

# Changes in long-lived rockfishes after more than a decade of protection within California's largest marine reserve

Aimee A. Keller<sup>1,\*</sup>, John H. Harms<sup>1</sup>, John R. Wallace<sup>1</sup>, Colin Jones<sup>2</sup>,  
Jim A. Benante<sup>3</sup>, Aaron Chappell<sup>4</sup>

<sup>1</sup>Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

<sup>2</sup>International Halibut Commission, 2320 West Commodore Way, Suite 300, Seattle, Washington 98199, USA

<sup>3</sup>Pacific States Marine Fisheries Commission, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

<sup>4</sup>Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Newport, Oregon 97365, USA

**ABSTRACT:** In 2001, the Pacific Fishery Management Council established 2 large (10 878 and 260 km<sup>2</sup>) Southern California Bight marine reserves called Cowcod Conservation Areas (CCAs) in response to declining abundance of west coast rockfishes, particularly overfished cowcod. Following closure, no fishery-independent monitoring took place for groundfishes within the CCAs through 2013. To assess the impact of the closures, we sampled multiple sites inside and outside CCAs from 2014 to 2016 via the Northwest Fisheries Science Center's Hook and Line Survey. We investigated variations in catch per unit effort (CPUE), size, length frequency and percent of sites with positive catch for 14 abundant groundfishes (bank, bocaccio, chilipepper, copper, cowcod, greenspotted, lingcod, olive, rosy, speckled, squarespot, starry, swordspine and the vermilion-sunset complex). General linear models that included area, year, depth and distance from port revealed significantly greater CPUE inside CCAs for 11 species. CPUE for lingcod, copper rockfish and vermilion-sunset was significantly or near-significantly lower inside the CCAs. We saw significant or near-significant differences in size (12 species) and length-frequency distributions (10 species), with larger fish present inside CCAs. The percentage of sites positive for individual species tended to be greater inside CCAs (11 species). We also observed significantly elevated species richness (species per site) and total CPUE inside CCAs. Results indicate larger individuals and greater CPUE for multiple rockfishes inside CCAs either as a result of effective management or perhaps pre-existing conditions.

**KEY WORDS:** Catch per unit effort · Hook and line research · Cowcod Conservation Areas · Richness · Length frequency

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## 1. INTRODUCTION

Establishment of marine reserves in oceanic ecosystems aims to fulfill multiple functions ranging from habitat protection to conservation of biodiversity and fisheries management (Russ et al. 2015, 2017,

Thompson et al. 2017). An expanding body of research centered on marine reserves highlights the potential impacts of closures on fish populations (Lubchenco et al. 2003, Miller & Russ 2014). Factors known to affect populations include reserve size and/or design, recruitment success, larval transport

across closure boundaries, rates of adult movement, environmental factors, compliance/enforcement, initial population size and concentration of fishing effort along reserve boundaries (Jennings 2000, McClanahan 2000, Denny et al. 2004, Babcock et al. 2010, Mason et al. 2012, Edgar et al. 2014, Thompson et al. 2016). Multiple studies have measured fishery spillover, including reproductive output, and fishing effects on areas adjacent to closures (McClanahan 2000, Wilcox & Pomeroy 2003, Bellman & Heppell 2007, Kellner et al. 2007, Goñi et al. 2008, Hitchman et al. 2012, Thompson et al. 2017). Further studies compared fishing effort and catch during and after establishment of reserves, although rarely prior to the closure (Murawski et al. 2005, Abbott & Haynie 2012).

Documented increases in size and abundance of fish species often occurred following establishment of closures (Cole et al. 2000, Paddock & Estes 2000, Willis et al. 2003), although the extent of recovery varied widely among studies (Babcock et al. 1999, Castilla 1999, Shears & Babcock 2003). In general, species richness and biomass of large fishes significantly increased across a broad range of protected areas (Edgar et al. 2014). Additionally, many studies concluded that reserves effectively produced increases in fecundity and species richness within their borders as well as enhanced reproductive output within and adjacent to protected areas (Hitchman et al. 2012, Miller & Russ 2014, Thompson et al. 2016, 2017). However, success of reserves in bolstering fish populations may be affected by the period of time examined, species-specific factors such as size and mobility, spatial alterations in localized fishing pressure, as well as reserve features such as large size and effective enforcement (Barrett et al. 2007, Jaworski et al. 2010, Edgar et al. 2014).

Despite recognition as important regulatory options for fisheries and ecosystem-based management, difficulties exist in determining the effectiveness of areas closed to fishing (Hilborn et al. 2004, Miller & Russ 2014, Egerton et al. 2018). Most commonly, the lack of baseline data prior to closures and the absence of long-term monitoring following closures prevent definitive assessment of actual value. Comparing density, size, richness and other population measures inside and outside closed areas offers one approach to bridge these inadequacies, particularly when similar habitat and environmental conditions exist across areas compared (Thompson et al. 2017, Egerton et al. 2018). Within the California Current system, Starr et al. (2015) noted that differences in fishes between marine protected areas (MPAs) and reference sites were slow to accumulate even with more and larger

fishes present inside MPAs when initially implemented (perhaps related to habitat quality). However, benefits did accrue to closed areas over time, with older reserves (>20 yr) subsequently characterized by significantly larger and more abundant fishes (Starr et al. 2015). This indicates that comparing established reserves, such as the Cowcod Conservation Areas (CCAs), with similar areas outside their borders, provides an effective approach for assessing response variables in the absence of preliminary data or long-term monitoring.

By the late 1990s, many commercially and recreationally important rockfishes (*Sebastes* spp.) severely declined in abundance along the US west coast due to overfishing and unfavorable oceanographic conditions (PFMC 2008). Seven of 9 species declared overfished by the Pacific Fishery Management Council (PFMC) between 1999 and 2002 belonged to the genus *Sebastes*. Rockfishes, particularly larger species within this diverse group, appear inherently vulnerable to overfishing because of their long life span (>100 yr), slow growth and late maturity (Love et al. 2002, Starr et al. 2016).

To counteract overfishing, the PFMC introduced a series of regulatory measures to reduce fishing pressure off the US west coast, including gear restrictions, reductions in allowable catch, buyback programs and closures of traditional fishing grounds (PFMC 2008). Within the Southern California Bight (SCB), managers established 2 large (10 878 and 260 km<sup>2</sup>) marine reserves, known as the CCAs, in response to severely overfished cowcod *S. levis*, estimated at only 7% of its unfished biomass. Site selection was based on elevated cowcod catch rate within the regions chosen for CCAs, although the higher catches might result from historical depletion elsewhere rather than the occurrence of prime habitat (Butler et al. 2003). Although managed as a no-retention fishery along the entire coast (California, Oregon and Washington), implementation of the CCAs afforded additional protection to cowcod by preventing incidental harvest within these large areas. Currently, bottom fishing remains restricted for all groundfishes within the CCAs at depths greater than 20 fathoms (36.6 m), thus potentially protecting the 50+ additional species of rockfishes found there (Love et al. 2002, Yoklavich et al. 2007). The CCAs remain the largest areas closed to fishing within California waters and coast-wide (Starr et al. 2015, Thompson et al. 2017).

Previous studies suggested that larvae of targeted rockfish species benefitted from closure of the CCAs (Hitchman et al. 2012, Thompson et al. 2016, 2017). Here we focused on changes in catch, size, distribu-

tion and richness for later life stages of multiple groundfish species related to the long-term closure of the CCAs. To evaluate the performance of these extensive, offshore closed areas, we compared local fish populations between the depth-based, no-take CCAs and adjacent fished areas of similar habitat. We incorporated year, depth and distance from port in our analyses to better understand factors related to differences between areas. We considered depth both because of its role in fish distribution and the known ontogenetic shift (linking depth and length) for many species encountered here (Love et al. 2002, 2009). We used distance from port as a proxy for fishing effort, since size and catch tend to decrease with increased travel time and greater fuel cost in recreational fisheries (Bellquist & Semmens 2016, Frid et al. 2016). We defined ports as locations with commercial passenger fishing vessels (CPFVs) participating in recreational fishing on an annual basis (Santa Barbara, Ventura, Oxnard, Port Hueneme, Marina del Rey, San Pedro, Long Beach, Newport Beach, Dana Point, Oceanside, Mission Bay, San Diego).

We used data collected as part of a fishery-independent hook and line (H&L) survey conducted in the SCB. Although initially excluded from the CCAs, the H&L survey received permission to sample there beginning in 2014. Since no regular monitoring of groundfishes occurred within the CCAs prior to establishment in 2001, and rarely since then (but see Yoklavich et al. 2007, Stierhoff et al. 2013), we lacked appropriate data for a pre- and post-closure comparison. Consequently, we compared current differences in species-specific catch per unit effort (CPUE), size, percent of sites with positive catch, richness and total catch between areas (defined throughout the manuscript as geographic areas open or closed to fishing) with similar habitat and depth, located inside and outside the CCAs.

## 2. MATERIALS AND METHODS

### 2.1. CCAs

The PFMC established 2 large, disconnected CCAs within the SCB in response to declining rockfishes (Yoklavich et al. 2007), including cowcod, bocaccio, blue, olive, chilipepper, swordspine and vermilion rockfishes (see Table 1 for scientific names). The CCAs represent the largest rockfish conservation areas established to date and are several times larger than most MPAs (Thompson et al. 2017). The western CCA encompasses a large area (10 878 km<sup>2</sup>) off the

Palos Verdes Peninsula, CA, extending southwards ~145 km and westward ~80 km. A relatively smaller (260 km<sup>2</sup>) eastern management area, the 43-fathom site, lies 75 km distant from the western site, ~64 km offshore San Diego, CA. Site selection was based on habitat characterized by historically high cowcod catch within the SCB (Butler et al. 2003, Thompson et al. 2017). Until the current study, fisheries-independent data to define fish catch, size or distribution within the CCAs remained lacking.

### 2.2. Survey design and samples

Since 2004, the H&L survey annually sampled ~121 fixed sites within the SCB from Point Arguello (34° 30' N) in the north to the US–Mexico exclusive economic zone boundary (32° 00' N) in the south (Harms et al. 2010). Selected sites included a range of reefs, banks and hard-bottom habitats at depths judged of likely importance to groundfishes in non-trawlable habitats throughout the region (Harms et al. 2008). Although the initial survey design excluded sites within the CCAs, we added these areas in 2014. Within the CCAs, we increased sampling from 42 sites in 2014 to 75 sites sampled annually thereafter (Fig. 1). The site selection process followed the same general guidelines used to develop the survey's 121 original fixed sites (Harms et al. 2010), with sites similarly selected in non-trawlable habitats. Potential sites, identified through meetings and outreach with members of the local sport and commercial fishing industry, revealed 371 suitable survey sites inside the 2 CCAs. Three major criteria used to guide final site selection included (1) approximating the depth range (37–229 m) sampled by the H&L survey outside CCAs; (2) ensuring adequate spatial coverage of reefs, banks and other hard-bottom habitats within CCAs; and (3) sampling a broad range of habitat quality, including areas of prime, average and marginal quality as reported by industry. Harms et al. (2010) provided additional details on the steps taken to ensure representative site selection throughout the study area, with similar considerations evaluated in the more recent selection of sites with the CCAs.

Since the addition of the CCAs in 2014, sampling occurred throughout the survey area using 3 chartered CPFVs from late September through early October. Each year, sites inside and outside the CCAs are apportioned among the vessels, with each site visited by a single vessel once annually to avoid depletion. We use a differential GPS navigation unit (Garmin 152) to locate fixed sites and establish a 91.4 m

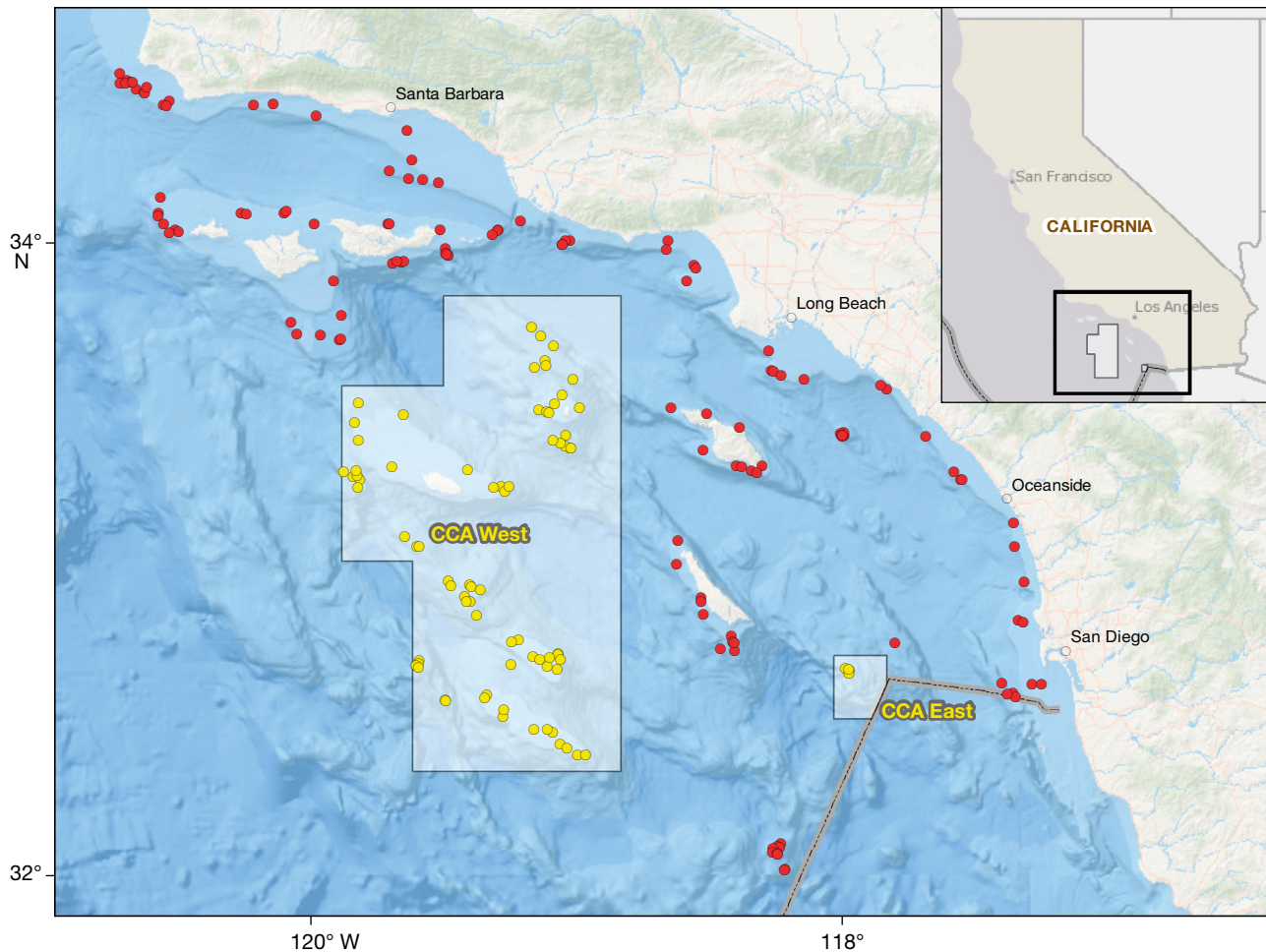


Fig. 1. Geographic extent of the Northwest Fisheries Science Center's Hook and Line Survey, showing the location of the study area in the Southern California Bight relative to the entire coast of California, USA (inset). Individual sampling sites shown outside (red) and inside (yellow) the 2 Cowcod Conservation Areas (CCAs). Boundaries of CCAs are demarcated by borders. Base chart credits: Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors

(100 yard) radius around each site. The radius allows vessel captains flexibility in targeting the site given year-to-year changes in prevailing wind and ocean conditions. Upon arrival at a designated sampling site, 3 deckhands conduct 5 coordinated drops using H&L gear deployed by rod and reel. The gear consists of a vertically arranged, 5-hook gangion appropriate for shelf rockfishes and similar to recreational gear traditionally used within the bight. Each hook includes both a shrimp fly lure (red and yellow bucktail bristle) and bait (frozen squid strip). Each set has a maximum soak time of 5 min, with combined sets resulting in a maximum catch of 75 fish site<sup>-1</sup>. Following capture, survey personnel identify, count, sex, measure (length and weight) and collect otoliths and tissue samples from managed species with limited data also taken for non-managed species. A Sea-Bird SBE 19plus conductivity, temperature, depth profiler

(Sea-Bird Electronics), provides site-specific details on bottom depth and other environmental variables. In this study, we restricted analyses to the years 2014–2016 with data collected both inside and outside CCAs.

During the current study, sampling ranged from 115 to 121 of the original fixed H&L sites per year, as weather permitted, and from 42 to 75 sites inside the CCAs (Fig. 1). To verify that hook saturation did not overly influence catch during the study, we examined the percentage of hooks deployed per year that caught fish. We examined the overall average percentage of hooks ( $\pm$  SD) that yielded catch and the percentage of sites with catch  $>50$  site<sup>-1</sup> (as a conservative but arbitrary measure of saturation at 67%) inside and outside the CCAs. We summarized hook saturation by examining the frequency (%) of hooks with positive catch, divided into 8 bins, with the first

bin including all catch  $\leq 10$  site<sup>-1</sup> and the last bin including all catch  $> 70$  site<sup>-1</sup>. We compared the frequency of catch with hooks between areas based on non-parametric, 2-sample Kolmogorov-Smirnov (K-S) analysis (SAS PROC NPAR1WAY, SAS v. 9.3, SAS Institute; Daniel 1990).

### 2.3. Distribution, CPUE and species richness

To provide general information on fish distribution within the SCB, we calculated catch-weighted average latitude (°N), depth (m) and distance from port (km) by species. Because of the importance of depth-related ontogenetic shifts (linking length and depth) and the relation between fishing pressure and distance from port, we further examined variations in these factors inside and outside CCAs. We statistically compared average depth and distance from port between the 2 areas using 2-sample *t*-tests with unequal variance. We compared frequency distributions for depth and distance from port between areas using non-parametric, 2-sample K-S analysis (SAS PROC NPAR1WAY, SAS v. 9.3, SAS Institute; Daniel 1990).

We examined the geographic distributions for 14 groundfishes including 1 species complex (Table 1) based on site-specific CPUE rates averaged across years (2014–2016) inside versus outside CCAs. We calculated species-specific CPUE for each site as the total number caught divided by the proportion of the

full complement of 75 hooks recovered at the end of each set (i.e.  $75 \times \text{catch} / \text{hooks recovered}$ ). We also examined species richness, defined as the total number of individual species taken per site (*n*), again weighted by the number of hooks recovered. This standardization allowed comparisons among sites when recovery of the full complement of 75 deployed hooks did not occur following a set.

We used Gaussian general linear models (GLMs) to examine variations from 2014 to 2016 in species-specific CPUE, total CPUE and species richness relative to the area sampled (inside and outside the CCAs), co-located geographic variables (depth in m and distance from the nearest major port in km) and year. CPUE values were log-transformed ( $\ln [\text{CPUE} + 0.5]$ ) before analysis to stabilize the variance (Gunderson 1993). Area (A), the main factor, had 2 levels within the study: open (outside the CCAs) or closed (inside the CCAs) to fishing. We tested the null hypothesis that no difference in CPUE or richness occurred between areas. The covariates included in the models (depth: Z; distance: D; year: Y) accounted for potential dependence of CPUE and richness on these variables. Because of our focus on variation in CPUE and richness relative to CCAs, we incorporated first-order interaction terms between area and other covariates in models (A:Z, A:D and A:Y; hereafter called 'interaction terms'). When significant, such interaction terms indicated important changes in CPUE and richness at different rates relative to Z, D or Y inside (I) versus

Table 1. Common and scientific names for 13 dominant demersal fish species and the vermilion-sunset rockfish species complex collected during the 2014–2016 Southern California Bight Hook and Line Survey. Mean, minimum and maximum latitude, depth and distance from port are shown by species and overall. The total catch (*n*), adjusted by the number of hooks, and the number of sites with positive catch (*n*) are also shown

Common name	Scientific name	— Latitude (°N) —			— Depth (m) —			— Distance (km) —			Catch Sites	
		Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	<i>n</i>	<i>n</i>
Bank rockfish	<i>Sebastes rufus</i>	33.07	32.02	34.22	174.3	99.7	236.8	103.3	13.9	173.3	853	67
Bocaccio	<i>Sebastes paucispinis</i>	33.08	32.01	34.52	115.8	41.9	236.3	92.2	4.4	173.3	5144	185
Chilipepper rockfish	<i>Sebastes goodei</i>	33.13	32.10	34.49	156.6	78.5	236.8	87.8	6.9	168.0	501	56
Copper rockfish	<i>Sebastes caurinus</i>	33.72	32.46	34.50	79.0	39.2	111.3	60.9	4.4	166.1	265	56
Cowcod	<i>Sebastes levis</i>	33.25	32.02	34.19	159.9	73.6	236.8	85.6	15.6	173.3	196	55
Greenspotted rockfish	<i>Sebastes chlorostictus</i>	33.28	32.07	34.52	132.4	73.9	206.1	89.5	4.4	167.8	1127	110
Lingcod	<i>Ophiodon elongatus</i>	33.82	32.38	34.52	110.6	47.4	225.5	80.2	4.4	167.8	327	88
Olive rockfish	<i>Sebastes serranoides</i>	32.93	32.41	34.50	68.6	41.4	100.8	124.3	6.3	167.4	172	31
Rosy rockfish	<i>Sebastes rosaceus</i>	33.02	32.09	34.00	78.5	43.2	225.0	102.4	5.7	167.4	176	78
Speckled rockfish	<i>Sebastes ovalis</i>	33.20	32.08	34.50	114.1	58.0	188.5	83.7	11.9	167.8	1440	105
Squarespot rockfish	<i>Sebastes hopkinsi</i>	33.14	32.40	34.39	86.7	43.7	176.8	74.5	4.4	167.4	462	69
Starry rockfish	<i>Sebastes constellatus</i>	32.88	32.02	34.53	109.7	44.7	198.6	101.7	5.7	167.8	449	97
Swordspine rockfish	<i>Sebastes ensifer</i>	33.07	32.02	34.04	148.4	82.5	239.9	90.2	6.9	173.3	281	96
Vermilion-sunset complex	<i>Sebastes miniatus/crocutulus</i>	33.66	32.01	34.52	119.8	42.5	218.1	79.3	4.4	173.3	5764	170
Total	All species	33.34	32.01	34.52	118.5	39.2	239.9	85.0	4.4	173.3	19233	196

outside (O) the CCAs. The analyses included all sites sampled per year, even those with 0 catch for a given species.

We evaluated support among models with different combinations of covariates and interaction terms based on Akaike's information criterion (AIC) (Sakamoto et al. 1986). We used a backwards-stepwise model selection process to account for area effects (inside or outside the CCAs). We removed competing covariates and interaction terms if they exhibited insignificant approximate p-values ( $p > 0.05$ ). If a covariate was removed from the model, its interaction term was also removed. We continued this process until AIC values no longer decreased when dropping covariates. For each species, the model with the best fit was determined based on minimum AIC values as:

$$\Delta_i = \text{AIC}_i - \text{AIC}_{\min} \quad (1)$$

The best model as defined above has  $\Delta_i = 0$ , while models with  $\Delta_i < 2$  have substantial support relative to the best model ( $\text{AIC}_{\min}$ ) (Burnham & Anderson 2002). Following selection of the most parsimonious model for each species, we used estimates for the area coefficients to identify directional differences for CPUE (and richness) between areas as  $I > O$  or  $O > I$ . We used R ver. 3.3.2 statistical programming language for statistical analyses (R Core Team 2016).

#### 2.4. Percent positive sites, size and length frequency

We compared the percentage of positive sites for each species inside and outside the CCAs. We calculated this metric each year based on the ratio of the number of sites with catch for a given species versus the total number of sites sampled annually by geographic area. We statistically compared percent positive sites inside and outside the CCAs using the 3 yearly values for each species via 2-sample *t*-tests with unequal variance.

We used Gaussian GLMs, similar to those for CPUE but without logarithmic transformation and with an added quadratic term for depth ( $Z^2$ ), to examine variations in size (length, cm) by species. We added the quadratic term since preliminary analyses (not shown) indicated an improved fit between length and depth with  $Z^2$  included in all species-specific models. As described in Section 2.3, we removed covariates and interaction terms until optimal models were developed for each species.  $Z^2$  was not retained for consideration in an optimal model when  $Z$  was eliminated, but  $Z$  was retained on occasion when  $Z^2$  was removed.

When a covariate was removed from a model, its interaction term was also removed; otherwise, interaction terms were removed when not significant.

To examine length-frequency distributions by species, we pooled lengths of individual fish collected by vertical H&L fishing sets, within and outside the CCAs, for all years (2014–2016). We compared species-specific length-frequency distributions between areas based on non-parametric, 2-sample K-S analysis. This non-parametric analysis of variance detects differences in length-frequency distributions between samples. To account for the large number of species-specific tests conducted, we applied Bonferroni corrections with a significance level of 0.05 to the data (Peres-Neto 1999).

### 3. RESULTS

#### 3.1. Samples

Throughout the study period, we collected data on 48 fish species from 196 sites with a total catch of 19 233 fish. With the exception of lingcod, the top 14 species taken during the survey belonged to the genus *Sebastes* (rockfishes) (Table 1). These species represent the most abundant demersal species (90% of the total CPUE) captured during the H&L survey from 2014 to 2016. Total CPUE ( $n \text{ site}^{-1}$ ), averaged by year, ranged from 35 to 49 inside (I) and 32 to 33 outside (O) the CCAs. Maximum site-specific CPUE of 73 (I) and 74 (O) indicated that on occasion gear saturation occurred; however, fewer than 3 sites per year caught greater than 70 fish  $\text{site}^{-1}$  (1.5% overall).

The 2 most abundant rockfishes (bocaccio and the vermilion-sunset complex) comprised 56.7% of the total catch ( $n$ ) from 2014 to 2016 (Table 1) and occurred at the greatest number of sites. The species with the lowest catch (olive rockfish) occurred at the fewest sites (Table 1). The overall species-specific catch ( $n$ ) and number of sites positive for catch ( $n$ ) (seen in Table 1) were significantly and positively related ( $p < 0.0001$ ,  $r^2 = 0.78$ ,  $n = 14$ ). The relationship proved significant even after elimination of the 2 most abundant outliers ( $p = 0.04$ ,  $r^2 = 0.34$ ,  $n = 12$ ).

Overall, 46–51% of hooks yielded catch each year, with a slightly higher annual percentage inside the CCAs (48–68%) versus outside (44–45%). Throughout the study,  $24.9 \pm 3.4\%$  (SD) of the sites inside the CCAs yielded catches  $>50$  fish  $\text{site}^{-1}$  (i.e. 50 hooks with positive catch equivalent to a catch rate of ~67%) while  $14.8 \pm 2.2\%$  of sites outside the CCAs caught  $>50$  fish  $\text{site}^{-1}$ . Significant differences existed

in frequency distributions for the percentage of hooks with catch (K-S asymptotic test) by area, with greater hook saturation within the CCAs relative to sites outside the CCAs (Fig. 2). Greater gear saturation inside the CCAs indicated that the significantly higher CPUE for multiple species (see Section 3.2) inside CCAs might have been even greater with deployment of more hooks.

### 3.2. Distribution, CPUE and species richness

Distribution data indicated species-specific differences in mean (weighted by CPUE), minimum and maximum latitude ( $^{\circ}$ N), depth (m) and distance from port (km) throughout the study area (Table 1). Average catch-weighted latitude varied, with olive, rosy and starry rockfishes concentrated in the more southerly portion of the sampling area and copper rockfish, lingcod and the vermilion complex being the more northerly-distributed species (Table 1). Species found at greater depths included bank and chilipepper rockfishes and cowcod, all at average depths ranging from 156.6–174.3 m while mean depths for the shallowest species (copper, olive and rosy rockfishes) ranged from 68.6–79.0 m. Although most species spanned much of the distance from nearshore to offshore (4.4–173.3 km), copper rockfish on average occurred considerably closer to port (60.9 km) while olive rockfish averaged the greatest distance from port (124.3 km) (Table 1). Both copper and olive rock-

fishes occurred at relatively shallow depths, despite representing either extreme for distance from port.

Within the CCAs, site-specific bottom depths ranged from 48.7–239.9 m (mean  $\pm$  SD:  $117.4 \pm 42.8$  m,  $n = 75$ ) while outside depths ranged from 39.2–234.6 m (mean:  $109.9 \pm 36.4$  m,  $n = 121$ ). Depths skewed deeper at sampling sites inside the CCAs (Fig. 3a), with significant differences in mean values by area ( $t$ -test:  $t = 2.31$ ,  $p = 0.02$ ). However, no significant differences existed in depth-frequency distributions inside versus outside CCAs. Distance from nearest port ranged from 45.4–173.3 km (mean:  $117.7 \pm 38.0$  km,  $n = 75$ ) within the CCAs and 4.4–119.3 km (mean:  $53.0 \pm 37.3$  km,  $n = 121$ ) outside. Significant differences existed in both mean distance ( $t$ -test:  $t = 11.86$ ,  $p < 0.0001$ ) and frequency distributions for distance by area, with sites located within the CCAs further offshore in comparison to sites outside the CCAs (Fig. 3b). Because of these differences, we incorporated depth and distance (as well as year) in models evaluating variation in CPUE and length of fishes captured inside and outside the CCAs.

Charts showing distributions (site-specific CPUE averaged across years) by species allow visual comparisons inside and outside the CCAs (Fig. 4). These figures demonstrate the variability in both species distributions and the higher CPUE within the CCAs for multiple species (see below). For example, bank (Fig. 4a) and chilipepper rockfishes (Fig. 4c) are widely distributed with elevated CPUE within the CCAs but rare throughout the remainder of the study area, while copper rockfish (Fig. 4d) and lingcod exhibit the opposite distribution and abundance patterns (Fig. 4g). Bocaccio (Fig. 4b) and the vermilion complex (Fig. 4n) appear widely distributed with relatively high CPUE throughout the study area, while olive (Fig. 4h) and rosy rockfishes (Fig. 4i) had relatively low CPUE with 0 catch at multiple stations, but higher CPUE inside the CCAs. Copper rockfish (Fig. 4d) and lingcod (Fig. 4g) frequent the northern range of the survey in high abundance, while high CPUEs of olive, rosy, squarespot and starry rockfishes were recorded in the southern half of the study site.

Because  $p$ -values generated by GLM analyses are approximate (Daskalov 1999), we based our final decisions to retain covariates on AIC values, even if, on occasion, the  $p$ -value for a covari-

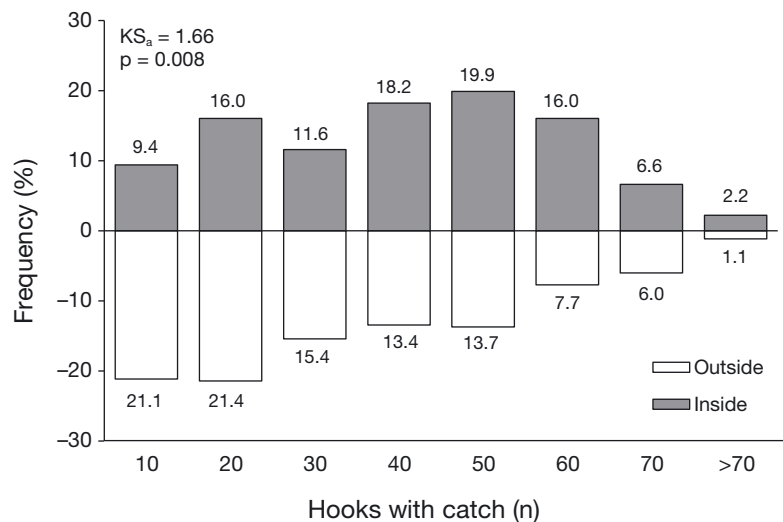


Fig. 2. Frequency distributions (%) for hooks with positive catch during the 2014–2016 Hook and Line Surveys comparing areas inside (upper gray bars) and outside (lower white bars) of the Cowcod Conservation Areas. Percentages for hooks with catch shown by intervals of 10 (n). Kolmogorov-Smirnov asymptotic statistics ( $KS_a$ ) and  $p$ -value are shown

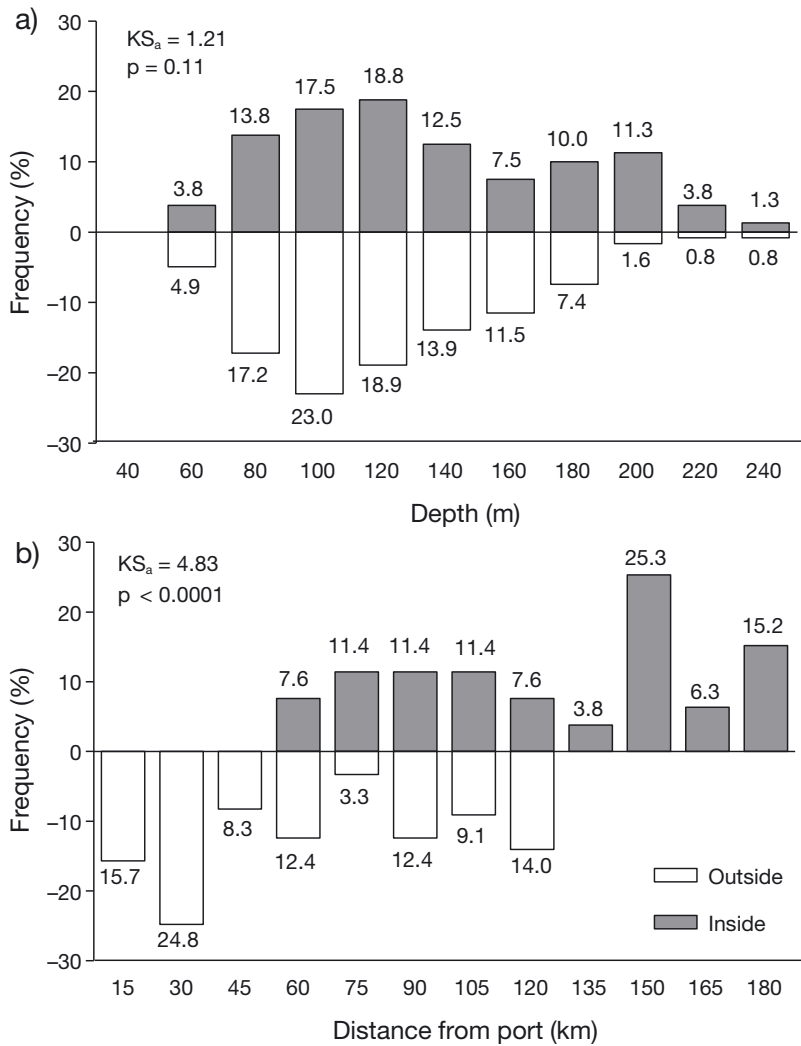


Fig. 3. Frequency distributions (%) for sites sampled during the 2014–2016 Hook and Line Surveys for: (a) depth (m) and (b) distance from port (km). Comparison shown of 2 areas defined as inside (upper gray bars) and outside (lower white bars) the Cowcod Conservation Areas, with percentages shown by depth for each 20 m interval and by distance for each 15 km interval. Kolmogorov-Smirnov asymptotic statistics( $KS_a$ ) and p-values are shown

ate was not significant. Overall, optimal models were highly significant ( $p < 0.001$ ) for all species, total CPUE and richness. Because of our interest in differences between open and closed areas, we also focused on the significance of the approximate p-values for area and noted that with the exception of copper rockfish ( $p = 0.10$ ), the area effect proved significant ( $p < 0.05$ ) for species-specific CPUE, total CPUE and richness (Table 2).

Even though  $\Delta_I$ -values for each step in the backwards elimination are not displayed, all covariates and interaction terms removed from optimal models are listed in Table 2. For 5 species (bank, bocaccio, olive, speckled, squarespot rockfishes, and the ver-

million-sunset complex), the best models ( $\Delta_i = 0$ ) included all covariates but not all interaction terms. Among covariates, depth was retained in the optimal models most frequently (13 of 14 species, total CPUE and richness). Depth was excluded from the optimal model for lingcod, while A:Z was removed for an additional 3 species (cowcod, green-spotted and squarespot rockfishes), total CPUE and species richness (Table 2). Year and/or A:Y were excluded from optimal models for 8 species and species richness (Table 2). Distance and/or A:D were also removed from optimal models for 8 species (Table 2). Six species (cowcod, bank, copper, greenspotted, rosy and speckled rockfishes) had at least 1 and up to 3 models with  $\Delta_i < 2$ , usually on removal or addition of 1 or 2 covariates from the final model (Table 2). The frequent retention (10 of 14 species) of A:Z signified an important difference in the rate of change in CPUE by depth for sites located inside versus outside the CCAs for multiple species (Table 2).

The coefficient of determination ( $r^2$ ) from the GLM analysis indicated that optimal models explained from 5.0% (lingcod) to 56% (bank rockfish) of the variation in species-specific CPUE (Table 2). The percent variance explained for total CPUE (25.0%) was greater than both the average variance explained (18.6%) for the 14 groundfish species examined and higher than the percent variance explained for species richness (10.0%) (Table 2).

Because of the focus on differences inside and outside CCAs, we additionally examined the directional relationships between species-specific CPUE, total CPUE and richness over the study period (Table 2). These analyses revealed significantly greater CPUE ( $n \text{ site}^{-1}$ ) for 11 of 14 species, total CPUE and species richness within the CCAs related to the area main effect (Table 2). Lower CPUE occurred for copper rockfish, lingcod and the vermilion complex inside the CCAs, with lingcod and vermilion significantly lower and copper rockfish close to significance ( $p = 0.10$ ). Mean CPUE by species from 2014 to 2016 generally reflected the results observed via the GLM analysis (Fig. 5).



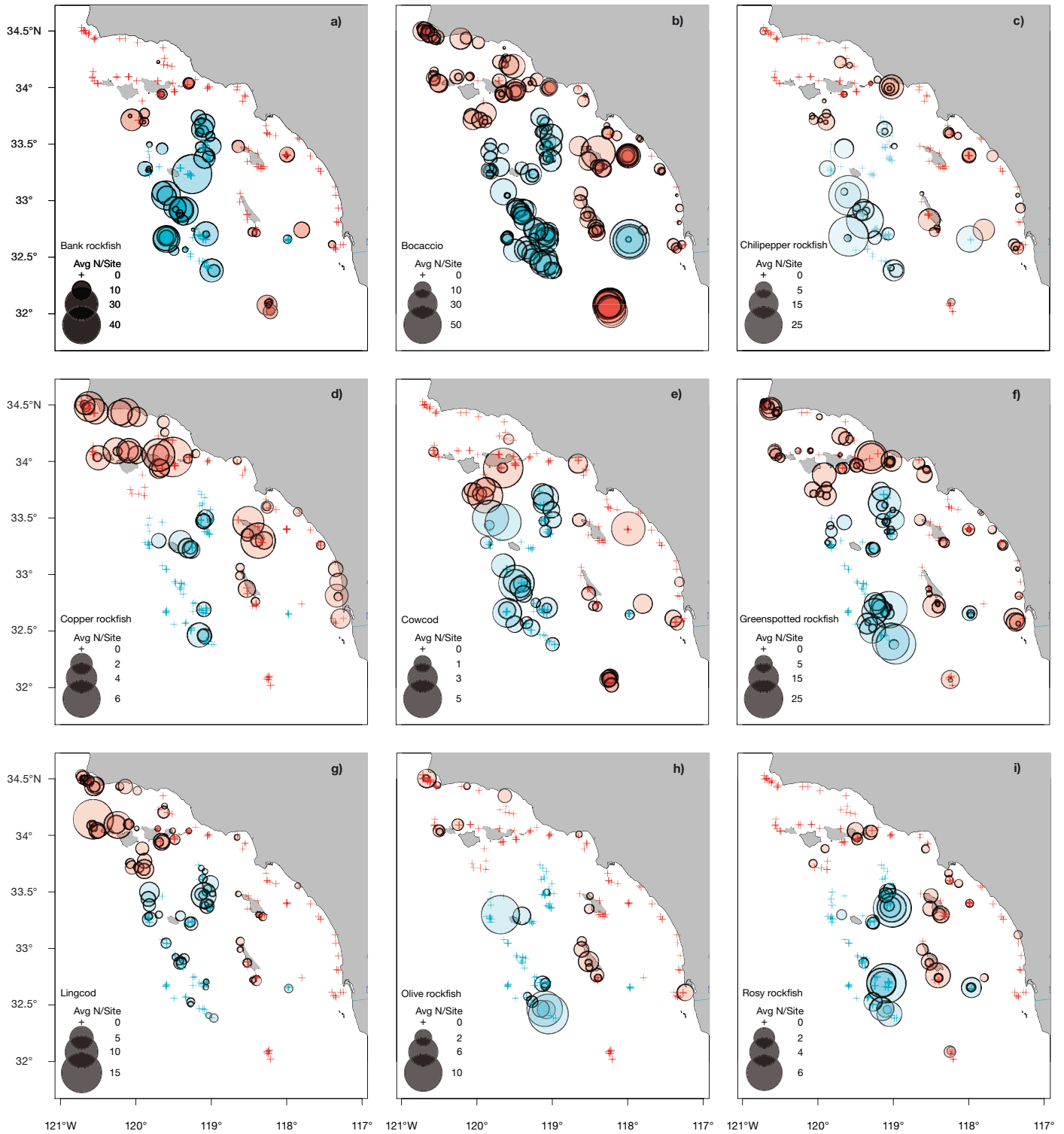


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Fig. 4. Distributions and relative abundance by species (site-specific catch per unit effort [CPUE] averaged across years) inside (blue circles) versus outside (red circles) of the Cowcod Conservation Areas for (a) bank rockfish, (b) bocaccio, (c) chilipepper rockfish, (d) copper rockfish, (e) cowcod, (f) greenspotted rockfish, (g) lingcod, (h) olive rockfish, (i) rosy rockfish, (j) speckled rockfish, (k) squarespot rockfish, (l) starry rockfish, (m) swordspine rockfish and (n) vermilion-sunset complex. For each species, the sizes of the circles represent the CPUE ( $n \text{ site}^{-1}$ ) adjusted by hooks recovered and averaged across years for each site. Note that the range of CPUE varies among species as shown in the key for each chart; (+) zero catch

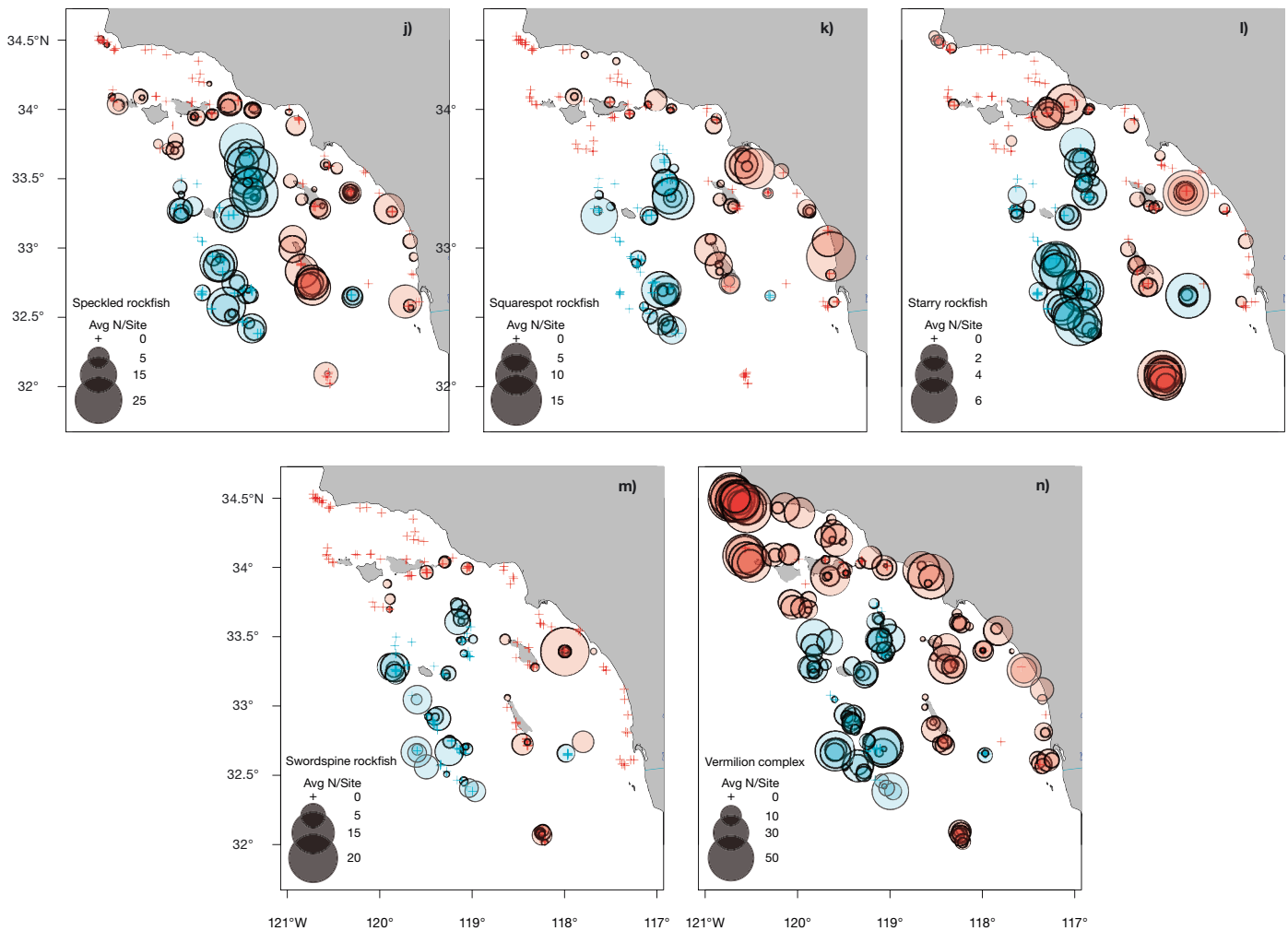


Fig. 4 (continued)

### 3.3. Percent positive sites, size and length frequency

Eleven of 14 species occurred more frequently at sites inside the CCAs (based on percentage of sites with positive catch averaged across all years; Fig. 6). Results of *t*-tests ( $n = 6$ ) indicated a significantly ( $p < 0.05$ ) elevated percentage of sites inside CCAs for bank, bocaccio, rosy, starry and swordspine rockfishes. Near significant ( $p < 0.10$ ) results occurred for lingcod, olive and speckled rockfishes, while insignificant ( $p > 0.10$ ) but elevated percentages of sites with positive catch occurred inside CCAs for cowcod, greenspotted and squarespot rockfishes. Copper rockfish demonstrated a significantly higher percentage of sites with positive catch outside the CCAs, while chilipepper rockfish and the vermilion complex tended to be present at a slightly higher percentage of sites outside the CCAs (Fig. 6).

Optimal GLMs for size (length, cm) consistently incorporated distance and/or depth and frequently (7 of 14 species) excluded year (Table 3). These models explained 3 to 65% of the variation in length inside and outside the CCAs from 2014 to 2016. Based on approximate *p*-values for area, we noted that 12 species were significantly ( $p < 0.05$ ) larger inside the CCAs (Table 3). In some cases, despite only small differences in mean size (e.g. bocaccio; Table 4) results indicated significantly larger fish inside CCAs, after accounting for covariates. No significant effects were seen for starry ( $p = 0.9$ ) and swordspine rockfishes ( $p = 0.35$ ).

All covariates ( $Z$ ,  $Z^2$ ,  $D$ ,  $Y$ ) and interaction terms ( $A:Z$ ,  $A:Z^2$ ,  $A:D$ ,  $A:Y$ ) removed from optimal models are listed in Table 3. For 3 species (bank, bocaccio and starry rockfishes), the best models ( $\Delta_i = 0$ ) included all covariates. Among covariates,  $D$  was retained in all optimal models, and  $Z$  and  $D$  were frequently retained

Table 2. General linear model (GLM) results for catch per unit effort ( $\ln [CPUE + 0.5]$ ,  $n \text{ site}^{-1}$ ) of demersal fishes and species richness ( $n$ ). Models were analyzed by Akaike's information criterion (AIC) with optimal models determined by the lowest  $\Delta AIC$  value ( $\Delta_i = 0$ ).  $\Delta AIC$  values are shown for candidate models that included treatment (area, A), defined as inside (I) and outside (O) the Cowcod Conservation Areas, and covariates: depth (Z, m), distance from port (D, km) and year (Y). All models initially included first-order interaction terms with area (e.g. A:Y). Covariates removed from optimal models are also shown. If a covariate was removed, its interaction term was also removed; otherwise, interaction terms were removed if not significant ( $p > 0.05$ ).  $F$ -values and  $r^2$  are shown for the optimal models ( $\Delta_i = 0$ ) (all highly significant with  $p < 0.001$  and  $n = 538$ ). Optimal models with significant ( $p < 0.05$ ) area effects indicated with \* and near-significant ( $p < 0.10$ ) area effects with +. GLMs with greater CPUE between areas are demarcated as I > O or vice versa

$\Delta_i$ for models with:	A	A,Z	A,D	A,Y	A,Z,D	A,Z,Y	A,D,Y	Full	Covariates removed	$F$	$r^2$	CPUE
Bank rockfish	382.3	5.9	374.0	382.2	6.4	1.1	374.1	0.0*	A:D	114.0	0.56	I > O
Bocaccio	118.2	89.3	27.9	105.2	15.6	75.2	13.0	0.0*	None	26.1	0.26	I > O
Chilipepper rockfish	115.8	14.5	113.9	119.3	0.0*	17.9	117.3	3.2	Y, A:Y	27.9	0.21	I > O
Copper rockfish	89.2	1.3	92.5	88.8	89.1	0.0+	92.1	2.3	D, A:D	23.2	0.18	O > I
Cowcod	125.7	1.9	115.0	129.3	0.0*	5.7	118.6	5.4	Y, A:Z, A:Y	39.3	0.22	I > O
Greenspotted rockfish	44.5	8.0	47.4	37.6	8.3	0.0*	41.0	1.3	D, A:Z, A:D	14.1	0.10	I > O
Lingcod	23.6	28.2	0.0*	29.6	3.6	31.9	3.8	7.5	Z, Y, A:Z, A:Y	10.2	0.05	O > I
Olive rockfish	92.2	30.7	68.7	89.0	3.6	26.4	66.8	0.0*	A:D	19.6	0.18	I > O
Rosy rockfish	80.5	0.0*	83.3	81.7	1.4	0.2	84.5	1.5	D, Y, A:D, A:Y	40.5	0.19	I > O
Speckled rockfish	18.8	13.9	8.0	16.8	1.1	11.8	7.0	0.0*	A:Y	9.8	0.10	I > O
Squarespot rockfish	61.9	15.8	55.9	50.7	15.5	3.2	43.1	0.0*	A:Z	13.5	0.13	I > O
Starry rockfish	40.7	22.2	15.1	71.1	0.0*	25.5	18.5	5.2	Y, A:Y, A:D	20.5	0.13	I > O
Swordspine rockfish	88.5	0.0*	90.6	92.1	103.1	3.6	94.2	6.6	D, Y, A:D, A:Y	43.8	0.20	I > O
Vermilion complex	36.5	24.5	13.3	38.3	0.0*	26.2	15.3	3.1	Y, A:D, A:Y	11.8	0.09	O > I
Total	111.2	66.7	40.0	104.4	9.4	58.9	32.8	0.0*	A:Z	27.3	0.25	I > O
Species richness	24.1	16.8	3.6	27.4	0.0*	21.1	7.0	5.4	Y, A:Y, A:Z	15.3	0.10	I > O

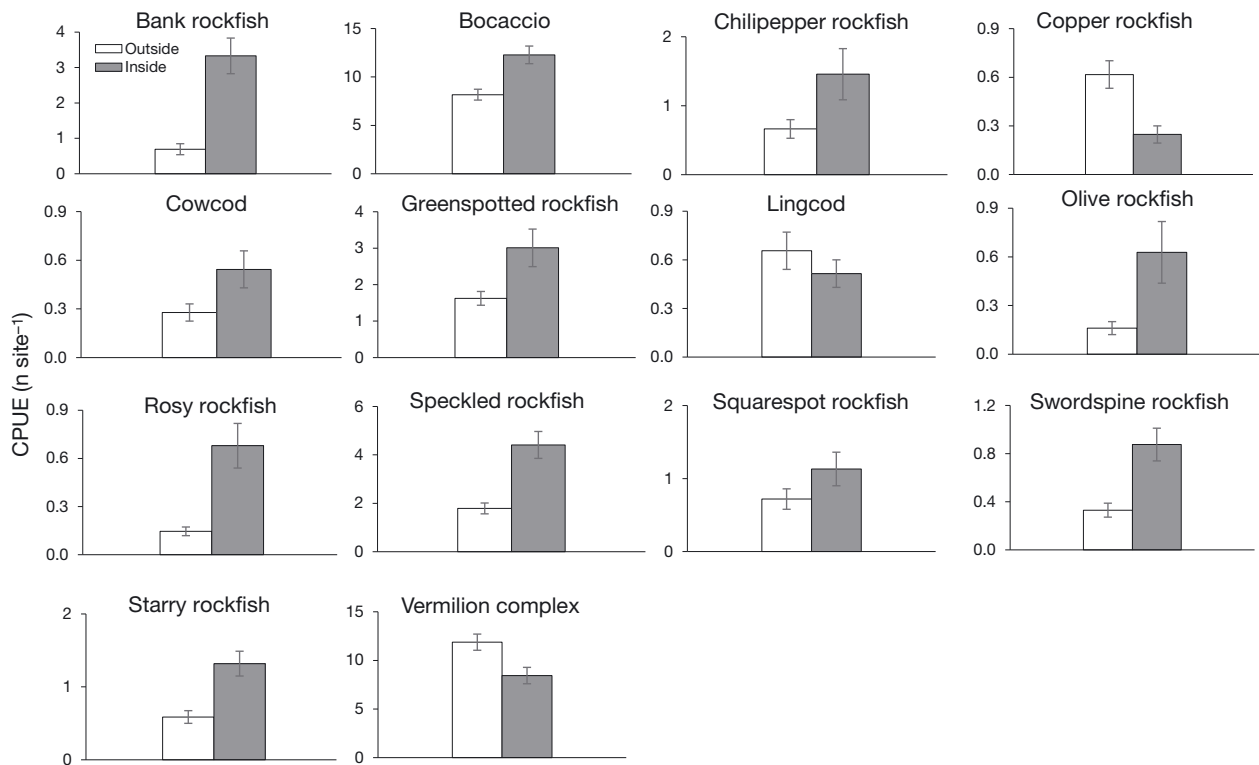


Fig. 5. Species-specific catch per unit effort (CPUE;  $n \text{ site}^{-1}$ ) for bank rockfish, bocaccio, chilipepper rockfish, copper rockfish, cowcod, greenspotted rockfish, lingcod, olive rockfish, rosy rockfish, speckled rockfish, squarespot rockfish, starry rockfish, swordspine rockfish and the vermilion-sunset complex collected during the 2014–2016 Hook and Line Surveys. Means  $\pm$  SE are shown for each species inside (grey bars) and outside (white bars) of the Cowcod Conservation Areas

Table 3. General linear model (GLM) for length (cm) of demersal fishes analyzed by Akaike's information criterion (AIC) with optimal models determined by the lowest  $\Delta AIC$  value ( $\Delta_i = 0$ ).  $\Delta AIC$  values are shown for candidate models that included treatment (area, A), defined as inside (I) and outside (O) the Cowcod Conservation Areas and covariates: depth (Z, m), distance from port (D, km), and year (Y). All models initially included a quadratic term for depth ( $Z^2$ ) and first-order interaction terms with area (e.g. A:Y).  $Z^2$  was not retained for consideration in an optimal model when Z was eliminated. Covariates removed from optimal models also shown. If a covariate was removed its interaction term was also removed; otherwise, interaction terms were removed if not significant ( $p > 0.05$ ). *F*-values and  $r^2$  are shown for the optimal models ( $\Delta_i = 0$ ) (all highly significant with  $p < 0.001$ ). Optimal models with significant ( $p < 0.05$ ) area effects indicated with \*. Models were followed by *t*-tests, with greater lengths between areas demarcated as I > O or vice versa

$\Delta_i$ for models with:	A	A,Z	A,D	A,Y	A,Z,D	A,Z,Y	A,D,Y	Full	Covariates removed	<i>F</i>	$r^2$	<i>t</i> -test
Bank rockfish	54.1	7.9	46.0	57.1	1.7	7.1	49.4	0.0*	None	8.3	0.08	I > O
Bocaccio	2040.3	147.0	1682.6	2012.8	6.8	132.8	1668.0	0.0*	None	282.3	0.33	I > O
Chilipepper rockfish	200.5	41.4	73.8	201.9	0.0*	36.0	73.1	34.6	Y, A:D, A:Z <sup>2</sup>	89.6	0.48	I > O
Copper rockfish	101.5	22.9	28.9	102.8	0.0*	21.6	31.0	1.9	Y, Z <sup>2</sup> , A:Y, A:Z, A:Z <sup>2</sup>	43.0	0.40	I > O
Cowcod	15.9	7.0	14.3	18.6	0.0*	8.6	17.3	0.9	Y, Z <sup>2</sup> , A:Y, A:Z <sup>2</sup>	11.0	0.23	I > O
Greenspotted rockfish	197.3	78.3	130.7	196.7	0.0*	77.2	133.9	5.7	Y, A:Y, A:Z, A:Z <sup>2</sup>	117.0	0.34	I > O
Lingcod	81.6	72.1	31.1	58.2	32.4	52.2	0.0*	4.8	Z, Z <sup>2</sup> , A:Z, A:Z <sup>2</sup> , A:Y	54.2	0.43	I > O
Olive rockfish	32.3	20.5	5.8	33.7	6.6	21.0	0.0*	3.1	Z <sup>2</sup> , A:Z, A:Z <sup>2</sup> , A:Y	15.7	0.32	I > O
Rosy rockfish	36.9	34.9	11.9	36.7	0.0*	34.4	15.4	5.9	Y, Z <sup>2</sup> , A:Y, A:Z <sup>2</sup>	12.5	0.28	I > O
Speckled rockfish	397.2	100.5	328.5	399.6	0.0*	100.1	331.3	1.0	Y, A:Y	95.1	0.32	I > O
Squarespot rockfish	46.7	15.3	38.3	31.1	0.0*	2.3	26.1	5.2	Z <sup>2</sup> , Y, A:Z, A:Z <sup>2</sup> , A:Y	15.0	0.12	I > O
Starry rockfish	94.8	44.9	45.7	88.2	0.6	41.0	41.5	0.0	None	27.5	0.20	O > I
Swordspine rockfish	5.6	5.3	0.0	5.3	1.5	6.5	1.9	1.9	Z, Z <sup>2</sup> , Y, A:Z, A:Z <sup>2</sup> , A:Y	3.8	0.03	O > I
Vermilion complex	4346.2	1904.0	2073.8	4331.1	40.9	1876.0	2050.0	0.0*	None	1178.0	0.65	I > O

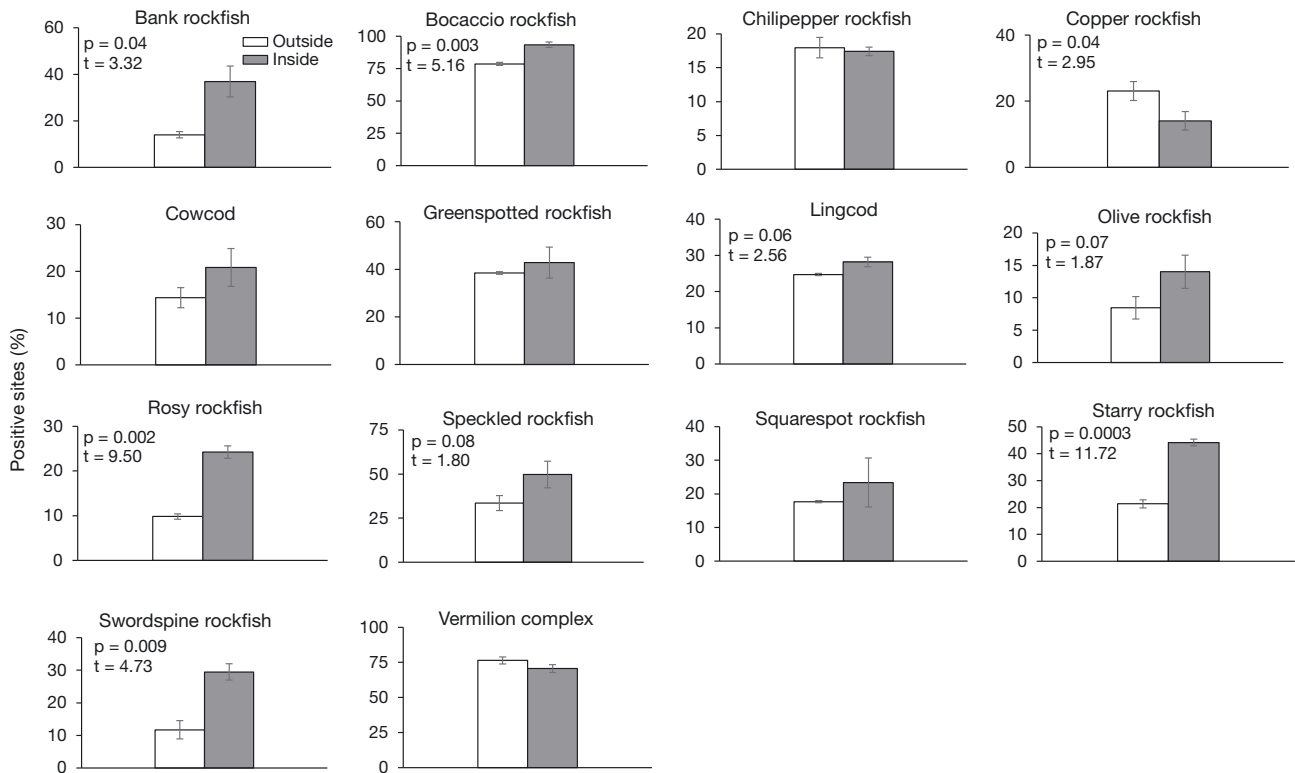


Fig. 6. Mean  $\pm$  SE percent of sites with positive catch by species (bank rockfish, bocaccio, chilipepper rockfish, copper rockfish, cowcod, greenspotted rockfish, lingcod, olive rockfish, rosy rockfish, speckled rockfish, squarespot rockfish, starry rockfish, swordspine rockfish and the vermilion-sunset complex) inside (grey bars) and outside (white bars) of the Cowcod Conservation Areas. *p*-values and *t*-statistics for significant ( $p < 0.05$ ) and near-significant ( $p < 0.1$ ) differences between areas shown for individual species

Table 4. Comparison of species-specific length-frequency distributions between regions based on a non-parametric, 2-sample Kolmogorov-Smirnov analysis. Shown are the Kolmogorov-Smirnov asymptotic statistics ( $KS_a$ ) with significant ( $*p < 0.05$ ) or near significant ( $+p < 0.10$ ) differences between areas inside and outside the Cowcod Conservation Areas (CCAs), following Bonferroni corrections. Mean (SD) length (cm), range (cm) and number of observations (n) are also shown for 13 demersal fish species and 1 species complex within the 2 geographic areas based on the CCAs from 2014–2016

Common name	$KS_a$	Outside CCA			Inside CCA		
		Length ( $\pm$ SD)	Range	n	Length ( $\pm$ SD)	Range	n
Bank rockfish	1.36	40.6 (4.23)	29–54	243	41.2 (4.15)	27–56	633
Bocaccio	2.59*	47.5 (7.75)	17–78	2824	48.0 (8.16)	25–82	2230
Chilipepper rockfish	4.05*	31.8 (8.92)	15–51	233	40.2 (7.62)	24–56	257
Copper rockfish	2.24*	35.3 (6.61)	18–50	217	40.7 (4.74)	32–50	45
Cowcod	2.14*	59.2 (11.09)	26–83	99	66.5 (8.99)	41–87	96
Greenspotted rockfish	6.93*	31.5 (5.51)	17–46	573	36.8 (4.61)	21–52	553
Lingcod	3.49*	60.4 (10.98)	35–101	197	73.7 (11.4)	48–101	85
Olive rockfish	2.75*	35.2 (5.83)	24–50	55	39.8 (5.05)	25–51	116
Rosy rockfish	1.56+	21.4 (2.51)	16–28	51	22.7 (2.41)	17–35	121
Speckled rockfish	5.54*	32.4 (4.32)	21–48	628	34.6 (2.93)	21–48	837
Squarespot rockfish	1.37	22.6 (2.08)	15–30	251	23.1 (2.71)	12–38	207
Starry rockfish	0.26	32.1 (4.76)	18–42	202	32.0 (4.72)	17–43	244
Swordspine rockfish	0.44	20.6 (2.15)	16–26	116	20.5 (2.26)	12–28	159
Vermilion complex	15.43*	39.8 (8.40)	16–63	4105	49.8 (5.82)	32–66	1541

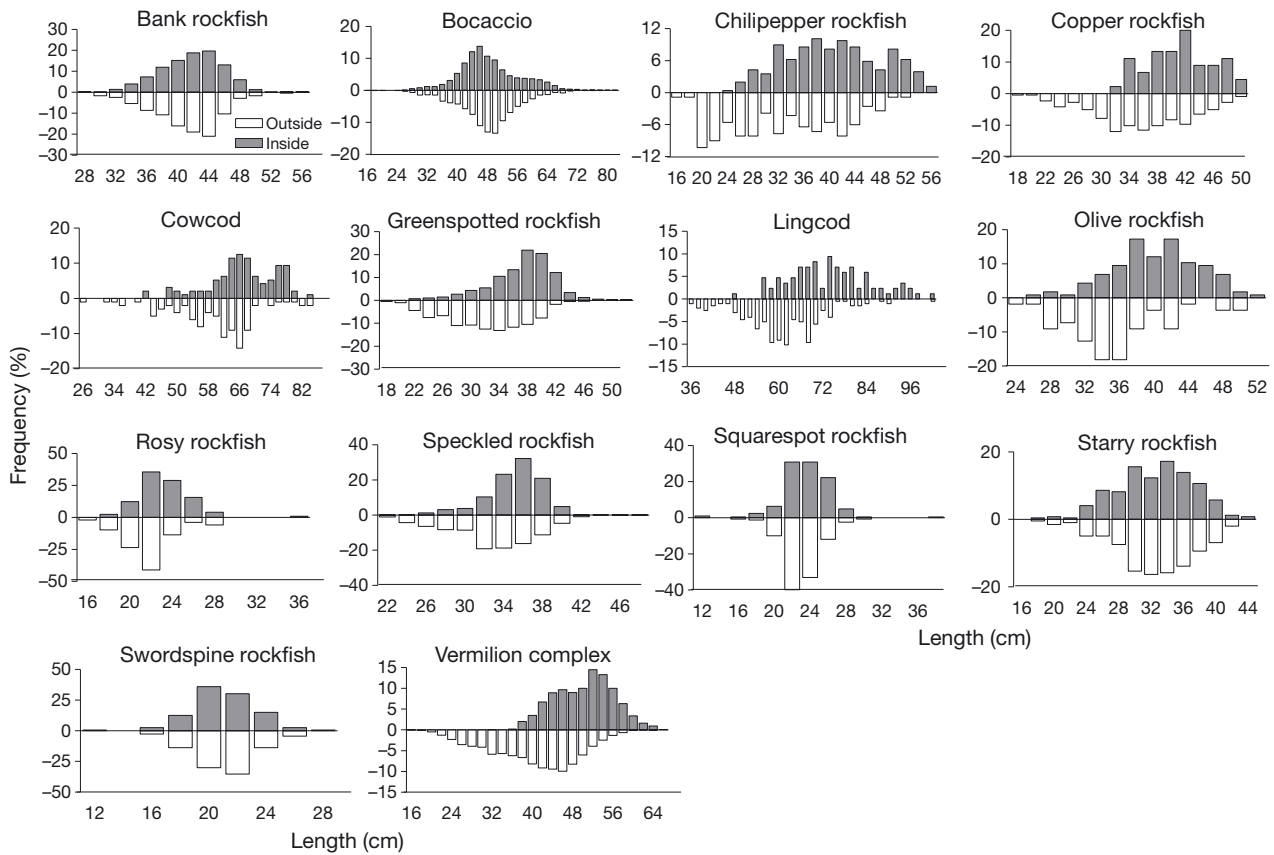


Fig. 7. Length (fork length, cm) frequency distributions (%) comparing fish size from 2014 to 2016 within 2 different areas defined as inside (upper gray bars) and outside (lower white bars) of the Cowcod Conservation Areas for bank rockfish, bocaccio, chilipepper rockfish, copper rockfish, cowcod, greenspotted rockfish, lingcod, olive rockfish, rosy rockfish, speckled rockfish, squarespot rockfish, starry rockfish, swordspine rockfish and the vermilion-sunset complex

together (10 of 14 species). Few species (bank, starry and squarespot rockfishes) had acceptable alternate models ( $\Delta_i < 2$ ) (Table 3).

Following Bonferroni corrections, our analysis also revealed significant ( $p < 0.05$ ) or near significant ( $p < 0.10$ ) differences in length-frequency distributions between areas for 10 of 14 demersal fish species ( $KS_{a_i}$ ; Table 4, Fig. 7). The results of the K-S analyses generally agreed with the GLM results for differences in lengths inside and outside CCAs, after accounting for covariates. Starry and sword-spine rockfishes did not have significant differences in length-frequency distributions or in mean length between areas (Table 4).

#### 4. DISCUSSION

During the 3 yr period examined here, abundance, richness, size and occurrence of multiple groundfish species appeared significantly elevated within the CCAs relative to similar habitat outside these areas. Although initially designed to protect overfished cowcod, closure of the CCAs in 2001 also afforded long-term protection to a large number of co-located demersal fish species (PFMC 2008). Despite the extended period since closure establishment, the short time frame for the current post-closure study (3 yr) did not support comparing trends in abundance or richness over time between areas. Similar to other studies, which lack pre-closure information and ongoing monitoring during the closed period, we elected to compare data collected from inside and outside CCAs using contemporaneous data from multiple sites with similar habitats (Lester et al. 2009, Starr et al. 2015). Despite clear evidence of larger-sized fish and greater abundance inside the CCAs, some of the observed differences may reflect variation present at the time of establishment.

The original site selection for the CCAs encompassed areas characterized as prime offshore habitat based on mean cowcod catch by commercial passenger fishing vessels from 1990 to 1998, without considering catch rate for other species (Butler et al. 2003). Beginning in 2001, regulations restricted fishing within CCAs to depths  $< 36.6$  m (20 fathoms) because adult cowcod commonly occur deeper (Love et al. 2002, PFMC 2008). Since many rockfishes and other species also inhabit these greater depths (Love et al. 2002), restricted fishing in deep waters of the CCAs thus protected other targeted species. Fishing regulations specified that at no time may rockfishes, lingcod and associated species (cabezon, greenlings,

California scorpionfish, California sheephead and ocean whitefish) be taken in these deeper waters within CCAs (PFMC 2008). Unlike other species, management further designated cowcod as a no-retention fishery throughout their range (also in January 2001), with take prohibited in commercial and recreational sectors statewide. Closure of the CCAs provided even greater protection for cowcod by sequestering a very large area where no incidental take would occur, eliminating discard mortality within CCA borders (Butler et al. 2003). Following these actions, cowcod catch dropped to less than  $1 \text{ t yr}^{-1}$ , indicating that the effort to eliminate cowcod catch has been effective (Dick & MacCall 2014). Discard mortality for cowcod continues to occur elsewhere, even with the no-retention policy, since when brought to the surface they often die following release. CCA boundaries therefore provided cowcod protection. Perhaps the existence of discard mortality for cowcod coupled with ongoing exploitation of other targeted species outside the CCAs explains the significantly higher CPUE observed for the majority of species inside the CCAs. However, as noted previously, in the absence of studies prior to closure of the CCAs, some of the differences in catch could be related to differences present at the time of establishment.

Although some periodic fishery-independent monitoring has occurred within CCAs since closure, there has been no consistent, synoptic coverage within these areas pre- or post-establishment (Yoklavich et al. 2007, Ralston & MacFarlane 2010, Hitchman et al. 2012, Stierhoff et al. 2013, Thompson et al. 2016). Past monitoring projects within the CCAs have either been short-term visual surveys conducted by manned submersible (Yoklavich et al. 2007) and a remotely operated vehicle (ROV) (Stierhoff et al. 2013) or recruitment studies focused on larval fishes (Ralston & MacFarlane 2010, Hitchman et al. 2012, Thompson et al. 2016, 2017). Yoklavich et al. (2007) conducted a visual survey of cowcod on 8 offshore banks within the CCAs at depths of 71–322 m in 2002. They made no comparisons with areas outside the CCAs but instead established a limited baseline estimate of cowcod abundance and biomass inside the CCAs while exploring a potential method for future monitoring. Stierhoff et al. (2013) built on their approach and presented encounter rates for cowcod both inside (12 sites) and outside (6 sites) the CCAs using a ROV at depths of 67–268 m. This later study (2012) observed cowcod encounter rates that were 1.88 times higher on average within the CCAs (Stierhoff et al. 2013). Their findings are very similar to the cowcod results observed here, with CPUE ( $n \text{ site}^{-1}$ ) on average 1.96

times more abundant within the CCAs (Fig. 5). Neither Stierhoff et al. (2013) nor Yoklavich et al. (2007) presented results for other demersal fish species or compared size and length-frequency distributions between areas.

Larval studies, conducted at various times and focused on a variety of species, demonstrated higher larval presence within the CCAs than in surrounding areas (Ralston & MacFarlane 2010, Hitchman et al. 2012, Thompson et al. 2016, 2017). Longer-term analyses of larval abundance benefitted from systematic sampling throughout southern California that included a time series of samples from inside and outside the closed areas before and after establishment of the CCAs (Thompson et al. 2017). In particular, Thompson et al. (2017) noted that larvae for 75 % of targeted rockfish species, but 0 % of non-targeted species, increased at a faster rate inside relative to outside CCAs from 1998 to 2013. They concluded that CCAs are facilitating recovery of rockfish species historically targeted in commercial and recreational fisheries by enhancing reproductive output. Additional studies focused on smaller protected areas in the Mediterranean, off South Africa and New Zealand, similarly concluded that enhanced larval abundance, with export into surrounding areas, fostered recovery beyond the boundaries of the protected sites (Willis et al. 2003, Pelc et al. 2009, Crec'hriou et al. 2010).

The lack of high-quality baseline measurements for juvenile and adult groundfishes prior to closure, as well as little ongoing monitoring throughout much of their history, required that we evaluate CCA effectiveness using recently collected data (2014–2016). Recommendations by stock assessment scientists, independent reviewers and the PFMC's science and statistical committee prompted expansion of the H&L survey into the CCAs in 2014 (Field et al. 2010, Dick et al. 2011, Kupschus 2012, PFMC 2013a,b, Dick & MacCall 2014, He et al. 2015). Ongoing, fishery-independent sampling within the CCAs will provide the added spatial coverage needed to evaluate rebuilding of overfished species and reduce uncertainty in abundance indices introduced by excluding such a large area from study (Ralston & MacFarlane 2010). In addition, these data provided an avenue to judge the value of the CCAs as a management tool for multiple demersal fish species. Prior to initiating the current comparison, we selected stations inside the CCAs to match similar habitat (i.e. depth, bottom type) monitored by the H&L survey within the SCB since 2003 (Harms et al. 2008). Although less than ideal, this approach bridged inadequacies resulting from the lack of prior sampling and/or ongoing long-

term monitoring, particularly since we selected similar habitat and environmental conditions across the areas compared (Hilborn et al. 2004, Miller & Russ 2014, Thompson et al. 2017, Egerton et al. 2018).

Despite the care taken in selecting sites with similar habitat, we found significant differences in mean depth and distance from port (a proxy for fishing effort), but not depth-frequency distributions. Because of these differences, we incorporated depth and distance from port (and year) in analyses comparing CPUE, richness and size inside and outside CCAs. Many of the groundfish species examined here exhibit ontogenetic shifts in depth as they mature (Love et al. 2002, 2009). The on-average greater depth of the CCAs, despite similarity in depth-frequency distribution, could thus account for some of the differential in size, making incorporation of depth in the analysis particularly important. Our use of covariates in statistical models thus reinforces our findings of greater species richness, larger size and elevated CPUE, for the majority of species examined here, inside the CCAs.

Prior research frequently reported similar findings when contrasting species richness, abundance and biomass of fish between protected and non-protected areas (Côté et al. 2001, Lester et al. 2009, Jaworski et al. 2010). Depth, in particular, played an important role in comparing demersal fish catch between areas opened and closed to fishing near Iceland (Jaworski et al. 2010). Jaworski et al. (2010) concluded that the inclusion of covariates in analyses when studying MPAs aids in detecting difference between areas, while their absence may cause results to be interpreted incorrectly. Others have consistently noted a significant relationship between depth and demersal fish distribution here and elsewhere along the US west coast (Tolimieri & Levin 2006, Juan-Jordá et al. 2009, Keller et al. 2014). Our prior analyses examining the effectiveness of the Rockfish Conservation Area (RCA), an area partially closed to commercial bottom fishing, revealed significantly greater CPUE for multiple demersal groundfish species, elevated species richness and larger fish inside the RCA after accounting for year and depth as covariates (Keller et al. 2014).

For the current study, we incorporated distance from port as a covariate in the analyses to account for fishing pressure. We reasoned that the majority of recreational fishers, particularly those in smaller boats, would typically fish closer to a nearby port, with fishing pressure thus decreasing at greater distances from land. In support of this, an analysis of recreational and commercial fishing off California showed much greater rockfish catches nearshore versus offshore (Miller et al.

2014). In general, the differential distribution of biomass with higher fish density inside protected areas (both target and non-target) appears influenced by elevated fishing effort outside these areas (Bellman & Heppell 2007, Mason et al. 2012, Keller et al. 2014).

After accounting for covariates, CPUE for the majority of species studied here was significantly greater inside the CCAs, suggesting that groundfishes within their borders were somewhat protected by the closures. Additionally, the siting of the CCAs in the more southerly, offshore waters of the SCB, where cowcod appeared more abundant at the time, favored species with similar spatial distributions, while affording less protection to more northerly and/or inshore species, as reflected in our results. The more northerly distributions for copper rockfish, lingcod and the vermilion-sunset complex, as well as the shallower location of copper rockfish, apparently contributed to their greater CPUE outside the CCAs. Despite lower CPUE within the CCAs, all 3 species were significantly larger within CCA boundaries, perhaps reflecting size-selective exploitation elsewhere.

Potential ongoing work on genetically separating the vermilion-sunset complex into the respective species may provide future additional insights into how the CCAs have affected this cryptic species pair. In particular, we suspect that once reconciled into separate species via genetic analysis, the deeper-dwelling sunset rockfish (Hyde et al. 2008) may exhibit significant differences in CPUE inside and outside the CCAs, differences currently masked by treating the species as a complex.

Multiple studies previously reported a greater proportion of larger fish in protected populations, most likely as a direct consequence of reduced fishing mortality and size-selective fishing (Harmelin et al. 1995, Tetreault & Ambrose 2007). Commercially exploited demersal fishes in the North Sea and off the coast of Iceland reportedly also exhibited variation in size distributions, with larger fish inside protected areas (Piet & Rijnsdorp 1998, Jaworski et al. 2010). Keller et al. (2014) observed larger sizes for 20 of 31 demersal fish species in the RCA. Those not exhibiting larger sizes tended to be slow-growing rockfish species or species with a known ontogenetic shift into waters deeper than the RCA as they age. In the current analysis, we saw larger sizes for 11 species and the vermilion-sunset complex inside the CCAs. Although not shown, we observed the same results based on weight for all species. Given the significantly greater average depth encountered within the CCAs relative to outside, some of the variation in size may be related to mean depth (inside CCAs, 117.4 m ver-

sus outside, 109.9 m). However, the magnitude of the depth difference is small (<8 m), despite being significant, and is unlikely the cause for the observed differences in mean length and length-frequency distributions. Additionally, size differences could result from the absence of smaller size classes inside CCAs, as seen for multiple species (e.g. chilipepper rockfish; see Fig. 7). Excluding the smaller size classes for chilipepper rockfish, copper rockfish, lingcod, olive rockfish and the vermilion-sunset complex and repeating the analyses confirmed significantly different size-frequency distributions, with larger fish still present on average within the CCAs. Consequently, we attribute the larger sizes inside CCAs to reduced fishing pressure and size-selective exploitation elsewhere, as reported by others, although the larger sizes could reflect pre-existing conditions related to habitat differences present at the time of implementation.

Our results suggest that a 13 yr time span following implementation of protection produced notable increases in both abundance and size even for the slow-growing, long-lived, late to mature rockfish species examined here. In contrast, Starr et al. (2015) found that a 7 yr period was too short for positive effects to be evident in several small reserves in central CA. However, Starr et al. (2015) reported that an older reserve, closed since 1973, displayed significantly more abundant and larger fish relative to reference areas, similar to findings noted here for the CCAs. Our results support the suggestion of Molloy et al. (2009) that a 10–20 yr closure produces positive reserve effects for species with the above life history characteristics. However, variations in longevity and age at maturity among rockfish species likely also impacts when reserve effects would be observed (Hamilton et al. 2010, Haggarty et al. 2016). In addition, the existence of high-quality rockfish habitat inside the CCAs likely influenced the observed results, although again the lack of measurements prior to closure decreases the certainty of the observed response (Rodwell et al. 2003, Friedlander et al. 2007, Claudet et al. 2010).

An additional metric, i.e. the comparison of the percentage of sites with positive species-specific catch inside and outside protected areas, supported our findings of positive reserve impacts. The metric revealed that when averaged across the 3 yr study period, 11 species occurred at a greater proportion of sites inside CCAs, signifying widespread distributions. On average, the frequency of occurrence of these species was 14% greater inside CCAs (range 4–23%). Although significant for only 5 of 14 species, we believe that given the small number of years



currently available, the metric will prove a useful response variable for detecting change over longer periods.

The CCAs demonstrated higher species richness (i.e. total fish species caught per site, adjusted by the number of hooks recovered) relative to areas open to fishing after accounting for covariates. Numerous studies similarly reported that protected areas have significantly elevated species richness and/or diversity (Piet & Rijnsdorp 1998, Côté et al. 2001, Fisher & Frank 2002, Abesamis & Russ 2005). Since fishing activity often leads to depletion of species, greater species richness is expected inside protected areas relative to fished sites (Jennings & Kaiser 1998, Hall 1999, Kaunda-Arara & Rose 2004, Lester et al. 2009). Worm et al. (2006) found that reserves enhanced diversity on average by 23% with accompanying large increases in fisheries productivity. However, in some cases, the opposite response occurred (i.e. decreased species richness), leading some to postulate that species richness or diversity is a less meaningful measure as a response variable for detecting change due to closures than changes in size or abundance (Bianchi et al. 2000, Stobart et al. 2009, Starr et al. 2015).

We conclude, based on data collected via fishery-independent H&L surveys from 2014–2016, that significant differences occurred in CPUE, species richness, size and length-frequency distributions for multiple demersal fish species inside and outside the CCAs. Long-term closures, such as those for the CCAs, produced discernable results even for long-lived, slow-growing and late to mature rockfishes. These differences were manifest even with a variety of other management measures enacted outside the CCAs, such as closures at 9 sites associated with other state and federal MPAs, intermittent closures associated with the RCAs and specific management measures aimed at a number of species. Monitoring within the CCAs will continue for the next several years to establish trends over time and affirm if differences observed here primarily result from protection afforded fishes within CCA boundaries rather than differences present at the time of implementation or enactment of other management measures.

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