

SPRING MIGRATION OF PACIFIC LOONS THROUGH THE SOUTHERN CALIFORNIA BIGHT: NEARSHORE FLIGHTS, SEASONAL TIMING AND DISTRIBUTION AT SEA¹

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Abstract. We studied the spring migration of Pacific Loons (*Gavia pacifica*) from a coastal promontory and during shipboard transects in the Southern California Bight. The coastline in the northern part of the bight acts as a leading line that diverts northbound migrants toward the west. We detected no effect of the onshore wind component on migration traffic rates along the coast and rejected the hypothesis that nearshore flights resulted from wind drift. Migration of Pacific Loons proceeded in headwinds up to 13 m/sec, but traffic rates decreased with increasing headwind strength, suggesting that loons avoided flying in the most energetically unfavorable conditions. The timing of peak migratory flights varied from mid-April to early May in different years, perhaps reflecting constraints imposed by the availability of food in wintering areas, at premigratory staging sites, and/or at *en-route* stopover sites. At sea, migrant loons were concentrated in cool waters in the northern part of the bight, and observations of loons on the water were associated with high densities of zooplankton at nearby sampling stations. We hypothesize that many northbound loons stop in the northern bight to feed on macrofauna attracted by concentrations of zooplankton near the frontal boundaries of upwelling plumes. Such stopovers should allow migrant loons to replenish energy stores efficiently and to resume northward migration rapidly.

Key words: *Gavia pacifica*; migration; Pacific Loon; seabirds; seasonal timing; Southern California Bight; stopovers.

INTRODUCTION

Compared with its terrestrial counterpart, the ecology of migration of marine birds has received little attention. This is unfortunate, because *en-route* environments probably are powerful selective agents in the biology of seabirds. In addition to immediate consequences for survival (e.g., Sefton 1926, Barry 1968, Bond 1971), migration through variable marine environments can have important effects on subsequent reproductive performance (Ebbinge 1989).

We studied the spring migration of Pacific Loons (*Gavia pacifica*; formerly considered a subspecies of Arctic Loon, *Gavia arctica pacifica* [AOU 1985]) in the Southern California Bight during a coastal seawatch in 1976-1978 and during shipboard transects in 1989 and 1990. This species was chosen for detailed study because it is an abundant and conspicuous migrant along much of the Pacific coast. Anecdotal accounts

dating back to 1910 describe thousands of loons migrating in continuous streams past coastal vantage points in Mexico and California (Bent 1919). Moreover, distributional reports published in *American Birds* suggest that loon migration may be subject to substantial variation among years: although large spring flights along the west coast normally are confined to April and May, large waves have been reported to continue along the Washington and Oregon coasts throughout June in some years (e.g., Harrington-Tweit and Mattocks 1984, Tweit and Mattocks 1987). Such interannual differences probably reflect variation in some aspect(s) of the marine environment, but the specific factors involved have not been identified.

In this study, we focused on three important components of loon migration strategies that were likely to be influenced by spatiotemporal patterns in the *en-route* marine environment—flight behavior, seasonal timing, and habitat selection during stopovers. Our specific objectives were: (1) to determine whether variations in the magnitude of nearshore loon flights were related to

¹ Received 9 September 1993. Accepted 14 January 1994.

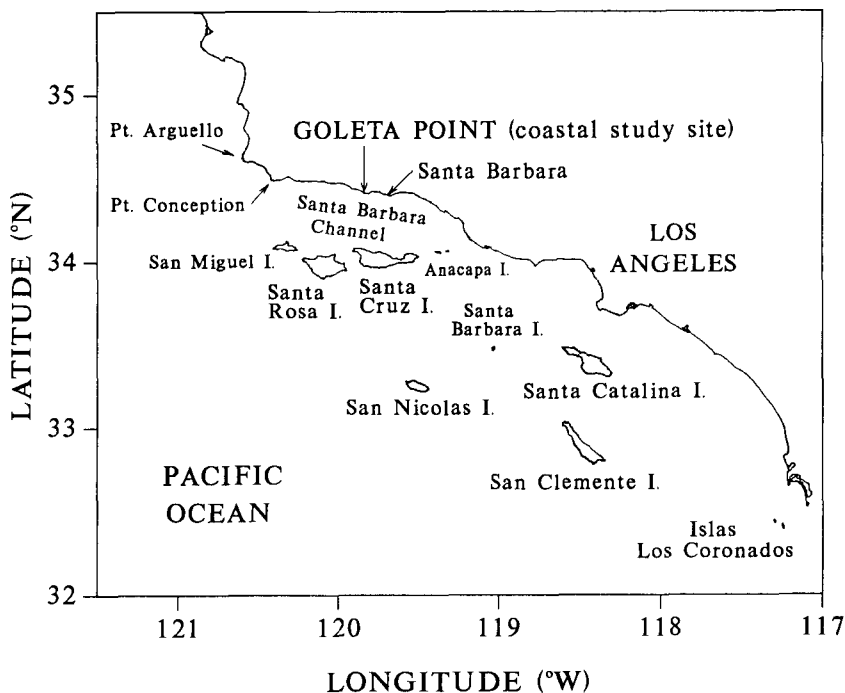


FIGURE 1. Map of study area.

ambient wind conditions; (2) to compare the seasonal timing of loon migration along the southern California coast to temporal patterns of coastal upwelling, which is well known to enhance marine productivity (Ryther 1969); and (3) to search for possible correlations between the geographic distribution of loons at sea and the availability of food resources for refueling.

METHODS

STUDY AREA

The Southern California Bight (hereafter referred to as "the bight") is defined as the "open embayment of the Pacific Ocean bounded on the north by Point Conception, on the west by the California Current and extending southward to Cape Colnett, Baja California" (Jones 1971). A number of islands are located within the bight; these are known collectively as the Channel Islands (Fig. 1).

Important features of the bight have been reviewed by Jones (1971), the Southern California Coastal Water Research Project (1973), Hickey (1979), Huyer (1983), and Jackson (1986). The California Current generally conforms to the Cal-

ifornia coastline until it reaches Point Conception, where it departs from the coast and continues southward, transporting cool, low-salinity water of subarctic origin that is continually modified by mixing, solar heating, and other processes. The flow turns landward off the northern coast of Baja California and divides into two branches, one continuing southward and the other turning toward the north. Water in the northward flowing branch, known as the Southern California Countercurrent, may flow through the northern part of the bight, mix with the California Current near Point Conception, and eventually re-enter the bight. This counterclockwise circulation is known as the Southern California Eddy.

Surface currents in the bight generally are dominated by the northward flow of comparatively warm, saline Southern California Countercurrent water, but the distinctness of the Southern California Eddy varies seasonally. During the spring, the California Current moves inshore, sometimes eliminating the Countercurrent in April and May (Wyllie 1966). Circulation patterns may also be influenced locally by the complex submarine topography in the region.

Coastal upwelling occurs along the west coast of North America in response to equatorward winds blowing parallel to the coastline. The interaction of wind stress and the Coriolis force causes surface water to move offshore (Ekman transport), resulting in a compensating upward vertical flow near the coast. This upwelling transports cold, nutrient-rich subsurface water to the ocean surface, and the influx of nutrients into the euphotic zone results in rapid growth of phytoplankton stocks, short food chains, and high trophic efficiencies (Ryther 1969). Because of the generally northwest-to-southeast orientation of the mainland coastline in the bight, coastal upwelling is caused primarily by northwesterly winds. The most intense upwelling usually occurs in the bight from April to June. Upwelling events occur intermittently, however, and are generally less frequent and less intense than elsewhere along the California coast (Jackson 1986). A notable exception is the Point Conception-Point Arguello area, which is an important and persistent upwelling center (Jones et al. 1983, Atkinson et al. 1986, Science Applications International Corp. [SAIC] 1987).

Spring migration of loons along the coast in the bight was studied at Goleta Point, California (34°24.2'N, 119°50.6'W; Fig. 1). Goleta Point protrudes several hundred meters into the ocean beyond the surrounding coastline, providing an excellent vantage point for observing seabirds migrating westward along the coast. Spring seabird flights at Goleta Point are usually dominated by Pacific Loons, Surf Scoters (*Melanitta perspicillata*), and Brant (*Branta bernicla*), with smaller numbers of Bonaparte's Gulls (*Larus philadelphia*), Red-throated Loons (*Gavia stellata*), Common Loons (*Gavia immer*), and other species; in some years, however, very large numbers of phalaropes (*Phalaropus lobatus* and *P. fulicaria*) and Sooty Shearwaters (*Puffinus griseus*) also pass Goleta Point (Lehman 1979).

STUDY SPECIES

Pacific Loons are widely distributed along the Pacific coast during winter (AOU 1983, Root 1988), but a large proportion of the North American population winters to the south of our study area, in coastal areas of Baja California and in the Sea of Cortez (Bent 1919, Palmer 1962). In adult Pacific Loons, simultaneous replacement of the remiges occurs in late winter (Woollfenden

1967). At that time, flocks of thousands of Pacific Loons in wing molt have been noted on the western coast of Baja California (Jehl 1990), suggesting that this area may be an important pre-migratory staging area. Beginning in late March, Pacific Loons migrate north to their breeding grounds, which stretch from the arctic coasts of Alaska and Canada south to southern Alaska and northwestern Quebec (AOU 1983).

Pacific Loons are pursuit divers, but few data are available on their diet during the nonbreeding season. Stomach contents of four birds wintering on Monterey Bay were dominated by the market squid (*Loligo opalescens*), with smaller numbers of pelagic fishes such as medusafish (*Icichthys lockingtoni*), northern anchovy (*Engraulis mordax*), and unidentified fish species (Baltz and Morejohn 1977). Palmer (1962) reported that two stomachs from birds in California contained only yellow shiner (*Cymatogaster aggregatus*) and minute surfperches (Embiotocidae), respectively, and one from British Columbia contained only herring (*Clupea pallasii*). Crustaceans and mollusks may also be taken (Palmer 1962).

FIELD PROCEDURES

Coastal seawatch. A seawatch was conducted by PEL at Goleta Point from March to late May or early June in 1976, 1977, and 1978 (1976: $n = 83$ hr; 1977: $n = 68$ hr; 1978: $n = 107$ hr). Pacific Loons were counted as they migrated singly or in flocks (usually at altitudes <20 m over the water) past the Point. Observations were made during the mid-afternoon, when heaviest seabird movement tended to occur, averaging about 2 hr/day (usually 14:00–16:00 Pacific Time). If conditions were windy, the observer stood in the lee of a large rock near the beach; otherwise, observations were conducted from a bluff directly above (about 15 m elevation).

Because of their high traffic rates on some days in April, numbers of loons had to be estimated when birds were passing continuously. On these occasions, exact counts were made during one 5-min period every 15 min. The hourly traffic rate (i.e., loons/hr) then was estimated by dividing the sum of the 5-min counts by the total amount of time during which exact counts were conducted.

In 1978, ambient wind conditions were recorded for each of the census periods. Average wind speed (m/sec) was measured with a wind

gauge, and wind direction was coded on an eight-point scale (e.g., north, northeast, east). Because wind conditions were not recorded during 1976 and 1977, data from these years were pooled into 10-day intervals (e.g., 1–10 April, 11–20 April) for comparisons among years. Monthly upwelling indices for 33°N, 119°W were obtained from Mason and Bakun (1986) for comparison with the 1976–1978 data on seasonal timing.

Shipboard studies. Observations of migrant loons were made at sea by RWR and others in the spring of 1989 and 1990 during cruises conducted by the California Cooperative Oceanic Fisheries Investigations (CalCOFI). The cruise track of the ship included transects both perpendicular to and parallel to the southern California coast, from about 32°N to about 35°N, and seaward from the coast to about 124°W. Observations were continuous throughout daylight hours, except when the ship was stopped at stations for oceanographic sampling. Times of observation were recorded for all loons sighted, and locations were calculated by interpolating between station positions. Directions of flying loons were estimated in 1989 with a precision sighting compass and a gyroscopic compass mounted on the ship's bridge.

A variety of oceanographic measurements were made by CalCOFI personnel during stops at sampling stations (Scripps Institution of Oceanography 1989, 1991). We report data on sea-surface temperature (SST) and sea-surface chlorophyll-*a* concentration from hydrographic casts, and data on macrozooplankton displacement volume from net tows. SSTs were read from paired reversing thermometers. For determination of chlorophyll concentrations ($\mu\text{g}/\text{liter}$), 140-ml samples of seawater were filtered through glass fiber filters, the filters were subjected to a cold extraction technique in 90% acetone to remove pigments, and fluorescence was determined with a fluorometer (Venrick and Hayward 1984). Macrozooplankton were sampled with a 71-cm diameter bongo net with 0.51-mm mesh, which was towed obliquely from 210 m (bottom depth permitting) to the surface. Filtered volumes of seawater were estimated from flowmeter readings and the area of the net opening. Large (>5 ml) jellies and tunicates were removed from the sample, and wet displacement volume ($\text{cm}^3/ [1,000 \text{ m}^3 \text{ strained seawater}]$) was determined later, following Kramer et al. (1972).

DATA ANALYSES

Seawatch data. Because serial autocorrelation in the loon count data violates the assumption of independence underlying the application of standard statistical techniques (Bartlett 1935), we first removed the effects of seasonal timing by fitting a curve to the data and performing all analyses on the residuals. Theoretically, the temporal distribution cannot be exactly normal, because a normal distribution has infinitely long tails (Preston 1966). Instead, we used a distribution made up of cosine-power functions of the form

$$y(x) = y_0 \cos^m x, \quad (1)$$

where $y(x)$ represents the migration traffic rate on day x (x has units of radians; $x = 0$ indicates the date of peak migration), $y_0 = y(0)$ indicates the peak migration traffic rate, and m is a parameter having a value greater than one. Preston (1966) used such cosine-power functions to analyze migration phenology in relation to temperature and the solar cycle. When m is large, $y(x)$ closely approaches a normal distribution (but still has finite tails).

Examination of the 1978 data suggested that the seasonal timing of migration at Goleta Point was bimodal. Noting that one Julian day is equivalent to 0.0172 radians, equation (1) may be used to express the composition of two approximately normal distributions as

$$y(x) = y_{1_0} \{\cos[0.0172(x - x_{1_0})]\}^{m_1} + y_{2_0} \{\cos[0.0172(x - x_{2_0})]\}^{m_2}, \quad (2)$$

where x is Julian day, $y(x)$ remains as before, y_{1_0} and y_{2_0} are the peaks of the two distributions, x_{1_0} and x_{2_0} are the respective Julian days corresponding to $x = 0$ in equation (1), and m_1 and m_2 are two parameters having values greater than one.

Nonlinear least squares regression was used to estimate y_{1_0} , y_{2_0} , x_{1_0} , x_{2_0} , m_1 , and m_2 . Because the magnitude of the residuals varied with the magnitude of the predicted migration traffic rates, we standardized the residuals by dividing them by the predictions for each date.

To examine the influence of wind on nearshore flights, we subjected the data on migration traffic rates (adjusted and standardized as described above) to a multiple regression analysis with on-shore and alongshore wind components as the independent variables. Values of the compo-

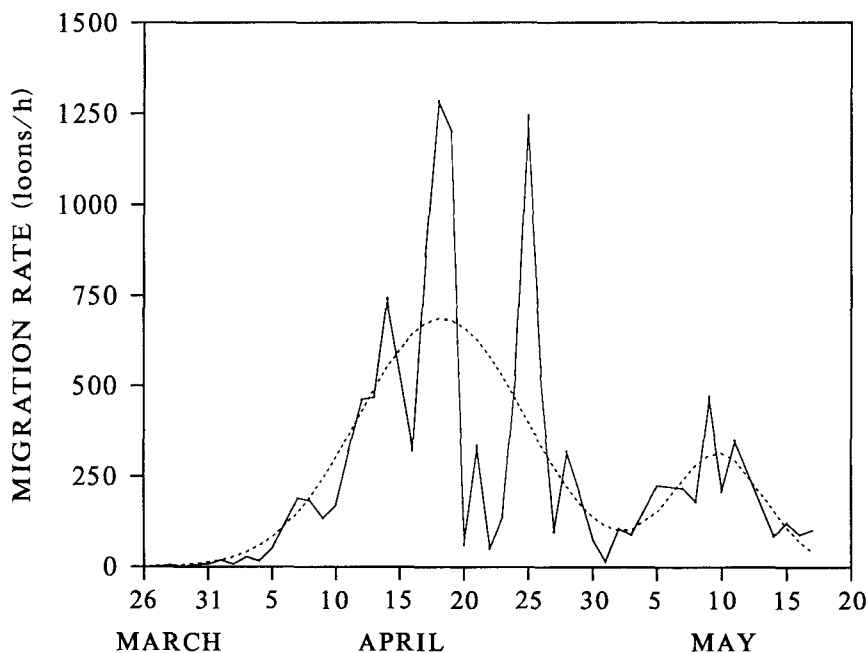


FIGURE 2. Seasonal timing of migration in 1978. The dotted line indicates the fitted cosine-power model (see text for details).

nents were computed with trigonometry by assuming an average coastline orientation of 290° in the vicinity of the study area. For this analysis, we only used data from days when at least 25 loons/hr were predicted by the cosine-power model (2 April through the end of the 1978 study on 18 May; $n = 40$ days).

Oceanographic data. To examine habitat selection, we analyzed the relationship between loon abundance near CalCOFI sampling stations and oceanographic variables measured at those stations. The distribution of loon counts at sea was highly non-normal, so we treated loon abundance as a categorical variable for statistical analyses. The three categories used were: (1) no loons observed near a station; (2) loons present near a station but only observed in flight; and (3) loons observed on the water near a station. "Near a station" was defined as within 30 min sailing time (about 9 km) of a station. Four habitat variables were analyzed: SST, surface chlorophyll concentration, macrozooplankton displacement volume, and distance to the nearest mainland. One-way ANOVAs followed by Tukey HSD multiple comparisons were used to determine which of these four variables were related to the occurrence of loons. Where appropriate, habitat variables were log-transformed prior to analysis

to improve normality and/or to ensure homogeneity of variances. Data from both years were combined for analysis, and only stations east of a line running from 35°N , 122°W to 31°N , 119°W were used ($n = 35$ CalCOFI sampling stations) because loons were never observed west of this line.

Data on flight directions were analyzed using circular statistics (Batschelet 1981). We computed the mean direction of the sample, the length of the mean vector (a measure of the dispersion of the data), and the 99% confidence interval around the mean direction.

RESULTS

COASTAL SEAWATCH

Nearshore flights. Very large numbers of Pacific Loons migrated west past our coastal study site, with typical traffic rates of 500–1,000 birds/hr from mid-April through early May. Migration traffic rates observed from the Goleta Point seawatch in 1978 are shown in Figure 2 together with fitted values from the cosine-power model. Migration traffic rates were not related to the onshore wind component, but did tend to vary with the alongshore component, decreasing with increasing headwind speed (Table 1).

TABLE 1. The relationship between nearshore loon flights and ambient winds at Goleta Point during spring, 1978. Values shown are from a multiple regression analysis ($n = 40$ d, $R^2 = 0.10$) with migration traffic rate (standardized as described in text) as the dependent variable.

Independent variable	Partial regression coefficient	Standard partial regression coefficient	<i>t</i>	<i>P</i>
Crosswind speed*	-0.052	-0.18	-1.12	0.27
Headwind speed	-0.054	-0.32	-1.96	0.057

* Southerly crosswinds were coded as positive, and northerly crosswinds were coded as negative.

Seasonal timing. The seasonal timing of migration varied among years, with peak traffic rates occurring in early May in 1976 and in mid-April in 1977 and 1978 (Fig. 3). The onset of intense upwelling in the region preceded the beginning of loon migration through the bight in all three years (Fig. 4). Upwelling peaked in May in 1976 and in June in 1977 and 1978; seasonal patterns of upwelling were otherwise quite similar in the different years, and did not appear to correlate with the interannual differences in migration timing (Figs. 3, 4).

SHIPBOARD STUDIES

Geographic distribution of loons at sea. Although Pacific Loons were observed throughout the Southern California Bight, the largest numbers

were present in the vicinity of the northern Channel Islands and in the Santa Barbara Channel (Fig. 5). This region was characterized by cold water and sharp horizontal gradients in ocean temperatures (Fig. 6).

Habitat selection. Of the four habitat variables that we examined, only SST and chlorophyll concentration were significantly cross-correlated (Table 2). Neither of these variables, however, was significantly related to the occurrence of loons near sampling stations (Table 3). Distance from the mainland differed significantly among the three classes of stations: stations where loons were observed were closer to the mainland than were stations without loons (Table 3). Multiple comparisons indicated that, among stations where loons were present, the distance from the main-

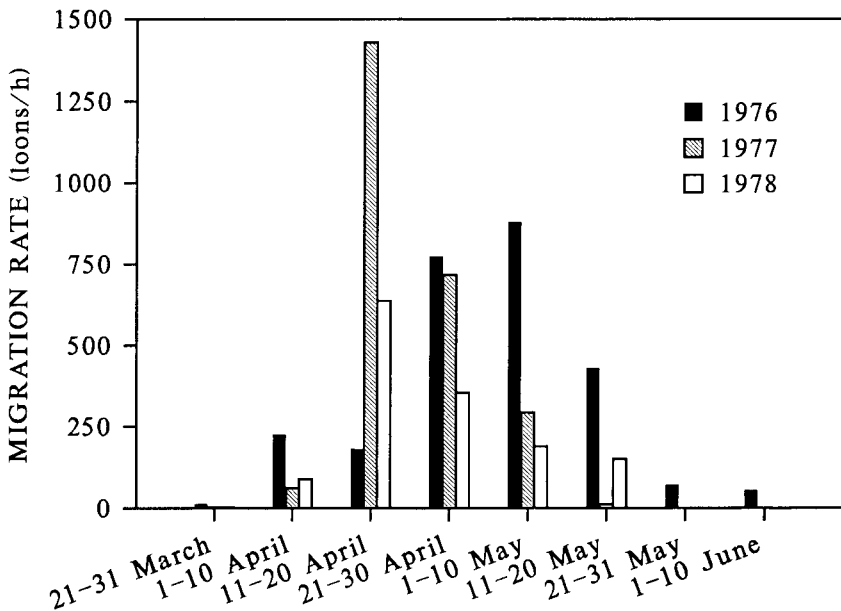


FIGURE 3. The seasonal timing of Pacific Loon migration (birds/hr) observed at Goleta Point in three different years.

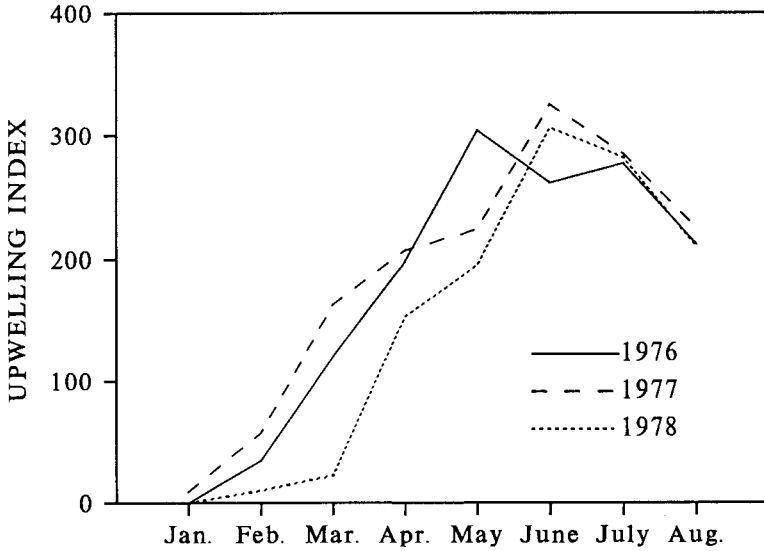


FIGURE 4. Temporal variation in the mean intensity of coastal upwelling measured at 33°N, 119°W. The units of the upwelling index are metric tons per second per 100 m of coastline. These units represent “the average amount of water upwelled through the bottom of the Ekman layer each second along each 100 m of a straight line directed along the dominant trend of the coastline on a scale of about 200 miles” (Mason and Bakun 1986:5).

land did not differ significantly between those stations where loons were observed on the water and those where loons were observed only in flight ($P = 0.66$). The presence of loons also was related to zooplankton displacement volume (Table 3). Multiple comparisons indicated that zooplankton volume was significantly higher at stations where loons were observed on the water than at stations where loons were observed only in flight ($P = 0.047$).

Flight orientation. The mean flight direction of loons observed at sea was toward 307° ($n = 13, r = 0.98$ [r is the length of the mean vector]). Because the axial orientation of the coastline in the northern part of the study area (290°) was not contained in the 99% confidence interval for the mean flight course ($298.8^\circ \leq \bar{x} \leq 314.2^\circ$), it

is likely that most northbound loons eventually intercepted the coastline at locations somewhere east of Point Conception (see Fig. 1).

DISCUSSION
NEARSHORE FLIGHTS

Large but highly variable numbers of migrating loons moved past our coastal seawatch in the northern part of the bight. Many aspects of these nearshore flights are explained most simply by geography. In the southeastern parts of the bight, loons migrate offshore over a broad front, and large nearshore flights rarely are observed (pers. observ.). Migrating loons observed at sea had courses that, if maintained, would eventually have brought the birds to the mainland coastline

TABLE 2. Pearson correlations among selected physical and biological variables measured at 35 sampling stations in the Southern California Bight during the 1989 and 1990 spring cruises. Significance levels were adjusted for multiple comparisons using the Bonferroni procedure. Symbols: NS, not significant; *, $P < 0.05$.

	SST	Chlorophyll concentration	Zooplankton volume
Chlorophyll concentration	-0.44 (*)		
Zooplankton volume	-0.41 (NS)	0.10 (NS)	
Distance to mainland	-0.07 (NS)	-0.21 (NS)	-0.35 (NS)

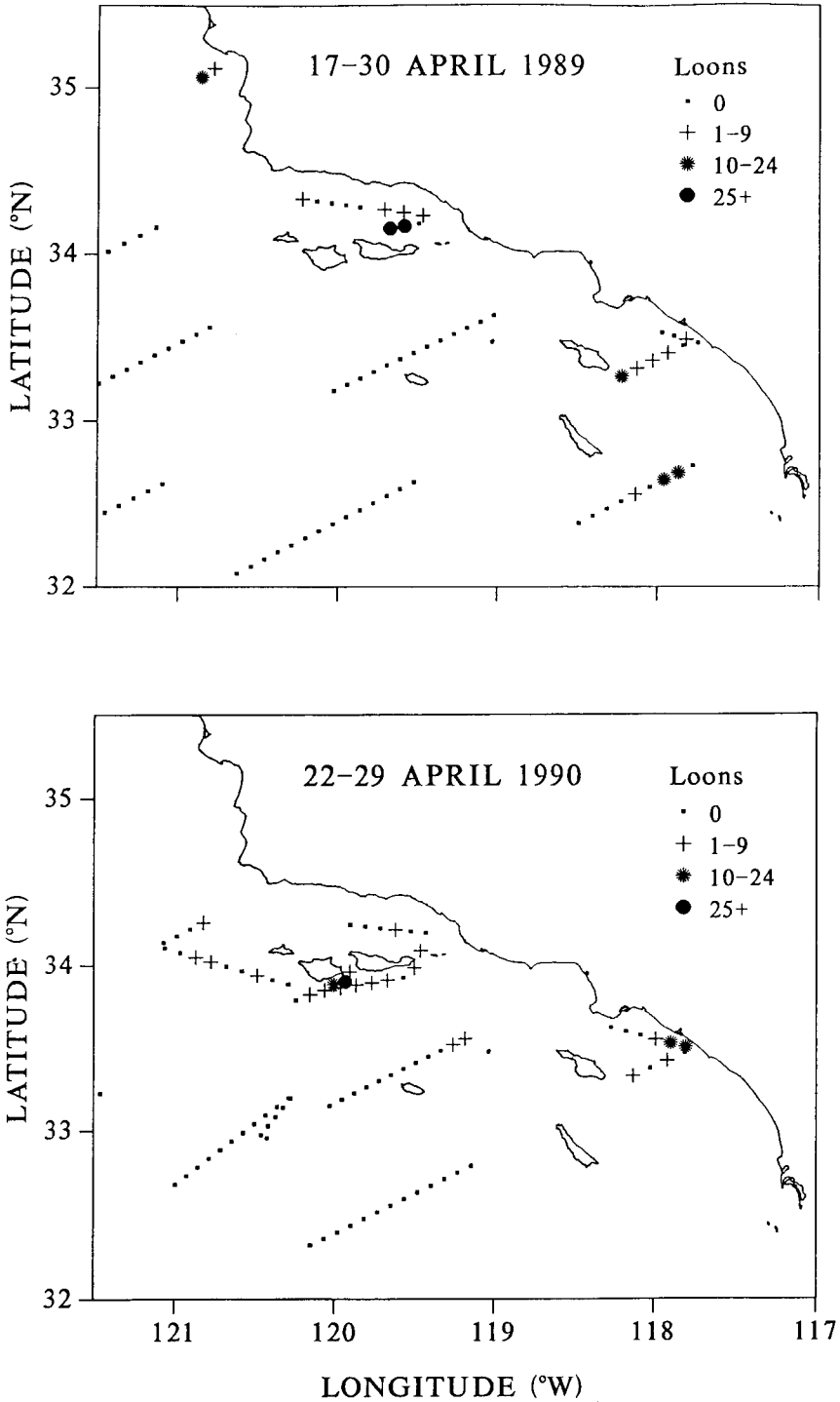


FIGURE 5. Distributions of Pacific Loons observed in the Southern California Bight during two cruises conducted around the peaks of spring migration. Symbols indicate numbers of loons observed during 30-min count periods. Top: 17-30 April 1989. Bottom: 22-29 April 1990.

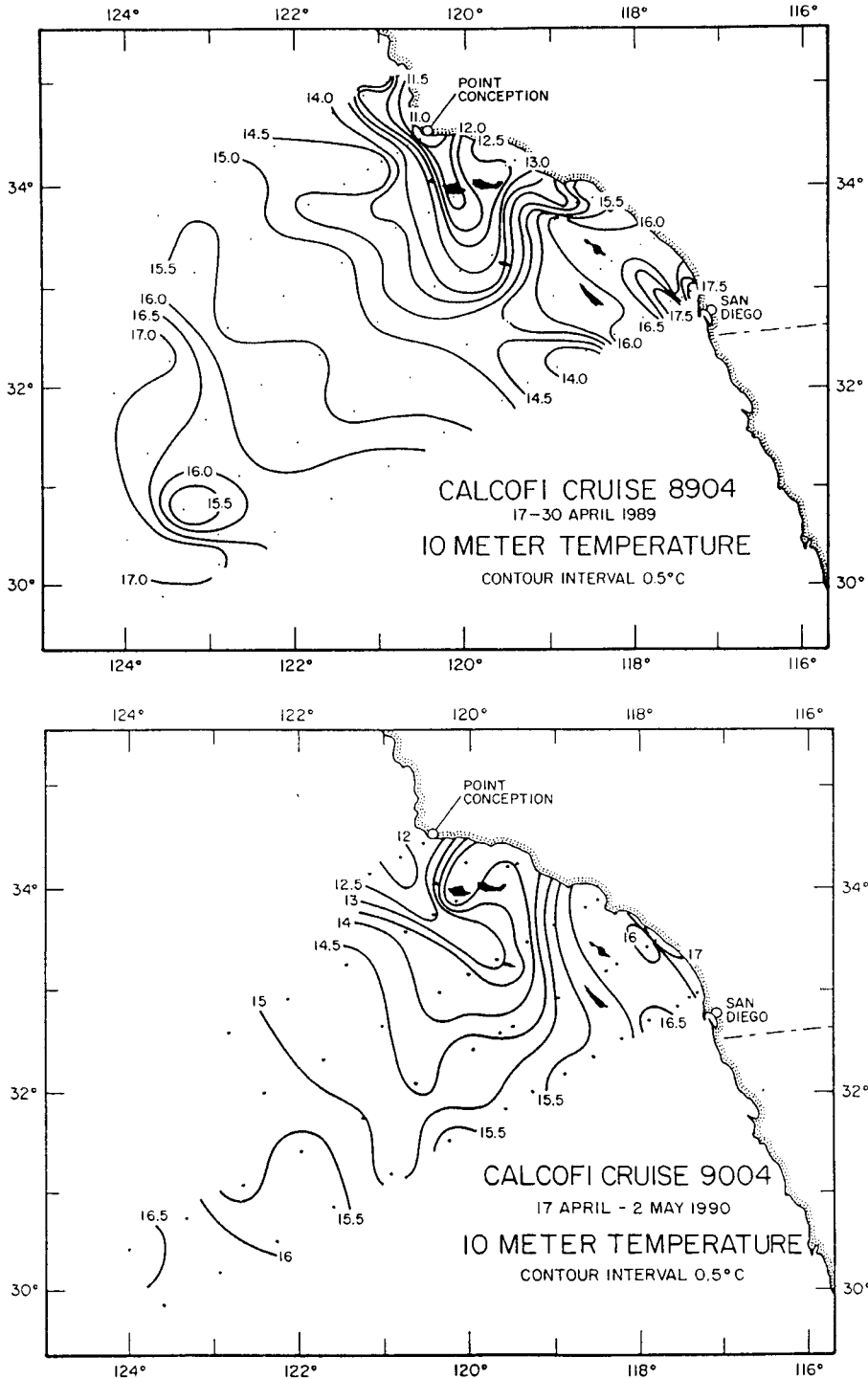


FIGURE 6. Contour plots of ocean temperature (depth = 10 m) during the 1989 and 1990 cruises. Reprinted from Scripps Institution of Oceanography (1989, 1991) with permission from the California Cooperative Oceanic Fisheries Investigations.

TABLE 3. Relationships between the distribution of loons at sea and physical and biological variables potentially involved in selection of stopover habitat. Sample sizes indicate numbers of sampling stations where oceanographic data were taken. Values shown are means and standard errors of the raw data. *F* statistics and *P* values indicate results from one-way ANOVAs. Data on chlorophyll, zooplankton, and distance were log-transformed prior to ANOVAs to achieve homogeneity of variances (Bartlett's test, $P > 0.05$).

Loons observed near station?	<i>n</i>	Habitat variable (units)			
		SST (°C)	Chlorophyll concentration (µg/liter)	Zooplankton displacement volume (cm ³ /1,000 m ³)	Distance to nearest mainland (km)
No	19	14.55 ± 0.28	0.90 ± 0.16	107.6 ± 16.4	92.6 ± 14.2
Yes, flight only	11	15.24 ± 0.58	1.42 ± 1.02	81.8 ± 15.6	39.1 ± 8.3
Yes, on water	5	14.12 ± 0.79	0.88 ± 0.21	334.6 ± 163.5	24.1 ± 10.4
	<i>F</i> _{2,32}	1.14	0.66	3.10	3.71
	<i>P</i>	0.33	0.52	0.059	0.036

somewhere east of Point Conception. Because this coastline is oriented nearly east-west, it serves as a leading line for birds encountering it, and the migrants are diverted to the west. Due to the fact that loons migrate over a wide range of distances from shore in the southern part of the bight, this diversion of broad-front migrants along the northern coastline barrier should result in increasing concentrations of birds westward toward Point Conception. Although few comparative data are available from sites other than Goleta Point, 11,000 Pacific Loons were counted as they passed Point Conception in 4 hr on 21 April 1984 (Lehman, unpubl. data; cf. Figs. 2, 3), giving an indication of the magnitude of the concentrating effect.

One possible explanation for the large daily variation in the magnitude of the nearshore loon flights involves passive wind drift. The wind drift hypothesis (Trowbridge 1902, Allen and Peterson 1936, Mueller and Berger 1967) argues that broad-front migrants may be drifted passively by the lateral component of the wind until they reach physiographic "leading lines" such as coastlines or mountain ranges, whereupon they reorient in a seasonally appropriate direction. Under the wind drift hypothesis, nearshore flights are expected to increase with wind speed when winds are onshore and decrease with wind speed when winds are offshore, in which case the daily variation in migration traffic rate that we observed would simply reflect a sampling bias. In detailed radar studies, Bergman and Donner (1964) demonstrated that this pattern characterizes the diurnal spring migrations of Black Scoters (*Melanitta nigra*) and Oldsquaws (*Clangula hyemalis*) over the Gulf of Finland. Our data do

not support the wind drift hypothesis for Pacific Loons (Table 1).

Alternatively, daily variation in the size of nearshore flights might reflect active behavioral responses to the wind component parallel to the coastal leading line. Specifically, migrants should select favorable tailwinds (which reduce the power output for flight and help to conserve valuable energy stores) and to avoid headwinds (for the opposite reasons). Ebbs (1989) showed that the breeding success of Brant was positively correlated with the frequency of tailwinds during their spring migration over the Baltic Sea, presumably because flight with headwinds requires energy to be shunted away from reserves that otherwise would be available for future reproduction. Kerlinger (1982) found that Common Loons usually flew nearly downwind, and never flew into headwinds during their overland migrations through New York. Tailwinds were rare during our study (e.g., only 6 of the 40 days analyzed in Table 1), and we observed Pacific Loons migrating in headwinds up to ca. 13 m/sec, which is 66% of the flight speed reported for this species (19.7 m/sec; Davis 1971). Nevertheless, the results shown in Table 1 suggest that migration traffic rates varied inversely with the headwind component, and are therefore consistent with the hypothesis that loons avoid flying in the most unfavorable wind conditions. However, this relationship was weak, accounting for only 10% of the variance in migration traffic rates (Table 1).

A negative relationship between traffic rate and headwind speed could result, even if migration proceeded regardless of wind conditions, simply because the rate at which migrants pass an observer varies with the ground speed of the mi-

grants. It is difficult to reject this null hypothesis, but simple computations using the raw data lend support to the alternative interpretation that loons are selective of flight conditions. For example, in 1978, the observed migration traffic rate decreased sharply from 1,200 birds/hr on 19 April to only 60 birds/hr the following day (Fig. 2), in concert with an increase in headwind speed from 5.8 to 12.6 m/sec. Assuming that Pacific Loons fly at a constant airspeed of 19.7 m/sec (Davis 1971), the expected reduction in visible migration rate is only 50%—considerably less dramatic than the twentyfold difference actually observed. The expected reduction would be even smaller if birds increased airspeed with increasing headwind strength, as predicted by flight mechanics theory (Pennycuik 1978).

A third possibility is that loons initiate migration in response to specific weather conditions at sites of departure, with subsequent migratory flight subject to little or no modifying influence of wind conditions *en route*. Under this hypothesis, the variable traffic rates are simply a result of the migration occurring in “waves” rather than in a steady stream. Migration seems to occur in such pulses in many species of birds, but in the absence of exhaustive measurements of all environmental variables, alternative explanations are usually nearly impossible to rule out. It is noteworthy, though, that spring migration of loons through the bight occurs in April and May, subsequent to the transition to the spring upwelling season along the coasts of Baja and southern California (Jones et al. 1983, SAIC 1987). The fact that migration apparently begins *after* prevailing winds in the region become unfavorable suggests that factors other than weather may be involved in the initiation of migration, casting some doubt on the “pulse migration” hypothesis (see below under SEASONAL TIMING).

Our findings also raise the question of why migrants don't orient directly toward Point Conception, which would seem to be the optimal flight strategy since it constitutes the shortest possible migration route. One reason may be the ubiquity of fog in the Point Conception-Point Arguello area. Loons attempting to take “short-cuts” may encounter fog and miss all visible signposts that tell them to swing to the north. Such individuals could conceivably end up very far off course, and over deep, relatively sterile waters that might preclude successful feeding. Thus, the

flight behavior of loons observed in this study probably represents a risk-averse strategy rather than an energetically optimal one.

SEASONAL TIMING

Seasonal timing is an extremely important component of migration strategies because it influences the timing of arrival at the migratory destination, as well as the quality of habitats encountered both *en route* and at the destination (Slagsvold 1985). For Pacific Loons, it should be important to arrive in the breeding area as early as possible to be able to procure an unoccupied pond for a territory. Our data, however, indicate that migration of loons peaked about three weeks later in 1976 than in 1977 and 1978. Such a difference suggests that the northward progress of migration may have been influenced by some environmental factor that varied among years.

As discussed earlier, the beginning of loon migration through the bight occurs after the seasonal transition to upwelling conditions (i.e., prevailing winds unfavorable for northbound flight). This suggests that some factor other than variable weather may be responsible for interannual differences in migration timing. A likely candidate is the availability of food. Loons might be constrained in their northward progress by reduced availability of food on the wintering grounds or at premigratory staging sites, which could occur either if resources are depressed overall or if reduced availability of preferred high-energy prey necessitates a switch to less profitable foods (cf. Hunt and Butler 1980, Chu 1984). Pacific Loons molt their flight feathers during late winter (Woolfenden 1967), and are obviously unable to migrate until new flight feathers permit them to do so. If the resource base in wintering or staging areas is good, it could allow an early molt; if it is poor, it might contribute to a delayed molt and slower energy storage, perhaps resulting in a later migration.

Constrained delays could also result from poor feeding opportunities at *en-route* stopover sites in the bight. Historical accounts suggest that feeding opportunities to migrant loons can vary radically. For example, Sefton (1926) described massive wrecks of starving loons in the bight during spring migration in 1926, the year of a very strong El Niño event (Quinn et al. 1987). Is there any indication that feeding conditions were regionally depressed in 1976, when loon

migration was apparently delayed? No such pattern is manifest in published data on sea surface temperature anomalies; in fact, a mild El Niño event occurred during the winter of 1976–1977 (Cole and McLain 1989), and should have affected the 1977 spring migration, if it had any effect at all. When we examined an index of upwelling intensity in the region, we detected neither a correlation between migration timing and temporal patterns of upwelling among the years of our study, nor any striking differences in the overall pattern or intensity of upwelling among years. An upwelling index is admittedly an extremely indirect measure of resource conditions, however, and direct data on food availability would be necessary for a critical evaluation of these ideas.

Pacific Loons are probably selected to arrive in breeding areas as early as possible to procure territories, but if they arrive too early, ponds will still be frozen (Petersen 1979) and the consequences could be disastrous (cf. Barry 1968, Prach et al. 1981). If the prevalence of relatively warm temperatures in the breeding range in early spring determines the availability of ice-free ponds and lakes, then it might benefit loons to wait for synoptic weather patterns that signal the occurrence of appropriate conditions further north. Under this hypothesis, plasticity in the timing of migration is viewed as an adaptive strategy, in that loons are assumed to be using environmental information to optimize their arrival on the breeding grounds. In contrast, the resource-based hypotheses discussed earlier view variation in migration timing as the result of environmental constraints that *prevent* loons from optimizing their arrival. The “adaptive waiting” hypothesis seems quite unlikely, because such waiting would best be done at productive foraging sites much further north, where weather cues would be more reliable indicators of conditions in breeding areas because of the much closer proximity of those areas. Variation in migration timing would then be apparent along the northern portion of the flyway but not along the southern portion. In any case, available data suggest that the timing of loon migration is not adjusted to compensate for whether the year is “early” or “late” with respect to ice melt (Petersen 1979).

Arrival on the breeding grounds takes place between mid-May and mid-June, indicating that roughly 5–10 weeks are required to complete the

journey from Mexican wintering areas (Table 4). The amount of actual flight time during this 5,000+ km migration, however, ranges from only several days to one week. These estimates suggest that, for most loons, >90% of the time spent *en route* is devoted to stopovers for resting and feeding (Table 4).

HABITAT SELECTION DURING STOPOVERS

Little information is available concerning the role of stopovers in loon migrations. Williams (1973) observed Common Loons departing northward from the Gulf of Mexico during spring and believed that they flew continuously overland to the Great Lakes without stopovers. McIntyre and Barr (1983) documented the occurrence of feeding flocks of Common Loons on a lake in Minnesota during autumn stopovers, but did not discuss possible factors affecting the loons' use of the lake. On the Atlantic coast, large aggregations of migrant Red-throated Loons have been noted in April off Cape May Point, New Jersey, feeding intensively along a “line of rough water” (probably a convergence front) at the confluence of the Atlantic Ocean and Delaware Bay (Stone 1937).

Pacific Loons were widespread in our study area but were concentrated in the Santa Barbara Channel and around Santa Cruz and Santa Rosa Islands. Concentrations of hundreds to thousands of feeding loons have also been observed in late April and early May in the passes between Santa Rosa, Santa Cruz, and Anacapa Islands (Dawson 1923, Briggs et al. 1987, pers. observ., R. R. Veit [pers. comm.]). This distribution suggests an association between migrant loons and hydrographic processes in the bight. Plumes of cold water frequently enter the western and southern portions of the Santa Barbara Channel, sometimes surrounding the northernmost Channel Islands (e.g., Traganza et al. 1981, Jackson 1986, Pelaez and McGowan 1986, Fielder and Bernard 1987, SAIC 1987, Dugdale and Wilkerson 1989). These plumes result from advection of upwelled water originating in the Point Conception-Point Arguello upwelling center (Atkinson et al. 1986, Dugdale and Wilkerson 1989), perhaps in combination with intrusion of California Current water into the bight (Wyllie 1966, SAIC 1987).

Zooplankton displacement volume was significantly higher at stations where loons were observed on the water than at stations where loons were absent or observed only in flight. This

TABLE 4. Estimates of the proportion of time devoted to stopovers while *en route*, calculated for representative locations along the migration route. Typical peak arrival dates at the different locations are taken from Bent (1919), Gabrielson and Lincoln (1959), Palmer (1962), Pyle and Henderson (1991), and this study. Flight distances were determined for birds departing from staging sites along the central coast of Baja California near Punta Eugenia, and migration times were estimated for a departure date of 8 April, which is probably typical (Palmer 1962). Flight times were estimated from flight distances assuming that birds maintain a constant groundspeed of 19.7 m/sec (Davis 1971). Proportion of time devoted to stopovers was then calculated by subtracting total flight time from total migration time, and dividing the result by total migration time. The validity of this reconstruction is contingent upon two important assumptions about the migration of Pacific Loons: 1) the migration is not of the "leapfrog" type, and instead involves a general shifting of the whole population; and 2) there is no overland migration route between the Pacific coast and north-central Canada. There is no evidence that either of these assumptions is incorrect (Palmer 1962).

Location	Typical peak arrival date	Total flight distance (km)	Total migration time (d)	Total flight time (hr)	Proportion of time devoted to stopovers	
					Cumulative	Last leg
Ensenada Bay, Baja Cal.	12 April	545	4	7.7	0.920	0.920
Goleta Point, Cal.	17 April	940	9	13.3	0.938	0.953
Farallon Is., Cal.	25 April	1,465	17	20.7	0.949	0.961
Kodiak I., Alaska	15 May	5,000	37	70.5	0.921	0.896
Wales, Alaska	25 May	7,260	47	102.4	0.909	0.867
Barrow, Alaska	5 June	8,175	58	115.3	0.917	0.951
Banks I., N.W.T.	11 June	9,600	64	135.4	0.912	0.860
King William I., N.W.T.	14 June	10,725	67	151.2	0.906	0.781

enhanced zooplankton volume may have reflected increased primary productivity associated with coastal upwelling. However, local growth of zooplankton volume is expected to lag behind increased nutrient input and primary production by up to 1–2 months, depending upon whether biomass fluctuations result from larval and juvenile growth-rate responses or adult reproductive response (Roesler and Chelton 1987). It is therefore not clear whether the interval between the onset of upwelling-favorable weather and the peak of loon migration allows sufficient time for zooplankton populations to respond to improved feeding conditions. Furthermore, although sea-surface temperatures were coolest at sampling stations where loons were observed on the water, the difference was not statistically significant. This suggests that loons were not simply using upwelled water *per se*.

Alternatively, many organisms may be advected into surface waters of upwelling areas and entrained in the adjoining frontal zones by convergent currents (Olson and Backus 1985, Franks 1992). Theory and observations suggest that upwelling fronts are the center of convergent flow, at least during certain stages of the wind event cycle (reviewed by Brink 1983), and dense concentrations of phytoplankton (Traganza et al. 1987) and copepods (Smith et al. 1986) have

been documented in the vicinity of upwelling fronts. Tunas select upwelling fronts as habitat (e.g., Laurs et al. 1977) and they increase the frequency of anchovies and other fish in their diet while in the vicinity of these fronts (Fiedler and Bernard 1987). This suggests that large numbers of small schooling fish aggregate at the fronts to graze the high densities of entrained plankton.

We hypothesize that, like tunas, some migrant loons may undertake stopovers near small-scale fronts in the northern bight to feed on aggregations of fishes attracted by dense plankton concentrations, or perhaps even to feed on the larger zooplankton themselves. In addition to upwelling fronts, loons might also make use of topographically controlled fronts (Wolanski and Hamner 1988) around the northern Channel Islands. Sharp thermal gradients along the boundaries of upwelling plumes in the northern bight are clearly visible in satellite thermal images (e.g., Fig. 1 in Traganza et al. 1981, Fig. 2.13 in Jackson 1986, Fig. 11 in Pelaez and McGowan 1986). The structure of these fronts is often complex and convoluted, but they are sometimes visible to shipboard observers, appearing as distinct color boundaries (pers. obs.). Presumably, they can be detected by migrating loons as well. The distribution of zooplankton (and, by inference, planktivorous fish) in the bight is notoriously

heterogeneous in both space and time (Smith 1971), and this hypothesis provides a plausible explanation of how migrant loons could identify suitable habitat for feeding without devoting large amounts of time to searching and sampling many different areas.

CONCLUSIONS

Our findings suggest that Pacific Loons migrate over a broad front through the Southern California Bight, but are diverted to the west by the coastline in the northern part of the bight. Near-shore flights along this leading line are large but highly variable from day to day. Wind drift did not seem to be implicated in this variation, suggesting that careful counts from coastal seawatches are unbiased indices of actual migration traffic and may be useful for monitoring loon population trends.

Several results from our study suggest that variation in the availability of energy may be an important ecological constraint on Pacific Loon migrations. The timing of migration varied substantially among the years of our study, and we argued that the most plausible explanation for the differences involved interannual variation in resource availability on the wintering grounds, at premigratory staging sites, or at *en-route* stopover sites. Hypotheses concerning interactions between resource availability and migration timing can be tested in future studies that combine oceanographic sampling with simultaneous observations of weather, nearshore flights, and the physiological condition of loons over the course of winter and spring during several years.

Migrant Pacific Loons appeared to select stopover habitats in the northern part of the bight where levels of zooplankton biomass are high. We hypothesize that loons may exploit upwelling fronts where fish aggregate to feed on high densities of plankton entrained by convergent flow. Brief stopovers at sites where prey populations are amplified by oceanographic processes should allow migrant loons to replenish energy stores efficiently and to resume northward migration rapidly. However, the methods used in this study did not allow us to judge what proportion of migrating loons used the bight as a stopover area. In fact, it is possible that only a minority of migrants stop to feed in the Southern California Bight, with most flying straight through, perhaps destined for productive foraging sites farther to

the north. Future studies conducted at a smaller spatial scale will be required to confirm the importance of the northern bight as a stopover area for migrant loons, as well as to identify which hydrographic features, if any, are exploited by the birds.

ACKNOWLEDGMENTS

We thank G. T. Hemingway and the CalCOFI program for generously facilitating RWR's participation in the 1989 cruise and R. R. Veit for providing CalCOFI data on birds from 1990. D. L. Russell provided valuable logistical assistance. We also thank R. H. Day, G. L. Hunt, Jr., R. R. Veit, G. E. Walsberg, and three anonymous reviewers for reading earlier drafts of this paper and offering many valuable suggestions for improvement.

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