

# Seabirds and fronts: a brief overview

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Oceanographic fronts are the sites of enhanced physical and biological activity, including locally concentrated feeding by marine birds. Two general hypotheses relating marine birds to fronts have been developed. The first is that enhanced primary production at fronts increases prey supply through increased animal growth, reproduction, or immigration. The second is that prey patches develop at fronts either through behavioural responses of prey to thermal or salinity gradients, or through interaction between prey behaviour and circulatory patterns. Several recent studies support the second hypothesis. The first hypothesis, that birds benefit from enhanced primary production at fronts, has yet to be evaluated. We need a better understanding of trophic mechanisms at fronts in order to determine (1) the proportion of daily energy requirements extracted by predators at fronts; (2) the proportion of natural mortality of prey populations at fronts; and (3) the probability of contact between seabirds and point source pollutants.

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## A definition of 'front', with example

Few people experience any practical difficulty in identifying a front from physical oceanographic data, yet formal definition of the term has proved elusive. Definitions that have been offered (Bowman & Esias 1978; Holligan 1981; Owen 1981) range from the phenomenological, emphasizing directly measureable quantities, to conceptual, emphasizing dynamic characteristics. The definition that I will use is that of Fedorov (1986): a frontal zone is a region of high spatial gradient in thermodynamic characteristics such as temperature, density, or velocity. A frontal interface is the two-dimensional distribution (surface) having the maximum spatial gradient in some property within this region. A front is the intersection of this surface with any given surface, particularly the free surface of the ocean, or an isopycnal (equal density) surface.

An example will serve to illustrate. Fig. 1 shows the distribution of temperature with depth along a transect beginning 6 km east of one of the Pribilof Islands, in the southeastern Bering Sea. One can see stratified water near the beginning of the transect, unstratified conditions in slightly shallower water near the end of the transect, and a strong gradient in sea-surface temperature at the transition between these two mixing regimes, near the middle of the transect. The frontal interface, seen from the side, is the line of maximum hori-

zontal thermal gradient, which separates mixed and stratified water. The front, seen from the side, is the intersection of this line with the sea

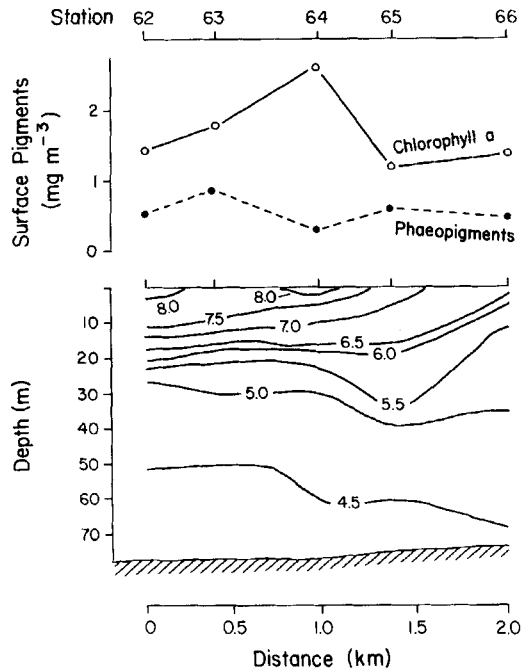


Fig. 1. Thermal structure along a transect running toward St. George Island, in the southeastern Bering Sea. Profile made on 5 August, 1982. Profile begins at 56° 38.22' N, 169° 22.32' W. Figure taken from Schneider, Harrison & Hunt (in press).

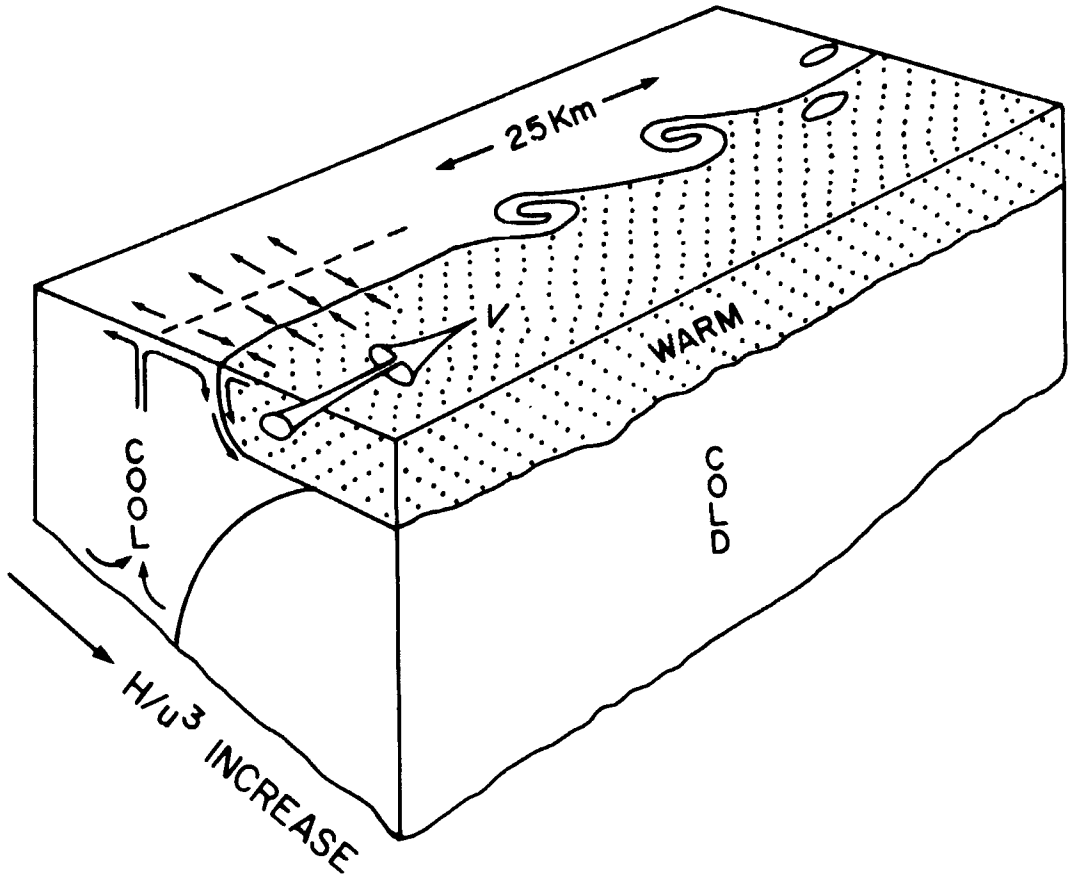


Fig. 2. Interpretation of circulation at front marking the transition from stratified to tidally mixed water.  $H/u^3$  is ratio of water depth to the cube of the tidal stream velocity. Redrawn from Simpson (1981).

surface. This occurs between the 7.5° C and 8° C isotherms where they intersect the sea surface (Fig. 1). Fig. 2 shows a further interpretation of such a feature, along dynamic lines. Simpson's (1981) interpretation is that of a lateral gradient in the balance between stabilizing (buoyant) and destabilizing (tidal mixing) forces, which result in a rapid shift from mixed to stratified water with a very small change in depth.

### Seabird distribution in relation to fronts

Michitaka Uda, who carried out the pioneering work on fronts ('siome'), reported that seabirds were present in 1 out of 14 crossings of small fronts near Japan (Uda 1938). Despite work on

small scale (<1,000 km) circulatory patterns by Uda and others, the term 'front' did not enter the oceanographic literature until the 1960s. The term does not appear in Bourne's comprehensive review (1963), which discusses several instances of seabird congregation at current boundaries. Subsequent reviews of work on pelagic birds reflect the recent increase in research on birds at fronts, as well as increasingly thorough scouring of older literature for published reports. Brown (1980) listed 8 published reports of birds at fronts. Bourne (1981) listed 8 published works on birds in a 3-paragraph discussion of fronts. By 1985 Hunt & Schneider (1987) had compiled 20 reports of seabirds at fronts. In early 1986 Brown (in press) tabulated 46 reports of marine birds at fronts inferred from a variety of physical and biological properties.

Statistical analysis has shown that, in general, fronts explain a significant but relatively small proportion of the observed variation in seabird abundance. In the Bering Sea the presence of a front explains less than 20% of the observed variability in abundance (Kinder et al. 1983; Schneider, Harrison & Hunt 1987). In the Southern Ocean Abrams (1985) reported stronger correlation of bird abundance with SST gradients than with other variables, but the variances explained by SST gradients generally fell short of 20%. In the California Current System Briggs et al. (1987) identified SST gradients as the third most important composite variable (after distance from shore and latitude), accounting for less than 20% of the observed variance in bird abundance.

On a seasonal basis seabird abundance has been correlated with seasonal change in the frequency of surface thermal gradients in shallow waters of the continental shelf east of the Gulf Stream (Haney & McGillivray 1985). Abundance was not correlated with seasonal frequency of thermal gradients due to eddy formation along the western side of the Gulf Stream (Haney 1986). In the eastern Bering Sea, energy dissipation by pelagic birds was associated with seasonal change in the depth-integrated salinity gradient across the shelf (Schneider, Duffy & Hunt 1988). On a smaller scale, abundance in frontal zones was not significantly greater than abundance in adjacent waters, but did depend on the strength of the physical gradient, as measured by the inverse of the width of the frontal zone (Schneider, Harrison & Hunt 1987). Strength of a front, as measured by the inverse of the width of the frontal zone, explained 27% of the variation in abundance of seabirds in 61 frontal crossings.

One potential source of low explained variance is a mismatch between the spatial scale of the front and the spatial scale at which variability in avian abundance is measured. To test this, Schneider, Pierotti & Threlfall (in press) measured spatial variability in the abundance of murre *Uria aalge* and puffins *Fratercula arctica* along transects across a strong upwelling front in the southern Labrador Current. Variability in abundance was measured at the scale of the first internal Rossby radius, which is the characteristic width of the front between cold upwelled water and adjacent stratified water. The calculated width of the front was confirmed by temperature profiles. During strong upwelling, the front

explained less than 15% of the observed variation in avian abundance. Low explained variance in this case could not be attributed to a mismatch between the scale of the physical phenomenon and the scale of the analysis.

Another potential source of low explained variance is the length of the causal chain linking seabirds to fronts. If the causal link is through prey responses to fronts, then low explained variances can be expected relative to the situation of a direct causal linkage. For example, if fronts explained half of the variation in prey abundance on average, and prey explained half of the variation in avian abundance, then the variance in avian abundance explained by fronts (in the statistical sense) would be 25%. Several recent analyses (Schneider & Piatt 1986; Hunt, Harrison, & Cooney in press; Ryan & Cooper in press; Erikstad this volume) have shown that prey density can explain more than half of the observed variation in avian abundance, often at spatial scales in excess of 5 km. These results suggest that the generally low variance in avian abundance explained by fronts may be due to intermediate levels of association along a 2 step causal chain—fronts to prey, and prey to birds.

## Feeding at fronts

Fronts may yet be determinants of spatial variation in prey capture, even though they are not major determinants of distribution. Work on feeding at small frontal features in the Bay of Fundy (Gaskin & Smith 1979; Brown & Gaskin 1988) has shown that phalarope feed during the day on copepods found near the sea surface in patches of cool water generated by tidal flow over banks and ledges. These authors attributed this feeding interaction to upward flushing of copepods, which normally migrate downward during the day. Feeding also occurs at convergent areas downstream from ledges, where copepod concentrations occur near the sea surface. Similarly detailed work in the Bering Sea has shown that murre capture euphausiids beneath the surface on the mixed side of a shallow sea front west of the Pribilof Islands (Schneider, Harrison & Hunt in press). Phalarope (*Phalaropus fulicarius*) and kittiwakes (*Rissa tridactyla*) captured injured euphausiids found swimming near the surface at the front. These authors attributed this feeding interaction to subsurface concentration of down-

ward swimming euphausiids beneath a surface convergence on the mixed side of the front (Simard, de Ladurantaye & Therriault 1986), upward flushing of euphausiids injured by diving murre, and concentration of injured euphausiids at the convergence associated with the thermal front at the sea surface. Enhanced standing stock of phytoplankton occurs on the stratified side of the front (Fig. 1), while avian predation on euphausiids occurred either at the front (kittiwakes and phalaropes), or on the mixed side of the front (murre). The Bay of Fundy and Pribilof Island studies demonstrate the importance of one of the two hypotheses relating marine birds to fronts, which is that avian predators respond to prey patches that develop through interaction between prey behaviour and circulatory patterns. Detailed work at more locations will be needed to determine whether this generalization applies to other frontal systems. The importance of the alternate general hypothesis, which is that enhanced primary production increases prey supply to birds through enhanced growth, has yet to be evaluated. We do not yet know whether enhanced primary production at fronts is passed along to consumers such as seabirds, or simply carried elsewhere.

Improved understanding of concentrating mechanisms and production processes still falls short of an important goal, which is estimating the magnitude of prey mortality and predator intake in a spatially heterogeneous environment. Both prey mortality and avian intake can be viewed as flux rates upward through the sea surface with dimensions of mass per unit area per unit time ( $M L^{-2} T^{-1}$  where M is mass, L is length, and T is time). Given the area of ocean used by pelagic populations and the difficulty in obtaining 2-dimensional measurements of seabird distribution, some form of interpolation has to be used. One solution is to develop a statistical model of spatial variation in upward flux of prey to avian predators. A wealth of such statistical models exists (Ripley 1981). At present, we cannot expect a statistical model to give us a very precise estimate of flux because of the generally low explained variances reported to date. Another solution, which is standard in physical and biological oceanography, is to construct a dynamic model that captures major features of spatial heterogeneity, such as fronts. The statistical route guarantees an immediate result in any given situation, with no guarantee of carryover to other

situations. The alternative route, construction of a model of the feeding dynamics of marine birds in a spatially heterogeneous environment, will take longer, but does hold out the hope of general applicability and greater insight into the sources of spatial variability in trophic interaction between seabirds and their prey.

A better description (and preferably, understanding) of spatial variation in energy flux to marine birds is needed in several contexts. One such context is the impact of changes in the abundance and dispersion of fish and other prey on the foraging success and reproductive output of marine bird populations. How much of a change in either abundance or patchiness of prey must occur, and at what scale, before we can expect a change in foraging success or reproductive output of avian predators? The obverse side of this coin is: can we use seabirds as monitors of change in prey stocks, or are seabirds so loosely coupled with prey as to make them of little practical use in monitoring changes in prey abundance or dispersion? A second important context is improved understanding of natural mortality of commercially important fish species. By tradition, fisheries biologists set natural mortality at 20% per unit time, a figure that seems to work despite known temporal and spatial variation in rate of prey removal by predators. Can we perhaps use birds as a convenient, highly visible group with which to investigate and attempt to understand spatial variation in natural mortality of commercially important fish stocks? A third important context is the impact of point-source pollutants (notably oil spills) on marine birds. We can be certain that aggregation will decrease the probability of contact between a spill and a group of birds, while increasing the number of encounters, given a contact. To make more specific statements, we need a model of spatial variability in seabird abundance at the spatial scale of oil spills, which range from  $10^0$  to  $10^{10}$  metres in area.

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