



**Abstract**—The distribution and abundance of demersal young of the year (YOY) of rockfish species (*Sebastes* spp.) were investigated over a 17-year period along the central coast of California at depths of 19–326 m. More than 87,000 YOY rockfish were counted during surveys of 1292 transects on the seafloor. The 3 most abundant species were the pygmy (*S. wilsoni*), halfbanded (*S. semicinctus*), and shortbelly (*S. jordani*) rockfish. Young of the year of many rockfishes were found at greater depths than have been previously reported. The highest densities of all species combined occurred in shallow and intermediate depths ( $\leq 100$  m). Most YOY rockfish occupied rock or mixed substrata, except the greenstriped (*S. elongatus*) and stripetail (*S. saxicola*) rockfish, which were associated primarily with soft substrata. Statistically significant ( $P < 0.01$ ) hot spots of YOY rockfish densities were located throughout the region, but only Soquel Canyon, a known refuge for large adult rockfish ( $> 50$  cm in total length), was a significant ( $P < 0.01$ ) cold spot. Biological processes (e.g., ontogenetic movement and predation) and environmental characteristics (e.g., seafloor habitat and oceanographic conditions) are potential influences on the distribution of YOY of rockfishes. The results of our study provide insights into the distributions of YOY of rockfishes in deep, complex seafloor habitats and can help improve estimation of year-class strength through targeted surveys of preferred habitats.

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## Distribution, abundance, and habitat associations of young of the year of rockfish species (*Sebastes* spp.) in deep waters along the central coast of California

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Over 70 rockfish species (*Sebastes* spp.) occur in the northeast Pacific Ocean from Alaska to Baja California, Mexico, and many of them are important to commercial and recreational fisheries. Rockfish species have long lifespans (from decades to more than 100 years for certain species), are slow growing, and mature late (Love et al., 2002), making them slow to recover from high levels of fishing mortality. In studies of the distribution and abundance of young of the year (YOY) of rockfishes, large interannual fluctuations in abundance have been found (Woodbury and Ralston, 1991; Sakuma et al., 2006; Ralston et al., 2013). Such variation in abundance is a contributor to variable year-class strength, which is largely determined within the first year of life (Ralston and Howard, 1995; Hobson et al., 2001; Laidig et al., 2007). Annual indices of YOY abundance are used in stock assessments for several rockfish species (He et al., 2011; Dick et al., 2017; Field et al., 2017; He and Field, 2018).

Young-of-the-year rockfish begin as pelagic larvae, transform to pelagic juveniles, and settle to a variety of benthic habitats generally after 3–6 months, typically at shallower depths than those occupied by conspecific adults

(Boehlert, 1977; Love et al., 2002). In nearshore areas (depths  $< 30$  m), species-specific habitat associations of settled YOY rockfish have been identified with kelp beds, estuaries, and man-made structures, such as piers and jetties (Anderson, 1983; Hallacher and Roberts, 1985; Carr, 1991; Gallagher and Huppell, 2010). In offshore areas, large numbers of YOY rockfish have been found in high-relief rocky habitats at depths of 30–100 m off central California and Oregon (Stein et al., 1992; Yoklavich et al., 2002), and newly settled YOY of 3 rockfish species were commonly found in a study on soft sediments at depths of 40–100 m in Monterey Bay, located south of the San Francisco Bay Area in California (Johnson et al., 2001).

Relatively few surveys of settled YOY rockfish have been conducted in high-relief, rocky habitats at depths  $> 30$  m compared to the number of surveys conducted in shallow nearshore areas (depths  $\leq 30$  m). The latter are often conducted by scuba divers or with small trawl nets deployed from small boats or from shore, and the former require large, specialized survey vehicles (such as human-occupied and remotely operated vehicles) and support vessels, as well as skilled equipment operators

(Yoklavich et al., 2015). The researchers that have conducted the few surveys that have been carried out in rocky habitats at depths >30 m have reported on YOY rockfish in general rather than on individual species, because of difficulties in identifying young fish to species. As a result, our understanding of the abundance and habitat use of YOY rockfish is lacking for those species that inhabit depths deeper than 30 m.

In our study, a manned submersible was used to conduct visual surveys of YOY of deep-living, demersal rockfishes along a 140-km section of the central coast of California from the seaward edge of kelp beds (depths ~30 m) to depths >300 m. Survey data were used 1) to characterize species composition, 2) to determine associations of YOY rockfish with seafloor substrata by species and for all species combined, and 3) to examine spatial patterns of density, as a measure of abundance, relative to depth. The resultant data on YOY rockfish distributions will help to unravel the complex life history strategies of many commercially important rockfish species and to discover vital rockfish nursery areas in deep waters that are not often surveyed.

## Material and methods

Visual surveys of demersal fish were conducted along the central coast of California from Big Creek (36°00'N, 121°35'W) to Ascension Canyon (37°02'N, 122°25'W) (Fig. 1) by using the 4.6-m-long *Delta* manned submersible (Delta Oceanographics<sup>1</sup>, Torrance, CA). A total of 11 research expeditions were completed over the 17-year period from 1992 through 2009 (Table 1) during late summer and fall (typically the time of the calmest waters along this coastline) at depths from 19 to 326 m (the maximum depth to which the submersible can travel safely is 365 m). All surveys were conducted during daylight hours from 0700 to 1700.

The submersible had space for 1 pilot and 1 scientific observer and was equipped with an external color video camera (fabricated by Delta Oceanographics) mounted on the starboard side above the observer viewports. Before 2002, tapes in the Hi8 format were used in the external camera, and in 2002, the tape format changed to MiniDV to improve video resolution. Also, in 2002, a handheld MiniDV video camera (DCR-VX1000, Sony Group Corp., Tokyo, Japan) was placed in the lowest viewport inside the submersible and angled down to document the fish that could be seen close to the submersible, along the inside edge of a transect. Two parallel lasers were mounted on either side of the external color camera about 20 cm apart (except during the research expedition in 1992, when the lasers were spaced 39.5 cm apart). These lasers were used to estimate fish length and as a tool to help in determining the width of transects.

<sup>1</sup> Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

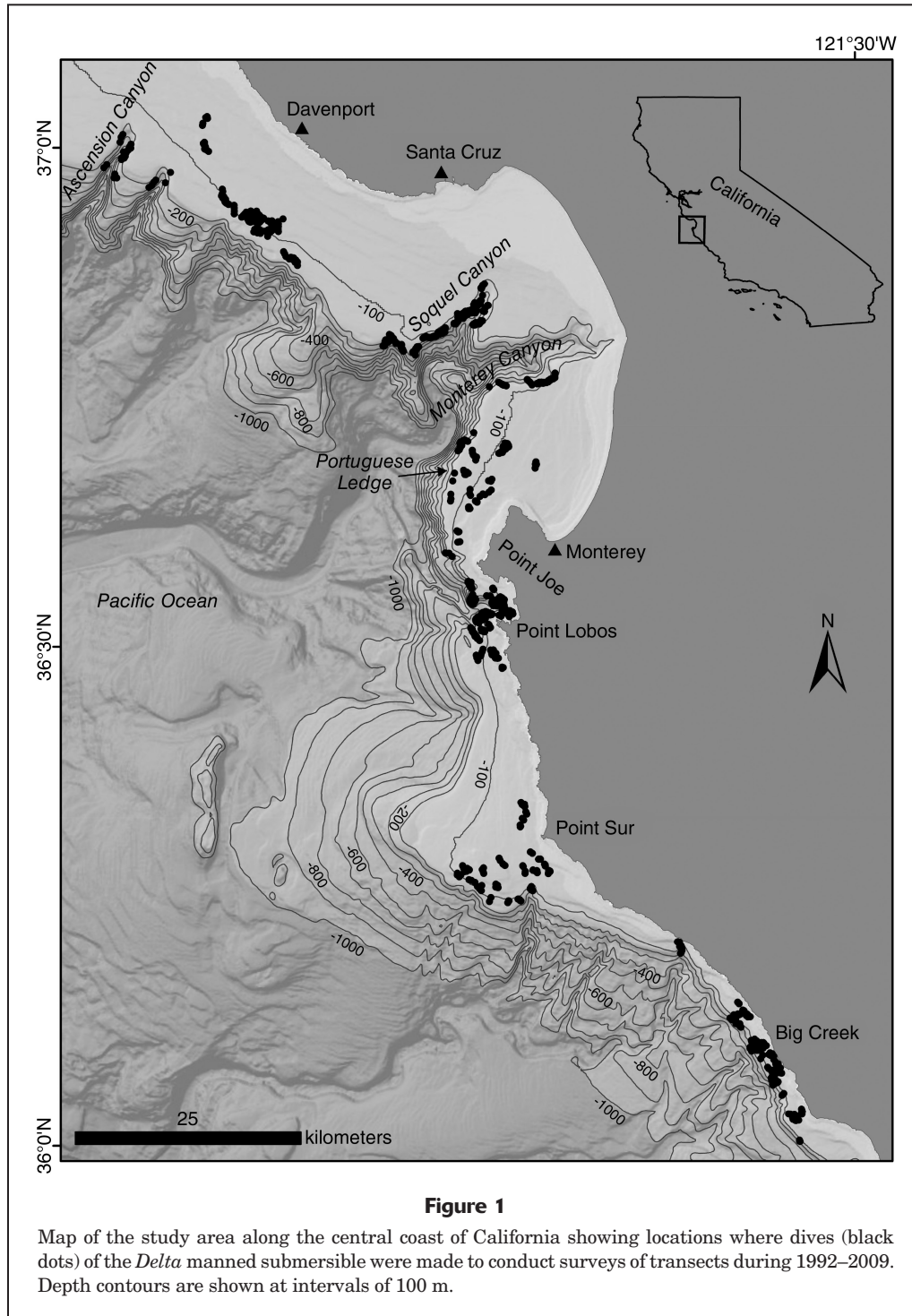
A conductivity, temperature, and depth instrument (SBE 19plus SeaCAT, Sea-Bird Scientific, Bellevue, WA) was attached to the submersible to accurately measure depth. From 2007 through 2009, a ring laser gyro and Doppler velocity log were affixed to the submersible to measure the distance travelled.

Strip-transect surveys were conducted to quantify the fish within a 2-m-wide swath along the seafloor and from the seafloor to a height 2 m above it. During transect surveys, the submersible transited approximately 1 m above the bottom at rates of 0.4–0.9 kt (depending on bottom topography). The surveys were conducted for either 10 or 15 min (depending on the year), with 2–6 transects surveyed during each submersible dive. The start position and direction of travel on transects were directed to the submersible pilot by a scientist aboard the support vessel who tracked the submersible's position using an ultra-short baseline acoustic system (ORE Trackpoint II, EdgeTech, West Wareham, MA) and WinFrog software (vers. 3.1; Fugro Pelagos Inc., San Diego, CA). During transect surveys, the submersible followed the depth contour with minor course corrections (e.g., for obstacle avoidance) left to the submersible pilot's discretion.

The scientific observer (all of whom were biologists experienced in fish identification) in the submersible identified (to the lowest possible taxon), enumerated, and estimated the length (to the nearest 5 cm in total length [TL] using the lasers spaced 20 cm apart) of all fish observed within the 2-m-wide transects and ≤2 m above the seafloor, verbally recording this information on an audio channel of each video tape (for more details, see Yoklavich et al., 2002, 2007). Few YOY rockfish were observed >2 m above the seafloor, and most were within 0.5 m of the seafloor. The 2-m width of transects was determined by using a combination of the distance of the laser spots from the submersible and measurements with a handheld sonar.

Young-of-the-year rockfish were identified to species by their body shape, length-specific pigment patterns, and physical characteristics (e.g., the bocaccio, *S. paucispinis*, has a large mouth; Butler et al., 2012). However, many of these patterns and characteristics were not easily observed from the submersible or in video footage because of the small size of some fish and their orientation, and these fish remained classified as unidentified YOY rockfish. All rockfish that were ≤5 cm TL were considered YOY, as were fish ≤10 cm TL that were identified as bocaccio, olive rockfish (*S. serranoides*), and shortbelly rockfish (*S. jordani*). These 3 species are relatively fast growing during their first year and can attain lengths >10 cm TL by the end of summer and fall of their first year (Anderson, 1983; Love et al., 2002).

All video footage was reviewed back in the laboratory. Data from the observer's verbal recordings were entered into a database, and fish identifications and counts were confirmed. Sections of seafloor observed in video footage for at least 5 s in duration along transects were characterized as a combination of primary and secondary substratum types. Primary substratum types covered at



least 50% of the seafloor, and secondary types represented at least 20% of the remaining seafloor. We used these substratum types, following Greene et al. (1999): rock outcrop (bedrock outcrops), rock pinnacle (vertical bedrock pinnacles), continuous flat rock (flat-topped bedrock), boulder (individual rocks >25 cm in diameter), cobble (stones 6–25 cm in diameter), pebble (stones <6 cm in diameter), sand, and mud. Combinations of

primary and secondary substrata were further classified as hard, mixed, or soft. Any combination of cobble, pebble, boulder, flat rock, rock outcrop, or rock pinnacle was considered hard, and a combination of mud and sand was deemed soft. For the mixed category, hard and soft substratum types each composed either the primary ( $\geq 50\%$ ) or the secondary ( $\geq 20\%$ ) portion of the observed substratum.

Table 1

Year, month or period, location, number of transects surveyed, total duration in minutes of all transect surveys, area surveyed, depth range surveyed, and total number of young-of-the year (YOY) rockfish (*Sebastes* spp.) observed for each of the 11 research expeditions conducted with the *Delta* manned submersible off the central coast of California from 1992 through 2009.

Year	Period	Location	Transects		Area (m <sup>2</sup> )	Depth range (m)	No. of YOY observed
			Number	Minutes			
1992	Aug	Soquel Canyon	42	420	14,142	95–305	3
1993	Oct	Monterey Bay	90	900	48,772	62–296	4557
1994	Sep	Ascension and Carmel Canyons	78	1170	49,872	79–316	8833
1997	Sep–Oct	Big Creek	64	640	25,768	19–222	20,119
1998	Sep	Big Creek	81	810	29,567	22–250	9827
2002	Oct	Soquel Canyon	10	115	5066	110–292	550
2003	Sep	Soquel Canyon	30	300	12,794	113–296	139
2004	Aug–Sep	Davenport and Monterey Bay	172	1880	104,630	66–260	2606
2007	Sep–Nov	Big Creek to Soquel Canyon	317	3170	162,694	23–325	21,617
2008	Sep–Nov	Big Creek to Soquel Canyon	391	3910	176,856	19–326	19,221
2009	Sep–Oct	Soquel Canyon	17	170	7972	99–288	215
Total			1292	13,485	638,133		87,687

Transect length was estimated by using 1 of 3 methods: 1) counting intervals of paired laser spots end-to-end in the video footage as it advanced (in 1992–1994, 1997, and 1998), 2) plotting transect lines in ArcGIS (vers. 10.3; Esri, Redlands, CA) with edited and smoothed latitudes and longitudes from the ultra-short baseline acoustic system (in 2002–2009), or 3) using distances travelled measured with a ring laser gyro and Doppler velocity log (in 2007–2009). Transect area was estimated by multiplying the transect length by the 2-m transect width. Densities of YOY rockfish on each transect were calculated by dividing the total number of YOY rockfish by the total transect area.

For analyses, data from all years were combined. We analyzed all YOY rockfish grouped together and YOY of the most common species that had overall densities  $\geq 0.01$  fish/100 m<sup>2</sup> (with a minimum of 64 individuals counted on all transects) and that occurred on at least 15 transects (Table 2). We excluded fish identified to species in the subgenus *Sebastomus* from analyses because multiple species (e.g., the rosy rockfish, *S. rosaceus*, and the greenspotted rockfish, *S. chlorostictus*) in this group had varied distributions that would confound these analyses. A Kruskal–Wallis (KW) test, a nonparametric method of one-way analysis of variance, was conducted for each species and for all rockfishes combined to determine if there was a statistically significant difference in overall YOY density with depth (average depths of transects were grouped in 10-m depth bins). A canonical correlation analysis was used to examine the relationships between densities of the most common species and environmental factors (i.e., average depth of transects [grouped in 10-m bins] and substratum type). We examined which substrata were used by YOY rockfish by using a chi-square test to test the null hypothesis that YOY of all species combined

were distributed proportionately to the relative availability of the substratum types.

We examined the spatial distribution of YOY rockfish densities on transects, using ArcMap in ArcGIS. We conducted hot-spot analyses (with the Spatial Analyst extension in ArcGIS), employing the Getis–Ord  $G_i^*$  statistic (Getis and Ord, 1992) to identify statistically significant spatial clusters of transects with high (hot spots) or low (cold spots) densities of YOY rockfish. Hot-spot analyses of YOY densities were conducted for each rockfish species, for all rockfishes and depths combined, and for all rockfishes combined within 50-m depth strata.

To calculate the Getis–Ord  $G_i^*$  statistic for each feature (i.e., transect) relative to its neighbors, inputs that define the spatial relationships among features and the size of the neighborhood are required. For each analysis, we chose the input of 3000 m as a fixed distance band that provided a reasonable spatial scale relative to the seafloor topography and the input of 8 or more neighbors for most transects (or a minimum of 6 neighbors for some transects). The input of a false discovery rate correction was also applied to adjust critical thresholds of  $P$ -values from analysis with the  $G_i^*$  statistic to account for multiple testing and spatial dependency issues (Caldas de Castro and Singer, 2006). As a local statistic, the  $G_i^*$  tests each feature in a data set (i.e., allows multiple testing), and the identification of some statistically significant hot or cold spots may actually be driven by random spatial processes (i.e., some results may falsely reject the spatial randomness null hypothesis). Spatial dependency is caused by the tendency of features near each other to be similar and can artificially inflate statistical significance. We considered  $Z$ -scores with  $P$ -values, adjusted with a false discovery rate procedure, at the 99% confidence level to be statistically significant; at this level, we rejected the



**Table 2**

Total number, overall density (the total number of fish observed per total area surveyed), and minimum, maximum, and mean depths of observed young of the year for all rockfish species (*Sebastes* spp.) identified during or in video footage from transect surveys conducted with the *Delta* manned submersible off the central coast of California from 1992 through 2009. An asterisk (\*) after a common name indicates that the species is one of the most abundant species that were used in analyses. A dagger (†) after a common name indicates that the species belongs to the subgenus *Sebastomus*. Some of the fish identified as blue rockfish (*S. mystinus*) may have been deacon rockfish (*S. diaconus*) because these species have not been differentiated at small sizes. Mean depths are rounded to the nearest 10 because 10-m depth bins were used in analyses. SD=standard deviation. N/A=not applicable because only 1 individual was observed.

Common name	Scientific name	Number	Density (fish/100 m <sup>2</sup> )	Depth			
				Min	Max	Mean	SD
Aurora rockfish	<i>Sebastes aurora</i>	1	<0.01	241	241	240	N/A
Pinkrose rockfish <sup>†</sup>	<i>Sebastes simulator</i>	1	<0.01	209	209	210	N/A
Swordspine rockfish <sup>†</sup>	<i>Sebastes ensifer</i>	1	<0.01	90	90	90	N/A
Yelloweye rockfish	<i>Sebastes ruberrimus</i>	1	<0.01	72	72	70	N/A
Chameleon rockfish	<i>Sebastes phillipsi</i>	2	<0.01	244	275	260	22.5
Gopher rockfish	<i>Sebastes carnatus</i>	2	<0.01	36	38	30	4.7
Black rockfish	<i>Sebastes melanops</i>	3	<0.01	39	45	40	2.9
Copper rockfish	<i>Sebastes caurinus</i>	3	<0.01	44	51	50	5.0
Vermilion rockfish	<i>Sebastes miniatus</i>	4	<0.01	29	48	40	11.2
Bank rockfish	<i>Sebastes rufus</i>	6	<0.01	140	249	210	52.2
Canary rockfish	<i>Sebastes pinniger</i>	9	<0.01	44	52	40	3.4
Rosethorn rockfish <sup>†</sup>	<i>Sebastes helvomaculatus</i>	12	<0.01	152	200	170	14.6
Bocaccio	<i>Sebastes paucispinis</i>	13	<0.01	28	78	50	11.6
Olive rockfish	<i>Sebastes serranoides</i>	17	<0.01	30	83	40	15.7
Darkblotched rockfish	<i>Sebastes crameri</i>	26	<0.01	89	262	220	46.1
Splitnose rockfish	<i>Sebastes diploproa</i>	35	0.01	159	302	200	32.8
Greenspotted rockfish <sup>*†</sup>	<i>Sebastes chlorostictus</i>	86	0.01	81	151	120	18.6
Stripetail rockfish <sup>*</sup>	<i>Sebastes saxicola</i>	112	0.02	41	257	130	41.5
Yellowtail rockfish <sup>*</sup>	<i>Sebastes flavidus</i>	147	0.02	28	50	50	3.7
Starry rockfish <sup>*†</sup>	<i>Sebastes constellatus</i>	150	0.02	44	131	80	17.7
Rosy rockfish <sup>*†</sup>	<i>Sebastes rosaceus</i>	174	0.03	33	126	60	16.0
Greenstriped rockfish <sup>*</sup>	<i>Sebastes elongatus</i>	236	0.04	82	203	120	19.5
Squarespot rockfish <sup>*</sup>	<i>Sebastes hopkinsi</i>	402	0.06	44	113	70	16.2
Widow rockfish <sup>*</sup>	<i>Sebastes entomelas</i>	533	0.08	30	81	40	6.9
Blue rockfish <sup>†</sup>	<i>Sebastes mystinus</i> / <i>diaconus</i>	541	0.08	24	81	40	11.1
Unidentified <i>Sebastomus</i>	<i>Sebastes</i> spp.	1359	0.21	32	227	90	32.1
Shortbelly rockfish <sup>*</sup>	<i>Sebastes jordani</i>	3656	0.57	38	181	70	27.7
Halfbanded rockfish <sup>*</sup>	<i>Sebastes semicinctus</i>	4143	0.65	39	149	60	10.1
Pygmy rockfish <sup>*</sup>	<i>Sebastes wilsoni</i>	11,292	1.77	43	177	70	14.7
Unidentified YOY	<i>Sebastes</i> spp.	64,720	10.15	22	314	70	21.8
Total		87,687	13.76				

null hypothesis that the density of YOY rockfish is completely spatially random.

## Results

Surveys of 1292 transects were conducted, resulting in >220 h of observations (Table 1). The depths of transects ranged from 19 to 326 m (from roughly the outer edge of the kelp bed to near the maximum depth to which the submersible can travel safely). The total area surveyed was 638,133 m<sup>2</sup>, and the mean transect area (with all transects included regardless of YOY presence) was 494 m<sup>2</sup> (standard deviation [SD] 151.6). The mean transect area for 10-min

transects (sample size [*n*]=1203) was 480 m<sup>2</sup> (SD 137.9) and for 15-min transects (*n*=89) was 647 m<sup>2</sup> (SD 137.1).

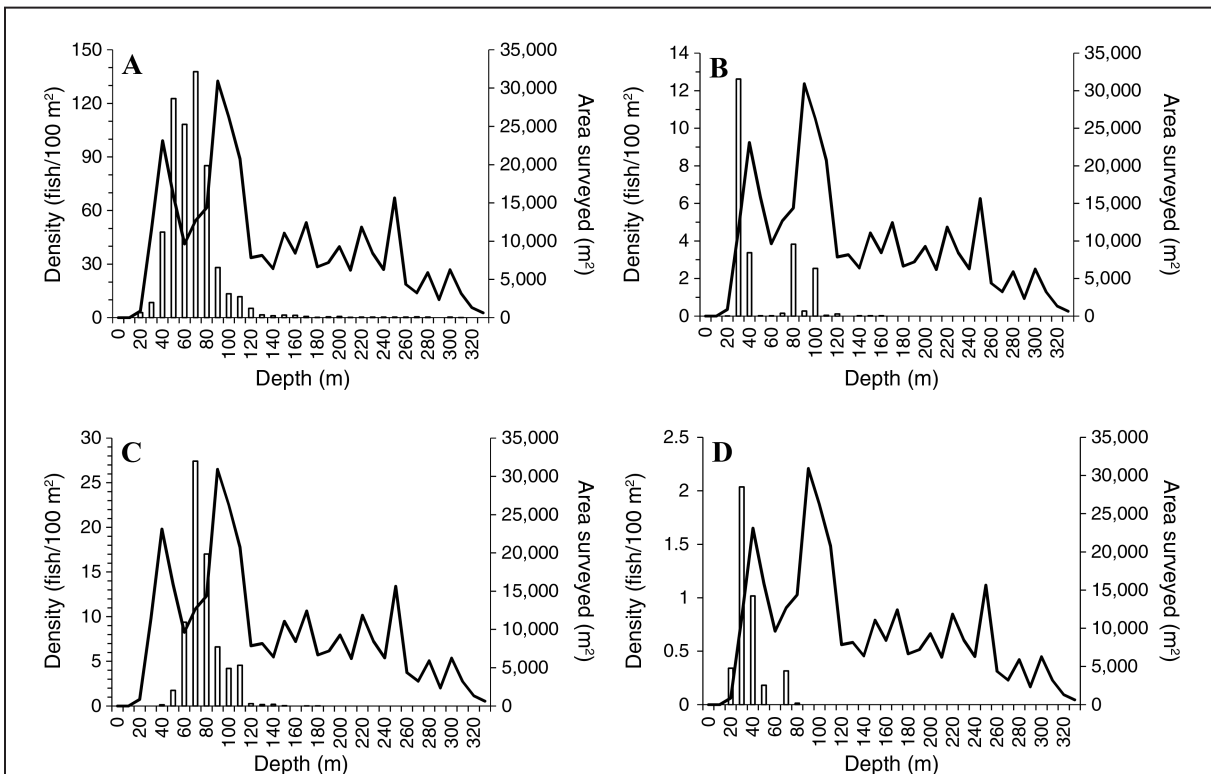
A total of 87,687 YOY rockfish from at least 28 different species were counted, with an overall density of 13.8 fish/100 m<sup>2</sup> (Table 2). Young-of-the-year rockfish were observed on nearly two-thirds of all transects (822 of 1292 transects). Approximately one-quarter (26%) of YOY were identified to a taxon lower than the genus *Sebastes* (*n*=22,967), with 94% of them identified to species. The most abundant identified species were as follows: the pygmy rockfish (*S. wilsoni*), with 11,292 individuals observed at a density of 1.8 fish/100 m<sup>2</sup>; the halfbanded rockfish (*S. semicinctus*), with 4143 individuals counted at a density of 0.7 fish/100 m<sup>2</sup>; and the shortbelly rockfish, with 3656

individuals observed at a density of 0.6 fish/100 m<sup>2</sup>. Individuals were also identified to the subgenus *Sebastomus*, a group of 11 similar-looking rockfishes characterized by 5 large white spots along the dorsal half of their body (Love et al., 2002; Butler et al., 2012). Species in this subgenus are difficult to identify as adults and even more so as YOY; however, in our study, rockfish were identified to 6 species in this group, and 3 of these species are among the most commonly identified (Table 2).

Young-of-the-year rockfish were found at depths from 22 to 314 m. Overall, the highest densities of all taxa combined within 10-m depth bins (i.e., the total number of fish divided by the total area sampled, for each 10-m depth bin) were found on transects at depths between 40 and 90 m (Figs. 2 and 3), and the densities in this depth range were significantly higher than they would have been if the depth distribution had been uniform as expected (KW test:  $P < 0.0001$ ). Most species had depth distributions of YOY that were significantly different from a uniform depth distribution (KW test:  $P < 0.0001$ ), except the stripetail rockfish (*S. saxicola*), which had a broad distribution ranging from 41 to 257 m. For the blue (*S. mystinus*), widow (*S. entomelas*), and yellowtail (*S. flavidus*) rockfish, YOY were found at the relatively shallow depths of 40 or 50 m. Young-of-the-year rosy, halfbanded, squarespot

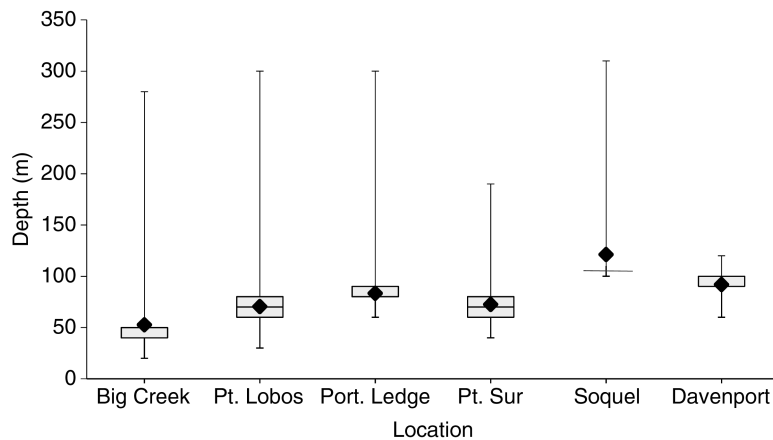
(*S. hopkinsi*), shortbelly, starry (*S. constellatus*), and pygmy rockfish were observed at mean depths ranging between 60 and 100 m, and greenspotted and greenstriped (*S. elongatus*) rockfish were found at mean depths  $> 100$  m (Table 2). The species for which YOY occurred at the greatest depths, such as the splitnose rockfish (*S. diploproa*) and the chameleon rockfish (*S. phillipsi*), were too scarce to include in our analyses. Sampling effort (measured as the area surveyed) for each 10-m depth bin varied from  $> 30,000$  m<sup>2</sup> at a depth of 90 m to  $< 1000$  m<sup>2</sup> at the depths of 10–20 m (the submersible could not sample kelp beds safely; therefore, few transects within this depth stratum were surveyed) and depths  $> 330$  m (Fig. 2).

Results from the canonical correlation analysis indicate that YOY are separated by depth in 3 groups of rockfish species (Fig. 4). The group with the negative second canonical coefficient includes the greenstriped rockfish, greenspotted rockfish, and stripetail rockfish. These species occurred at the deepest average depths (120–130 m) and had generally high densities (0.3–0.4 fish/100 m<sup>2</sup>) on soft substrata. The group with high second canonical and low first canonical coefficients includes the fishes that occupied average mean depths between 60 and 100 m (i.e., pygmy, starry, rosy, squarespot, and halfbanded rockfish), and YOY of all rockfishes combined (mean depth for all



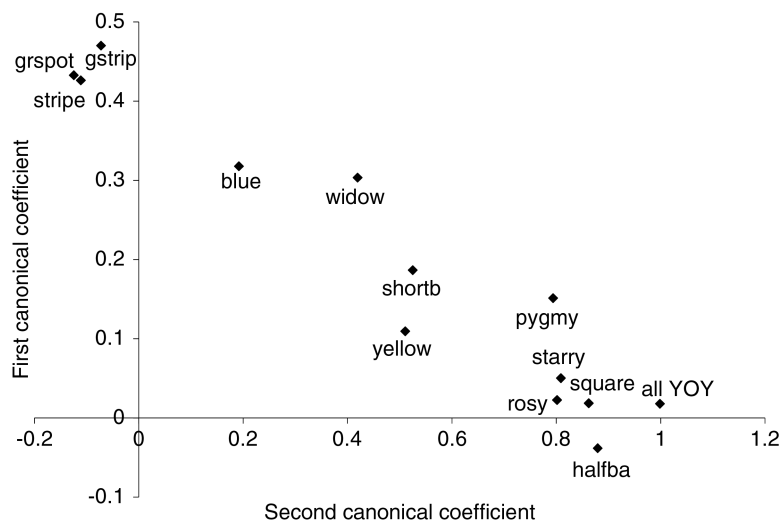
**Figure 2**

Densities of young-of-the-year (YOY) rockfish (*Sebastes* spp.) by depth (grouped in 10-m bins), for (A) all YOY rockfish combined, (B) shortbelly rockfish (*S. jordani*), (C) pygmy rockfish (*S. wilsoni*), and (D) blue rockfish (*S. mystinus*), from surveys conducted with the *Delta* manned submersible off central California from 1992 through 2009. The black line in each graph indicates the total area surveyed for each depth.



**Figure 3**

Box plots of the mean depth at which all young-of-the-year (YOY) rockfish (*Sebastes* spp.) were observed at the 6 locations along the coast of central California that were surveyed the most during 1992–2009. Each box shows the mean depth (diamond), the distribution between the first and third quartile (top and bottom lines), and the median depth (horizontal line). The whiskers indicate the maximum and minimum depths at which YOY rockfish were observed. Port. Ledge=Portuguese Ledge, a marine protected area located at the southern end of Monterey Bay.



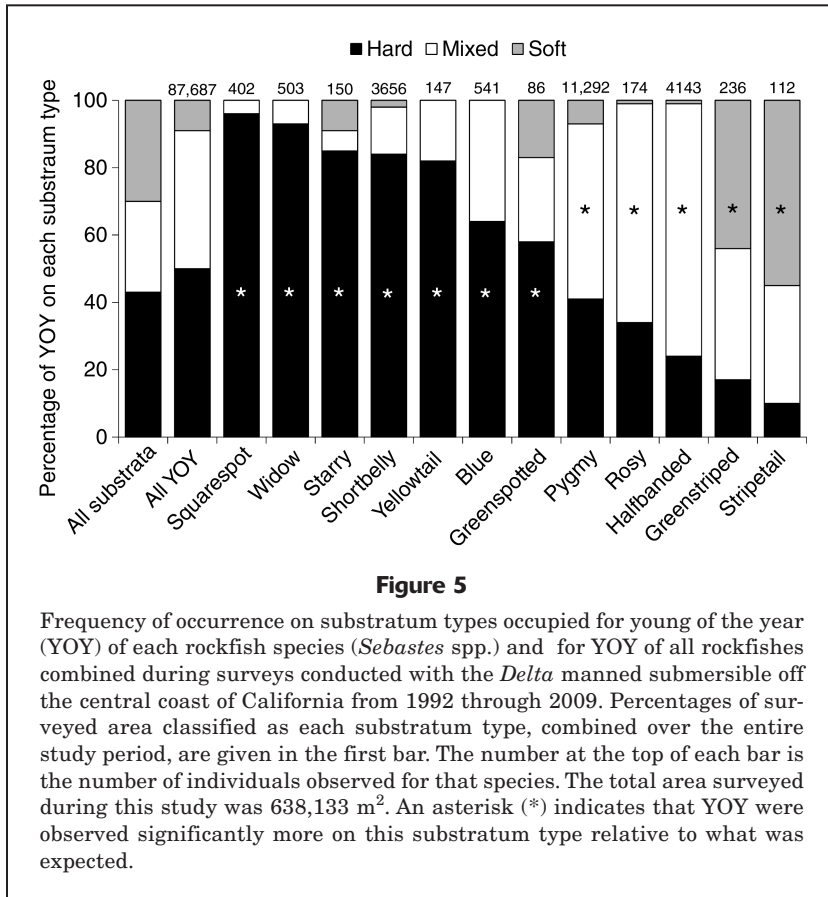
**Figure 4**

Comparison of first and second canonical correlation coefficients for densities of young of the year (YOY) of the 12 most abundant rockfish species (*Sebastes* spp.) and of all rockfishes combined from surveys conducted with the *Delta* manned submersible along the central coast of California during 1992–2009. The species with abbreviated common names are the greenstriped rockfish (*Sebastes elongatus*) (gstrip), greenspotted rockfish (*S. chlorostictus*) (grspot), stripetail rockfish (*S. saxicola*) (stripe), shortbelly rockfish (*S. jordani*) (shortb), yellowtail rockfish (*S. flavidus*) (yellow), squarespot (*S. hopkinsi*) (square), and halfbanded rockfish (*S. semicinctus*) (halfba).

YOY was 67 m) had similar results in this analysis. The remaining species grouped in the middle of Figure 4 (i.e., blue, widow, yellowtail, and shortbelly rockfish) occurred at mostly shallow depths in high densities on hard substrata. Although shortbelly rockfish were found at a mean depth equal to that of the mid-depth group, over 2000 individuals of this species were found at shallow depths of 50 m or less (Fig. 2B).

The breakdown of seafloor substrata types for all transects combined (over the entire survey area of 638,133 m<sup>2</sup>), is as follows: 43% hard, 27% mixed, and 30% soft (Fig. 5). Most YOY rockfish occupied hard and mixed substrata (Fig. 5). The frequency of occurrence of YOY for each of 7 species was disproportionately greater on hard substrata relative to its availability (chi-square test:  $P < 0.0001$ ), with frequencies varying from 58% (greenspotted rockfish) to 96% (squarespot rockfish). For 4 of these species, the squarespot, widow, yellowtail, and blue rockfish, YOY were never observed on soft substrata. Each of 3 species, the halfbanded, pygmy, and rosy rockfish, occurred disproportionately more on mixed substrata relative to its availability (chi-square test:  $P < 0.0001$ ), with 75% of halfbanded rockfish occurring on this substrata. Each of 2 species, the greenstriped and stripetail rockfish, occurred disproportionately more on soft substrata relative to its availability (chi-square test:  $P < 0.0001$ ).

Although YOY of rockfish species were present throughout the study area at densities ranging from 0.1/100 m<sup>2</sup> to 3236/100 m<sup>2</sup>, density hot spots for all but greenstriped rockfish were located within the southern region from Point Joe to Big Creek. For all taxa combined, there was a statistically significant ( $P < 0.01$ ) hot spot at Big Creek (Table 3, Fig. 6), where hot spots of YOY densities were found for individual species, including the stripetail, blue, shortbelly, and halfbanded rockfish, and for unidentified rockfish. Point Sur was a statistically significant hot spot for 7 taxa: greenspotted, yellowtail, starry, rosy, widow, and pygmy rockfish and unidentified rockfish (hot spots for pygmy rockfish are shown in Figure 6, as an example). Three species, the starry, squarespot, and pygmy rockfish, had a hot spot at Point Lobos. Point Joe,



Davenport, and Monterey Canyon were statistically significant hot spots for YOY pygmy, greenstriped, and stripetail rockfish, respectively. The greenstriped rockfish was the only species that had a cold spot, which was a statistically significant ( $P < 0.01$ ) cluster of transects with low densities located in Soquel Canyon inside Monterey Bay.

In the spatial examination of the density at depth for YOY of all rockfishes combined, no statistically significant hot spots were found at depths  $\leq 50$  m, depths of 150–200 m, or depths of 250–300 m. Statistically significant ( $P < 0.01$ ; Table 4) hot spots were located at Big Creek at depths of 50–100 m, Point Sur at depths of 100–150 m, and Point Lobos at depths of 200–250 m. A statistically significant cold spot was located at Soquel Canyon at depths of 200–250 m.

**Discussion**

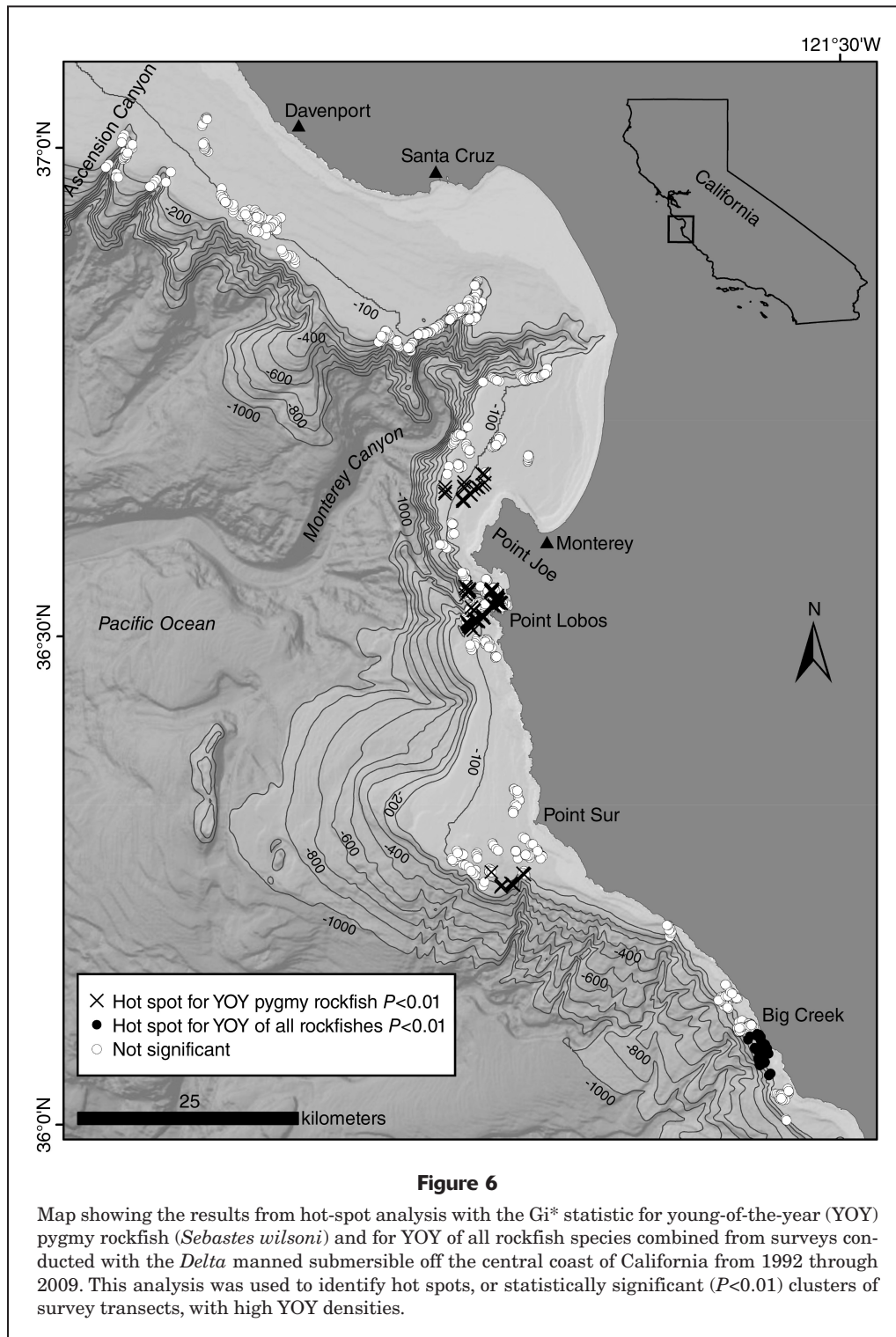
In most previous studies, YOY of all rockfish species have been categorized into a single group. In this study, we were able to identify individuals of 28 species, because of recent progress in

**Table 3**

Results from hot-spot analysis with the  $G_i^*$  statistic for young of the year (YOY) of rockfish species (*Sebastes* spp.) along the central coast of California from 1992 through 2009. This analysis was used to identify locations of statistically significant ( $P < 0.01$ ) clusters of survey transects with high (hot spots) and low (cold spot) densities of YOY rockfish, by species.

Species	Location	
	Cold spot	Hot spots
All rockfishes	None	Big Creek
Blue rockfish	None	Big Creek
Greenspotted rockfish	None	Point Sur
Greenstriped rockfish	Soquel Canyon	Davenport
Halfbanded rockfish	None	Big Creek
Pygmy rockfish	None	Point Sur, Point Lobos, Point Joe
Rosy rockfish	None	Point Sur
Shortbelly rockfish	None	Big Creek
Squarespot rockfish	None	Point Lobos
Starry rockfish	None	Point Sur, Point Lobos
Stripetail rockfish	None	Big Creek, Monterey Canyon
Widow rockfish	None	Point Sur
Yellowtail rockfish	None	Point Sur
Unidentified rockfish	None	Point Sur, Big Creek





the identification of rockfishes for individuals at the YOY stage along the West Coast of the United States (Butler et al., 2012). In 2002, YOY were identifiable for less than 30 species (Love et al., 2002); currently, about 40 of the over 70 rockfish species have detailed, descriptive developmental series of the larval and juvenile stages, allowing

for more accurate identifications (Anderson, 1983; Love et al., 2002; Butler et al., 2012).

Most of the rockfishes that occur along the central coast of California have had their juvenile pigment patterns identified and documented, and many of these species (i.e., pygmy, halfbanded, shortbelly, and squarespot

**Table 4**

Results from hot-spot analysis with the  $G_i^*$  statistic for young of the year (YOY) rockfish (*Sebastes* spp.) along the central coast of California from 1992 through 2009. This analysis was used to identify locations of statistically significant ( $P < 0.01$ ) clusters of survey transects with high (hot spots) and low (cold spot) densities of YOY rockfish, by 50-m depth bin. The number of transects in the >300-m depth bin was insufficient for analysis.

Depth (m)	Location	
	Cold spot	Hot spots
≤50	None	None
>50 and ≤100	None	Big Creek
>100 and ≤150	None	Point Sur
>150 and ≤200	None	None
>200 and ≤250	Soquel Canyon	Point Lobos
>250 and ≤300	None	None

rockfish) are among the most numerous that we observed. Many of them, such as the halfbanded rockfish with its large, dark, diamond-shaped pigment spot on the side of its body and the blue rockfish with its blue coloration, are quite distinctive. Young-of-the-year blue rockfish have not been positively differentiated from the more northerly distributed deacon rockfish (*S. diaconus*) (Butler et al., 2012). Therefore, some of the YOY rockfish identified as blue rockfish in our study may be deacon rockfish. Bizarro et al. (2020) found that, as adults, blue rockfish were more frequently observed from Monterey Bay south with from two-thirds to three-quarters of the catch identified as blue rockfish. Further studies are needed to determine the identification and distribution of YOY blue and deacon rockfish. It is more difficult to differentiate between species in a few groups, including species in the subgenus *Sebastes*, the yellowtail and olive rockfish, and a group consisting of the widow, pygmy, squarespot, and shortbelly rockfish. The species in the latter group are all tan-colored and, even though their pigment patterns are distinctive as large individuals, they have only subtle differences at small sizes (e.g., shortbelly rockfish are more elongated than the other species in this group).

Advances in high-definition camera systems that take high-resolution images allow researchers to see the definitive characters needed for identification of YOY in video and still images. Despite these advances, species identification for YOY rockfish during visual surveys remains difficult, and we were able to identify to species only one-quarter of the total number of individuals observed on transects in our study. Most of the unidentified rockfish were small individuals (≤5 cm TL), partially obstructed from view, or not observed with enough resolution in video images to get a positive identification. However, on the basis of the number of individuals of each species that we identified, their tan color, and lack of obvious pigment patterns, we believe that most of the unknown YOY

rockfish were probably pygmy, squarespot, or shortbelly rockfish. The number of YOY rockfish that can be identified to species can only be expected to increase in the future, along with increases in camera quality and resolution. With these improvements in identification and image quality and with the advent of emerging technologies (i.e., environmental DNA and light-field cameras), it may be possible in the future to identify most YOY rockfish to species during visual surveys.

Rocky substrata have been shown to be important habitats for YOY rockfishes living in shallow water (depths <30 m) (Anderson, 1983; Carr, 1991; Laidig et al., 2007). In our study, we observed the highest densities of YOY rockfish on hard or mixed substrata at depths between 40 and 90 m and the lowest densities at depths >160 m or over soft bottom habitat. Love et al. (2006) found the highest densities of YOY bocaccio on oil platforms (hard man-made substrate) and on shell mounds near platform bases in Southern California at depths between 25 and 80 m. High abundances of YOY rockfish have also been seen in rocky substrata at depths <100 m in southeast Alaska and in Oregon, with low numbers of YOY rockfish observed in soft sediments (Carlson and Straty, 1981; Stein et al., 1992). Although densities were not available from these studies, these results indicate that rocky substrata at these depths may be important to YOY of rockfishes along the West Coast.

For many rockfish species, YOY had statistically significant associations with rocky areas, but soft sediments served as a habitat for YOY greenstriped and stripetail rockfish. Not surprisingly, the highest densities of these 2 species were located in areas with high amounts of muddy seafloor (at Monterey Canyon and Davenport), at the deep average depths of 120 m for greenstriped rockfish and 130 m for stripetail rockfish. Soft sediments are also the common habitats of conspecific adults, but adults have been found at deeper depths than YOY (Love et al., 2002). Young-of-the-year stripetail rockfish have been observed in large numbers on soft sediments off Big Creek in central California at depths of about 70 m and in Southern California at depths of 18–150 m (Mearns et al., 1980; Yoklavich et al., 2002), and, for YOY, both the greenstriped rockfish and the stripetail rockfish have been found to be the most abundant rockfishes surveyed on the soft sediments of Monterey Bay from the depth of 60 m to the 100-m limit of their sampling (Johnson et al., 2001).

Most settled YOY of rockfishes live at shallower depths than their adult counterparts. Ontogenetic shifts in depth are most obvious in the deepwater species that recruit initially to kelp beds (e.g., the shortbelly and yellowtail rockfish; Anderson, 1983; Love et al., 1991, 2002, 2009; Butler et al., 2012). The YOY of a handful of kelp-bed-settling species remain in shallow depths (e.g., kelp rockfish, *S. atrovirens*, and black-and-yellow rockfish, *S. chrysomelas*), and YOY of most species either remain for only a short time (days to a month; e.g., halfbanded and shortbelly rockfish) or for many months until the first big storms of winter hit in October or November (e.g., copper rockfish, *S. caurinus*;

stripetail rockfish; and yellowtail rockfish; Anderson, 1983). Most YOY blue and olive rockfish move to deeper water in fall, but some individuals remain in kelp beds throughout the winter.

Although these ontogenetic habitat movements have been recorded in nearshore areas, the movements of only a few species that recruit to deeper waters have been observed. Johnson et al. (2001) used a size-frequency analysis to document the ontogenetic movement to deeper waters for cowcod (*S. levis*), greenstriped rockfish, and stripetail rockfish in Monterey Bay. Love et al. (1991) found that bocaccio move successively deeper as they mature, with a shallow-water-dwelling juvenile taking around 5 years to move to deeper adult habitats. In our study, YOY rockfish were observed living in habitats similar to, but shallower than, habitats utilized by conspecific adults, according to data on depth distributions from Love et al. (2002).

The average depth at which YOY of most rockfishes were found was over 50 m shallower than the average depth at which adults have been found. For example, YOY widow and yellowtail rockfish in our study were found at average depths of 40 and 50 m, respectively, and in contrast the average depth of adults has been reported as well over 100 m (Love et al., 2002). However, some species make an ontogenetic depth change of well over 100 m; for example, stripetail rockfish can settle in depths as shallow as 15 m but as adults live at 200 m (Love et al., 2002).

Some rockfish species recruit to nearshore kelp beds, but many of these same species also recruit to deeper depths. Young-of-the-year blue, widow, and yellowtail rockfish have been recorded in large numbers in nearshore kelp beds (Anderson, 1983; Carr, 1991; Laidig et al., 2007). These beds reach maximum depths of 20–30 m depending on water clarity (Schiel and Foster, 2015). The highest densities of blue rockfish in our study occurred at depths around 30–40 m, and widow and yellowtail rockfish were most abundant at depths of 40–50 m. These species utilize both shallow nearshore areas (depths <30 m) and deeper rocky habitats. Carr (1991) counted YOY blue rockfish in kelp beds and estimated densities of 180–400 fish/100 m<sup>2</sup> over a 2-year period. Laidig et al. (2007) surveyed YOY of rockfishes in the kelp beds off Northern California and found large interannual fluctuations in abundance for YOY blue and yellowtail rockfish with densities varying from 0.07 to 655 fish/100 m<sup>2</sup>. In this study, the density of blue rockfish at the depth of 30 m was 2 fish/100m<sup>2</sup>, and the density of yellowtail rockfish at the same depth was 0.1 fish/100 m<sup>2</sup>. The submersible could not survey within the kelp bed; therefore, a substantial proportion of each of the populations of blue and yellowtail rockfish may have been missed.

The differences in densities may also be explained through the interannual variation in recruitment strength realized in all rockfishes (Carr, 1991; Ralston et al., 2013). Some species that recruit to the kelp bed, including the bocaccio and the black (*S. melanops*), gopher (*S. carnatus*), olive, and vermilion (*S. miniatus*) rockfish, were rarely seen at deeper depths in this study. The YOY of these species may be more restricted to shallow depths than YOY of

other rockfish species. Other species have more protracted distributions that stretch from the kelp bed to depths >100 m. Stripetail, halfbanded, and shortbelly rockfish all occasionally recruit to kelp beds (Anderson, 1983), but distributions of their YOY occur at much deeper depths. Love et al. (2009) surveyed rockfishes in Southern California and found YOY halfbanded rockfish in areas ranging from the kelp bed (<30 m) to depths over 200 m. Therefore, recruitment numbers for many species in kelp bed environments provide only a relative measure of their abundance, and the numbers of these species living in deeper waters should be considered.

The abundance of YOY pygmy, halfbanded, and shortbelly rockfish in our study reflects the dominance of adults of these dwarf species in the fish assemblages of deepwater rocky habitats off California (Yoklavich et al., 2002; Baskett et al., 2006). Love et al. (2009) found that the 4 most abundant species in Southern California at depths between 19 and 365 m were the squarespot, halfbanded, shortbelly, and pygmy rockfish. In a study of marine protected areas (MPAs) along the central coast of California, Starr and Yoklavich (2008) observed that at most depths between 100 and 200 m, the dominant species group was dwarf rockfishes. In another study at the Big Creek Ecological Reserve also along the central coast of California, Yoklavich et al. (2002) observed that the halfbanded and shortbelly rockfish were the 2 dominant fish species as adults within the reserve.

Although dwarf species dominate many reefs, some protected areas harbor many old fish of larger species. An example of a relatively pristine refuge is Soquel Canyon. There, considerable numbers of large (>50 cm TL), old individuals of piscivorous rockfishes have been reported, but, not surprisingly, few adults of dwarf rockfishes have been observed there (Yoklavich et al., 2000). As expected, with so many large predators there, few YOY rockfish were observed in Soquel Canyon during this study. Much of the deep rocky habitat off the U.S. West Coast has been heavily fished, and fishing has disproportionately removed rockfish of large, slow-growing, piscivorous species that prey on small, fast-growing dwarf rockfish species (O'Farrell et al., 2009). With the decline in abundance of larger species, populations of dwarf species have increased in abundance. The recovery of large rockfish species may be slowed by competition with these highly abundant dwarf rockfish species (an outcome referred to as the *cultivation effect*; Walters and Kitchell, 2001).

Initial settlement of pelagic juvenile rockfish to benthic areas is dependent on many factors, including upwelling, fronts, depth, available habitat, and temperature (Anderson, 1983; Love et al., 2002; Laidig, 2010). Upwelling has been suggested as a settlement mechanism for winter-spawned rockfish off California, with pelagic juveniles actively descending through the water column into the deeper shoreward currents that transport them to the appropriate shallow habitats (Lenarz et al. 1991; Larson et al., 1994; Johnson et al., 2001). Markel and Shurin (2020) observed high recruitment of black rockfish off Canada during a year with strong upwelling. Conversely, they



ascertained that periods of downwelling were correlated to higher settlement of other species: the copper, quillback (*S. maliger*), and brown (*S. auriculatus*) rockfish. Woodson et al. (2012) found that ocean fronts in the California Current Large Marine Ecosystem were positively correlated with recent settlement of winter-spawned fish of *Sebastes* species. Larson et al. (1994) found an unusually shallow distribution of late-stage pelagic juvenile rockfish above the thermocline in Monterey Bay and suggested that this behavior may contribute to shoreward transport of these large juveniles. They also described a multistage settlement process, with moving to shore as the first stage and finding suitable settlement habitat as the second stage.

The distribution of settled YOY rockfish is determined by the availability of food and shelter, mortality, the number of rockfish that initially settled there, or the redistribution of YOY rockfish on different substrata (Love et al., 1991). Once settled, predator avoidance (West et al., 1994; Hobson et al., 2001; Love et al., 2002) and food availability (Hallacher and Roberts, 1985; Love et al., 1991) are likely factors affecting distribution. Stein et al. (1992) observed clouds of YOY rockfish near the top of a rocky bank (at depths of 60–80 m) and larger adults in deeper areas (at depths of 100–150 m), indicating that predation is a potential cause for this distribution. The tops of rocky banks have more ambient light than deeper areas, aiding in predator detection and avoidance. In a laboratory study, predator avoidance by YOY black rockfish was higher when the predator was visible to the YOY rockfish than when they had only chemical cues (Giger, 2015).

In a study of artificial reefs, West et al. (1994) determined that abundance of demersal YOY rockfish was greatest on the most complex reefs, with aggregations near crevices. Small rockfish near the top of reefs may also be feeding on planktonic organisms in open waters above the reef more than from the reef itself (Carlson and Haight, 1976; Singer, 1985). Love et al. (1991) found evidence that food resources were less abundant in deeper, offshore areas than in shallow reefs. Besides food resources, temperature may be a factor in determining YOY rockfish distributions. Boehlert and Yoklavich (1983) studied YOY black rockfish in the laboratory and determined that growth rates increased at warmer temperatures. The YOY rockfish that settle in shallow zones may have an advantage by growing faster than deeper-living conspecifics.

The spatial distribution of settled YOY rockfish varied by species within our study area. Big Creek was the hot spot for YOY of all rockfishes combined, with the identification of this hot spot driven by high densities of half-banded and shortbelly rockfish and of unidentified YOY rockfish there during 1997 and 1998. These taxa along with the blue and striptail rockfish also each had statistically significant hot spots at this location. For several species (i.e., the greenspotted, pygmy, rosy, starry, widow, yellowtail rockfish) and unidentified rockfish, hot spots of high densities were found at Point Sur, a major upwelling center (Traganza et al., 1981).

Four other locations were also hot spots for 1 or 2 species: Davenport, Point Joe, Point Lobos, and Monterey Canyon. None of these locations was a hot spot for all rockfish species combined (Table 3), and the oceanographic currents differ between locations. Therefore, it is unlikely that ocean current transport alone is the basis for these distributions because many of these species aggregate together as pelagic juveniles before settling to the seafloor (Lenarz et al., 1991; Larson et al., 1994; Field et al., 2021). If they had all settled together and not migrated after settlement, we would expect hot spots to be populated by the species that aggregated together in the planktonic environment, and that is not the case. In a study of pelagic juveniles of rockfishes off central California during 2001–2019, only the shortbelly rockfish was in the top ten of the most abundant rockfish species over the 19-year study (Field et al., 2021). If ocean currents brought fish to these locations, we would expect the most abundant species of settled YOY rockfish to be proportional to the abundances of pelagic juvenile rockfish in the same areas, and they are not. It is more likely that the fish migrated after settlement to specific regions of high food availability or of low predation at appropriate species-specific depths and seafloor habitats (Love et al., 1991; Hobson et al., 2001; Auster et al., 2003). Those individual YOY rockfish that remain in the less desirable areas may perish or experience reduced growth rates.

Some of the areas of highest abundance of YOY rockfish were located within or near an MPA. The fish living in these areas receive increased protection from fishing and other human activities, leading to increased numbers of rockfish that can translate into greater larval production and greater numbers of YOY rockfish settling there. Most of the MPAs in our study area were established in 2007 (information on the MPAs in California are available on the [website](#) of the California Department of Fish and Wildlife); therefore, they were too new to have a significant effect on larval production. However, 2 MPAs were established prior to 2007, the Point Lobos and Big Creek Ecological Reserves in 1973 and 1994, respectively (McArdle, 1997). There may have been some additional contribution of larval rockfish from within these 2 reserves, but these reserves are small and their contribution may have been minimal. Also, high numbers of YOY were observed at Big Creek in 1997, only 3 years after the reserve was established, likely not enough time for rockfish abundance to increase enough to result in a substantial increase in the number of larvae produced. In the future, the added larval production from these MPAs should increase the numbers of YOY rockfish recruiting along the coast of central California.

A better understanding of the habitats and areas of importance to YOY rockfish can improve estimates of year-class strength and management measures to protect them. Marine protected areas, gear restrictions, and other protective measures can be employed to reduce human effects in these areas, which may prove to be nursery areas where juveniles may be able to thrive and survive to maturity, increasing their contribution to the population. Year-class



strength is a valuable component of assessing the status of fish populations and forecasting future growth. Indices of year-class strength for YOY rockfishes have traditionally been estimated by using catch-per-unit-of-effort data from midwater trawl and scuba surveys (Laidig et al., 2007; Ralston et al., 2013). Visual surveys conducted routinely in deep, complex rock habitats can enhance these traditional indices and provide indices of year-class strength for YOY rockfish species not represented in traditional surveys. Habitat-specific estimates of YOY abundance improve our ability to manage rockfish populations on an ecosystem basis.

## Conclusions

Young-of-the-year rockfish were distributed throughout the central coast of California at depths of 22–314 m. In the visual surveys of YOY in this study, 28 species of rockfish were identified, and for many this study was the first time they were identified in situ, leading to new depth distributions and habitat associations for them. The highest YOY densities for rockfishes were found in hard or mixed habitats at depths of 40–90 m. For YOY, rockfishes fell into 3 groups, the group found on soft substrata in deep water, the mid-depth group, and the shallow-water group. The shallow-water group consisted of many species that also recruit to kelp beds. For 2 of the species that recruit to shallow kelp beds, the blue and yellowtail rockfish, densities were generally higher in these beds than at deeper depths. However, the maximum depths at which these 2 species were observed in this study were 81 and 50 m, respectively, depths that are much deeper than the edge of the kelp beds (depths of ~30 m). Therefore, estimating species densities from surveys of kelp beds alone may result in underestimation of population density for YOY of species that recruit to kelp beds.

The hot spots of YOY rockfish densities coincided with 3 MPAs at Big Creek, Point Sur, and Point Lobos. These MPAs offer protection for these young fish, potentially allowing more individuals to reach maturity. Understanding of the species-specific distributions and habitat preferences of rockfish in these early life stages will improve fisheries management by enhancing 1) the reliability of density estimates with sampling of correct depths and habitats, 2) the protection of potential nursery areas and placement of future MPAs, and 3) estimates of year-class strength for stock assessment models.

## Resumen

Se investigó la distribución y abundancia de juveniles demersales del año de especies de peces de roca (*Sebastes* spp.) durante un periodo de 17 años a lo largo de la costa central de California a profundidades de 19–326 m. Se contaron más de 87,000 juveniles de peces de roca durante los estudios de 1292 transectos en el fondo marino. Las 3 especies más abundantes fueron el rocote pigmeo

(*S. wilsoni*), el rocote inspector (*S. semicinctus*) y rocote pancita (*S. jordani*). Los juveniles del año de muchas especies de peces de roca se hallaron a profundidades mayores que las registradas anteriormente. Las mayores densidades de todas las especies combinadas se dieron en profundidades someras e intermedias. La mayoría de los juveniles ocuparon sustratos rocosos o mixtos, excepto el rocote reina (*S. elongatus*) y el rocote cola listada (*S. saxicola*), que se asociaron principalmente con sustratos blandos. En toda la región se localizaron puntos calientes de densidades de juveniles de peces de roca estadísticamente significativos ( $P < 0.01$ ), pero sólo el cañón Soquel, un conocido refugio de grandes peces de roca adultos ( $> 50$  cm de longitud total), fue un punto frío significativo ( $P < 0.01$ ). Los procesos biológicos (ej., el movimiento ontogénico y la depredación) y las características ambientales (ej., el hábitat del fondo marino y las condiciones oceanográficas) pueden influir en la distribución de juveniles del año de peces de roca. Los resultados de nuestro estudio proporcionan información sobre la distribución de juveniles del año de peces de roca en hábitats profundos y complejos del fondo marino, y pueden ayudar a mejorar la estimación de la fuerza de la cohorte anual mediante estudios específicos de los hábitats preferidos.

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