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

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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 sedi-

ments 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. 10^9 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 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. Law-

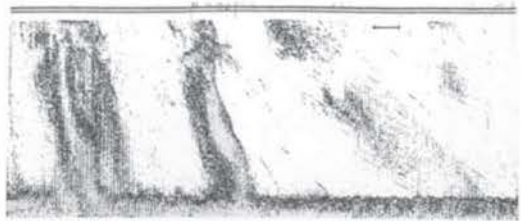


Fig. 1. Echogram of mud plumes formed during three successive blows by the same gray whale. To obtain the echogram, we used a 200-kHz echo sounder while the ship was virtually stationary. Settling rates of particles in the plumes ranged between 5–40 m/min. Scale bar is equal to 1 min. Note the high density and the ephemeral nature of the material in the patches.

rence 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 (*Cyclorhynchus 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

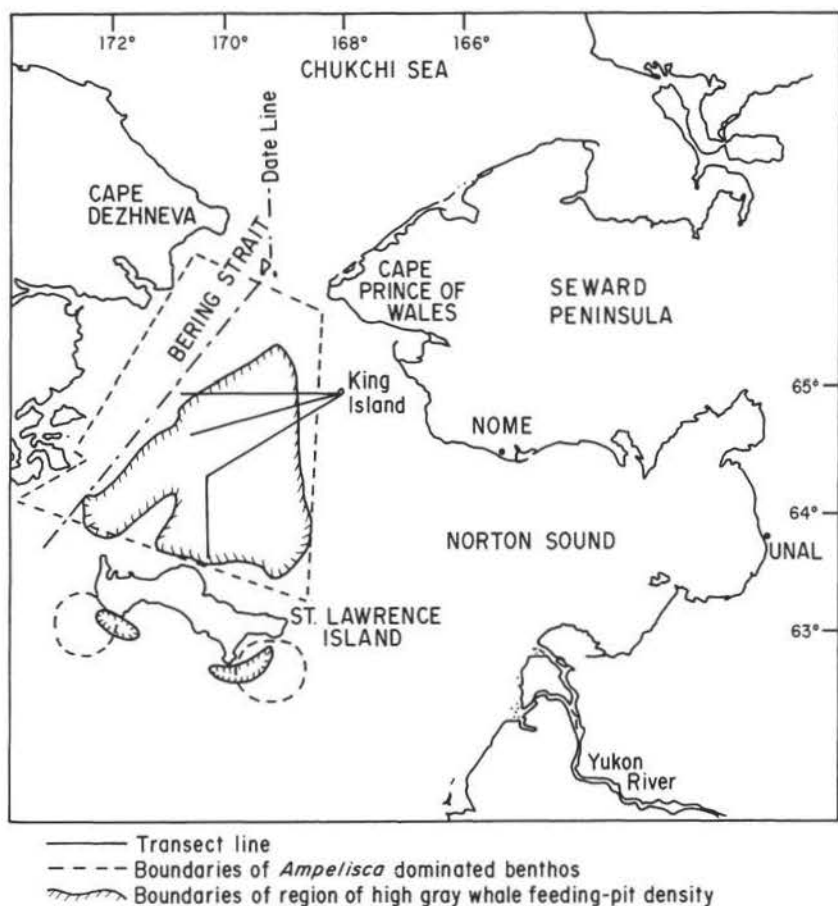


Fig. 2. Location of seabird transect lines in relation to the principal feeding grounds of the gray whale in the Chirikov Basin, northern Bering Sea. Boundaries of the whale feeding grounds are taken from Johnson and Nelson (1984: 1150), and the rough limits of the Ampeliscid benthic community are drawn after Nerini (1984: 423).

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

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 (n)	At plumes (%)	Birds per 10-min transect segment*			Birds per flock		
				With whales ($\bar{x} \pm SE$)	Without whales ($\bar{x} \pm SE$)	Ratio	At plumes ($\bar{x} \pm SE$)	Away from plumes ($\bar{x} \pm SE$)	Ratio
Northern Fulmar	157	190	55	2.68 \pm 0.69	0.81 \pm 0.16	3.3***	3.91 \pm 0.55 (46)	1.78 \pm 0.25 (87)	2.2***
Red Phalarope	80	505	87	5.17 \pm 1.50	1.17 \pm 0.51	4.4**	19.28 \pm 3.25 (25)	7.89 \pm 2.94 (9)	2.4*
Black-legged Kittiwake	23	155	87	1.72 \pm 0.56	0.18 \pm 0.06	9.6***	4.05 \pm 1.02 (37)	1.72 \pm 0.30 (18)	2.4*
Thick-billed Murre	271	56	17	1.59 \pm 0.26	1.00 \pm 0.15	1.6	2.08 \pm 0.48 (24)	1.22 \pm 0.04 (176)	1.7***
Species combined	531	906	63	11.16 \pm 1.92	3.16 \pm 0.68	3.5***	9.83 \pm 1.44 (90)	1.74 \pm 0.18 (289)	5.7***

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

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 whale plumes comprised more than one species. At plumes, the frequency of flocks encountered declined as species' diversity increased. Monospecific 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 resetttle to match its progress, as long as mud was being released. The kittiwakes always fed in the most recently formed plume. After the whale ceased to eject mud, or it dove, the kittiwakes remained on the water, where they continued to peck at the surface for a few minutes. Kittiwakes were often the first birds to arrive at a fresh plume, and were typically the first birds to abandon it (Fig. 3). Black-legged Kittiwake flocks ($n = 14$) spent an average of 6.16 ± 0.60 min at individual whale plumes. Mean time spent in feeding was only 4.46 ± 0.74 min per plume.

TABLE 2. Correlations* between seabird density (four primary whale-associating species, on water or feeding) and the density of gray whales sighted along six transect lines in the Chirikov Basin, northern Bering Sea.

Transect segment length (NM)	n	Correlation statistics			No. of transects $P < 0.05$
		r	Variance explained ($r^2 \times 100$)	P	
For the best of 6 transect lines					
1.5	18	0.73	54%	<0.01	5/6
3.0	15	0.89	79%	<0.01	3/6
5.0	14	0.79	62%	<0.01	3/6
10.0	7	0.79	62%	<0.05	1/6
For all 6 transects pooled					
1.5	195	0.33	11%	<0.001	
3.0	88	0.37	13%	<0.01	
5.0	59	0.33	11%	<0.02	
10.0	29	0.36	13%	0.06	

* Correlation is by least squares, linear regression analysis. Abbreviations: NM = nautical miles, n = number of individual transect segments, r = correlation coefficient, and P = significance level of correlation.

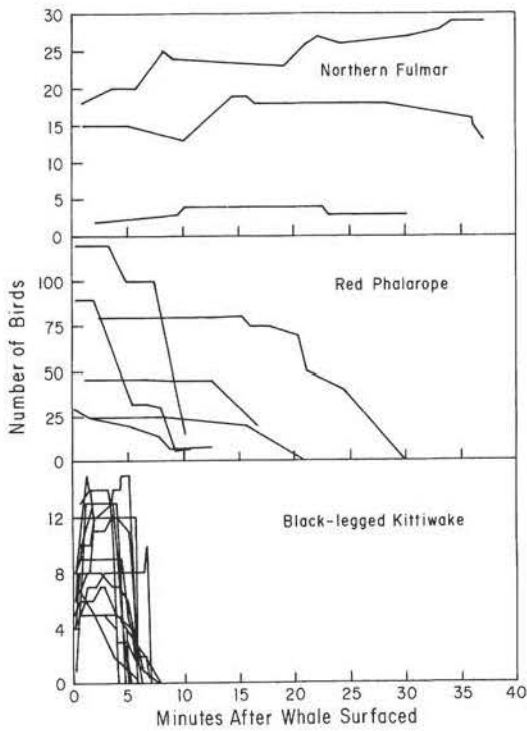


Fig. 3. A comparison of the time spent on gray whale mud plumes by three surface-feeding bird species. Time zero marks the surfacing of the whale and the origin of a mud plume. Each curve tracks the subsequent arrival, aggregation, and disappearance of birds at a single plume. Northern Fulmars commonly feed at plumes for 30 min or more, whereas Black-legged Kittiwakes abandon plumes within 5-10 min after the plumes are formed.

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 div-

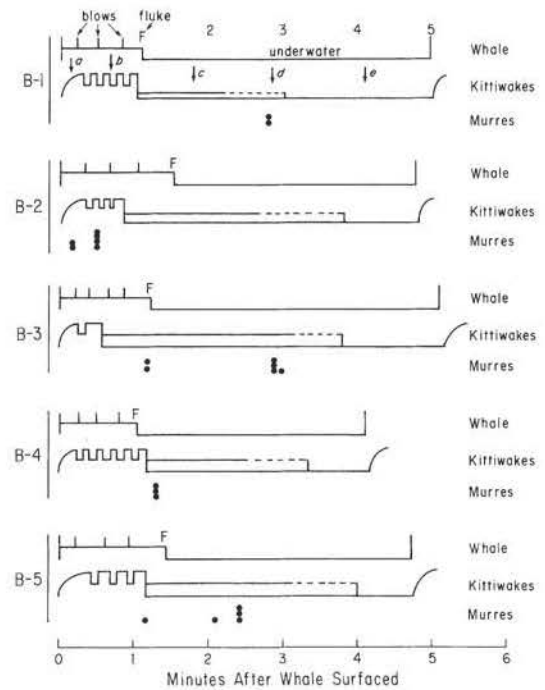


Fig. 4. Synchronization of foraging behavior of a Black-legged Kittiwake flock with the dive cycle of a feeding gray whale. Note that when the whale moved at the surface, the kittiwakes followed; when the whale was submerged, the kittiwakes sat on the water, first feeding, then waiting for it to resurface. Each successive dive cycle represented (B1-B5) began immediately at the end of the cycle depicted above it. Symbols: *a* = flock takes flight; *b* = flock alternately flies and settles in wake of whale; *c* = entire flock on water, all feeding; *d* = flock on the water, occasional pecking; and *e* = flock resting on the water, not feeding. Note that unlike the kittiwakes, the arrival of Thick-billed Murres ● is not synchronized with the whale's behavior.

ing 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 dabbled 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 ± 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 ≥ 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

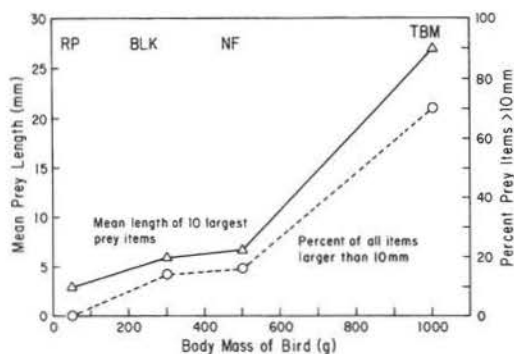


Fig. 5. The length of prey (amphipods) taken from the stomachs of seabird species collected while they fed at gray whale mud plumes as a function of body mass. In general, the average size of the largest prey items increased with the size of the predator, and the majority of large (> 10 mm) prey items 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.

swam on the surface to join groups of surface-feeding birds at a plume; they dove when they reached the feeding group. Less commonly, murres surfaced unexpectedly in plumes where we had not previously seen murres arrive. This suggests that some individuals arrived at plumes underwater, either by searching for regions of turbid water or by entering these zones accidentally. Because the murres fed exclusively underwater, we could not track individuals or monitor the time course of feeding activities. Thick-billed Murres occurred mostly as individuals or pairs at whale events (Table 1), and exhibited no obvious coordination as flocks. We saw no evidence that Thick-billed Murres tracked individual whales.

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*

TABLE 4. Percent occurrence of some common, benthic amphipods in the stomachs of seabirds collected near gray whale mud plumes. Sample size is seven for each bird species.

Amphipod	Northern Fulmar	Red Phalarope	Black-legged Kittiwake	Thick-billed Murre
<i>Ampelisca</i> spp.	100	71	100	57
<i>Byblis</i> spp.	100	71	14	57
<i>Protomedea</i> spp.	71	14	29	0
<i>Anonyx</i> spp.	43	14	14	71
<i>Lembos</i> spp.	0	0	0	86

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* sp.) 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 ^a	How identified ^b	Scale ^c	Bird-density increase in transects with prey patch?	P	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 Piatt 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	—	Yes	0.2-0.6
Haney 1986	<i>Sargassum</i> 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	?	—

^a All subsurface except whale plumes and *Sargassum* reef.

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

^c NM = nautical mile.

bird density and measures of patch density in these studies are typically either weak or not statistically significant (Table 5). The whale plumes were unmistakable in their surface manifestation: a 12-m mammal spewed water 10 or more meters into the air while striping the sea surface with prey-rich mud. Perhaps for this reason, the correlation between the density of patches (whale events) and the density of seabirds was unusually high. Up to 79% of the variability in the density of bird species between segments along a transect line was explained by the number of patches (Table 2).

Although correlations between seabird densities and marine processes have been demonstrated at larger scales, the amount of variability explained by these correlations has often been very low (Abrams 1981, Abrams and Griffiths 1981, Haney and McGillivray 1985, Schneider and Duffy 1985, Briggs and Chu 1986, Schneider et al. 1988). Hunt and Schneider (1987) suggested that patchiness at fine scales (e.g. interactions with prey patches) may be a source of apparent "noise," which can impede the quantification of habitat usage by seabirds at larger scales. The highly significant correlations we found over a wide range of measurement scales indicate the potential importance of identifying and quantifying relevant fine-scale patches in correlative studies of seabird distribution.

Several pursuit-diving alcid species were never observed in association with gray whales,

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 murre, 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 Murre 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 Murre, 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 staging by inland migrating Wilson's (*Phalaropus tricolor*) and Red-necked (*P. lobatus*) phalaropes at terminal lakes of the western United States (Jehl 1981, 1986). Kumlien (1878) reported that associations between postreproductive Red Phalaropes and bowhead whales (*Balaena mysteceti*) were once so regular in waters adjacent to Greenland that early whalers routinely tracked aerial flocks of phalaropes to locate surfacing bowheads. Migratory staging with whales may have formerly occurred widely in this species.

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.

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