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Canary rockfishes *Sebastes pinniger* return from the brink: catch, distribution and life history along the US west coast (Washington to California)

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ABSTRACT: A standardized bottom trawl survey monitored the recovery of canary rockfishes *Sebastes pinniger* along the US west coast. We examined catch-per-unit-effort (CPUE), distribution and life history parameters for canary rockfishes, an important groundfish that severely limited other US west coast fisheries from 2000 to 2015 due to their overfished status. Average catch varied among years, but CPUE, tows with positive catch and biomass significantly increased since 2007. Weight–length and size-at-age relationships varied by regions separated at key biogeographic breakpoints. Weight increased more rapidly as a function of length north of Point Conception, California, regardless of gender. Growth rates of females and maximum size of males increased with latitude, with the greatest increases north of Pt. Conception. Mature females most commonly occurred north of Cape Mendocino and at depths >115 m. Observed variations in spatial patterns (CPUE and distribution) and life history characteristics combined with reduced occurrence of large/old canary rockfishes south of Cape Mendocino suggest coast-wide differences that imply the existence of distinct biological stocks. However, since annual von Bertalanffy growth coefficients and slopes of weight–length regressions appear related to basin-wide (Pacific Decadal Oscillation) and regional (based on *in situ* data) climatic effects, environmental variation may also contribute to the differences observed here.

KEY WORDS: Canary rockfish · Weight–length · Size-at-age · US west coast · Groundfish surveys

INTRODUCTION

In the northeastern Pacific Ocean, canary rockfishes *Sebastes pinniger* range from the western Gulf of Alaska, USA, to northern Baja California, Mexico, with greatest abundance from British Columbia, Canada to central California (Miller & Lee 1972, Love et al. 2002). Although occasionally found deeper, adults generally inhabit the continental shelf in waters shallower than 300 m (Love et al. 2002). Canary rockfishes display ontogenetic migration; adults move into deeper waters as they mature (Love et al. 2002). They are a relatively large, sexually dimorphic rockfish with females reaching a maximum size of ~70 cm and generally larger than males of the same age. Like many rockfish species, they are long-lived with observed ages greater than 80 yr (Love et al. 2002). Within the California Current system, older females (>30 yr) are infrequently encountered, although catches of older males up to 50 yr of age occasionally occur (Stewart 2009). Like all *Sebastes*, canary rockfishes are viviparous (live-bearing fish), and spawn in the winter months (Love 1996, Thorson & Wetzel 2015).

Distribution is patchy and varies by bottom type, with adults off Washington, Oregon and California most abundant in and around rocky shelf habitats (Love 1996), perhaps in association with upwelling conditions (Juan-Jordá et al. 2009) and occasionally

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near soft-bottom areas (Tissot et al. 2007, Vestfals 2009). In Alaskan waters, canary rockfishes observed via remotely operated vehicles were associated primarily with complex boulder–cobble habitat (Johnson et al. 2003).

After being declared overfished in 2000, the recovery plan for this recreationally and commercially important species constrained fishing opportunities for multiple healthy fish stocks along the US west coast. The Pacific Fishery Management Council recently determined canary rockfish populations to be rebuilt following adoption of the 2015 stock assessment (Thorson & Wetzel 2015). Although lightly exploited before the early 1940s, the stock was heavily fished thereafter, with a minimum spawning stock biomass reached in the mid-1990s (Wallace & Cope 2011). After being declared overfished in 2000, a rebuilding plan placed several constraints on the fisheries in which canary rockfishes co-occur with other groundfish. Implemented protections included limited catch, spatial closures and gear restrictions to reduce coincident catch in rocky habitats and shelf flatfish trawls (Bellman et al. 2005, Thorson & Wetzel 2015). These restrictions, along with a shift towards favorable ocean conditions (e.g. elevated productivity) in 2006 (Schwing et al. 2009), led to a gradual increase in canary rockfish biomass to the management target of 40% of unfished biomass. Subsequently, new harvest specifications and regulations were implemented in 2017.

Although the Northwest Fisheries Science Center's (NWFSC) bottom trawl survey encounters canary rockfishes somewhat infrequently, its 13 yr time series of catch-per-unit-effort (CPUE) and biological data provides background information of interest to scientists and of value to fishery managers. Despite being an important species in the management of west coast fisheries, life history parameters of canary rockfishes have rarely been described, including latitudinal trends in life history traits (coast-wide age and growth structure) (Boehlert & Kappenmann 1980, Boehlert 1980, McClure 1982). In an effort to support management of this species, we evaluated differences in age and growth of canary rockfishes throughout the study area, extending from the US–Canada to US–Mexico borders. Information for the southern portion of the survey incorporated size-at-age data collected as part of the NWFSC's 2003 to 2015 Southern California Shelf Rockfish Hook and Line Survey, as well as the NWFSC's fishery-independent west coast groundfish bottom trawl survey (WCGBTS). Differences in weight–length relationships and growth curves were explored as a function of gender and locality. We related annual changes in the slope of weight–length regressions and growth between 2003 and 2015 to biomass and environmental indices, including the Pacific Decadal Oscillation (PDO), a widely used El Niño-like pattern of Pacific climate variability representative of basin-wide climatic effects (Mantua et al. 1997, Schwing et al. 2009), and an *in situ* temperature-based index, developed here, indicative of local conditions within the survey area.

MATERIALS AND METHODS

Survey design

The annual WCGBTS sampled groundfish, including canary rockfishes *Sebastes pinniger*, from 2003 to 2015 off the US west coast (Bradburn et al. 2011, Keller et al. 2015). Surveys occurred from late-May through October from the US–Canada border (48° 28′ N) to the US–Mexico border (32° 30′ N) at depths of 55 to 1280 m. The entire geographic extent of the survey was covered twice each year during late May to July and mid-August to October using a stratified (by geographic location and depth) random sampling design with an average of 750 sites sampled each year. The survey was subdivided into 2 geographic strata with a north–south division at 34° 30′ N (Point Conception, California) and 3 depth strata (shallow: 55 to 183 m; mid: 184 to 549 m; and deep: 550 to 1280 m). Chartered west coast fishing vessels were equipped with customized Aberdeen-style trawls with a 3.8 cm mesh (stretched measure) liner in the codend, a 25.9 m headrope and a 31.7 m footrope. Trawling occurred within randomly selected cells with a target fishing time of 15 min at a target speed of 1.13 m s^{-1} (2.2 knots). All fishing operations strictly complied with national and regional protocols detailed in Stauffer (2004).

The annual (2003 to 2015) NWFSC's Southern California Shelf Rockfish Hook and Line Survey occurs aboard commercial sportfishing vessels during fall (September to October) using hook and line gear deployed via rods and reels. This cooperative fishery-independent survey utilizes a fixed-site design with sampling occurring once annually at 200 stations from Point Arguello (34° 35′ N) to the US–Mexico exclusive economic zone (EEZ) boundary (32° 00′ N) at depths between 36 and 229 m. Three anglers concurrently sampled each site with a maximum of 75 fish captured $site^{-1}$ (Harms et al. 2008). On average ~50% of the hooks deployed at each site caught fish, suggesting that depletion was not an issue.

Samples

Canary rockfishes captured during trawling (2003 to 2015) were identified to species, weighed and enumerated. CPUE (kg ha^{-1}) was calculated by dividing catch (kg) by area swept (ha) tow^{-1}. Area swept was computed from the mean trawl wingspread for each tow multiplied by the distance fished.

We used a spatial delta-generalized linear mixed model (delta-GLMM; R package geostatistical_delta-GLMM, version 3.4.0: https://github.com/nwfsc-assess/geostatistical_delta-GLMM) to estimate annual biomass indices (metric tonnes, t), spatial variation in density (ln kg km^{-2}) and effective area occupied over time (ln km^2) for canary rockfishes (Thorson et al. 2015, Thorson & Barnett 2016). The GLMM implements a conventional delta-model for biomass-sampling data (Maunder & Punt 2004):

$$\Pr(b_i = B) = \begin{cases} 1 - p(s_i, c_i, t_i) & \text{if } B = 0 \\ p(s_i, c_i, t_i) \times g\{B \mid \log[w_i \times r(s_i, c_i, t_i)], \sigma_c^2\} & \text{if } B > 0 \end{cases} \quad (1)$$

where the probability distribution for catch data b_i is composed of 2 components, the probability of encounter, $p(s_i, c_i, t_i)$, and the expected catch-density, $r(s_i, c_i, t_i)$, given a species is encountered for the location s_i, taxon c_i, and year t_i of the ith sample. The model further includes g, a lognormal probability distribution function (PDF) for positive catches with variance σ_c^2 and w_i the area swept for the ith sample. This delta-model decomposes density into 2 components: encounter probability (representing species distribution) and expected biomass given encounter (representing positive density). Each component is specified via a linear predictor and link-function. Encounter probability for canary rockfishes is:

$$\text{logit}[p(s_i, t_i)] = \beta_p(t_i) + \omega_p(s_i) + \varepsilon_p(s_i, t_i) + \delta_p(v_i) + \sum_{j=1}^{N_j} \lambda_p(j) q(j, i) \quad (2)$$

where $\beta_p(t_i)$ is an intercept, $\omega_p(s_i)$ is spatial variation, $\varepsilon_p(s_i\ t_i)$ is spatio-temporal variation and $\delta_p(v_i)$ represents variation in catchability for vessel v_i relative to the average vessel. We included pass level (j, first or second) as a catchability covariate $q(j,i)$ to account for unbalanced sampling between the first and second passes in 2004 and 2013 when the WCGBTS design was modified by using fewer vessels. λ_p (j) is the estimated impact of catchability covariates.

Expected biomass for canary rockfishes is specified as:

$$\log[r(s_i, t_i)] = \beta_r(t_i) + \omega_r(s_i) + \varepsilon_r(s_i, t_i) + \delta_r(v_i) + \sum_{j=1}^{N_j} \lambda_r(j) q(j, i) \quad (3)$$

where parameters are defined similarly except with subscript r indicating their use for predicting positive catch rates. Encounter probability and positive catch densities incorporate variation in average density among years (as a fixed effect estimated via maximum marginal likelihood) and incorporate variation among sampling vessels as a random effect (Helser et al. 2004, Thorson & Ward 2014). Spatial variation (variation that is constant among years) and spatio-temporal variation (variation over space which differs among years) are approximated as Gaussian Markov random fields (Thorson et al. 2015). The model was used to generate coast-wide indices of biomass (t), density (ln kg km^{-2}) and an annual measure of effective area occupied (ln km^2) (Thorson et al. 2016a,b). Effective area occupied represents the area required to contain a population given an average population density (kg km^{-2}) (Thorson et al. 2016a,b). Biomass was estimated by summing across predicted densities for the entire spatial domain of the survey, where each density is weighted by area. Effective area was used to evaluate shifts in range (expansion or contraction) over time.

We examined trends in CPUE over time using regression analysis (GLM) in R v.3.3.2 statistical programming language (R Development Core Team 2016). Given the variable catch and patchy distribution characteristic of canary rockfishes sampled by the trawl survey, we also examined trends over time via changes in the percent of positive tows (the number of tows per year with positive canary rockfish catch divided by the total number of successful tows) and the modeled biomass indices using regression analysis. Biomass indices are assumed proportional to population abundance (Maunder & Punt 2004).

Biological sampling

For the WCGBTS, a subsample of canary rockfishes (n ≤ 100) was randomly selected from each tow to determine individual sex, fork length (cm), weight (kg), age (yr) and maturity. If gonads were not sufficiently well developed to visually determine sex, gender was recorded as unidentified (unsexed). For the Hook and Line survey, similar information was collected for all canary rockfishes captured (n = 195). These supplementary data were included in the size-at-age analyses since age data south of Point Conception were relatively sparse and age structures collected in 2015 during the WCGBTS were not yet available. Overall, less than 4 % of the age samples used in the analysis came from the Hook and Line survey (2003 to 2015).

For both surveys, extracted otoliths were aged using the break and burn method (Chilton & Beamish 1982), a generally accepted method for aging Pacific rockfishes (MacLellan 1997). Double-reads were conducted for a subset of otoliths to analyze the precision and bias of age estimates (Punt et al. 2008). For evaluating maturity, ovaries from randomly selected females associated with age samples were removed and stored in 10% neutral buffered formalin (sodium bicarbonate).

We examined variation in fork length and age of canary rockfishes relative to changes in both latitude (° N) and depth (m) using regression analysis (GLM) in R v.3.3.2 (R Development Core Team 2016). We also explored changes in both length and age frequency distributions over time. Length frequency distributions were summarized by year and sex using twenty-eight 2 cm bins from 10 to 64 cm. Age frequencies were divided into thirty-five 1 yr bins from age 1 to 35 with the last bin including all fish older than 35 yr and first fish age 1 or younger.

Weight–length relationship

Weight–length relationships for canary rockfishes were based on the allometric equation:

$$W = aL^b \tag{4}$$

where W is fish weight in kg, L is fork length in cm and a and b are constants. A GLM using R v.3.3.2 (R Development Core Team 2016) estimated regression equations for natural-log transformed weight and fork length. Obvious outliers (±2 SD) were removed from the data set following examination of plots of raw and natural-log transformed variables (<0.5% of the observations). To examine variation in weight–length regressions by latitude and gender, we initially subdivided the survey area into 3 regions with geographic boundaries based on prominent biogeographic features at Cape Mendocino, CA (40° 26′ N) and Point Conception (34° 27′ N). Akaike's information criterion (AIC) was used to compare analysis of covariance (ANCOVA) models for weight–length, which incorporated geographic regions and sex as covariates. Relative support among competing models was determined based on minimum AIC values as:

$$\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{\min} \tag{5}$$

The best model as defined above has $\Delta_i = 0$ while models with $\Delta_i < 2$ have substantial support relative to the best model ($\mathrm{AIC}_{\min}$) (Burnham & Anderson 2002).

We also used the slope (b; Eq. 4) of annual weight–length regressions as a proxy for population-level changes in the rate at which weight increased with length for canary rockfishes. This biometric indicator does not account for changes in body form with size (Froese 2006), but captures annual variability in weight–length relations for comparison with environmental effects (see below).

Size-at-age

We analyzed variation in size-at-age of canary rockfishes by sex and geographic area via von Bertalanffy growth relationships. Based on AIC values, we selected between 2 potential model treatments (Akaike 1992) (with and without measurements from the Southern California Shelf Rockfish Hook and Line Survey) and determined that it was appropriate to combine age data from the 2 surveys despite methods that varied in how rockfishes were sampled. Growth curves were fit to length-at-age data by nonlinear regression using R v.3.3.2 (R Development Core Team 2016). Growth was described as:

$$L_t = L_\infty[1 - \mathrm{e}^{-k(t-t_0)}] \tag{6}$$

where L_t is fork length (cm) at age t, k is growth rate (yr^{-1}), L_∞ is the theoretical maximum fork length (cm), t is age in years and t_0 is the theoretical age in years of fish at length zero (von Bertalanffy 1938). The null hypothesis that gender and regions have no effect on growth parameters was tested via ANCOVA and evaluated by AIC. Models were fit in stages starting with a von Bertalanffy fit to all data without accounting for other effects, followed by adding the gender effect and then accounting for geographic area. The most parsimonious model is the model with the smallest AIC. Since the survey occurred during the same period each year and von Bertalanffy growth coefficients (k; Eq. 6) capture interannual variation in growth across multiple cohorts (Love et al. 2002, Szalai et al. 2003, He & Bence 2007), we also estimated k by year and sex for comparison with annual variability in environmental indices.

Maturity

We estimated maturity using histological measurements from 808 canary rockfish ovaries collected by the Oregon Department of Fish and Wildlife and the WCGBTS between 2009 and 2015. Tissue samples from individual ovaries were embedded in paraffin, thin-sectioned to 4 µm, mounted on slides and stained with hematoxylin and eosin (H&E) stain (Sheehan & Hrapchak 1980). Each prepared ovary section was examined using a Leica DM1000 binocular microscope, at 40 to 400× magnification, equipped with a Leica DFC295 camera and imaging software (Leica Microsystems LAS EZ 4.0). Maturity for each ovary was determined by whether oocytes had reached developmental stage 4.2 or later using classification criteria similar to those described for multiple rockfish species (McDermott 1994, Nichol & Pikitch 1994, Frey et al. 2015, Head et al. 2016). Ovaries with significant (>25%) atresia were classified as 'immature'.

Logistic regression was used to fit sigmoid curves to the proportion of canary rockfish females mature at length and age:

$$P = \frac{1}{1+e^{-(\alpha+\beta x)}} \tag{7}$$

where P is the proportion mature at length or age x and α and β are parameters that define the shape and location of the fitted sigmoid curve. Parameters α and β were estimated using a GLM in R v.3.3.2 (R Development Core Team 2016). The length or age at 50% maturity (L_{50}, A_{50}) was calculated as:

$$L \text{ (or } A)_{50} = -\alpha/\beta \tag{8}$$

Variance and 95% confidence intervals for L_{50} and A_{50} were estimated using the delta method (Seber 1982):

$$S^2(L_{50}, A_{50}) = \frac{S^2(\hat{\alpha})}{\hat{\beta}^2} - \frac{2\hat{\alpha}S(\hat{\alpha})S(\hat{\beta})r}{\hat{\beta}^3} + \frac{\hat{\alpha}^2 S^2(\hat{\beta})}{\hat{\beta}^4} \tag{9}$$

where $S^2(L_{50}, A_{50})$ is the variance of L_{50} or A_{50}, $\hat{\alpha}$ and $\hat{\beta}$ are estimates of parameters α and β generated by the GLM model and $S(\hat{\alpha})$ and $S(\hat{\beta})$ are the standard errors of $\hat{\alpha}$ and $\hat{\beta}$.

Environmental effects

We compared variation in annual population level metrics (b; the slope of Eq. 4) and growth coefficients (k; Eq. 6) to environmental change within the survey area using regression models (R Development Core Team 2016). We utilized 2 measures of environmental variability: annual PDO values (2003 to 2015) and a second index, specific to the groundfish survey, based on near-bottom temperature and depth measured during each tow. Since average annual bottom temperature alone does not account for variations in depth among randomly sampled stations each year, we utilized the slopes (slope$T$-Z) of annual regressions comparing site-specific near-bottom temperature (ln temperature, °C) to bottom depth (m) as a local measure of changing environmental conditions. The PDO represents basin-wide climatic effects (Mantua et al. 1997, Schwing et al. 2009) and the newly developed temperature-based index is reflective of more regional conditions for the specific areas within the California Current System sampled during the WCGBTS each year.

Because of the potential influence of density-dependent effects on growth, incorporating annual biomass indices in the relationships with b and k was initially explored using ANCOVA. AIC with bias correction term for small sample size (AIC$_c$) was subsequently used to select which variables (biomass and/or environmental indices) to include in the final model for the slope of the weight–length regressions and von Bertalanffy growth coefficients (Johnson & Omland 2004). We additionally compared annual PDO values and the newly developed regional temperature-based index using standard regression analysis (R Development Core Team 2016).

RESULTS

CPUE

Canary rockfishes *Sebastes pinniger* exhibited variable annual CPUE (kg ha^{-1}) with average annual values of tows with positive catch ranging from a low of 0.29 kg ha^{-1} in 2009 (n = 33) to a high of 8.44 kg ha^{-1} in 2006 (n = 32) (Fig. 1a). Relatively few tows caught canary rockfishes each year (range: 32 to 77 tows yr^{-1}). Years with the highest and lowest average annual CPUE had approximately the same percentage of positive tows (4.8% in 2009 and 5.0% in 2006) (Fig. 1b).

Annual coast-wide biomass indices estimated via the spatial delta-GLMM ranged from 8483 to 22 550 t throughout the survey period (Fig. 1c). Biomass indices closely mirrored the annual pattern exhibited by percent positive tows over time (Fig. 1b) but not CPUE (Fig. 1a). An extreme catch event (4942 kg) in 2006 resulted in an exceptionally high CPUE (3984.4 kg ha^{-1}) for a single tow.

Fig. 2 depicts the estimated relative depletion (%) of canary rockfish spawning stock biomass along the US west coast (Thorson & Wetzel 2015). Relative depletion declined from unfished levels (B$_{100\%}$) in 1920, through the 1990s until being declared overfished (biomass < 25% of unfished level, B$_{25\%}$) in 2000, followed by recovery (B$_{40\%}$) beginning in 2006.

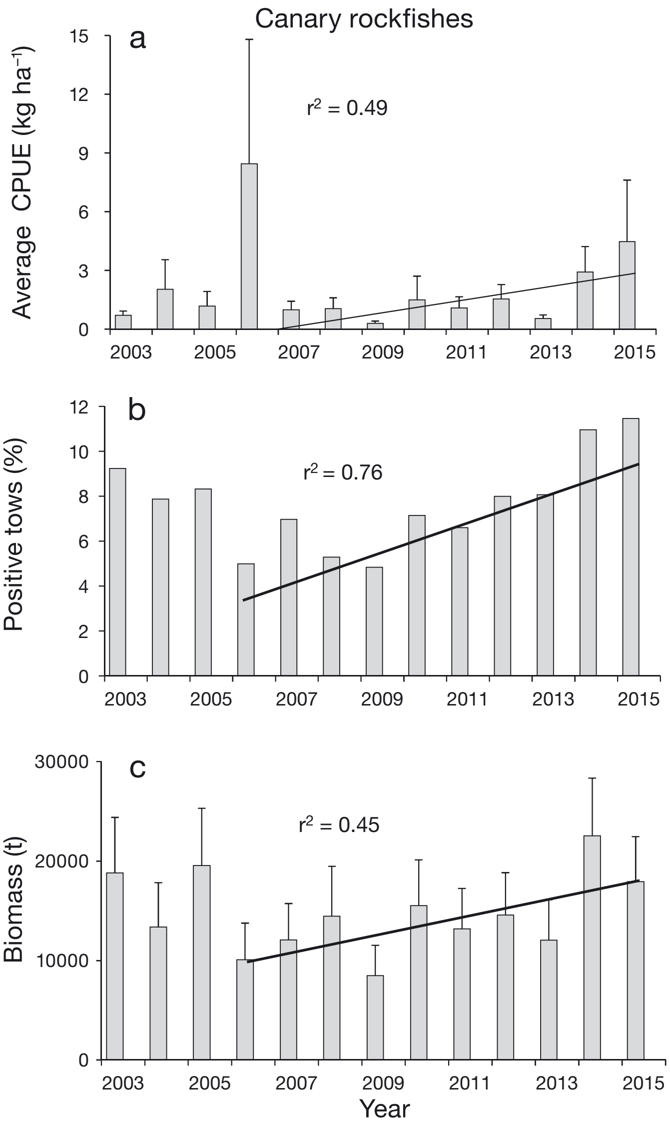


Fig. 1. Variation in (a) average (±SE) catch per unit effort (CPUE), (b) percent positive tows, and (c) average (±SE) biomass indices for canary rockfish from 2003 to 2015. Significant regressions and r^2 values shown as CPUE increased from 2007 to 2015 and both percent positive tows and biomass increased since 2006

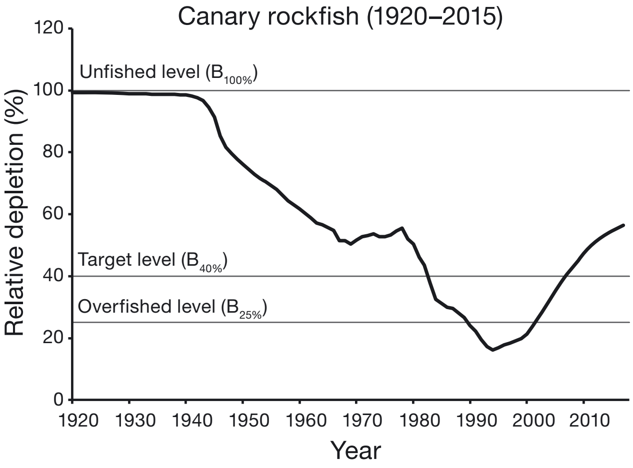


Fig. 2. Relative depletion (%) of spawning stock biomass (age 5+) for canary rockfish from 1920 through 2015 showing management levels for unfished biomass ($B_{100\%}$), the management target of 40% depletion ($B_{40\%}$) for healthy rockfish stocks, and overfished level ($B_{25\%}$)

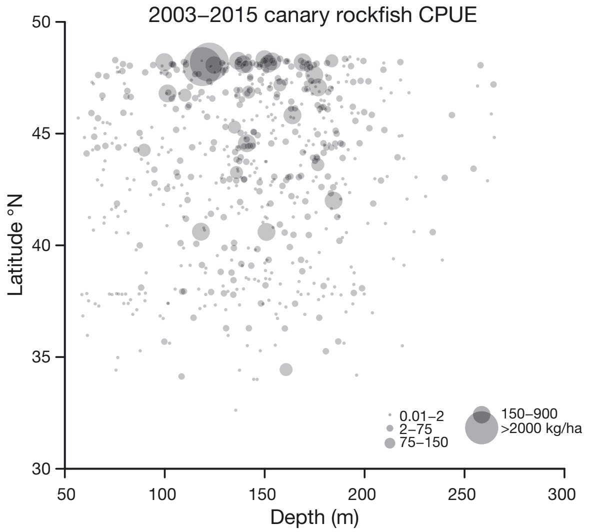


Fig. 3. Catch per unit effort (CPUE; kg ha^{-1}) for canary rockfish showing distribution by latitude (° N) and depth (m) for tows with positive catch from 2003 to 2015, with the increasing size of the circle representing increased ranges for CPUE (0–2, 2–75, 75–150, 150–900 and >2000 kg ha^{-1})

CPUE, biomass indices and the percent of positive tows exhibited insignificant ($p > 0.05$) trends over the entire time series (Fig. 1). However, following recovery, increases occurred in recent years with CPUE significantly increasing ($F_{1,7} = 6.67$, $r^2 = 0.49$, $p = 0.04$, $n = 9$) from 2007 to 2015 and both biomass ($F_{1,8} = 6.71$, $r^2 = 0.45$, $p = 0.03$) and the percent positive tows ($F_{1,8} = 24.6$, $r^2 = 0.75$, $p = 0.001$) significantly increasing since 2006 ($n = 10$). The extreme catch in 2006 and resulting high annual average CPUE caused the dissimilarity in periods over which significant increases occurred for the 3 variables.

Distribution

Canary rockfishes exhibited a highly patchy distribution occurring from 32° 37′ to 48° 26′ N at depths of 56.7 to 351 m (mean ± SE: 143.3 ± 1.69 m) (Fig. 3). The majority of tows with canary rockfish catch (90%) occurred at depths between 56.7 and 193 m. Rockfishes occurred in 632 tows at longitudes ranging from 124° 6′ to 125° 18′ W (mean 124° 22′ ± 54′). High CPUE occurred most commonly north of 47° N with additional areas of elevated CPUE recorded in the vicinity of 40 and 42° N and rarely as far south as 34° 24′ N (Fig. 3).

We estimated spatial variation in density (ln kg km^{-2}) of canary rockfishes via the geostatistical delta-GLMM over time. The model consistently predicted the occurrence of the highest densities in northern Washington (Fig. 4), where extreme catch events most often clustered (Fig. 3). Annual density plots indicate moderate density north of San Francisco, California, and suggested increased density in the southern reaches of the bottom trawl survey over time. This expansion is captured by the variability in effective area occupied over time (Fig. 5). Effective area has increased since 2011 and reached its highest level in recent years (2014 and 2015). Overall, the area occupied increased by ~215 km^2 or 1.4 % over the survey period.

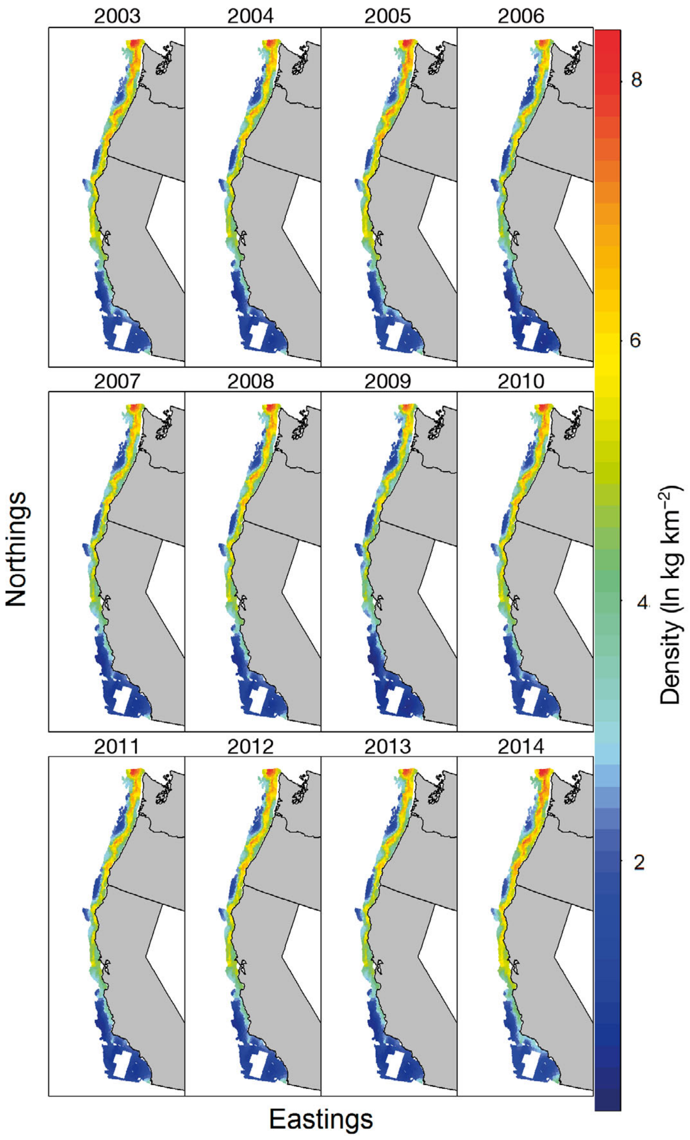


Fig. 4. Spatial variation in density of canary rockfish by year as estimated by the geostatistical delta-generalized linear mixed model (delta-GLMM) within the survey area (32° 30′ to 48° 28′ N at depths of 55 to 1280 m)

Biological sampling

Fork lengths (cm) were determined for 8995 canary rockfishes collected during the 2003 to 2015 period. Lengths ranged from 9 to 64 cm with females on average larger (mean ± SE: 41.6 ± 0.18 cm) than males (39.7 ± 0.15 cm). Lengths for fish with undefined sex (n = 263) ranged from 9 to 31 cm (13.7 ± 0.34 cm).

Ages ranged from 0 to 65 yr for male canary rockfishes (10.03 ± 0.14 yr, n = 2688) while ages for females ranged from 1 to 33 yr (9.88 ± 0.12 yr, n = 2159). For unsexed fish (n = 162), ages ranged from 1 to 8 yr (1.4 ± 0.06 yr). Estimated aging error from double reads (19 %) indicated that the standard deviation for age increased from 1.37 at age 10 to 5.48 at age 40, with ages of less than 35 yr well represented in the data. Exact agreement between age readers occurred for 50.8 % of double-read otoliths (19 %) with no bias observed between the first and second age reader.

Length and age of canary rockfishes varied significantly by depth (Table 1), with smaller and younger individuals occurring at shallower depths. The relationships for females, males, unsexed and pooled (all) data versus depth are described by significant quadratic equations (Table 1). Model selection, based on $\Delta_i = 0$, indicated that the most parsimonious models for both length and age versus depth included sex as a covariate (Table 1). Predicted length at depth was greatest for females, while age was greatest at depth for males, perhaps since males included in the analysis reached greater ages than females (see above). Greater than 56 % of the variation in length and 26 % of the variation in age were explained by depth (Table 1).

Length and age, averaged by 25 m depth intervals (Fig. 6a,b), gradually increased to ~175 m depth for male and female fish. At depths >175 m, the fitted

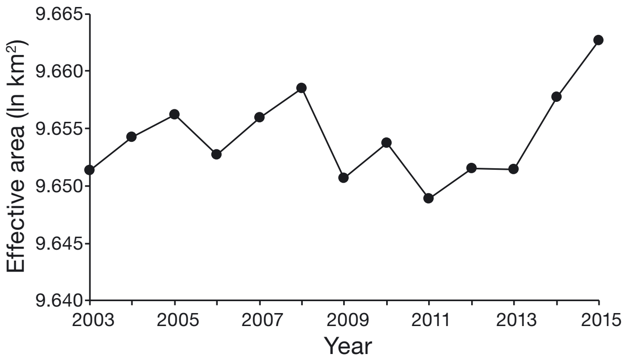


Fig. 5. Variation in effective area occupied by canary rockfish from 2003 to 2015 as estimated by the geostatistical delta-generalized linear mixed model (delta-GLMM)

Table 1. Estimated parameters for canary rockfish curves relating length (cm) and age (yr) to depth (m) and latitude (°N) based on the fitted relationship $y = a + bx + cx^2$ by sex (male, female, unsexed) or all data, where y is either length or age and x is either depth or latitude. Also shown are standard errors (±SE) for parameters, F-values and degrees of freedom (F_{df}), r^2, associated probabilities (p) and Δ_i (difference between Akaike's information criterion [AIC] and the minimum AIC value) comparing models with (male, female, unsexed) and without (all) sex

Model	*a* (±SE)	*b* (±SE)	*c* (±SE)	n	F_{df}	r^2	p	Δ_i
Length vs. depth								
Female	−20.20 (1.35)	0.78 (0.02)	−0.002 (0.000)	3944	$2504_{2,3941}$	0.56	<0.0001	0
Male	−18.04 (1.01)	0.73 (0.02)	−0.002 (0.000)	4788	$5591_{2,4785}$	0.59	<0.0001	
Unsexed	21.84 (2.40)	−0.34 (0.05)	0.003 (0.000)	263	$517_{2,260}$	0.71	<0.0001	
All	−21.92 (0.78)	0.78 (0.01)	−0.002 (0.001)	8995	$6747_{2,8992}$	0.60	<0.0001	793.2
Age vs. depth								
Female	−12.37 (1.04)	0.27 (0.02)	−0.001 (0.000)	2158	$693_{2,2155}$	0.39	<0.0001	0
Male	−14.41 (1.14)	0.31 (0.02)	−0.001 (0.000)	2688	$461_{2,2685}$	0.26	<0.0001	
Unsexed	2.18 (0.59)	−0.05 (0.01)	0.000 (0.000)	162	$123_{2,159}$	0.61	<0.0001	
All	−14.43 (0.75)	0.30 (0.01)	−0.001 (0.001)	5008	$1232_{2,5005}$	0.33	<0.0001	38.8
Length vs. latitude								
Female	247.9 (18.7)	−10.65 (0.89)	0.13 (0.01)	3944	$216_{2,3941}$	0.10	<0.0001	0
Male	203.2 (15.9)	−8.58 (0.76)	0.11 (0.01)	4788	$289_{2,4785}$	0.11	<0.0001	
Unsexed	306.6 (85.8)	−13.91 (3.96)	0.17 (0.05)	263	$8.9_{2,260}$	0.06	0.0002	
All	291.0 (12.8)	−12.78 (0.61)	0.16 (0.01)	8995	$544_{2,8994}$	0.11	<0.0001	1440.6
Age vs. latitude								
Female	107.9 (12.2)	−5.14 (0.58)	0.07 (0.01)	2159	$136_{2,2156}$	0.11	<0.0001	0
Male	123.6 (14.4)	−5.98 (0.69)	0.08 (0.01)	2688	$165_{2,2685}$	0.11	<0.0001	
Unsexed	42.4 (13.9)	−1.96 (0.65)	0.02 (0.01)	162	$5.8_{2,159}$	0.07	0.004	
All	134.5 (9.6)	−6.46 (0.46)	0.08 (0.01)	5009	$311_{2,5007}$	0.11	<0.0001	253.9

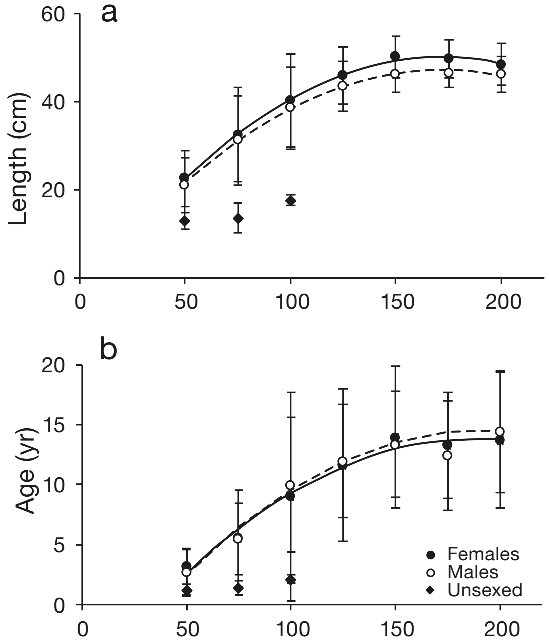


Fig. 6. Mean (±SD) (a) canary rockfish standard length and (b) age displayed by 25 m depth intervals for females (closed circles), males (open circles) and unsexed (closed diamonds). The fitted curvilinear relationships (see Table 1: $y = a + bx + cx^2$) for length (females, n = 3944; males, n = 4788) and age (females, n = 2158; males, n = 2688) versus depth shown in the figures are based on all data by sex (see Table 1) rather than the binned averages displayed here

relationships (based on equations in Table 1 rather than fit to binned data) declined slightly. Females were significantly larger but younger than males by depth (Fig. 6). Unsexed individuals also exhibited increases in size and age with depth but across a relatively narrow depth range (55 to 105 m) (Fig. 6).

When subdivided by 2° increments of latitude, beginning at the southern limit of distribution for all years pooled (2003 to 2015), mean length and age of canary rockfishes declined to about 38° N then increased, with the greatest increases occurring North of Cape Mendocino (Fig. 7). Age gradually increased towards the northern extent of the survey for both male and female canary rockfishes while length did not show such a clear trend. Regression analysis indicated significant ($p < 0.004$) quadratic relationships between length and age measurements with latitude; subdividing samples by sex resulted in the most parsimonious models ($\Delta_i = 0$) (Table 1). For both males and females, latitude explained about 11% of the variation in length and age (Table 1). However, some of the variation in size and age by latitude was a function of average sampling depth, which varied among latitudinal bins. The 37 to 38° N bin exhibited the shallowest average depth coast-wide. We saw significant ($p < 0.05$) linear relationships between both length ($F_{1,7} = 7.39$, $r^2 = 0.55$, p = 0.03) and age

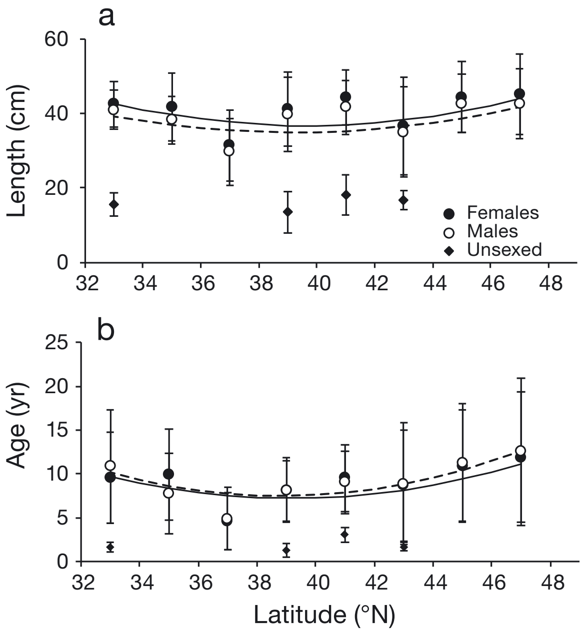


Fig. 7. Average (±SD) canary rockfish (a) standard length and (b) age by 2° of latitude beginning at the US–Mexico border (32° 30′ N) for females (closed circles), males (open circles) and unsexed (closed diamonds). The fitted curvilinear relationships ($y = a + bx + cx^2$) for length (females, n = 3944; males, n = 4788) and age (females, n = 2158; males, n = 2688) versus latitude are based on all data by sex (see Table 1) rather than the binned values displayed here

($F_{1,7}$ = 9.14, r^2 = 0.60, p = 0.02) versus depth based on averages calculated by 2° latitudinal bins.

Size frequency distributions varied by year (Fig. 8), with the average length of females greater than males for all years. Overall, mean size progressively increased from 2003 to 2006, 2008 to 2011 and 2013 to 2015, with similar increases observed for females and males over time. Higher percentages of small individuals were apparent in multiple years, suggesting recruitment events may have occurred in 2008, 2010 and 2013 or in the years just preceding the appearance of these smaller fish (Fig. 8). Although there is little evidence of strong year classes moving through the population over time, increasing size in years following the appearance of high proportions of small individuals indicates occurrence of at least moderate recruitment events (Fig. 8). To highlight the recruitment events and aid in interpretation of these plots, we added smoothed lines showing dominant length modes by year to the right of each bubble series.

Although age data are sparser than length measurements, there is generally good agreement between age and length frequency distributions (Figs. 8 & 9). Both size and age progressively increased from 2003 to 2006, with few small or young canary rockfish captured during this period (Figs. 8 & 9). Higher percentages of young individuals occurred in 2008, 2010 and 2013 when smaller canary rockfishes also occurred. Additionally, the highest portion of age-1 individuals occurred in 2010 (Fig. 9), the year with the highest frequency of small fish (Fig. 8). The occurrence of younger individuals in recent years (2008, 2010 and 2013) further confirms the presence of moderate recruitment events.

There is very little difference in the overall age distribution for males and females over the survey period (Fig. 10). However, a higher proportion of older males was evident relative to females at ages above 24 to 25 yr. Additionally, the oldest females aged during the survey reached 33 yr (Fig. 10), while 39 males occurred within the 34 to 65 age range.

Weight–length relationships

Model selection for weight–length relationships, based on measurements from male (n = 3098) and female (n = 2470) canary rockfishes, indicated variation by gender and region (Table 2). Although the weight–length curves for the North of Cape Mendocino, Central and South of Point Conception regions exhibited some differences, the best model incorporated only a single geographic subdivision at Point Conception in addition to gender (Table 2a). Predicted weight at length was greatest for males relative to females regardless of geographic region. Additionally, weight of canary rockfishes north of Point Conception tended to increase more rapidly as a function of length relative to further south (Table 2b).

Size-at-age

Both geographic variation and gender played significant roles in the size-at-age relationships for canary rockfishes. AIC values comparing relative support among models with sex and 2 or 3 geographic regions demonstrated that von Bertalanffy model fits improved with the addition of further information (Table 3a). The best fit occurred with the inclusion of both sex and a subdivision of the coast into 3 regions (Table 3a). Growth curves show a tight range of ages at a given length and demonstrate that the growth trajectory for females reaches larger sizes than males for a given age (Table 3b, Fig. 11) in all regions. In general, the maximum size (L_∞) was greatest for females relative to males

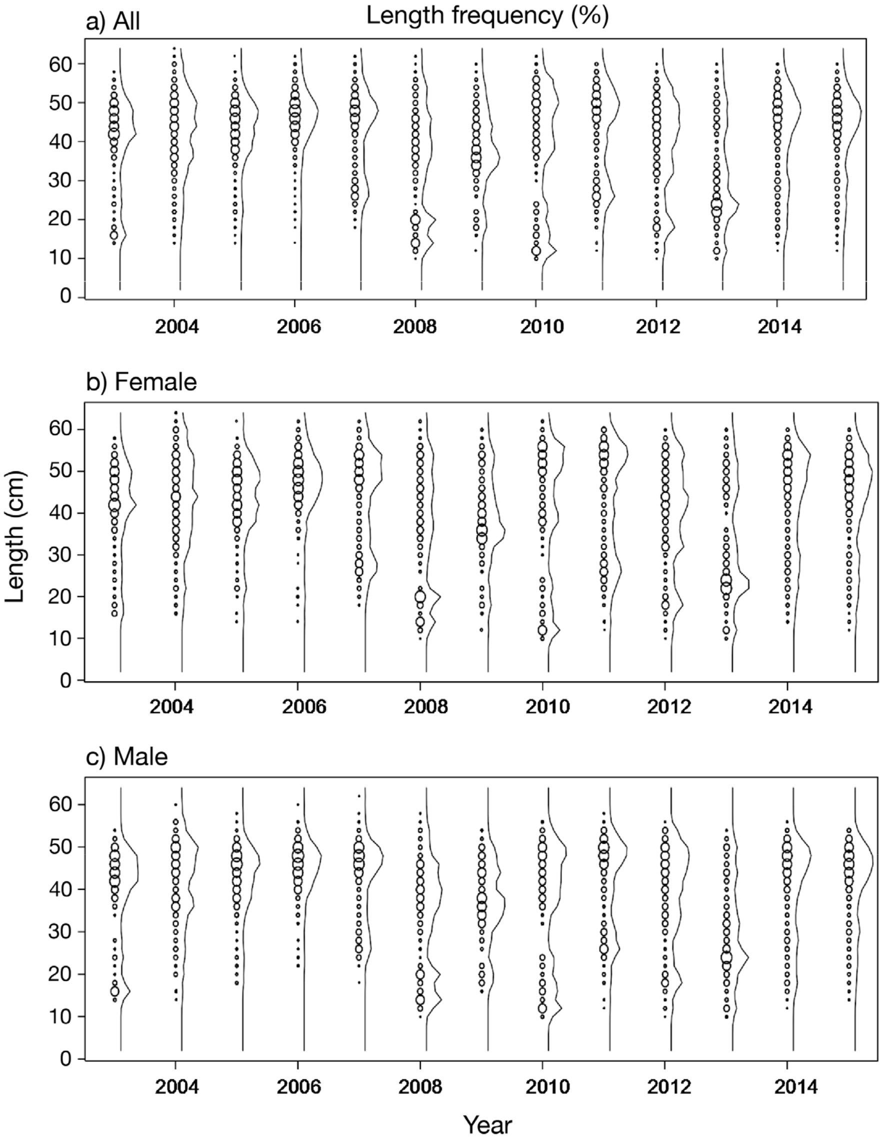


Fig. 8. Length frequency distributions (%) summarized by year for (a) all; (b) female; and (c) male canary rockfishes using 28 bins from 10 to 64 cm (fork length). The largest bubble for all fish is 17.2%, females 17.6% and males 19.5%. To aid in interpretation of these plots, we added smoothed lines showing dominant length modes by year to the right of each bubble series

regardless of geographic area and L_∞ for males increased in size with latitude (Table 3b, Fig. 11). Growth rates (k, yr^{-1}) for females progressively increased south to north with a similar pattern observed North of Point Conception for males (Table 3b). Variation in gender-specific growth rates by year (range 0.120 to 0.191 yr^{-1} for females and 0.134 to 0.271 yr^{-1} for males) correlated with changing environmental conditions from 2003 to 2015 as described in the results for environmental effects. Overall, less than 4% of the data utilized in the size-at-age analysis came from the Hook and Line survey (range 0.8 to 8.2% yr^{-1}).

Maturity

Mature canary rockfishes (n = 347) ranged from 41 to 61 cm (51.73 ± 0.22 cm), while smaller, immature females (n = 461) ranged from 17 to 55 cm with an average size of 37.04 ± 0.36 cm. Examination of the estimated maturity schedule illustrates a length at 50% maturity of 46.28 cm (95% CI: 45.82 to 46.74 cm) (Fig. 12a). The estimated age at 50% maturity (n = 412) for female canary rockfishes was 10.94 yr (95% CI: 10.73 to 11.16 yr) (Fig. 12b).

The proportion of immature versus mature female canary rockfishes varied with latitude and depth

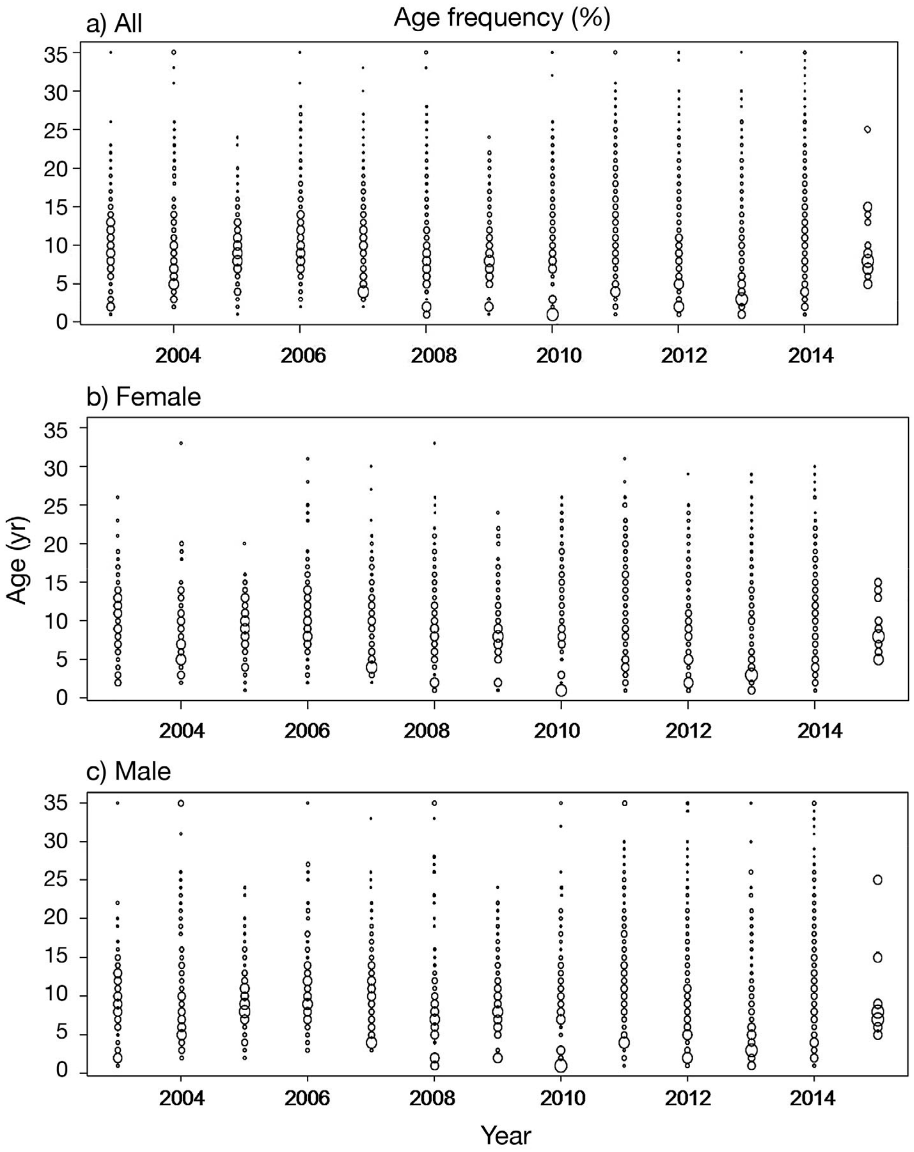


Fig. 9. Age frequency distributions (%) summarized by year for (a) all; (b) female; and (c) male canary rockfishes using 35 bins from 1 to 35 yr with the last bin including all fish older than 35 yr and the first all fish age 1 or younger. The largest bubble for all fish is 24.2%, females 25.5% and males 22.8%. Data for 2015 are restricted to fish sampled during the Southern California Shelf Rockfish Hook and Line Survey since ages for fish from the Northwest Fisheries Science Center's west coast groundfish bottom trawl survey (WCGBTS) were not yet available

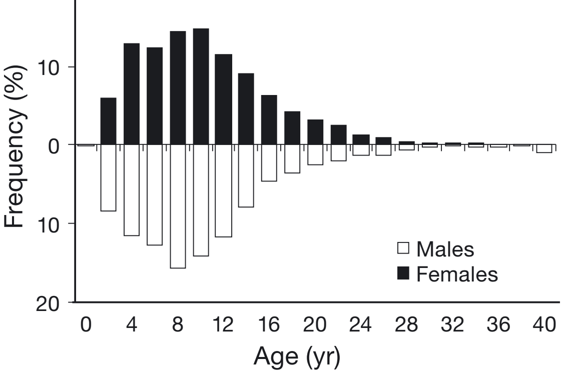


Fig.10. Overall age distribution (%) for male (open bars) and female (closed bars) canary rockfishes from 2003 to 2015 using 20 bins from 0 to 40 yr, with the last bin including all fish (males) age 39 or older

based on 513 maturity samples with paired latitude and depth measurements (Fig. 13). Of 437 specimens sampled north of Cape Mendocino (40° 26′ N), 224 (51.3%) were mature. South of Cape Mendocino, 6 of 76 samples (8%) were mature. Depth was also positively correlated with maturity (Fig. 13). Mean depth for immature females was 117.1 ± 1.5 m, compared to

156.8 ± 1.2 m for mature females. Overall, ~95% of mature canary rockfishes occurred North of Cape Mendocino at depths greater than 115 m (Fig. 13).

Environmental effects

As previously described, we used slope *T-Z* (Table 4) to represent variation in local environmental conditions and annual PDO indices as proxies for basin-scale change. Since prior analyses detected sexually dimorphic differences in weight–length (Table 2) and von Bertalanffy relationships (Table 3), we examined variation in slope (*b*) and growth rates (*k*) versus the above 2 measures of environmental variability separated by sex. We initially used ANCOVA and AIC$_c$ (Δ_i = 0) to determine if biomass should be included in the analyses. Results indicated that the most appropriate models for both *b* and *k* tended to include significant environmental effects ($p < 0.05$), but no significant effects for biomass with or without the inclusion of environmental measures ($p > 0.05$) and no acceptable alternatives.

Table 2. (a) Delta AIC values (Δ_i, the difference between Akaike's information criterion [AIC] and the minimum AIC value) for canary rockfish weight–length relationships. For fitted relationships, models incorporated sex (F: female, M: male) and evaluated 3 geographic subdivisions with bounds as 40° 26′–48° 28′ N, 34° 27′–40° 26′ N, and 32° 30′–34° 27′ N. The best model ($\Delta_i = 0$) included separation by sex and 2 geographic regions (with a subdivision at 34° 27′ N; Pt. Conception, CA). Models are shown in order of complexity (number of parameters, n). (b) Estimated parameters for the best fit canary rockfish curves relating weight (ln kg) and length (ln cm) based on fitted allometric equations by sex and areas north (N) and south (S) of Pt. Conception. Also shown are standard errors (±SE), number of observations (n), *F*-values (*F*), and r^2. $p < 0.0001$ for all equations

(a)

Model description	Δ_i	n
Without regions, sex	10.19	2
By sex, without regions	6.41	4
By region, without sex		
with 2 regions (subdivided at 40° 26′ N)	10.16	4
with 2 regions (subdivided at 34° 27′ N)	4.24	4
with 3 regions (subdivided at 34° 27′ N and 40° 26′ N)	7.46	6
By region, with sex		
with 2 regions (subdivided at 34° 27′ N)	0.00	8
with 2 regions (subdivided at 40° 26′ N)	6.42	8
with 3 regions (subdivided at 34° 27′ N and 40° 26′ N)	3.53	12

(b)

Sex	Area	Intercept (±SE)	Slope (±SE)	n	*F*	r^2
F	N	−11.413 (0.021)	3.109 (0.006)	2343	303 000	0.99
M	N	−11.501 (0.019)	3.135 (0.005)	2986	364 300	0.99
F	S	−10.642 (0.176)	2.911 (0.047)	127	3846	0.97
M	S	−10.693 (0.192)	2.921 (0.051)	112	3246	0.97

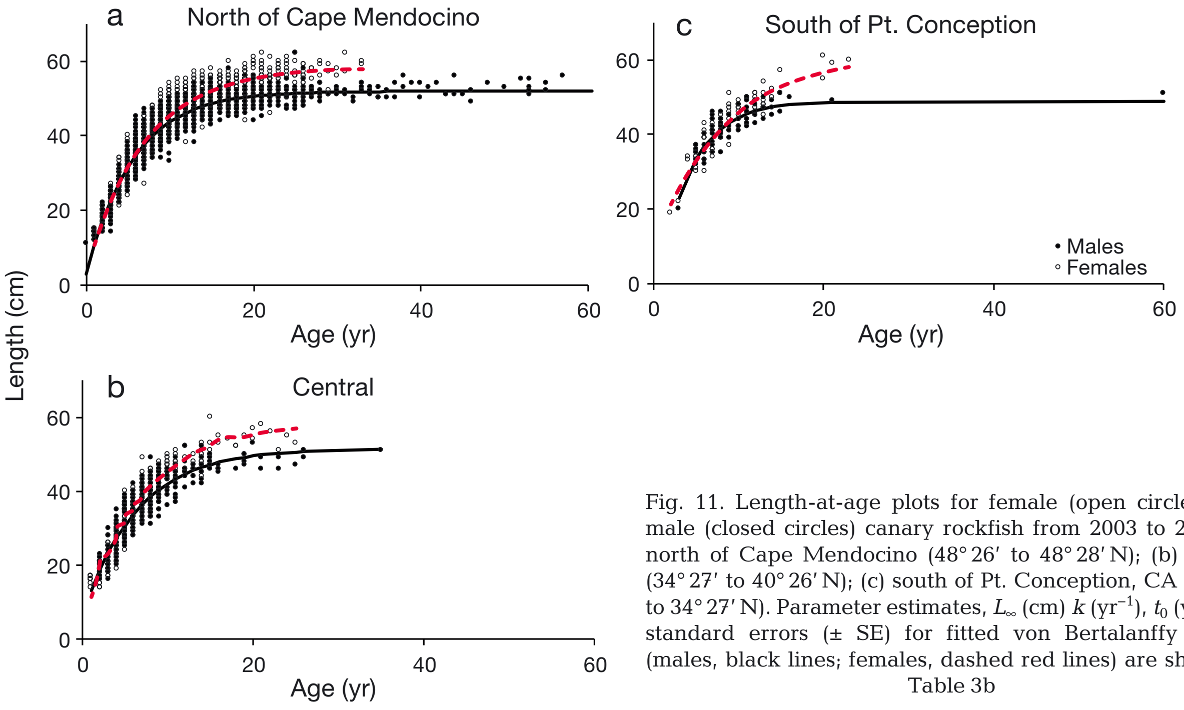
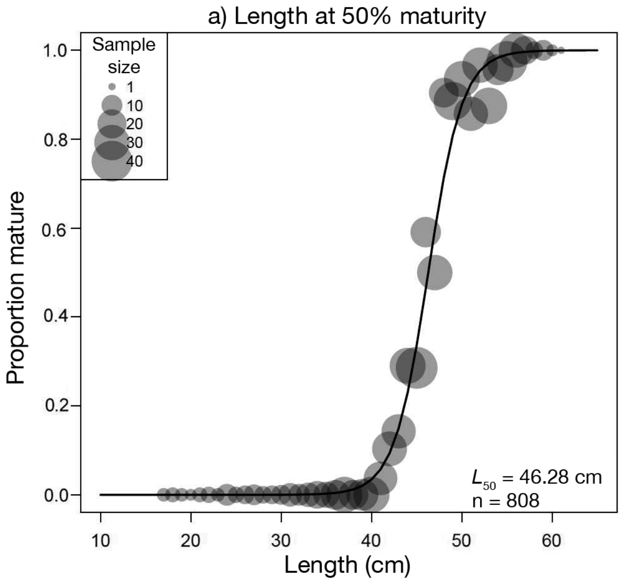


Fig. 11. Length-at-age plots for female (open circles) and male (closed circles) canary rockfish from 2003 to 2015 (a) north of Cape Mendocino (48° 26′ to 48° 28′ N); (b) central (34° 27′ to 40° 26′ N); (c) south of Pt. Conception, CA (32° 30′ to 34° 27′ N). Parameter estimates, L_∞ (cm) k (yr^{-1}), t_0 (yr) with standard errors (± SE) for fitted von Bertalanffy curves (males, black lines; females, dashed red lines) are shown in Table 3b



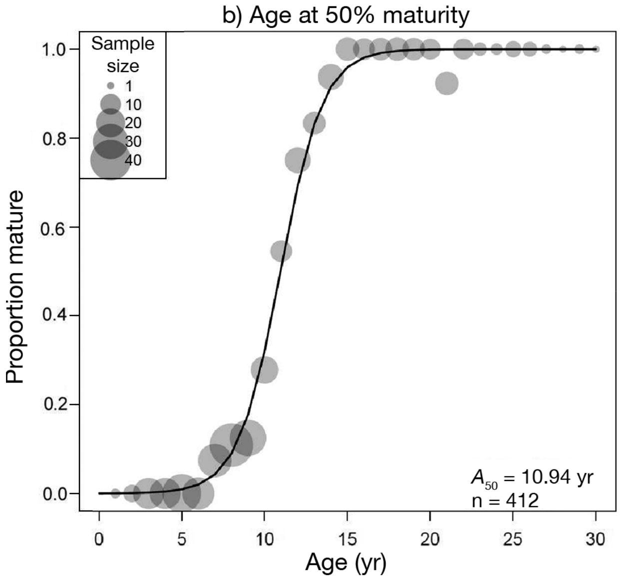


Fig. 12. (a) Logistic maturity curve fitted to length for female canary rockfish collected from 2009 to 2015 by the Northwest Fisheries Science Center's west coast groundfish bottom trawl survey (WCGBTS) (n = 513) and the Oregon Department of Fish and Wildlife (n = 295); and (b) age for the WCGBTS (n = 412). The proportion mature is shown versus length (cm) and age (yr) with the size of the circle representing the number of samples at each length

Table 3. (a) Delta AIC values (Δ_i, the difference between Akaike's information criterion [AIC] and the minimum AIC value) for different stages in fitting von Bertalanffy models. For fitted relationships, models incorporated sex (F: female, M: male) and evaluated 3 geographic subdivisions with bounds as 40° 260′–48° 28′ N, 34° 27′–40° 26′ N, and 32° 30′–34° 27′ N. The best model ($\Delta_i = 0$) included separation by sex and 3 geographic regions. Models are shown in order of complexity (number of parameters, n). (b) Estimated parameters for the best fit von Bertalanffy models for canary rockfish: L_∞ (cm), k (yr^{-1}), t_0 (yr) with standard errors (±SE) and number of observations (n). Results shown by sex and region: north (N: Cape Mendocino, CA to the US–Canada border), central (C: Pt. Conception, CA to Cape Mendocino and south (S: US–Mexico border to Pt. Conception, CA)

(a)

Model description	Δ_i	n
Without regions, sex	999.5	3
By sex, without regions	125.1	6
By region, without sex		
with 2 regions (subdivided at 40°26′N)	940.1	6
with 2 regions (subdivided at 34°27′N)	981.7	6
with 3 regions (subdivided at 34°27′N and 40°26′N)	885.3	9
By region, with sex		
with 2 regions (subdivided at 40°26′N)	58.7	12
with 2 regions (subdivided at 34°27′N)	104.1	12
with 3 regions (subdivided at 34°27′N and 40°26′N)	0.0	18

(b)

Sex	Area	L_∞ (±SE)	k (±SE)	t_0 (±SE)	n
F	N	58.24 (0.26)	0.147 (0.003)	−0.383 (0.059)	1710
M	N	51.88 (0.16)	0.180 (0.002)	−0.302 (0.046)	2091
F	C	59.97 (1.32)	0.123 (0.007)	−1.043 (0.147)	365
M	C	51.64 (0.80)	0.156 (0.007)	−0.885 (0.114)	517
F	S	61.55 (2.73)	0.118 (0.018)	−1.615 (0.700)	84
M	S	48.98 (1.08)	0.252 (0.038)	0.483 (0.605)	80

The fit between slope b and the PDO explained a higher percentage of the variation for females ($F_{1,11}$ = 16.33, r^2 = 0.60, p = 0.002) relative to the newly developed local index of environmental change ($F_{1,11}$ = 3.9, r^2 = 0.27, p = 0.07) (Fig. 14a,b). Note that the fit for females was close to significance at p = 0.07. For males, we observed significant fits for the slope of weight–length regressions versus the PDO ($F_{1,11}$ = 9.2, r^2 = 0.46, p = 0.01) and slope *T-Z* ($F_{1,11}$ = 7.9, r^2 = 0.42, p = 0.02) (Fig. 14a,b).

Analyses also indicated significant differences in regressions relating growth coefficients (k, yr^{-1}) by sex to annual PDO indices (females: $F_{1,11}$ = 11.55, r^2 = 0.51, p = 0.006; males: $F_{1,11}$ = 12.73, r^2 = 0.54, p = 0.004) but no significant relationships between growth coefficients and slope *T-Z* ($p > 0.05$) (Fig. 14c,d). We observed increases in growth coefficients during the warm phase of the PDO with greater than 51 % of the variation in growth coefficients explained for male and female canary rockfish (Fig. 14c). We found no significant relationship between growth and slope *T-Z*

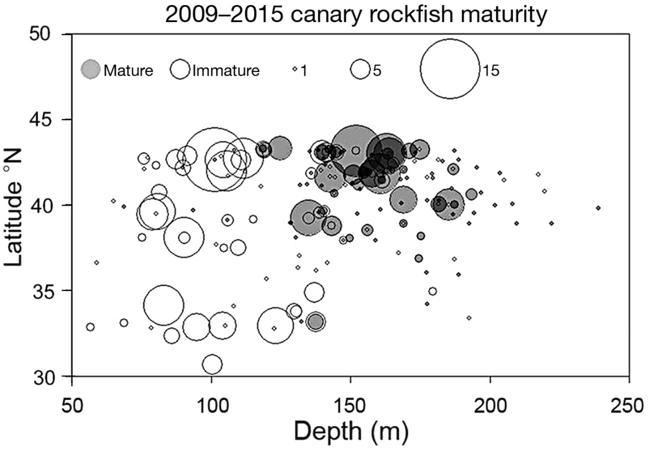


Fig. 13. Distribution by latitude and depth of mature (closed circles, n = 230) and immature (open circles, n = 283) female canary rockfish with paired latitude and depth measurements sampled during the 2009 to 2015 Northwest Fisheries Science Center's west coast groundfish bottom trawl survey (WCGBTS). The size of the circles represents the number of mature and immature samples at each latitude and depth

Table 4. Slope of annual regressions relating temperature (ln °C) to depth (m) used here as a survey-specific proxy for changing oceanographic conditions (slope *T-Z*). Also shown are *F*-values with degrees of freedom (F_{df}) and r^2, with $p < 0.0001$ for all years

Year	Slope	F_{df}	r^2
2003	−0.00088	$2896_{1,496}$	0.85
2004	−0.00088	$2896_{1,463}$	0.86
2005	−0.00088	$3440_{1,571}$	0.86
2006	−0.00084	$3718_{1,522}$	0.88
2007	−0.00083	$3740_{1,680}$	0.85
2008	−0.00085	$3124_{1,669}$	0.82
2009	−0.00087	$3332_{1,669}$	0.83
2010	−0.00086	$4364_{1,704}$	0.86
2011	−0.00083	$4227_{1,689}$	0.86
2012	−0.00087	$3342_{1,695}$	0.83
2013	−0.00082	$2624_{1,459}$	0.85
2014	−0.00089	$3408_{1,680}$	0.83
2015	−0.00092	$3554_{1,667}$	0.84

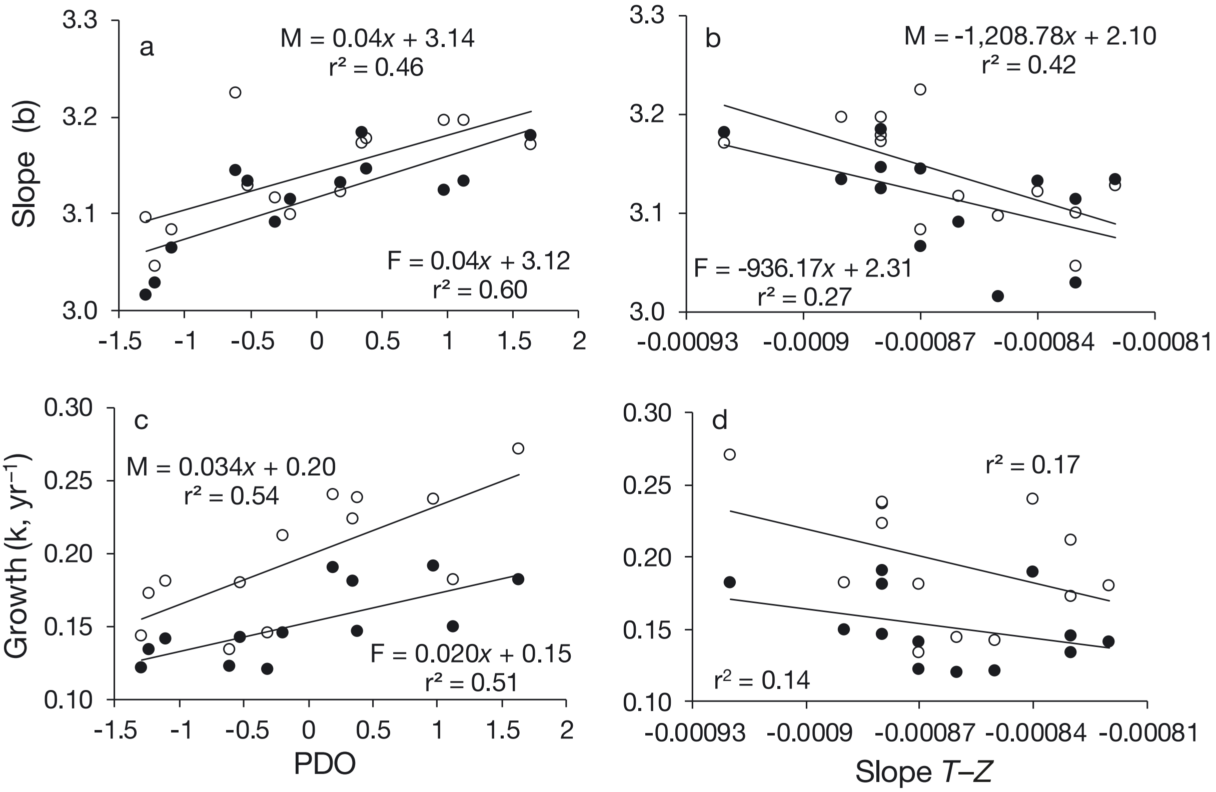


Fig. 14. Annual condition factors (*b*, slope of weight–length relationships) for male (M; open circles) and female (F; closed circles) canary rockfishes relative to annual (a) basin-scale indices of environmental change (Pacific Decadal Oscillation; PDO); and (b) survey-specific indices of change (slope *T-Z*, slope of annual regression between bottom temperature and depth). Also shown are significant linear regressions between slope *b* versus the PDO for females (p = 0.002) and males (p = 0.01) and significant or near significant regressions versus slope *T-Z* for males (p = 0.02) and females (p = 0.07). Annual growth rates (k, yr^{-1}) for male (open circles) and female (closed circles) canary rockfishes relative to (c) the PDO; and (d) slope *T-Z* during the 2003 to 2015 Northwest Fisheries Science Center's west coast groundfish bottom trawl survey (WCGBTS). Also shown are the significant regressions between growth rates for males (p = 0.004) and females (p = 0.006) versus the PDO over the study period

(Fig. 14d) with only 14 to 17% of the variation in growth coefficients tied to the local index for changing environmental conditions.

We observed similar results relating both biometric indicators (b, k) to other large-scale environmental indices, including the Multivariate El Niño–Southern Oscillation Index (MEI: $p < 0.05$). Note that as conditions warmed, as reflected in annual PDO index values, slope T-Z decreased such that the slopes for the years with the warmest temperatures (2014 and 2015) were the lowest observed (–0.00089 and –0.00092). The PDO in turn was significantly and negatively related to slope T-Z ($F_{1,11} = 10.98$, $r^2 = 0.50$, $p = 0.007$).

DISCUSSION

The current study focused on canary rockfish *Sebastes pinniger*, quantifying spatial patterns in life history characteristics and population demographics (catch and distribution) essential for management of this important commercial and recreational groundfish species. The life history parameters, growth and stock structure examined here supplement the relatively few prior publications devoted to canary rockfish along the US west coast (Phillips 1964, Boehlert 1980, McClure 1982) and contribute to assessment models used for ongoing management of this important resource (Thorson & Wetzel 2015).

The analyses revealed significant increases in coast-wide biomass indices and the percentage of tows with positive catch (i.e. non-zero CPUE), for this long-lived, slow growing species. Similarly, the study revealed recent increases in WCGBTS's CPUE but no steady increase over the temporal extent of the survey period (2003 to 2015). The increases observed here coincided with the finding that the stock is fully rebuilt and has been since 2006 (Thorson & Wetzel 2015). The 2015 assessment, however, noted that the estimated canary rockfish rebuilding rate is highly sensitive to assumed values of recruitment compensation (steepness) and natural mortality rate. In particular, the value of steepness increased dramatically in 2015 (J. T. Thorson pers. comm.). While current meta-analytic estimates of steepness represent 'best available science' for this species, they are liable to continue changing as new information becomes available, and these changes could have a large impact on future estimates of rebuilding rates.

The WCGBTS infrequently encountered canary rockfishes; generally in less than 12% of the tows conducted annually (632 of 8280 tows). However, canary rockfish aggregations encountered during the survey occasionally resulted in catches as large as 4.9 t tow^{-1}. These large tows occurred primarily off the northern Washington coast near the Canadian border, with some located off the Oregon or Northern California coasts. Vestfals (2009) similarly noted high density of canary rockfishes off Washington and Oregon based on commercial catch data. Neither very large nor very small individuals dominated the catch from the WCGBTS's largest tows. Consequently, these areas of high density did not represent either recruitment 'hot-spots', or unexploited 'pockets' of very old canary rockfishes (Thorson & Wetzel 2015) and are likely associated with habitat preferences (Juan-Jordá et al. 2009, Vestfals 2009).

The elevated average CPUE in 2006 that resulted largely from a single extremely large catch highlights the patchy distribution characteristic of canary rockfishes and emphasizes the importance of utilizing geostatistical models for analyzing survey data for such species. In the absence of modeling, the observed patchy distribution, low encounter rate and infrequent large tows of canary rockfishes could result in calculated population indices from design-based or conventional GLMM models that are relatively uninformative about trends in population abundance (Thorson et al. 2015). Utilizing a geostatistical model that accounted for catch in high- or low-density habitats explained a portion of the variability in CPUE and revealed the increasing trend in abundance in recent years. This modeling approach allowed us to estimate canary rockfish distribution and revealed an increasing trend measured as effective area over time, particularly since 2011. Such an expansion is expected during recovery from overfishing as a population grows followed by expansion into additional areas (Thorson et al. 2015, 2016a,b). Thorson et al. (2016b) found a significant relationship between increasing effective area occupied and density for multiple fish species from 6 marine regions.

The information compiled on depth distribution by the WCGBTS agrees with the range (57 to 307 m) described by Vestfals (2009) based on surveys conducted by the Alaska Fisheries Science Center (AFSC) from 1977 to 2001. Ninety percent of the AFSC tows with canary rockfish catch occurred from 57 to 199 m. Additionally, results presented here are consistent with Williams & Ralston's (2002) characterization of canary rockfish as a shelf species, infrequently encountered in deep water. Average size of canary rockfishes encountered in the trawl survey demonstrated a characteristic ontogenetic shift to deeper water with increased size as previously reported by others (Boehlert 1980, Sampson 1996).

Boehlert (1980) noted a general trend of increasing size with latitude in canary rockfishes along the US west coast. Similarly, Sampson et al. (2008) reported that median fork length (n = 528) for canary rockfishes caught in 2005 was largest in Washington, slightly less in Oregon and significantly smaller in California. Similarly, age (n = 427) decreased southwards along the coast, with ages ranging from 4 to 25 yr and the median age of fish from Washington (13 yr) greater than those from Oregon (12 yr) and California (8 yr) (Sampson et al. 2008). We also observed decreasing mean size and age along the coast from the northern most reaches of the survey to the 37–38° N latitudinal bin followed by a slight increase. However, part of the observed decrease in size and age within the 37–38° N latitudinal bin most likely relates to the relatively narrow shelf along that portion of the coast where the average depth of capture for canary rockfishes was shallower (94.0 m) than within all other 2° latitudinal bins (range 102.6 to 141.6 m).

Sampson et al. (2008) found that canary rockfishes older than 10 yr were predominantly female, but their reported maximum age (25 yr) was considerably less than the maximum age observed in the trawl survey (65 yr). The majority of their samples came from depths of 91 to 152 m (Sampson et al. 2008), most likely explaining the differences in age between their study and the trawl survey. Recall that both size and age increased with depth to greater than 200 m in the current study.

Age frequency throughout the current study was not markedly different by gender for canary rockfishes younger than 25 yr of age. However, for fish older than 25 yr, males (n = 104) outnumbered females (n = 37) by ~3:1. Stanley et al. (2005) also observed a decrease in females older than 20 to 25 years in Canadian waters. Recent stock assessment models account for the deficit in older females observed in age-composition samples from the bottom trawl survey by assuming an elevated natural mortality rate for females (Thorson & Wetzel 2015). Alternatively, behavioral differences that alter the availability of older females to capture could explain these results. Yellowtail rockfishes *Sebastes flavidus* exhibit similar patterns (Wallace & Lai 2005).

Both the size and age frequency distributions show evidence of recent recruitment during the survey period, with the highest percentage of young fish observed in 2010. These findings generally agree with the timing of observed rockfish recruitment events reported by coast-wide pre-recruit and young-of-year midwater trawl surveys (Ralston et al. 2013, 2015, Santora et al. 2014). Thorson & Wetzel (2015) noted that strong recruitment in 2001 to 2003, 2007 and 2010 aided the recovery of canary rockfishes after fishing decreased in the early 2000s. The pattern of reduced recruitment observed from 2003 to 2006 is consistent with many other groundfishes within the California Current (Thorson et al. 2013).

Multiple studies previously reported difference in weight–length relationships between sexes for canary rockfishes (McClure 1982, Thorson & Wetzel 2015). McClure (1982) noted that males and females have similar weights at fork lengths <45 cm, but females become increasingly heavier than males of equal length >45 cm. We observed coast-wide differences in estimated life history parameters among geographic sub-regions along the US west coast. The data examined suggested that males increase weight faster than females as a function of length, and that canary rockfishes north of Point Conception significantly increase weight faster than those to the south irrespective of sex. The biological significance of variation in weight–length relationships may be relatively small but when added to variation in other biological parameters (size-at-age and maturity) could suggest that stock structure exits latitudinally along the US west coast.

Other studies also found significant variation in growth curves for canary rockfishes between sexes (Westrheim & Harling 1975, Six & Horton 1977, Boehlert & Kappenmann 1980). Boehlert (1980) indicated that growth rate for canary rockfishes along the US west coast varied little with latitude; however, his samples came primarily from specimens collected north of 45° 32′ N with ages ≤20 yr. They and others noted latitudinal differences in growth, as well as variation between sexes, for other rockfish species (Keller et al. 2012, West et al. 2014). As observed here, males grew more rapidly than females but females reached larger asymptotic sizes. Growth rates and asymptotic sizes varied significantly among areas and generally increased in the northern portion of the study area. Similar species such as widow and yellowtail rockfishes also reportedly grow faster off Washington and Oregon than off California (Love et al. 2002). In addition to stock structure, environmental conditions and fishing pressure may individually or collectively contribute to regional variation in growth rates, although the reasons are unknown (Gertseva et al. 2010, West et al. 2014).

Previous studies reported lengths at 50% maturity for canary rockfishes ranging from 36 to 49.2 cm and ages at 50% maturity from 5 to 10 yr (Phillips 1964, Westrheim 1975, Gunderson et al. 1980, McClure 1982, Wyllie Echeverria 1987, Thorson & Wetzel

2015, Head et al. 2016). Estimates for L_{50} and A_{50} varied over time, with Phillips (1964) reporting L_{50} = 36 cm and A_{50} = 5 to 6 yr for canary rockfish (both sexes) from California while McClure (1982) recorded somewhat larger values for females off Oregon (L_{50} = 42.6 cm and A_{50} = 10 yr) with all females mature by age 12. Westrheim (1975) and Gunderson et al. (1980) reported L_{50} from northern Washington and southern British Columbia ranging from 48.5 to 49.2 cm. Based on coast-wide samples (n = 131) of female canary rockfishes from 2009 and 2011, we recently estimated L_{50} of 43 to 44 cm (Head et al. 2016), while the more extensive data described here (2009 to 2015) indicated L_{50} = 46.3 cm (n = 808) and A_{50} = 10.9 yr (n = 412). Prior studies reported reductions in length and age at 50% maturity for heavily exploited fish populations (Jørgensen 1990, Morgan & Colbourne 1999, Frey et al. 2015) while the results reported above for canary rockfishes suggest an increase in L_{50} and A_{50} since the 1960s. These contradictory findings suggest that historical variations noted over time for canary rockfishes most likely result from differences in sample size, area, methods and metrics used (total versus fork length). For example, earlier studies (Phillips 1964, Westrheim 1975, Gunderson et al. 1980, McClure 1982) based assessment of maturity on visual observations, while more recent results (Thorson & Wetzel 2015, Head et al. 2016) are based on histological examination of ovaries. Despite the unknown source of temporal variation, the spatial variation observed in the current study could indicate stock structure along the US west coast.

Our study revealed spatial patterns in canary rockfish maturity along the US west coast, including a notable decrease in the proportion of mature females present south of 40° 26′ N and at depths less than 115 m. The timing of the groundfish survey, which progresses seasonally north to south, does not account for the low number of mature fish observed south of Cape Mendocino. Since specimens from south of Cape Mendocino are taken closer to the spawning season (Love 1996), a higher proportion of mature fish might be expected unless other factors, such as stock structure, influence these results.

We initially included annual biomass indices, as well as environmental factors, in the analysis of variation in canary rockfish growth and weight–length relationships over time. However, the most parsimonious models exploring changes in these metrics for canary rockfishes did not include biomass. This suggests that at current population levels, density-dependent effects did not exert as strong an influence as environmental change on these parameters. Although we explored 2 different environmental indices, a basin-wide measure of oceanographic conditions (PDO) and an index site-specific to the survey (slope T-Z), we noted more robust relationships with the PDO and the MEI, particularly for growth. Slopes of weight–length regressions were significantly lower during the cool phase of the PDO or MEI and a regional measure of environmental change (slope T-Z). However, although growth rates tended to be lower during the cool phase of the local index (r^2 = 0.17 males; 0.14 females), significant relationships only occurred with basin-scale indices (PDO and MEI), with rates higher during warm conditions. The relatively short length of the time series examined here (13 yr) may increase the likelihood that these results are spurious. However, longer records of rockfish growth rates, based on otolith structure, also revealed elevated growth in another region (Alaska Coastal Current) during years with warmer conditions (Helser et al. 2011). Increases in condition similarly occurred for other groundfish species (petrale sole and arrowtooth flounder) during the warm phase of the PDO and MEI within the California Current System (Keller et al. 2013). Some support for elevated growth of canary rockfishes during warmer conditions is also provided by stomach content analyses. Euphausiids form a major component of the canary rockfish diet (54% by weight), occurring in ~71% of stomachs (J. Buchanan pers. comm.) and euphausiids tended to increase in abundance during warm PDO years through 2008 (Bograd et al. 2010). Ralston et al. (2015) indicated that euphausiids are part of the micronekton assemblage of lower trophic level species that transfer production from primary and secondary trophic levels (e.g. phytoplankton and zooplankton) to fish. Also, as noted by Harvey (2009), simulated growth of rockfish increased with warming temperatures based on bioenergetics models.

Other studies have reported linkages between growth of numerous taxa and environmental indices such as the PDO in North Pacific ecosystems (Mantua & Hare 2002, Martinez et al. 2009). Previous long-term (10 to 30 yr) studies have found correlations with changes in biota (Hare & Mantua 2000), productivity (Schwing et al. 2009), landed catch (Norton et al. 2009) and production of commercial fish stocks (Hollowed et al. 2001). These climate–growth relationships indicate broad-scale oceanographic factors may be important processes affecting the growth rates of rockfishes in the North Pacific Ocean, although the mechanism behind these relationships remains unknown.

CONCLUSIONS

We saw significant increases in CPUE, percent of tows with positive catch and biomass of canary rockfishes *Sebastes pinniger* during the period of population recovery. Evidence presented here, based on geographical variation in biological parameters, also indirectly implies that canary rockfish may exhibit stock structure off the US Pacific coast. Variations in spatial patterns, combined with the reduced capture of large/old rockfish south of Cape Mendocino further suggest geographic differences. Limited direct evidence from protein polymorphisms also supports separation of canary rockfish stocks geographically between California and Washington (Wishard et al. 1980). However, tagging data indicate significant movement of adult canary rockfishes across depth and latitude, and conclusive data in the form of genetic analyses are currently lacking (Stewart 2007). Since regional environmental effects, such as temperature and productivity differences, perhaps in association with local or regional upwelling (Juan-Jordá et al. 2009, Vestfals 2009) could drive the differences observed here, we recommend addressing stock structure directly through DNA studies.

Stringent management coupled with support from fishers and good ocean conditions resulted in canary rockfish achieving rebuilt status along the west coast in less time than anticipated. Ongoing monitoring by fisheries-independent surveys with associated improvements in knowledge about life history parameters will allow managers to remain vigilant as ocean conditions continue to shift with changing climate. Future research should focus on exploration of stock structure and associations between canary rockfish and specific habitat types as the population continues to expand and grow.

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