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Rockfish assemblage structure and spawning locations in southern California identified through larval sampling

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ABSTRACT: Differences in oceanographic conditions over short distances can dramatically affect the distribution of marine organisms over small spatial scales. In southern California, oceanographic conditions vary widely from east to west as the offshore region is impacted by cool, southern flowing California Current water, while the inshore is typically warmer and more productive. We investigated how patterns of distribution and abundance of larval, genetically-identified rockfishes related to environmental conditions off southern California, the world's center of rockfish *Sebastes* spp. species diversity. The rockfish assemblage was dominated by small and short-lived species not typically targeted by recreational or commercial fishing (i.e. shortbelly, *S. jordani* and squarespot, *S. hopkinsi* rockfishes), but also contained moderate abundances of a few larger, targeted species (bank, *S. rufus* and bocaccio, *S. paucispinis* rockfishes). Spawning locations of many species were affected by environmental variability, as abundances of young (0 to 2 d old), targeted larvae were mainly found offshore in the cool, low primary production waters that also were relatively shallow and contained hard substrate. In contrast, untargeted species were more widespread and correlated positively only with hard substrate. Hotspots of species richness and targeted species were high within a large managed region, the Cowcod Conservation Area, indicating that it is effectively protecting important rockfish spawning habitat. This research highlights the need to account for environmental variation in habitat and assemblage structure when conducting marine spatial planning.

KEY WORDS: *Sebastes* · Southern California · Ecosystem based management · Conservation · Biogeography

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INTRODUCTION

The suitability of spawning habitat in any ecosystem is affected by prevailing environmental conditions. Within marine ecosystems, habitat variability is often not immediately apparent, but nonetheless can exert a major effect on species composition and abundance (Witman & Roy 2009, Belanger et al. 2012, Fenberg et al. 2015). In particular, locations where 2 or more water masses with differing physical properties adjoin (i.e. ocean fronts), are an example of a type of transition zone in oceanic systems. Studies from around the world have demonstrated that species assemblages often vary dramatically on either side of an ocean front (Moser & Smith 1993, John et al. 2001, 2004, Keane & Neira 2008, McClatchie et al. 2012). Whereas some fronts are spatially ephemeral (e.g. eddies), others are present in roughly the same location for long periods of time. These fronts can thus affect the distribution of organ-

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isms such as rockfishes *Sebastes* spp. in marine ecosystems.

Southern California is the world's center of rockfish biodiversity (at least 55 species have been observed in this region; Love et al. 2002) and is highly spatially variable in terms of its oceanography and bathymetry. The ocean off southern California is characterized by several frontal zones as cool, low-salinity Pacific subarctic water (i.e. California Current) flows into the region from the north and abuts relatively warm, saline Equatorial Pacific water inshore that enters the region at depth from the south (California Undercurrent) and relatively high temperature, saline water (North Pacific Central) offshore (see Figs. 1 & 2; reviewed by Checkley & Barth [2009], McClatchie [2013]). These oceanographic transitions, along with shifts in depth and benthic habitat composition, affect the biogeographic distribution of marine organisms and may impact the assemblage structure of rockfishes (Horn & Allen 1978, Blanchette et al. 2008, Hamilton et al. 2010, Fenberg et al. 2015). In fact, rockfishes may be particularly affected by long-term oceanographic conditions because most adults reside in benthic habitats and are relatively site-attached. Understanding how rockfish spawning is affected by this spatial environmental variability is crucial for marine spatial planning.

Rockfishes fill integral ecological and economic roles throughout the west coast of North America. From an ecological perspective, smaller, short-lived species such as halfbanded rockfish *Sebastes semicinctus* that grow to only 25 cm and live to 15 yr as well as larvae and juveniles from all species provide important forage for higher trophic level fishes, marine mammals, and birds (Thompson et al. 2012). By contrast, larger species such as cowcod *S. levis* that live at least 55 yr and grow to 94 cm, and yelloweye rockfish *S. ruberrimus* that can live to 118 yr and grow to 91 cm are apex predators (Love et al. 2002). From an economic perspective, the larger rockfishes are important components of recreational and commercial fisheries off the west coast of Canada, the United States, and Mexico (Love et al. 2002). Given the ecological and economic importance of the rockfish assemblage, more information on the distribution of the various species is needed to better manage them in an ecosystem-based context.

Many of the larger rockfish species were historically overfished and their populations have been severely depleted, leading the United States National Marine Fisheries Service (NMFS) to formally declare several species as 'overfished'. As a ramification of this designation, highly constraining management measures, such as the establishment of marine protected areas (MPAs; spatially delineated regions where fishing is restricted to some degree) were established to help rebuild depleted populations (Butler et al. 2003, Berkeley et al. 2004, Field et al. 2006). Ideally, MPAs protect important spawning locations such that larvae help replenish not only populations within the reserve itself, but also seed locations in the broader region (Pelc et al. 2010). These spatially-delineated areas may be particularly suitable for mediating rockfish exploitation as many rockfishes are site-attached and maintain small home ranges relative to pelagic fishes (Love et al. 2002). Therefore, to determine where to place reserves, it is important to identify spawning hotspots and define the environmental factors that characterize these regions.

Determining the relative abundances and distribution of the entire rockfish assemblage is difficult. Since traditional sampling methods such as hook and line fishing or trawling are typically lethal, these techniques are constrained within the bounds of some Rockfish Conservation Areas (RCAs) (Field et al. 2006). Furthermore, these methods capture only a subset of the assemblage, as smaller species will often not bite hooks (M. Love pers. comm.) and trawls cannot operate in rocky habitats where many species reside. In addition, because of the large sample frame, thorough sampling throughout southern California is logistically difficult using direct observation techniques such as submersibles (Yoklavich et al. 2007, Stierhoff et al. 2013). Fortunately, all rockfish species release pelagic larvae that are susceptible to capture by plankton nets. Several studies have shown that larval abundance and female spawning stock biomass for groundfishes are highly correlated; thus, larval abundances can be used as proxies for relative population sizes (Moser et al. 2000, Ralston et al. 2003, Ralston & MacFarlane 2010) and have been employed as such in stock assessments of shortbelly rockfish *S. jordani* (Field et al. 2007), cowcod *S. levis* (Dick & MacCall 2014), and *S. paucispinis* (Field 2014). Here, we utilized larval samples to evaluate the relative abundance and spawning locations of rockfishes off the coast of southern California.

Identification of spawning habitat through larval sampling can be problematic because larvae have the potential to drift away from their natal habitat. To overcome this issue, we measured the total length of each larvae and assessed ages based on published length–age relationships. We then focused distribution analyses only on very young larvae (0 to 2 d old), which have been shown to remain close to their birth

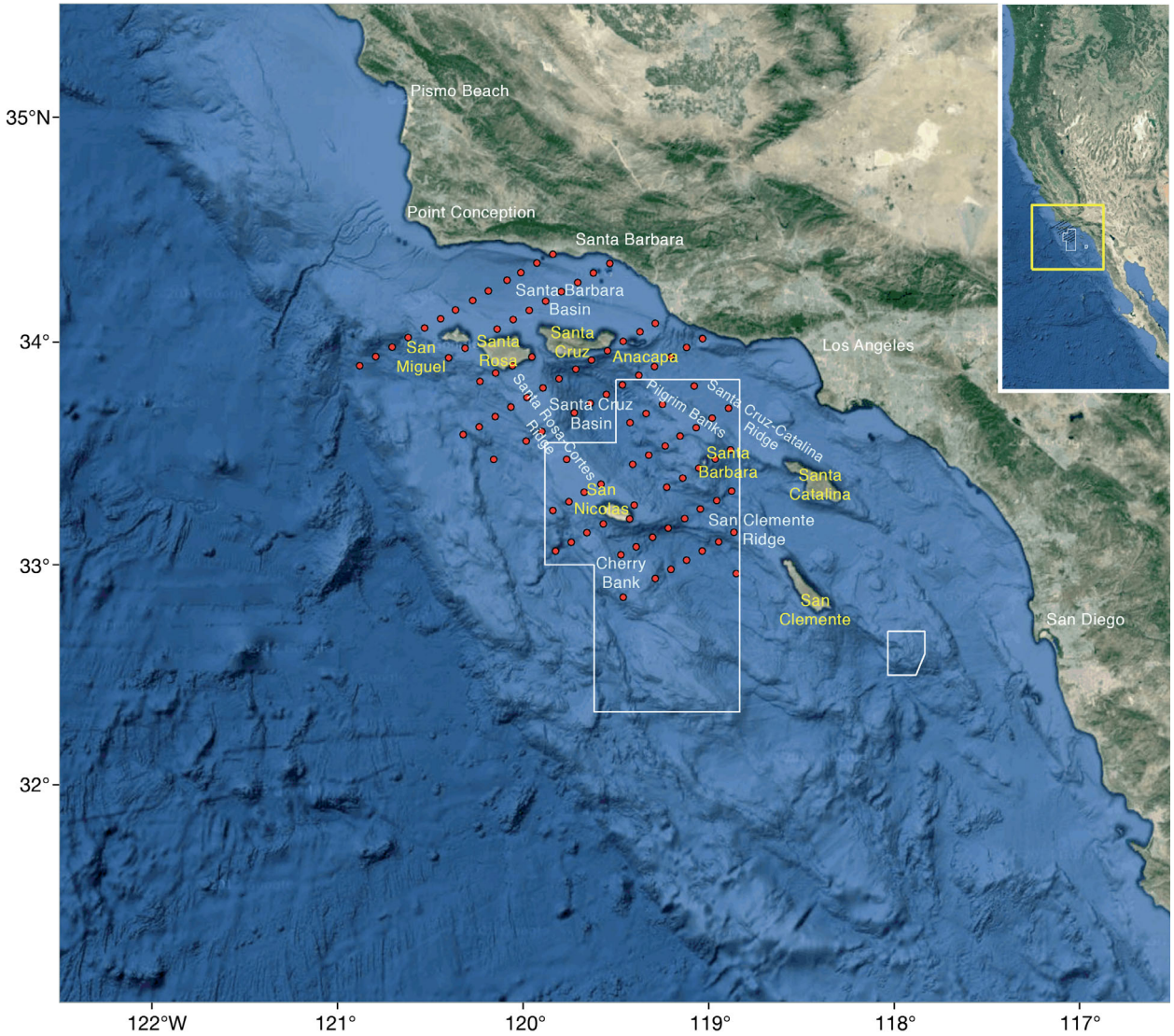

Fig. 1. Study site off the coast of California (yellow border on inset map) depicting location of sampling stations (circles). Channel Island names are in yellow, geological features in light green, and cities in white. Areas outlined in white within the study frame: Cowcod Conservation Areas

locations during the winter in southern California (Hitchman et al. 2012). Winter is the ideal time to identify spawning locations with larval data as this is the peak spawning time for rockfishes (Moser et al. 2001) and currents are typically relatively weak (Lynn & Simpson 1987, Taylor et al. 2004). Although most rockfish larvae cannot be reliably identified to species based on morphology, they can be identified using molecular genetics techniques (Taylor et al. 2004). In this study, we genetically identify rockfish larvae collected in southern California in order to (1) characterize community structure to determine the relative prevalence of small, untargeted versus large, targeted species, and (2) better understand where hotspots of rockfish species richness and the abundances of species that are and are not targeted by fishers are located, and how environmental conditions affect these patterns.

MATERIALS AND METHODS

Sampling and data acquisition

Plankton tows and oceanographic measurements were taken from 95 locations (Fig. 1) between 4 and 20 February 2005, which is the peak annual parturition period of rockfishes (Wyllie Echeverria

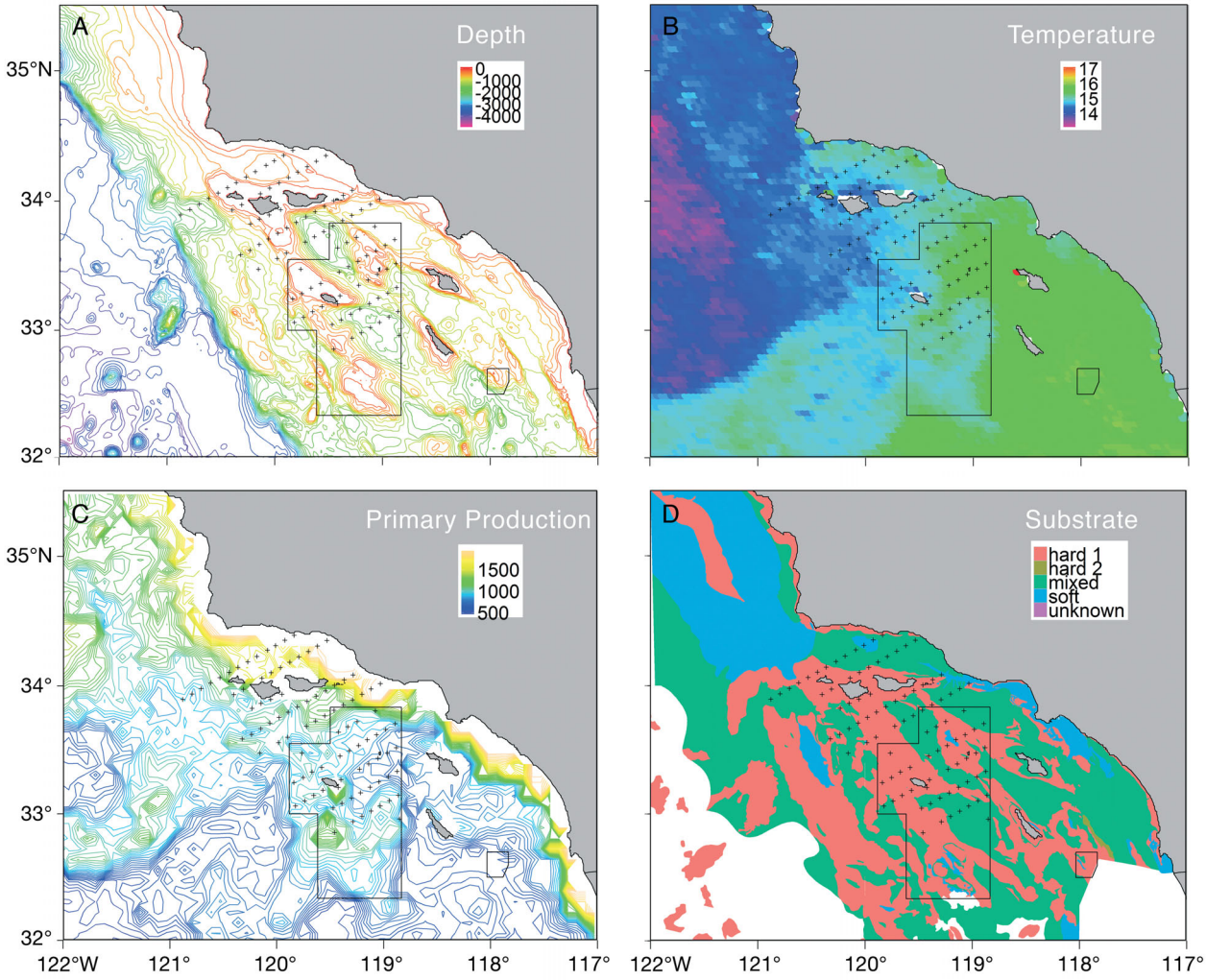

Fig. 2. Distribution of habitat features used as dependent variables: (A) depth (in m), (B) temperature (°C), (C) primary production (mg C m^{-2} d^{-1}), and (D) location of hard substrate making up the benthic environment. 'Hard' 1 and 'Hard' 2 categories were combined into the 'hard substrate' category used in the analyses

1987). The sampling area was environmentally variable and included at least 3 regions known to be oceanographically distinct: one influenced by the California Current in the west, one by the Santa Barbara Channel in the northeast, and one affected by the California Undercurrent in the southeast (Fig. 2). Samples were taken along 10 lines, positioned roughly perpendicular to the coast; lines were separated by 18 km, and stations within lines by 9.5 km.

Plankton collection followed techniques utilized by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program (McClatchie 2013). Bongo nets (71 cm mouth opening, 0.505 mm mesh) equipped with a flowmeter were lowered to 210 m (or 15 m from the bottom at shallow stations), then towed to the surface at a 45° angle at an in-water speed of 0.51 to 1.03 m s^{-1}. For this study, we analyzed the contents of the port side of the bongo nets, which were preserved in 95% ethanol.

In contrast to standard CalCOFI sampling, CTD samples were not collected alongside plankton tows. Therefore we used satellite measurements of sea surface temperature (SST; Pathfinder v.5 5.5 km SST monthly composite) and surface primary production (PP; SeaWiFS 7.6 km monthly composite) data that was downloaded from NOAA's CoastWatch Browser website (http://coastwatch.pfeg.noaa.gov/). We then determined average temperature and primary production within 5 km of each station. To account for the potential effect of benthic substrate on rockfish distribution, we obtained shapefiles delineating the

benthos into hard, soft, and mixed substrate throughout the study region from the Seafloor Mapping Lab at California State University, Monterey Bay (http://seafloor.otterlabs.org/contact.html). These data were used to determine the proportion of each substrate type within 5 km of each station. Bottom depth was also logged from all stations at the time of larval collection.

In the laboratory, all fish larvae were sorted from each plankton sample, and those morphologically identified as rockfish were separated from the remainder. Most rockfish larvae were identified by sequencing 625 base pairs of the mitochondrial cytochrome *b* gene and comparing this sequence to that of reference adult rockfishes (see Appendix 1A). Individuals that were unambiguously determined to be *S. jordani* based on their morphology were not sequenced.

Samples with >100 individuals were subsampled. Here, larvae other than *S. jordani* were sorted into 2 crude categories: with or without dorsal pigment. At least 50% of the larvae from each category were sequenced and the proportion of individuals of each species was extrapolated to the total number in a sample. In total, 3326 of 5018 larvae were genetically identified. To account for (typically slight) differences in tow lengths or depths among stations, we standardized the raw larval count data by multiplying by a 'standard haul factor' (Smith & Richardson 1977) to express larval abundances as larvae under 10 m^2 of sea surface area.

Total lengths of all genetically identified larvae were measured using a micrometer. Sizes of larvae not included in subsampled stations were estimated based on the size distributions of larvae that were identified. Specifically, we determined the mean and standard deviation of sizes from each identified species and randomly selected from this distribution size estimates for the unidentified larvae.

Analysis

Overview of the larval rockfish assemblage

Our first goal was to characterize relative abundances and proportion of stations occupied by each species. In addition, we evaluated the proportions of the assemblage comprised of species that were (and were not) targeted by fishers. Categorization of fishes into targeted (moderate or high fishing pressure) and non-targeted (no or low pressure) were based on species descriptions in Love et al. (2002).

Univariate analyses: influence of environment on spawning locations

We evaluated the influence of temperature, primary production, hard substrate and depth of spawning locations on 3 variables that are important to conservation and management: overall species richness (the total number of species spawning at a given station), and the abundances of fishes targeted and not targeted by fishers. To minimize the potential that drift disassociated larvae from their natal habitat, we restricted this analysis to larvae that were <5 mm total length. Previous research on age–length relationships using otolith analysis of *S. paucispinis* larvae indicated that 86% of larvae <5 mm were <3 d old and 72% were <2 d old (Hitchman et al. 2012). We thus made the assumption that these smaller larvae were very young and likely close to their birth location.

We used generalized linear models with a negative binomial distribution and a log link to evaluate the relationship between the abundance of <5 mm larvae (i.e. dependent variables) and the 4 environmental (i.e. independent) variables. Preliminary analyses indicated that the dependent variables were all not normally distributed (thus precluding the use of simple general linear models) and that a negative binomial model was more appropriate than either Poisson or zero-inflated models. We also found that residuals from species richness models were spatially autocorrelated, which violates the model assumption that samples are independent from one another (Dormann et al. 2007). Thus, we used a spatial generalized linear mixed model where the spatial covariance structure was explicitly included with a Gaussian correlation structure in the variance–covariance matrix (Dormann et al. 2007) to evaluate the effect of the environment on species richness.

We tested the relative plausibility of 15 candidate models that included various combinations of depth, proportion of hard substrate, and satellite-derived estimates of primary production and sea surface temperature (Table 1) using a model-selection approach based on Akaike's Information Criterion controlled for small sample size (AICc) scores. We limited models to include only additive (not interactive or quadratic) terms. To assess which independent variables impacted the dependent variables, we calculated model-averaged slopes and 90% confidence intervals for depth, hard substrate, primary production, and temperature. Independent variables were considered important if the confidence intervals did not overlap with zero.

Table 1. Candidate models used to evaluate the effect of covariates on rockfish species richness, abundance of targeted and non-targeted species, and assemblage structure

Model	Independent variables
1	~Temperature
2	~Primary production
3	~Hard substrate
4	~Depth
5	~Temperature + primary production
6	~Temperature + hard substrate
7	~Temperature + depth
8	~Primary production + hard substrate
9	~Primary production + depth
10	~Hard substrate + depth
11	~Temperature + primary production + hard substrate
12	~Temperature + primary production + depth
13	~Temperature + hard substrate + depth
14	~Primary production + hard substrate + depth
15	~Temperature + primary production + hard substrate + depth

Assemblage structure

To visualize assemblage structure, we performed a non-metric multidimensional scaling (NMDS) analysis on log-transformed abundances. To correct for bias induced by rare species, we included only species with total abundances >100 under 10 m^2 (Table 2) and stations with at least 50 larvae under 10 m^2. The stress value for this plot was <0.20, thus suggesting that 2 dimensions were sufficient to characterize assemblage structure (Clarke & Gorley 2001). To visualize how NMDS values varied geographically, we color-coded points according to whether stations were found in the northeast, northwest, southeast, or southwest regions and created maps in which stations were colored according to values of NMDS axes 1 and 2 (NMDS1 and NMDS2). We then tested the relative plausibility of

Table 2. Rockfish *Sebastes* spp. larval abundance (no. under 10 m^2 sea surface area), proportion of total larval abundance, and proportion of stations where a species was present at least once. Species are ordered by abundance. Fishing pressure is based on Love et al. (2002). Shading scales to relative values within each column

Species	Common name	Fishing pressure	Abundance (no. 10 m^{-2})	Proportion of total	Proportion of stations present
S. jordani	Short belly	Low	9195	0.3783	0.81
S. hopkinsi	Square spot	Low	6756	0.278	0.65
S. wilsoni	Pygmy	None	1962	0.0807	0.45
S. ensifer	Swordspine	Low	1374	0.0565	0.43
S. semicinctus	Halfbanded	Low	810	0.0333	0.28
S. paucispinis	Bocaccio	High	791	0.0325	0.43
S. rufus	Bank	High	632	0.026	0.38
S. moseri	Whitespeckled	None	491	0.0202	0.28
S. mystinus	Blue	High	447	0.0184	0.12
S. ovalis	Speckled	High	326	0.0134	0.17
S. rufinanus	Dwarf-red	None	163	0.0067	0.15
S. entomelas	Widow	High	138	0.0057	0.11
S. serranoides	Olive	Moderate	136	0.0056	0.13
S. levis	Cowcod	High	130	0.0053	0.11
S. goodei	Chilipepper	High	125	0.0052	0.17
S. melanostomus	Black	High	123	0.005	0.12
S. saxicola	Stripetail	Low	103	0.0043	0.08
S. caurinus	Copper	High	102	0.0042	0.12
S. elongatus	Greenstriped	Moderate	94	0.0039	0.09
S. rosaceus	Rosy	Low	86	0.0035	0.07
S. aurora	Aurora	Moderate	49	0.002	0.07
S. rosenblatti	Greenblotched	Moderate	45	0.0018	0.03
S. diploproa	Splitnose	Moderate	44	0.0018	0.07
S. constellatus	Starry	High	30	0.0012	0.03
S. macdonaldi	Mexican	Low	24	0.001	0.02
S. simulator	Pinkrose	Low	19	0.0008	0.01
S. crocotulus	Sunset	High	19	0.0008	0.04
S. rastrelliger	Grass	High	18	0.0008	0.01
S. helvomaculatus	Rosethorn	Moderate	14	0.0006	0.02
S. gilli	Bronzespotted	Low	10	0.0004	0.02
S. flavidus	Yellowtail	High	10	0.0004	0.01
S. phillipsi	Chameleon	Low	10	0.0004	0.02
S. carnatus/chrysomelas	Gopher/black and yellow	High	10	0.0004	0.02
S. miniatus	Vermillion	High	9	0.0004	0.02
S. rubrivinctus	Flag	Moderate	5	0.0002	0.01
S. umbrosus	Honeycomb	Moderate	5	0.0002	0.01

the same 15 candidate models used previously (Table 1) to explain variability in NMDS1 and NMDS2. The NDMS scores met normality assumptions so we used general linear models for these analyses. There was no evidence of spatial autocorrelation in model residuals.

All analyses and figures were produced using various packages (see Appendix 1B) in program R v.3.1.1 (R Development Core Team 2014).

RESULTS

Overview

The rockfish assemblage off southern California was dominated by non-targeted species as the 4 most common species (*Sebastes jordani*, *S. hopkinsi*, *S. wilsoni*, and *S. ensifer*) comprised 79% of the total larval abundance. Within the non-targeted category, *S. jordani* and *S. hopkinsi* were particularly important and together made up 66% of the untargeted larval abundance (Table 2, Appendix 1). *S. jordani* and *S. hopkinsi* were also spatially widespread as they were present in 81 and 65% of the sample stations, respectively. Driven by the prevalence of these 2 species, non-targeted species were 6.4 times as abundant as targeted species. Among the 22 observed targeted species, 3 (*S. rufus*, *S. paucispinis*, and *S. mystinus*) made up 57% of the total targeted abundance. *S. paucispinis* and *S. rufus* were the most widely dispersed targeted species and were found at 43 and 38% of stations, respectively (Table 2).

Univariate analyses

Species richness tended to be highest in the western region of the sample area, along the Santa Rosa-Cortes Ridge that connects Santa Rosa and San Nicolas Islands (Figs. 1 & 3A). In particular, an especially specious station was found just south of San Nicolas Island over Cherry Bank where 21 species were detected (Fig. 3A). Model selection (Table 3) indicated that the 3 most plausible models relating environment to species richness contained hard substrate and primary production (Table 3). The best model (hard substrate + primary production) explained 12%

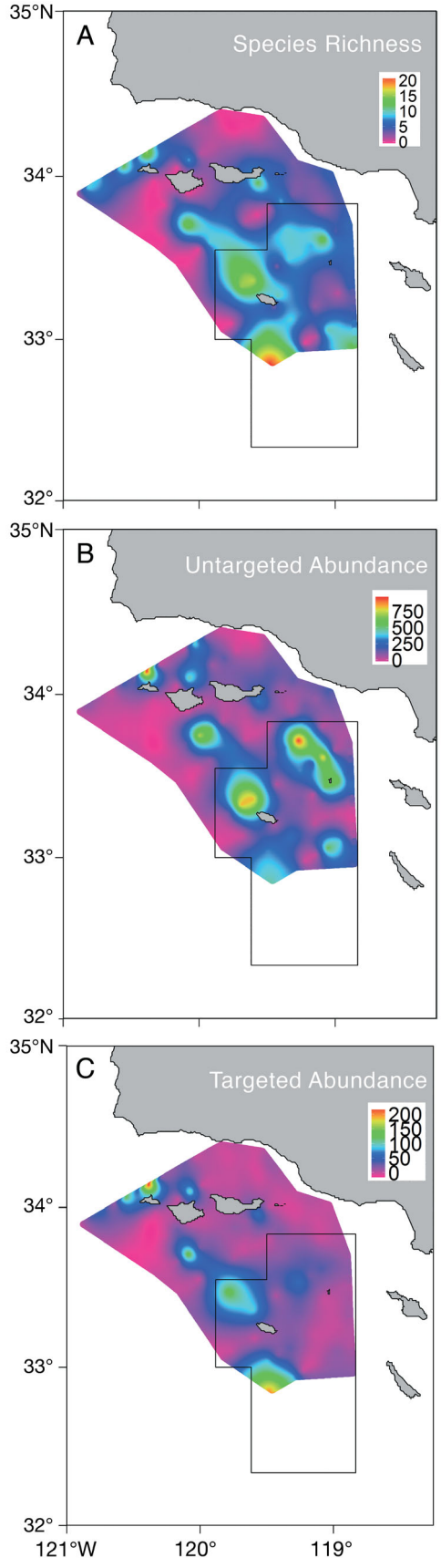

Fig. 3. Krige maps of rockfish *Sebastes* spp. (A) species richness, and abundances of (B) untargeted and (C) targeted species. Color shading gradient represents number of rockfish larvae under 10 m^2 of sea surface area

Table 3. Most plausible models relating rockfish *Sebastes* spp. species richness and the abundances of targeted and untargeted species to the environment. *K*: number of parameters in the model; AICc: Akaike's Information Criterion score adjusted for small sample size; ΔAICc: difference in AICc scores between a given model and the most plausible model; AICcWt: weight of a given model; Cum.Wt: cumulative weight of a given model plus the weight of more plausible models; LL: log likelihood; Prop. deviance: proportion of total deviance explained by the most plausible model. PP: primary production; temp: temperature

Dependent variable	Model	*K*	AICc	ΔAICc	AICcWt	Cum.Wt	LL	Prop. deviance
Species richness	Hard substrate + PP	3	512.43	0	0.35	0.35	−253.08	0.12
	Hard substrate + PP + temp	4	514.15	1.72	0.15	0.5	−252.85	
	Hard substrate + PP + depth	4	514.42	1.99	0.13	0.62	−252.99	
Untargeted abundance	Hard substrate + temp	3	897.65	0	0.35	0.35	−445.66	0.09
	Hard substrate	4	899.76	2.11	0.12	0.47	−445.6	
	Hard substrate + temp + depth	4	899.86	2.21	0.11	0.58	−445.66	
Targeted abundance	Hard substrate + PP + temp	4	670.77	0	0.54	0.54	−331.16	0.20
	PP + temp + depth	4	671.69	0.93	0.34	0.87	−331.62	

Table 4. Model-weighed estimates of slope and 90% confidence intervals (in parentheses) for each environmental parameter for the dependent variables rockfish *Sebastes* spp. species richness, abundance of untargeted species and abundance of targeted species. Slopes with confidence intervals that do not overlap 0 are in **bold**

	Species richness	Untargeted species	Targeted species
Temperature	0.28 (−0.30 to 0.86)	1.037 (−0.019 to 2.09)	**−2.46 (−3.67 to −1.26)**
Primary production	**−0.00069 (−0.0012 to −0.00017)**	−0.00049 (−0.0016 to 0.00063)	**−0.0031 (−0.0045 to −0.0017)**
Depth	0.00016 (−0.00036 to 0.00068)	−0.00042 (−0.0012 to 0.00034)	**−0.00098 (−0.0018 to −0.00021)**
Hard substrate	**0.76 (0.24 to 1.27)**	**1.25 (0.51 to 1.20)**	**1.53 (0.67 to 2.38)**

of the deviance. Model averaging showed that primary production and hard substrate were negatively and positively related to species richness, respectively (Table 4).

Distribution patterns were quite different between non-targeted and targeted species (Fig. 3B,C; grouping of each species is defined in Table 2). While abundances of non-targeted species were fairly evenly spread between the west (Santa Rosa-Cortez Ridge) and east (Pilgrim Bank) (Fig. 3B), targeted species were much more abundant in the west (Fig. 3C). Indeed, the 10 stations with the highest abundances of fished species were all found in the west. The 2 stations with the highest abundance of fished species were detected on Cherry Bank and just north of San Miguel Island.

There were also differences between the environmental factors affecting untargeted and targeted species (Tables 3 & 4). The top 3 models for untargeted species all contained hard substrate, which was the only variable in which the 90% confidence intervals of the slope did not overlap zero (Tables 3 & 4). By contrast, the top 2 models for targeted species contained some combination of all independent variables and the confidence intervals for the slopes of each did not overlap with zero (Table 4). Notably, the model correlating all 4 independent variables to targeted species failed to converge and thus was excluded from model selection and averaging. The best model for untargeted species (positive relationship with hard substrate) explained 9% of the total deviance, whereas the top model for targeted species (negative relationships with temperature, primary production and depth, positive with hard substrate) explained 20% of the deviance.

Assemblage structure

Negative values of NMDS1 characterized stations that were largely dominated by 2 untargeted species: *S. jordani* and *S. semicinctus*. By contrast, high values of NMDS1 depicted stations with several targeted species such as *S. levis*, *S. paucispinis*, *S. ovalis*, and *S. entomelas*, as well as untargeted, diminutive species such as *S. rufinanus* and *S. wilsoni* (Fig. 4A,B). There was clear geographic separation between locations with high and low NMDS1 values, as most of the stations with negative scores were found in the northeast and southeast, all stations in

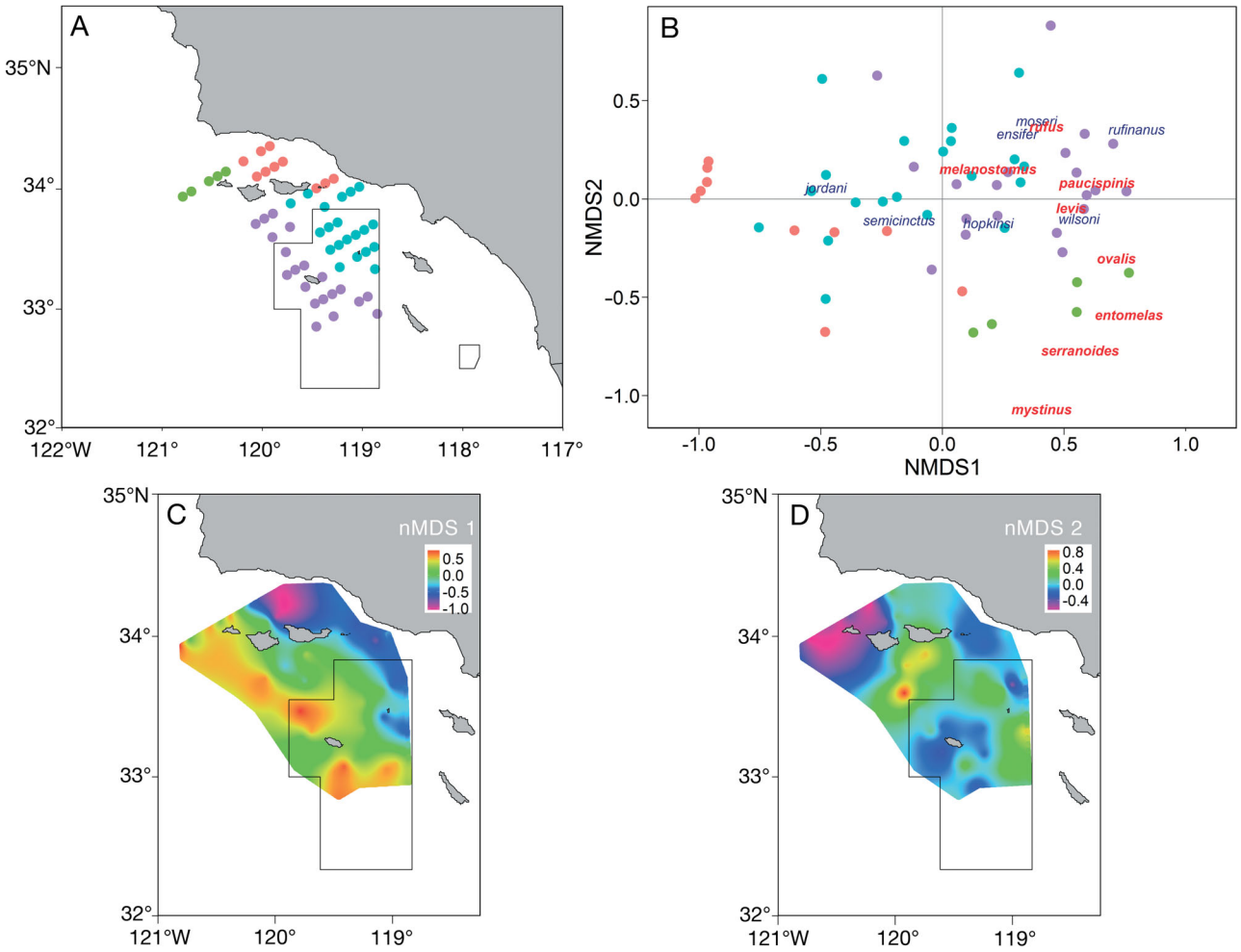

Fig. 4. (A) Sampling locations of rockfish *Sebastes* spp., color-coded by region (red: northeast; green: northwest; blue: southeast; purple: southwest). (B) Non-metric multidimensional scaling (NMDS) plot of species and stations (stress = 0.17). Stations are colored as in (A); red species names are targeted and blue species are not targeted by fishers. Krige maps of (C) NMDS1 and (D) NMDS2. Only species with total abundances >100 under 10 m^2 sea surface area (see Table 2) and stations with at least 50 larvae under 10 m^2 were included in this analysis

the northwest had positive NMDS1 values, and 85% of stations in the southwest had positive NMDS1 (Fig. 4A–C). The most plausible model evaluating the relationship between NMDS1 and the environment explained 48% of the variation and included all 4 environmental variables (Table 5). Model averaging indicated that NMDS1 was negatively related with temperature and primary production and positively correlated with depth and hard substrate (Table 6).

Table 5. Most plausible models relating non-metric multidimensional scaling (NMDS) axes 1 and 2 to the environment. Column headings and abbreviations are the same as in Table 3

Dependent variable	Model	*K*	AICc	ΔAICc	AICcWt	Cum.Wt	LL	Adj R^2
NMDS1	Hard substrate + PP + temp + depth	6	52.41	0	0.7	0.7	−19.33	0.48
	PP + temp	4	56.23	3.83	0.1	0.8	−23.72	
NMDS2	Temp	3	32.14	0	0.33	0.33	−12.83	0.09
	PP + temp	4	33.95	1.82	0.13	0.47	−12.58	
	Temp + depth	4	34.09	1.96	0.13	0.59	−12.65	

Table 6. Model-weighed estimates of slope and 90% confidence intervals (in parentheses) for each environmental parameter for non-metric multidimensional scaling (NMDS) axes 1 and 2. Slopes with confidence intervals that do not overlap 0 are in **bold**

	NMDS1	NMDS2
Temperature	**−0.57 (−0.90 to −0.24)**	**0.36 (0.11 to 0.61)**
Primary production	**−0.00058 (−0.00094 to −0.00021)**	−0.000087 (−0.00030 to 0.00013)
Depth	**0.00038 (0.00010 to 0.00065)**	0.000064 (−0.000087 to 0.00021)
Hard substrate	**0.54 (0.16 to 0.93)**	0.070 (−0.15 to 0.29)

Extreme (negative) values of NMDS2 described stations with high abundances of *S. mystinus* and *S. serranoides* (Fig. 4B). There was also geographic separation in NMDS2 scores as all stations in the northwest had low values on this axis (Fig. 4A,B,D). Model selection indicated that the best model characterizing the variation in NDMS2 contained only temperature (Table 5). Model averaging showed that NMDS2 correlated positively with temperature (Table 6).

DISCUSSION

The primary goals of this study were to determine the relative abundance of larvae from targeted versus untargeted rockfishes and to understand how environmental variability affects spawning locations in terms of overall species richness and the abundances of targeted and untargeted species. Results suggest that the larval rockfish assemblage is dominated by smaller, short-lived species such as *Sebastes jordani* and *S. hopkinsi*, a finding that has also been documented with underwater submersible surveys (Love et al. 2009). In addition, we found significant correlations between temperature and the abundance of targeted species and overall community structure; between primary production and species richness and the abundance of targeted species; between depth and targeted species and overall assemblage structure; and between hard substrate and all dependent variables.

Ecological theory can help contextualize our finding that small species dominate the rockfish assemblage. According to successional theory, mature ecosystems are characterized by organisms of large average sizes and high trophic levels (Odum 1969). However, anthropogenic actions often induce reverse succession by, for example, targeting large, high trophic level fishes (Pauly et al. 1998). Because this dynamic occurs in many marine ecosystems worldwide, recent efforts have focused on evaluating ecosystem health, in part by monitoring trophic positioning within an ecosystem (Sandin & Sala 2012). The preponderance of small, non-targeted rockfish species found in our study suggests that this rockfish assemblage is in 'poor' health. That small, non-targeted rockfishes dominate the benthic fish community in southern California was also found through extensive submersible surveys between 1995 and 2006 (Love et al. 2009), and by genetically-identified larval rockfishes collected during the April 1999 CalCOFI survey (Taylor et al. 2004). Although there are currently no species-specific, fishery-independent time series of rockfish assemblage dynamics, analysis of recreational fishing data shows that catch per unit effort of large rockfishes such as *S. paucispinis*, olive rockfish *S. serranoides*, *S. mystinus*, and *S. levis* declined by 2 to 3 orders of magnitude between 1980 and 1996, and that the relatively small and short-lived *S. hopkinsi* went from being the 16th to the 1st most commonly caught fish during that time (Love et al. 1998). This suggests that the assemblage was in a more mature successional state in 1980 than in the mid-2000s. In an attempt to facilitate the recovery of the rockfish assemblage, several marine reserves including the large Cowcod Conservation Areas (CCAs) were instituted over the past 25 yr in southern California (Fig. 1) (Butler et al. 2003, Hamilton et al. 2010, CDFW 2014). It is possible, however, that succession has been impeded if the copious smaller species compete or directly consume larvae or juveniles of larger species (Baskett et al. 2006). We are currently working to build a time-series of genetically-identified rockfish larvae to determine whether the influence of targeted versus untargeted species has changed over the past decades (A. R. Thompson unpubl. data).

Hard substrate correlated positively with each dependent variable. This finding agrees with manned submersible surveys of 25 adult rockfishes, which demonstrated that each species mainly associated with high or low relief rocky substrate (Love et al. 2009). In addition to direct observation, surveys focusing on young rockfish larvae also found that larvae in this life stage are found near adult spawning habitat. For

example, the distribution of *S. paucispinis* larvae that were identified to be 0 to 2 d old by counting daily deposited rings on otoliths were significantly negatively associated with depth, while older larvae were not (Hitchman et al. 2012). Similarly, Taylor et al. (2004) demonstrated that the youngest larvae of some rockfishes were associated with potential adult habitat in southern California. Notably, correlation between larvae and hard substrate broke down in our study when larvae of all sizes were analyzed (results not shown), emphasizing the need to focus on young individuals when seeking to use larvae to elucidate spawning locations. Our results, along with those of other studies demonstrate the strong association of rockfishes with coarse benthic habitat.

Depth correlated negatively with the abundance of targeted species, suggesting that these rockfishes were found in relatively shallow areas. This result superficially contrasts with depth ~ rockfish correlations identified by Love et al. (2009), who concluded that 3 clusters of rockfish species were divided among shallow, medium, and deep habitats. This discrepancy, however, can be explained by differences in the range of depths analyzed by their study and ours. Whereas their deep habitat averaged 168 m, depths in our study ranged from 51 to 1800 m. Indeed, examination of abundance ~ depth relationships for targeted species in our study showed that most individuals were located at depths <500 m. In addition to targeted species, NMDS1 correlated positively with depth. Further examination of this pattern revealed that this relationship is actually driven by a negative relationship between *S. jordani* and depth, as this species loaded heavily, and negatively on NMDS1. *S. hopkinis*, the second most common untargeted species, however, had no relationship with depth, thus likely rendering the relationship of combined untargeted species with depth insignificant.

Temperature correlated negatively with the abundance of targeted species and NMDS1 (which characterized a gradient between untargeted and targeted species) and positively with NMDS2 (*S. mystinus* loaded strongly and negatively on NMDS2). The negative relationship with temperature reflects the presence of many species in the western part of the sampling area, which is influenced by the relatively cool and fresh southward-flowing California Current (Figs. 2 & 3). The affinity for cooler water in southern California is likely a product of a greater northern than southern extent of biogeographic ranges of many of the targeted species. For example, the ranges of the 3 most common targeted species, *S. rufus*, *S. paucispinis*, and *S. mystinus*, all extend more than 2500 km to the north, but only approximately 600 km to the south of Point Conception (Love et al. 2002). Therefore, it is likely that these fishes prefer cooler water, and that the warmer water in southern California is approaching their thermal tolerance. The lack of correlation between non-targeted species and temperature was driven by the most abundant species in our study, *S. jordani*. In contrast with the majority of species that we collected, Point Conception is approximately in the center of this species' range (which extends from the tip of Baja California to the state of Washington) and thus it likely has broad tolerance of the thermal habitat throughout southern California. In addition to our work, studies of fish distributions also found an effect of temperature on assemblage structure in the continents of Africa (John et al. 2001), Australia (Keane & Neira 2008), Europe (Roussel et al. 2010), North America (Funes-Rodríguez et al. 2011), and South America (Landaeta et al. 2008). These findings suggest that thermal tolerance may affect the distribution of rockfishes within southern California and around the world.

Primary production was negatively correlated with species richness, the abundance of targeted species, and NMDS1. Primary production tended to be highest in nearshore areas as well as the northeast region (i.e. the Santa Barbara Channel). Midwater trawl surveys in the Santa Barbara Channel revealed that this region was depauperate relative to other areas in the Southern California Bight, and that the presence of fishes was highly dependent on the formation of a cyclonic eddy within the channel (Nishimoto & Washburn 2002). Further, CalCOFI surveys from 1951 to 1998 in southern California showed that the abundance of unidentified rockfish larvae (*Sebastes* spp.) was much lower at stations inshore and in the Santa Barbara Channel than in the regions we defined (Fig. 4A) as northwest, southwest, and southeast (Moser et al. 2001). This suggests that the overall lack of rockfishes in areas with high primary production is a long-term characteristic of the rockfish assemblage in southern California.

The negative relationship between primary production and larval abundance was interesting as it has been hypothesized that spawning takes place in productive regions where there is ample food for larvae to consume (i.e. the match–mismatch hypothesis; Cushing 1975). Indeed, studies have documented a positive correlation between primary production as reflected by chlorophyll *a* (chl *a*) and larval or egg abundances for species such as northern anchovy

(Weber & McClatchie 2010) and Pacific sardine (Weber & McClatchie 2010, Zwolinski et al. 2011) in the California Current ecosystem. However, Auth (2009) also found a negative correlation between fluorescence (a proxy for primary production) and the abundance of rockfish larvae off the coasts of Oregon and Washington between 2004 and 2009, suggesting that this may be a general pattern within the California Current System. A potential explanation for these negative correlations is that because fish larvae typically feed on zooplankton rather than phytoplankton (Arthur 1976, Sumida & Moser 1984, Heath & Lough 2007, Swalethorp et al. 2014), primary production does not accurately reflect the larval rockfish prey field. It is possible, in fact, that phytoplankton standing stock would be lower in areas with abundant zooplankton if the zooplankters were grazing down the phytoplankton. Future research that includes the composition of the zooplankton assemblage as a potential predictor of larval abundance would help resolve this issue. Another possibility is that locations with high primary production (e.g. the Santa Barbara Channel and nearshore) coincidentally happen to be located in places with unsuitable rockfish benthic habitat. Specifically, the Santa Barbara Channel has the lowest amount of hard substrate of the 4 zones defined in this study, and as discussed previously, many rockfishes prefer hard substrate (Love et al. 2009).

The relationship between oceanographic conditions and assemblage structure likely reflects long-standing oceanographic variability that affects the biogeography of many marine species in southern California. Due to the equatorward offshore flow of the California Current and poleward, inshore flow of the California Undercurrent, the western and eastern portions of the study area are often separated by a front with cooler water in the west. In addition, coastal upwelling typically fuels primary production in the eastern portion of the study area. Previous studies on fish assemblage structure in this area also documented abrupt changes over relatively small spatial scales. Evaluation of the biogeographic range of 280 coastal fishes in California indicated that a faunal split divided assemblages located north and south of the Channel Islands (Horn & Allen 1978). More recently, Hamilton et al. (2010) conducted surveys of fishes at depths <30 m off of Santa Barbara, Anacapa, Santa Cruz, Santa Rosa, and San Miguel Islands and found that communities differed significantly among these regions. In particular, they also found that *S. mystinus* was common in the northwest, absent in the southeast, and rare in the northeast. Similarly, remotely operated vehicle surveys at depths between 31 and 100 m throughout the northern Channel Islands revealed biogeographic shifts in fish community structure (Karpov et al. 2012). In addition, stable isotope analysis revealed that California sheephead *Semicossyphus pulcher* diet varied with geographic location throughout southern California (Hamilton et al. 2011), likely reflecting biogeographically-mediated variability in prey availability among zones, suggesting that the entire marine ecosystem is affected by biogeography in southern California. These findings and ours suggest that marine assemblages vary due to long-standing oceanographic processes in southern California.

Changes over relatively short (<100 km) distances in the structure of fish assemblages in association with oceanographic fronts have also been identified in ichthyoplantkon studies throughout the world. Off the coast of Angola (Africa), for example, the Angola-Benguela Frontal Zone separates relatively cool and warm water masses, and assemblages were only 22% similar on either side of this front (John et al. 2001). Similarly, off the east coast of Australia, Keane & Neira (2008) found that the assemblage changed rapidly between waters characterized by the cool Tasmanian Current and the warm East Australian Current. Holliday et al. (2012) also detected a sudden change in assemblage structure within and outside of the Leeuwin Current off the west coast of Australia. Closer to our study region, a major transition from species with primarily southern to northern biogeographic affiliations were documented over short (<20 km) distances across the Ensenada Front, a semi-permanent frontal zone approximately 200 km offshore from San Diego, CA (Moser & Smith 1993). Thus, it appears that fish assemblage structure worldwide changes rapidly across ocean fronts.

In addition to habitat, it is possible that fishing pressure contributed to the higher diversity and abundance of targeted species in the west. A recent analysis of spatially explicit fishing pressure on groundfishes from recreational and commercial fisheries between 1933 and 2010 showed that rockfish catches were much greater nearshore compared to offshore in California (Miller et al. 2014). Specifically, Miller et al. (2014) found that between 1957 and 2000, recreational catch of rockfish was up to an order of magnitude higher nearshore and along the eastern banks than within the southwestern banks. Further, recreational catch correlated significantly with distance from port, depth, and chl *a* (a proxy for primary production) and commercial catch with distance from port and depth. The effect of spatial distri-

bution of fishing pressure on depletion of groundfish in California was also demonstrated by Bellquist (2015), who showed that from 1966 to 1989 recreational anglers traveled <25 km to catch the largest size classes of rockfishes, whereas from 1990 to 2013 anglers had to travel 50 to 100 km to catch the largest rockfishes. In addition, the largest rockfishes caught 51 to 100 km from home port during the 1990 to 2013 period were similar in size to those caught <25 km from home port from 1966 to 1989. Spatially heterogeneous fishing effort may also explain the negative relationship between primary production and both the abundance of targeted species and diversity. For the most part, locations with high primary production (close to shore and within the Santa Barbara Channel) were also subjected to high fishing pressure (Miller et al. 2014). As such, these areas could be more greatly impacted by fishing, leading to a reduction in species richness and abundance of targeted species, and even some non-targeted species since relatively undesirable species such as *S. hopkinsi* are now frequently landed since the larger, targeted species have become rare (Love et al. 1998). Since management actions have eased fishing pressures in many of the eastern, previously highly exploited areas, an interesting future study would be to determine if the abundance of larvae from targeted species has increased in this region since 2005.

Our research was largely motivated by a need to assist ecosystem based management (EBM) efforts in southern California (Harvey et al. 2014). The goals of EBM are typically to preserve biodiversity, assist the recovery and sustainability of fished species, and generally maintain 'healthy' ecosystems (Field & Francis 2006). Marine reserves have been utilized extensively throughout southern California to help meet these EBM goals. Our sample frame encompassed 2 major reserve systems: the Channel Island National Marine Sanctuary (CINMS), which covers 488 km^2 of state waters around the Channel Islands (Hamilton et al. 2010), and the approximately 11000 km^2 CCAs. The boundaries of the CINMS were explicitly designed to include locales throughout the biogeographic zones defined in our paper to maximally protect biodiversity (Airame et al. 2003), and the delineation of the CCAs were based on the historic distribution of *S. levis* landings (Butler et al. 2003). Sampling has identified species richness hotspots within the western portion of the main CCA and around the western Channel Islands. In addition, abundances of targeted rockfishes were high in the western CCA and Channel Islands. Previous analyses of larval rockfish distributions also showed that the CCA is an important spawning area for targeted species. For example, Ralston & MacFarlane (2010) demonstrated that the center of *S. paucispinis* abundance was located in the western part of the CCA in 2002 and 2003. Similarly, rockfish larvae were found in high abundances in the western CCA between 2002 and 2004 (Hitchman et al. 2012) and 1999 (Taylor et al. 2004). These studies and ours, therefore, indicate that the reserves were appropriately placed in locations that protect important rockfish spawning habitat.

Our results provide insight into how rockfish larvae are distributed throughout southern California, and should provide valuable information for further delineation of RCAs in the future and for EBM in this region. A key issue to resolve, however, is the temporal stability of the patterns observed in this study. Genetic identification of larval rockfish samples over a broader time scale should help elucidate whether the mean trophic level of the rockfish community has changed in response to the establishment of the CCAs and/or environmental fluctuations, and further help guide EBM.

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Appendix 1.

(A) Detailed methods for genetic analysis.

A Chelex-based boiling protocol was used to extract genomic DNA from each larva (Hyde et al. 2005). Tissue was typically taken from the eye. If an eye was unavailable, tissue was extracted from the posterior region of the larva. Subsequent to tissue removal each individual was retained for future analyses. The target genomic region was amplified by polymerase chain reaction (PCR) using the primers GLURF2-5′ and CB3RF2-5′ (Hyde et al. 2008). Each PCR was conducted in 10 µl volumes with buffer (67 mM Tris-HCl pH 8.8, 16.6 mM $[NH_4]_2SO_4$, 10 mM β-mercaptoethanol, 2 mM $MgCl_2$), 800 µM dNTP, 0.4 µM of each primer, 0.5 mg ml^{-1} bovine serum albumin, 0.5 units *Taq* DNA polymerase (New England Biolabs), and 1 µl of chelex supernatant containing DNA template. The thermal profiles of the PCRs were: denature at 92°C for 2 h and 30 min; followed by 40 cycles of 94°C for 30 min, 55°C for 90 min, 70°C for 90 min; then a final extension of 72°C for 3 h. Negative, no template controls were run for each PCR to monitor for possible contamination. PCR products were enzymatically cleaned using ExoSap-IT (Affymetrix) in accordance with the manufacturer's protocol. The resultant cleaned products were sequenced in one direction using the internal primer CBINR3 (5′-ATG AGA ART AGG GGT GGA AGC T-3′) and BigDye v.3.1 Dye Terminator chemistry following manufacturer's protocols, and analyzed using an ABI3730 Genetic Analyzer (Life Technologies). Sequences were edited and aligned using Sequencher v.4.9 (GeneCodes), aligned with templates from reference adult rockfishes (Hyde & Vetter 2007) and identified by creating Neighbor Joining phylogenetic trees with MEGA v.6.06 (Tamura et al. 2013).

(B) Detailed methods for statistical analysis: statistical packages

All figures were constructed using the R packages 'ggplot2' (Wickham 2009) or 'ggmap' (Kahle & Wickham 2013). The depth contours (Fig. 2A) were made using the package 'marmap' (Pante & Bouhet 2014) while the data for the image plots (Figs. 3 & 4) were generated using the package 'kriging' (Olmedo 2011). The package 'AER' (Kleiber & Zeileis 2008) was used to test for overdispersion in Poisson models while the 'pscl' package (Jackman 2015) was used to run zero-inflated negative binomial models and test their performance relative to their negative binomial counterparts. The negative binomial models that did and did not include spatial autocorrelation in the error term were run using the 'MASS' package (Venables & Ripley 2002). The package 'ncf' (Bjornstad 2013) was used to evaluate the significance of spatial autocorrelation while the package 'sp' (Bivand et al. 2013) was used to convert coordinates between UTM and decimal degrees. Model selection based on AICc scores were carried out using the package 'AICcmodavg' (Mazerolle 2013).

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