Distribution and Diet of Cassin's Auklet and Common Murre in Relation to Central California Upwellings

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Abstract
Cassin's Auklets (*Ptychoramphus aleuticus*) and Common Murres (*Uria aalge*) nesting in California feed on euphausiids and fish whose life histories are adapted to coastal upwellings. Employing ship, aerial, and satellite observations, we determined responses in distribution and diet of these alcids to onset and variations in upwelling near the Farallon Islands. Birds and their prey aggregated at shorter spatial scales across the shelf than along it. Feeding centers persisted as long as 60 d, but auklet distribution changed within a few days in response to formation of an upwelling "filament." Diets changed slowly, differing before and after upwelling.

Introduction

Concurrent studies of seabird abundance, prey availability, and the ocean environment have been relatively few, but this combination is necessary to understand seabird occurrence patterns. Usually one of the elements is missing, or the scales of measurement are mismatched. In some cases bird and prey concentrations were found to correlate locally and over larger areas (e.g., Bradstreet 1979; Brown 1980; Briggs *et al.* 1984; Schneider and Piatt, in press), but in others correlation at local scales was poor (Woodby 1984; Obst 1985).

Off the California coast, the frontal zone between the offshore California Current and continental-shelf upwellings constitutes the main habitat of some seabirds and limits the distribution (seaward or shoreward) of others. Colonies of Cassin's Auklet (*Ptychoramphus aleuticus*), a planktivore, occur at only three sites; upwellings and frontal formation recur frequently at these sites. Colonies of Common Murres (*Uria aalge*) exist at two of these sites, as well as at others where upwellings are frequent. The murre dives much deeper than the auklet (Tuck and Squires 1955; Krasnow and Sanger 1982; Dolphin and McSweeny 1983) and feeds on fish, squid, and zooplankton. Both alcids are abundant near their Farallon Islands breeding colonies (Fig. 1), where they feed primarily on euphausiids and rockfish during nesting season (Manuwal 1974; DGA, unpublished data). These prey are adapted to reproducing in the upwelling environment and probably move toward shore from seaward of the shelf with the onset of upwelling during spring (Parrish *et al.* 1981; PBA and SES, unpublished data).

Methods

By concurrent use of ship and aerial surveys and satellite imagery during 1985, we attempted to determine responses of these two alcids to onset and variations in upwelling. Continuous daylight transects for seabirds were complemented by concurrent hydrographic data, and trawls provided a measure of rockfish and plankton abundance.

We sampled before and after establishment of persistent upwelling. Prior to 20 April, brief periods of upwelling and offshore transport were interrupted by south storms and coastal convergence. Following a strong "coast-wide wind pulse" from 21 to 25 April, upwelling recurred frequently in May and much of June. Heavy winds in mid-June intensified upwelling for 200 km north of Point Reyes, and a warm-core eddy, centered off the shelf, entrained some of this upwelled water into a long "filament" extending southwest. Where the cold water passed 40 km west of Point Reyes, strong thermal (and density) gradients marked the edges.

Results and Discussion

During six cross-shelf aerial surveys in March through May, Common Murres were consistent in distribution relative to mainland and Farallon colonies. Occurring in large numbers to about 20 km from the colony, murre densities correlated negatively with water depth, distance to the mainland, and distance to the Farallones. A feeding area 8–25 km northeast of the islands was occupied by numerous large flocks from mid-April to early June. After that, murres favored waters within 12 km of the colonies on the mainland and Farallones (Fig. 1).

In June, murres occupied waters having a variety of temperature and salinity conditions. They preferred turbid water near colonies, but their abundance was not correlated with water density at 10 m (an index to the recency of upwelling; Fig. 1). A regression model explaining 31% of density variation in murres incorporated optical depth (OD) and distance to the nearest colony (DC):

$$\log \text{density} = -0.02\ \text{OD} - 0.005\ \text{DC} + 0.41 \qquad (1)$$

$$(\text{ANOVA } F_{2,49} = 12.07,\ P < 0.001)$$

Where birds fed near the coast, surface estuarine outflow from San Francisco Bay was underlain by salty, cold water that probably had been upwelled along the outer shelf. Fish such as anchovies (*Engraulis mordax*), smelt (Osmeridae), and small lingcod (*Ophiodon elongatus*) constituted the nearshore diet. From

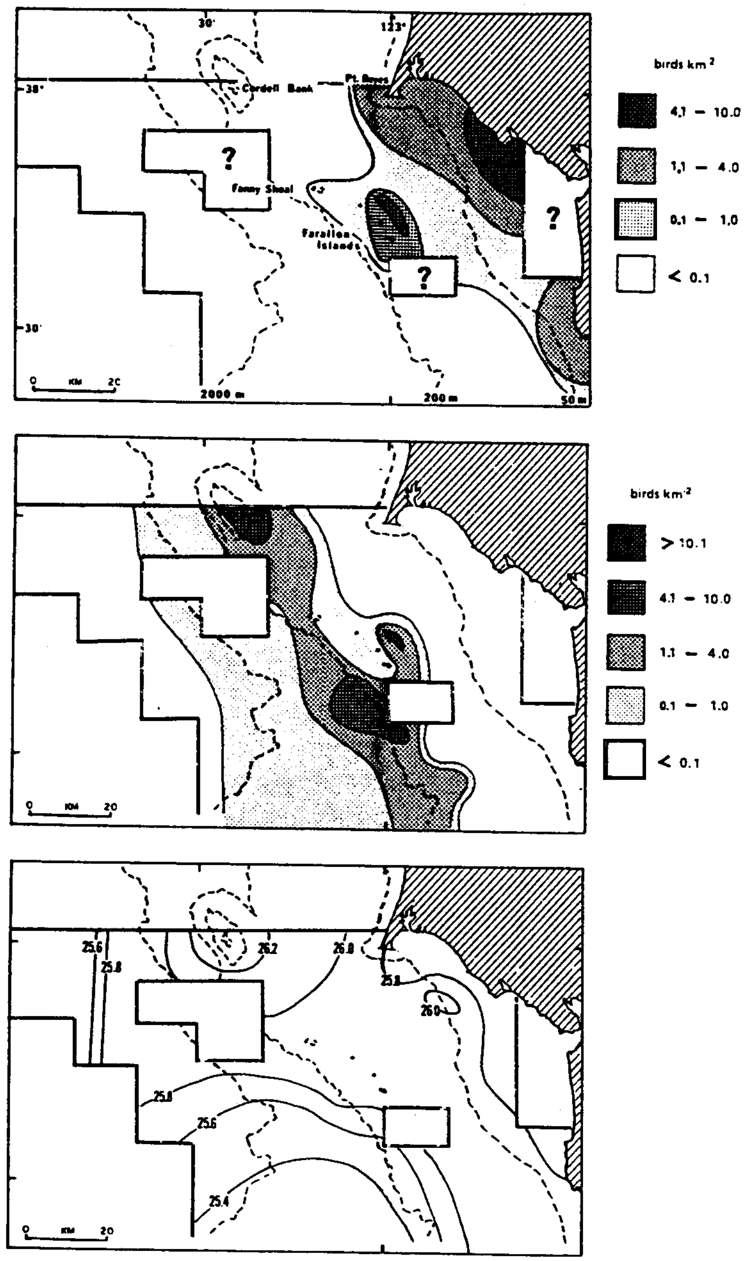

Figure 1. Distributions of Common Murres (top) and Cassin's Auklets (middle) compared with plot of water density (sigma t) at 10 m (bottom), 12–17 June 1985. Areas not sampled are delimited by double lines.

the Farallones, murres foraged in waters intermediate in character between recent upwellings (cold and salty) and estuarine outflow. Diets on the outer shelf changed after 20 April from almost all euphausiids to almost all juvenile rockfish (Table 1).

From continuous ship-transect data, we determined the variance to mean ratios for bird density in transect intervals ranging from 1 to 64 km (Ord 1972; Schneider and Duffy 1985). At all measurement intervals, density variation in murres was greater in the cross-shelf than the along-shelf direction. Peak variance to mean ratios (I′), which we interpret to indicate the scales at which bird aggregation was most intense, occurred at measurement intervals of 8–24 km across the shelf and 16–24 km along the shelf (Fig. 2).

The center of auklet distribution shifted at onset of egg laying in late March from offshore of the continental slope (200–2000 m in depth) toward the shelf break. Auklets were usually abundant north, rather than south, of the colony. In April, May, and early June, auklet density varied inversely with distance from the shelf break and distance from the colony, but did not correlate with depth or distance to the mainland. In late March, as auklets shifted toward the shelf break, they aggregated at shorter spatial scales than in mid-March, when they were widely dispersed off the shelf; the scale of maximum intensity of aggregation in the cross-shelf direction diminished from I'_{max} = 32 km to I'_{max} = 16 km (Fig. 2). In the along-shelf direction, peak auklet aggregation occurred at 48+ km in all months.

In mid-June, we began to see auklets 15–25 km southwest of the colony. At this time, we encountered no auklets over the inner shelf, large numbers in the edges and core of the cold upwelling filament west of Point Reyes (to 63 km from the colony), and none for 50 km seaward of the filament. Returning southeast toward the colony, we again encountered a few auklets in the core of the filament and many within 20 km of the island, where temperature and salinity characteristics were those of a relict upwelling.

Along the inner edge of the filament and at Fanny Shoal, auklets ate euphausiids (Table 1). Adults of one prey species, *Thysanoessa spinifera*, concentrated at or below the thermocline by day during the nonupwelling season. After the onset of upwelling, surface swarms became frequent. In June 1985, *T. spinifera* was abundant along the outer shelf, avoiding nearshore waters and those seaward of the shelf break. *Euphausia pacifica* inhabited the upper continental slope, where most adults apparently remained below the thermocline until dark. In deep water southwest of the colony, auklets ate mainly small (30 mm) rockfish (*Sebastes* spp.). These offshore surface waters were relatively fresh and warm, and a strong thermocline existed at 15–30 m. A regression model incorporating water density (sigma t) at 10 m, optical depth (OD), and distance to the colony (DC) explained 36% of variation in auklet density:

$$\log \text{density} = 0.34 \text{ sigma t} - 0.006 \text{ DC} - 0.06 \text{ OD} - 8.2 \quad (2)$$

$$(\text{ANOVA } F_{2,49} = 26.22, P < 0.001)$$

In previous years, auklets occurred in large numbers at Cordell Bank (Briggs *et al.* 1983). During 1985, they mostly avoided the area until the upwelling

Table 1. Major components of diets of Cassin's Auklets and Common Murres off the central California coast, March–July 1985.*

Bird species	Period	Location[†]	Sample size	No. of prey species	Prey species	% occurrence	% frequency
Cassin's Auklet	Late March	FS–CB	13	3	*Thysanoessa spinifera*	54	15
					Euphausia pacifica	100	85
	Mid-April	NFAR	5	2	*T. spinifera*	80	12
					E. pacifica	100	88
	Early June	FS–CB	8	4	*T. spinifera*	38	23
					E. pacifica	88	73
					Sebastes spp.	50	40
		NFAR	6	4	*T. spinifera*	67	59
					Sebastes spp.	83	15
		SFAR	11	8	*T. spinifera*	9	7
					E. pacifica	9	7
					Sebastes spp.	73	26
	Mid-June	FS–CB	7	4	*T. spinifera*	28	1
					E. pacifica	86	96
					Sebastes spp.	86	3
		NFAR	4	3	*T. spinifera*	50	18
					E. pacifica	75	27

					Sebastes spp.	100	55
	Late July	NFAR	10	3	*T. spinifera*	70	24
					E. pacifica	80	75
Common Murre (offshore samples only)	Mid-April	NFAR	7	4	*T. spinifera*	71	7
					E. pacifica	57	92
					Brachyistius frenatus	28	1
		SFAR	5	4	*T. spinifera*	80	85
					E. pacifica	60	2
					Sebastes spp.	100	13
	Mid-June	NFAR	7	3	*E. pacifica*	14	6
					Sebastes spp.	100	87
	Late July	NFAR	5	3	*Sebastes* spp.	100	99

*Only birds containing food are reported.

† Locations: FS-CB: Fanny Shoal to Cordell Bank, 20–35 km northwest of Farallones colony.
NFAR: Near North and Middle Farallones, 6–11 km northwest of Farallones colony.
SFAR: Near South Farallon, 1–15 km west, southeast, or east of Farallones colony.

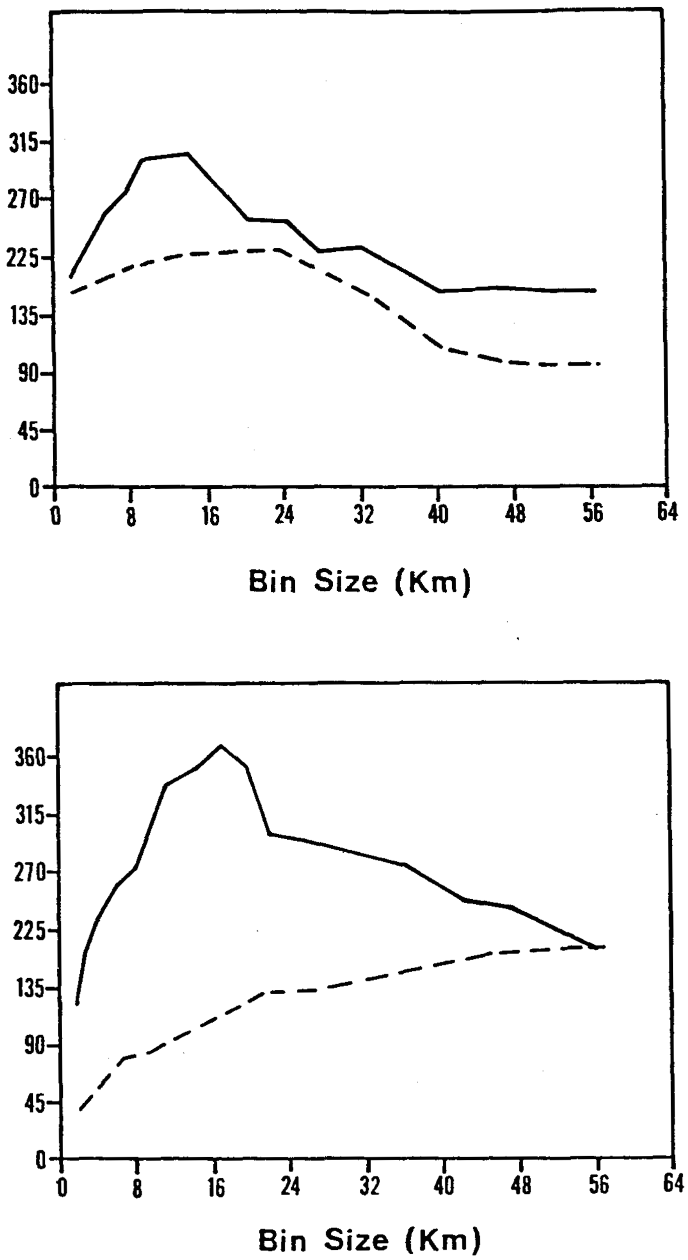

Figure 2. Intensity of aggregation (I′ of Ord 1972) as a function of scale of measurement for Common Murres (top) and Cassin's Auklets (bottom) for ship transects, late May to mid-June 1985. Cross-shelf data are shown with solid lines and along-shelf data with dashed lines.

filament appeared with its strong thermal and optical gradients. Analysis of extensive bird surveys and satellite imagery from central California (J.C. Mueller, L.C. Breaker, and KTB, unpublished data) indicated that auklets are abundant primarily in waters having moderate thermal gradients (0.01–0.10°C·km^{-1}) and moderate clarity (optical depth narrowly restricted to 7.5–8.3 m). Almost all auklets we observed in June 1985 occurred in waters having an optical depth of 5–7 m.

Many questions about links between physical processes, prey populations, and these seabirds remain unanswered. Depths at which the birds obtain food are not known, nor are the specifics of the vertical distributions or scales of aggregation of the prey. During 1985, juvenile rockfish and *E. pacifica* occupied bands along the shelf break with considerable along-shelf continuity (tens of kilometers). This pattern was matched by the auklet but not the murre. A possible explanation lies in the occurrence of murres in relatively murky coastal water northeast of the Farallones; waters were much clearer along the shelf break. Might the greater escape capabilities of small fish (relative to euphausiids) be offset in murky water, where murres can closely approach prey before being detected (Ainley 1977)? On the other hand, why do auklets frequent relatively clear water? Is this the type of water where detection and capture of euphausiids is easiest? Or is this optical characteristic merely a "tracer" for the kind of habitat having the highest numbers of prey? Detailed sonographic transects might provide an answer.

The distribution of auklets relative to the upwelling filament in mid-June suggests that foraging success is enhanced at the upwelling frontal zone. Auklets concentrated only in newly upwelled water or where the same dense subsurface waters lay beneath a shallow thermocline. Fanny Shoal, where auklets fed for more than two months, was bathed much of the time in recently upwelled water. Studies of satellite archives show that the Farallones / Point Reyes / Cordell Bank is one region where upwelling fronts frequently recur and persist up to several weeks (J.C. Mueller and L.C. Breaker, pers. commun.). Such consistency should allow auklets to track the evolution of these features.

A variety of seabirds now have been shown to concentrate at mesoscale ocean features having large property gradients (e.g., midshelf fronts, ice edges, tidally forced divergences, boundaries of Gulf Stream eddies) (Brown 1980; Ainley and Jacobs 1981; Schneider and Hunt 1982; Haney 1985). Off the California coast and elsewhere, the shelf break and associated upwelling fronts appear to segregate different elements of the seabird community. As interdisciplinary studies of the shelf-break zone go forward, we may find that birds such as auklets are uniquely adapted to exploit this intensely variable environment.

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