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Long-term variation in a central California pelagic forage assemblage

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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.

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,

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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 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.

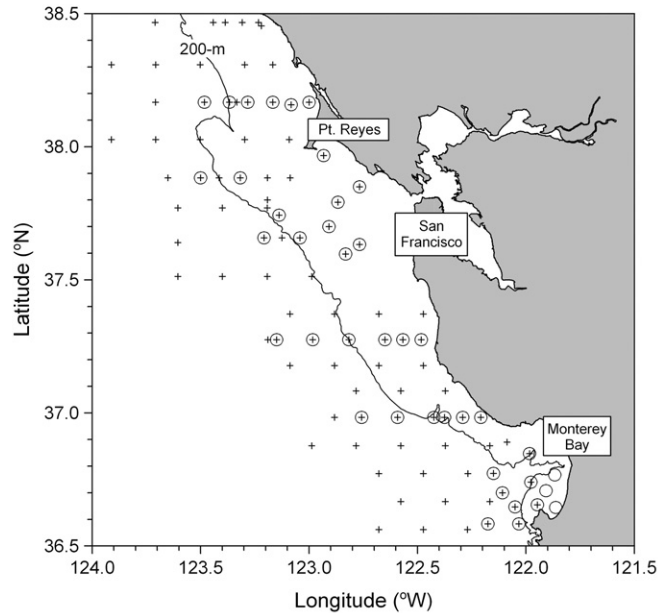

Fig. 1. Map of the core survey area showing station locations where midwater trawling is conducted (circles) and conductivity–temperature–depth (CTD) casts are completed (+).

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