OCEANIC FACTORS INFLUENCING DISTRIBUTION OF YOUNG ROCKFISH (*SEBASTES*) IN CENTRAL CALIFORNIA: A PREDATOR'S PERSPECTIVE

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ABSTRACT

We used the diet of a seabird, the common murre (*Uria aalge*), to assess the abundance of juvenile rockfish (*Sebastes* spp., mostly *S. jordani*) in the Gulf of the Farallones, California, 1973–90. On the basis of an exploratory analysis of the data and of several oceanographic factors, we hypothesize that availability of fish in the study area during June–July was a function of advection during the January–February period of rockfish parturition. When upwelling or downwelling was persistent in winter, there were few juveniles in late spring, but when upwelling had been mild or pulsed, juveniles were abundant. Rockfish availability also decreased when turbulence, sea level, and sea-surface temperature were high during winter. Stepwise multiple regression analyses indicated that, among these variables, advective transport significantly affects the distribution of juvenile rockfish.

RESUMEN

Usamos la dieta del ave marina alca piquilarga (*Uria aalge*) para estimar la abundancia de rocot juveniles (*Sebastes* spp., principalmente *S. jordani*) en el Golfo de Farallones, California, 1973–90. Basándonos en un análisis exploratorio de los datos así como en factores oceanográficos, presentamos la hipótesis que la disponibilidad de peces en Junio–Julio fué función de la advección durante Enero–Febrero (la temporada de cría los rocot). Cuando hubo surgencias o hundimientos de masas de agua persistentes en invierno, disminuyó la abundancia de juveniles en primavera tardía, mientras que cuando las surgencias fueron poco intensas u ocurrieron intermitentemente, la abundancia de los juveniles incrementó. La disponibilidad de los rocot disminuyó cuando en invierno hubo valores altos de turbulencia, nivel del mar o temperatura superficial. Análisis de regresión múltiple por pasos indicaron que de entre ésas variables, la advección afecta significativamente la distribución de rocot juveniles.

INTRODUCTION

Eastern boundary currents contribute roughly a third of the world's fishery resources (Thompson 1981). Such productivity is attributable, in part, to the dominant oceanographic feature of these areas — upwelling of cold, nutrient-rich waters to the surface, which in turn leads to enhanced phytoplankton growth. Parrish and MacCall (1978) examined the relations between several environmental variables and the recruitment success of Pacific mackerel (*Scomber japonicus*) in southern California, and found the highest correlation with the upwelling index (Bakun 1973) at 30°N during the early part of the spawning season. The correlation was positive, and Parrish and MacCall stated that "upwelling is obviously related to recruitment, because it determines the basic productivity of the California Current."

Associated with upwelling, however, is wind-generated turbulence, which could lead to impaired nutrient and carbon transfer to higher trophic levels. For example, Peterman and Bradford (1987) found a negative linear relationship between the mortality rate of northern anchovy (*Engraulis mordax*) during the first 15 days of the larval period and a measure inversely related to turbulence, i.e., the number of periods of calm at 33°N during the main spawning season. Neither cannibalism, as measured by the biomass of adults, nor advection, as measured by offshore Ekman transport, improved the explanation of variability in early mortality. Further, as noted by Methot (1983), even though advection may not have increased mortality during the first 15 days of the larval period, it may have reduced the proportion of larvae that remain in favorable habitat, thereby contributing to late mortality.

Bailey and Francis (1985) found strong year classes of Pacific whiting (*Merluccius productus*) only when sea-surface temperature (SST) in the Los Angeles Bight was relatively high, and when upwelling at 36°N was relatively low at the beginning of the spawning season. They showed that whiting larvae are found farther offshore and to the south in cold years and in years of relatively high upwelling. They concluded that this could be either because spawning takes place farther offshore and to the south or

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[Manuscript received April 1991.]

because of advection. They cited evidence that the larvae grow more slowly during cold years and that prey densities are relatively low offshore and to the south.

Fishery oceanographers have long believed that advection could be an important factor in the reproductive success and recruitment of fish. Bakun (1986) and Simpson (1987) discuss some of the physical mechanisms involved in advection and some physical phenomena that would retain eggs and larvae in favorable habitat.

In order to deter the offshore transport of larvae, fishes in eastern boundary currents tend to reproduce when advection (Ekman transport) is low. They also tend to bear their young alive; relatively large larvae are more capable of swimming than, for instance, newly hatched northern anchovies (Parrish et al. 1981). We found that prevalence of the young-of-the-year (YOY) of one genus of live-bearing fish, *Sebastes*, varies from year to year in the diet of an apex predator, the common murre (*Uria aalge*), in California (Ainley and Boekelheide 1990). To determine what factors might explain the availability of rockfish, we analyzed the relations between several oceanographic factors and the prevalence of rockfish in the murre diet.

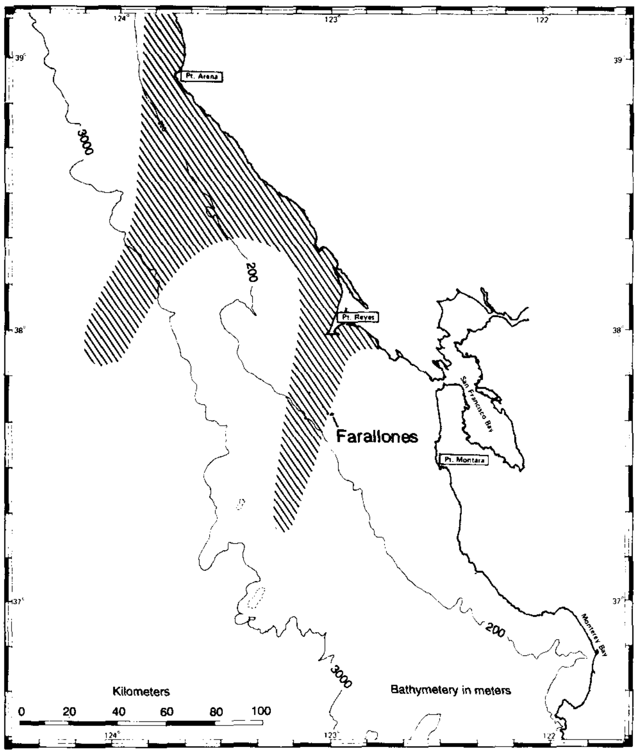

Figure 1. Upwelling plumes of a size and shape typical of early spring in central California, and the location of the Gulf of the Farallones study area (shape of the plume drawn according to figure 4.2.2-27 in SAIC 1987).

METHODS

A seabird, the common murre, was our fish-sampling tool. We studied murre diet at Southeast Farallon Island (SEFI), 42 km offshore of central California (figure 1), each June and July for 18 years, 1973–90. Murres carry fish in their beaks, in full view, to feed their offspring. From within a blind that overlooked a group of approximately 100 pairs of breeding murres within 10 m of the blind, we observed birds returning from the sea with fish (Ainley and Boekelheide 1990). Observations were made every 3 to 5 days throughout the chick-rearing season, from late May to early July. Using 8 × binoculars (for a "frame-filling" view of each murre), we identified, to the closest taxon possible, 800 to 4000 prey items per year (Ainley and Boekelheide 1990). Years when sample sizes were smaller were oceanographically anomalous years, such as during El Niño events, when fewer pairs were breeding (Ainley and Boekelheide 1990).

We used the proportion of juvenile rockfish in the diet as an index to rockfish availability within the foraging range of the murres. Murres' preferred prey were juvenile rockfish (Ainley and Boekelheide 1990). When rockfish were not available, the murres fed along the mainland coast on other species of fish, principally anchovies. Murres dive to a depth of about 100 m, which corresponds to the depth of the continental shelf in the study area. They forage up to 80 km from breeding sites. Thus, allowing for the shape of the mainland coastline and the fact that it lies only about 40 km from SEFI, the murre population can sample about 7000 km^2 of ocean during the summer breeding season, including the entire volume of water overlying the continental shelf and upper slope.

During June 1985 and 1986, we collected 24 and 42 common murres, respectively, at various locations within the study area. Gut contents analysis revealed 274 juvenile rockfish in the 1985 sample, and 87 in the 1986 sample (PRBO unpubl. data), and many rockfish were fresh enough to identify to species. These data provided a check for the identifications made at SEFI.

From 1983 to 1991, the National Marine Fisheries Service, Tiburon Laboratory (NMFS), estimated the abundance and distribution of juvenile rockfish in waters off central California, including those surrounding the Farallon Islands (our murres were collected on these cruises). The more classical research method used by NMFS — a grid of trawl stations during late May and June (Wyllie Echeverria et al. 1990; Adams 1992) — overlapped the time of our observations at SEFI. The proportion of juvenile rockfish in the murre diet (as a measure of annual variability in the abundance of the fish) correlated with the NMFS trawl data during overlapping years when trawl results were consistently derived from year to year (1986–91, including 1991 to increase the sample size); a regression between murre diet and log-transformed trawl results for fishes in the size classes appropriate to murre foraging (>39 mm; see Results) was highly significant ($R^2 = 0.87$, $t = 5.27$, $P < 0.01$; figure 2). Therefore, we believe that the bird diet serves as a valid index to the availability of juvenile rockfish in the Gulf of the Farallones region during early summer. We use the diet data for comparison with oceanographic conditions because this time series is much longer than that of the trawl data.

We related the proportion of rockfish in the murre diet to indices of upwelling ($m^3/sec^{-1}/100\ m^{-1}$ of coastline; Bakun 1973) and turbulence (wind speed^3), SST, and sea level. We used the upwelling index as a surrogate measure of Ekman transport (advection). Monthly upwelling indices were taken from Bakun (1973), Mason and Bakun (1986), and unpublished updates. A turbulence index consisting of monthly wind-speed-cubed values was derived from 6-hr wind-speed values that were inferred by Bakun from atmospheric pressure fields supplied by the U.S. Navy's Fleet Numerical Oceanography Center. A preliminary analysis with these data indicated that the upwelling index and turbulence estimates derived for 36°N are more representative of conditions in the study area than those at 39°N (F. Schwing, Pacific Fisheries Environmental Group, NMFS, Monterey, pers. comm.). At SEFI we measured SST daily. We used sea level measured at San Francisco (units in mm) as an index to the strength of northerly flow in the California Current and an integration of temperature by depth and region—factors known to affect the marine climate of eastern boundary currents (Norton et al. 1985). Finally, we related rockfish values to measures of wind pulsation, defined as the number of wind events (velocity >9 kts terminated by winds <9 kts) per month. At SEFI we measured winds daily at 0800 PST.

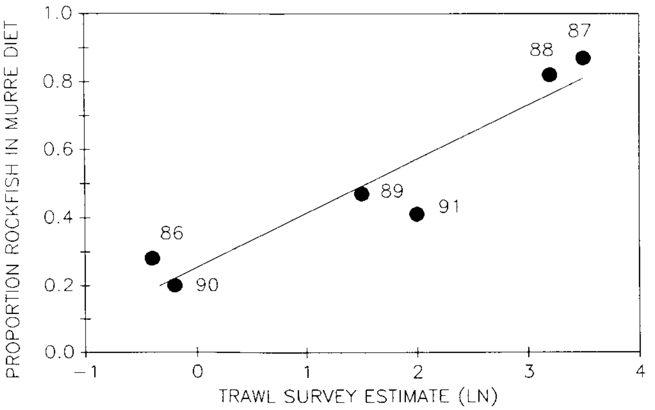

Figure 2. The relation between the proportion of the murre diet contributed by rockfish and the log of the number of juvenile rockfish (>39 mm) in NMFS trawl samples, 1983–91. The relation is described by the equation, $Y = 0.272 + 0.165X$.

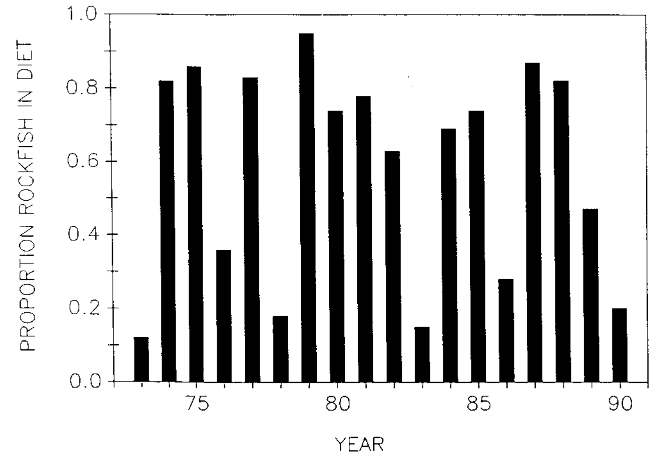

Figure 3. Annual variability in the proportion of rockfish in the diet of the common murre, Southeast Farallon Island, June and July 1973–90.

We correlated the percentage of rockfish in the birds' diet with the above oceanographic and meteorological values averaged for individual and combined monthly periods, October to June, preceding the June–July chick-feeding period. Initially, we used simple regression analyses to investigate relations among these variables; we also tested for correlations among the measures. We used quadratic values of upwelling, turbulence, and SST to model apparent curvilinear relations. To examine the relative effect of each oceanographic variable on rockfish availability, we used forward and backward stepwise multiple regression. Statistical significance was assumed if nominal $P < 0.05$. We recognized that the large number of tests increases the probability of failing to reject false hypotheses, and thus consider this an exploratory analysis.

RESULTS

Rockfish in the common murre diet varied substantially from one year to the next (figure 3). Regression analyses of rockfish in the diet against the upwelling index, turbulence, SST, and sea level indicated which values provided significant correlations (figure 4). The average January-plus-February upwelling index ($UJ+F$) related to rockfish availability in a parabolic fashion (figure 5) and explained 61% of the variation in interannual abundance ($Y = 79.54 + 1.51\,(UJ+F) - 0.11\,((UJ+F)^2)$; separately, neither month was significantly related to rockfish abundance. Rockfish were most available when the

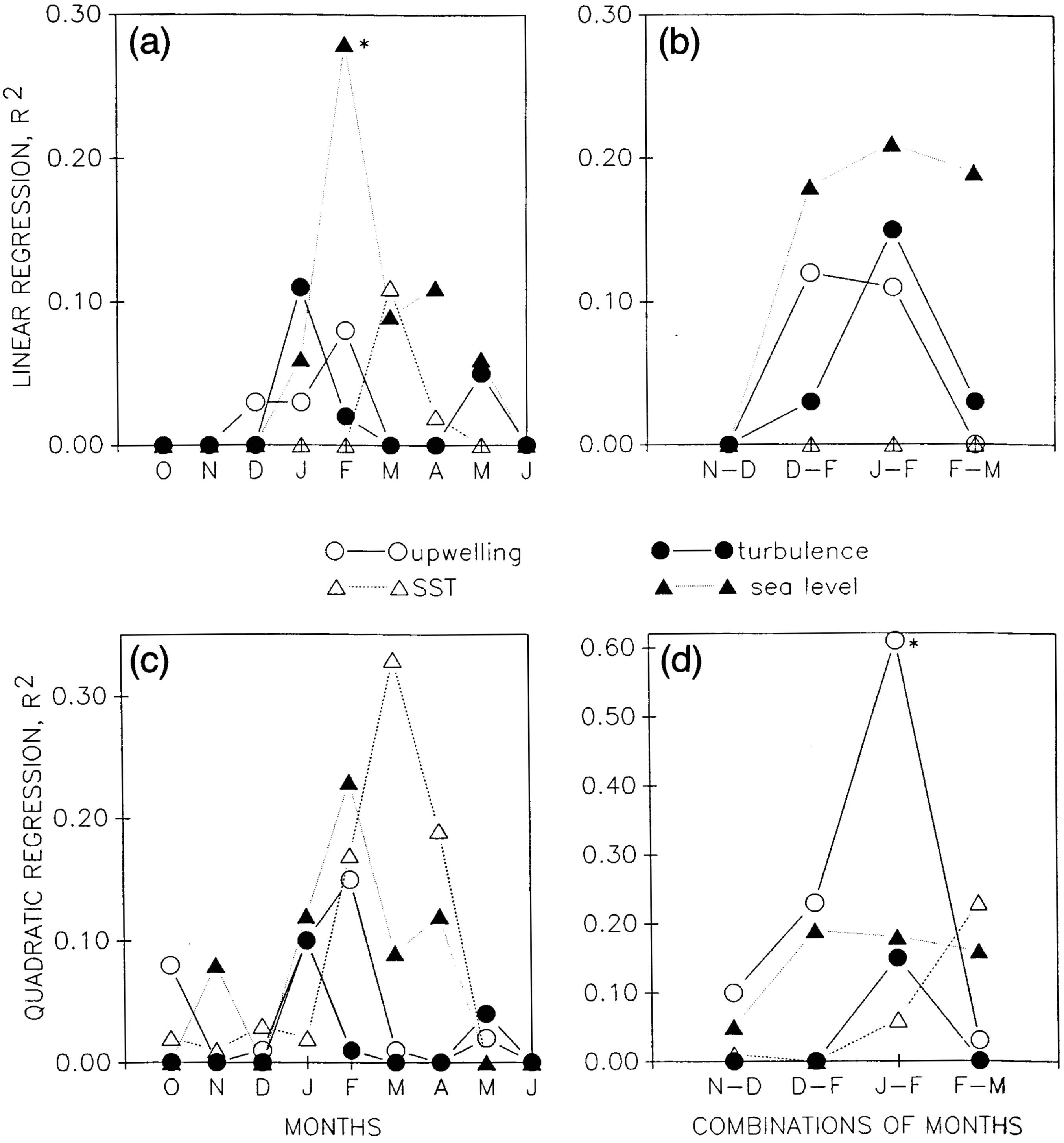

Figure 4. Values of R^2 for regressions between prevalence of rockfish in the murre diet and four oceanographic parameters: *a*, linear regression by month, and *b*, by combinations of months; *c*, quadratic regression by month, and *d*, by combinations of months. Significant values are indicated by an asterisk (*).

average January–February upwelling index was slightly above zero. During years of prevalent winter downwelling (1973, 1978, 1983, and 1986), or years when winter upwelling was overly persistent (1976, 1989, 1990), rockfish were less abundant (figure 3; see also Ainley and Boekelheide 1990). We found no significant relations between rockfish abundance and monthly upwelling indices later in the spring and summer, when upwelling reaches its maximum intensity in the California Current sys-

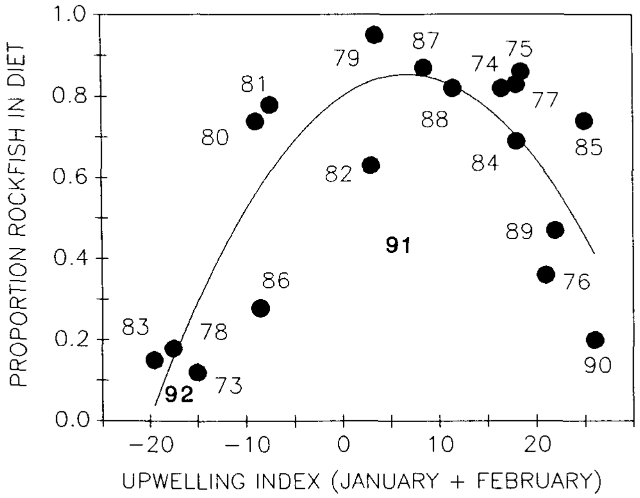

Figure 5. Parabolic relation between rockfish in the diet of murres in the Gulf of the Farallones during June and July and the upwelling index during the preceding January and February, 1973–90. The relation is described by the equation $Y = 79.54 + 1.51(UJ+F) - 0.11((UJ+F)^2)$.

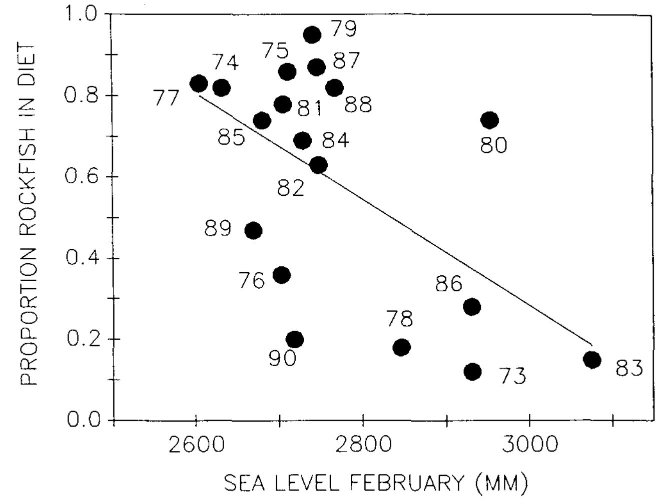

Figure 6. The relation between rockfish in the diet of murres in the Gulf of the Farallones during June and July and sea level during the preceding February, 1973–90.

tem (Breaker et al. 1983). Neither did we find any relation with wind pulsation.

Rockfish availability was negatively, but not significantly, correlated with turbulence during January–February (figure 4; $P = 0.0635$). This variable accounted for only 15% of the yearly variation in fish prevalence. Again, separate turbulence values for January or February were even more weakly related to rockfish availability. Turbulence was greatest during 1978, 1980, 1983, and 1986; the winters of 1978, 1983, and 1986 were also characterized by intense downwelling and elevated sea level. We detected no departure from linearity ($P > 0.10$) between turbulence and rockfish availability.

In March, SST was negatively, but weakly, correlated with rockfish abundance. The quadratic of March SST accounted for 33% of the variation in annual rockfish prevalence, but was again not significant (figure 4; $P = 0.052$). The warmest March SSTs were noted in 1978, 1983, and 1986.

Sea level during February was negatively and significantly correlated with rockfish prevalence (figures 4 and 6; $P = 0.014$), when it accounted for 28% of the yearly variation in rockfish abundance. Sea level was highest in 1973, 1978, 1980, 1983, and 1986. Although sea level in 1976, 1989, and 1990 was low, rockfish were scarce. A linear relation was more significant and explained more of the variance than did a quadratic relation.

The January–February upwelling index, March SST, February sea level, and January–February turbulence values correlated significantly (table 1). The upwelling index was negatively correlated with SST, sea level, and turbulence. SST was positively correlated with sea level and turbulence, and sea level and turbulence also were positively associated. Forward multiple regression indicated that January–February turbulence ($F = 0.10$), March SST ($F = 0.25$), and February sea level ($F = 0.80$) were insignificant when January–February upwelling was first entered into the model. A backward regression analysis confirmed these findings (table 2). The explan-

TABLE 1

Correlation Coefficients among Four Environmental Factors in Central California, 1973–90

	1	2	3	4
1. Upwelling, Jan.–Feb.	1.000			
2. Temperature, Mar.	−0.8416	1.000		
3. Sea level, Feb.	−0.8192	0.7455	1.000	
4. Turbulence, Jan.–Feb.	−0.7736	0.6823	0.7964	1.000

Each value alone had significant or nearly significant correlation to the prevalence of rockfish in the diet of murres at the Farallon Islands.

TABLE 2

Backward Regression of January + February Upwelling Index (UI), February Sea Level (SL), and March Sea-Surface Temperature (SST) with Rockfish Prevalence in the Murre Diet

Model	R^2	F	P
UI, UI^2, SST, SL	0.58	6.81	0.0035
UI, UI^2, SST	0.59	9.17	0.0013
UI, UI^2, SL	0.60	9.50	0.0011
UI, UI^2	0.61	14.03	0.0004
SL, SST	0.23	3.55	0.0547
UI	0.11	3.11	0.0971
SL	0.28	7.54	0.0144
SST	0.11	3.08	0.0986

R^2 values were adjusted by the degrees of freedom and sample size (n = 18 years).

atory power of the model was greatest when only the upwelling index was included. SST and sea level contributed little to explaining variation in rockfish prevalence in the diet and could be dropped from the model with no effect on R^2 values.

DISCUSSION

Most of the rockfish eaten by murres at Southeast Farallon are YOY shortbelly rockfish (*S. jordani*) — on average, 70% of rockfish in the summer diet (Ainley and Boekelheide 1990). This species has also dominated midwater trawl catches of YOY rockfish in the study area (Wyllie Echeverria et al. 1990; Adams 1992), as well as the fish contained in murre stomachs during the two years of collections (Briggs et al. 1987; Ainley, unpublished data). The shortbelly constitutes the largest biomass of any rockfish off California and is a species of the continental shelf and upper slope (Pearson et al. 1991). January and February are the peak months of parturition for this and most other abundant rockfish species that inhabit offshore central California (Wyllie Echeverria 1987), and are the months just before the spring transition from winter conditions to the upwelling period (Breaker et al. 1983). Murres begin to feed on these fish, along with other prey of the same size, as soon as the prey appear in winter (PRBO unpublished data). By the time the rockfish have increased from about 1 cm to 4 cm they are big enough to be carried to chicks at SEFI breeding sites.

The correlation with the upwelling index indicates to us that intense and persistent midwinter winds, either onshore (negative upwelling) or offshore (positive upwelling), transport larvae and perhaps small juveniles away from the foraging range of murres at the Farallones. It is at this time, just after birth and when they are smallest, that YOY rockfish are most vulnerable to advection. Figure 1 depicts an upwelling plume typical of this coast during the early upwelling period (March–April; see also figure 3 in Parrish et al. 1981). Later (June), when upwelling is intense and continuous, plumes in this area of the coast are much broader and extend much farther offshore (SAIC 1987). Along this coast, murres tend to feed at the periphery of upwelling plumes, because there are no prey in recently upwelled water (Briggs et al. 1988). On the basis of this pattern and our analysis herein, we conjecture that large, intense plumes may completely displace YOY rockfish from the foraging range of Farallon-based murres. Advection outside of the murre foraging range — i.e., away from the continental slope (the main habitat of shortbelly and certain other rockfish) — may remove young rockfish from the population unless they can compensate by swimming, or survive until fortuitous currents carry them back to suitable habitat. Whether or not such advection strongly affects recruitment of rockfish, however, remains to be determined (and is being investigated by NMFS). Hobson and Howard (1989) reported mass mortality of YOY shortbelly rockfish on the California shore, not the usual shortbelly habitat (and certainly outside of murre foraging habitat), and conjectured that they had been transported in waters propelled by intense shoreward winds.

Upwelling has the potential to increase primary production in coastal waters of eastern boundary currents, as well as to decrease the egg and larval survival of spawning pelagic fishes because of turbulence and advection (Bakun 1990; Cury and Roy 1989). Our analysis indicates that increased transport of young (larval and small) juvenile fish away from traditional areas for recruitment is an important factor. We base our hypothesis — "The observed pattern of presence or absence of fish is explained by advection" — partly upon the reasoning of Cury and Roy (1989): fish (in this case, rockfish) should bear their young within the central upwelling area of the California Current just before the seasonal onset of intense upwelling. By eliminating the passive (planktonic) egg and reducing the early larval stage, they should be better able to cope with turbulence and advection, which are also caused by the intense, upwelling winds that are the nemesis of smaller developmental stages of the fish. Indeed, by bearing their young alive, rockfish eliminate about 40 days' free existence in the passive stages. This idea assumes that incubation time would be the same as gestation time if rockfish spawned eggs rather than bearing viable larvae. If it is assumed that incubation time of (hypothetical) egg-laying rockfish would be similar to that of other egg layers, then only about one week of passive drifting would be eliminated.

On the other hand, many rockfish species apparently bear their young when they do in order to avoid the intense offshore transport characterizing late spring in the California Current region, as well as perhaps to take advantage of spring plankton blooms. Through natural selection, the release of rockfish larvae during late winter may have evolved because upwelling events are usually intermittent at that time. Upwelling events that are mild or short lead to an enhanced food web. Resulting upwelling plumes may displace the fish slightly offshore, but the young fish are able to return because, between the upwelling events, slack or onshore winds propel them or allow them to return shoreward. We failed to find a correlation with wind pulsation because years of extended weak transport and intermittent strong winds were those in which YOY rockfish were abundant. In such conditions the swimming ability of the young, but relatively well developed, rockfish larvae is sufficient to accommodate to the food dispersal caused by turbulence.

Our analyses suggest that advection is an important factor determining the occurrence patterns of YOY rockfish in central California. Other factors that perturb the oceanic environment in which these rockfish live also appear to play a role. These factors are represented by SST and sea level in our analyses and, like upwelling, correlated most closely with variability of YOY rockfish during late winter.

ACKNOWLEDGMENTS

Our work on the Farallon National Wildlife Refuge was made possible through a contractual agreement and the logistic support of the U.S. Fish and Wildlife Service and the National Weather Service, as well as the generosity of the members of and donors to PRBO. PRBO participation in NMFS rockfish cruises was funded during various years by the Environmental Protection Agency, Fish and Wildlife Service, Gulf of the Farallones National Marine Sanctuary, Minerals Management Service, and PRBO itself. Collection of SST at SEFI was accomplished through our participation in a shore-station program managed by the Scripps Institution of Oceanography. Upwelling indices were supplied by D. Husby, Pacific Fisheries Environmental Group, NMFS, Monterey; sea-level data were supplied by G. Mitchum, University of Hawaii. We benefited from discussions of rockfish biology with R. Larson, A. MacCall, S. Ralston, D. Woodbury, and coworkers at the NMFS Tiburon Laboratory. Farallon biologists of PRBO, research personnel at the Tiburon Lab, and the officers and crew of the R/V *David Starr Jordan* aided immensely in the determination of rockfish abundance and murre diet. We thank S. Emslie and A. MacCall for their reviews and constructive comments on this and an earlier version. This is contribution no. 486 of PRBO.

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