged Kittiwakes and Thick-billed Murres, and their breeding seasons coincide with the nearby foraging (June–August) of gray whale herds.

The Northern Fulmars and Red Phalaropes
in the study region represented nonbreeding or postbreeding individuals, but their association with gray whales may also be important. Both species are migratory, and the phalarope winters at sea off Central America and South America. Based on the high densities we observed and their regular attendance at whale events, migratory Red Phalaropes may use the gray whale feeding-grounds of the Bering Sea as an important staging area, perhaps analogous to postbreeding individuals, but their associations between marine birds and various rorquals have been widely reported (Evans 1982).

California gray whales in the Bering Sea have returned to historic levels after decimation by whalers during the late 19th and early 20th centuries (Jones et al. 1984). Many other cetacean species have been less fortunate. Although gray whales are unique in their ability to deliver large quantities of benthic sediments within reach of surface-feeding birds, feeding associations between marine birds and various rorquals have been widely reported (Evans 1982). The impact of the virtual extirpation of great whales from many coastal and pelagic ecosystems upon the status and ecology of their former seabird associates is unknown.

ACKNOWLEDGMENTS

We are grateful to Z. Eppley, N. Harrison, C. Williams, and B. Young for their valuable assistance with observations of bird distribution and behavior at sea. We thank the Captain and crew of the R.V. 'Alpha Helix' for their efforts on our behalf. N. Harrison provided the analyses of the birds' stomach contents. D. Au and D. Nettleship provided valuable comments on an earlier draft of this manuscript. This work was funded in part by National Science Foundation grant DPP 8308232.

LITERATURE CITED

ABRAMS, R. W. 1981. Environmental determinants of pelagic seabird distribution in the African sector of the Southern Ocean. J. Biogeograph. 12: 473–492.

---. & A. M. GRIFFITHS. 1981. Ecological structure of the pelagic seabird community in the Benguela current region. Mar. Ecol. Prog. Ser. 5: 269–277.

AU, D. W. K., & R. L. PITMAN. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. Condor 88: 304–317.

BRIGGS, K. T., & E. W. CHU. 1986. Sooty Shearwaters off California: distribution, abundance and habitat use. Condor 88: 355–364.

BROWN, R. G. B. 1980. Seabirds as marine animals. Pp. 1–39 in Behavior of marine animals, vol. 4 (J. Burger, B. Olla, and H. E. Winn, Eds.). New York, Plenum Press.

---. 1986. Foraging at patches: interactions between Common and Roseate terns. Ornis Scandinavica 17: 47–52.

EVANS, P. G. H. 1982. Associations between seabirds and cetaceans: a review. Mammal. Rev. 12(4): 187–206.

HANEY, J. C. 1986. Seabird patchiness in tropical oceanic waters: the influence of Sargassum “reefs.” Auk 103: 141–151.

---. & P. A. MCGILLIVARY. 1985. Midshelf fronts in the South Atlantic Bight and their influence on seabird distribution and seasonal abundance. Biol. Oceanogr. 3: 401–430.

HARRISON, C. S. 1979. The association of marine birds and feeding grey whales. Condor 81: 93–95.

HARRISON, N. M. 1987. Foraging behavior and coexistence of seabirds in the Bering Sea. Ph.D. dissertation, Irvine, Univ. California.

HEINEMANN, D., G. HUNT, & J. EVERSON. 1989. Relationships between the distributions of marine avian predators and their prey Euphausia superba in Bransfield Strait and Drake Passage, Antarctica. Mar. Ecol. Prog. Ser. 58: 3–16.

HOFMANN, W., D. HEINEMANN, & J. A. WEINS. 1981. The ecology of seabird feeding flocks in Alaska. Auk 98: 437–456.

HULSMAN, K. 1978. Feeding and breeding biology of six sympatric species of tern (Laridae) at One Tree Island, Great Barrier Reef. Abstr., Ph.D. thesis, Univ. Queensland 1977. Australian J. Ecol. 3: 240–241.

HUNT, G. L., J. EVERSON, R. R. VEIT, & D. W. HEINEMANN. 1985. Distribution of marine birds and their prey in Bransfield Strait and Southern Drake Passage. Antarctic J. U.S. 1985 Review: 166–168.
