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Long-term variation in a central California pelagic forage assemblage

Stephen Ralston *, John C. Field, Keith M. Sakuma

Fisheries Ecology Division, Southwest Fisheries Science Center, NOAA Fisheries, 110 Shaffer Road, Santa Cruz, CA 95060, United States

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ABSTRACT

A continuous 23 year midwater trawl survey (1990–2012) of the epipelagic forage assemblage off the coast of central California (lat. 36°30′–38°20′ N) is described and analyzed. Twenty taxa occurred in ≥10% of the 2037 trawls that were completed at 40 distinct station locations. The dominant taxa sampled by the 9.5 mm mesh net included a suite of young-of-the-year (YOY) groundfish, including rockfish (*Sebastes* spp.) and Pacific hake (*Merluccius productus*), two clupeoids (*Engraulis mordax* and *Sardinops sagax*), krill (Euphausiacea), cephalopods (*Doryteuthis opalescens* and *Octopus* sp.), and a variety of mesopelagic species, i.e., *Diaphus theta*, *Tarltonbeania crenularis*, "other" lanternfish (Myctophidae), deep-sea smelts (Bathylagidae), and sergestid shrimp. Annual abundance estimates of the 20 taxa were obtained from analysis of variance models, which included year and station as main effects. Principal components analysis of the abundance estimates revealed that 61% of assemblage variance was explained by the first three components. The first component revealed a strong contrast in the abundance of: (a) YOY groundfish, market squid (*D. opalescens*), and krill with (b) mesopelagics and clupeoids; the second component was associated with long-term trends in abundance. An evaluation of 10 different published oceanographic data sets and CTD data collected during the survey indicated that seawater properties encountered each year were significantly correlated with abundance patterns, as were annual sea-level anomalies obtained from an analysis of AVISO satellite information. A comparison of our findings with several other recent studies of biological communities occurring in the California Current revealed a consistent structuring of forage assemblages, which we conjecture is primarily attributable to large-scale advection patterns in the California Current ecosystem.

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1. Introduction

The Fisheries Ecology Division of the Southwest Fisheries Science Center (SWFSC), National Marine Fisheries Service (NMFS), has conducted a midwater trawl survey off of central California every year since 1983, with a focus on quantifying the abundance of young-of-the-year (YOY) rockfish (*Sebastes* spp.), Pacific hake (*Merluccius productus*), and other groundfish stocks. The principal objective of the survey has been to develop indices of pre-recruit abundance for use in groundfish stock assessments, as well as to improve our understanding of the physical and biological processes that lead to variation in year-class strength. More recently the survey has also been used to describe and understand spatial and temporal variability in the broader micronekton assemblage that is vulnerable to capture by midwater trawling, particularly with respect to the role that YOY groundfish play in a broadly defined forage assemblage that supports the production of higher trophic level fishes, seabirds, and marine mammals.

The California Current ecosystem has long been known to exhibit high- and low-frequency variability in physical forcing as the basis of primary and secondary planktonic production (Checkley and Barth, 2009; Chelton et al., 1982; Hickey, 1998; Mackas et al., 2001). However, variability in micronekton abundance has been less well understood until recently. Both high- and low-frequency variability in the abundance, productivity, and distribution of this assemblage have been previously inferred by virtue of work on coastal pelagic species abundance and productivity (Baumgartner et al., 1992; MacCall, 1996; Schwartzlose et al., 1999), rockfish YOY abundance (Ralston and Howard, 1995; Ralston et al., 2013), and seabird diets (Mills et al., 2007; Sydeman et al., 2001). More recently, it has also been shown that a broad community assemblage, dominated in large part by mesopelagic fishes, also varies over high- and low-frequencies throughout the southern California Bight, based on a 60 year time series of ichthyoplankton data (Koslow et al., 2013a,b). In this study, we focus on a micronektonic forage assemblage over a small, but important, geographical area using a 23 year time series of survey abundances and evaluate the physical forcing mechanisms that appear to be linked to observed variability in this community.

The micronekton assemblage sampled by this survey includes a suite of YOY groundfish, pelagic invertebrates, coastal pelagic fishes,

* Corresponding author. Tel.: +1 831 420 3949; fax: +1 831 420 3977.
E-mail address: sralston10@gmail.com (S. Ralston).

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mesopelagic fishes, and several other fish taxa. Collectively, they represent a very large fraction of the mid-trophic level forage assemblage that is preyed upon by higher trophic level predators in this region, including adult rockfishes (Adams, 1987; Philips, 1964), Chinook salmon (*Oncorhynchus tshawytscha*; Merkel, 1957; Thayer et al., 2014), albacore tuna (*Thunnus alalunga*; Glaser, 2010), as well as a wide range of seabirds (Ainley and Boekelheide, 1990; Mills et al., 2007; Sydeman et al., 2001) and marine mammals (Clapham et al., 1997; Stroud et al., 1981; Weise and Harvey, 2008). As such, this assemblage represents a micronekton "forage" assemblage, or a suite of lower-trophic level species as defined by Smith et al. (2011), as those that are often present in high abundance, forming dense schools or aggregations, and are generally plankton feeders for much of their life cycle. These lower-trophic level species are the principal means of transferring production from primary and secondary trophic levels (e.g., phytoplankton and zooplankton) to piscivorous fishes, marine mammals and seabirds, and thus represent an assemblage of considerable importance in marine ecosystems.

Previous studies have developed spatial climatologies for many of these groups and have quantified their relationships to both fixed (e.g., depth, distance from shore, etc.) and dynamic (e.g., temperature, chlorophyll, stratification, etc.) habitat variables (Santora et al., 2011, 2012). More recent work has evaluated the spatiotemporal dynamics of a subset of the overall assemblage, indicating that the abundance of some components of this assemblage (such as krill and anchovy) appear to be less variable in offshore regions relative to nearshore habitats. In contrast, others (e.g., YOY rockfish and YOY sanddabs) co-vary strongly throughout all regions (Santora et al., in press). However, none of this work has yet examined the temporal dynamics of the broader micronekton assemblage, particularly as related to climate or ocean conditions, which is the focus of our study.

2. Materials and methods

2.1. Sampling procedures

The NMFS SWFSC has conducted an annual midwater trawl survey off central California since 1983. During that time cruises have started as early as April 9th and have ended as late as June 30th, but since 1990 the preponderance of sampling has occurred during the six weeks spanning May through the first half of June. The latitudinal range of the survey within the "core" sampling region spans 200 km from 36°30′ to 38°20′ N (Fig. 1). Survey design is based on occupying an array of fixed station locations, which have been altered somewhat over time to improve and optimize sampling efficiency. Although the survey was expanded in 2004 to encompass most of the State of California (Ralston and Stewart, 2013; Sakuma et al., 2006), for this analysis we only included stations sampled within the core region of the survey, as they have been sampled continuously from 1983 to the present. The majority of those stations are occupied several times each year to account for short-term temporal variation in juvenile rockfish abundance (Ralston et al., 2013).

From its inception the survey has sampled with a standardized modified-Cobb midwater trawl fitted with a 26-m headrope and a 9.5-mm mesh cod-end liner that retains epipelagic micronekton. Based on net mensurations the height and width of the net are 12 m, producing a sampled swath ≈ 144 m^2. The standard target depth for the trawl's headrope is 30 m, based on results that showed pelagic juvenile rockfish are most abundant below the thermocline (Ross and Larson, 2003). However, at a few nearshore stations (<60 m) the net is fished at 10 m to avoid bottom contact. Time–depth recorders and, in recent years, SIMRAD ITI acoustic sensors are attached to the net on all tows to ensure proper gear performance. Due to net avoidance by juvenile rockfish, trawling is only conducted at night. Quantitative samples are obtained by deploying 85 m of trawl warp and adjusting the ship's speed in real time to maintain the headrope at 30 m, which results in a ship speed

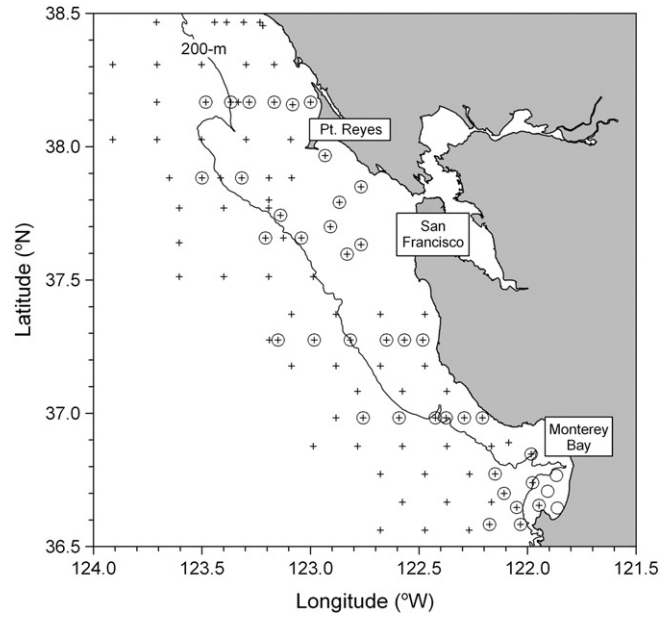

Fig. 1. Map of the core survey area showing station locations where midwater trawling is conducted (circles) and conductivity–temperature–depth (CTD) casts are completed (+).

of ≈2.0 knots (3.7 km h^{-1}). Tows are further standardized by fishing the net for exactly 15 min at the target depth.

Upon completion of a trawl the contents of the cod-end are immediately sorted and all fish, cephalopods, and selected decapod crustaceans identified and enumerated to the lowest possible taxon, given time and efficiency constraints. Several key taxa (e.g., krill) are usually estimated by volumetric expansion from a subsample. Pelagic juvenile rockfish are all identified to species, frozen, and returned to the laboratory for further study (see Ralston et al., 2013). Beginning in 1990 a concerted effort was made to improve and standardize abundance estimates of several important, but previously poorly quantified, taxa (e.g., krill and mesopelagic fishes). Thus, we limit our analysis to data collected from that point forward. A total of 2037 standard midwater trawls were completed within the core study area during the 23 years spanning 1990–2012, which were distributed among 40 different standard stations, with a minimum total occupancy per station of 13 and a maximum of 71 trawls (median N = 60) (Fig. 1).

Beginning in 1987 oceanographic data were collected using a SeaBird conductivity–temperature–depth (CTD) instrument. CTD casts to a maximum depth of 500 m (10 m off the bottom for shallower stations) are conducted at nearly all trawl stations, with additional casts completed during daylight hours throughout the study region (Fig. 1). All CTD data are post-processed following the cruise and are stored in a database (e.g., Baltz et al., 2006).

2.2. Data analysis

Year-specific abundance estimates for each taxon under study were derived by a model-based estimation procedure. In particular, the observed catch of a taxon in a valid standard haul was log-transformed and the haul-specific data were fitted by analysis of variance (ANOVA) to a model that included year and station as main effects, i.e., $\log(CPUE_{ijk} + 1) = Y_i + S_j + \varepsilon_{ijk}$, where $CPUE_{ijk}$ is the catch-per-unit-effort based on the number of individuals taken in a 15-minute tow conducted at standard depth, Y_i is the survey year, S_j is a standard station, and ε_{ijk} is a normal error term. Year effects were calculated from the parameter estimates by averaging over station effects and solving the model for each year (see LSMEAN option in PROC GLM; SAS, 1988). Similarly, station effects were similarly calculated by averaging over year effects. In this application the use of main effects

ANOVA models has its advantages and disadvantages. It is advantageous because it accommodates unbalanced sampling (e.g., inclusion of stations that were not sampled every year). That is also its weakness, however, especially if abundance patterns are strongly influenced by year × station interactions. Nonetheless, the 2-factor ANOVA models we developed performed reasonably well at explaining catch variability, with r^2 values ranging from 14.4 to 72.0%. While we believe the standardized indices we developed robustly reflect general trends in abundance, we also recognize that other estimation techniques may prove to be superior for specific individual taxa.

To ascertain assemblage relationships among the taxa we conducted a principal components analysis (PCA) on the estimated year effects from the taxon-specific ANOVA models (Green and Carroll, 1978). In the analysis we treated taxa as variables and years as cases and the ordination was applied to the correlation matrix. Examination of latent roots and eigenvectors from the PCA was studied to reveal assemblage characteristics.

We analyzed the CTD data to characterize among-year variation in water type within the core survey area at the time of the survey. The data were first filtered to only include temperature, salinity, and density (σ_t) observations taken within the depth range of the headrope (28–32 m). For each cast, mean values for each variable were calculated and three separate ANOVAs were conducted, again employing year and station as main effects. For example, the temperature model was $T_{ijk} = Y_i + S_j + \varepsilon_{ijk}$, where T_{ijk} is the mean temperature at 30 m in the kth cast conducted in year Y_i $\{i \in 1987, 1988, \ldots, 2012\}$ at CTD station S_j and ε_{ijk} is a normal error term. Temperature year-effects were calculated from the ANOVA model using the LSMEAN option in PROC GLM, as were station effects to represent the spatial climatology. Similar analyses of salinity and density also were completed.

2.3. Published oceanographic variables

A variety of published oceanographic indices were examined to understand and potentially explain the biological variability we observed in the survey (Table 1). The first five of these are spatially integrated and reflect oceanographic conditions in the northeast Pacific Ocean, whereas the last five are site-specific. We therefore restricted our consideration of the latter to the central California region where the survey is conducted. In particular, we considered the Bakun upwelling index at 39° N, AVISO sea-level anomalies from 36.5° to 38.3° N, tide gauge data collected at San Francisco (37.7° N), and wind stress estimates at 37.5° N. Because all indices are available on a monthly basis, we compared the annual time series of May–June midwater trawl assemblage characteristics to index values in the five months preceding and leading up to the survey (January–May). Given the breadth of oceanographic information that we evaluated, here we limit our full consideration to AVISO sea surface height deviations because overall those data were most revealing *vis-à-vis* our biological findings.

Our collection and summarization of the AVISO data set proceeded by querying the data at http://coastwatch.pfeg.noaa.gov/erddap/index.html. From there we obtained the "Sea Surface Height, AVISO, Global, Science Quality (Monthly Composite)" dataset, which extends from October 1992 to January 2010. This limited our summarization to the months of January–May from 1993 to 2009 (17 years). Moreover, the data are spatially explicit in bins 0.25° lat. × 0.25° long., allowing us to subset the analysis to 34 central California cells bounded by 36.50–38.25° N and 122.00–124.00° W (Fig. 1). Lastly, to understand how sea surface height deviations covary within the region and to develop a composite monthly statistic, we performed separate PCAs on the five monthly data sets.

3. Results

3.1. Biological findings

The assemblage of organisms commonly collected in the midwater trawl survey includes a wide variety of forage species. Thirty-seven regularly identified taxa were collected in those samples, but many were rare (e.g., Pacific mackerel, *Scomber japonicus*). We therefore limited our consideration to taxa that were collected in at least 10% of trawls (Table 2). Note that thirteen of the taxa are identified to species and seven are identified at a higher taxonomic level (e.g., family, order, etc.). For example, krill were by far the most commonly encountered taxon, occurring in 86% of all trawls. Krill taken in the survey are composed almost entirely of two species (*Euphausia pacifica* and *Thysanoessa spinifera*) (Santora et al., 2011, 2012), but they were not identified to species until 2002 and so we combine them here. Note also that we consolidated all YOY rockfish (*Sebastes* spp.) into a single genus-level taxon because previous results had shown very high concordance among 10 common YOY rockfishes sampled in the survey (Ralston et al., 2013). It is also noteworthy that the assemblage included six YOY groundfish species, including rockfish, speckled sanddab (*Citharichthys stigmaeus*), Pacific sanddab (*Citharichthys sordidus*), Pacific hake, rex sole (*Glyptocephalus zachirus*), and lingcod (*Ophiodon elongatus*). As we distinguish young-of-the-year (YOY) from age-1+ fish whenever possible, Pacific hake (*M. productus*) are included as two categories (YOY and older fish). Taxa wherein that ontogenetic distinction was ambiguous were classified as unknown age, which included all of the invertebrates. Four invertebrate taxa were regularly encountered (krill, market squid [*Doryteuthis opalescens*], octopus, and sergestid shrimp), as well as a group of mesopelagic fishes (California headlightfish [*Diaphus theta*], blue lanternfish [*Tarltonbeania crenularis*], "other" lanternfish [Myctophidae], California smoothtongue [*Leuroglossus stilbius*], and "other" deep-sea smelts [Bathylagidae]). We note that prior to 2006 some lanternfish, while abundant, were not identified to species due to constraints on processing time at sea (e.g., northern lampfish [*Stenobrachius leucopsarus*]). Thus, other than rockfish, the taxa presented here represent the lowest level of taxonomic resolution achieved consistently from 1990 onwards.

Table 1
Published oceanographic data sets examined in relation to variation in the biological assemblage observed in the SWFSC midwater trawl survey.

	Internet URL
Northeast Pacific Ocean Global Indices	
North Pacific Index (NPI)	http://gcmd.nasa.gov/records/GCMD_NCAR_NP.html
Multivariate ENSO Index (MEI)	http://www.esrl.noaa.gov/psd/enso/mei/
Pacific Decadal Oscillation (PDO)	http://jisao.washington.edu/pdo/
Northern Oscillation Index (NOI)	http://www.pfeg.noaa.gov/products/pfel/modeled/indices/NOIx/noix.html
North Pacific Gyre Oscillation (NPGO)	http://www.o3d.org/npgo/
Central California Regional Indices	
Bakun Upwelling Index	http://www.pfeg.noaa.gov/products/las/docs/global_upwell.html
Sacramento–San Joaquin River System DayFlow	http://www.water.ca.gov/dayflow/
Archiving, Validation, and Interpretation, of Satellite Oceanographic Data (AVISO)	http://www.aviso.oceanobs.com/en/
Coastal Tide Gauge Stations	http://uhslc.soest.hawaii.edu/
Wind Stress Data	http://www.pfel.noaa.gov/products/PFEL/modeled/sfc_wind/sfc_wind.html

Table 2
Commonly sampled organisms collected in the midwater trawl survey, listed in rank order of frequency of occurrence in trawls conducted from 1990 to 2012. Ontogenetic stage codes distinguish young-of-the-year (Y), age 1+ (A), and unknown age (U). Note that taxonomic abbreviations are employed in subsequent tables and figures.

Rank	Common name	Scientific name	Ontogenetic stage	Abbreviation	Frequency of occurrence
1.	Krill	Euphausiacea	U	krill	0.862
2.	Rockfish	*Sebastes* spp.	Y	rock	0.719
3.	Speckled sanddab	*Citharichthys stigmaeus*	Y	sdab	0.613
4.	Pacific sanddab	*Citharichthys sordidus*	Y	pdab	0.573
5.	Pacific hake	*Merluccius productus*	Y	hakeY	0.561
6.	market squid	*Doryteuthis opalescens*	U	dory	0.489
7.	Lanternfish	Myctophidae	U	myct	0.343
8.	Octopus	Octopoda	U	oct	0.268
9.	Pelagic shrimp	Sergestidae	U	serg	0.252
10.	California smoothtongue	*Leuroglossus stilbius*	U	smth	0.226
11.	Pacific hake	*Merluccius productus*	A	hakeA	0.225
12.	Northern anchovy	*Engraulis mordax*	A	anch	0.206
13.	Rex sole	*Glyptocephalus zachirus*	Y	rex	0.191
14.	California headlightfish	*Diaphus theta*	U	diaph	0.173
15.	Plainfin midshipman	*Porichthys notatus*	U	por	0.173
16.	Blue lanternfish	*Tarletonbeania crenularis*	U	tarl	0.167
17.	Lingcod	*Ophiodon elongatus*	Y	ling	0.165
18.	Goby	Gobiidae	U	goby	0.152
19.	Pacific sardine	*Sardinops sagax*	A	sard	0.148
20.	Deep-sea smelt	Bathylagidae	U	bathy	0.144

Annual estimates of log-abundance for these 20 taxa obtained from the ANOVA modeling are presented in Table 3. To illustrate abundance variability in six important taxa we graph annual anomalies of ANOVA estimates from their long-term means in Fig. 2. Autocorrelation in the estimates of all six taxa is obvious. For example, during the five years spanning 1990–1994 Pacific sardine (*Sardinops sagax*) was below average in abundance, whereas from 2004 to 2008 that species was relatively abundant. Because in any particular year the sardines that are collected include multiple cohorts, the autocorrelation might be attributable to age structure. Note, however, that autocorrelated patterns are also evident in taxa that lack multi-cohort age structure, for example YOY groundfishes and market squid.

We also examined the expected spatial distribution of each taxon within the study area. Presented in Fig. 3 are the results for six species, which collectively illustrate three general spatial patterns we observed. Market squid and northern anchovy (*Engraulis mordax*) demonstrated a distribution that was largely limited to the continental shelf (≤200 m depth). In contrast, the mesopelagic California headlight fish and California smoothtongue were, not surprisingly, distributed off the shelf. Lastly, YOY speckled sanddab and YOY rex sole were ubiquitous within the study region. In general, we observed that each of the 20 taxa we considered could be classified into one of these three basic spatial patterns, although more subtle aspects to the catch distributions have been described (Santora et al., 2012, in review).

PCA of the 20 taxon-specific annual estimates of log-abundance indicated that 94% of the collective variance was captured by the first 10 components (Table 4). We graph the taxon loadings (eigenvectors) for the first three components ($\lambda \geq 2$) in sorted order graphically in Fig. 4. Note that taxon loadings for the first principal component (PC-1) indicate that YOY rockfish, YOY Pacific sanddab, YOY speckled sanddab, and YOY Pacific hake are all strongly positive, indicating positive covariation with PC-1. In contrast, northern anchovy and Pacific sardine load strongly negative, indicating negative covariation with the first component. Similarly, note that the largest positive loadings on

Table 3
Time series of log-abundance estimates for 20 frequently sampled taxa in the midwater trawl survey (see Table 2). Abundance statistics are the estimated year effects derived from an ANOVA (see text).

Year	krill	rock	sdab	pdab	hakeY	dory	myct	octo	serg	leur	hakeA	anch	rex	diaph	por	tarl	ling	goby	sard	bath
1990	7.42	1.24	1.30	0.72	1.15	2.06	1.23	0.39	1.33	0.85	0.65	0.74	0.01	0.49	0.36	0.39	0.25	0.01	0.02	0.25
1991	8.64	2.43	2.22	1.41	2.12	1.13	1.07	0.33	1.03	0.70	1.90	−0.08	0.43	0.36	0.53	0.22	0.64	0.03	0.02	0.24
1992	4.18	1.12	0.64	0.54	0.77	3.21	1.49	0.03	0.88	0.37	0.27	1.09	0.02	0.61	0.45	0.51	0.06	0.09	0.07	0.12
1993	7.75	2.79	1.38	1.89	3.22	1.70	1.65	0.33	1.18	0.75	0.29	0.49	0.05	0.65	0.52	0.34	0.56	0.28	0.11	0.45
1994	8.11	1.10	1.65	2.26	2.19	1.60	1.44	0.37	1.01	0.49	0.80	0.66	0.04	0.20	0.39	0.39	0.14	0.58	0.22	0.38
1995	6.73	0.89	0.91	0.86	0.82	2.15	1.32	0.50	1.38	0.52	0.57	1.80	0.03	0.28	0.44	0.40	0.44	0.26	0.59	0.14
1996	6.07	1.84	1.53	1.96	2.09	1.35	1.68	0.19	2.13	0.93	0.25	0.43	0.13	0.45	0.41	0.42	0.33	0.35	0.15	0.37
1997	7.24	1.45	0.84	0.56	1.56	2.39	0.96	0.29	0.65	0.53	0.52	0.86	0.12	0.28	0.27	0.26	0.16	0.54	0.65	0.08
1998	3.86	0.37	0.10	−0.07	0.64	0.52	1.12	0.03	0.94	0.21	0.05	1.08	0.03	0.39	0.24	0.58	0.09	0.08	0.83	0.19
1999	7.26	0.88	1.11	1.18	2.05	0.76	0.85	0.10	0.57	0.23	0.13	1.37	0.04	0.11	0.00	0.20	0.37	0.01	0.43	0.28
2000	8.04	1.98	0.49	0.87	2.34	1.51	0.75	0.69	0.15	0.45	1.63	0.32	1.17	0.20	0.27	0.47	0.25	0.12	0.22	0.28
2001	8.72	2.68	2.11	1.46	2.39	2.54	0.80	0.63	1.09	0.65	0.64	0.40	0.40	0.09	0.26	0.36	0.47	0.24	0.33	0.23
2002	6.50	2.82	2.35	2.57	1.86	2.41	1.05	0.40	1.21	0.40	0.74	0.16	0.95	0.24	0.39	0.12	0.25	0.04	0.13	0.07
2003	8.37	1.63	0.41	1.40	0.96	1.19	1.56	0.73	2.14	0.21	0.08	0.32	0.05	1.36	0.27	0.87	0.27	0.10	0.11	0.34
2004	7.48	2.31	0.71	1.50	3.09	1.26	1.72	0.39	1.24	0.47	1.00	1.53	1.01	0.93	0.18	0.96	0.37	0.05	0.40	0.62
2005	6.60	0.17	0.36	0.46	−0.03	0.79	1.47	0.02	1.03	0.64	0.26	2.01	0.01	1.02	0.17	0.70	0.12	0.32	0.93	0.51
2006	6.89	0.28	0.15	0.24	0.08	0.41	1.25	0.14	0.82	0.54	0.89	2.24	0.00	0.66	0.07	0.43	0.03	0.07	0.65	0.31
2007	8.23	0.72	0.33	0.35	0.52	0.73	1.09	0.18	0.72	0.45	0.41	1.07	0.05	0.75	0.06	0.43	0.36	0.01	0.77	0.18
2008	10.13	1.42	0.63	0.11	1.42	0.71	1.59	0.39	0.86	0.37	1.11	0.27	0.13	1.21	0.07	0.88	0.68	0.00	0.92	0.47
2009	8.37	2.05	0.75	0.27	1.24	1.17	1.95	0.60	1.73	0.09	0.21	0.30	0.43	1.54	0.01	1.28	0.43	0.10	0.23	0.35
2010	8.40	1.88	2.03	1.51	1.80	1.25	2.24	0.64	1.74	0.87	−0.03	0.17	0.69	0.91	0.02	0.61	0.46	0.11	0.03	0.35
2011	9.05	2.36	1.90	2.49	1.35	1.61	0.36	0.36	1.00	0.12	0.44	0.25	0.18	0.03	0.11	0.08	0.50	0.07	0.06	0.18
2012	9.54	1.05	1.22	2.27	1.12	3.46	0.92	0.36	1.04	0.15	0.30	0.03	0.01	0.20	0.01	0.32	0.32	0.08	0.07	0.09

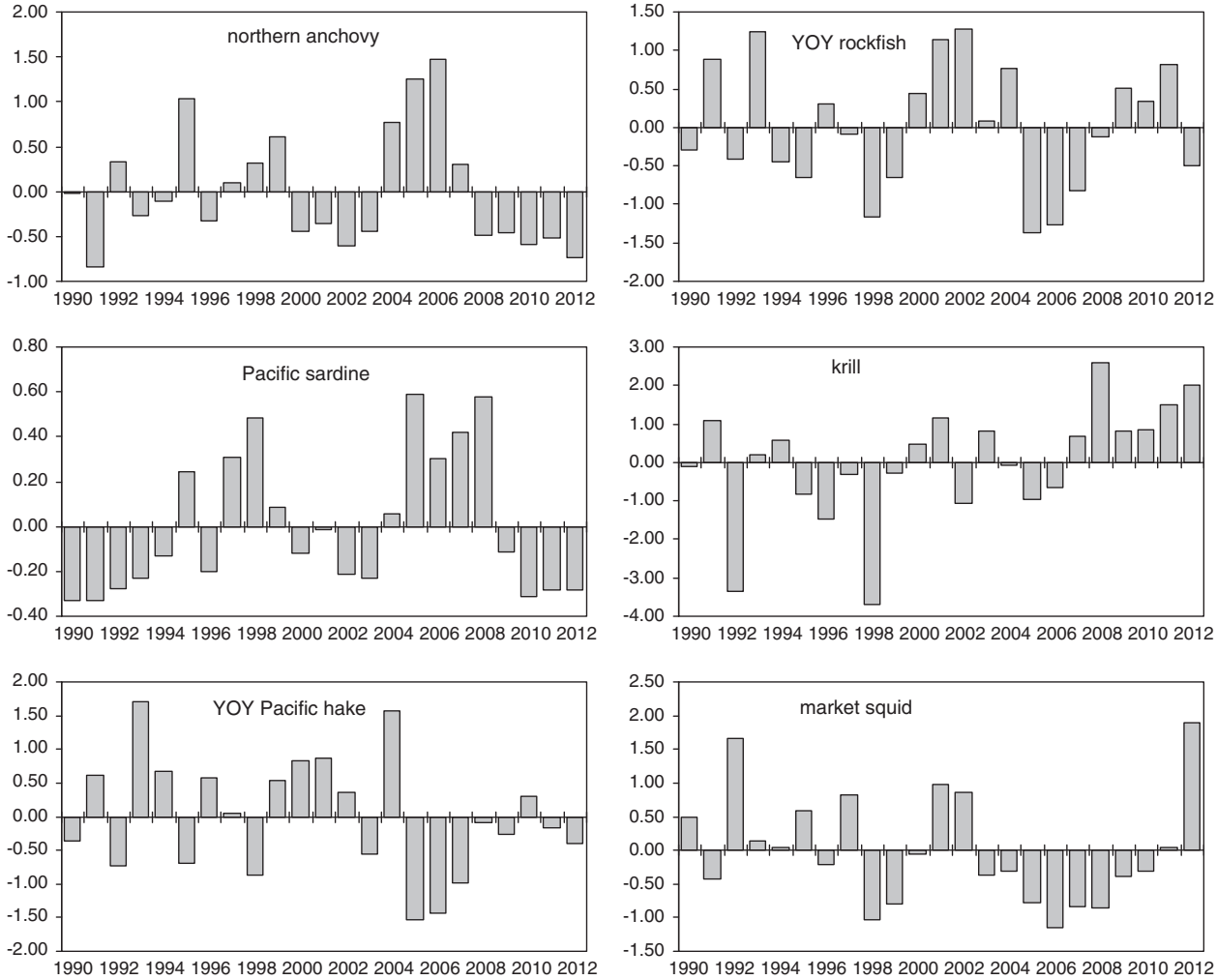

Fig. 2. Annual anomalies in log-abundance of selected taxa collected in the SWFSC midwater trawl survey based on deviations of ANOVA estimates from their 23 year means.

PC-2 are mesopelagic scattering layer taxa (myctophids, bathylagids, and sergestids), indicating positive correlation with that component. Coastal species (i.e., northern anchovy, gobies, plainfin midshipman, and market squid) are negatively correlated with this component. PC-3 is more difficult to interpret, but appears to discriminate taxa that are favored, or not, by upwelling within the study area (see below).

Scores for 1990–2012 for the first three components are displayed in Fig. 5. A Durbin–Watson test for autocorrelation shows that PC-1 is significantly autocorrelated ($d = 1.217$, $n = 23$, $P < 0.05$), whereas results for PC-2 are inconclusive ($d = 1.334$) and PC-3 is not significant ($d = 1.557$). Note that the PC-1 time series demonstrates a run of positive scores from 2000 to 2004, a run of negative scores from 2005 to 2009, and a run of positive scores for the last three years of the series. In this instance we conjecture that the positive autocorrelation of ($\hat{r} = 0.378$) is due to low-frequency environmental forcing that affects the distribution of the communities in the epipelagic zone that are vulnerable to our survey.

3.2. Oceanographic findings

CTD data were collected at 97 different stations from 1987 to 2012 (Fig. 1), collectively representing 4333 individual casts. All three ANOVA models that were fitted to the data (i.e., temperature, salinity, and σ_t) and their main effects were highly significant ($P < 0.0001$), with 61–64% of the dependent variable variance explained by the model.

To illustrate the expected oceanographic topography encountered by the midwater trawl within the study region we contoured the estimated station effects from the density (σ_t) ANOVA model (Fig. 6). Results show that nearshore waters around Point Reyes and the Gulf of the Farallones are characterized by elevated isopycnals ($\sigma_t \geq 26.0$) indicative of upwelled water (Wing et al., 1998). Throughout the study region expected seawater densities at 30 m decrease with increased distance from shore.

Results presented in Fig. 7 show the annual temperature–salinity (TS) relationship based on the year effects estimated from the respective ANOVA models. Clearly evident is a tendency for warm years to be associated with low salinity water and vice versa, a pattern consistent with annual variation in the extent of upwelling within the study region (Schwing et al., 2000). Given the strong association between these variables ($r = -0.806$), we extracted their common trend by conducting a PCA on the annual TS estimates (Fig. 8). Plotted in the figure are component scores from the analysis, which reflect the long axis of the values shown in Fig. 7 (PC-1) and an axis orthogonal to that (PC-2). Note that positive PC-1 scores correspond to weak upwelling years and negative scores occur in strong upwelling years. In that regard, the greatest contrast in water types occurred between 1998 (an El Niño year) and 1999 (a La Niña) year; the 1992–93 El Niño is also clearly evident.

PC-1 reflects a density continuum that follows interannual variation in upwelling, i.e., cold-saline versus warm-fresh seawater (Smith, 1968). In contrast, PC-2 being orthogonal to PC-1, is related to isopycnal thermohaline variability, i.e., differences in the relative contributions of

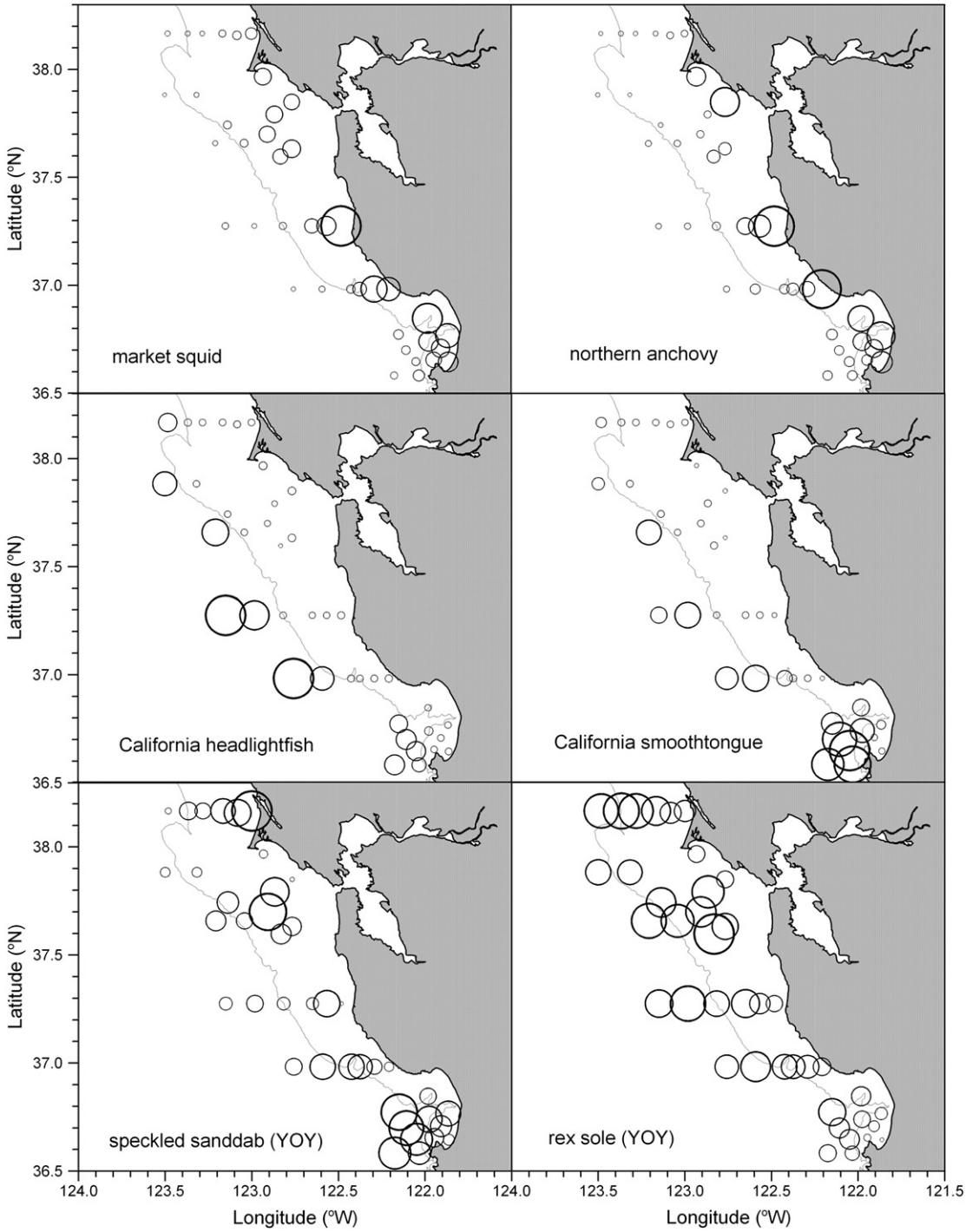

Fig. 3. Station effects estimated from taxon-specific ANOVA models for six species, representing three general patterns. Circles are proportional to log-abundance, which for each species are scaled similarly from maximum to minimum values.

temperature and salinity to density. For a given density warmer–saltier water has more "spice" than cooler–fresher water (Flament, 2002). For example, note that while PC-1 scores for 1997 and 2004 are similar (0.63 and 0.95, respectively), PC-2 scores for those years are quite different (0.85 and −1.04). In particular, 1997 is similar in density to 2004 but has more spice. Such differences are useful in identifying distinct water types, which often have different origins.

The 34 sites that were included in our analysis of AVISO satellite altimetry are shown in Fig. 9. Note that they broadly overlap the midwater trawl stations, extending from nearshore to well off the continental shelf. Also shown in the figure are shaded contours of PC-1 eigenvector loadings from the January analysis. Note that all 34 loadings are positive, ranging 0.098–0.183. In fact, 30 of the 34 values were ≥0.16, demonstrating that in January there is strong positive covariation in sea surface height deviations throughout the study area. That conclusion is further supported by the observation that, among the five months analyzed, PC-1 explained 74.3–83.3% of the combined variation among the 34 sites. Moreover, the smallest loading observed

Table 4
Eigenvalues and variance terms from a principal components analysis of the assemblage of fishes and invertebrates taken in the midwater trawl survey (1990–2012).

Principal component	Eigenvalue	Percentage of variance explained	Cumulative variance explained
1	5.733	29%	29%
2	3.929	20%	49%
3	2.441	12%	61%
4	1.935	10%	70%
5	1.253	6%	76%
6	0.965	5%	81%
7	0.896	4%	86%
8	0.631	3%	89%
9	0.499	3%	91%
10	0.453	2%	94%

in any analysis was 0.098, i.e., the most northwestern AVISO site in January. Hence, scores taken from PC-1 effectively capture the general trend in sea surface height anomalies.

3.3. Biological-oceanographic comparisons

We compared interannual variation in the biological structure of the epipelagic forage community, as reflected in trawl component scores (Fig. 5), with the time series of seawater properties observed through CTD sampling (Fig. 8). Simple correlation analysis revealed that both PC-1 and PC-3 are significantly correlated with "upwelling" as we have defined it, although biological variability is apparently unrelated to seawater "spice" (Table 5). The inverse relationship between upwelling and PC-1 implies that years with enhanced upwelling are associated with greater representation of YOY groundfish, market squid, and krill in survey catches. Conversely, clupeoids and mesopelagics rise in importance when upwelling is relatively weak. A similar biological outcome is implied by the positive correlation between upwelling and PC-3, i.e., mesopelagics are more dominant in low upwelling years.

Also presented in Table 5 are correlation results for comparisons of assemblage structure (PC-1, PC-2, and PC-3) with five published oceanographic data sets in the months leading up to the survey. It is striking that only AVISO sea-level anomalies are significantly correlated with PC-1, whereas all five indices are correlated with PC-3. Note also that January and February AVISO anomalies are associated with PC-1 (Fig. 10) whereas March and April anomalies are correlated with PC-3 (Fig. 11). This implies that conditions preceding and following the spring transition to the upwelling season (Bograd et al., 2009) influence the composition of the trawl survey catch independently of one another (Black et al., 2011). Moreover, because the eigenvalue for PC-1 (λ_1) is over twice as large as λ_3 (Table 4), winter sea-level anomalies appear to have a dominant impact on the assemblage structure of the epipelagic forage community encountered by the survey in May–June.

The three global indices in Table 5 (NPGO, PDO, and MEI) are significantly correlated with PC-3 in all five months leading up to the survey (January to May). This is doubtless due to strong positive autocorrelation in all three indices. For example, the monthly NPGO and PDO indices from January 1990 to May 2012 are significantly autocorrelated at least through order 10. Likewise, the monthly MEI index over the same time is autocorrelated through order 7.

Oceanographic conditions appear to have no discernible relationship with PC-2 (Table 5). Rather, that component is statistically associated with long-term trends in the abundance of the twenty taxa collected in the survey. Here we quantify an abundance trend simply as the correlation coefficient between ANOVA abundance estimates and year, calculated over the 23 years of available data (Table 3). Plotted in Fig. 12 are those correlation coefficients and PC-2 eigenvector loadings. The relationship is significant ($r = 0.656$, $P = 0.0017$) and indicates that plainfin midshipman (*Porichthys notatus*), California smoothtongue, and "goby" (Gobiidae) have declined in abundance while krill, California headlightfish, and blue lanternfish have increased.

4. Discussion

We describe multi-decadal variation in a central California forage community based on annual sampling in a midwater trawl survey. Standardized abundance estimates were derived by application of a model-based ANOVA estimation procedure to 20 commonly occurring taxa in the survey. While effective at utilizing all the trawl samples and extracting the primary temporal and spatial patterns in the data, more subtle variations in abundance attributable to year × station

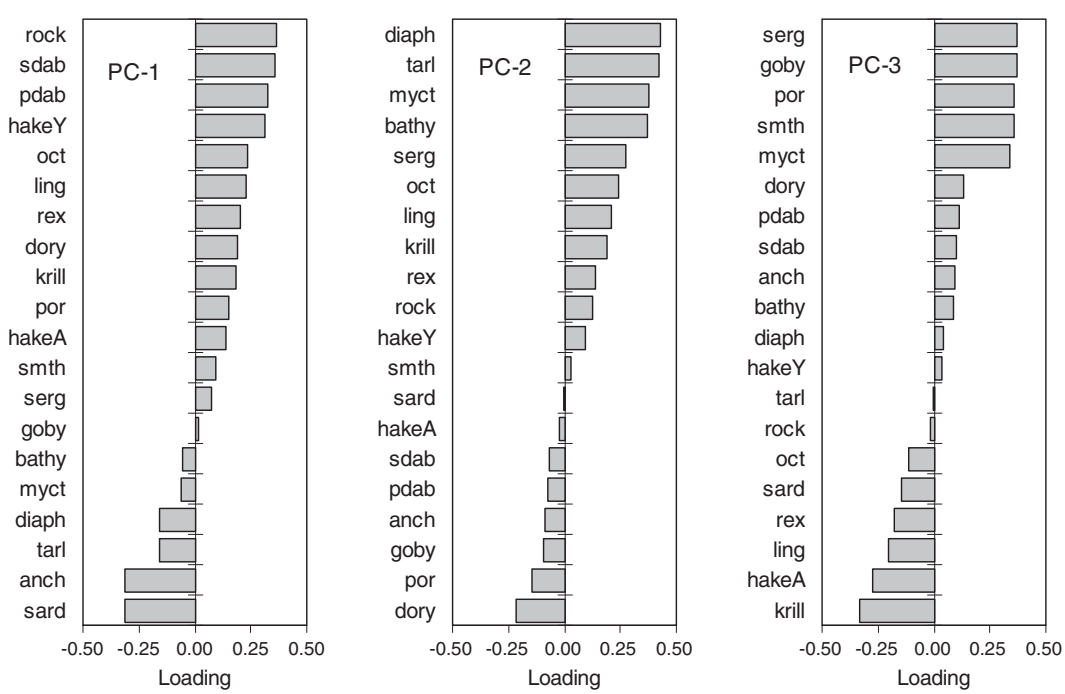

Fig. 4. Taxon-specific loadings sorted in descending order for the first three principal components. Taxa with positive loadings are positively correlated with a component while negative loadings indicate a negative correlation (a zero loading is uncorrelated).

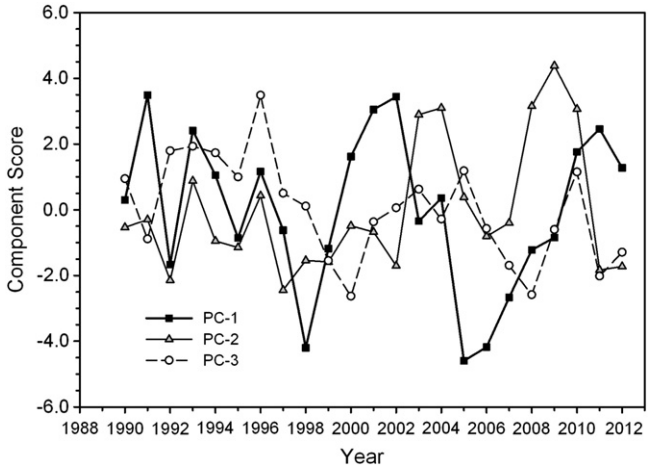

Fig. 5. Scores for the first three principal components over the period 1990–2012.

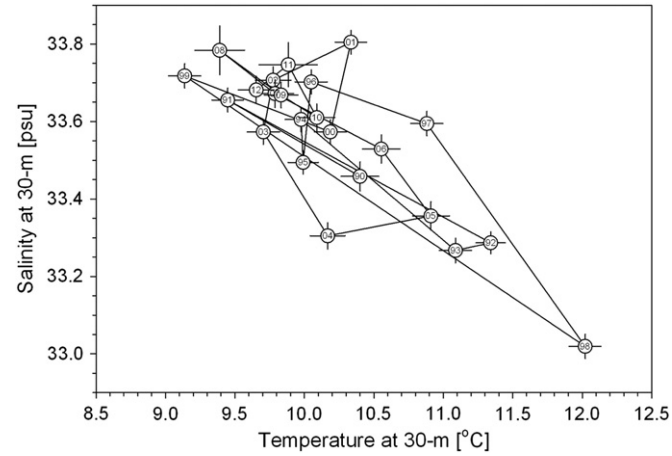

Fig. 7. TS plot of the estimated year effects from temperature and salinity ANOVA models (1990–2012). Error bars represent ±2 standard errors of the mean.

interactions are unaccounted for. Likewise, the spatial scale of our study is less than ideal, spanning only 200 km of coastline. For YOY rockfish this issue was studied in some detail by Ralston and Stewart (2013), who showed that an accurate characterization of abundance patterns, for the purpose of estimating impending fisheries recruitment, required coast-wide sampling. Given that the trawl survey was expanded to cover a much broader region in 2004 (Sakuma et al., 2006), it would be possible to conduct a more spatially extensive study, albeit over a much shorter time period. Our focus, however, has been on developing a long-term, multi-decadal view of the assemblage.

Principal components analysis of the 20 dominant taxa occurring in the survey was effective in extracting the dominant modes of variability. The first three components explained 61% of the combined variability exhibited by the assemblage. The dominant mode (PC-1) revealed a contrast between the abundance of YOY groundfish versus clupeoids (Fig. 4). The second component expressed differences in occurrence between mesopelagic species and several continental shelf-associated species (e.g., market squid, plainfin midshipman, and gobies). From a species composition point of view, the contrast that was defined by the third component was characterized by an assortment of taxa that seemed to have little in common.

We compiled and evaluated a variety of oceanographic data sets (Table 1) in an effort to explain our biological findings (Table 5). It is revealing that the CTD data we collected during the survey was similarly effective in explaining variation in PC-1 and PC-3, even though the two components are orthogonal (=independent) to one another. This indicates that the thermohaline characteristics of the seawater encountered during the survey interacts with the species composition of the catch in a complex manner. Similarly, we found that sea-level height anomalies in the central California region are effective in explaining variability in PC-1 and PC-3 (Table 5, Figs. 10 and 11), although there is a seasonal contrast to those findings. In particular, variation in PC-1 is tied to winter (January) ocean conditions, whereas PC-3 is linked to spring (April). It is striking that none of the indices that are most commonly cited in biological oceanographic studies (i.e., the NPGO, PDO, MEI, and Bakun upwelling) are significantly related to the dominant mode of variation in the trawl survey, although all of them are correlated with our PC-3.

Black et al. (2011) described a contrast between upwelling modes on the U.S. west coast (lat. 33°–45° N). The first mode reflected upwelling during the summer months and was characterized by low-frequency processes, whereas the second mode was attributable to wintertime upwelling and was dominated by high frequency processes. Their findings

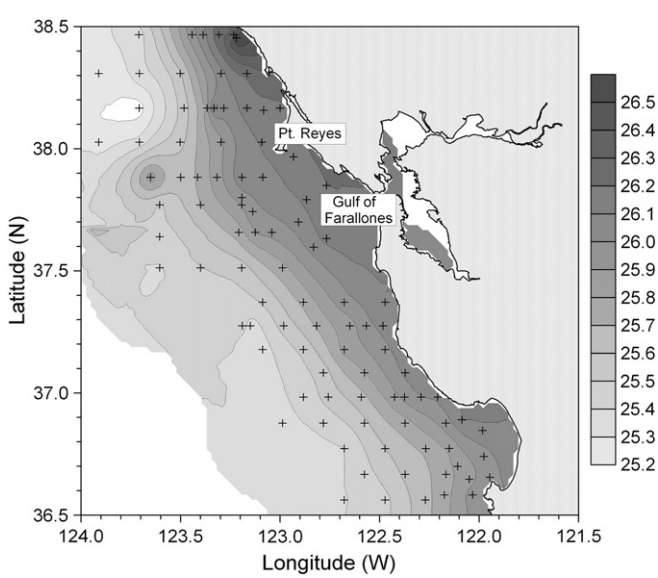

Fig. 6. Contour map of estimated CTD station effects from an ANOVA of seawater density (σ_t) at 30 m depth. Plus signs (+) indicate station locations. The gray scale on the right indicates density. Cold-saline water indicative of upwelling ($\sigma_t > 26.0$) is generally evident in nearshore waters, especially in the vicinity of Point Reyes and the Gulf of the Farallones.

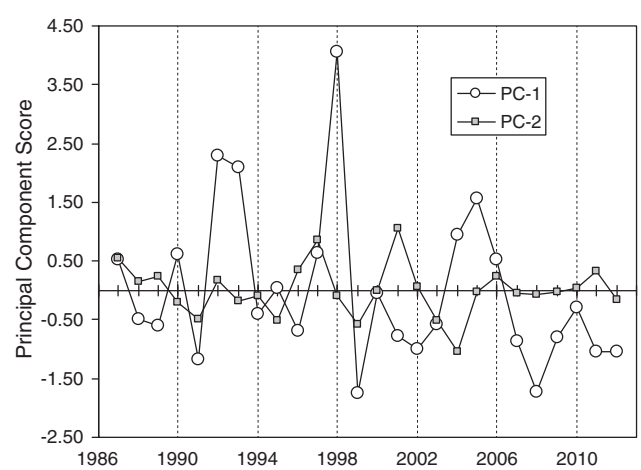

Fig. 8. Annual scores from a principal components analysis of the temperature–salinity results shown in Fig. 6. The dominant component (PC-1) reflects interannual variation in upwelling within the study region; the second component (PC-2) shows fluctuations in "spice" as an indicator of source waters (see text).

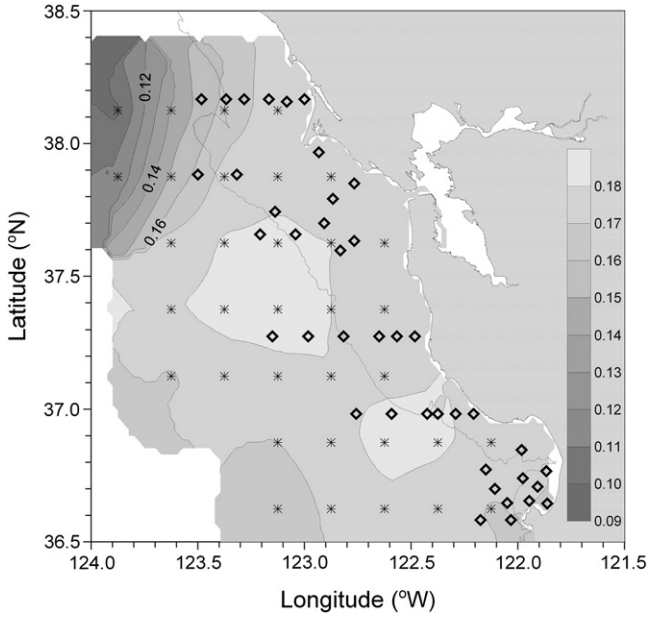

Fig. 9. Contour plot of site-specific loadings from the first principal component for AVISO altimetry sea surface height deviations in the month of January. In the figure the 34 asterisks represent the locations (=variables) of the altimetry estimates and the bold diamonds indicate trawl station locations. Note that lighter shades of gray represent stronger loadings, as indicated in the scale bar on the right.

support the view that events occurring pre- and post-spring transition (Bograd et al., 2009) independently affect the growth and reproductive success of seabirds, Chinook salmon (*O. tshawytscha*), and rockfishes. It is also telling that their winter mode was related to four of the six biological responses they examined.

Further support for the view that in central California ocean conditions prior to the spring transition play a major role in structuring biological communities during the upwelling season is provided by Ralston et al. (2013). They studied variation in the distribution and abundance of YOY rockfish collected in the midwater trawl survey and showed that time series of standardized CPUE (1983–2010) for the 10 most commonly sampled rockfish species were highly correlated. A principal components analysis conducted in that study revealed that 77% of the variation exhibited by the 10 species was accounted for by the first component, with species' loadings ranging 0.27–0.34. They also showed that sea-level anomalies were well correlated with fluctuations in YOY rockfish catch, so it is not surprising that there is a strong positive correlation ($r = 0.846$, $P < 0.0001$) between their rockfish PC-1 and our assemblage PC-1. It is notable that our PC-1 is correlated with winter sea-level anomalies and the YOY rockfish considered by Ralston et al. (2013) were all winter-spawning species. Together these findings support the view that conditions in the winter months preceding the May–June survey have a dominant influence on survey catches.

While Koslow et al. (2013a,b) and this study have focused on the southern portion of the California Current, other studies of somewhat shorter duration have examined interannual variation in pelagic forage communities in the northern California Current. For example, Brodeur

Table 5
Correlations between SWFSC midwater trawl principal component scores and selected oceanographic and biological time series. For each comparison the Pearson correlation coefficient ($\boldsymbol{r}$) is provided, along with the significance probability of the null hypothesis (H_o: $\boldsymbol{r} = 0$) in parenthesis. Cases where the correlation is nominally significant ($\boldsymbol{\alpha} = 0.05$) are shown in bold.

	Variable	PC-1	PC-2	PC-3
Physical				
CTD (May)	Temperature @ 30 m	−0.3986 (0.0596)	−0.2588 (0.2330)	**0.4378 (0.0367)**
	Salinity @ 30 m	**0.4541 (0.0295)**	0.0507 (0.8183)	−0.3852 (0.0695)
	σ_t @ 30 m	**0.4585 (0.0278)**	0.1444 (0.5109)	**−0.4157 (0.0485)**
	Depth 26.0 isopycnal	**−0.4235 (0.0440)**	−0.1457 (0.5070)	**0.4732 (0.0226)**
	"Upwelling" (PC-1)	**−0.4470 (0.0325)**	−0.1634 (0.4562)	**0.4309 (0.0401)**
	"Spice" (PC-2)	0.0905 (0.6814)	−0.3401 (0.1123)	0.0860 (0.6964)
NPGO	Jan	0.1717 (0.4334)	0.2123 (0.3308)	**−0.4264 (0.0425)**
	Feb	0.1671 (0.4460)	0.1600 (0.4657)	**−0.5974 (0.0026)**
	Mar	0.2236 (0.3051)	0.1527 (0.4868)	**−0.6131 (0.0019)**
	Apr	0.2853 (0.1869)	0.1704 (0.4369)	**−0.6841 (0.0003)**
	May	0.2374 (0.2754)	0.2091 (0.3380)	**−0.7485 (<0.0001)**
PDO	Jan	−0.2842 (0.1887)	0.0705 (0.7491)	**0.5679 (0.0047)**
	Feb	−0.4006 (0.0582)	0.0343 (0.8766)	**0.5668 (0.0048)**
	Mar	−0.3099 (0.1502)	−0.0811 (0.7129)	**0.5688 (0.0046)**
	Apr	−0.2237 (0.3048)	−0.2121 (0.3313)	**0.7008 (0.0002)**
	May	−0.2129 (0.3294)	−0.0912 (0.6790)	**0.8204 (<0.0001)**
MEI	Jan	−0.3217 (0.1345)	0.0286 (0.8970)	**0.4924 (0.0170)**
	Feb	−0.3167 (0.1409)	0.0188 (0.9322)	**0.5425 (0.0075)**
	Mar	−0.2891 (0.1809)	−0.0735 (0.7391)	**0.6102 (0.0020)**
	Apr	−0.1988 (0.3631)	−0.1202 (0.5849)	**0.5252 (0.0101)**
	May	−0.1038 (0.6375)	−0.2308 (0.2893)	**0.4414 (0.0350)**
Upwelling at 39° N	Jan	0.0424 (0.8476)	−0.0944 (0.6683)	−0.3177 (0.1396)
	Feb	−0.0137 (0.9504)	−0.0061 (0.9779)	−0.0934 (0.6716)
	Mar	−0.0886 (0.6877)	0.3873 (0.0679)	**−0.4363 (0.0374)**
	Apr	−0.0519 (0.8140)	−0.0032 (0.9886)	−0.4115 (0.0511)
	May	0.1377 (0.5309)	−0.0425 (0.8473)	−0.4067 (0.0541)
AVISO sea-level	Jan	**−0.6346 (0.0062)**	0.0680 (0.7954)	0.3391 (0.1831)
	Feb	**−0.4859 (0.0480)**	0.0339 (0.8971)	0.4309 (0.0842)
	Mar	−0.2147 (0.4079)	−0.0049 (0.9850)	**0.5138 (0.0349)**
	Apr	−0.2319 (0.3706)	−0.2140 (0.4096)	**0.6526 (0.0045)**
	May	−0.2803 (0.2759)	−0.1204 (0.6454)	0.3693 (0.1446)
Biological				
Garcia-Reyes	PC1	**0.6850 (0.0024)**	0.1364 (0.6015)	0.4446 (0.7272)
Garcia-Reyes	PC2	0.1633 (0.5311)	0.1170 (0.6546)	0.0944 (0.7185)
Sacramento	Index	**0.5404 (0.0139)**	0.3512 (0.1289)	0.1630 (0.4922)
Koslow	PC1	0.0483 (0.8309)	**0.4377 (0.0416)**	**0.5979 (0.0033)**
Koslow	PC2	**0.5414 (0.0093)**	0.1460 (0.5167)	0.0883 (0.6961)
Koslow	PC3	0.3770 (0.0837)	0.0355 (0.8752)	**0.5177 (0.0136)**

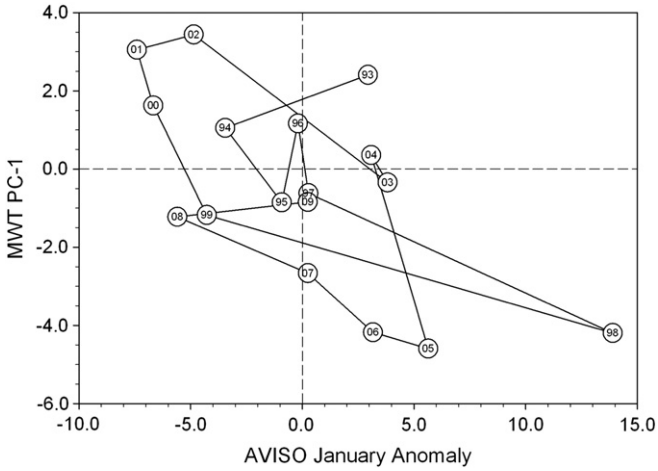

Fig. 10. Covariation between January AVISO sea level anomalies and the first principal component from an analysis of the forage assemblage sampled by the SWFSC midwater trawl survey.

et al. (2005) describe a 5 year time series of daylight collections of pelagic nekton sampled with a surface rope trawl off the Oregon–Washington coast. The period of their study (1998–2002) encompassed major fluctuations in the abiotic environment due to El Niño, La Niña, low Columbia River flows, and a significant intrusion of a nutrient rich subarctic water mass. The nekton communities they describe seemed to vary in response to fluctuations in the physical environment, being explained primarily by onshore/offshore and north/south gradients. Likewise, Auth (2011) presented results of a 6 year time series of collections of ichthyoplankton sampled at night by bongo net off Oregon and Washington. He also showed substantial year to year variability in the spring–fall ichthyoplankton community, which he linked to adverse impacts on spawning stocks arising from anomalously late upwelling in 2005, but also highlighted the importance of onshore/offshore gradients in community structure. Finally, Litz et al. (2014) describe an 11 year time series (1999–2009) of nighttime collections of epipelagic nekton and micronekton sampled with a surface rope trawl in and around the Columbia River plume. They also found significant variation in the community structure of the dominant forage and predator species, although there was little linkage of their biological findings to basin scale oceanographic indicators (i.e., MEI, PDO, and the NPGO).

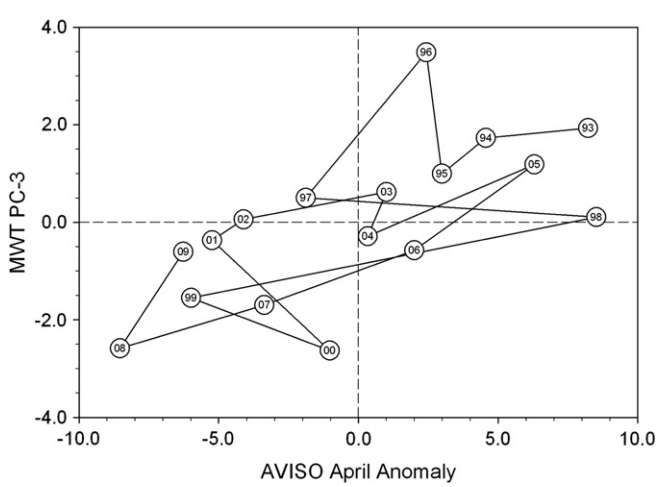

Fig. 11. Covariation between April AVISO sea level anomalies and the third principal component from an analysis of the forage assemblage sampled by the SWFSC midwater trawl survey.

4.1. An ecosystem perspective

The California Current (CC) is an upwelling ecosystem, in which the dynamics of the waters over the continental shelf-break are primarily forced by regional wind fields that drive coastal upwelling. However, the CC itself is typically defined as a year-round basin-scale feature consisting of a massive equatorward flow of cool North Pacific Current waters, with both the intensity of the transport and the physical characteristics of the source waters varying considerably, depending on both the intensity of the North Pacific Current and the nature of the bifurcation of the current when it reaches the North American continent (Chelton et al., 1982; Cummins and Freeland, 2007). The large scale dynamics associated with this flow have long been associated with variability in the characteristics of both the physical properties of the water masses, as well as shifts in the species composition and overall productivity of the plankton communities entrained into the CC (Chelton et al., 1982; Mackas et al., 2001; McGowan et al., 1998; Wickett, 1967). Similarly, sea-level anomalies have been identified as a proxy for the magnitude and direction of transport in the CC. Specifically, elevated sea-levels indicate anomalous poleward geostrophic flow typical of El Niño events, while depressed sea-levels indicate enhanced equatorward geostrophic flow, which is often associated with La Niña events (Checkley and Barth, 2009; Chelton and Davis, 1982; Hickey, 1998). Like Koslow et al. (2011, 2013) and Ralston et al. (2013), we have shown that the relative abundance and species composition of the micronektonic forage assemblage off central California varies substantially in response to sea-level variation, which we interpret as both a shift in the spatial distribution of habitat and productivity of these communities.

Such shifts have important implications for both the abundance and distribution of this forage assemblage, as well as higher and lower trophic levels. During high transport years the central California micronekton assemblage includes increased numbers of YOY groundfish, krill, market squid and sergestid shrimps. During low transport years the same region experiences reduced numbers of those species, and greater representation of coastal pelagic and mesopelagic species. In our view, the observed dynamics of the former (YOY groundfish and high turnover invertebrates) largely represents shifts in productivity associated with higher survival of early life history stages for these species. In contrast, the distribution and abundance of the latter group (coastal pelagic and mesopelagic species) are more likely related to their overall coastwide distribution and their availability to the midwater trawl survey. For example, the May–June distribution of reproductively active coastal pelagic fishes is often shifted both southward and seaward of the core study area during years of high transport, strong upwelling and/or cool sea surface temperatures (e.g., Song et al., 2012; Wells et al., 2013).

From a "bottom-up" perspective, our results are consistent with the hypothesis that large-scale transport mechanisms in the CC lead to variable bottom-up production and ramify throughout the food web via intermediate trophic level species like those studied here. For example, we found a strong correspondence between our PC-1 and the first principal component derived from a set of biological indicators reported by Garcia-Reyes et al. (2013). Their analysis includes a suite of seabird breeding success indices from central California and time series of rockfish and salmon growth anomalies (Table 5). The seabirds in that study are primarily central-place foragers from the Farallon Islands that feed preferentially on some of the species in our assemblage (YOY rockfish, YOY sanddabs, and northern anchovies). We also found a strong relationship between our PC-1 and the Sacramento Index, an indicator of salmon abundance and year class strength that is used to manage the largest central California Chinook salmon stock (O'Farrell et al., 2013). This relationship is strongest when the time series is lagged by two years to correspond to the time when salmon outmigrate from San Francisco Bay into the Gulf of the Farallons (Table 5). Relationships between krill availability and juvenile salmon survival have been

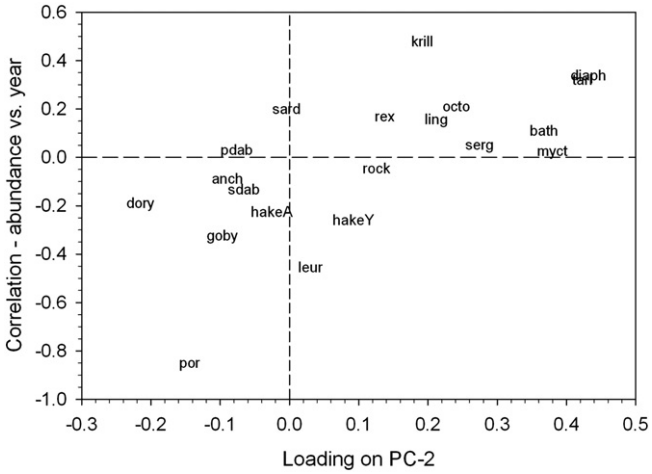

Fig. 12. Relationship between taxon loadings obtained from the trawl assemblage second principal component and taxon-specific trends in abundance from 1990 to 2012 (abbreviations as in Table 1).

described previously (Wells et al., 2012). Moreover, adult salmon are known to prey largely on a subset of the forage assemblage described here and a linkage between the assemblage and salmon productivity has been previously suggested (Thayer et al., 2014).

Finally, we note that our forage assemblages share similar dynamics as those described by Koslow et al. (2011, 2013a,b, in press), who studied variation in southern California fish assemblages based 60 years of ichthyoplankton data. They link major shifts in community structure to the PDO, as well as to oxygen concentrations. Their analyses are weighted heavily towards mesopelagic and epipelagic fishes like anchovy and sardine, but also include groundfish species (rockfishes, sanddabs, and Pacific hake). In addition, their indices are based on reproductive output (=larval production), rather than pelagic juvenile year-class strength arising from highly variable larval survival rates (see Ralston et al., 2013). Despite this difference in ontogenetic stage, and the clear spatial differences between the studies, a comparison of our results with Koslow et al. suggests that both are measuring the same processes. Specifically, PC-1 from the Koslow analysis is heavily weighted towards the mesopelagic community and is strongly correlated with the PC-3 of our analysis (Table 5), which is also weighted towards the mesopelagic community. Not surprisingly then, both of these components correlated strongly with the PDO, as well as the MEI. Koslow et al. (2013a,b) also found that the strongest physical variable related to their PC-1 was oxygen concentration at 200–400 m, suggesting that PDO related processes are the ultimate driver of shifts in oxygen concentration in the southern California Bight, which by virtue of habitat compression has influenced the relative distribution and abundance of mesopelagic and benthic fish communities. Koslow et al. (2013a,b) also found that their PC-2 and PC-3 time series (which correlate to our PC-1 and PC-3 time series) were strongly correlated with advection as indicated by coastal sea level, as well as to temperature indices.

Although the hypotheses related to both habitat compression and advection have considerable appeal, a full understanding and validation of the processes that drive these shifts remain elusive. More importantly, however, may be the notion that the communities that collectively represent the micronektonic forage base vary coherently throughout the California Current region, as demonstrated by the Koslow et al. studies in conjunction with our findings. Given the differences in spatial scale among these studies, we suggest that this is primarily in response to those large-scale physical factors that drive advection of different water masses throughout this ecosystem. As such, tracking variations in this assemblage could and should help to inform managers with respect to the sensitivity and vulnerability of higher trophic level predators to the combined effects of climate variability and fishing intensity. Ongoing efforts have linked the abundance of many of these species to the productivity of higher trophic level predators (Abraham and Sydeman, 2004; Ainley and Boekelheide, 1990; Cury et al., 2011; Field et al., 2010; Ruzicka et al., 2012; Thayer et al., 2014). Other studies have recently demonstrated spatially-variable associations in such predator–prey relationships (Santora et al., in press; Wells et al., 2012). Moreover, an improved understanding of the dynamics driving lower trophic level productivity and the predator–prey relationships between both exploited and unexploited forage species has been highlighted as a critical component of ecosystem-based approaches to fisheries management (Cury et al., 2011; PFMC, 2013; Smith et al., 2011). Ultimately, through ongoing study, we hope to better understand the chain of processes that lead to variable production of commercially and ecologically important species, with the goal of refining and improving management activities that support healthy interactions between humans and the California Current ecosystem.

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