SHORT COMMUNICATIONS

MARINE BIRD ATTRACTION TO THERMAL FRONTS IN THE CALIFORNIA CURRENT SYSTEM[1]

CHRISTOPHER J. HOEFER[2]
Department of Natural Sciences, The Evergreen State College, Olympia, WA 98505

Abstract. I relate marine bird density to the 55 strongest thermal fronts encountered during a survey of much of the eastern portion of the California Current and the adjacent coastal upwelling region. Elevated densities were recorded for all marine bird taxa except the Leach's Storm-Petrel (*Oceanodroma leucorhoa*). The variance explained by the regression models ranged from 3% for the Leach's Storm-Petrel to 85% for all marine birds. The response observed is notably stronger than previous analyses with similar data.

Key words: California Current System, Leach's Storm-Petrel, Oceanodroma leucorhoa, pelagic ecology, seabird distribution, thermal fronts.

Because of the spatial and temporal variability of the marine environment and because marine birds are only weakly correlated with their prey at relatively small spatial scales (Obst 1985, Heinemann et al. 1989), marine bird distributions may reflect a selection of regions or habitats that produce a regular supply of accessible prey as well as the strongly opportunistic nature of their environment. Hydrographic events that concentrate prey, particularly those that are persistent or recurring, are potentially important to marine birds because they can provide a spatially and temporally predictable food supply (Hunt 1990, Schneider 1990). Fronts, areas adjoining two different water masses, are one example of biologically important hydrographic events.

Fronts have been defined more specifically as lines of horizontally convergent flow where vertical flow is often vigorous and highly localized (Owen 1981). They occur on scales ranging from Langmuir circulations (10–100 m) to the major current boundaries and other transition zones that result from large-scale atmospheric circulation. Sea floor topography, coastal prominences, coastal upwelling, circulatory patterns, and wind events are physical features that contribute to the production of fronts (Owen 1981). Even though the degree to which frontal systems affect prey of marine birds, the width over which they do this, and the

trophic dynamics of frontal regions are all complex, it is now becoming clear that frontal systems affect organisms at all trophic levels.

Although statistically significant responses of organisms to frontal regions and the associated causal relationships are often difficult to demonstrate (Owen 1981, Schneider 1990), elevated densities of organisms from phytoplankton to high level predators like marine birds and mammals have been observed near fronts (Olson and Backus 1985). Marine birds have been associated with fronts and other biologically important oceanographic features in the Bering Sea (Kinder et al. 1983), North Atlantic (Brown and Gaskin 1988), subtropical Gulf Stream (Haney and McGillivary 1985), as well as regions in the Southern Hemisphere (Abrams and Underhill 1986). Briggs et al. (1987) found marine bird affinities for temperature gradients off California using primarily aerial surveys and primary components analysis (PCA). The present study demonstrates significant associations by marine birds to frontal regions in the California Current. Marine bird densities are related to 55 of the "strongest" thermal fronts that were encountered.

METHODS

The survey area consisted of waters from the coast to 300 km offshore of California, Washington, and Oregon, from 30 to 46°N latitude. This area comprises the coastal upwelling zone and much of the eastern portion of the California Current, an eastern boundary current that is characterized by a surface flow that is equatorward and between 1,000 and 1,500 km wide (Huyer 1983).

The numerous fronts that were encountered during this study are a result of the complexity of this region. The California Current and coastal upwelling, including their interaction, are two primary features of biological significance within this region. Coastal upwelling can occur sporadically throughout the year as a result of strong wind events. It is most intense during the spring and summer when winds from the north are prevalent along the entire coast (Huyer 1983). Upwelling typically occurs within 10 or 20 km of the coast (Walsh 1981). At these distances, the cool, nutrient-rich waters that move offshore after being upwelled along the coast are downwelled below the warmer, stratified waters of the California Current. However, disturbances such as meanders and eddies

occur along this convergence front which allow the upwelled water to remain at the surface and to enter the equatorward flow of the current. For instance, particularly strong upwelling occurs near capes and promontories. These "upwelling centers" apparently generate narrow (~40 km) offshore surface jets which carry filaments of coastal water several hundred kilometers offshore (Landry and Hickey 1989). One such jet occurs near Haceta Banks (~44°N) where the continental shelf doubles in width.

Bird observations were made from July to November 1996 aboard two National Oceanic and Atmospheric Administration (NOAA) research vessels—the *McArthur* and the *David Starr Jordan*. Ship speed was maintained at 18.5 km hr^{-1}. Two observers rotated on a 2-hr schedule from dawn to dusk when observation conditions allowed. The observers recorded all birds in a 300 m bow-to-beam strip transect on the side with best visibility (Tasker et al. 1984). Distance was estimated with a pelagic rangefinder (Heinemann 1981). In addition to species identification, data recorded for each sighting included association with other marine animals and whatever animals were foraging, flying, or sitting. Ship-following birds were excluded from density estimates. Beaufort and general observation conditions were recorded at the beginning of each transect. If conditions changed, a new transect was started. Data were entered into a laptop computer in real-time format. This allowed comparison with the oceanographic data that were collected simultaneously with a flow-through thermosalinograph.

DATA ANALYSES

Linear regression was used to relate marine bird distributions with fronts (Sokal and Rohlf 1981). Bird density, the dependent variable, was regressed against distance from front, the independent variable. Log-transformed bird density (birds km^{-2}) was calculated over both 15 and 30-min intervals (4.6 and 9.3 km, respectively) starting at the center of the fronts. This allowed comparison with other studies that were done on similar spatial scales. Curvilinear regression was run for the 4.6-km density data to check for second or third-order effects. Because the density data could not be normalized sufficiently with log transformations, significance values for regression lines were set at $P < 0.02$. Despite the lack of normality, regression still provides the best analysis of these data (Seber 1977). Fronts were defined as areas where sea surface temperature (SST) gradients were at least one order of magnitude above the mean SST gradient. SST gradients were calculated over 2-min intervals (0.6 km) to gain fine spatial resolution when defining the center of the thermal fronts. The mean rate of change in SST was 0.05°C km^{-1}, and fronts used for the study had a gradient of at least 0.51°C km^{-1}. The number of fronts with this characteristic was 55.

I examined intermediate spatial scales to avoid autocorrelation problems associated with short distances and spatial resolution problems found with long distances. For example, Schneider and Piatt (1986) found that the strength of association between murres (*Uria* spp.) and schooling fish was greatest at the scale of several kilometers, and the association decreased rapidly at progressively smaller spatial scales.

RESULTS

A total of approximately 1,020 hours of observation were completed and 5,665 km^2 were surveyed. Numerically dominant species, including information on their food and feeding habits and guild composition, are listed in Table 1. Although the less common species observed were excluded from this table, they were included in the density estimates for regression purposes.

All taxa, excluding the Leach's Storm-Petrel, exhibited elevated densities in frontal regions. However, the responses were variable. Only five taxa showed significant responses to fronts (Table 2). Leach's Storm-Petrels and Cassin's Auklet (scientific names in Table 1) had nonsignificant slopes and low amounts of variance explained. Linear regression equations accounted for 3 to 85% of the variation in seabird density when using distance from front as the predictor variable and the 4.6-km scale (Table 2). The 9.3-km scale examination resulted in slightly higher amounts of variance explained, but the significance values were lower.

Curvilinear regression was run for the 4.6-km density estimates because the data suggested second or third-order effects. This resulted in slightly higher amounts of variance explained for some taxa. With quadratic (second order) equations, Common Murre and the combined marine bird categories both had 92% variance explained ($P < 0.01$), and shearwaters had 59% variance explained ($P < 0.01$). Third-order equations did not noticeably improve the variance explained for any of the taxa from the quadratic fit.

DISCUSSION

I found elevated densities of seabirds near fronts for most taxa and both surface and subsurface feeding guilds, and a relatively high amount of variance explained by distance from front for some taxa. Although prior studies have shown elevated densities of marine birds in frontal regions, the results are often variable or there is low explained variance. Schneider (1990) suggested a two step causal linkage—fronts to prey, and prey to birds—as an explanation for the weak, although apparently significant, association between seabirds and fronts. Another possible explanation for the weak associations found in previous studies is that correlation with SST gradients is often used instead of regressing density against distance from front. In the former type of analysis, all elevated gradients will affect the relationship and possibly diminish the variance explained. Marine birds may not be attracted to all elevated or relatively high SST gradients. Rather, they may respond, directly or indirectly, to only the highest SST gradients that could represent biologically important fronts. Even if marine birds are associating with most of the elevated gradients but the association is not tight in that the birds are generally over waters nearby rather than directly over the gradients, a significant correlation will depend upon the scale used to both detect and define the location of fronts and estimate bird densities. Also, it will depend on the definitions used for fronts, which do not always corre-

TABLE 1. Dominant marine bird species that were observed associated with ocean fronts in the California Current with information on food, foraging techniques, and guild composition.

Species	No. observed	Food[a]	Foraging habits[a]
Sooty Shearwater[b] *Puffinus griseus*	8,769	Fish, cephalopods, crustaceans	Surface-seizing, pursuit-diving
Phalaropes[c] *Phalaropus* spp.	2,798	Zooplankton, fish eggs	Surface-seizing
Leach's Storm-Petrel[c] *Oceanodroma leucorhoa*	1,756	Crustaceans, molluscs, fish	Pattering, surface-seizing, dipping
Western Gull[c] *Larus occidentalis*	1,396	Fish, crustaceans, carrion	Surface-seizing, scavenging, piracy
Pink-footed Shearwater[b] *Puffinus creatopus*	1,350	Fish, cephalopods, crustaceans	Pursuit-diving, surface-seizing
Northern Fulmar[c] *Fulmarus glacialis*	684	Fish, cephalopods, crustaceans	Surface-seizing, filtering, little diving
California Gull[c] *Larus californicus*	677	Fish, crustaceans, carrion	Surface-seizing, scavenging, piracy
Cassin's Auklet[b] *Ptychoramphus aleuticus*	669	Crustaceans, zooplankton, larvae	Pursuit-diving, surface-seizing
Common Murre[b] *Uria aalge*	651	Fish, crustaceans	Pursuit-diving, surface-seizing
Fork-tailed Storm-Petrel[c] *Oceanodroma furcata*	644	Fish, crustaceans, floating oil	Pattering, surface-seizing, dipping
Buller's Shearwater[c] *Puffinus bulleri*	511	Fish, cephalopods, crustaceans	Surface-seizing
Arctic Tern[c] *Sterna paradisaea*	465	Fish, crustaceans	Plunging, dipping
Jaegers[c] *Stercorarius* spp.	343	Fish, crustaceans, carrion	Piracy, dipping, surface-seizing
Brown Pelican[c] *Pelecanus occidentalis*	80	Fish	Plunging, surface-filtering
Xantus'/Craveri's Murrelet[b] *Synthliboramphus* spp.	71	Fish, crustaceans, zooplankton	Pursuit-diving, surface-seizing
Sabine's Gull[c] *Larus sabini*	68	Fish, crustaceans	Dipping, surface-seizing

[a] Sources include Ashmole (1971) and Cramp (1977).
[b] Members of the subsurface-foraging guild.
[c] Members of the surface-foraging guild.

TABLE 2. Linear regression statistics for seabird density (calculated in 15- and 30-min intervals; 4.6 and 9.3 km, respectively) regressed against distance from front. All slopes (b) were negative except for the Leach's Storm-Petrel.

Dependent variable (y)	Scale (km)[a]	R^2	P-values
All marine birds	4.64	0.76	<0.01
	9.27	0.85	0.03
Sooty/Pink-footed Shearwaters	4.64	0.57	0.01
	9.27	0.69	0.08
Leach's Storm-Petrel	4.64	0.03	0.65
	9.27	0.07	0.66
Phalaropus sp.	4.64	0.52	0.02
	9.27	0.72	0.07
Western Gull	4.64	0.85	<0.01
	9.27	0.91	0.01
Common Murre	4.64	0.85	<0.01
	9.27	0.89	0.02
Cassin's Auklet	4.64	0.06	0.50
	9.27	0.05	0.72
Subsurface[b]	4.64	0.51	0.02
	9.27	0.73	0.07
Surface[b]	4.64	0.48	0.03
	9.27	0.58	0.13

[a] Size of block used for the independent variable, distance from front.
[b] Dominant members of the foraging guilds are listed in Table 1.

spond to biological significance concerning both prey species and higher level consumers.

This response does not necessarily need to be causally related to the SST gradients. That is, birds may not be searching for the high gradients directly. Instead, they may be tracking something else such as actively or successfully foraging birds, another covarying surface feature not generally measured, or some combination of inadequately measured or unmeasured variables.

The highest gradients may represent the temporally more predictable or longer lasting frontal regions. Indeed, if the smallest frontal systems are usually accounted for by cellular convections due to wind or thermocline effects (Owen 1981) that are short-lived and temporally less predictable than, for example, upwelling convergence or shelf-break fronts, we can hypothesize that marine birds may not be able to locate these systems reliably. The high amount of variance explained for most taxa found here suggest that this might be the case. Also, Elphick and Hunt (1993) suggest that a marine bird's ability to recognize a habitat patch depends on both the size of the patch and its degree of contrast with adjacent waters. Thus, the strongest gradients may represent the frontal systems that, through predictability, size, and degree of contrast, marine birds can recognize and respond to. The degree of contrast does not have to be the actual temperature gradient, but rather just a covariate that the birds can actively track.

The differential response of marine bird guilds to fronts has been reported by Haney and McGillivary (1985) and Briggs et al. (1987). The results of the present study overlap considerably with the Briggs et al.

study. In both studies, the Leach's Storm-Petrel showed a distribution that was distinctly away from these systems. Despite storm-petrel affinities for regions of upwelling (Stallcup 1976), the distribution of the Leach's Storm-Petrel seems to be distinctly seaward of the continental shelf and slope and in the California Current proper. This area is practically devoid of the high SST gradients that were looked at except for areas with, for example, the offshore surface jets and meanders mentioned previously. This storm-petrel may be competitively excluded from these high density areas. Briggs et al. (1987) found a strong negative correlation between this species and other birds.

There is another potentially simpler explanation for our results concerning the Leach's Storm-Petrel. This species apparently feeds extensively at night (Watanuki 1985, Steele and Montevecchi 1994). Although we observed this species on several occasions feeding diurnally, a correlation with frontal regions may only exist nocturnally. It also is likely that our results parallel the observations made by Duffy (1986). He found that a less competitive species, the Roseate Tern (*Sterna dougallii*), foraged more successfully in smaller feeding groups and in regions where prey was more dispersed. We observed the Leach's Storm-Petrel most commonly in small, widely dispersed groups. Although this seems the most probable explanation of our results, whether or not these small groups were actually foraging and, if so, more successfully remains to be demonstrated. A combination of these factors could both exclude this species from frontal regions and/or diminish any diurnal response to them.

Primarily piscivorous species, including shearwaters, gulls, and the Common Murre, were strongly correlated with fronts. The correlation between gulls (primarily Western Gulls) and fronts, however, seems to be an indirect relationship. I observed gulls most often associated with shearwater flocks. This association, apparently lacking in the South Atlantic Bight in Haney and McGillivary's (1985) study, may explain the difference. The food and feeding habits of the species observed in that study (regarded as scavengers) may differ substantially from that of the Western Gull.

In summary, distance from front is an important predictor of marine bird distributions, and it has been neglected as such in deference to correlational studies using temperature gradients as the predictor. The high amount of variance explained suggests that the tracking of thermal fronts by marine birds is potentially more direct than once thought, at least for some taxa. In this case, it may be enlightening to compare the variability in occurrence at fronts between taxa or foraging guilds such as olfactory foragers versus non-olfactory foragers. Fronts are often biologically important. Marine birds often congregate near fronts. How do they do this? How marine birds distribute themselves across the heterogeneous, yet deceptively monotonous, ocean remains elusive.

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