

SEABIRD DIET AT A FRONT NEAR THE PRIBILOF ISLANDS, ALASKA

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Abstract. Large concentrations of murre (*Uria aalge* and *U. lomvia*) have been reported on the water at sites where bathymetry generates flow gradients near breeding colonies in North America. One such site was located in August 1982, by following streams of murre flying away from the colony on St. George Island, Alaska. We found a well-defined tidal front where murre were diving and feeding on euphausiids on the mixed (landward) side of the front, an area of subsurface convergence. Surface-foraging birds (Black-legged Kittiwakes *Rissa tridactyla* and Red Phalaropes *Phalaropus fulicaria*) were feeding on euphausiids at the surface convergence seaward of the murre aggregation. The feeding success of surface foragers was attributed to surface convergence acting on weakly swimming (injured) euphausiids; that of murre to subsurface convergence acting on negatively phototactic euphausiids. Successful foraging at spatially predictable locations around colonies has important implications for population monitoring, impact assessment, and theoretical treatments of the foraging distribution of colonial seabirds.

Key Words: Bering Sea; marine birds; diet; fronts.

The hypothesis that bathymetrically-induced flow gradients increase the availability of prey to marine birds in shelf ecosystems was proposed to explain the patchiness of diving birds along transects away from colonies in the southeastern Bering Sea (Schneider et al. 1986). Several lines of evidence (summarized by Schneider et al. 1990) suggest that this hypothesis can be extended to colonially nesting alcids foraging around their colonies. There have been no detailed studies of the diets or feeding success of alcids in areas of flow gradient generated by bathymetry. Here we report the prey number, prey condition, and stomach volume of Common and Thick-billed murre (*Uria aalge* and *U. lomvia*) at such a site east of St. George Island, in the southeastern Bering Sea. We also report the prey of surface-foraging birds feeding at the same site.

LOCATION AND METHODS

The number of seabirds on St. George Island (Fig. 1) has been estimated at 2.6×10^6 birds, including 1.5×10^6 Thick-billed Murres (Hickey and Craighead 1977). The number of seabirds on St. Paul Island, 63 km to the northeast, has been estimated at 2.5×10^5 birds, including 1.1×10^5 Thick-billed Murres and 3.9×10^4 Common Murres (Hickey and Craighead 1977). The site that we investigated was located at $56^{\circ}38.22'N$, $169^{\circ}22.32'W$, which is 6 km east of Tolstoi Point, St. George Island. Surveys in 1977 and 1978 (Kinder et al. 1983) showed that during the summer a front associated with the 70 km isobath separates vertically homogeneous water near the island from stratified water away from the island. We attempted to relocate the front described by Kinder et al. (1983) by steaming outward from St. George on 5 August 1982 until we encountered water depths of 70 m. A series of conductivity, temperature, and depth (CTD) casts showed that the water was vertically homogeneous. During the casts we noticed streams of murre flying by the ship,

so rather than searching for a front along our radial transect from the island, we simply followed the murre. Over the next hour we steamed northward through a heavy fog (visibility less than 0.5 km), while murre continued to overtake the ship from the stern and then disappear into the fog ahead. Eventually we came to a location where murre were abundant on the water as well as in the air, so we stopped and carried out a series of CTD casts normal to the prevailing bathymetry at this location. The casts showed a well-defined front, with murre confined almost entirely to the island (mixed) side. Murre abundance on the water was on the order of 10–50 birds within a 10 m radius of the bow, as we slowed to a stop over a distance of approximately 1 km.

We then carried out a more detailed CTD profile across the front. Depth casts were made at 0.5 km intervals. Surface measurements of chlorophyll and phaeopigments (a measure of phytoplankton) were obtained at each CTD station. As the fog lifted we visited the front in a skiff to collect birds. No birds were present on the stratified side of the front, but they were abundant on the mixed side of the front, where six Thick-billed Murres were collected in less than an hour.

We then returned to the ship and used the ship's depth-sounder to obtain a profile of zooplankton and nekton abundance across the front. The depth-sounder showed a dark trace at and below the depth of the thermocline identified from CTD casts. The trace was 15–20 m below the surface on the stratified side of the front, rising toward the surface on the unstratified side of the front. We made several tows with a bongo net to identify the source of the dark trace, but only a few euphausiids (primarily *Thysanoessa raschii*) were captured. The mesh size was less than 1 mm, so the poor catch may have been due to net avoidance by euphausiids (Nemoto 1983).

While making bongo tows we noticed that surface-feeding birds (Black-legged Kittiwakes *Rissa tridactyla* and Red Phalaropes *Phalaropus fulicaria*) were increasing at the slick marking the front. We revisited the front in the skiff to collect kittiwakes and phala-

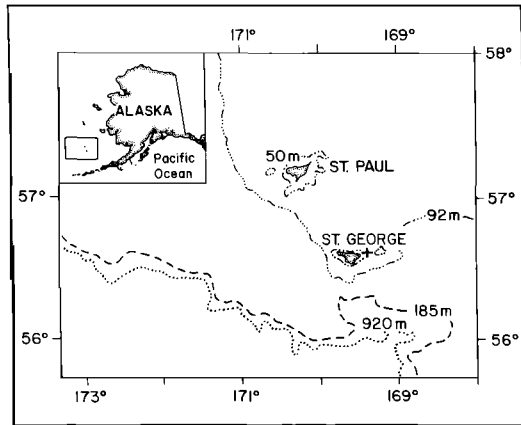


FIGURE 1. Location of bathymetrically fixed front (shown as +) east of St. George Island, southeastern Bering Sea.

ropes feeding along the surface slick. This collection was 4.2 km SSE of the earlier collection. Drift over the 6-hr period since the previous collection was 0.2 m/s. During this second trip we collected three more murres landward of the front. As before, we could not find murres at the front or seaward, for comparison with murres collected on the landward side of the front.

All birds were tagged in the skiff with a unique number. Approximately 20 ml of 95% ethanol was injected down the throat of each bird. The digestive tract of each bird was removed in the ship's laboratory within 1 hr of collection. Each tract was gently slit to allow entry of preservative, and placed in 95% alcohol. The sex, reproductive condition, and approximate mass of each bird were noted and recorded. Masses were approximate because birds had been injected with ethanol, and gravimetric measurements are unreliable on a rolling ship. Carcasses were frozen, and eventually deposited at the Los Angeles County Museum.

Crop, stomach, and gizzard contents were later identified using standard keys and a set of reference specimens. The volume of material in the stomach was measured by water displacement. The length of intact prey was measured to the nearest mm. Seabirds digest the soft parts of prey rapidly, so stomach volume and prey condition (intact or not) were used as indices of recent foraging success.

RESULTS

The front located east of Tolstoi Point in 1982 was structurally similar to the fronts described by Kinder et al. (1983). Upward deflection of the thermocline was associated with a slight change in bottom contour at the 75 m isobath (Fig. 2). Notable physical features included a surface slick at the front (Station 65, Fig. 2), thickening of the surface layer at the slick (Station 65), and upward deflection of the thermocline landward of the slick (Station 66). Gelatinous zooplankton, seaweed, and floating debris were observed at this

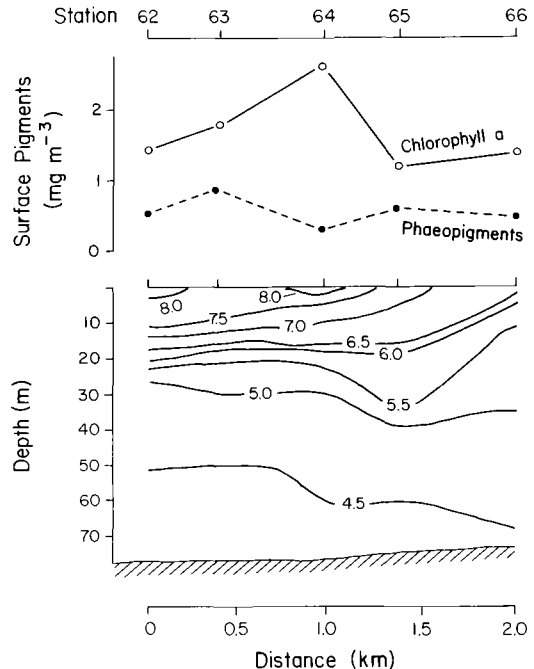


FIGURE 2. Surface chlorophyll distribution in relation to the temperature depth profile across the Tolstoi Point front.

slick. Highest chlorophyll concentrations occurred slightly seaward of the slick (Fig. 2). Chlorophyll concentrations were lower on the stratified than on the mixed side, as reported in transects across similar fronts in Europe (Le Fevre 1986). The structure of the front was consistent with Simpson's (1981) conceptual model of circulation, which is that of convergent flow marked by a surface slick running parallel to divergent flow on the landward side of the surface slick (Fig. 3). We observed considerable meandering of the front, which is also characteristic of the tidally-generated convergent fronts described by Simpson (1981).

A secondary slick occurred at Station 63, seaward of the main slick (Fig. 2). Very little debris was observed at this slick, and no birds were observed feeding there. Detailed temperature profiles (Fig. 4) showed multiple thermoclines at this minor slick (Station 63), at the major slick (Station 65), but not between the slicks (Station 64). Comparison of the horizontal profile (Fig. 2) with the detailed vertical profiles (Fig. 4) suggests that an eddy may have been present on the seaward side of the front. Other explanations for lateral variation in the depth of the thermocline (e.g., passage of internal waves) cannot be ruled

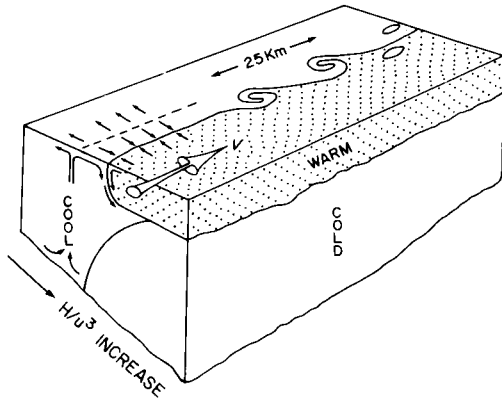


FIGURE 3. Summary of frontal structure and circulation due to bathymetrically induced gradient in rate of tidal stirring. Redrawn from Simpson (1981). Dotted lines show subsurface convergence required to maintain upwelling. The ratio of water depth to the cube of tidal stream velocity (H/u^3) measures the relative importance of buoyant and mixing energy.

out. A fully upwelled thermocline was observed landward of the front (Station 66).

Thick-billed Murres collected landward of the front had been eating euphausiids, primarily *T. raschii* (Table 1). Nearly all birds had foraged successfully, as indicated by number of intact prey and number of birds with full stomachs. Intact euphausiids ranged from 19 to 24 mm, rostrum to tail. The volume of material in the stomachs of nine murres averaged 8.5 ml, ranging from 0.3 to 21.5 ml.

Kittiwakes and phalaropes collected at the front had also been feeding actively on euphausiids. The sizes taken by Black-legged Kittiwakes and by murres were similar (Table 1). Many of the euphausiids found in the proventriculus of these birds were missing their tails, so total length could not be measured. In the field, euphausiids missing either heads or tails floated or swam weakly in the slick at the surface. This, and the fact that euphausiids are generally unavailable to surface-foraging birds during the day, suggests that euphausiids were injured by murres beneath the surface, then carried toward the slick and concentrated by the frontal circulation (Fig. 3), where they were fed on by kittiwakes and phalaropes.

DISCUSSION

Our results show that both diving and surface-foraging birds fed on the same prey at a front located east of the Pribilof Islands. However, surface-foraging birds fed along the surface convergence, while subsurface-foraging murres were observed on the landward side of the front. These

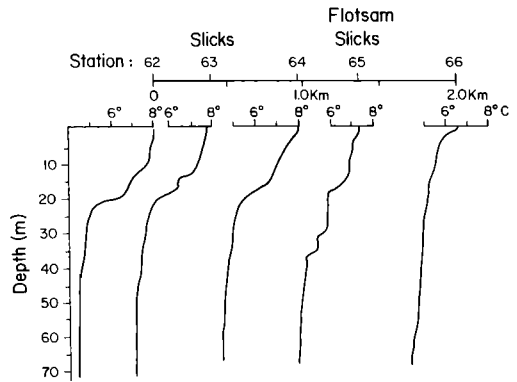


FIGURE 4. Temperature-depth profiles along transect across the Tolstoi Point front. Stations are the same as in Figure 2.

observations were interpreted in light of Simpson's (1981) model of circulation at tidal fronts (Fig. 3). The feeding success of kittiwakes and phalaropes at the surface slick was attributed to convergent flow acting on dead or weakly swimming euphausiids at the sea surface. The mechanism responsible for the feeding success of murres on the landward (mixed) side of the front is less clear. We speculate that euphausiids, which are normally negatively phototactic during the day, were being concentrated by subsurface convergence beneath a surface divergence (upwelling) in a manner similar to that proposed by Simard et al. (1986) at a coastal upwelling in the Gulf of St. Lawrence.

If our interpretation is correct, then the success of surface-foraging kittiwakes and phalaropes was due to a complex interaction of physical processes (surface convergence immediately adjacent to subsurface convergence) and biological processes (negative phototaxis of euphausiids unless injured). Similarly, at St. Matthew Island, injury of euphausiids by murres foraging beneath the surface increased the foraging success of surface feeding kittiwakes (Hunt et al. 1988). At St. Matthew, surface-foraging by kittiwakes occurred immediately above subsurface-foraging murres, whereas at St. George, surface-foragers were displaced laterally relative to subsurface-foragers.

During the field work and up until the work by Simard et al. (1986) on euphausiids we considered a series of alternative interpretations. These deserve brief comment.

1. Euphausiids avoid warm water, remaining just below the thermocline, and hence were closer to the surface on the landward side than the seaward side of the front. However, lack of diving birds immediately adjacent to the surface

convergence suggests that proximity of prey to the surface was not responsible for the foraging success of birds at this site.

2. Water clarity was reduced on the seaward side of the front, increasing the availability of euphausiids to murres foraging visually beneath the sea surface. Water clarity at the sea surface appeared to be greater on either side of the front than at the front. If water clarity were important, then murres should have been less abundant at the front. Instead, they attained a local maximum on the landward side. Looking landward from the front, murre density first increased with distance from the front, then decreased.

3. Euphausiids aggregate in response to increased primary production. This explanation may be correct at the scale of several kilometers, as euphausiids and newly produced chlorophyll were abundant in the same area (frontal zone of Federov 1986). At a smaller scale, however, chlorophyll occurred in highest concentration on the stratified side of the front (as expected), whereas foraging murres and targets recorded on the depth sounder occurred in mixed water landward of the front.

4. Spawning behavior of euphausiids increased their availability at the sea surface. We did not observe swarms of euphausiids at the surface during the two collecting trips in the skiff.

5. Pursuit divers concentrate euphausiids near the surface, or delay the ascent of euphausiids from the surface, as has been hypothesized for fish (Hoffman *et al.* 1981, Grover and Olla 1983). It is possible that behavioral responses of euphausiids to murres did contribute to successful feeding by surface-foragers. This mechanism does not account for the continued association of a laterally structured foraging aggregation with a front over more than 6 hr.

The number of intact prey found in Black-legged Kittiwake and murre stomachs at this site was, in our experience, high for birds collected at sea. We attempted to determine whether quantity of prey was lower away from the front, but were unable to find birds on the water there. We tabulated the number of Black-legged Kittiwakes and murres with intact prey during the same cruise. Birds were collected on 26–29 July, 30–31 July, and 2–3 August in Bristol Bay, at latitudes ranging from 54°50.3' to 57°47.3'N, between 163°10.1' and 167°55.3'W. Of 14 kittiwakes and one murre, only one kittiwake had intact prey in the digestive tract. Comparison with Table 1 indicates the recent foraging success of birds collected near the Pribilof front.

These data, plus our experience in observing and collecting marine birds at sea, indicate that energy gain occurs at a limited number of sites around colonies, some of which are the result of



FIGURE 5. Conceptual model of foraging costs and bathymetrically fixed food concentrations along a radius running outward from a breeding colony.

physical structuring of the fluid environment of prey by topography. This concept is based on physical theory combined with observations of prey and seabird aggregations around alcid colonies in the Bering Sea (Kinder *et al.* 1983, Hunt and Harrison 1990) and in the southern Labrador Current (Schneider and Piatt 1986, Schneider *et al.* 1990). In shelf ecosystems, flow gradients depend on topography, because upward and downward mixing act through significant fractions of the water column (Csanady 1982). These flow gradients can increase prey aggregation through a variety of mechanisms (e.g., Simard *et al.* 1986). Empirical support for this concept comes from the observation that feeding aggregations are observed in areas of strong flow gradient (e.g., Brown 1980), that seabird patchiness depends on the strength of salinity gradients generated by flow gradients at topographic features (Schneider *et al.* 1987), and that bathymetric charts have been used to locate an active feeding site (Schneider *et al.* 1990).

Spatially predictable variation in prey supply has a number of implications. One is that the difference between energy gain and foraging costs depends on location (Fig. 5), rather than simply on distance from a colony. The recognition of spatially predictable sites of prey concentration due to bathymetric influence shows that models of foraging behavior need to include oceanographic heterogeneity in order to be realistic. Furthermore, learning where to forage may occur as birds mature and increase their foraging efficiency (Orians 1969, Porter and Sealy 1982). Another implication of spatially predictable feeding sites is that the probability of contact with a point source contaminant (e.g., oil spills) will be reduced unless contamination occurs at feeding sites. Knowledge of regularly used feeding sites near a colony will allow more effective monitoring in the event of a release of contaminants (Ford *et al.* 1982).

Our observations around the Pribilof Islands indicate that physical processes may contribute to the structure and function of mixed-species feeding flocks. Other investigators (Sealy 1973, Hoffman *et al.* 1981, Porter and Sealy 1982, Grover and Olla 1983, Chilton and Sealy 1987) have described ways that the foraging behavior

of individual species can affect the formation and structure of feeding aggregations. Further study of predator behavior in relation to prey behavior and physical processes can increase our understanding of the formation, composition, and evolution of mixed species feeding flocks.

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LITERATURE CITED

- BROWN, R. G. B. 1980. Seabirds as marine animals. Pp. 1-39 in J. Burger, B. L. Olla, and H. E. Winn (eds.), Behavior of marine animals, Vol. 4. Plenum Press, New York.
- CHILTON, G., AND S. G. SEALY. 1987. Species roles in mixed-species feeding flocks of seabirds. *J. Field. Ornithol.* 58:456-463.
- CSANADY, G. T. 1982. Circulation in the coastal ocean. Reidel, Dordrecht, 279 pp.
- FEDOROV, K. N. 1986. The physical nature and structure of oceanic fronts. Springer-Verlag, Berlin. 333 pp.
- GROVER, J. J., AND B. L. OLLA. 1983. The role of the Rhinoceros Auklet (*Cerorhinca monocerata*) in mixed-species feeding assemblages of seabirds in the Strait of Juan de Fuca, Washington. *Auk* 100:979-982.
- HICKEY, J. J., AND F. L. CRAIGHEAD. 1977. A census of seabirds on the Pribilof Islands. Environmental assessment of the Alaskan continental shelf. Annual reports of Principal Investigators. Boulder, Colorado, Natl. Oceanic Atmospheric Administration Environmental Research Laboratory 2:96-195.
- HOFFMAN, W., D. HEINEMANN, AND J. A. WEINS. 1981. The ecology of seabird feeding flocks in Alaska. *Auk* 98:437-456.
- HUNT, G. L., JR., N. M. HARRISON, AND R. T. COONEY. 1990. Foraging of Least Auklets: the influence of hydrographic structure and prey abundance. *Studies in Avian Biology* 41:7-22.
- HUNT, G. L., JR., N. M. HARRISON, W. M. HAMNER, AND B. S. OBST. 1988. Observations of a mixed-species flock of birds foraging on euphausiids near St. Matthew Island, Bering Sea. *Auk* 105:345-349.
- KINDER, T. H., G. L. HUNT, JR., D. C. SCHNEIDER, AND J. D. SCHUMACHER. 1983. Correlation between seabirds and oceanic fronts around the Pribilof Islands, Alaska. *Estuar. Coast. Shelf Sci.* 16:309-319.
- LE FEVRE, J. 1986. Aspects of the biology of frontal systems. *Adv. Mar. Biol.* 23:163-299.
- NEMOTO, T. 1983. Net sampling and abundance assessment of euphausiids. *Biol. Oceanogr.* 2:211-226.
- ORIAN, G. H. 1969. Age and hunting success in the Brown Pelican (*Pelecanus occidentalis*). *Anim. Behav.* 17:316-319.
- PORTER, J. M., AND S. G. SEALY. 1982. Dynamics of seabird multispecies feeding flocks: age-related feeding behaviour. *Behaviour* 81:91-109.
- SCHNEIDER, D. C., N. M. HARRISON, AND G. L. HUNT, JR. 1987. Variation in the occurrence of marine birds at fronts in the Bering Sea. *Estuar. Coast. Shelf Sci.* 25:135-141.
- SCHNEIDER, D. C., G. L. HUNT, JR., AND N. M. HARRISON. 1986. Mass and energy transfer to marine birds in the southeastern Bering Sea. *Cont. Shelf. Res.* 5:241-258.
- SCHNEIDER, D. C., AND J. F. PIATT. 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. *Mar. Ecol.—Progr. Ser.* 32:237-246.
- SCHNEIDER, D. C., R. PIEROTTI, AND W. THRELFALL. 1990. Alcid patchiness and flight direction near a colony in eastern Newfoundland. *Studies in Avian Biology* 14:23-35.
- SEALY, S. G. 1973. Interspecific feeding assemblages of marine birds off British Columbia. *Auk* 90:796-802.
- SIMARD, Y., R. DE LADURANTAYE, AND J. THERRIAULT. 1986. Aggregation of euphausiids along a coastal shelf in an upwelling environment. *Mar. Ecol.—Progr. Ser.* 32:203-215.
- SIMPSON, J. H. 1981. The shelf-sea fronts: implications of their existence and behaviour. *Phil. Trans. Roy. Soc. Lond.* A302:531-546.