

Abstract—The coastal Pacific Ocean off northern and central California encompasses the strongest seasonal upwelling zone in the California Current ecosystem. Headlands and bays here generate complex circulation features and confer unusual oceanographic complexity. We sampled the coastal epipelagic fish community of this region with a surface trawl in the summer and fall of 2000–05 to assess patterns of spatial and temporal community structure. Fifty-three species of fish were captured in 218 hauls at 34 fixed stations, with clupeiform species dominating. To examine spatial patterns, samples were grouped by location relative to a prominent headland at Point Reyes and the resulting two regions, north coast and Gulf of the Farallones, were plotted by using nonmetric multidimensional scaling. Seasonal and interannual patterns were also examined, and representative species were identified for each distinct community. Seven oceanographic variables measured concurrently with trawling were plotted by principal components analysis and tested for correlation with biotic patterns. We found significant differences in community structure by region, year, and season, but no interaction among main effects. Significant differences in oceanographic conditions mirrored the biotic patterns, and a match between biotic and hydrographic structure was detected. Dissimilarity between assemblages was mostly the result of differences in abundance and frequency of occurrence of about twelve common species. Community patterns were best described by a subset of hydrographic variables, including water depth, distance from shore, and any one of several correlated variables associated with upwelling intensity. Rather than discrete communities with clear borders and distinct member species, we found gradients in community structure and identified stations with similar fish communities by region and by proximity to features such as the San Francisco Bay.

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Regional and seasonal patterns of epipelagic fish assemblages from the central California Current

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Twenty five percent of marine fisheries catch comes from regions that encompass a mere five percent of the world's oceans: within the Benguela, California, Canary, Peru, and Somalia currents (Jennings et al., 2001). Management of these highly productive coastal upwelling ecosystems has historically been based on single species assessments, although the science informing management has long recognized the limited power of this approach. After the dramatic and unexpected collapse of several major small-pelagic fisheries worldwide circa 1945–72, scientists began to advocate the need to incorporate climate, ocean conditions, and other sources of uncertainty into management (Fréon et al., 2005; MacCall, 2009). In the last two decades the momentum to achieve this goal has increased, and some form of ecosystem-based management is now a stated policy objective of government agencies in several nations (Link et al., 2002; Ecosystem Principles Advisory Panel¹). Ecosystem management plans have now been proposed for most U.S. fisheries including the U.S. west coast and large portions of the California Current ecosystem,

and various agencies and institutions are actively collecting the biological and environmental data that will be needed to bring these plans to action (Ecosystem Plan Development Team²).

The high productivity of the California Current (CC) is primarily the result of local wind-driven seasonal upwelling and the interaction of alongshore currents with prominent coastal features such as capes, headlands, and bays that advect upwelled water masses into complex patterns of offshore filaments and coastal retentive eddies (Davis, 1985; Gan and Allen, 2002). The zone of maximum spring and summer wind stress and wind-driven upwelling occurs between Cape Blanco in southern Oregon (43°N) and Point Conception in central California (34°N) (Nelson, 1977). Headlands in this region including Cape Mendocino, Point Arena, Point Reyes, and Point Año Nuevo are the main locales of newly upwelled water. Bays located down-current act as retention zones where eddies form and trap aging upwelled water (Paduan and Rosenfeld, 1996), allowing concentrated phytoplankton blooms to develop nearshore (Vander

¹ Ecosystem Principles Advisory Panel. 1999. Ecosystem-based fishery management. A report to Congress by the National Marine Fisheries Service, 54 p. National Marine Fisheries Service, Office of Science & Technology, 1315 East-West Highway, Silver Spring, MD 20910.

² Ecosystem Plan Development Team. 2010. Ecosystem fishery management planning for U.S. west coast fisheries. A report to the Pacific Fisheries Management Council, 35 p. Pacific Fisheries Management Council, 7700 N.E. Ambassador Pl., Ste. 101, Portland, OR 97220.

Woude et al., 2006). Blooms in this region often occur at cape-and-bay spatial scales and are ephemeral, typically lasting several days after an upwelling wind event (Largier et al., 2006).

Coastal topographical features also affect the distribution of zooplankton and larval invertebrates in this region (Ebert and Russell, 1988; Largier, 2004). Localized differences in zooplankton density and community structure have been measured across distances of 10 km or less in the vicinity of headlands and their upwelling shadows (Graham et al., 1992; Wing et al., 1998; Mace and Morgan, 2006), and across-shelf variation in zooplankton (Morgan et al., 2003) and ichthyoplankton (Auth, 2008) community structure is well described. A complex field of mesoscale eddies and fronts off coastal Oregon in the summer of 2000 correlated spatially with four or five different zooplankton assemblages, and dynamic water-mass attributes influenced by recent strong upwelling and advection appear to be the principal factors driving horizontal planktonic distribution (Keister et al., 2009). Seasonal zooplankton shifts have been linked to intensity of upwelling and variation in the timing and delivery rate of subarctic and subtropical water onto the shelf (Peterson and Miller, 1977; Roesler and Chelton, 1987), and interannual patterns appear related to El Niño–Southern Oscillation (ENSO) events and other multiyear climate cycles that impact the ocean on basin-scales (Rebstock, 2003). The physical processes that promote rapid growth and patchiness among plankton have additional downcurrent trophic effects among krill, fishes, seabirds, and marine mammals (Ainley, 1990; Croll et al., 2005; Ware and Thomson, 2005; Jahncke et al., 2008).

Assemblage patterns of epipelagic fishes in the CC are known mostly from studies in the northern portion. Orsi et al. (2007) summarized broad-scale species associations from surface trawls in both the California and the Alaska Current, in a region spanning 1100 km of coastline and identified three or four spatially distinct assemblages. In a study covering about 400 km of coastline in Washington and Oregon, Brodeur et al. (2005) sampled across-shelf transects and described seven different fish assemblages, some of which were spatially distinct. At the finest scales yet examined for epipelagic fishes in this region, Emmett et al. (2006) found significant differences in abundance among years, months, and stations for several common predator and forage species in a region influenced heavily by the Columbia River plume. These and several prior studies (summarized in Brodeur et al., 2003) highlight the scales of variation found among epipelagic nekton in the northern CC, but the area south of the Oregon–California border was sampled in only a few of these studies.

The central CC supports vast schools of clupeiform fishes that are essential prey items for fish and avian predators. Food-web models constructed for the CC ecosystem are an essential component of ecosystem-based fishery management; these models require data from

surveys of forage fishes and their associates, details of the spatial and temporal structure of their populations, and measurement of the oceanographic variables that drive local abundance (Field et al., 2006; Samhoury et al., 2009). This area is also home to several large state and federal marine sanctuaries and is one of the primary testing grounds for Marine Protected Areas (MPAs) in the United States. Although these MPAs are designed primarily for the conservation of demersal fish and invertebrates, knowledge of pelagic fish habitat and community structure could also be used to inform decisions on size and placement of MPAs (Reese and Brodeur, 2006).

Our study covered a strip of coastal ocean running north–south above the inner continental shelf in a region of strong seasonal upwelling off northern and central California. The region encompasses several prominent headlands and bays, a small group of offshore islands, and the outflow of the largest river in the state through the San Francisco Bay. Detailed patterns of spatial and temporal community structure of epipelagic fishes in this portion of the CC are undescribed. The objectives of this study were 1) to test for regional, seasonal, and interannual patterns of fish abundance in catch data from six years of summer and fall surface trawl surveys; 2) to identify dominant species associated with patterns of community structure, and correlate biotic patterns to a suite of water properties that may be influencing fish distribution; and 3) to provide a detailed baseline record of species abundance and distribution for the region, against which future change may be measured, and to provide primary data for ecosystem-based management for the California Current ecosystem.

Materials and methods

The study area encompassed a 185-km strip of coastal ocean between Point Arena (38°55'N) and Point San Pedro (37°35'N) in northern and central California (Fig. 1). Ocean sampling stations were located from 1 to 39 km offshore at a depth of 18–141 m mostly over the inner portion of the continental shelf and largely within the boundaries of three national marine sanctuaries (Cordell Bank National Marine Sanctuary [NMS], Gulf of the Farallones NMS, and Monterey Bay NMS). Fish obtained for this study were collected as part of a more detailed examination of Chinook salmon (*Oncorhynchus tshawytscha*) growth and energy status during their first ocean year (MacFarlane, 2010). Because Chinook salmon are thought to remain very close to shore during this life-history stage, we chose to extend our nearshore north–south coverage as much as possible. This spatial arrangement of stations restricted our analysis to tests of primarily along-shelf latitudinal patterns, with less emphasis on onshore–offshore gradients.

We divided our study area into two geographic regions, the north coast (NC) and the Gulf of the Farallones (GF), separated by a prominent headland at Point

Reyes (38°00'N) (Fig. 1). Point Arena defined the northern border of NC, and Pt. San Pedro the southern border of GF. The boundaries of the GF are generally well recognized, and similar borders have been reported elsewhere (Ainley, 1990; MacFarlane et al., 2005). We worked from chartered commercial trawlers and the NOAA ship *David Starr Jordan*. Samples were collected over 5–13 consecutive days in June or July (hereafter “summer” cruises) and for 5–11 consecutive days in September or October (hereafter “fall” cruises) for six years, from 2000 to 2005. All sampling was conducted during daylight hours, between sunrise and sunset. There were 23 and 11 fixed trawling stations in the NC and GF, respectively, and both regions were sampled during every cruise, although not every station was visited each time (Table 1). Effort was not equally distributed among years, seasons, or regions because of operational constraints, weather, and other project objectives.

We used a Sea-Bird SBE 19 CTD (conductivity, temperature, and depth) profiler with added sensors for hydrographic sampling conducted immediately before or after trawling at each station. Five environmental variables were measured in 1-m depth bins from the surface to the bottom: water temperature, °C (TMP); salinity, ppt (SAL); water density, kg/m³ (DEN); photosynthetically available radiation, (μE/sec)/m² (PAR); and chlorophyll-*a* concentration, μg/L (CHL). Values from 1 to 15 m depth were averaged for each cast, and therefore represented about the same range as the vertical spread of the trawl net. Owing to occasional instrument failures, not all of the CTD sensor data were collected on every cast (Table 1). Bottom depth in m (DEP) and distance offshore (DIS) in km were measured for every haul.

Trawling and sample processing

We used a 264 Nordic rope trawl and 3.0-m² foam-filled pelagic doors to collect epipelagic fish and invertebrates. Net dimensions were approximately 14 m (vertical at mouth) by 27 m (horizontal at mouth) by 194 m (length). Vertical spread was measured in the field with depth recorders attached to the head and footrope, and the measurement of horizontal spread had been estimated and provided previously by the manufacturer (NET Systems, Bainbridge Island, Washington). Effective mouth area was assumed constant at 380 m². The codend liner was constructed of 6×10 mm knotless nylon and did not usually retain fish <40 mm total length or small invertebrates such as krill. Floats on the headrope and bridles helped maintain the net near the surface (usually within 1.0–1.5 m) continuously during tows. Sets were made at depths of ≥37 m, except at four shallower stations where the bottom was thought to be free of snags. Tow duration was 6–40 min (mean=22

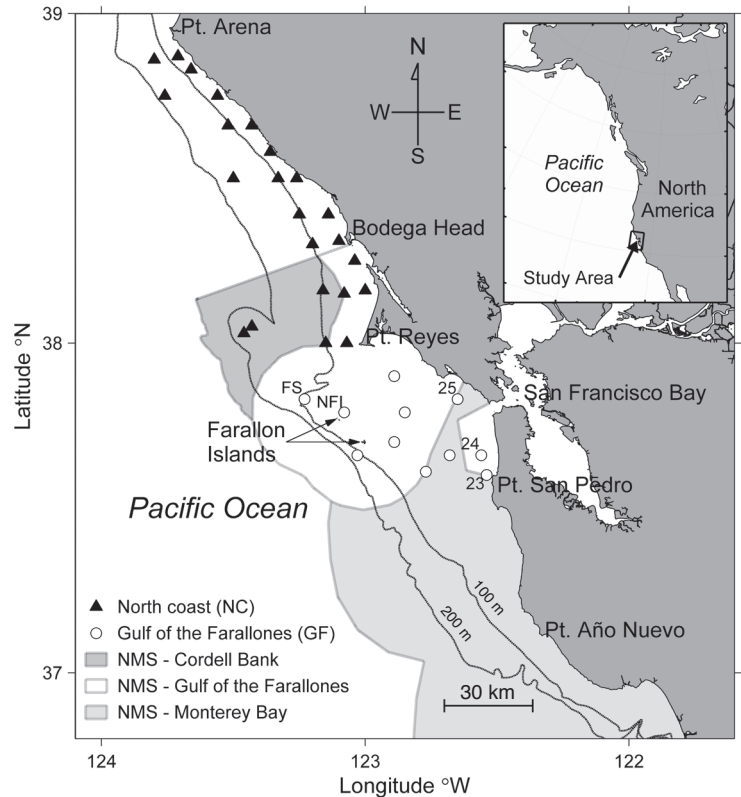


Figure 1

Location of trawl stations off central and northern California where epipelagic fish species were collected during 2000–05. Symbols show stations of the two regional sampling groups: north coast (NC) and Gulf of the Farallones (GF). Also shown are station labels for selected eastern GF (23, 24, 25) and western GF stations (FS=Fanny Shoal, NFI=North Farallon Island). Three National Marine Sanctuaries (NMS) are indicated.

min) and inversely proportional to jellyfish (*Chrysaora fuscescens* and *Aurelia* spp.) density. When abundant, these large jellyfish reduce sampling efficiency and can damage nets. Tow speed varied from 5.0 to 8.0 km/h (mean=6.5 km/h), depending on sea conditions and vessel. Tow distance was measured either with a mechanical flow meter pulled alongside the boat or calculated with GPS; tow distance varied from 0.5 to 4.8 km (mean=3.0 km).

Most fishes retained in the codend were identified to species, or occasionally to higher taxonomic levels, and counted. Larval and other small fish <40 mm were seldom retained. However, postlarval osmerids, scorpaenids, and flatfishes were occasionally captured and these were identified to family or sometimes to broader groups (e.g., “flatfish larvae”). Very large hauls were subsampled by volume or weight, and total species abundance was estimated from the composition of subsamples. Size class distinctions were made for only one species: juvenile Chinook salmon (≤250 mm fork length) were counted separately from larger individuals (>250 mm fork length, hereafter called “adults”). Adult salmon and other highly mobile species are thought to

Table 1

Number of stations sampled and hauls completed by region, year, and season, for trawl hauls and environmental variables obtained from CTD casts. Region: NC=north coast of California, GF=Gulf of the Farallones; season: S=summer, F=fall; variables: TMP=water temperature, SAL=salinity, DEN=water density, PAR=photosynthetically available radiation, CHL=chlorophyll-*a* concentration, DEP=water depth, DIS=distance of station from shore.

Region	Year	Season	Stations	Hauls	TMP	SAL	DEN	PAR	CHL	DEP	DIS	
NC	2000	S	1	1	1	1	1	0	1	1	1	
		F	2	2	2	2	2	2	0	2	2	
	2001	S	2	2	2	2	2	2	2	2	2	
		F	6	6	5	5	5	1	5	6	6	
	2002	S	6	6	5	5	5	5	5	6	6	
		F	10	11	10	10	10	10	10	11	11	
	2003	S	11	11	11	11	11	11	11	11	11	
		F	11	13	13	13	13	13	13	13	13	
	2004	S	17	17	17	17	17	16	17	17	17	
		F	21	21	21	21	21	20	21	21	21	
	2005	S	22	24	24	24	24	24	24	24	24	
		F	17	17	16	16	16	16	16	17	17	
	GF	2000	S	4	6	4	4	4	2	4	6	6
			F	6	8	7	7	7	5	2	8	8
2001		S	5	7	6	6	6	6	6	7	7	
		F	3	5	4	4	4	1	4	5	5	
2002		S	6	10	9	9	9	9	9	10	10	
		F	5	8	6	6	6	6	6	8	8	
2003		S	5	8	6	6	6	6	6	8	8	
		F	7	10	10	10	10	9	10	10	10	
2004		S	5	8	5	5	5	5	5	8	8	
		F	4	6	5	5	5	5	5	6	6	
2005		S	5	6	6	6	6	6	6	6	6	
		F	4	5	5	5	5	5	5	5	5	

be undersampled because they avoid the net (Emmett et al., 2006), although at times they were captured in large numbers. Macroinvertebrates—primarily jellyfish, squid, ctenophores, and salps—although often abundant in the catch, were not consistently identified or counted and therefore are not included here. To account for differences in tow distance and duration, fish abundance was standardized to a volume of 10^6 m^3 for all hauls—a standard that is about equal to a typical tow of 30 minutes at 5.6 km/h (3.0 knots).

Individual hauls were often sparse in diversity, sometimes containing only one or two species. For this reason, it was necessary to combine all hauls into larger sample groupings to run statistical tests and produce meaningful ordinations. Because sampling effort was not equal among stations, regions, or years, averaging the standardized abundance of each species (rather than pooling) was the appropriate method to cumulate hauls. For regional and seasonal comparisons, hauls at each station were averaged across all six years to obtain species abundance (averaged for each station) for each season and region. For interannual comparisons, hauls were grouped more broadly, by averaging for region and season within each of the six years separately. The analytical methods we used were robust to the inclusion of rare species and unaffected by zero values in

the community matrix, so that the full species matrix was used throughout the study, thus avoiding arbitrary omissions. Standardized abundances were square-root transformed to mildly reduce the disproportionately large influence of highly abundant species in the community analysis.

Assemblage structure: tests and ordinations

We used multivariate statistical tests and ordinations to search for patterns of community structure in space and time. PRIMER analytical software (vers. 6.1.6, PRIMER-E Ltd, Plymouth, U.K.) with PERMANOVA+ (Anderson et al., 2008) was used for all multivariate routines. We first tested for differences among main effects (regions, years, and seasons) and interaction terms by using a type-III permutational multivariate analysis of variance (PERMANOVA) with hauls averaged by region, year, and season in a three-way crossed design. PERMANOVA is a semiparametric group difference test directly analogous to multivariate analysis of variance but with pseudo- F ratios and P -values generated by resampling (permutation) the resemblance measures of the actual data; thus it is less sensitive to assumptions of parametric tests that are frequently violated by community data sets (Anderson, 2001; Anderson et al., 2008). For all biotic

data we used the Bray-Curtis coefficient to construct resemblance matrices. The variance components and degrees of freedom of highly nonsignificant interaction terms in the full model were consolidated by sequentially pooling them with the residuals to generate the final reduced model. Regions and seasons were treated as fixed effects: the examination and testing of variations in community structure between regions and seasons was the *a priori* objective of the study. Years were treated as random effects because there was no *a priori* reason for the timing or duration of the study: years have no particular meaning except to serve as replicates for the fixed effects of primary concern. Moreover, interannual patterns may be complicated by other sources of uncontrolled variation such as weather and sea state, or different ships and captains.

To examine community patterns in finer detail (specifically, among all four combinations of the two fixed factors [2 regions×2 seasons]), we used a two-way crossed PERMANOVA type-III design with hauls averaged by station and season across all six years. This method of cumulating samples provided greater replication and more degrees of freedom for each factor than was possible in the previous three-way arrangement. After this global test, pairwise comparisons were made between the two levels of each significant factor.

We used nonmetric multidimensional scaling (MDS), an unconstrained ordination technique, to create graphical summaries of relationships among samples based on the abundance of the various species present and to highlight spatial and temporal patterns of community structure. Unlike PERMANOVA, MDS operates on the rank orders of the elements in the resemblance matrix, rather than on the resemblance matrix itself, and constructs a map of the samples in a specified number of dimensions. The axes in MDS plots have no meaning other than for orientation, and scaling in MDS plots, if shown, is arbitrary. A stress value ranging from 0 to 1.0 is used to measure the reliability of the ordination, with zero indicating a perfect fit and all rank orders correctly represented by the relative distance between all pairs of points in the graph, and with values >0.3 indicating that points are close to being arbitrarily placed in the graph (Clarke and Warwick, 2001).

Where group differences in community structure were found ($\alpha < 0.05$ in PERMANOVA tests), we used another exploratory method to identify those species most responsible for the difference. For any two groups, SIMPER (similarity percentages) calculates the percent contribution each species makes to the total between-group dissimilarity (Clarke and Warwick, 2001). SIMPER identifies a small subset of species that are more consistently present or more abundant in one group than another, thus helping to reveal the major contributors to each group's biotic identity and simplifying the interpretation of community patterns. Because the routine incorporates both abundance and frequency of occurrence, it allows species at low abundance to be major contributors to community patterns if they are consistently present in one place or time.

Water properties: tests and ordinations

To match the approach used for the community analysis, we also ran multivariate tests for group differences in environmental structure using PERMANOVA and graphically summarized the relationships among hydrographic samples using ordination—in this case principal components analysis (PCA). In order to make direct comparisons with the biological patterns, oceanographic variables were grouped, averaged, and plotted in the same arrangements as those used for hauls in the species analysis. Because we were interested in examining water properties only as they relate to biotic patterns, the starting point for the PERMANOVA environmental model was the reduced model from the biotic analysis, with all three main effects included and all interaction terms pooled with residuals. Four variables with skewed distributions required transformation before PCA, and appropriate transformations were selected by using log-likelihood profiles of Box-Cox transformations. A square-root transformation was used for DIS and PAR, and a $\log_{10}(x)$ transformation for DEP and CHL. Environmental variables were normalized before PCA analysis, and Euclidian distance was used to measure sample similarity.

Oceanographic variables were also individually tested for regional and seasonal differences by using univariate analysis of variance (ANOVA) type-II tests. The same transformations described above were applied. After transformation, the distributions of all environmental variables met the requirements necessary for parametric testing and ANOVA was an appropriate choice in this instance.

The degree of similarity between corresponding species and environmental patterns was measured by using a matrix-matching permutation test (the BIO-ENV routine in PRIMER). With this procedure, biotic and abiotic samples are compared from matching locations and a subset of water properties are determined that maximize their correlation to the community pattern (Clarke and Warwick, 2001). To accomplish this goal, the elements of the two corresponding sample similarity matrices (Bray-Curtis for biotic and normalized Euclidian distance for abiotic) are ranked, the ranks are ordered by sample number or location, and the two matching sets of ordered ranks are compared by calculating a correlation coefficient—in this case the familiar Spearman coefficient (ρ_s). The significance level of the match is determined by comparing the observed value of ρ_s to a large set of ρ_s values generated by repeated random reassignment of sample labels in one of the two similarity matrices. Only samples that are jointly present in both matrices are considered in the test.

Results

We caught a total of 53 different species of fish during this study, of which a few common mid-trophic level

Table 2

Results of permutational multivariate analysis of variance (PERMANOVA) pairwise tests for differences in fish assemblages and environmental variables between regions of the north coast (NC) of California and the Gulf of the Farallones (GF) for both seasons, and between summer and fall for both regions.

Factor	Level	Pairs	Fish assemblages		Environmental variables	
			pseudo- <i>t</i>	<i>P</i>	pseudo- <i>t</i>	<i>P</i>
Season	summer	NC, GF	2.05	0.0001	1.80	0.0149
	fall	NC, GF	2.17	0.0001	3.26	0.0001
Region	NC	summer, fall	2.69	0.0001	2.30	0.0022
	GF	summer, fall	1.03	0.3471	2.04	0.0073

fishes heavily dominated the catch. One hundred and thirty-one hauls were taken in summer and fall cruises along the NC. The catch in that area was dominated numerically by jacksmelt (*Atherinopsis californiensis*, 39%) and Pacific herring (*Clupea pallasii*, 39%), with smaller landings of northern anchovy (*Engraulis mordax*, 6%), juvenile Chinook salmon (5%), and surf smelt (*Hypomesus pretiosus*, 2%). The five most frequently captured species were juvenile Chinook salmon (60%), jacksmelt (48%), adult Chinook salmon (34%), medusafish (*Icichthys lockingtoni*, 30%), and Pacific sardine (*Sardinops sagax*, 21%).

Eighty-seven hauls were taken in summer and fall cruises in the GF. Species composition was dominated numerically by northern anchovy (45%) and Pacific herring (44%), followed by jacksmelt (4%), Pacific sardine (4%), and whitebait smelt (*Allosmerus elongates*, 2%). The five most frequently captured species in this region were juvenile Chinook salmon (55%), Pacific herring (44%), jacksmelt (33%), adult Chinook salmon (32%), and medusafish (31%).

Although the interpretation of yearly patterns along the NC (but not the GF) was hampered somewhat by the increasing sample size over time in the north, the haul-averaged catch density indicated that 2004 and 2005 stand out as unusual years for several of the common species (those with >15% frequency of occurrence) (Appendix 1). In the NC, the average density of jacksmelt was much higher in both seasons in 2004 and 2005 than at any other time; Chinook salmon (both juveniles and adults) and Pacific herring average density was highest in summer of 2004 and 2005; northern anchovy and Pacific sardine density was highest in fall of 2004 and 2005; and jack mackerel (*Trachurus symmetricus*) were captured only in 2004 (both seasons) and during the summer of 2005. In the GF, the average density of jacksmelt was especially high in the fall of 2004 and during both seasons in 2005, sardine density was especially high in spring of 2004 and 2005, anchovy density was above average in both seasons in 2005, and Pacific butterfish (*Peprilus similimus*) average density was highest in both seasons in 2005. No common species were notably absent in these two years.

Multivariate biotic patterns

All interaction terms in the three-way PERMANOVA were highly nonsignificant ($P > 0.40$); these terms were sequentially removed by pooling their components of variation and degrees of freedom with residuals to increase statistical power for the remaining terms in the final reduced model. Main effects in the reduced model were all significant (region: pseudo- $F_{1,16} = 6.14$, $P = 0.0001$; season: pseudo- $F_{1,16} = 2.07$, $P = 0.0334$; year: pseudo- $F_{5,16} = 1.52$, $P = 0.0293$). The two-way PERMANOVA for regional and seasonal community differences was also highly significant for both main effects (region: pseudo- $F_{1,60} = 7.60$, $P = 0.0001$; season: pseudo- $F_{1,60} = 4.62$, $P = 0.0001$) and not significant for *region* × *season* interaction (pseudo- $F_{1,60} = 1.30$, $P = 0.196$). Subsequent pairwise comparisons (Table 2) showed strong differences in community structure between the NC and GF regions for both seasons, and strong seasonal differences within the NC region. However, there was no apparent seasonal difference within the GF region, where summer and fall communities were not statistically distinguishable.

Interannual community pattern The ordination of trawl catch averaged broadly by region, year, and season (Fig. 2A) showed clear separation of samples by region, but other differences due to years and seasons are not well supported by this configuration. With the exception of one point ('04 GF-summer), 2004 and 2005 occupied a separate quadrant of the data cloud, indicating that there may have been some commonality of structure shared by those two years alone. Samples from the remaining four years did not show an annual pattern at this level of resolution. Seasonal (summer vs. fall) samples also appeared to be randomly mixed in this configuration, especially for the GF region. Seasonal differences in community structure must be examined at a finer scale of resolution, and samples averaged more narrowly by station and season across all six years, for recognizable seasonal patterns in MDS plots to emerge.

Regional community pattern Ordinations of samples averaged by station and season visually supported the result of the two-way PERMANOVA and subsequent

pairwise comparisons. In MDS plots of community structure, stations in summer cruises separated fairly well by region (Fig. 3A), with NC stations forming a central cloud and GF stations scattered more widely around the perimeter and mostly to one side of the plot. Within the GF region there was further recognizable spatial structure: stations 23, 24, and 25 are the three easternmost nearshore stations, closest to the mouth of the San Francisco Bay in real space. Stations FS (Fanny Shoal) and NFI (North Farallon Island), the two westernmost GF stations, were dissimilar in the summer ordination. Stress was moderate at 0.13, indicating a fairly reliable plot. Samples from fall cruises formed a similar regional pattern, with NC stations falling in a (mostly) separate central cloud surrounded by more widely scattered and dissimilar GF stations (Fig. 3B). Further spatial structure within the GF was again apparent; the eastern nearshore trio of stations (23, 24, and 25) were placed together and opposite most of the remaining GF stations. The two westernmost GF stations (FS and NFI) were structurally similar to each other in fall. Stress was moderate at 0.19.

Seasonal community pattern Ordinations of seasonal community patterns also supported their corresponding statistical tests. Along the NC there was clear separation of summer and fall samples (Fig. 3C), consistent with the significant seasonal test for this region, whereas in the GF there was broad overlap of summer and fall samples (Fig. 3D) consistent with the nonsignificant test for seasonal differences in this area. Summer samples in both regions were more widely spread across the plots, and hence more variable, than fall samples, and stress was moderate for both plots.

Representative species The SIMPER routine identified a small subset of species most responsible for the observed differences between the NC and GF communities, and between summer and fall communities along the NC (Table 3). Over 80% of the total dissimilarity between communities was attributed to about 12 species, and six of these were high ranking contributors to all three of the paired SIMPER comparisons between significantly different communities. Variation in the relative abundance and frequency of occurrence of these six species, in particular, allowed the multivariate tests and ordinations to discriminate among groups. For example, the three common clupeiform species (Pacific herring, Pacific sardine, and northern anchovy) were much more abundant in the GF than along the NC, regardless of season. Among the other principal species, jacksmelt and juvenile Chinook salmon were more abundant in the NC-summer community, whereas medusafish were more abundant in the GF-summer community. In the fall, juvenile Chinook salmon were still more abundant in the NC community, and jacksmelt and medusafish were more abundant in the GF.

Significant seasonal differences were only observed along the NC. Here, the NC-summer community was

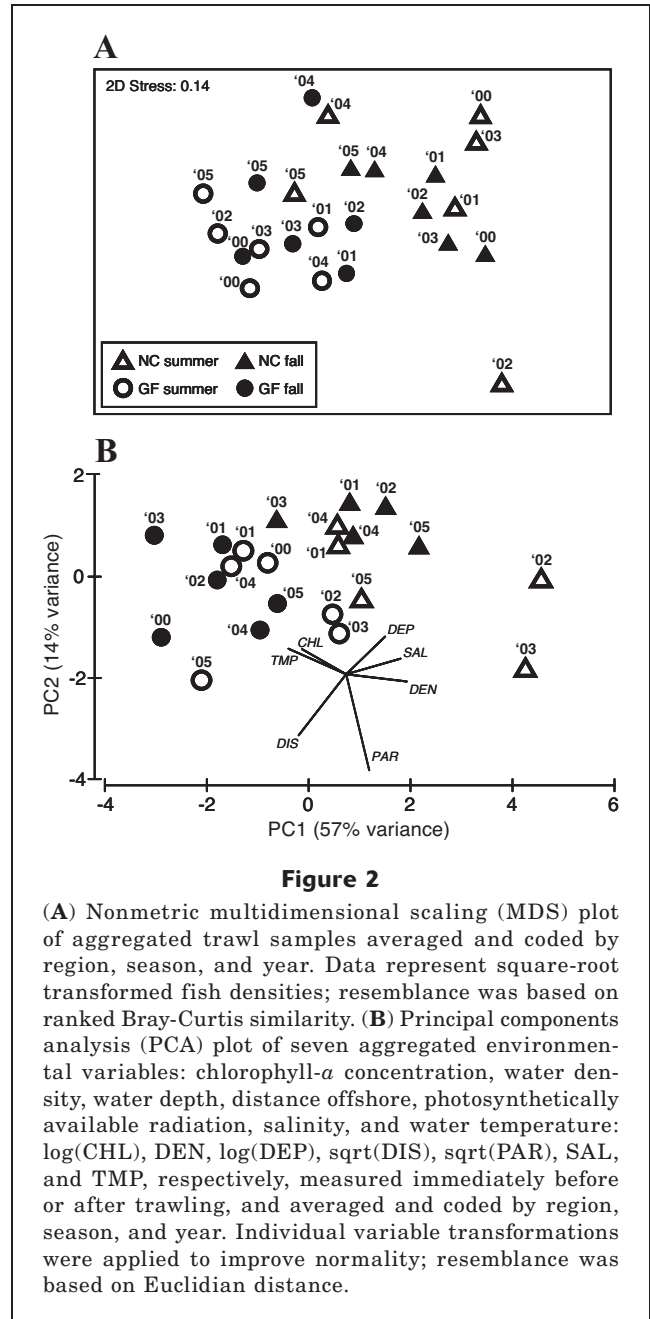


Figure 2
(A) Nonmetric multidimensional scaling (MDS) plot of aggregated trawl samples averaged and coded by region, season, and year. Data represent square-root transformed fish densities; resemblance was based on ranked Bray-Curtis similarity. (B) Principal components analysis (PCA) plot of seven aggregated environmental variables: chlorophyll-*a* concentration, water density, water depth, distance offshore, photosynthetically available radiation, salinity, and water temperature: log(CHL), DEN, log(DEP), sqrt(DIS), sqrt(PAR), SAL, and TMP, respectively, measured immediately before or after trawling, and averaged and coded by region, season, and year. Individual variable transformations were applied to improve normality; resemblance was based on Euclidian distance.

dominated by jacksmelt, Pacific herring, and juvenile Chinook salmon, and the NC-fall community was dominated by northern anchovy, Pacific sardine, and medusafish. Other important contributors to regional dissimilarity were adult Chinook salmon, jack mackerel, and Pacific saury (*Cololabis saira*) (all more strongly associated with the NC), and Pacific tomcod (*Microgadus proximus*), surf smelt, and Pacific butterfish (all more strongly associated with the GF). Along the NC, adult Chinook salmon and jack mackerel were more abundant in summer than in fall, whereas Pacific tomcod were more abundant in fall than in summer.

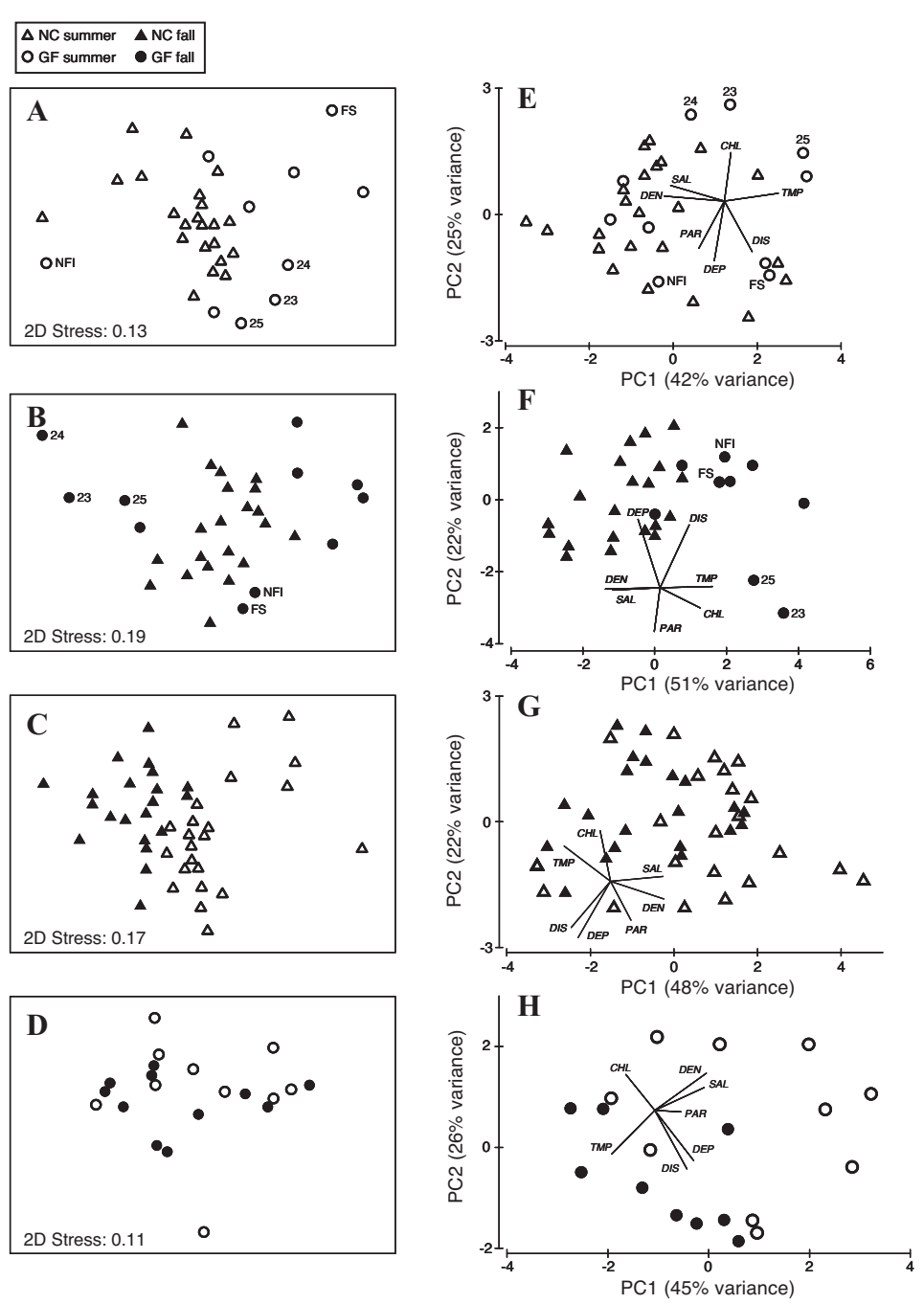


Figure 3

(A–D) Nonmetric multidimensional scaling (MDS) plots of aggregated trawl samples averaged by season and station across all years, and coded by region and season. Data are square-root transformed fish densities; resemblance based on ranked Bray-Curtis similarity. (E–H) Principal components analysis (PCA) plots of seven aggregated environmental variables: chlorophyll-*a* concentration, water density, water depth, distance offshore, photosynthetically available radiation, salinity, and water temperature: log(CHL), DEN, log(DEP), sqrt(DIS), sqrt(PAR), SAL, and TMP, respectively, measured immediately before or after trawling, averaged by season and station across all years, and coded by region and season. Individual variable transformations were applied to improve normality; resemblance was based on Euclidian distance. Selected Gulf of the Farallones stations are labeled: eastern nearshore (23, 24, 25) and western offshore (FS=Fanny Shoal, NFI=North Farallon Island) groups.

Table 3

Species contributions to between-group dissimilarity for three pairs of communities with significantly different community structures (i.e., $\alpha < 0.05$ in pairwise PERMANOVA tests), determined by using the SIMPER (similarity percentages) routine. Species are listed in order of decreasing percent dissimilarity contribution with an 80% cumulative dissimilarity cutoff imposed. Abundance is the untransformed average number of fish/10⁶ m³ within each group: NC=north coast, GF=Gulf of the Farallones, S=summer, F=fall. Dominant (Dom.) region and dominant (Dom.) season indicate the region and season, respectively, where each species was more abundant in each of the three comparisons presented. For the species Chinook salmon: ad=adult (>250 mm fork length); jv=juvenile (≤ 250 mm fork length).

Species	Dissimilarity	Contribution	NC abundance	GF abundance	Dom. region
Summer NC vs. summer GF, $\Sigma(\text{dissimilarity})=86.38$					
Pacific herring, <i>Clupea pallasii</i>	18.10	20.96	127.46	1644.41	GF
jacksmelt, <i>Atherinopsis californiensis</i>	15.48	17.92	99.12	55.56	NC
Pacific tomcod, <i>Microgadus proximus</i>	7.23	8.36	0.08	8.94	GF
Pacific sardine, <i>Sardinops sagax</i>	5.95	6.88	0.07	184.68	GF
Chinook salmon, jv, <i>Oncorhynchus tshawytscha</i>	5.47	6.33	13.70	9.48	NC
northern anchovy, <i>Engraulis mordax</i>	4.89	5.66	0.06	2166.27	GF
medusafish, <i>Icichthys lockingtoni</i>	3.80	4.40	0.28	1.65	GF
Chinook salmon, ad, <i>Oncorhynchus tshawytscha</i>	3.51	4.06	2.20	2.07	NC
jack mackerel, <i>Trachurus symmetricus</i>	3.27	3.79	2.91	0.00	NC
surf smelt, <i>Hypomesus pretiosus</i>	2.65	3.07	6.40	6.82	GF
Fall NC vs. fall GF, $\Sigma(\text{dissimilarity})=81.04$					
Pacific herring, <i>Clupea pallasii</i>	16.11	19.88	0.30	756.19	GF
northern anchovy, <i>Engraulis mordax</i>	14.64	18.07	17.30	204.83	GF
jacksmelt, <i>Atherinopsis californiensis</i>	13.91	17.17	24.42	184.51	GF
Chinook salmon, jv, <i>Oncorhynchus tshawytscha</i>	5.75	7.09	2.90	1.79	NC
medusafish, <i>Icichthys lockingtoni</i>	5.08	6.27	2.74	2.80	GF
Pacific sardine, <i>Sardinops sagax</i>	4.85	5.98	3.22	6.92	GF
Pacific saury, <i>Cololabis saira</i>	3.41	4.21	4.71	0.82	NC
Pacific butterfish, <i>Peprilus simillimus</i>	3.16	3.90	0.42	2.43	GF
Species	Dissimilarity	Contribution	Summer abundance	Fall abundance	Dom. season
Summer NC vs. fall NC, $\Sigma(\text{dissimilarity})=75.35$					
jacksmelt, <i>Atherinopsis californiensis</i>	17.24	22.88	99.12	24.42	S
Pacific herring, <i>Clupea pallasii</i>	10.89	14.46	127.46	0.30	S
northern anchovy, <i>Engraulis mordax</i>	7.16	9.51	0.06	17.30	F
Chinook salmon, jv, <i>Oncorhynchus tshawytscha</i>	6.70	8.88	13.70	2.90	S
Pacific sardine, <i>Sardinops sagax</i>	4.47	5.93	0.07	3.22	F
jack mackerel, <i>Trachurus symmetricus</i>	4.23	5.62	2.91	0.48	S
medusafish, <i>Icichthys lockingtoni</i>	3.82	5.06	0.28	2.74	F
Chinook salmon, ad, <i>Oncorhynchus tshawytscha</i>	3.54	4.70	2.20	0.39	S
Pacific tomcod, <i>Microgadus proximus</i>	2.26	3.00	0.08	0.91	F

Water properties

The analysis of environmental structure was designed to mirror the community analysis. Samples were averaged, tested, and plotted in the same arrangements in order to facilitate direct multivariate comparison of ocean conditions and community patterns. Interaction terms in the three-way PERMANOVA for differences in environmental structure were consolidated with residuals before tests were run, and all main

effects in the reduced model were found to be significant (region: pseudo- $F_{1,14}=8.08$, $P=0.0002$; season: pseudo- $F_{1,14}=2.58$, $P=0.0438$; year: pseudo- $F_{5,14}=1.88$, $P=0.0352$). The two-way PERMANOVA for regional and seasonal differences was also highly significant for both main effects (region: pseudo- $F_{1,59}=10.92$, $P=0.0001$; season: pseudo- $F_{1,59}=8.58$, $P=0.0001$) and not significant for *region* × *season* interaction (pseudo- $F_{1,59}=1.47$, $P=0.20$). All subsequent pairwise comparisons were highly significant (Table 2).

Interannual hydrographic pattern The ordination of hydrographic variables averaged broadly by region, year, and season (Fig. 2B) showed clear separation of samples by region, but failed to show evidence of other groupings due to years or seasons at this scale of resolution. Unlike the corresponding MDS community plot, the years 2004 and 2005 did not occupy a distinct quadrant of the PCA environmental plot.

Regional hydrographic pattern Stations in summer cruises did not form clearly distinct regional groups based on PCA (Fig. 3E). Rather, GF stations overlapped broadly with those of the NC, and weak regional separation was apparent on a gradient described mostly by PC1 axis. Most GF stations fell on the right of the first axis (characterized by higher TMP, lower SAL, and lower DEN) and most NC stations fell on the left (characterized by the opposite conditions). The trio of eastern nearshore GF stations (23, 24, and 25) was again placed together and was characterized by higher CHL and lower DIS, DEP, and PAR than other summer stations. Stations in fall cruises (Fig. 3F) showed greater regional separation than summer stations. This division also fell along an environmental gradient captured mostly by the first axis, with the GF characterized by higher TMP, higher CHL, lower DEN, and lower SAL, and the NC characterized by the opposite conditions. The finding that water properties within the two regions were more dissimilar in fall than in summer was consistent with PERMANOVA pairwise tests. One GF station (number 24) and two NC stations were excluded from the fall analysis because of incomplete CTD data sets.

Seasonal hydrographic pattern Summer and fall samples along the NC overlapped broadly but on average occupied mostly different sides of their PCA plot (Fig. 3G) and separated primarily along a gradient described by PC1; most summer samples were characterized by higher SAL and DEN and lower TMP than fall samples. Summer and fall samples in the GF (Fig. 3H) showed greater separation on the PC1 gradient, composed of roughly equal parts DEN, SAL, and TMP and capturing most of the seasonal variance. Summer samples in both regions were more variable than fall samples.

Univariate pattern ANOVA tests showed that water properties varied significantly between regions for six of the seven variables and between seasons for four variables (Fig. 4). TMP increased from north to south and from summer to fall, indicating stronger coastal upwelling in summer and north of Pt. Reyes. CHL also increased significantly from north to south, but the seasonal pattern was not consistent in the two regions and summer and fall differences in CHL were not significant. SAL and DEN were positively correlated ($r^2=0.97$, $P<0.001$) and showed similar patterns, with higher values along the NC and a significant decrease from summer to fall in both regions. PAR was the only variable not significantly different between regions, but it was significantly higher in summer than in fall. DEP

and DIS varied regionally but not seasonally. On average, GF stations were shallower and farther from shore, reflecting the broader shelf in the GF. The interaction between region and season was not significant for any of the variables, although it was close for TMP ($P=0.06$) and PAR ($P=0.08$).

Relationship of environment to community structure

The ordination of samples based on species similarity (Fig. 2A) was structurally related to the ordination of samples based on environmental similarity (Fig. 2B), as determined by direct comparison of their underlying similarity matrices with the BIO-ENV routine. Using first the full set of seven environmental variables with the BIO-ENV protocol, we found significant similarity of multivariate pattern between the biotic and the environmental data ($\rho_s=0.439$, $P=0.001$). However, a reduced subset of these seven variables generated an improved match with the community pattern. The solution that maximized the Spearman rank correlation between the two resemblance matrices was a four-variable combination of DEP, DIS, TMP, and SAL ($\rho_s=0.471$, $P=0.001$) that performed slightly better than the full seven-variable comparison. Closely following this four-variable solution were three three-variable combinations (DEP, DIS, DEN; DEP, DIS, TMP; DEP, DIS, SAL) that gave ρ_s -values only slightly smaller than the four-variable combination. These three are arguably the best solutions because they achieve essentially the same level of correlation with one less variable.

Discussion

Abundance data from a six-year survey of coastal marine fishes captured in surface trawls revealed significant differences in community structure based on region, year, and season. These patterns were mirrored by differences in a small suite of mostly physical oceanographic variables collected along with the biotic samples, indicating that epipelagic fish communities were responding to interannual, seasonal, and relatively small-scale spatial variability in oceanography. Multivariate ordination placed samples with similar fish communities in arrangements that corresponded with a boundary somewhere in the vicinity of the headland at Pt. Reyes. GF stations were more dispersed and variable in ordinations than NC stations, and the plotted arrangement of several GF stations appeared to be influenced by their common proximity to features such as the San Francisco Bay outflow and possibly the Farallon Islands. Differences in community structure were due primarily to differences in relative abundance and occurrence of about 6–12 ubiquitous species, most of which were regularly caught in both regions and during both seasons of the study. Thus, community patterns were not driven by abrupt turnover of dominant taxa across regional boundaries or between seasons, but rather by gradients in local abundance. Most of the dominant species identi-

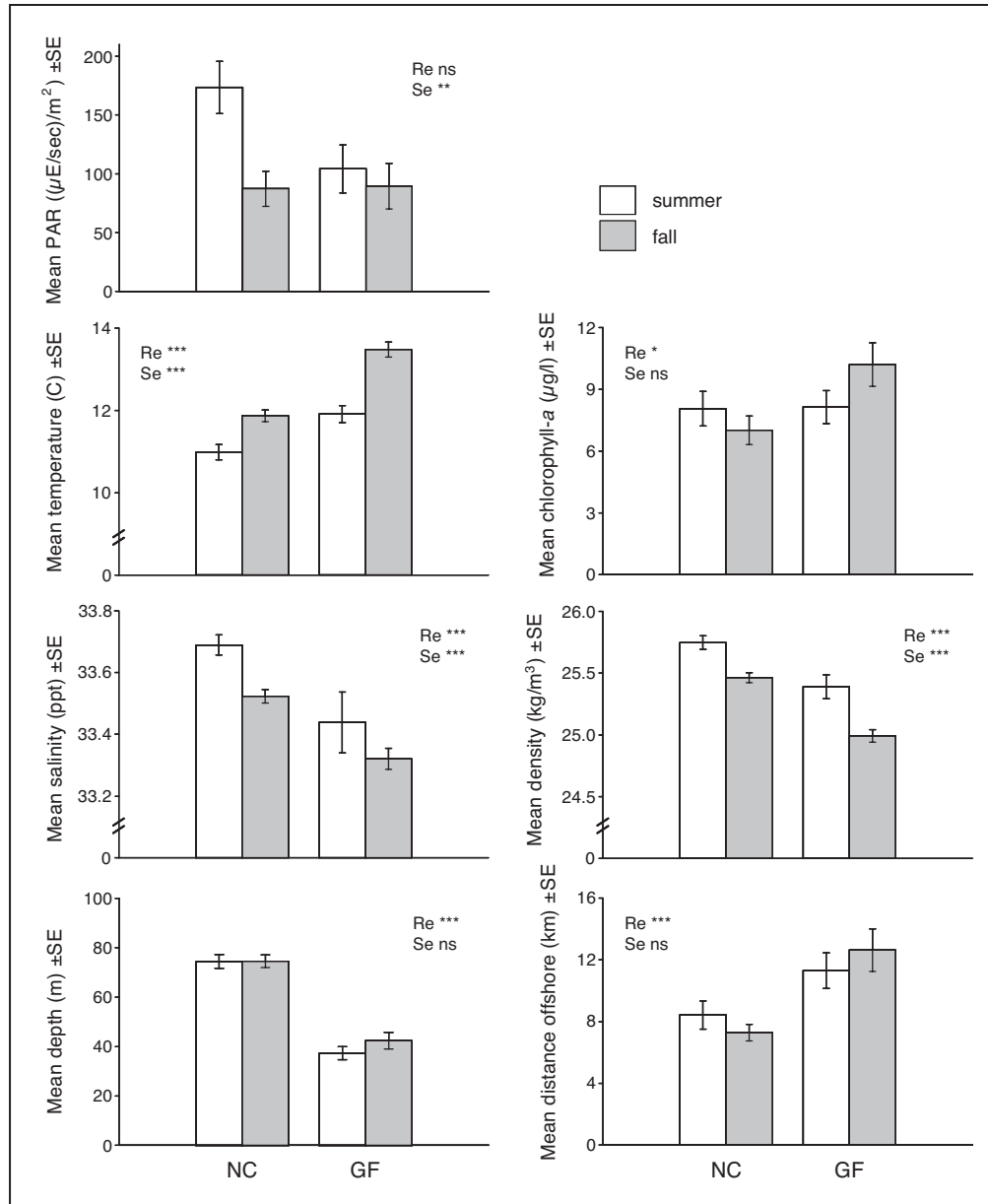


Figure 4
 Environmental variables measured immediately before or after trawling at stations off northern and central California, averaged by region and season across years and shown here untransformed. NC=north coast, GF=Gulf of the Farallones. Significance levels for two-way analysis of variance (ANOVA) tests were determined separately for each variable and are represented in each graph: Re=region, Se=season, ns= not significant at $P>0.05$, * $P\leq 0.05$, ** $P\leq 0.01$, *** $P\leq 0.001$. All Re \times Se interaction terms were not significant.

fied by the SIMPER routine were typical of more than one assemblage, which is not surprising for communities consisting of mobile pelagic species.

The arrangement of stations in PCA plots, based solely on environmental measures, was broadly similar to MDS ordinations based on fish abundance and diversity. Because the resemblance matrices underlying the corresponding PCA and MDS plots were independently derived, the match is unlikely to be purely coincidental.

It is reasonable to assume that one or more of the oceanographic variables are potentially causal factors affecting fish community structure in this region. Matrix-matching tests, where community patterns were compared to oceanographic features, helped narrow the field down to three or four important variables, namely DEP, DIS, and any one or two of the upwelling-related variables TMP, SAL, and DEN, which together proved to be fairly good indicators of variation in the commu-

nity. Future studies of a possible link between middle and upper trophic level community structure and pelagic ocean habitats in this region could expand our efforts with the inclusion of additional hydrographic variables (e.g., dissolved oxygen, nitrates, silicates, turbidity, and frontal intensity). The relationship between zooplankton abundance and fish community structure is of particular interest. For example, cold-water copepod biomass has been shown to correlate strongly with survival of age-1 northern anchovy and may ultimately determine adult anchovy density (Litz et al., 2008).

In the most comprehensive study of nekton community structure and oceanography off Oregon and Washington to date, Brodeur et al. (2005) identified a larger set of water properties with significant correlations to fish assemblages. In their study, differences in community structure were primarily related to seven environmental variables associated with distance offshore and upwelling intensity: water depth and temperature, water transparency, chlorophyll concentration, and three different macronutrients. The authors propose that future studies could develop a single metric combining multiple oceanographic variables as a means of quantifying suitable habitats for pelagic species. Among the other surface trawl surveys in the CC during which environmental variables were measured, onshore–offshore differences in fish community structure were usually present, but north–south patterns were weak or absent. Several oceanographic features that vary with distance offshore (depth, temperature, salinity, and turbidity) were correlated with species distributions (Emmett et al., 2006). In a study describing the physical properties of biological hotspots in the coastal zone off southern Oregon, Reese and Brodeur (2006) found that distance offshore, water depth, temperature, density, and salinity accounted for the strongest correlations with species ordination axes, although the order of importance among these physical variables was different among years and seasons and chlorophyll was of little value in explaining community structure. Curiously, although the hotspots themselves persisted, the fish species inhabiting them did not. The authors found different sets of indicator species within each of two hotspots on four separate cruises. In all of these studies, an area farther offshore than that of the present study was sampled, usually at least to the shelf break.

Our catch was dominated by a few highly abundant mid-trophic level species, as is typical of temperate upwelling zones worldwide. Examples include *Engraulis mordax* and *Sardinops sagax* in the California Current, *E. ringens* and *S. sagax* in the Peru Current, *E. capensis* and *S. ocellatus* in the Benguela Current, and *E. encrasicolus* and *Sardina pilchardus* in the Canary Current (Parrish et al., 1983). Chief among these “forage” species in our study were northern anchovy and Pacific herring; lesser contributions were made by jack-smelt and Pacific sardine, depending on location and season. Northern anchovy composed more than half of the overall catch and were abundant in both regions

but ranked seventh overall in frequency of occurrence, indicating large but scattered schools. Northern anchovy abundance in surface trawls was also notably high and variable off Oregon (Brodeur et al., 2005; Litz et al., 2008), and larval anchovy were the most abundant fish in plankton samples from the Columbia River plume (Parnel et al., 2008). In midwater trawls off central California (Pt. Reyes to Pt. Conception), Mais (1974) reported that 55% of hauls contained northern anchovy and greatest concentrations were in the south and <18.5 km offshore. In surface trawls in the northern CC, Brodeur et al. (2005) reported that Pacific herring, Pacific sardine, and northern anchovy together accounted for 76% of the catch, although their frequency of occurrence was relatively low. This pattern of clupeiform abundance was attributed to schooling behavior and patchy distribution. Subadult Chinook salmon were far less abundant in catches but were taken in a higher overall percentage of hauls, consistent with our findings and indicating a lower density and a more uniform distribution than for clupeids. In a broad survey of the CC between Vancouver Island and central California, 75% of 1.5 million fish taken in surface trawls were Pacific sardine and Pacific herring (Orsi et al., 2007). Pacific herring were positively associated with osmerids (true smelts) and juvenile salmonids, and together these three taxa (sometimes in combination with northern anchovy and other species) formed a distinct group typical of inshore habitats (Brodeur et al., 2004, 2005; Emmett et al., 2006; Orsi et al., 2007). In the present study, Pacific herring and juvenile Chinook salmon were co-dominant summer species in the NC region based on SIMPER analysis, but spatially herring were more dominant in the GF and juvenile Chinook salmon more dominant along the NC. Osmerids were far less abundant in our study than in those conducted farther north off Oregon and Washington and contributed little to the distinctions among communities in our area.

Unlike herring and juvenile salmonids, Pacific sardines are usually grouped with an offshore migratory assemblage that includes Pacific mackerel (*Scomber japonicus*) and jack mackerel off Oregon (Brodeur et al., 2003; Reese and Brodeur, 2006). These three species appear to migrate from the southern CC farther north and onshore in unusually warm years (Brodeur et al., 2005; 2006). In spite of our limited cross-shelf coverage, the consistent importance of the variables DEP and DIS in matrix-matching tests strongly indicates that onshore–offshore gradients structure fish communities in our region as well, and implies that a distinct offshore assemblage perhaps similar to that of the northern CC exists in our area. However, in classification analysis of selected species in our study (not shown), fishes typically associated with offshore habitats, such as Pacific sardine and jack mackerel, showed no clear relationship to each other or to distance offshore, and Pacific mackerel were too infrequently caught to allow assessment of their distribution. The spatial coverage of ongoing trawl surveys conducted by

the U.S. National Marine Fisheries Service (NMFS) along the northern California coast beginning in 2010 has been expanded well beyond the shelf break to help resolve this point.

During this study ocean conditions in the northern CC shifted from a phase of cool, generally productive coastal water with strong upwelling and La Niña-like conditions (2000–02) to a warmer, less productive phase with weaker upwelling and El Niño-like conditions (2003–05) (Goericke et al., 2005). This gradual but progressive shift culminated in a major oceanographic anomaly in 2005 when upwelling in the northern CC was delayed by ~2 months, during which time sea surface temperatures remained abnormally high (Peterson et al., 2006; Schwing et al., 2006). Ecosystem effects caused by this delay were dramatic and included unusually low chlorophyll (phytoplankton) levels in some areas, a crash in recruitment of intertidal mussels and barnacles, reduction and redistribution of copepods and other zooplankton, extremely low numbers of rockfish larvae, and the complete breeding failure of a krill-eating seabird (Peterson et al., 2006; Sydeman et al., 2006; Barth et al., 2007). In the epipelagic fish community off Oregon, anomalous abundance patterns were seen during 2004–05 for northern anchovy, Pacific sardine, Pacific herring, jack mackerel, osmerids, and juvenile salmonids, and several southern species were recorded far north of their usual range (Brodeur et al., 2006). In the present study we obtained larger than average catches of several common species during 2004–05, most notably along the NC. The patterns we observed were generally consistent with the catch anomalies seen in Oregon (except for juvenile salmon, where the above average densities we recorded were opposite the Oregon pattern). The years 2004 and 2005 grouped together weakly in community ordination but the hydrographic data we collected at that time failed to show a multivariate signal of an anomaly, probably because the 2005 climate event was much stronger in the northern CC off Oregon and Washington than in the central CC off California, and it had a much greater effect on more northern fish populations (Peterson et al., 2006; Schwing et al., 2006). Along the NC and especially in the GF, localized oceanographic processes operating on smaller (cape-and-bay or less) spatial scales may have been more important to the community than coastwide climate forcing, at least in the short run (i.e., the six-year period of our study) and may have masked any broader effects.

Water origins and transport patterns could account for much of the spatiotemporal variability we observed. During upwelling-favorable northwest spring winds, shelf water transport along the NC is characterized by a strong jet that originates in the Pt. Arena upwelling center and travels south over the outer shelf and slope (20–50 km from the coast), to be deflected offshore by Pt. Reyes. Inner shelf water (<20 km from the coast) derives from more localized upwelling centers along the NC and is transported south past Pt. Reyes but more slowly, whereupon it enters GF circulation or is

entrained offshore (Kaplan and Largier, 2006). When upwelling-favorable winds relax, the southward-flowing offshore jet slows or stalls, while inner-shelf transport reverses direction completely and flows poleward up the coast. Gulf water is entrained in these poleward flows and travels north around Pt. Reyes toward the NC, remaining close to shore with little offshore dispersion until upwelling resumes (Kaplan and Largier, 2006). This scenario may also predominate in fall, when upwelling-favorable winds are generally absent. Thus, connectivity between the NC and the GF is punctuated by alternating water sources and directions of nearshore transport, although net transport is to the south in most years. In 2004–05 when upwelling was weak and delayed, longer periods of poleward transport of GF water toward the NC during spring and summer may have resulted, perhaps leading to the higher densities of clupeiform fishes, jacksmelt, and juvenile salmon we observed off the NC during that period.

In contrast to the NC, water transport and circulation in the GF (described by Steger et al., 2000) is characterized by persistent poleward flow of Pacific equatorial water along the shelf break and slope (40–80 km from the coast). Over the shelf (<40 km from the coast) circulation is more variable and net transport is to the south. The jet of cool upwelled water arriving from the NC slows and some portion is captured and retained in a coastal cyclonic eddy in the northern and eastern GF, where it is sheltered from wind forcing in the lee of Pt. Reyes. In the central GF, cross-shelf Ekman transport carries surface water offshore during upwelling-favorable periods and onshore during relaxation, and submesoscale (10–50 km diameter) vortices are common in all seasons. These circulating features transport and mix large volumes of different water types within the GF and their presence effectively masks any regular seasonal hydrographic patterns in some years. Up to four different water masses meet in the GF, and the frontal mixing zones between oceanic, bay outflow, upwelled cold and upwelled warm water have sinuous and shifting locations depending on the intensity of wind forcing, river volume, and other variables that change seasonally and annually (Schwing et al., 1991). Fundamentally different water circulation patterns north and south of Pt. Reyes set the GF apart as a hydrographically unique location along the northern California coast (Steger et al., 2000; Largier et al., 2006). It is also the only coastal region in California to receive substantial nutrient enrichment from a major fresh water source, here the eutrophic estuarine waters of the Sacramento River exiting through the San Francisco Bay (Wilkerson et al., 2002).

Fronts are common ocean features that form where distinct water masses collide or opposing currents meet. Long bands of concentrated flotsam, plankton, and neuston often form at surface convergent fronts, sometimes as visible meandering features. The intensity, persistence, and locations of nearshore fronts correlate positively with larval fish density (Bjorkstedt et al., 2002) and invertebrate recruitment (Roughgarden

et al., 1991). Forage and predatory fishes, seabirds, and marine mammals actively seek out and concentrate at fronts in order to feed (Olson et al., 1994; Sims and Quayle, 1998). Nearshore frontal probability, measured in fine-scale (5 km) bins, during the upwelling season in 2006 was much higher in the GF than elsewhere along the northern California coast (Woodson et al.³)—further evidence of the unique oceanographic properties of the GF and a possible reason for the much higher density of clupeiform fishes that we recorded there, than along the NC. Wing et al. (1998) described the spatial pattern of Gulf mesoscale fronts in 1994 and 1995 and collected several taxa of larval crabs and rockfish whose distributions in the GF and along the north side of Pt. Reyes were strongly correlated with specific water masses, water movement and locations of fronts. The highest abundance of larval crabs was found in the northern GF retention zone and the highest abundance of rockfish larvae along fronts farther offshore. The catch variability and higher average fish densities that we observed in six years of trawling in the GF is consistent with this view of the region as a complex frontal mixing and retention zone downcurrent of a major headland and also indicates that adjacent coastal regions may be less complex hydrographically and thus more predictable biologically. With different water masses impinging on the Gulf from all four sides and shifting frontal boundaries in different years and seasons, a more variable pelagic community would be expected here than elsewhere.

Conclusions

In this study we provide the first detailed baseline data on epipelagic fish abundance in a highly dynamic yet less studied portion of the CC. As such it can be used to evaluate the effects of future perturbations, such as climate-induced oceanographic changes or variation in fishing pressure, on fish communities. The analytical techniques employed offer a powerful method to reveal community structure and relationships with environmental conditions, and their use in other systems is encouraged. The analyses reveal spatial and temporal gradients in community structure between two adjacent but oceanographically different regions. Our results indicate that waters within the GF and nearshore to the estuary exit are oceanographically complex transition zones in contrast to more uniform but separate coastal communities; hence they reveal the importance of the GF and similar zones elsewhere as connectors or corridors between coastal and estuarine communities, where

more closely spaced biological and physical sampling is required to untangle the inherent complexity of such areas compared to open coastlines (Schwing et al., 1991). In order to move incrementally toward ecosystem-based management, the Pacific Fisheries Management Council may consider adopting a more regional “nested approach” to spatial management of living marine resources in the CC, in which smaller segments of the ecosystem could be defined for management purposes on cape-and-bay scales that better match the scales of variation in community and habitat structure (Ecosystem Plan Development Team²).

The gradual implementation of ecosystem-based management will continue to involve regular ship-based oceanographic and biological sampling. It will be necessary to measure species diversity within smaller cohesive regions, to account for multispecies patterns of distribution, to identify and describe essential fish habitat, and to model and understand food-web dynamics including predator-prey relationships, interspecific competition, and guild membership and biomass, among other things (Francis et al., 2007). Quantitative indicators for describing fish communities and for tracking ecosystem status are used in current modeling (Rice and Rochet, 2005). The best indicators are easily measured and are reliable proxies for a suite of desirable ecosystem attributes, and often include species that are not themselves the targets of any fishery and would likely have been ignored in previous single-species management plans.

Indicators of ecosystem status often consist of species with common properties such as foraging guild membership, spatial distribution, ecotype, or some combination of these (e.g., small planktivorous fish, migratory mesopelagic fish, all sharks) (Fulton et al., 2005). Among the best performing indicators for a set of north Pacific ecosystem models are biomass groups consisting of detritivores, flatfish, and zooplanktivorous fish, as well as some surprising compound metrics such as the ratio of forage fish to jellyfish biomass (Samhuri et al., 2009). The use of indicators such as these to track and evaluate ecosystem attributes is a central part of the integrated ecosystem assessment process and an important policy objective of the NMFS (Levin et al., 2009).

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Appendix 1

Summary of 2000–05 trawl catch by species or broader taxa as defined in the text, averaged over all available hauls by region, year, and season. Numbers are fish abundance/10⁶ m³, not transformed. Sample size for each reporting period is given in Table 1. Haul avg.=overall average fish density (abundance/10⁶ m³) within each region from 2000 to 2005; % Total = percentage of species contribution to the total regional catch during 2000–05; % F.O.=percent frequency of species occurrence within regional hauls during 2000–05. Only species contributing ≥5% of individuals to one or more hauls in a region are shown. C-O is named for the distinctive geometric pattern seen on the tail.

Common name	Family	Species	2000		2001	
			Summer	Fall	Summer	Fall
North coast (NC)						
thresher shark	Alopiidae	<i>Alopias vulpinus</i>
wolf-eel	Anarrhichadidae	<i>Anarrhichthys ocellatus</i>
sablefish	Anoplopomatidae	<i>Anoplopoma fimbria</i>
jacksmelt	Atherinidae	<i>Atherinopsis californiensis</i>	0.90	...	1.01	...
plainfin midshipman	Batrachoididae	<i>Porichthys notatus</i>
speckled sanddab	Bothidae	<i>Citharichthys stigmaeus</i>
jack mackerel	Carangidae	<i>Trachurus symmetricus</i>
blue shark	Carcharhinidae	<i>Prionace glauca</i>	1.79
medusafish	Centrolophidae	<i>Ichthyosoma lockingtoni</i>	...	18.35	4.92	1.20
Pacific sardine	Clupeidae	<i>Sardinops sagax</i>	2.54
Pacific herring	Clupeidae	<i>Clupea pallasii</i>
Pac. staghorn sculpin	Cottidae	<i>Leptocottus armatus</i>
northern anchovy	Engraulidae	<i>Engraulis mordax</i>	0.28
Pacific tomcod	Gadidae	<i>Microgadus proximus</i>
lingcod	Hexagrammidae	<i>Ophiodon elongatus</i>
Pacific hake	Merlucciidae	<i>Merluccius productus</i>
ocean sunfish	Molidae	<i>Mola mola</i>
bat ray	Myliobatidae	<i>Myliobatis californica</i>
surf smelt	Osmeridae	<i>Hypomesus pretiosus</i>	0.28
whitebait smelt	Osmeridae	<i>Allosmerus elongatus</i>
smelt, unidentified	Osmeridae	smelt, unidentified
C-O turbot	Pleuronectidae	<i>Pleuronichthys coenosus</i>
starry flounder	Pleuronectidae	<i>Platichthys stellatus</i>
longnose skate	Rajidae	<i>Raja rhina</i>
Chinook salmon, jv	Salmonidae	<i>Oncorhynchus tshawytscha</i>	2.69	3.13	5.04	3.22
Chinook salmon, ad	Salmonidae	<i>Oncorhynchus tshawytscha</i>	0.91
coho salmon	Salmonidae	<i>Oncorhynchus kisutch</i>
steelhead	Salmonidae	<i>Oncorhynchus mykiss</i>
white seabass	Sciaenidae	<i>Atractoscion nobilis</i>
Pacific saury	Scomberesocidae	<i>Cololabis saira</i>	...	60.39
Pacific mackerel	Scombridae	<i>Scomber japonicus</i>
rockfish, unidentified	Scorpaenidae	rockfish, unidentified
squarespot rockfish	Scorpaenidae	<i>Sebastes hopkinsi</i>
shortbelly rockfish	Scorpaenidae	<i>Sebastes jordani</i>
spiny dogfish shark	Squalidae	<i>Squalus acanthias</i>
Pacific butterfish	Stromateidae	<i>Peprilus simillimus</i>	...	1.27	2.02	...
Pacific electric ray	Torpedinidae	<i>Torpedo californica</i>
king-of-the-salmon	Trachipteridae	<i>Trachipterus altivelis</i>
flatfish, unidentified		flatfish, unidentified

2002		2003		2004		2005		NC		
Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall	Haul avg.	% Total	% F.O.
...	0.03	0.00	0.00	0.8
...	0.25	0.29	...	0.27	...	0.11	0.07	10.7
...	4.25	0.55	0.36	3.1
...	0.21	...	1.78	266.53	27.08	63.02	65.62	59.21	39.16	48.1
...	0.04	0.05	...	0.01	0.01	1.5
...	0.27	0.02	0.02	0.8
...	8.78	1.61	1.18	...	1.61	1.07	15.3
...	0.04	0.06	0.03	0.02	3.1
0.92	4.76	...	4.33	0.11	1.62	...	0.29	1.59	1.05	29.8
...	1.23	...	5.26	0.17	4.93	1.75	1.16	21.4
...	1.70	0.08	...	1.88	0.04	322.59	0.09	59.51	39.36	18.3
...	0.05	0.01	0.00	0.8
...	0.29	0.11	7.00	0.08	62.27	9.27	6.13	16.0
...	2.45	0.15	...	0.17	1.77	0.52	0.35	12.2
14.69	...	0.14	...	0.04	0.69	0.46	3.8
0.43	0.04	...	0.03	...	0.03	0.02	2.3
...	0.97	0.13	0.15	0.10	8.4
...	0.04	0.05	...	0.04	0.02	0.01	2.3
...	4.64	22.95	0.07	...	0.05	3.40	2.25	6.1
...	0.05	...	0.01	0.01	0.8
...	0.05	...	0.01	0.01	0.8
...	0.03	0.01	0.00	0.8
...	0.05	...	0.01	0.01	0.8
...	0.04	0.01	0.00	0.8
...	5.88	3.38	0.92	25.93	1.90	14.37	3.56	7.93	5.24	60.3
...	0.09	0.94	...	4.37	0.07	2.07	1.15	1.23	0.82	33.6
...	...	0.23	0.37	...	0.09	0.06	4.6
...	0.16	...	0.09	...	0.04	0.02	3.8
...	0.05	...	0.01	0.01	0.8
...	13.51	...	1.36	0.15	0.28	2.54	1.68	7.6
...	0.09	0.01	0.01	1.5
6.81	0.06	0.05	0.32	0.21	4.6
...	0.03	...	0.01	0.00	0.8
...	0.03	0.01	0.00	0.8
...	0.36	...	0.07	0.04	0.8
0.22	1.60	0.27	0.18	6.9
...	0.10	...	0.02	0.01	1.5
...	...	0.08	0.01	0.00	0.8
...	0.54	...	0.41	0.03	0.09	0.10	0.07	3.8

continued

Appendix 1 (continued)

Common name	Family	Species	2000		2001	
			Summer	Fall	Summer	Fall
Gulf of the Farallones (GF)						
thresher shark	Alopiidae	<i>Alopias vulpinus</i>
wolf-eel	Anarhichadidae	<i>Anarhichthys ocellatus</i>	0.50	...
jacksmelt	Atherinidae	<i>Atherinopsis californiensis</i>	...	0.54	23.86	4.66
California grunion	Atherinidae	<i>Leuresthes tenuis</i>	1.24
plainfin midshipman	Batrachoididae	<i>Porichthys notatus</i>
Pacific sanddab	Bothidae	<i>Citharichthys sordidus</i>	0.23
jack mackerel	Carangidae	<i>Trachurus symmetricus</i>
medusafish	Centrolophidae	<i>Icichthys lockingtoni</i>	0.36	5.32	7.61	0.63
Pacific herring	Clupeidae	<i>Clupea pallasii</i>	757.09	3381.56	422.49	38.58
Pacific sardine	Clupeidae	<i>Sardinops sagax</i>	...	0.18	3.46	0.40
American shad	Clupeidae	<i>Alosa sapidissima</i>	0.25
Pac. staghorn sculpin	Cottidae	<i>Leptocottus armatus</i>	0.29
shiner surfperch	Embiotocidae	<i>Cymatogaster aggregata</i>	...	1.14	...	0.29
northern anchovy	Engraulidae	<i>Engraulis mordax</i>	0.91	90.97	...	8.41
Pacific tomcod	Gadidae	<i>Microgadus proximus</i>	4.56	0.88
threespine stickleback	Gasterosteidae	<i>Gasterosteus aculeatus</i>
lingcod	Hexagrammidae	<i>Ophiodon elongatus</i>
ragfish	Icosteidae	<i>Icosteus aenigmaticus</i>
Pacific hake	Merlucciidae	<i>Merluccius productus</i>
ocean sunfish	Molidae	<i>Mola mola</i>	...	0.18
bat ray	Myliobatidae	<i>Myliobatis californica</i>
whitebait smelt	Osmeridae	<i>Allosmerus elongatus</i>	367.78	2.18
smelt, unidentified	Osmeridae	smelt, unidentified	1.44	141.28
surf smelt	Osmeridae	<i>Hypomesus pretiosus</i>
longfin smelt	Osmeridae	<i>Spirinchus thaleichthys</i>	1.59	...	0.16	...
night smelt	Osmeridae	<i>Spirinchus starksi</i>
English sole	Pleuronectidae	<i>Parophrys vetulus</i>
big skate	Rajidae	<i>Raja binoculata</i>	0.58
Chinook salmon jv	Salmonidae	<i>Oncorhynchus tshawytscha</i>	15.71	1.32	5.52	0.84
Chinook salmon ad	Salmonidae	<i>Oncorhynchus tshawytscha</i>	0.29	...	0.52	0.29
white croaker	Sciaenidae	<i>Genyonemus lineatus</i>	13.14	3.47
Pacific saury	Scomberesocidae	<i>Cololabis saira</i>	...	4.17
Pacific mackerel	Scombridae	<i>Scomber japonicus</i>	1.44
rockfish, unidentified	Scorpaenidae	rockfish, unidentified	0.38	...
yellowtail rockfish	Scorpaenidae	<i>Sebastes flavidus</i>
blue rockfish	Scorpaenidae	<i>Sebastes mystinus</i>
California barracuda	Sphyraenidae	<i>Sphyraena argentea</i>
spiny dogfish shark	Squalidae	<i>Squalus acanthias</i>	0.29
Pacific butterfish	Stromateidae	<i>Peprilus simillimus</i>	...	2.15	0.54	0.59
Pacific electric ray	Torpedinidae	<i>Torpedo californica</i>	0.32	...
flatfish, unidentified		flatfish, unidentified

2002		2003		2004		2005		GF		
Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall	Haul avg.	% Total	% F.O.
...	0.07	0.01	0.00	1.1
0.37	0.35	0.15	0.37	0.20	...	0.31	...	0.21	0.01	13.8
0.42	12.53	4.56	...	1.50	1169.64	380.09	120.75	117.81	4.31	33.3
...	0.07	0.00	1.1
0.12	0.08	0.02	0.00	2.3
...	5.21	0.15	0.38	0.01	3.4
...	0.30	...	4.32	...	0.15	0.34	0.01	5.7
0.38	1.37	...	4.32	1.89	2.92	2.20	0.08	31.0
4884.23	40.74	1162.64	330.65	60.84	...	1311.41	176.41	1215.61	44.48	43.7
4.94	...	151.11	10.15	829.45	28.50	65.38	2.90	98.86	3.62	26.4
2.77	...	0.71	...	0.11	0.41	0.01	6.9
...	0.02	0.00	1.1
...	0.18	0.14	0.01	3.4
1076.73	1.41	0.14	61.39	0.87	1.45	14450.22	1439.88	1219.37	44.62	28.7
0.22	0.35	8.07	2.07	37.82	...	0.19	...	4.94	0.18	25.3
0.84	0.10	0.00	1.1
0.12	...	0.09	0.02	0.00	2.3
...	0.43	0.04	0.00	1.1
3.52	0.41	0.01	1.1
...	0.11	1.01	0.15	0.13	0.00	6.9
...	0.20	0.12	0.03	0.00	3.4
1.05	16.65	214.01	8.70	4.26	...	48.11	1.76	20.7
...	0.46	...	1.45	0.76	...	8.50	0.31	9.2
30.68	0.12	3.53	0.13	3.4
0.22	0.15	0.01	3.4
...	0.25	0.03	0.00	1.1
...	0.09	0.01	0.00	1.1
...	0.04	0.00	1.1
13.56	3.46	8.43	0.75	3.35	0.51	10.65	4.45	5.77	0.21	55.2
2.10	0.67	1.03	0.09	3.42	0.32	5.22	0.21	1.19	0.04	32.2
0.57	1.17	0.04	5.7
...	0.10	0.40	0.01	2.3
...	0.31	0.12	0.00	2.3
...	0.03	0.00	1.1
3.36	0.39	0.01	1.1
1.26	0.14	0.01	1.1
...	0.23	0.02	0.00	1.1
...	0.02	0.00	1.1
1.82	0.12	...	0.84	0.10	...	8.22	14.47	2.00	0.07	20.7
...	...	0.14	0.40	0.28	0.12	0.12	0.00	8.0
...	1.31	0.81	...	0.18	0.01	2.3