DISTRIBUTION OF PELAGIC JUVENILE ROCKFISH (*SEBASTES* SPP.) IN RELATION TO TEMPERATURE AND FRONTS OFF CENTRAL CALIFORNIA

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ABSTRACT

We analyzed a 17-year time series of midwater trawl data examining the relationship between pelagic juvenile rockfish (*Sebastes* spp.) catches and temperature and temperature fronts (gradients) along two cross-shelf transect lines off Davenport (36°59.0'N) and Pescadero (37°16.5'N), California. Hydrographic conditions and catches varied substantially from year to year, with general coherence observed between the two lines. However, there was greater variability in temperature and salinity off Pescadero in most years, while gradient intensity differed between the two lines in several years with no consistency as to which line had the strongest and most frequent fronts. Visual inspection of pelagic juvenile rockfish distribution in relation to kriged temperature at 30 m frequently showed elevated catches associated with fronts. Using linear mixed effects models, we found no statistically significant relationship between catch and temperature gradients, although the relationship between gradient strength and catch was universally positive. By excluding anomalous El Niño years, this trend was strengthened, with the combined data set showing a significant positive effect of maximum temperature gradient on catch. We consistently observed the strongest gradients at intermediate temperatures of 10–12°C, coincident with more frequent occurrences of pelagic juvenile rockfish, suggesting that fronts can influence distribution.

INTRODUCTION

The spatial distribution of larval and juvenile fishes has been linked to hydrographic structure, especially fronts between dissimilar water masses, in several oceanographic settings (Grimes and Finucane 1991; Kingsford et al. 1991; Lochmann et al. 1997). Previous studies off central California have presented detailed examination and quantitative description of distributions of rockfish (*Sebastes* spp.) early life history stages (larvae through pelagic juveniles) in the context of hydrographic structure off central California and provide compelling evidence that distributions of larvae and juveniles are affected by features such as upwelling fronts (e.g., Larson et al. 1994; Sakuma and Ralston 1995; Wing et al. 1998; Bjorkstedt et al. 2002; Sadrozinski 2008; Woodson et al. 2013). Moreover, correlations between spatial patterns in rockfish settlement to shallow nearshore habitats and the occurrence of fronts near the coast suggest that frontal structures play an important role in the transport during rockfish early life history (Woodson et al. 2012).

Understanding how hydrographic structure influences distributions of larval and juvenile fishes can also have practical benefits, particularly with respect to the design of surveys and interpretation of their results. Since 1983, the Fisheries Ecology Division (FED) of the Southwest Fisheries Science Center (SWFSC), National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA) has conducted a midwater trawl survey off central California to enumerate pelagic juvenile rockfish and assess the general state of the ecosystem. Recruitment indices based on the abundance and size (age) of pelagic juvenile rockfish have been used to investigate factors that determine year-class strength in economically important rockfish stocks and have been incorporated as data in assessments for several species (Field et al. 2010; PFMC 2008; Ralston et al. 2013). A key consideration in the use of any survey data is how well the survey represents the state of the populations being studied. Comparisons to estimates of recruitment strength derived from catch histories and the dynamic age structure of the adult stock suggest that indices based on age-standardized pelagic juvenile rockfish abundance perform reasonably well and are useful for capturing recruitment variability well in advance of estimates available through conventional stock assessment methods (Field and Ralston 2005; Ralston et al. 2013). One potential source of uncertainty is whether the survey design is sensitive to variability in hydrographic conditions at the time that data are collected, particularly with respect to the general characteristics of water masses in the survey region and how pelagic juvenile rockfish are distributed in relation to hydrographic structures such as fronts.

Discerning general patterns in how water mass characteristics and upwelling fronts influence distributions of pelagic juvenile rockfish, particularly in the context of the annual midwater trawl survey, is complicated by the highly dynamic nature of the coastal ocean off central California. This region tends to experience weak and highly variable upwelling (and storm-driven downwelling) during the winter months and more sustained, albeit fluctuating, upwelling during the spring and summer; the "spring transition" between these two general patterns (and the corresponding ecosystem response) varies in timing from year to year, but typically occurs between late March and late April (Parrish et al. 1981; Schwing et al. 1991). Upwelling fronts form between warmer, fresher oceanic water and colder, saltier water that upwells along the coast in response to wind-driven cross-shelf advection. Off central California, these fronts are most commonly generated at discrete upwelling centers anchored by headlands, but more develop through the spring and summer upwelling season as the cumulative effects of upwelling and relaxation events build up and influence coastal waters (Castelao et al. 2006; Largier et al. 2006).

Many of the rockfish species encountered in the midwater trawl survey (including some of the most abundant species, which have the greatest economic value) release their larvae into the plankton during the winter yet settle to nearshore demersal habitats as large, well-developed juveniles in the late spring and early summer months. Year-class strength appears to be determined in these stocks during the larval period (i.e., by oceanographic conditions during the winter and early spring) (Ralston and Howard 1995; Laidig et al. 2007; Ralston et al. 2013). For those species of rockfish that release their larvae into the plankton during the winter and early spring (i.e., when upwelling off central California is weaker and highly variable) there is limited evidence that larval rockfish can encounter and be influenced by upwelling fronts during winter months (Sadrozinski 2008), but it remains unclear whether associations with hydrographic features are established early in life or emerge later, after the onset of more sustained upwelling and the development of robust frontal systems. Two studies that identified close associations between fronts and rockfish early life history stages were focused on rockfish that exhibit a spring–summer reproductive strategy (Bjorkstedt et al. 2002; Woodson et al. 2012).

In this study, we analyze a 17-year time series of pelagic juvenile rockfish catches and concurrent hydrographic observations to assess patterns in distribution in relation to the state of the coastal ocean, using temperature and temperature fronts (gradients) as our primary indicators of hydrographic structure. We focus our analysis on observations made along two cross-shelf transects that have been consistently sampled each year: the Davenport line (36°59.0'N) and the Pescadero line (37°16.5'N) (fig. 1). These transects lie in a dynamic region influenced by the Point Año Nuevo upwelling center and the southern extent of the Point Reyes upwelling plume. Other key hydrographic features include the San Francisco Bay plume (which includes outflow from San Francisco Bay and oceanic waters trapped inshore of the Point Reyes upwelling plume) (Schwing et al. 1991; Sakuma et al. 1995; Wing et al. 1998) and occasional intrusions of oceanic water from offshore or warmer water from the northern part of Monterey Bay (i.e., from the upwelling shadow in the lee of the Point Año Nuevo upwelling plume) (Graham and Largier 1997; Woodson et al. 2009). The study spans a period (1987–2003) of dynamic variability in climate and environmental forcing, including two El Niño events (1992–93 and 1997–98 [Hayward 1993; Lynn et al. 1998]), a strong La Niña event (1999 [Hayward et al. 1999]), and an anomalous freshening event that originated in the subarctic and broadly affected the California Current in conjunction with a weak El Niño in 2002 (Venrick et al. 2003; Peterson et al. 2006; Ralston et al. 2013).

METHODS

Midwater trawl survey

Pelagic juvenile rockfish were collected during midwater trawl surveys conducted aboard the NOAA RV *David Starr Jordan* off central California (36°30'–38°20'N) from 1983 to 2003. While the survey area expanded to the U.S. Mexico border and just south of Punta Gorda (32°45'–40°00'N) from 2004 to the present (Sakuma et al. 2006; Ralston et al. 2013), we restricted our analysis to surveys conducted from early May through mid-June of 1987 to 2003, a period during which (a) surveys included three replicate quasi-synoptic "sweeps" off a grid of fixed stations off central California (fig. 1); and (b) the sampling protocols included collection of synoptic hydrographic data (conductivity, temperature, and depth [CTD] data, see below). Inclement weather or other logistical constraints occasionally disrupted sequential occupation of CTD and CTD-trawl stations, but every effort was made to preserve quasi-synoptic observations during each sweep.

Pelagic juvenile rockfish sampling

Samples were collected at night (typically 2100–0600 PDT) using a modified Cobb midwater trawl with a 26 m headrope and 9.5 mm mesh cod end and theoretical mouth opening of 12 m x 12 m, which was fished for 15 minutes at a target headrope depth of 30 m except at shallow water stations (<60 m) where the target headrope depth was 10 m (Wyllie-Echeverria et al. 1990; Sakuma et al. 2006; Ralston et al. 2013). For this analysis,

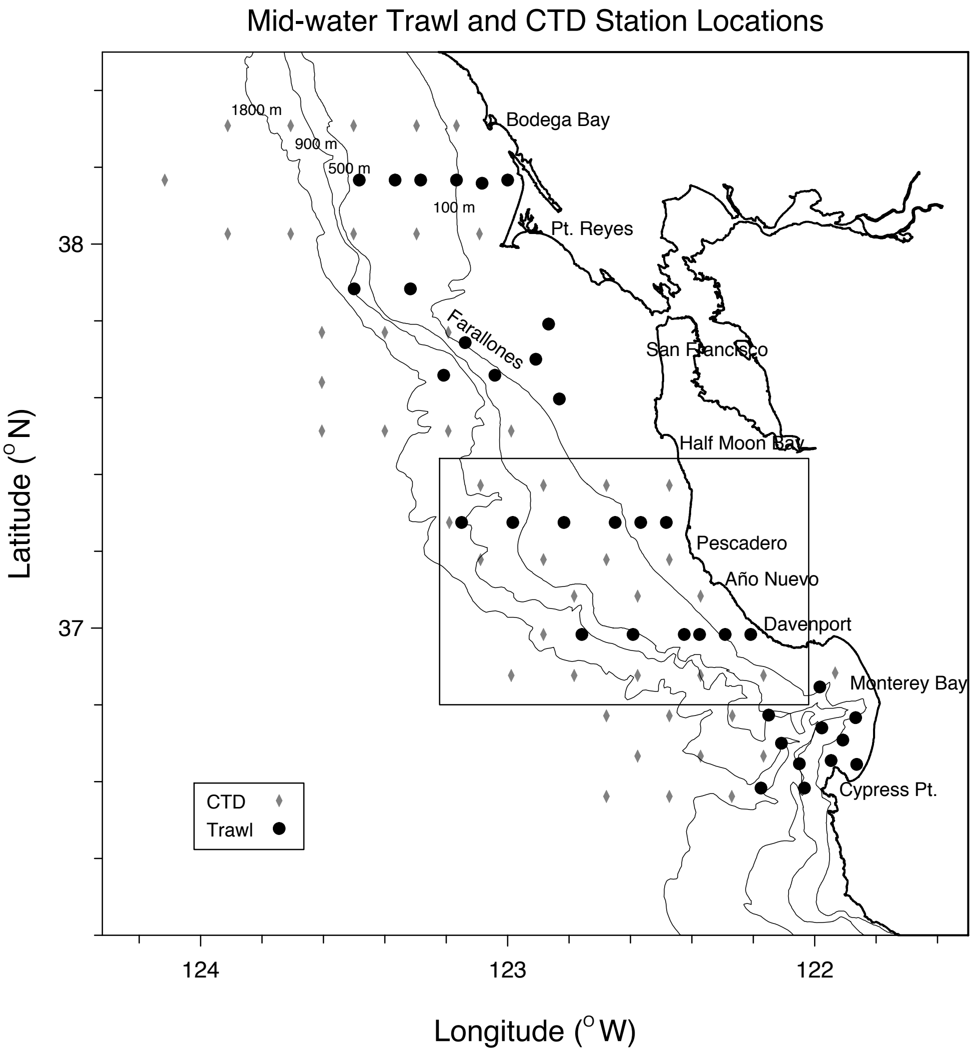

Figure 1. Midwater trawl and CTD station locations off central California. Observations from stations along the Davenport and Pescadero lines (within the rectangle) are analyzed in this study.

we restrict the data to stations where the trawl was fished at 30 m and exclude more inshore stations where shallower bathymetry required the net to be fished at 10 m. These shallow nearshore stations were also excluded from analysis because of difficulties in collecting consistent samples due to the frequency of large jellyfish catches that damaged the net or prevented quantitative sampling. All fish and select invertebrates from each trawl were sorted and enumerated at sea. More details on midwater trawl sampling and processing can be found in Ralston et al. 2013.

Hydrographic data

Vertical profiles of temperature, salinity, density, and other water properties were collected with CTD casts to a maximum depth of 500 meters (or within a few meters of the sea floor at stations over the shelf or upper slope). CTD casts were conducted at each trawl station, with additional casts conducted during the day at a series of stations that enveloped the trawl transect. Data from each cast were processed using SeaBird software; details on CTD deployments and data processing can be found in Sakuma et al. 1994.

We estimated spatial fields of temperature at 30 m depth by kriging quasi-synoptic observations collected during each sweep using functions in the 'fields' package in R (version 6.7; Furrer et al. 2012). From these fields, we extracted for each trawl station estimates of hydrographic conditions at 30 m and estimated the magnitude and heading of the strongest thermal gradient (i.e., the maximum increase in temperature over a 2 km line segment centered on each station). From the magnitude and heading of the maximum gradient vector, we calculated zonal (east-west) and meridonal (north-south) components of the gradient vectors. Zonal gradients represented the change in temperature in an east to

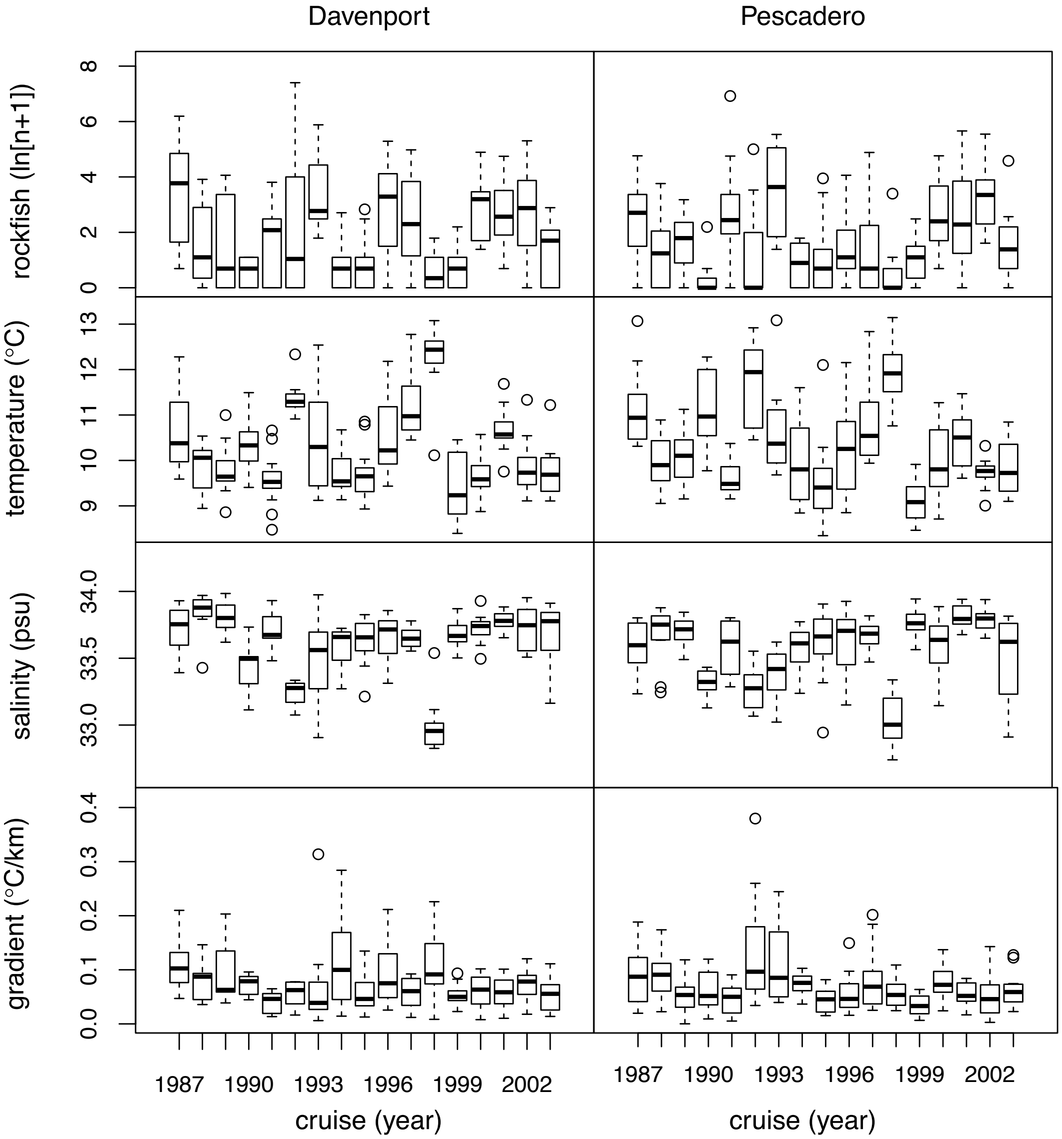

Figure 2. Summary of pelagic juvenile rockfish catch (ln(n+1)) and on-station temperature, salinity, and temperature gradient at 30 m for annual cruises along the Davenport and Pescadero lines. Dark central bars indicate median, box indicates interquartile range (IQR; i.e., 25th to 75th percentile), thin bars at end of lines indicate range of observations within 1.5 IQR of the median, and circles indicate more extreme low or high values.

west direction (e.g., a positive gradient indicated warmer water to the west), and meridional gradients were the change in temperature from north to south (e.g., a positive gradient indicated warmer water to the south). We also kriged temperature fields at 10, 20, and 40 m depth to supplement our interpretation of results from our main analysis, but do not include these in the quantitative analysis presented here.

Analysis

We visually inspected the spatial distribution of pelagic juvenile rockfish catches, scaled as a percentage of the total number captured on a given sweep, overlaid on contour plots of temperature at trawl depths (30 m) to identify cases where distributions suggested association with hydrographic features.

We fit linear mixed effects models (using package 'nlme' [version 3.1-104; Pinheiro et al. 2012] in R 2.15.1 [R Core Team 2012]) to examine relationships between abundance of pelagic juvenile rockfish in each haul, transformed as ln(n + 1), temperature, and temperature gradient. Based on visual inspection of bivariate relationships, fixed effects of temperature and temperature gradients on catch were modeled as, e.g.,

$$\ln(n + 1) \sim T + T^2 + \nabla_T$$

where T is water temperature and ∇_T is maximum gradient (a scalar value) of one of its two vector components (i.e., zonal or meridional gradients). Cruise and sweep (nested within cruise) were treated as random effects within the model. We examined the effects of maximum gradient and its zonal and meridonal components separately by fitting models to the combined data set and independently to data for each line. Preliminary analysis included models with quadratic gradient terms and models with interaction terms, but analysis returned non-significant parameter estimates for these additional terms, so we focus on results from the simpler models.

RESULTS

Hydrographic conditions encountered by the survey varied substantially from year to year, with years affected by the 1992–93 and 1997–98 El Niño events exhibiting expected increases in temperature and decreases in salinity (fig. 2). The abundance of pelagic juvenile rockfish captured along the Davenport and Pescadero lines varied coherently from year to year (fig. 2). Hydrographic conditions also varied more or less coherently, although there appears to be somewhat greater variability in temperature and salinity among stations along the Pescadero line in most years (fig. 2). The intensity of temperature gradients differed between the Davenport and Pescadero lines in several years, yet the line on which fronts were stronger or more commonly encountered was not consistent from year to year (fig. 2).

Over the course of the study period, most stations sampled water between ~9°–11°C and ~33.5–34 psu (figs. 2–3). Under warmer, fresher water conditions, substantial catches of pelagic juvenile rockfish were more common off Davenport than off Pescadero, while under cooler, saltier water conditions catches at Pescadero generally tended to be moderately higher (fig. 3). Catch-weighted mean temperature and salinity for the Davenport line was higher (10.33°C and 33.65 psu) than for the Pescadero line (10.18°C and 33.61 psu), counter to the pattern in mean conditions encountered at the trawl stations (10.20°C and 33.64 psu off Davenport and 10.25°C and 33.57 psu off Pescadero).

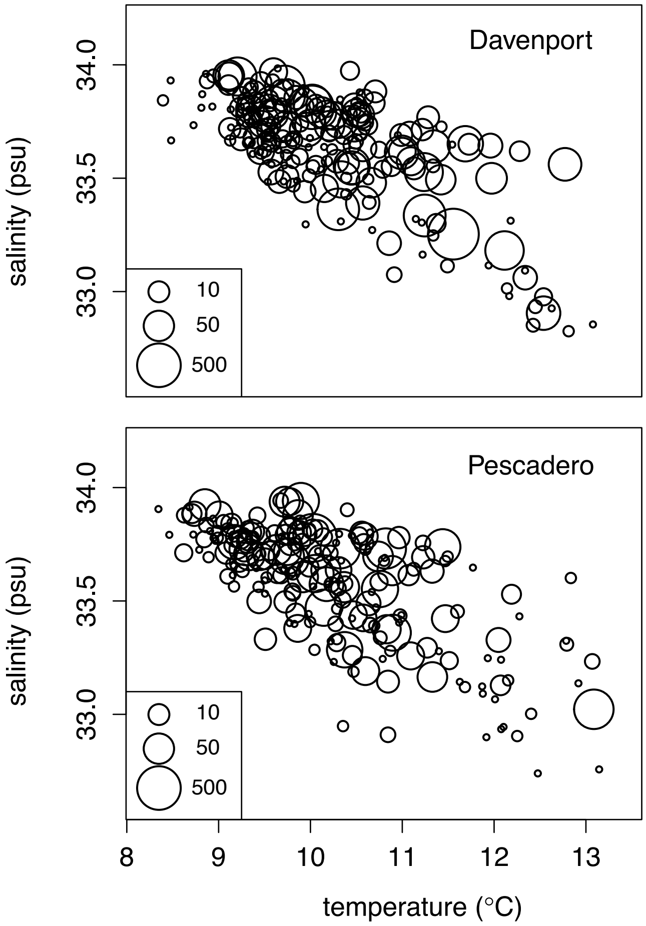

Figure 3. Pelagic juvenile rockfish catch in relation to temperature and salinity at 30 m off Davenport and Pescadero. The size of the circle represents the size of the abundance of pelagic juvenile rockfish.

Visual inspection of the distribution of pelagic juvenile rockfish catches in relation to temperature fields at 30 m depth frequently identified patterns indicating elevated catch densities associated with fronts (fig. 4). On any given sweep, elevated densities of pelagic juvenile rockfish might be observed at fronts that fell into one of three non-exclusive classes: (1) along the Davenport line, rockfish were commonly associated with fronts bounding the southern extent of the upwelling plume anchored at Point Año Nuevo, including the offshore and inshore "corners" of this front (e.g., fig. 4a), (2) along the Pescadero line, rockfish were commonly associated with frontal structure formed by shoaling of isotherms towards the coast, often in connection with upwelled water from the Point Reyes upwelling center (e.g., fig. 4h), and (3) on either or both lines, rockfish could be associated with a more extensive, offshore upwelling front (e.g., fig. 4e for Davenport and fig. 4f for Pescadero). In many cases, such interpretations were corroborated or more strongly supported by examination of thermal structure at shallower depths, although often with some increase in the spatial offset between hydrographic structures and the apparent distributions of juvenile rockfish (data not shown). This appeared to be especially true in years affected by warmer conditions and downwelling, when temperature fields at 30 m depth near the coast were often more homogeneous, yet elevated densities of pelagic juvenile rockfish tended to coincide with weaker and shallower frontal structures consistent with one of the cases identified above (e.g., especially structure associated with upwelling off Point Año Nuevo).

Catches of pelagic juvenile rockfish exhibited a dome-shaped relationship to temperature along the Pescadero line and a non-significant trend towards higher

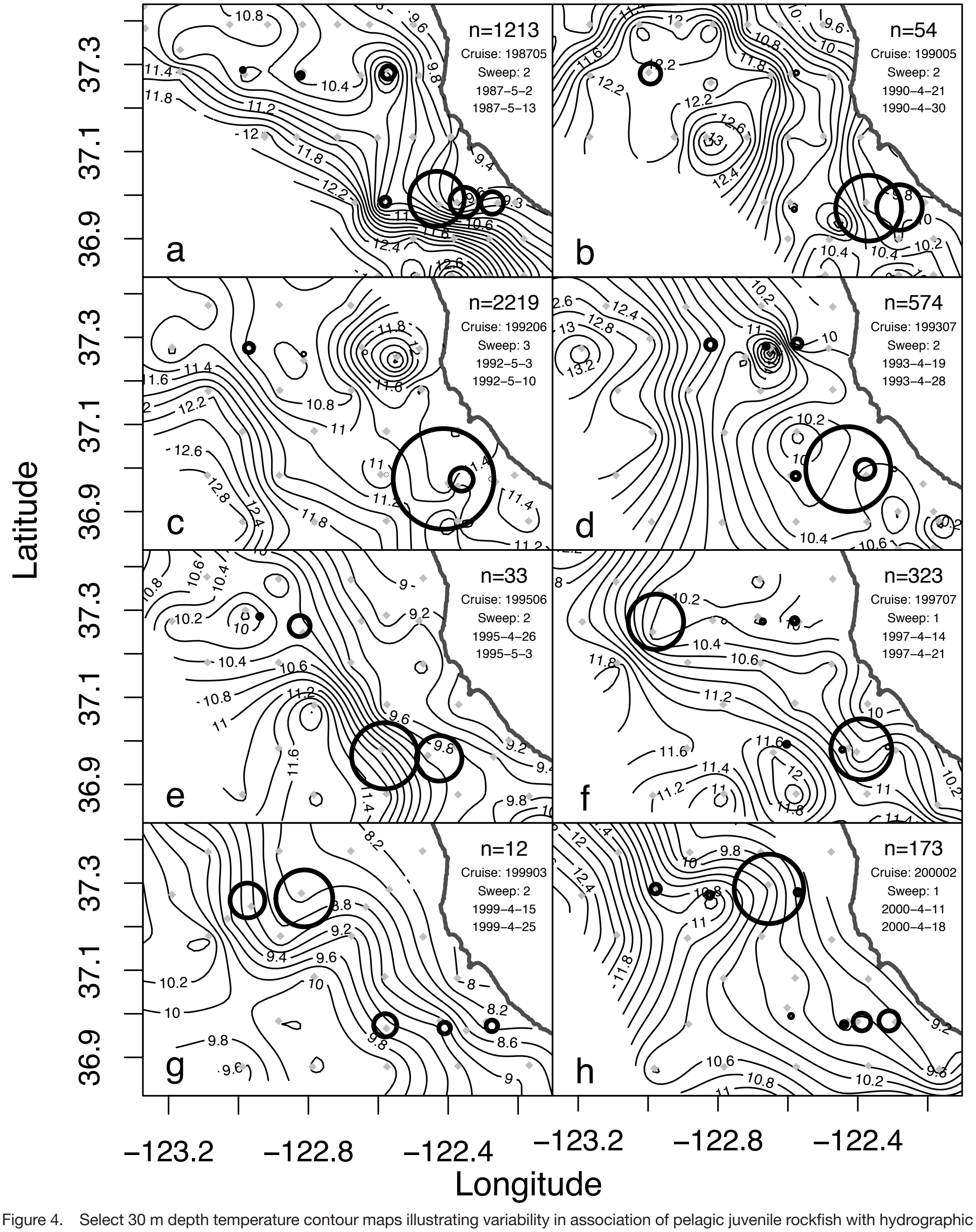

Figure 4. Select 30 m depth temperature contour maps illustrating variability in association of pelagic juvenile rockfish with hydrographic structure. Number in upper right corner of each plot indicates number of pelagic juvenile rockfish captured on the sweep. Also indicated are the cruise, sweep, and the dates over which the entire sweep throughout the core survey area (Monterey Bay to Point Reyes) was conducted. Solid circles indicate catch scaled by the proportion of the sweep's catch at each station. Grey diamonds indicate CTD stations from which data were used in developing the temperature map.

catches at stations with stronger maximum gradients (fig. 5, table 1). Catches along the Davenport line also were not significantly related to either gradient strength or temperature (table 1), but the lack of a relationship to temperature appears, at least in part, to be due to a bimodal distribution in the catch-temperature relationship (figs. 3, 6). Dome-shaped relationships between temperature and catch and non-significant (but positive) trends between gradient and catch were also observed when data were aggregated (using means) within sweeps

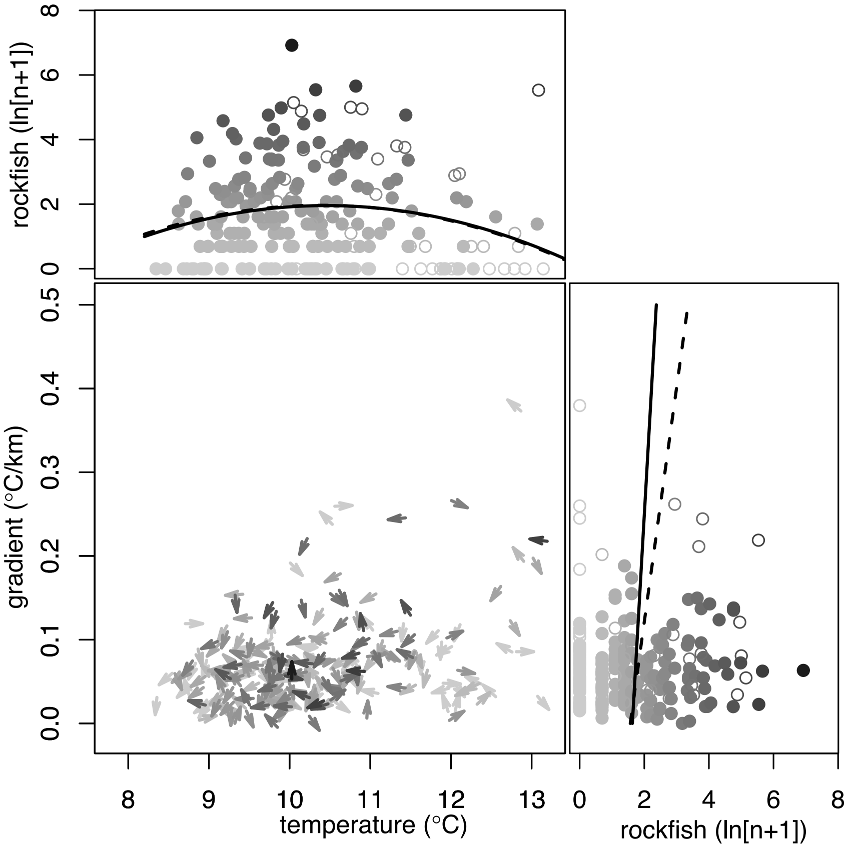

Figure 5. Relationships between pelagic juvenile rockfish catch, temperature, and gradient by station for the Pescadero line. Arrows indicate heading of gradient vector (i.e., direction of increasing temperature). Solid lines indicate model fits to full data set; dashed lines indicate model fits to data excluding "El Niño" years (open symbols). Greyscale shading scales with size of catch.

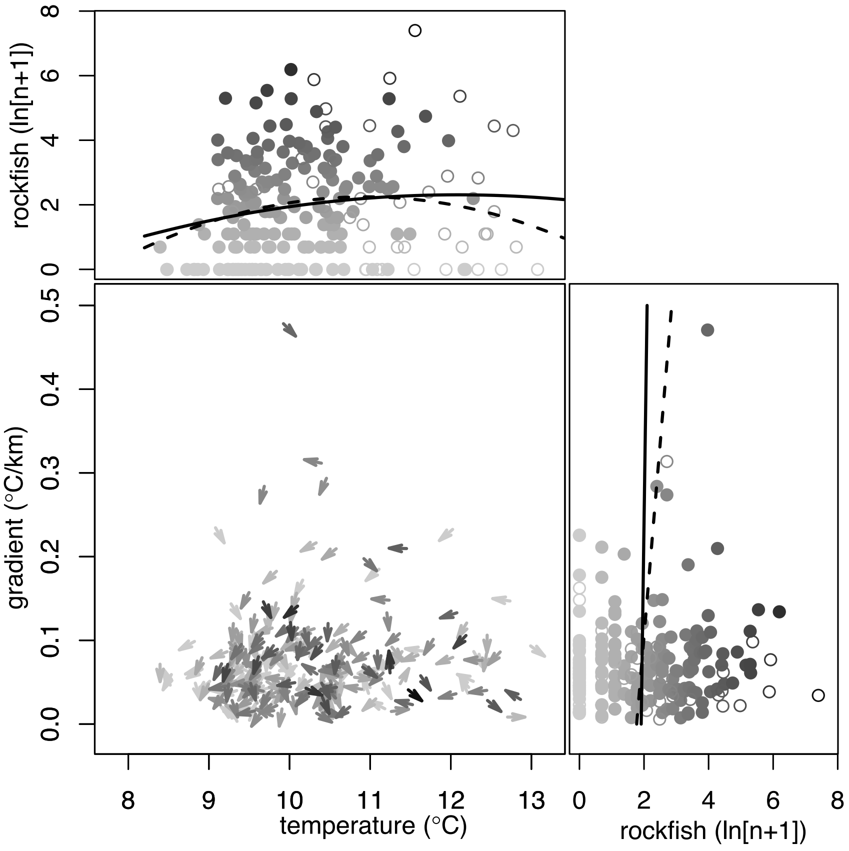

Figure 6. Relationships between pelagic juvenile rockfish catch, temperature, and gradient by station for the Davenport line. Arrows indicate heading of gradient vector (i.e., direction of increasing temperature). Solid lines indicate model fits to full data set; dashed lines indicate model fits to data excluding "El Niño" years (open symbols). Greyscale shading scales with size of catch.

TABLE 1
Linear mixed effects models of the relationships between pelagic juvenile rockfish catch (transformed as ln(n + 1)), temperature, and temperature gradient with cruise and sweep (nested within cruise) treated as random effects. For each gradient variable, upper row gives coefficients from fitted model, and lower row gives p-value associated with that coefficient.

All Years					Cool/non-ENSO				
Both Lines	**Int**	**T**	**T2**	**Gradient**	**Both Lines**	**Int**	**T**	**T2**	**Gradient**
Maximum	–15.389	3.232	–0.150	0.636	Maximum	–20.743	4.291	–0.204	3.191
	0.016	0.007	0.008	0.595		0.012	0.008	0.009	0.031
Zonal	–15.426	3.244	–0.151	0.445	Zonal	–21.178	4.400	–0.208	0.114
	0.160	0.007	0.008	0.679		0.012	0.007	0.008	0.935
Meridional	–15.052	3.166	–0.147	0.879	Meridional	–20.875	4.334	–0.205	1.742
	0.019	0.009	0.009	0.448		0.012	0.007	0.008	0.189
Davenport	**Int**	**T**	**T2**	**Gradient**	**Davenport**	**Int**	**T**	**T2**	**Gradient**
Maximum	–10.098	2.049	–0.085	0.366	Maximum	–23.095	4.604	–0.210	2.170
	0.356	0.324	0.387	0.834		0.122	0.116	0.141	0.243
Zonal	–12.672	2.556	–0.109	2.080	Zonal	–24.455	4.887	–0.223	0.985
	0.245	0.217	0.265	0.204		0.102	0.096	0.119	0.584
Meridional	–9.894	2.000	–0.082	1.308	Meridional	–22.471	4.480	–0.203	1.698
	0.362	0.331	0.397	0.475		0.136	0.130	0.159	0.369
Pescadero	**Int**	**T**	**T2**	**Gradient**	**Pescadero**	**Int**	**T**	**T2**	**Gradient**
Maximum	–18.770	3.944	–0.189	1.483	Maximum	–18.346	3.865	–0.186	3.576
	0.023	0.011	0.009	0.454		0.076	0.054	0.054	0.221
Zonal	–18.307	3.864	–0.184	–1.019	Zonal	–16.612	3.546	–0.170	–1.092
	0.026	0.012	0.010	0.483		0.109	0.077	0.079	0.627
Meridional	–18.118	3.831	–0.183	–0.473	Meridional	–17.252	3.680	–0.176	0.388
	0.027	0.013	0.011	0.776		0.098	0.069	0.071	0.860

or within cruises (figs. 7–8). Considered independently, neither zonal nor meridonal gradients had a significant effect on catch along the Pescadero line, though the trend was towards greater catches at stations where cooler water lay to the south and west, i.e., where fronts lay between upwelled water offshore and warmer waters associated with the San Francisco Bay Plume or poleward intrusions of oceanic water (figs. 4–5). Examination of catches in relation to zonal and meridonal temperature gradients along the Davenport line also yielded statistically non-significant results, with a weak trend for greater catches at stations where cooler water lay to the north and east, i.e., in a configuration consistent with upwelling extending from the Point Año Nuevo upwelling center (figs. 4, 6).

We repeated the station-level analysis for a data set that excluded years dominated by warmer temperatures related to strong El Niño events (1992, 1993, 1997, and 1998). In this analysis, catches of pelagic juvenile rockfish along the Davenport line exhibited a dome-shaped relationship to temperature (fig. 6) analogous to that observed along the Pescadero line (fig. 5), albeit with a somewhat higher range of temperatures. For both Davenport and Pescadero, the relationship between catch of pelagic juvenile rockfish and maximum temperature gradient strengthened yet remained non-significant (table 1). However, when the combined data set was considered, maximum temperature gradient was found to have a significant, positive effect on catch of pelagic juvenile rockfish (table 1). General trends between catch and temperature gradients remained the same for the Davenport line in the reduced data set, but the pattern for Pescadero switched to a (non-significant) tendency for catches to be larger at stations where cooler water lay to the north and west during non-El Niño years, i.e., at fronts affected by the southern, inshore end of the upwelling plume extending south from Point Reyes (figs. 4–6, table 1).

On any given cruise, much of the region surrounding the Davenport and Pescadero lines was marked by relatively weak horizontal temperature gradients, but the strongest gradients were most commonly and consistently observed in association with water between 10°C and 12°C (fig. 9). This pattern was also observed at shallower and deeper layers, with modest shifts in temperature related to depth (data not shown).

DISCUSSION

Our analysis of 17 years of midwater trawl survey data revealed several trends consistent with the hypothesis that pelagic juvenile rockfish are associated with hydrographic fronts. The relationship between gradient strength and catches of pelagic juvenile rockfish was universally positive (although typically not statistically significant) and was strengthened when the analysis excluded El Niño years. Moreover, the relationships

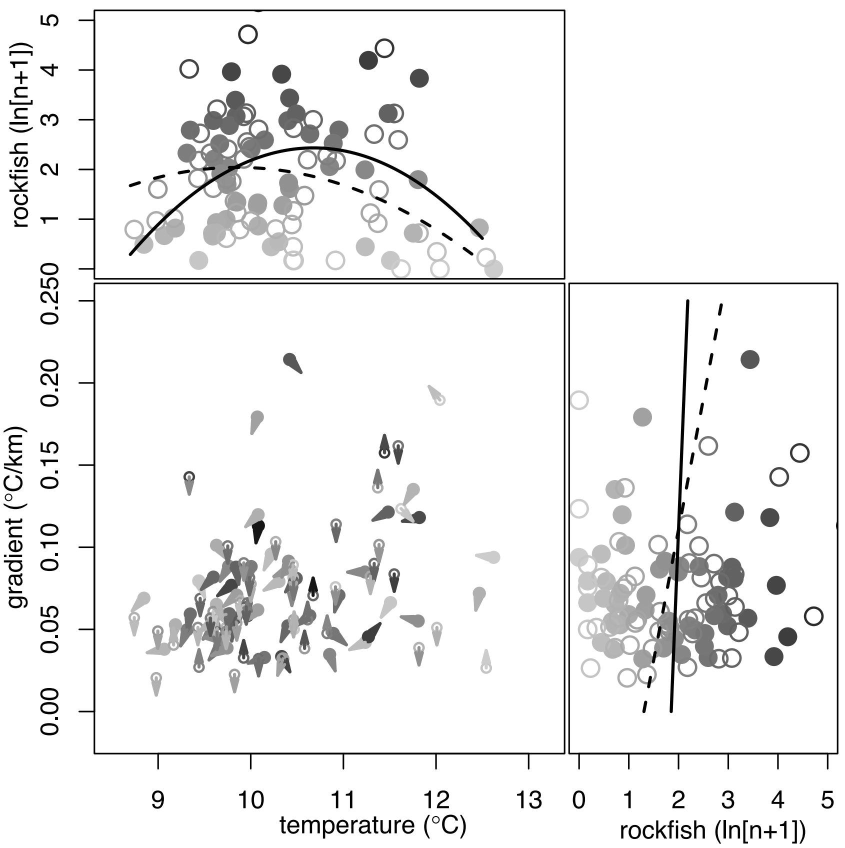

Figure 7. Relationships between pelagic juvenile rockfish catch, temperature, and gradient averaged by sweep. Solid symbols and lines indicate observations and model fits along the Davenport line, open symbols and dashed lines indicate results for the Pescadero line. Arrows indicate heading of gradient vector (i.e., direction of increasing temperature). Greyscale shading scales with size of mean catch.

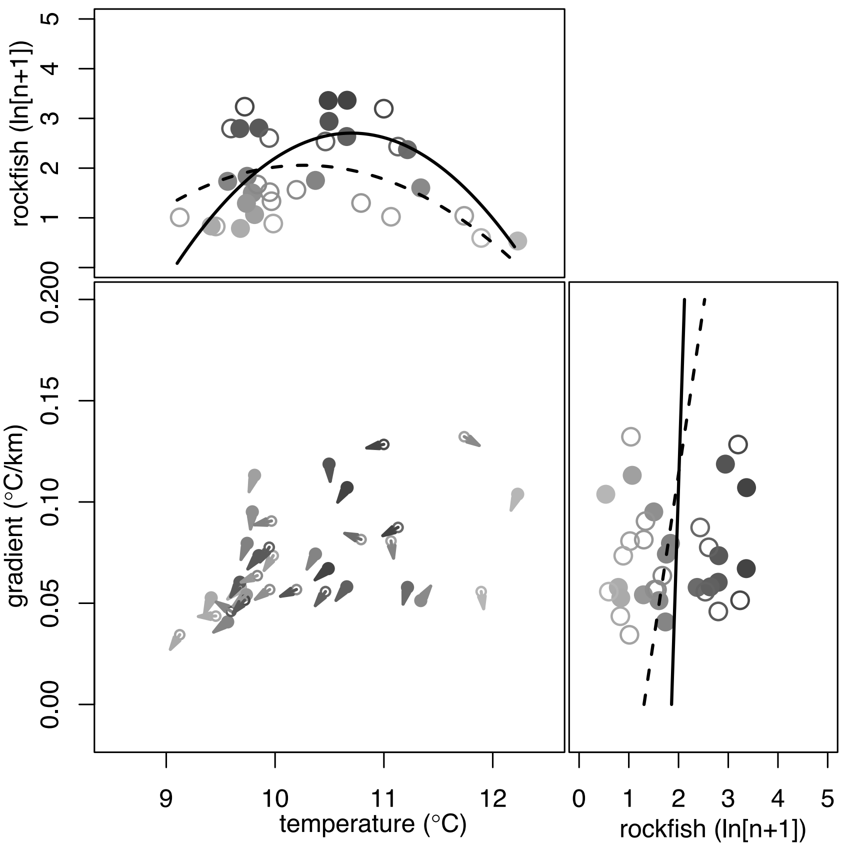

Figure 8. Relationships between pelagic juvenile rockfish catch, temperature, and gradient averaged by cruise. Solid symbols and lines indicate observations and model fits along the Davenport line, open symbols and dashed lines indicate results for the Pescadero line. Arrows indicate heading of gradient vector (i.e., direction of increasing temperature). Greyscale shading scales with size of mean catch.

between gradient heading (or the vector-valued zonal and meridional measures of thermal gradients) and catches of pelagic juvenile rockfish observed on each line is consistent with the dominant oceanographic structure typical of the region. This includes classical upwelling fronts with onshore-offshore structure or those bounding the southern and inshore extent of the upwelling plume advected from Point Año Nuevo and Point Reyes and "reverse" fronts between warmer water trapped inshore of upwelling plumes (e.g., warmer water from northern Monterey Bay trapped in the shadow of the Point Año Nuevo upwelling plume; Graham and Largier 1997) or advected poleward during relaxation events (e.g., Send et al. 1987; Wing et al. 1995). Further corroboration of these trends comes from visual inspection of catches overlaid on temperature fields, which indicates that pelagic juvenile rockfish are often more abundant at temperature fronts within the study area off central California (fig. 4).

We found that pelagic juvenile rockfish tend to be more frequently encountered in waters of intermediate temperature (i.e., around 10°C to 12°C at 30 m depth; figs. 5 and 6), which offers some circumstantial evidence that hydrographic fronts influence distribution off central California. These intermediate temperatures correspond to those typically observed in the thermocline in this region and thus are expected to be associated with fronts that form when the thermocline shoals in response to upwelling (Schwing et al. 1991; Sakuma et al. 1994 and 1995). Observed salinities also corroborate this interpretation (fig. 3). Moreover, the strongest temperature gradients observed in the study region consistently coincided with water in this temperature range (fig. 9). Together, these observations suggest that pelagic juvenile rockfish are commonly found in water masses linked to fronts, even when they are not in an area where the local horizontal gradients are particularly sharp. This conclusion is consistent with the results of simple visual inspection of catch distribution relative to the temperature field on almost any given sweep.

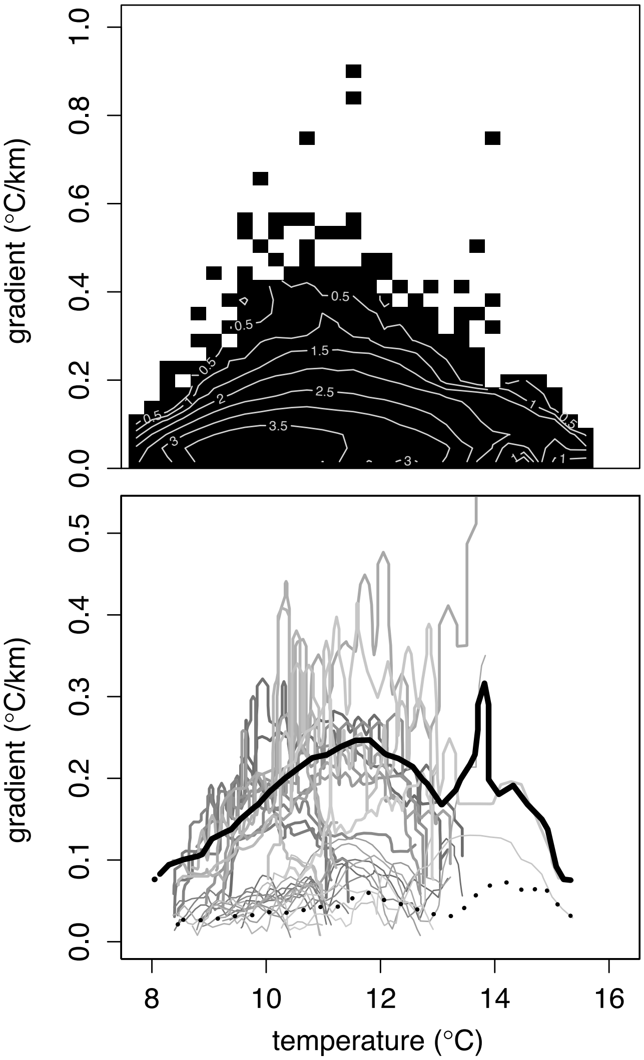

Figure 9. Upper panel: distribution of gradient strength as a function of temperature at 30 m for all cruises and sweeps. Dark areas indicate occurrence of particular (binned) combinations of temperature and gradient; grey contours indicate number of observations of each combination (in thousands). Lower panel: 99.5th (thick black line) and 50th (thick dashed line) percentile gradient strength v. temperature at 30 m. Cruise-specific 99.5th (thick grey lines) and 50th (thin grey lines) percentiles illustrate consistency of stronger gradients associated with intermediate temperatures for most cruises.

In some respects, the fact that we detected any pattern is somewhat surprising. The survey was not designed to target hydrographic features in this dynamic region, so opportunities to sample across hydrographic fronts were serendipitous and only recognized after the fact. Even when trawls occurred in the vicinity of fronts, the orientation of transects sometimes limited the potential for contrast in the data (e.g., due to stations falling along a front rather than spanning a front from one side to the other). Moreover, although each repeated sweep provides some opportunity for a quasi-synoptic view of this region, the observed distributions of pelagic juvenile rockfish relative to their hydrographic setting remain snapshots of a dynamic process contingent on the recent (and not so recent) history of the system. Otolith microchemistry studies by Woodson et al. 2013 showed that over a temporal period of five days, upwelling associated pelagic juvenile rockfish could in some instances traverse distances of up to 50–100 km. Furthermore, the age, extent, and spatial continuity of a front may matter as much or more than the strength of the gradient that defines the front in determining how it influences the distribution of pelagic juvenile rockfish and other elements of the coastal ecosystem. Indeed, it is possible that localized effects of fronts on distributions of pelagic juvenile rockfish may persist even as fronts weaken, or, especially in the case of larger juveniles, fish may not be advected offshore with fronts during active upwelling (cf. Larson et al. 1994), thus breaking any association with hydrographic structure that may have previously existed.

Our analysis provides insights to how pelagic juvenile rockfish are distributed with respect to hydrographic structure, but does little to explain absolute variability in abundance. Indeed, the analysis assigned a very small amount of variability in the abundance of pelagic juvenile rockfish to the fixed effects of temperature and temperature gradient, with much of the variability instead being attributed to the random effects of cruise (year) and sweep within cruise or remaining unexplained. This is entirely consistent with the hypothesis that large fluctuations in abundance reflect variability in recruitment success and supports previous reports linking the bulk of variability in abundance of pelagic juvenile rockfish to conditions that affect larval stages in the winter and early spring rather than conditions coincident with the midwater trawl survey (e.g., Ralston and Howard 1995; Laidig et al. 2007; Ralston et al. 2013). Unexplained variability is likely due to patchiness in the distribution of pelagic juvenile rockfish, changes in the structure of the coastal ocean, changes in response to variable wind forcing, and ontogenetic changes in how juveniles utilize pelagic habitats over the course of successive sweeps (e.g., changes in whether and how individuals maintain cross-shelf position, or attrition from the pelagic environment through settlement; Larson et al. 1994).

We recognize that our operational definition of a front (horizontal gradients in temperature at trawl depth) also constrains our ability to detect fish-front associations quantitatively. In several cases, catches of pelagic juvenile rockfish appear to be associated with shallow fronts that have weak signatures at depth. In some of these cases the apparent distribution of pelagic juvenile rockfish appears to be closely co-located with shallower fronts, while in others, their distribution appears to be slightly offset from the shallower hydrographic structure. This pattern is consistent with theoretical and empirical evidence that plankton associated with fronts are often located some distance away from the near-surface signature of the front (Franks 1992). Such interpretations must be made cautiously, however, given the limitations of our station-based sampling for resolving the spatial distribution of pelagic juvenile rockfish.

Notwithstanding these caveats, we believe that the trends that emerge from our analysis are informative and warrant further investigation of associations between spatial distributions of pelagic juvenile rockfish and hydrographic fronts. A greater understanding of these relationships offers the potential to improve the utility of the pre-recruit indices derived from the survey results. For example, the 1999 year class was exceptionally strong for many rockfish stocks, yet few pelagic juveniles were captured during that year's survey. However, the survey that year encountered universally cold water—the trawls fished waters colder than the lower range of the "optimal" temperature range identified here. This raises the possibility that pelagic juvenile rockfish were not as available to the survey in 1999 as in other years, although it is not clear whether this was because they were offshore of the survey area, in slightly warmer waters shallower than the target trawl depth, or had already settled out (perhaps assisted by onshore flow at depth associated with the strong upwelling that occurred during 1999).

Understanding fish-front associations also has implications for improving our ability to link recruitment success to environmental and climate variability. Recruitment success of commercial groundfish species has been shown to be related to variability in the timing of spring transition (Holt and Mantua 2009) as well as sea level anomalies during/after the spawning season (Ralston et al. 2013). Results from this and previous studies suggest that association with hydrographic fronts may occur throughout rockfish early life history stages (Bjorkstedt et al. 2002; Sadrozinski 2008), although factors that affect the establishment and continuity of such associations and their ecological consequences for growth and survival require further investigation. In this regard, observations of unusually high catches of pelagic juvenile rockfish at fronts during warm, El Niño years (e.g., 1992) suggests that such years may provide a useful contrast to more productive years for evaluating the ecological consequences of fronts for rockfish early life history stages. Indeed, it may be that what fronts are formed in such years play a stronger role in selecting individuals who survive. For example, greater productivity and reduced temperatures in frontal regions may yield a more favorable energetic balance or starker variability in the distribution of prey and may promote aggregation (i.e., limit the likelihood that individuals' foraging behaviors will lead them away from fronts). In any case, understanding how fronts affect the ecology of larval and juvenile rockfish during unproductive years is likely to yield insights into how fronts influence recruitment more generally.

Looking forward, we are developing methods to quantify three-dimensional frontal structure and how pelagic juvenile rockfish associate with these structures. Analyses based on results from realistic ocean circulation models (e.g., Petersen et al. 2010) may also prove informative in teasing out mechanisms that influence fish-front associations and the implications of variable forcing and our ability to observe these dynamics, as well as the implications of variable forcing on distribution of pelagic juvenile rockfish relative to the survey region. Ideally, statistical and modeling analysis of data sets such as the one considered here will be complemented by process-oriented field studies intensively sampling hydrographic features to resolve the distribution of pelagic juvenile rockfish relative to frontal structures (e.g., Sakuma and Ralston, unpublished data; Bjorkstedt et al. 2002) and how rockfish early life history stages are exposed to upwelling processes in general (e.g., Woodson et al. 2013). Such analyses will need to account for how catches (and front strength) vary relative to the regional environment and at more local scales (e.g., account for whether a front is a locally strong feature, even if stronger fronts exist elsewhere at the same time) and will lay the foundation for investigating how swimming and other behaviors affect the distribution of larval and juvenile rockfish during periods when year-class strength and settlement patterns are determined.

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