

SPATIAL AND TEMPORAL VARIATION IN ROSY ROCKFISH
(SEBASTES ROSACEUS) LIFE HISTORY TRAITS

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Ryan T. Fields

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The Undersigned Faculty Committee Approves the

Thesis of Ryan T. Fields:

**SPATIAL AND TEMPORAL VARIATION IN ROSY ROCKFISH (SEBASTES
ROSACEUS) LIFE HISTORY TRAITS**

Scott L. Hamilton, Chair
Moss Landing Marine Laboratories

Richard M. Starr
Moss Landing Marine Laboratories

Michael H. Graham
Moss Landing Marine Laboratories

Kris Roney, Dean
Associate VP for Academic Programs and Dean of Undergraduate and Graduate Studies

Approval Date

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ABSTRACT

Spatial and Temporal Variation in Rosy Rockfish (*Sebastes rosaceus*) Life History Traits

By
Ryan T. Fields
Master of Science in Marine Science
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Spatial and temporal variability in environmental conditions and fishing pressure across a species' geographic range may result in differences in life history traits, population demography, and abundance of marine species. Understanding spatial and temporal patterns of life history and demographic differences is essential for sustainable fisheries management because stock assessment models are sensitive to differences in stock productivity. The Rosy Rockfish (*Sebastes rosaceus*) is a small, commonly encountered, and ecologically important species in California whose life history and biological traits are only partially understood. I used central California collections of Rosy Rockfish from 2001-14 and data from the 1980s to revise outdated growth models, determine if changes in growth rates, longevity and survivorship have occurred over the past four decades, identify sex-specific differences in growth, and determine the spatial scale of Rosy Rockfish life history trait variations.

Break and burn otolith analysis techniques indicated that Rosy Rockfish live at least 30 years (yr) – over twice as long as previously reported – though validation of age structures is still needed. Mean lengths of Rosy Rockfish collected from 1980-83 (246 mm) were greater than those collected from 2012-14 (209 mm). The asymptotic length of Rosy Rockfish collected in central California from 1980-83 was 31 mm greater than Rosy Rockfish collected during 2012-14 (256 mm vs. 225 mm). Maximum ages estimated for the 1980-83 and 2012-14 periods were 32 and 30 yr, respectively. Total mortality (Z) was reduced and survivorship was greater in the 1980s compared to the 2010s collections. These changes are especially interesting because fisheries do not directly target Rosy Rockfish.

Male and female Rosy Rockfish exhibited different life history traits. Collections in central California from 2012-14 were comprised of a greater proportion of smaller females than males, and male Rosy Rockfish were larger than females in Half Moon Bay (2012-14) and Santa Cruz (2001-05). Longevity was greater in male Rosy Rockfish; females had

greater mortality and reduced survivorship with age. Age and length at 50% maturity was similar between the sexes as both matured at age 8 and 171 mm and male and female growth parameters (L_{inf} and K) were not significantly different.

Central California Rosy Rockfish exhibited greater longevity and maximum age compared to southern California Rosy Rockfish, despite similar sample sizes and sampling techniques. Total mortality was reduced and survivorship was greater in southern California compared with central California, indicating potential differences in predation or fishing pressure between areas. Surprisingly, asymptotic size (L_{inf}) was smaller in central California (225 mm) than in southern California (232 mm). A greater portion of midsized fishes in the southern California sample may explain some of these differences.

The use of whole otoliths in previous age and growth studies resulted in age estimates that significantly underestimated the oldest age classes in Rosy Rockfish and future stock assessments should revise growth parameters to reflect new age estimates. Using the break and burn technique, there were significant changes in mean length, longevity, survivorship and growth parameters between the 1980s and 2010s samples. The differences in life history and population demography characteristics are consistent with increased mortality from direct fishing removals or indirect, density-dependent effects of competition and predation. Climate conditions were favorable for rockfish over the lifespan of fishes I collected and were probably not responsible for the temporal patterns observed. Likewise, recreational and commercial removals for Rosy Rockfish steadily declined since the mid 1990s, giving Rosy Rockfish populations nearly 20 years of relief from intense fishing pressure. Changes in Rosy Rockfish life history traits are most likely due to the indirect effect of community level changes caused by intense historical fishing pressure on larger rockfish and the subsequent recovery of many species and their predators including lingcod and pinnipeds. Increases in rocky reef population abundances may have increased density-dependent interactions with Rosy Rockfish such as predation and competition leading to increased total mortality. Small species like Rosy Rockfish are susceptible to changing ecosystems; this study highlights the need to account for changes in life histories and population demography within fisheries management.

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INTRODUCTION

Temporal or spatial variability in oceanographic conditions, fishing intensity, and predation or competition through time or across the range of a species can lead to significant shifts in fish life history traits and population demography (Conover and Present 1990, Choat et al. 2003, Ruttenberg et al. 2005, Levin et al. 2006, Trip et al. 2008). Due to limited financial resources and the logistical challenges of small-scale sampling, fisheries managers seldom take into consideration spatial differences in species' life history and demographic characteristics (see Gunderson et al. 2008 and Hamilton et al. 2011b for exceptions). Additionally, averaging life history traits across the geographic range of a species, a common practice in many stock assessments, can lead to over- or under-utilization of a species (Gunderson et al. 2008, Prince 2010, Hamilton et al. 2011b). Understanding the patterns and scales of species specific life history trait variations is therefore critical to meeting sustainability objectives, as stock assessment models can be sensitive to differences in stock productivity (Wilson and Boehlert 1990, Choat et al. 2003, Mollet et al. 2015).

Spatial Variation in Life History Traits

Evidence of environmentally-driven life history variation over large scales can be seen in traits such as diet composition, size at age, reproductive timing, and fecundity (James 1970, Robertson et al. 2005, Trip et al. 2008). In temperate regions, shifts in these traits are often correlated with latitude; northern latitudes have cooler temperatures that shorten the growing season (Conover and Present 1990) and increase productive (Blanchette et al. 2007). Several studies reported substantial population demographic differentiation over a few degrees of latitude where strong environmental gradients exist (Ruttenberg et al. 2005, Caselle et al. 2011).

Spatial variation in life history traits is often caused by strong differences in fishing removals or density-dependent mortality such as predation or competition. Gradients in fishing pressure across a species' range can lead to regional variation in population size and age structure and significantly alter community composition and top predator abundance (Hamilton et al. 2007, DeMartini et al. 2008, Ruttenberg et al. 2011). Spatial differences in predator abundance mimic the selective pressures of fishing and lead to divergence in prey life history traits (Rodd and Reznick 1997, Reznick and Ghalambor 2005). Where predators are more abundant, prey fishes often exhibit reduced longevity, smaller size at age, and reduced size and age at maturity (Ruttenberg et al. 2005, 2011). In locations where conspecific densities are elevated and intraspecific competition is intense, fish grow slower, and may also attain smaller sizes, and mature and change sex at small sizes and younger ages (Gust 2004, Caselle et al. 2011).

Temporal Variation in Life History Traits

Temporal variation in life history traits may result from variability in environmental conditions as well as changes in competition, predator abundance, and fishing pressure through time (Reznick and Endler 1982, Pearson and Hightower 1990, Law 2000, Vamosi and Schluter 2002). On shorter time scales, commercial and recreational fishing pressure is one of the greatest sources of change in the growth of fishes (Myers and Worm 2003). Fishing pressure is highly selective and alters fish population dynamics by removing the largest, oldest, most fecund individuals (Conover and Munch 2002, Law 2000, Hamilton et al. 2007), and favors slow-growing, early-maturing individuals that reproduce before recruiting into the fishery (Ricker 1981, Rijnsdorp 1993, Conover and Munch 2002, Hamilton et al. 2007).

Fishing alters community structure within fish assemblages. The presence of large predators in an ecosystem, or their removal, affects the demographics of lower trophic level prey species (Rodd and Reznick 1997, Rundle et al. 2003). High predation results in smaller, slower growing individuals that mature at younger ages (Reznick et al. 2001, Reznick and Ghalambor 2005). The removal of top-piscivorous predators in tropical reefs significantly alters reef fish community structure, potentially increasing the abundance of lower trophic level species (DeMartini et al. 2008, Ruttenberg et al. 2011).

Rockfish background

Many rockfish species are long-lived (Andrews et al. 2002, 2007, Black et al. 2005, Thompson and Hannah 2010), late to mature (Echeverria 1987), and have variable reproductive success (Berkeley et al. 2004). As a result, rockfish are susceptible to overfishing (Parker et al. 2000, Levin et al. 2006). Historically, rockfishes are among the most important groups of fishes caught along the West Coast (Parker et al. 2000). Intense fishing pressure has altered rockfish community structure, mean lengths, and size and age at maturity (Mason 1995, 1998, Love 1998, Harvey et al. 2006, Levin et al. 2006, Schmidt 2014). Rockfish life history parameters also vary across time and space (Pearson and Hightower 1991, Malecha 2007, Keller et al. 2012, Schmidt 2014).

Management policies resulting from an incomplete understanding of rockfish life history traits contributed to the decline of many stocks in the 1980s and 1990s and the federal declaration of seven rockfish species as overfished in 2001 (Mason 1995, Love 1998, 2002, Levin et al. 2006). It is possible that small species of rockfish were also affected during these years of heavy fishing, either directly or by severe shifts in community structure and relative abundance of larger species (Levin et al. 2006).

Rosy Rockfish

Rosy Rockfish (*Sebastes rosaceus*; Girard, 1854) are a small and ecologically important species whose life history and biological traits are only partially understood (Love 2002). Rosy Rockfish are commonly encountered between northern California and central Baja California and have reportedly been found as far north as Puget Sound (Phillips 1957; Chen 1971). However, Chen (1971) speculated that the northernmost samples in Washington were likely Rosethorn Rockfish (*Sebastes helvomaculatus*) due to frequent misidentification with Rosy Rockfish. Rosy Rockfish often are associated with high relief rock and cobblestone substrates at depths of 50 to 90 m (Love et al. 2002, Wedding and Yoklavich 2015). They reportedly attain a maximum size of 360 mm, though Chen (1971) also suspected this record may reflect a misidentification of Rosethorn Rockfish.

Rosy Rockfish are generalist predators; their diet consists of euphausiids, shrimp, small fishes, crabs, and other prey items associated with the benthos and water column (Love 2002). Rosy Rockfish first reach maturity in central California between 120-250 mm total length, with 50% of the population maturing by 200 mm, at an age of 6 yr (Echeverria 1987). In southern California, Rosy Rockfish are 50% mature at 150 mm (Love 1990).

Though seldom targeted due to their small size, Rosy Rockfish have historically been caught by commercial and recreational fisheries along the California coast (Karpov et al. 1995, Mason 1998, Love et al. 2002). Reports to the Pacific Fisheries Management Council from the PacFIN database estimated that Rosy Rockfish commercial catch peaked in both 1988 and 1994 at approximately 17 and 21 metric tons (mt) (PacFIN 2015). Trawl and net gear were responsible for 97% of estimated Rosy Rockfish catch in 1988, whereas 98% of estimated commercial catch in 1994 was due to hook and line fishing (PacFIN 2015). Commercial catch of Rosy Rockfish steadily declined from 1994 to 2000 when it stabilized

to less than 0.6 mt per year on average. RecFIN recreational catch estimates for Rosy Rockfish peaked coastwide in 1980 and 1986 at 76 mt and 53 mt, respectively (RecFIN 2015). Statewide recreational landings declined to an annual average of 5 mt over the past decade (RecFIN 2015). A majority of the recreational Rosy Rockfish take in the past decade was caught south of Point Conception in southern California.

Rosy Rockfish are rarely targeted by fishers, although they are commonly caught and discarded by anglers aboard Commercial Passenger Fishing Vessels (CPFVs), experiencing high mortality rates due to barotrauma (Mason 1998). In addition, the decline of the rockfish complex in the 1980s and 1990s and the removal of large, piscivorous species may have led to predator release and increased food availability. As a result juvenile Rosy Rockfish mortality rates may have decreased and growth rates increased – though little is known about the feeding ecology of juvenile Rosy Rockfish.

Over the past 15-20 years, there have been significant recoveries of several important West Coast predators including larger rockfish species, Lingcod (*Ophiodon elongatus*), Harbor Seal (*Phoca vitulina*) and California Sea Lion (*Zalophus californianus*) (Hamel et al. 2009, Keller et al. 2014, Marks et al. 2015). Other small species of rockfish increased in abundance between 1977 and 2001 (Harvey et al. 2006, Levin et al. 2006). Rosy Rockfish population demography could be significantly altered by increased predation or competition with other rockfish (Hallacher and Roberts 1985, Hobson et al. 2001, Beaudreau and Essington 2007).

Much remains unknown about Rosy Rockfish longevity, age and growth, and the scale of variation in those traits along the California coast (Love 2002). Previous ageing studies used whole otoliths to age Rosy Rockfish to 14 yr (Chen 1971, Lea et al. 1999); however, surface-ageing techniques underestimate ages for long-lived, slow-growing fish

(Beamish 1979, Chilton and Beamish 1982, Wilson and Boehlert 1990). Additionally, many rockfish exhibit sexual dimorphism in growth and age at maturity; females often attain larger maximum lengths and mature at older ages (Echeverria 1987, Love 1990). Sex-specific differences were not detected in patterns of age and growth of Rosy Rockfish in earlier studies; however, the use of whole otoliths to age Rosy Rockfish may have obscured true differences in growth parameters between the sexes.

The goal of this study was to provide new information about spatial and temporal variation in the demography and life history of Rosy Rockfish. My specific objectives were to revise an outdated growth model for Rosy Rockfish, determine if changes in growth rates, longevity, and survivorship have occurred over the past four decades in central California, identify sex-specific differences in growth, longevity and survivorship, and determine at which spatial scales Rosy Rockfish life history traits vary. Finally, I sought to identify the environmental and ecological drivers of the observed changes in Rosy Rockfish population demography and life history traits within the California Current ecosystem.

METHODS

Study Area and Sample Collection

I used Rosy Rockfish collections from sites in central and southern California to compare geographic variation in rates of growth, maturation, longevity, and annual survivorship. I used additional samples from the 1980s in central California to investigate temporal differences in growth. For the purpose of this thesis, southern California included latitudes south of Point Conception (34.45 °N), whereas central California included latitudes north of Point Conception and south of Bodega Bay (34.45 °N to 38.32 °N)

Central California

I collected Rosy Rockfish in central California as incidental catch as part of the 2012-14 Rockfish Conservation Area (RCA) Project being conducted by the National Marine Fisheries Service (NMFS) in collaboration with the Fisheries Conservation and Biology Lab at Moss Landing Marine Laboratories (MLML) (Marks et al. 2015). In that project, fishing was conducted at similar locations and depths, and with similar terminal gear, as the 1980s-90s recreational fishery. Fish were collected during standardized hook-and-line fishing trips using 5-hook shrimp fly ganions with and without squid bait. Rosy Rockfish were caught in depths between 29 and 91 m. Of 338 Rosy Rockfish caught during the RCA Project, 272 were retained from Half Moon Bay, the Farallon Islands and Cordell Bank combined. All fish collected during this project were done so under NMFS collection permits: NOAA SRP-22-2012, NOAA SRP-22-2013, NOAA SRP-22-2014; as well as CDFW collection permits SWC-008, and SC-12372. Rockfish collected by NMFS were retained with IACUC permit CARC-Hayes1304, while permit #964 permitted later use of non-living tissue. The

University of California Santa Cruz Institutional Animal Care and Use Committee (IACUC) approved this research.

All rockfish collected through the RCA Project were processed at the NMFS Southwest Fisheries Science Center (SWFSC) lab in Santa Cruz within 48 hours of capture. For each fish, we recorded whole weight (g), fork length (mm), liver weight (mg), and gonad weight (mg). NMFS technicians determined maturity and reproductive stage of the gonads according to (Echeverria 1987). Finally, the otoliths were removed from the rockfish, rinsed of organic matter in water and stored dry in plastic vials for future ageing. All other Rosy Rockfish collected were dissected at MLML.

NMFS SWFSC, in collaboration with the Monterey Bay Aquarium, collected additional Rosy Rockfish in Monterey Bay for the purposes of ongoing fecundity studies and aquarium displays. The Monterey Bay Aquarium donated forty-six Rosy Rockfish during 2014 that were too small for either project for use in my study. These Rosy Rockfish were collected under the Monterey Bay Aquariums collection permit; however, I also possessed a CDFW scientific collection permit (# SC-12738). Finally, 200 Rosy Rockfish were collected by NMFS during a series of hook and line research cruises near Santa Cruz between 2001 and 2005. A subsample of 100 otoliths from this collection was made available for my study. Samples from the Santa Cruz region (2001-05) were collected in significantly deeper water than the rest of the central California or southern California Rosy Rockfish samples (ANOVA, Subregion, $F_{2,587} = 106.6$, $p < 0.001$). There were no clear relationships, however, between either Rosy Rockfish length or age with sample depth across the areas sampled (Table 1). I therefore proceeded under the assumption that depth did not represent a serious confounding factor within my data for the depths sampled during this study.

Table 1. Linear relationship between average size and age of Rosy Rockfish with depth (1 m increments). Slope, p-value and r^2 were derived from standard least squares regression. Significant relationships are in bold.

Location	Years	Age:Depth			Size:Depth				
		slope	+/- SE	p-value	r^2	slope	+/- SE	p-value	r^2
Central CA	2012-14	0.08	0.01	< 0.001	0.07	-0.323	0.04	0.015	0.02
Santa Cruz	2001-15	0.22	0.02	0.715	< 0.01	-0.089	0.10	0.795	< 0.01
Southern CA	2004-14	0.01	< 0.01	0.469	< 0.01	0.160	0.02	0.005	0.03

Southern California

Each year since 2004, NMFS has conducted standardized hook and line fishing in the Southern California Bight (SCB) as part of an annual survey to assess relative abundance of several shelf rockfish species (Harms et al. 2008). Each year, approximately 100 sites are sampled in the SBC; of those, 60 are considered fixed and sampled annually while 40 additional sites are chosen randomly from a list of known fishing locations (Harms et al. 2008). Sites were selected to sample across a range of historical exploitation levels as recommended from local captains. All sampling was conducted between the depth ranges of 37 and 229 m (Harms et al. 2008). Fishing was conducted using 5-hook shrimp fly gangions with squid mantle bait. Rockfish fork lengths were measured to the nearest centimeter (cm), and fish were dissected to determine sex and retain otolith pairs. Between 2004 and 2013, 308 pairs of Rosy Rockfish otoliths were retained from 53 sample sites and within 19 sample areas across the SCB. During the 2014 SCB hook-and-line survey, NMFS retained an additional 35 Rosy Rockfish for my thesis project. Whole fish samples were shipped frozen to MLML after the conclusion of the 2014 sampling season and subsequently dissected. Finally, the NMFS SWFSC lab in Santa Cruz also used hook and line fishing to collect 70

southern California Rosy Rockfish during 2006 and 2007. The otoliths retained were made available for my thesis.

Central California 1980s

In order to compare growth rates between contemporary collections of Rosy Rockfish and Rosy Rockfish populations from the 1980s, I collaborated with fisheries biologist Don Pearson of the SWFSC, Santa Cruz to age a historical set of otoliths. The historical samples were collected during the NMFS dockside sampling surveys in the 1980s and consisted of approximately 500 otoliths from the early 1980s. CDFW sampling block numbers were recorded for fish sampled, providing estimates of approximate catch location. The NMFS collections were stored dry in manila coin folders at the SWFSC; however, many otoliths did not have biological data (sex and length) associated with them, and were excluded from further analysis. Ultimately, only 200 otoliths from the 1980s were available for my study.

When I subsampled Rosy Rockfish otoliths from a larger collection, I used Komolgorov-Smirnov 2-sample test (i.e., KS-test) to compare the subsampled length frequency distributions with the full dataset. No statistical differences were detected between subsamples and original sample populations for either Central 1980-83 ($D = 0.081$, $p = 0.264$) or Southern 2004-14 Rosy Rockfish ($D = 0.050$, $p = 0.927$). I therefore proceeded under the assumption that my subsamples were good representations of the populations from whence they came.

Ageing

Bony fish have three pairs of otoliths, which facilitate hearing and balance (Popper et al. 2005). The largest of these otoliths, the sagittae, are used for ageing studies (Chilton and Beamish 1982). As fish age, new layers of calcium carbonate are deposited seasonally in concentric zones called annuli (Popper et al. 2005). These alternating opaque and translucent zones are interpreted as annual growth patterns; although annuli in younger or fast growing fish may represent shorter time scales (Chilton and Beamish 1982). Most round-bodied teleost otolith pairs are considered symmetrical (Matta and Kimura 2012) and, under that assumption, I used either side interchangeably.

Previous studies of Rosy Rockfish in southern and central California used whole otoliths to count annual growth rings and estimate Von Bertalanffy growth function (VBGF) parameters (Chen 1971, Lea 1999). These studies estimated that Rosy Rockfish live 13 and 14 yr in southern and central California, respectively; however, annuli from central California Rosy Rockfish otoliths were difficult to identify beyond age 7 and surface ageing techniques were not always accurate (Lea et al. 1999). Surface ageing techniques using the whole otolith underestimate the age structure of a species' population because older fish deposit calcium carbonate asymmetrically across the surface of the otolith (Beamish 1979). Otoliths in older fish grow in thickness, not in width, making detection of annuli around the edge difficult (Matta and Kimura 2012). Preliminary investigations using the break and burn sectioning technique indicated that Rosy Rockfish may actually live at least 40 years (Love 2011, Don Pearson, *pers. comm.*, Fisheries Ecology Division, Southwest Fisheries Science Center, NOAA, 110 Shaffer Rd., Santa Cruz, CA 95060, USA).

Fisheries biologist Don Pearson helped me develop general aging criteria for Rosy Rockfish. We agreed upon guidelines for identifying annuli, checks, and winter growth patterns while considering established aging techniques (Chilton and Beamish 1982, Matta and Kimura 2012). We decided that the break and burn technique, outlined by Chilton and Beamish (1982), was the most appropriate for this project due to its efficiency and wide acceptance in fisheries biology (Matta and Kimura 2012). This technique involved splitting the otolith in half across the nucleus and burning the exposed edge over an ethanol flame to increase contrast between annuli. I split most otoliths by applying pressure with my thumbnails; however, thicker otoliths needed to be scored first using an Isomet low speed saw or hand held Dremel tool (Chilton and Beamish 1982, D. Pearson, *pers. comm.*, Fisheries Ecology Division, Southwest Fisheries Science Center, NOAA, 110 Shaffer Rd., Santa Cruz, CA 95060, USA). I smoothed the broken otolith surface with a Dremel tool prior to burning. I set otoliths burned-side-up in dark modeling clay, brushed the surface with a thin coat of mineral oil, and viewed them with reflected light under a stereovision Nikon NI-150 dissecting scope at 20-60X magnifications. I took photos of otolith surfaces using an AmScope MU800 camera attached to a dissecting scope in conjunction with Toup View[®] image software; photographs often lacked nuanced details needed to age otoliths that were available by manipulating light levels, otolith angle, and microscope zoom and focus.

To test the assumption that break and burn was a suitable technique, I aged a subsample of otoliths by thin sectioning. I mounted otoliths on glass slides using Crystal Bond[™] adhesive and polished them with a Bueler Ecomet III polisher using 600-grit and 9-micron sanding pads. Ages were evaluated under a compound Leica DM 4000B microscope at 50-75X magnification in conjunction with ImagePro[®] software. I obtained three independent age estimates for each thin section.

I aged a subset of otoliths from a southern California NMFS hook-and-line survey using surface aging techniques to determine if Rosy Rockfish ages were underestimated by using whole otoliths. Seventy-six whole otoliths available between the years 2009 and 2013 were selected. In cases where break and burn was already performed, the remaining otolith was used for analysis under the assumption that otolith pairs are identical (Matta and Kimura 2012). Age estimates were obtained by submerging the otolith in water against a black backdrop and using an Olympus SZX-ILLD2-100 stereovision dissection scope with reflected light. Three independent age estimates were produced for each otolith.

Age structure validation is recommended for all age and growth studies but was not logistically feasible for this project (Chilton and Beamish 1982, Campana 2001). Identical aging criteria were applied evenly across all samples making relative differences in growth a valid comparison and I made every effort to increase the precision of my age estimates throughout the study. Rosy Rockfish population studies would benefit from validation.

Precision

Rosy Rockfish are a challenging species to age because their otoliths contain many checks (false annuli marks). To increase ageing precision, I evaluated each otolith at least three times. Each new age estimate was made independent of size data and a minimum of one week after previous estimates. Don Pearson provided age estimates for all NMFS SWFSC otoliths, including: 320 RCA Project otoliths, 187 1980s otoliths, and 21 southern CA otoliths. I used the coefficient of variation (CV) to calculate each estimate's relative deviation from the mean estimated age and re-read otoliths until the CV for three age estimates was within 10%. Due to differences between multiple reads that could not be

reconciled, I excluded five otoliths from the 1980s and one otolith from the 2012-14 collection from analysis.

Only otoliths from fish with known fork length were aged. Otoliths without associated sex information were considered in the full growth model only after further analysis revealed no statistical difference between male and female growth parameters.

STATISTICAL ANALYSIS

Ageing Precision

In order to determine error levels between independent age estimates, I calculated the CV as a proxy for of inter-reader precision (Chang 1982). I measured the magnitude of standard deviation relative to the mean using this formula:

$$CV_j = 100 \times \frac{\sqrt{\frac{\sum_{i=1}^R (x_{ij} - x_j)^2}{R - 1}}}{x_j}$$

Where x_{ij} is the i^{th} age estimate, x_j is the mean age estimate, and R is the total number of age estimates produced for the j^{th} sample. To look for systematic ageing bias, I produced age-bias plots by plotting mean estimated ages from one reader against the ages estimated by the second reader according to techniques described by Campana et al. (1995).

When I needed a single age estimate per fish for a calculation (e.g., longevity, survivorship, maturity), I used a mean value of the three closest age estimates for each fish and the between-reader bias was reduced to values between 6.4% and 9.9%. I determined that this level of precision was acceptable for the purposes of this study by convening with NMFS fisheries biologist Don Pearson. When calculating final Von Bertalanffy growth coefficients, I used all age estimates and random effects techniques, which explicitly

incorporated the error from multiple age estimates into the final model (Cope and Punt 2007).

Growth

In order to answer my questions about growth rate variability between populations of Rosy Rockfish, I fitted the Von Bertalanffy growth function (VBGF) to my size-at-age data using the following equation and least squares techniques in R (R Core Team 2015):

$$L_t = L_{inf} (1 - e^{-K(t-t_0)})$$

where L_t is predicted length-at-age, L_{inf} is predicted average maximum length, K is a growth coefficient that describes how quickly an individual reaches its maximum length, t equals age, and t_0 equals the time when length equals 0. I set t_0 equal to 0 and used a two-parameter estimation of the VBGF. This is justified because rockfish larvae are 3-7 mm at parturition (Love 2002) and small size classes were not well represented among all sample groups (Pardo et al. 2013). I calculated 95% confidence intervals for the VBGF parameters L_{inf} and K following methods in Kimura (1980) and Hamilton et al. (2011b). If these confidence intervals did not overlap, the two populations being compared were considered significantly different in their growth parameters at the $\alpha = 0.05$ level (Kimura 1980).

I used these methods to first identify differences in growth rates between the 1980s and 2010s Rosy Rockfish collections. I then identified sex-specific differences in male and female Rosy Rockfish growth rates and average maximum length. Sexes were combined to compare growth rates among geographic areas within central California and between central and southern California where Rosy Rockfish were obtained.

I also used a 2-sample KS-test between the 1980s and 2010s collections of Rosy Rockfish, as well as between sexes and among sample locations in central and southern

California. In this way, I was able to investigate whether differences in average maximum length between Rosy Rockfish populations, as measured by von Bertalanffy techniques, were due in part to larger or smaller length-frequency distributions. Additionally, KS tests were used to confirm that the subsamples of otoliths represented the original, full collection.

Because all populations did not have equal sample sizes, I used bootstrap resampling techniques to test the effect of varying sample size on the estimates of growth parameters. When greater than 100 samples were used in the regression the differences in growth parameter estimates between the subsample and the entire collection became negligible.

Age-based catch curves and longevity

To estimate mortality rates and survivorship, I plotted log-linear regressions (i.e., catch curves) for age-frequency data in each area and by sex. Rosy Rockfish younger than peak mode age were excluded from analysis because we assumed that the youngest fish had not recruited fully to the fishery and were under sampled (Robertson et al. 2005, Hamilton et al. 2011a, Ruttenberg et al. 2011). Similar logic was used to exclude three fish older than 29 years old in order to improve regression fit.

Log-transformation of age counts reduce heterogeneity of variance and the slope (Z) of the log-linear regression is an estimate of total mortality (Robertson et al. 2005). This estimate of total mortality was used to calculate estimates of Rosy Rockfish survivorship (S) using the equation:

$$S = e^{-Z}$$

Spatiotemporal differences in mortality were tested using analysis of covariance (ANCOVA), which accounted for variability due to a continuous covariate factor that varies along with the fixed factor. Accounting for covariate factors can reduce variability in the

error term and make the subsequent ANOVA comparison between fixed factors more powerful (Gotelli 2004).

The ANCOVA model is:

$$Y_{ij} = A_i + B_i(X_{ij} - \bar{X}_i) + \epsilon_{ij}$$

A_i is the treatment effect, B_i is the slope from the regression of the covariate, X_{ij} is the covariate measurement, \bar{X}_i is the average value of the covariate, and ϵ_{ij} is the error term for the i^{th} group (Gotelli 2004).

Longevity was calculated by taking the mean of the top quartile of ages for each study area and by sex (Robertson and Choat 2002). This technique allowed for comparability between fish collections with variable samples sizes. Longevity values were compared using student's t-test and ANOVA.

Maturity

Logistic regression techniques in R were used to assess sex-specific differences in ages at 1st, 50% and 100% maturity (Gelman and Hill 2006, James 2013).

The logistic equation is:

$$P_x = \frac{1}{(1 + e^{-(a+bx)})}$$

Where P_x is the proportion of fish mature at a given age, a is the intercept and b is the coefficient on the first predictor variable x . These variable can be rearranged in order to calculate age and length at 1st, 50% and 100% maturity (Echeverria 1987).

$$\ln\left(\frac{1}{P_x}\right) - 1 = ax + b$$

Length-at-maturity were also calculated for both sexes and 95% confidence intervals were used to test for statistical differences.

Condition Factors

I calculated several additional indexes to assess the condition of Rosy Rockfish recently collected. Fulton's condition factor K_{Fulton} was calculated as a general measure of individual fish health.

$$K_{Fulton} = 100 * \frac{Total\ Weight\ (g)}{Total\ length^3\ (cm)}$$

Larger values signified that a fish was heavy (and potentially had greater energy stores and fat reserves) for a given size. In addition, I calculated a closely related condition factor K_C that controls for changes in gonad weight throughout a reproductive season where:

$$K_C = 100 * \frac{Total\ Weight\ (g) - Gonad\ Weight\ (g)}{Total\ length^3\ (cm)}$$

K_C was included to make these data comparable with a previous study of southern California Rosy Rockfish (Love 1990). Gonad weights were not collected during the NMFS SCB hook-and-line survey and all contemporary comparisons used Fulton's condition K_{Fulton} . The gonadosomatic index was a proxy for reproductive potential of mature Rosy Rockfish at time of capture, which represented the gonad weight standardized by fish weight (de Vlaming 1982). The equation for GSI is:

$$GSI = 100 * \frac{Ovary\ Weight\ (g)}{Body\ Weight\ (g)}$$

Climate Analysis

In order to investigate the possible environmental effects of oceanographic changes upon Rosy Rockfish life history traits, I accessed historical databases collected by the California Cooperative Oceanic Fisheries Investigations (CalCOFI 2015). Scripps Institution of Oceanography, NMFS, and CDFW have collaborated to conduct quarterly CalCOFI research cruises since 1949. The CalCOFI surveys utilize CTDs and provides information about ocean temperature at depths where Rosy Rockfish commonly occur. I used the CalCOFI database to investigate temporal changes in central California ocean temperatures at the depths Rosy Rockfish were collected (approximately 30-100 m). I filtered the CalCOFI data to include CTD casts between 30-100 meters as well as filtered the years between 1965-1983 and 1999-2014. I chose these two time periods as approximate years that most Rosy Rockfish in my samples would have grown up. CalCOFI CTD cast data was averaged to attain one temperature estimate per sample station per year.

I used the Pacific Decadal Oscillation (PDO) index as a proxy for oceanographic conditions along California's coast over the past four decades. The PDO is a Pacific basin-wide climactic event that oscillates between warm and cool phases, much like the El Niño Southern Oscillation, but with phase shifts lasting 20-30 years (Mantua et al. 1997, Hare and Mantua 2000). Cool phases of the PDO have benefited growth in several deeper dwelling species of rockfish (Black et al. 2005, 2008, Thompson and Hannah 2010). Historical monthly averages of PDO values are maintained by University of Washington (<http://research.jisao.washington.edu/pdo>).

Fishing Pressure

In order to investigate the possible effects of changes in fishing pressure on rosy rockfish life history and demography, I obtained historical estimates of Rosy Rockfish landings from the PacFIN and RecFIN databases, which contain information on estimated commercial and recreational landings since 1980. Estimates of total catch are extrapolated from observed landings; therefore, total catch estimates can vary between data sources based on the algorithm used (Bob Leos, *pers comm*, Groundfish Management Team, California Department of Fish and Wildlife, 20 Lower Ragsdale Dr. Monterey, CA 93940). Until recently, processors were not required to differentiate between rockfish species and reported Rosy Rockfish catch was likely 'hidden' in market categories such as 'red' and 'unidentified' rockfish categories (Bob Leos, *pers comm*, Groundfish Management Team, California Department of Fish and Wildlife, 20 Lower Ragsdale Dr. Monterey, CA 93940).

RESULTS

Summary of Samples

Between 2012-14, I retained a total of 272 Rosy Rockfish from Cordell Bank, Farallon Islands, and Half Moon Bay and used 259 individuals for analysis (Fig.1, Table 2). I collected an additional 45 Rosy Rockfish from Monterey Bay. NMFS in southern California provided 436 otoliths and I subsampled 250 individuals between 2004 and 2014 (Fig.2, Table 2). Rosy Rockfish collected during the 1980s NMFS dockside-sampling program were retained with inconsistent biological information; I excluded otoliths missing corresponding sex and length data and used a total of 184 otoliths from 1980-83 (Fig.1, Table 2).

The mean fork length (FL) of Rosy Rockfish collected during the 2012-14 RCA-Project, excluding fish collected in Monterey Bay, was 208.5 mm (± 1.7 SE), whereas FL averaged 138.1 mm (± 3.3 SE) in Monterey. The latter were specifically targeted for their smaller sizes. Rosy Rockfish collected in the Santa Cruz region from 2001-05 and in the broader central California region from 1980-83 had a mean FL of 211.8 mm (± 2.4 SE) and 245.8 mm (± 1.8 SE) respectively. The subsample of Rosy Rockfish from southern California had a mean FL of 212.7 mm (± 1.5 SE).

Table 2: Summary of Rosy Rockfish collections used during this project by time period including fork length (FL). Latitudes for 1980s Rosy Rockfish are based on CDFW sample block locations and should be considered approximate. Southern California Bight (SCB) was divided into a northern and southern region. All fish were caught using hook and line fishing gear.

	Years	N	Min FL (mm)	Max FL (mm)	Min Lat (°N)	Max Lat (°N)
Central California						
	1980-83	184	188	318	36.2	38.6
	2001-05	98	162	281	36.59250	36.99680
	2012-14	305	98	300	36.64527	38.05202
Southern California						
SCB North	2004-14	81	135	262	33.21988	34.48432
SCB South	2004-14	169	135	270	32.08722	33.46355

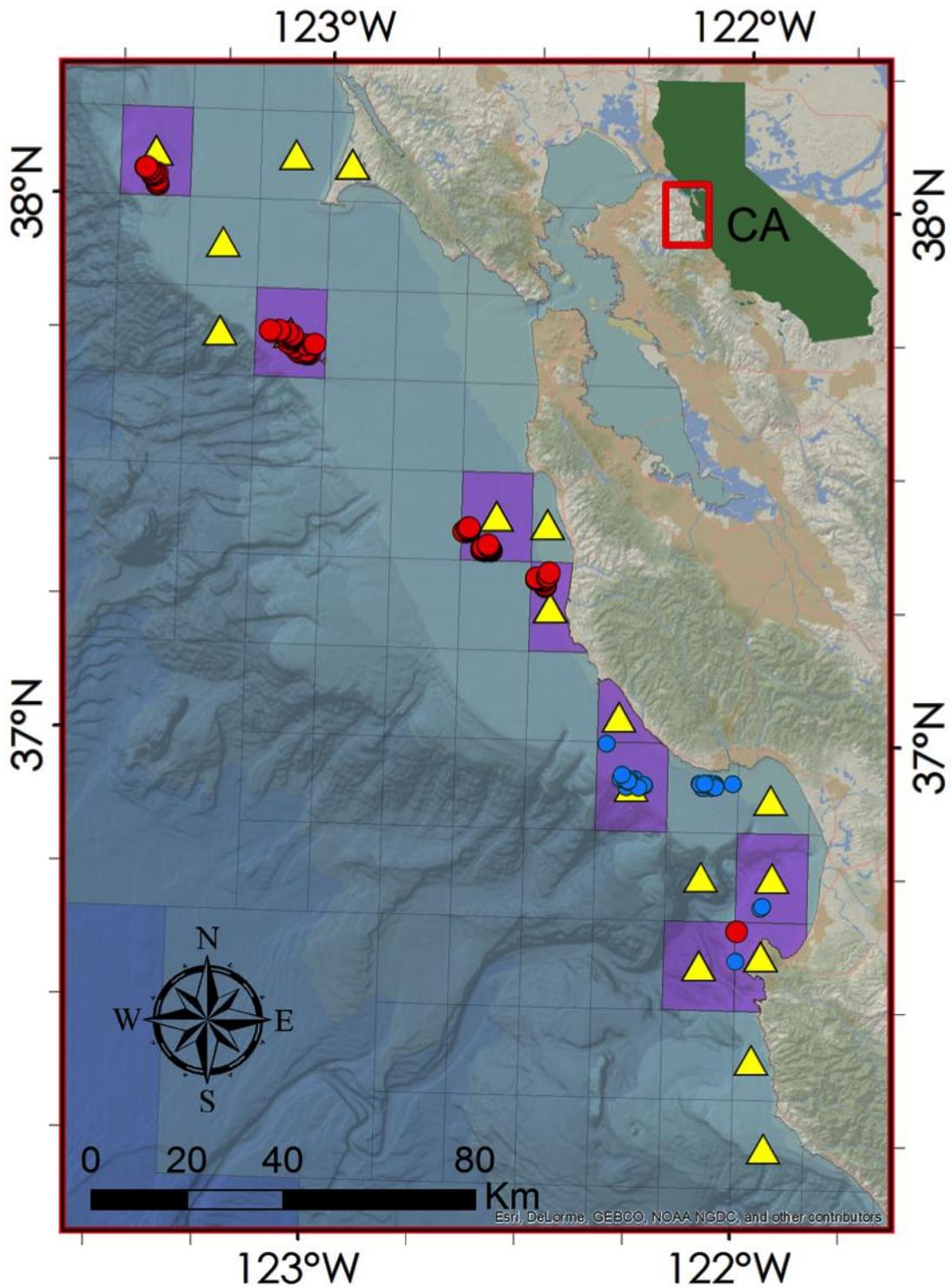


Figure 1. Rosy Rockfish collection locations in the Central California study area. Gold triangles denote CDFW sample blocks where Rosy Rockfish were caught during 1980-83. Red circles denote Rosy Rockfish collected during 2012-14 and blue circles denote NMFS collections during 2001-05. CDFW blocks are highlighted in purple to note areas of sample overlap between 1980-83 and 2000-10s sampling.

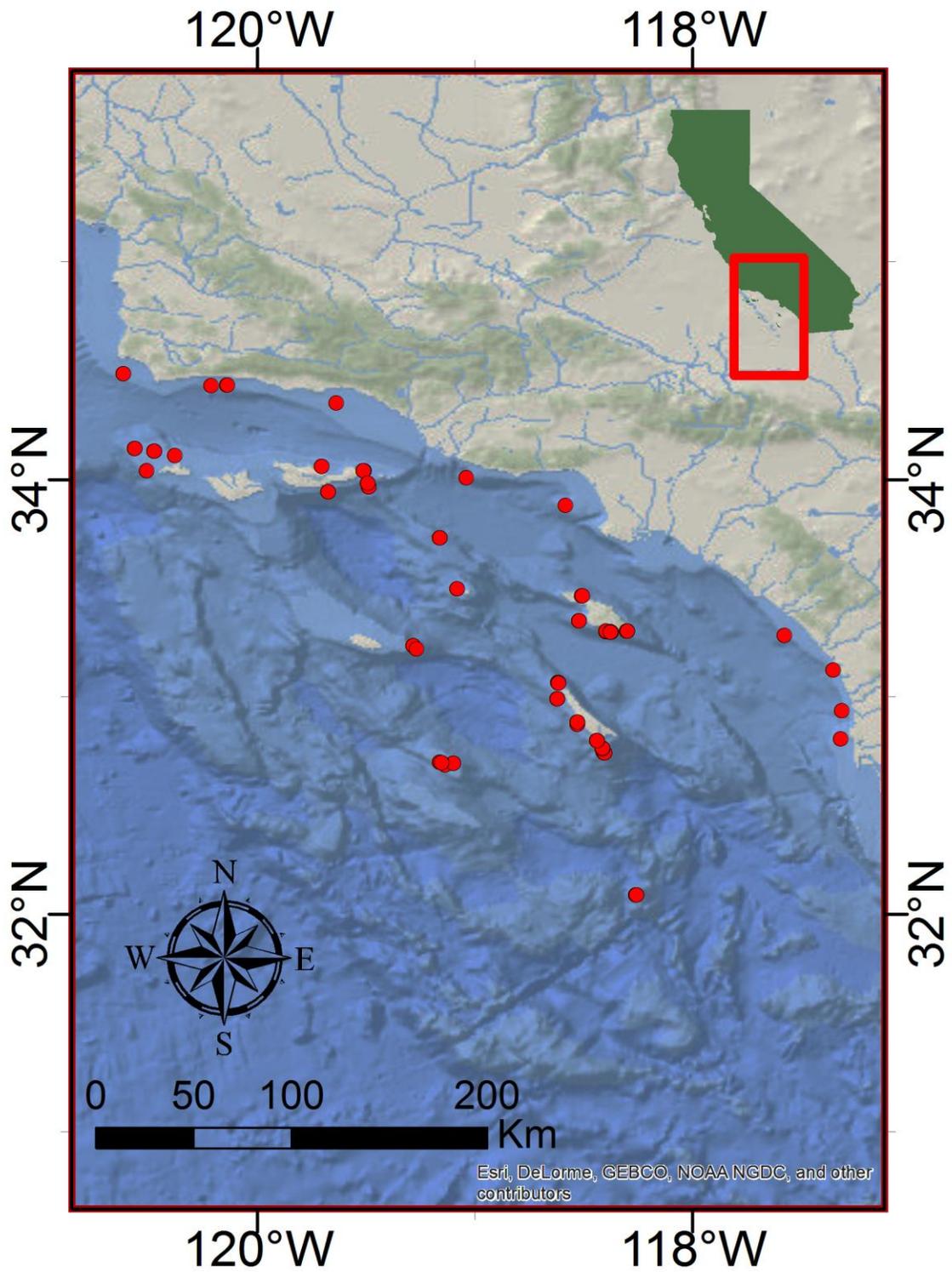


Figure 2. Locations of Rosy Rockfish collections in the Southern California Bight study area between 2004-14.

Age estimate bias

I used a total of 837 otoliths from central and southern California in the age and growth analysis (Table 2). Numerous checks were present during the first few years of otolith growth as well as during the transition zone, the age range which a fish transitions to maturity. I primarily used the dorsal axis to estimate Rosy Rockfish age, as other otolith axes were difficult to interpret (Fig. 3).

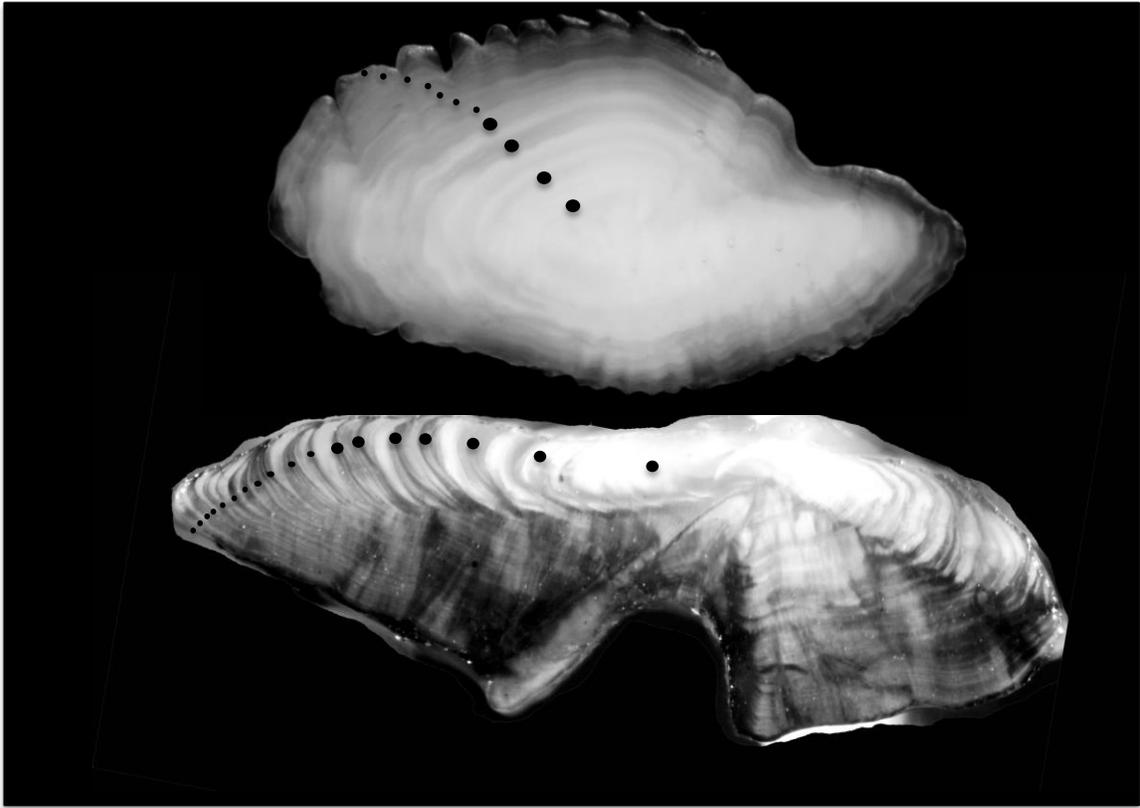


Figure 3. Whole otolith (top) and break and burn (bottom) comparison using the same fish (Sample R243) – a 277 mm male Rosy Rockfish collected at the Farallon Islands in October 2014. Estimated annuli for the whole otolith (11) and break and burn section (18-19) are overlaid with black circles.

Comparing my first two age estimates with those of my second reader (Don Pearson), the CV for age estimates ranged between 14.2-19.5% and 16.5-20.8% for the 1980s and 2012-14 central California Rosy Rockfish collection (Fig. 4 a-c). I aged southern California Rosy Rockfish without a second reader and the CV for the first three age estimates ranged between 13.7-14.5%. The most significant disagreements between readers were in age-classes older than 20 yr.

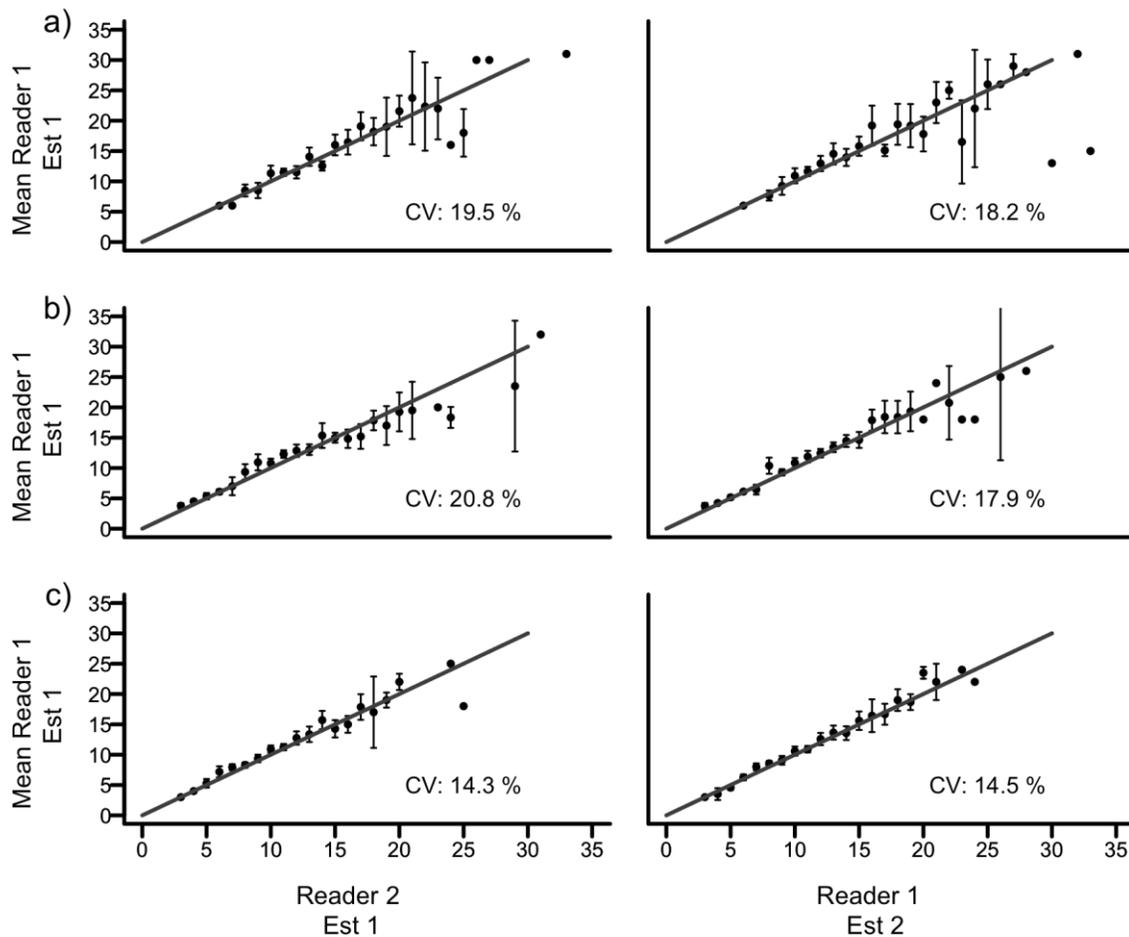


Figure 4. Mean age estimates (\pm SE) by one reader compared against subsequent age estimates for three populations: a) Central California 1980-83, b) Central California 2012-14, and c) Southern California 2004-14. Note that author produced all three age estimates for the Southern California population.

I aged 76 otoliths using surface reading techniques to determine the potential bias of using whole otoliths to estimate Rosy Rockfish age compared with break and burn. Rosy Rockfish. VBGF parameter L_{inf} was 20.2 mm greater and the growth coefficient K was 0.06 smaller when using surface ageing techniques compared to break and burn. Kimura's (1980) 95% maximum likelihood intervals revealed there was not a significant difference in either growth rate K or L_{inf} between the two techniques. Using an age-bias plot, I determined that the discrepancy in ageing Rosy Rockfish using the two techniques increased as a function of age based on the break and burn estimate (Fig. 5a). Estimated ages were similar for young fish but the oldest age estimates were only read with the break and burn technique. Non-linear regression revealed mean surface-age estimates attained an asymptotic value of 13 years, whereas maximum ages for break and burn were around 30 years.

Thin sections were prepared from 26 Rosy Rockfish otoliths selected across a range of possible age classes to compare with the break and burn method. There was a strong relationship between age estimates derived from the two methods ($r^2 = 0.86$, $F_{1,24} = 145.7$, $p < 0.001$). Thin section age estimates were described by the equation:

$$T = 2.13 + 0.758 * B$$

where T was the thin section age estimate and B was the break and burn age estimate (Fig. 5b). The coefficient of variation among the first four age estimates ranged from 0%–19.1%. Many more marks were visible on thin-sectioned otoliths, making the distinction between annuli and checks difficult. Thin-sectioned otoliths produced younger age estimates for the oldest age classes of Rosy Rockfish, which was likely the result of being overly conservative. Without proper age validation, thin-sectioned Rosy Rockfish otoliths proved difficult to interpret consistently and the break and burn technique was determined most appropriate for this study.

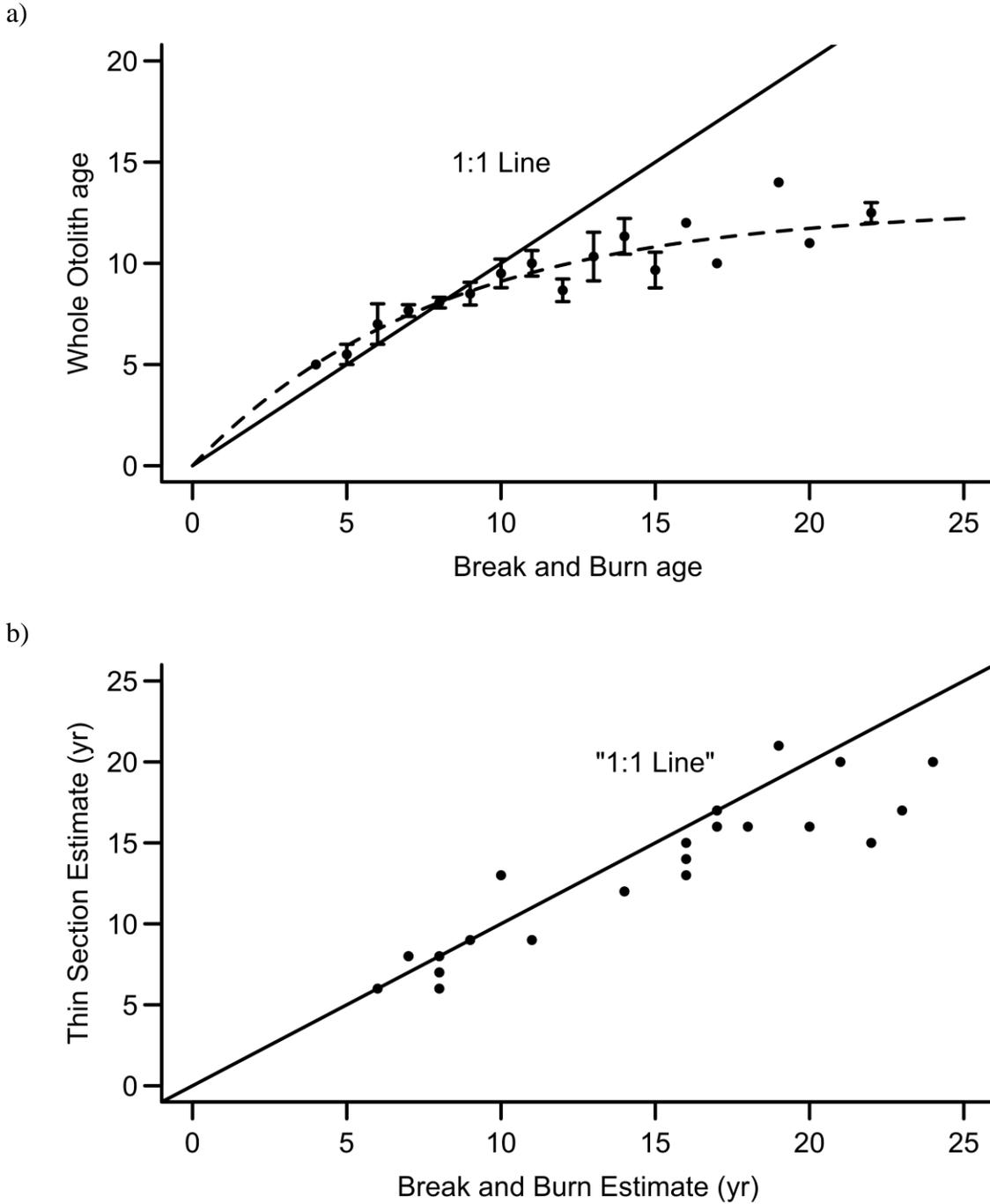


Figure 5. a) Relationship between mean surface-aged otolith and break and burn estimate of same fish (\pm SE). Logistic regression (dashed line) was fitted to relationship to show asymptotic age estimate from surface ageing: 13 yr. b) Relationship between thin-section and break and burn age estimates from same fish (Thin Section age = $2.13 + 0.76 * \text{Break and Burn age}$).

Temporal Comparison

Length frequency distributions of Rosy Rockfish differed significantly between 1980-83 and 2012-14 (Fig 6; $D= 0.562, p < 0.001$). Mean lengths were greater during 1980-83 ($245.8 \text{ mm} \pm 1.85 \text{ SE}$) than during 2012-14 ($208.5 \text{ mm} \pm 1.74 \text{ SE}$, Welch $t_{405.4} = 14.7, p < 0.001$).

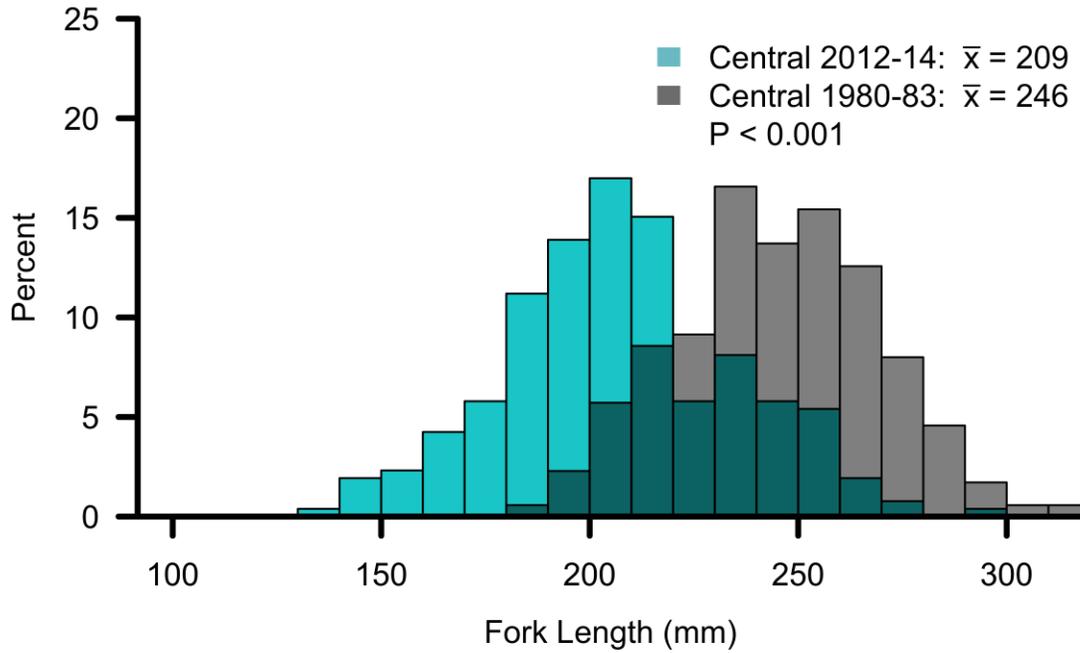


Figure 6. Length frequency distribution shown for central California Rosy Rockfish used in age and growth analysis with result from KS-test.

Growth

Significant changes in the VBGF growth parameters occurred over the past four decades (Fig. 7, Table 3). Rosy Rockfish collected in central California during 1980-83 had an asymptotic length (L_{inf}) of 256.0 mm (SD \pm 0.3.27) and growth coefficient K equal to 0.241 (SD \pm 0.02). In contrast, Central California Rosy Rockfish collected during 2012-14 had a lower L_{inf} of 225.0 (SD \pm 3.01 and K equal to 0.221 (SD \pm 0.01). 95% confidence intervals around growth parameters L_{inf} and K did not overlap (Fig. 7b), indicating that lifetimes growth curves were significantly different between the historical and current collections; the greatest difference between the two populations was in the asymptotic size

L_{inf} .

Table 3. Rosy Rockfish VBGF parameters L_{inf} , K , and t_0 and standard deviation (SD) within central California between the 1980-83 and 2012-14 sample groups.

Area	Year	N	L_{inf} (\pm SD)	K (\pm SD)	CV_{age}
Central California	1980-83	184	256.0 (3.27)	0.241 (0.02)	0.13
Central California	2012-14	296	225.0 (3.01)	0.221 (0.01)	0.12

Longevity and Survivorship

Longevity of Rosy rockfish was significantly greater for fish in the 1980-83 samples than the fish from the 2012-14 collections (Welch $t_{110,9} = -4.46$, $p < 0.001$). The 1980-83 population had displayed a mean maximum age of 20.3 yr (SE \pm 0.45), whereas mean maximum age was only 17.7 yr (SE \pm 0.36) for the central 2012-14 population (Fig. 8a). Maximum ages estimated for the 1980-83, and 2012-14 year groups were 32, and 30 yr, respectively. Total mortality (Z) was greater and survivorship was lower in the 2010s compared to the 1980s collections (ANCOVA: Age, $F_{1,25} = 215.36$, $p < 0.001$; Time Period, $F_{1,25} = 1.01$, $p = 0.33$; Age * Time Period, $F_{1,25} = 8.06$, $p = 0.009$; Fig. 8b).

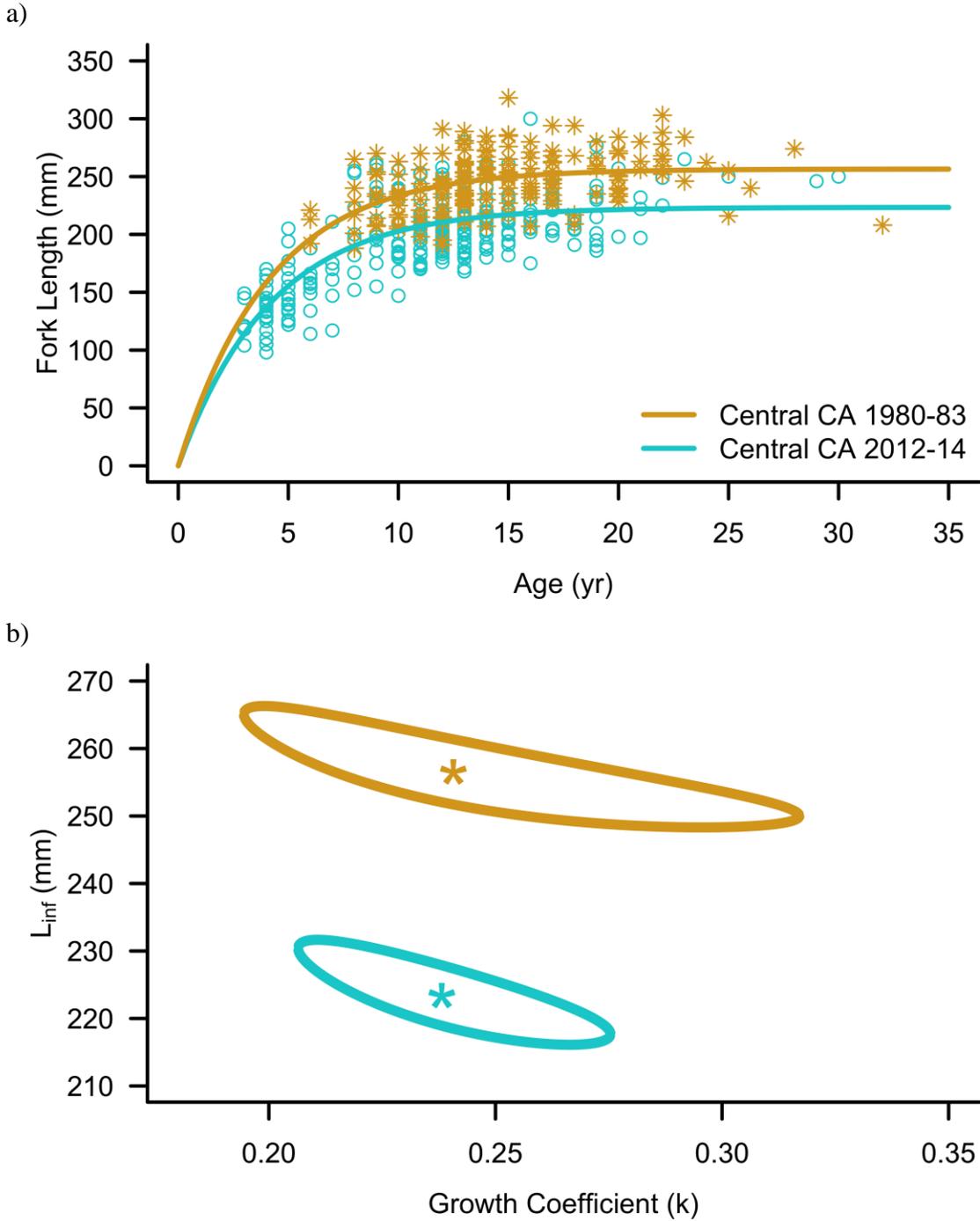
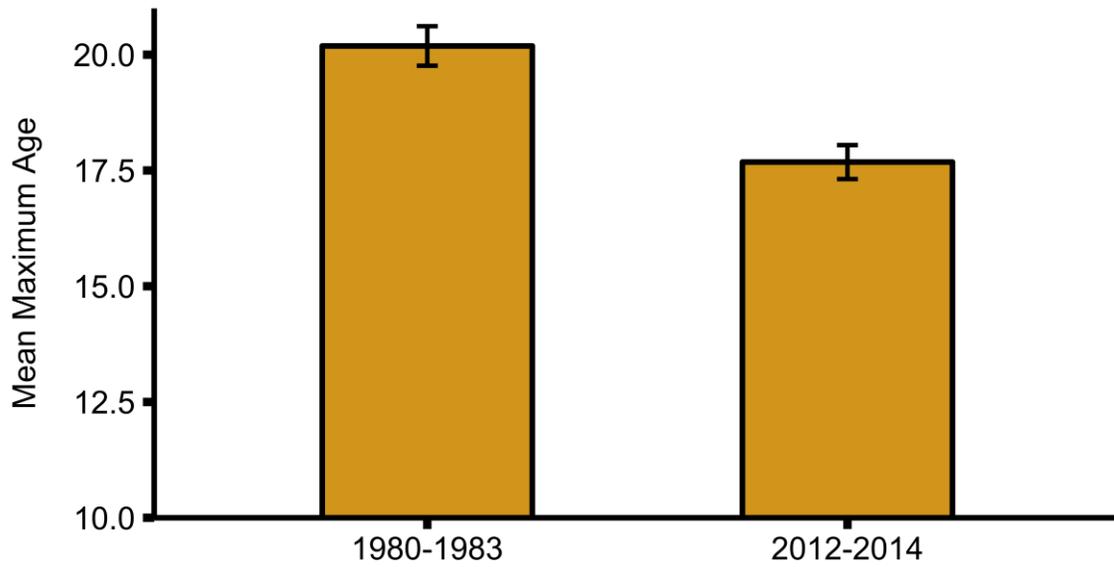


Figure 7. Central California Rosy Rockfish from the 1980-83 and 2012-14 collections. a) estimated age vs. fork length (mm) with VBGF growth function overlaid. b) 95% confidence intervals around VBGF estimates for L_{inf} and growth coefficient K (Kimura 1980).

a)



b)

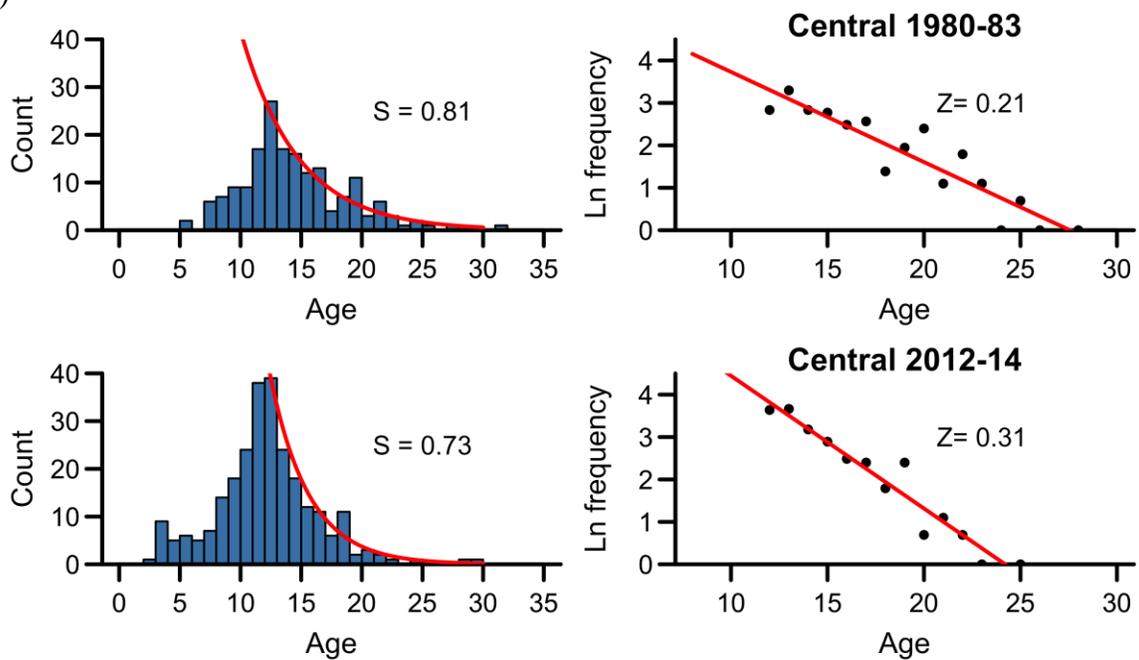


Figure 8. a) 1980-83 vs 2012-14 Central California Rosy Rockfish mean maximum age (\pm SE). b) Log-transformed counts of age estimates fitted with linear regression where slope is the instantaneous estimate of total mortality (Z), and survivorship (S).

Year Classes

The modal year classes were 1967 and 1999 for fish collected in central California between 1980-83 and 2012-14 respectively (Fig. 9). These peak years were used as guides to investigate environmental conditions during the early life stages of the Rosy Rockfish collected during both time periods.

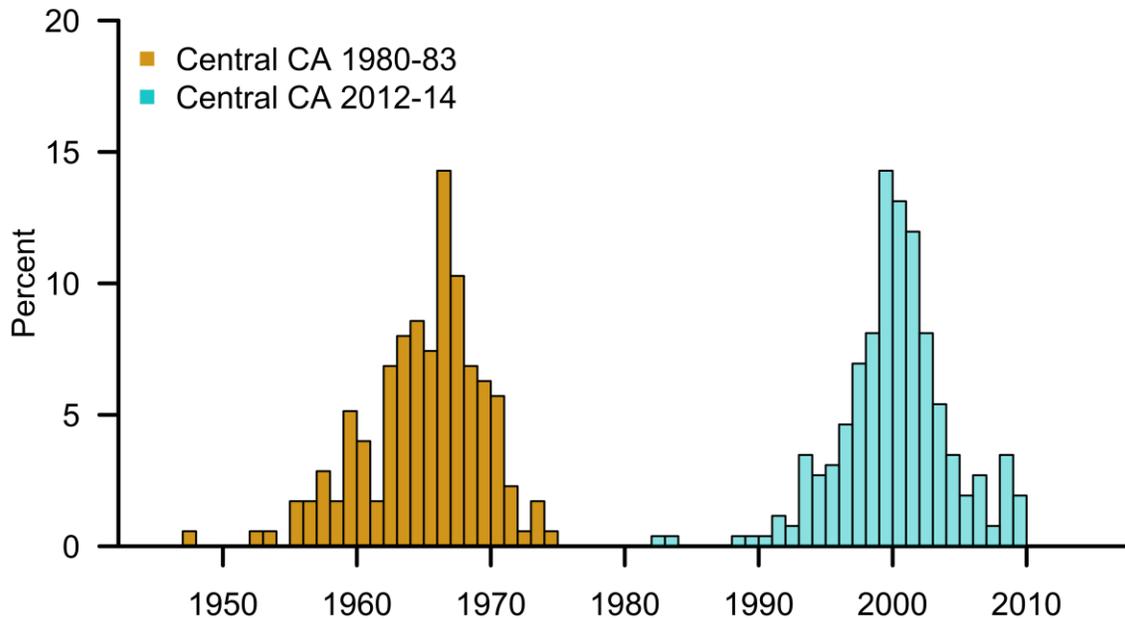


Figure 9. Rosy Rockfish year classes for central California 1980-83 and 2012-14 sample groups. Young Rosy Rockfish intentionally targeted from Monterey were excluded.

Environmental

The average temperatures between the depths of 30 -100 m and the years 1999-2014 were slightly cooler in central California than southern California (central CA, $10.50\text{ }^{\circ}\text{C} \pm 0.19\text{ SE}$; southern CA, $11.03\text{ }^{\circ}\text{C} \pm .07\text{ SE}$, Welch $t_{45.7} = -2.63$, $p = 0.012$). No differences were detected in mean temperature at these depths between 1965-1983 and 1999-2014, indicating that Rosy Rockfish did not experience a large shift in ocean temperature conditions between the time periods associated with the two temporal collections. Starting at peak year classes 1967 and 1999, I analyzed monthly PDO anomaly data to investigate

differences in environmental conditions between the two time periods. I examined the years 1965-1982 and 1999-2014 to capture the majority of time that the fish sampled were growing. There were no significant differences in PDO monthly anomalies (Welch $t_{352} = 0.452$, $p = 0.65$), indicating that Rosy Rockfish experienced similar PDO phases during development in the years preceding the two sampling periods (Fig. 10).

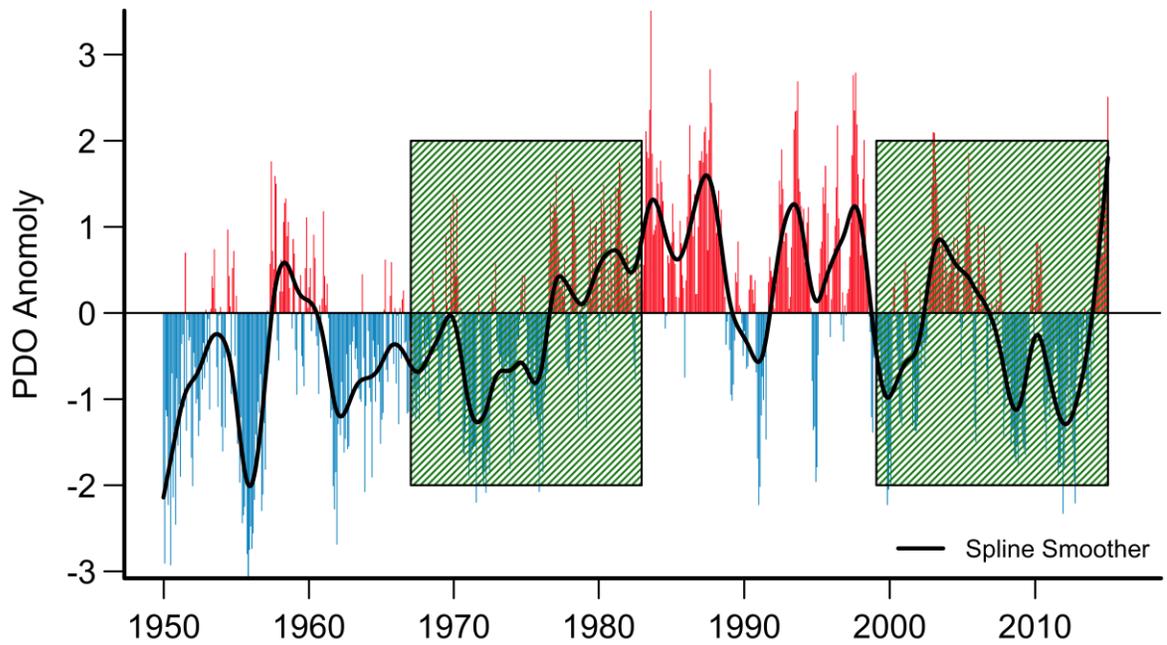


Figure 10. Monthly Pacific Decadal Oscillation (PDO) Anomalies (1950-2014) with smoothing spline. Hashed rectangles overlay 1967-1982 and 1999-2014, the years a majority of Rosy Rockfish samples were growing. Data obtained from '<http://research.jisao.washington.edu/pdo/PDO.latest>'.

Sex-Specific Comparison

KS-tests revealed significant differences in the length distributions between male and female Rosy Rockfish collected in central California during 2012-14 ($D = 0.196$, $p = 0.014$), with a greater proportion of smaller, mid-sized females being responsible for this result (Fig. 11a). Within the Central 2012-14 sample group, Half Moon Bay was the only subregion that exhibited significant differences between male and female length frequency distributions (Table 4; $D = 0.272$, $p = 0.010$). Sample size was similar for both sexes during this time period (males: $n = 133$, females: $n = 126$). Male mean length was significantly greater than females by 10 mm at Half Moon Bay (Welch $t_{138.5} = -2.87$, $p = 0.005$); however, there were no differences in sex-specific mean length among other areas sampled in 2012-14. There were also no differences in male and female Rosy Rockfish mean length in the Central 1980-83 samples nor the southern California 2004-14 samples; however, the Central 2001-05 samples from Santa Cruz did have slightly larger males (Welch $t_{85.4} = -2.10$, $p = 0.039$; Fig. 11b).

Table 4. KS-test results for sex-specific differences in Rosy Rockfish length-frequency distribution. KS-test statistic D and p -value are reported.

	Year	N_{Male}	N_{Female}	D	p-value
central California	1980-83	72	88	0.085	0.939
central California	2012-14	133	126	0.196	0.014
<i>Farallon Islands</i>	2012-14	42	46	0.169	0.560
<i>Half Moon Bay</i>	2012-14	80	64	0.272	0.010
Santa Cruz	2001-05	38	59	0.241	0.136
southern California	2004-14	132	118	0.079	0.834

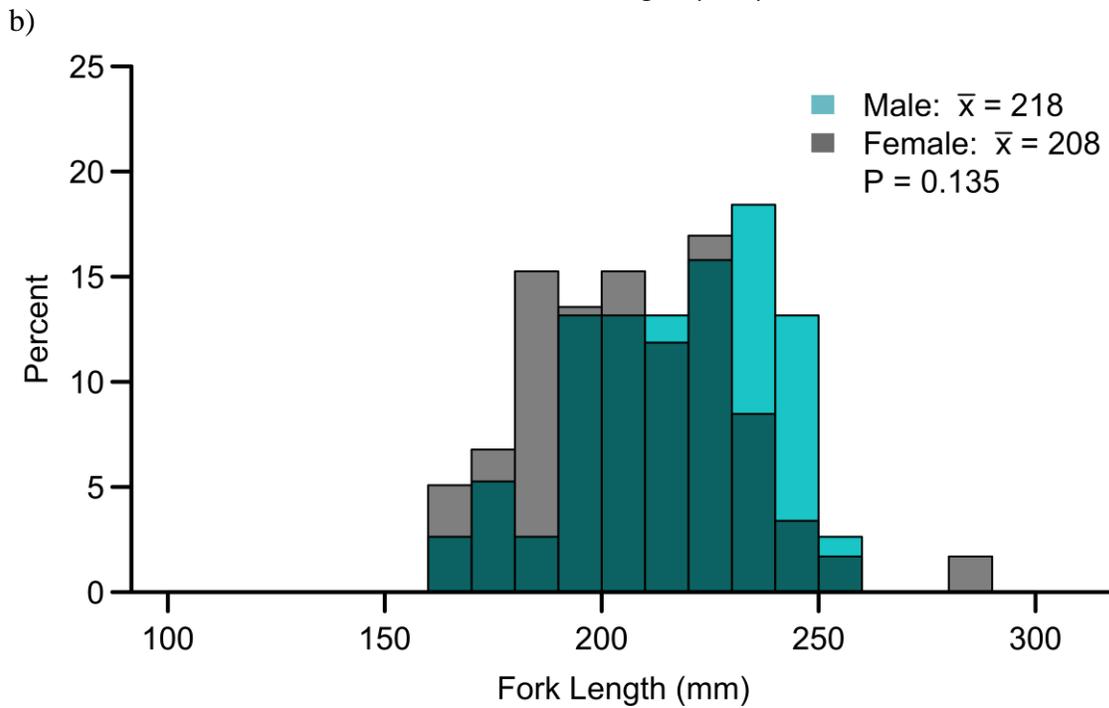
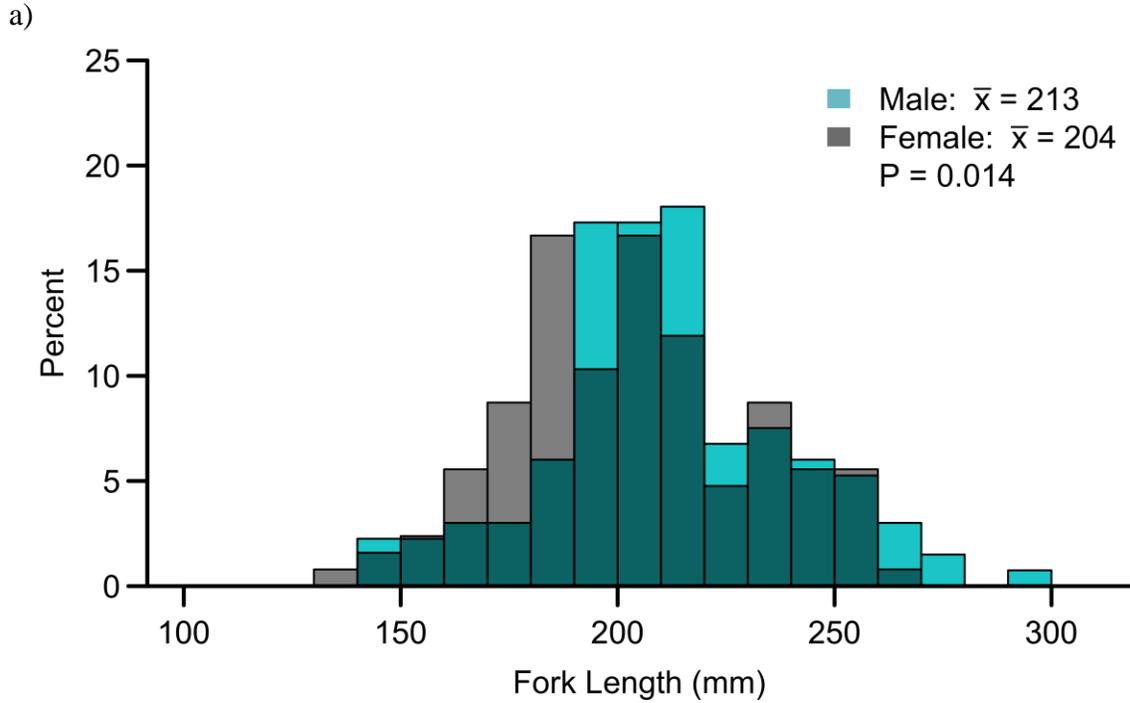


Figure 11. Sex-Specific length-frequency distributions for a) central California Rosy Rockfish (2012-14) and b) Santa Cruz region (2001-05). KS test p -values are displayed.

Growth

No significant differences were found between male and female Rosy Rockfish growth parameters L_{inf} and growth coefficient K among the sample groups (Fig. 12a-b, Table 5).

Female Rosy Rockfish tended to have larger L_{inf} in the central California 1980-83 and southern California 2008-14 sample groups, whereas males attained larger L_{inf} in the Santa Cruz 2001-05 and central California 2012-14 sample groups. Because these differences were insignificant, Rosy Rockfish data from 2001-14 were combined for further sex-specific analysis.

Table 5. Sex-specific VBGF growth parameters.

	Year	Female			Male		
		N	L_{inf}	K	N	L_{inf}	K
central California	1980-83	92	256.0	0.245	76	254.0	0.257
central California	2001-05	59	228.8	0.196	38	237.1	0.183
central California	2012-14	155	217.5	0.239	150	228.5	0.243
<i>Farallon Islands</i>	2012-14	46	229.9	0.286	42	246.7	0.237
<i>Half Moon Bay</i>	2012-14	64	204.1	0.308	80	215.5	0.309
southern California	2008-14	82	235.8	0.262	87	227.9	0.309
<i>SCB South</i>	2008-14	57	236.8	0.234	66	225.8	0.304
<i>SCB North</i>	2008-14	21	257.9	0.233	16	233.9	0.315

Longevity and Survivorship

Male Rosy Rockfish tended to live longer than females across the regions sampled (Fig. 13a). In the pooled central and southern California populations, male Rosy Rockfish longevity was 18.0 yr ($\pm .35$ SE), whereas female longevity was 16.5 yr (± 0.244 SE) (Welch $t_{155.6} = -3.51$, $p < .001$). Across the California coast, male Rosy Rockfish had lower instantaneous mortality rates (Z) and higher survivorship (S) compared to females (ANCOVA: Age, $F_{1,24} = 299.66$, $p < 0.001$; Sex, $F_{1,24} = 2.28$, $p = 0.14$; Age*Sex, $F_{1,24} = 5.49$, $p = 0.03$; Fig 13b)

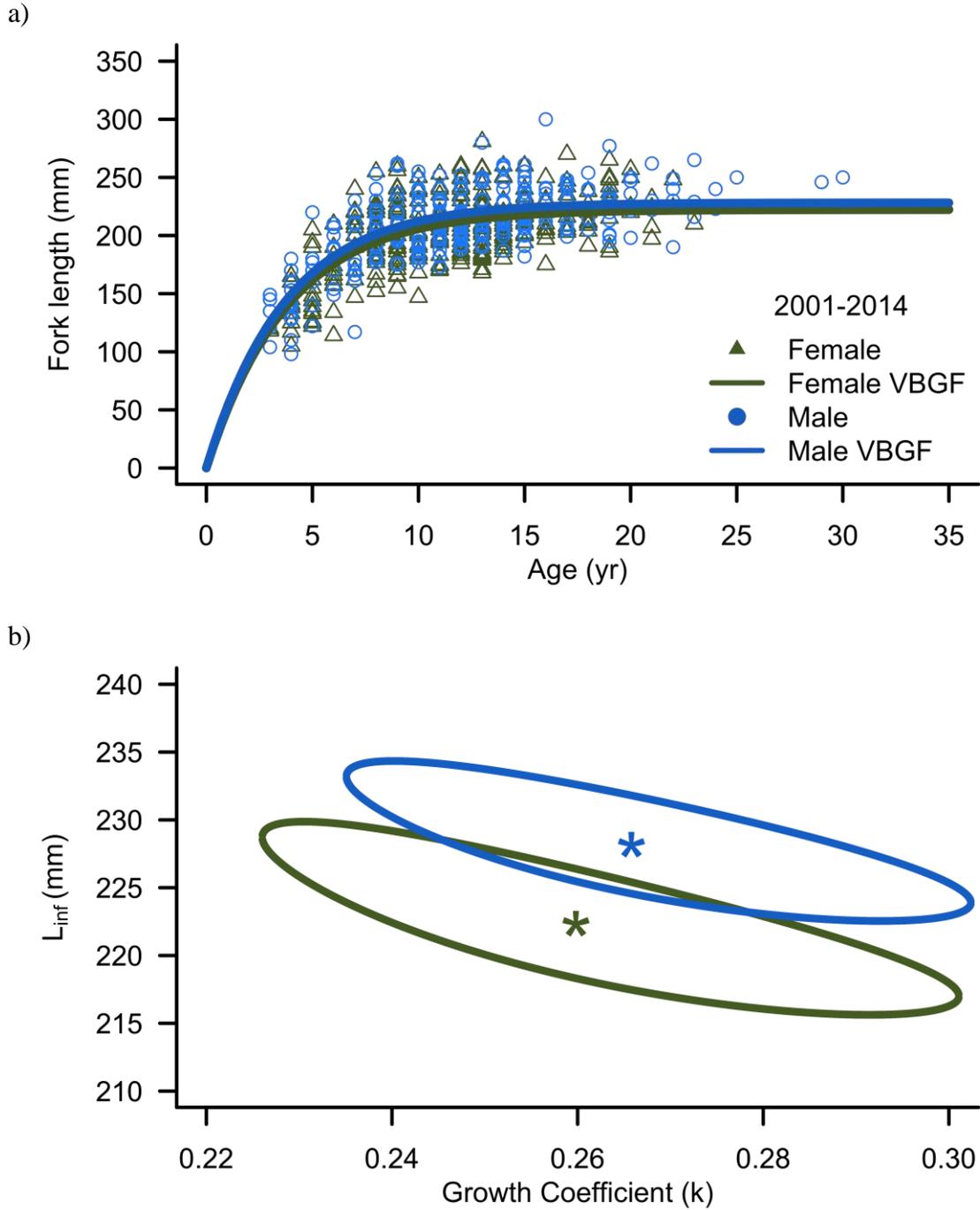
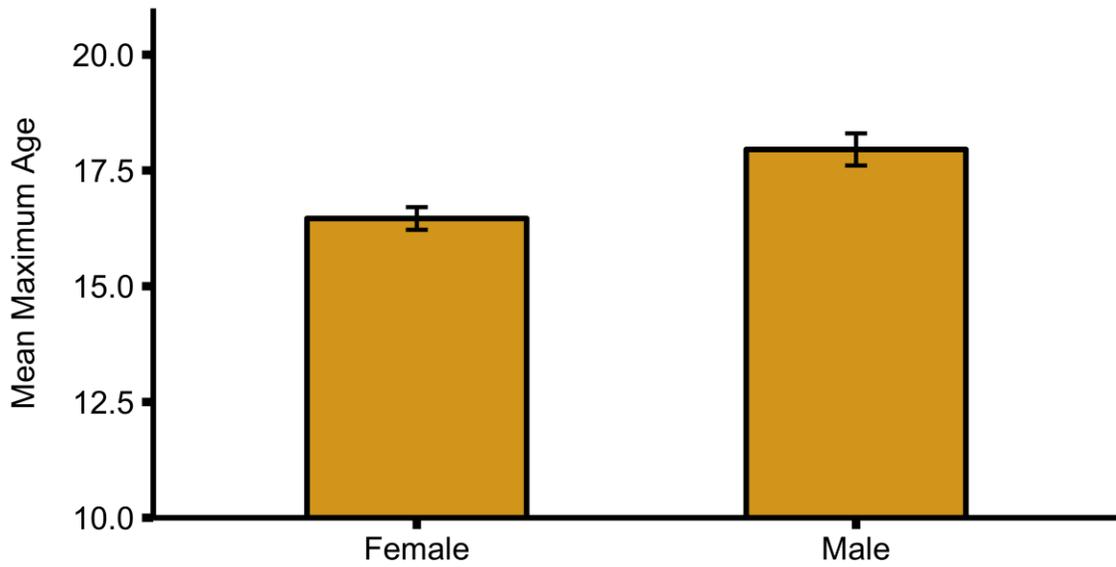


Figure 12. a) Sex-specific Rosy Rockfish lifetime growth curves for combined samples from 2001-14. Non-linear regression VBGF lines are overlaid. b) 95% confidence intervals for estimates of L_{inf} and growth coefficient K for male and female Rosy Rockfish.

a)



b)

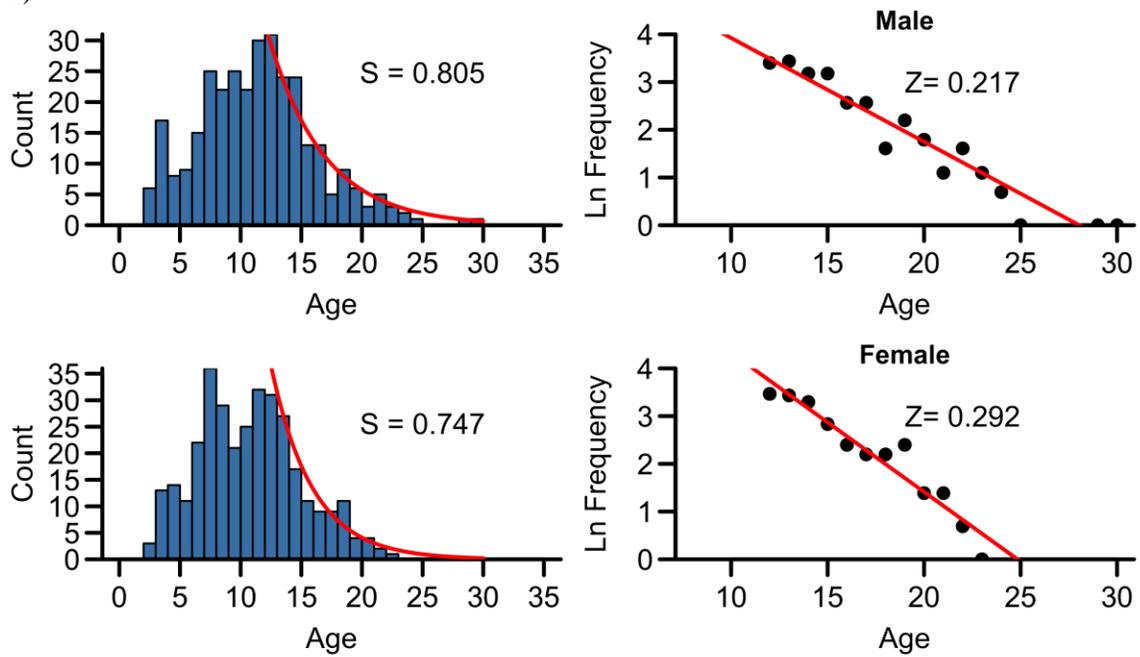


Figure 13. a) Mean maximum age (\pm SE) of Rosy Rockfish from central and southern California, 2001-14. b) Log-transformed counts of age estimates fitted with linear regression where slope is the instantaneous estimate of total mortality (Z) and survivorship (S).

Gonadosomatic Index

One hundred forty-eight central California female Rosy Rockfish were available for analysis of the gonadosomatic index (GSI) between January-May and August-December 2012-14; however, 82 of these fishes were collected in August, which resulted in uneven sample sizes across months (Fig 14a). GSI peaked for female Rosy Rockfish between February and April. GSI was reduced to a minimum during the months of August through December. GSI of male Rosy Rockfish peaked later during November and December (Fig 14b).

Across all months sampled, no sex-specific differences in condition factor (K_C) were detected in central California (2012-14) (Table 6, Welch $t_{320.3} = -1.20$, $p = 0.23$). Within each sex, condition factor K_C was significantly greater during December-May than June-November (Table 6; male, Welch $t_{52.6} = 4.52$, $p < 0.001$; female, Welch $t_{157.4} = 5.22$, $p < 0.001$).

Table 6. Condition factor (K_C) by sex and season. This study is compared with Love et al.'s 1990 publication from the Southern California Bight with sample size (N), standard deviation (SD), t-statistic (t), and p-value (P).

		Fields 2016					Love et al. 1990				
		N	K_C	SD	t _{df}	P	N	K_C	SD	t _{df}	P
<i>Male</i>											
	Dec-May	132	1.78	0.16	4.52 _{52.6}	< 0.001	129	1.62	0.13	2.00 _{NA}	0.045
	June-Nov	36	1.64	0.17			59	1.58	0.14		
<i>Female</i>											
	Dec-May	119	1.77	0.23	5.22 _{157.4}	< 0.001	124	1.61	0.14	-0.61 _{NA}	0.552
	June-Nov	50	1.63	0.12			69	1.62	0.16		
<i>All</i>											
<i>Seasons</i>	Male	168	1.75	0.17	-1.20 _{320.3}	0.230	188	1.61	0.14	-0.58 _{NA}	0.570
	Female	169	1.72	0.21			193	1.61	0.15		

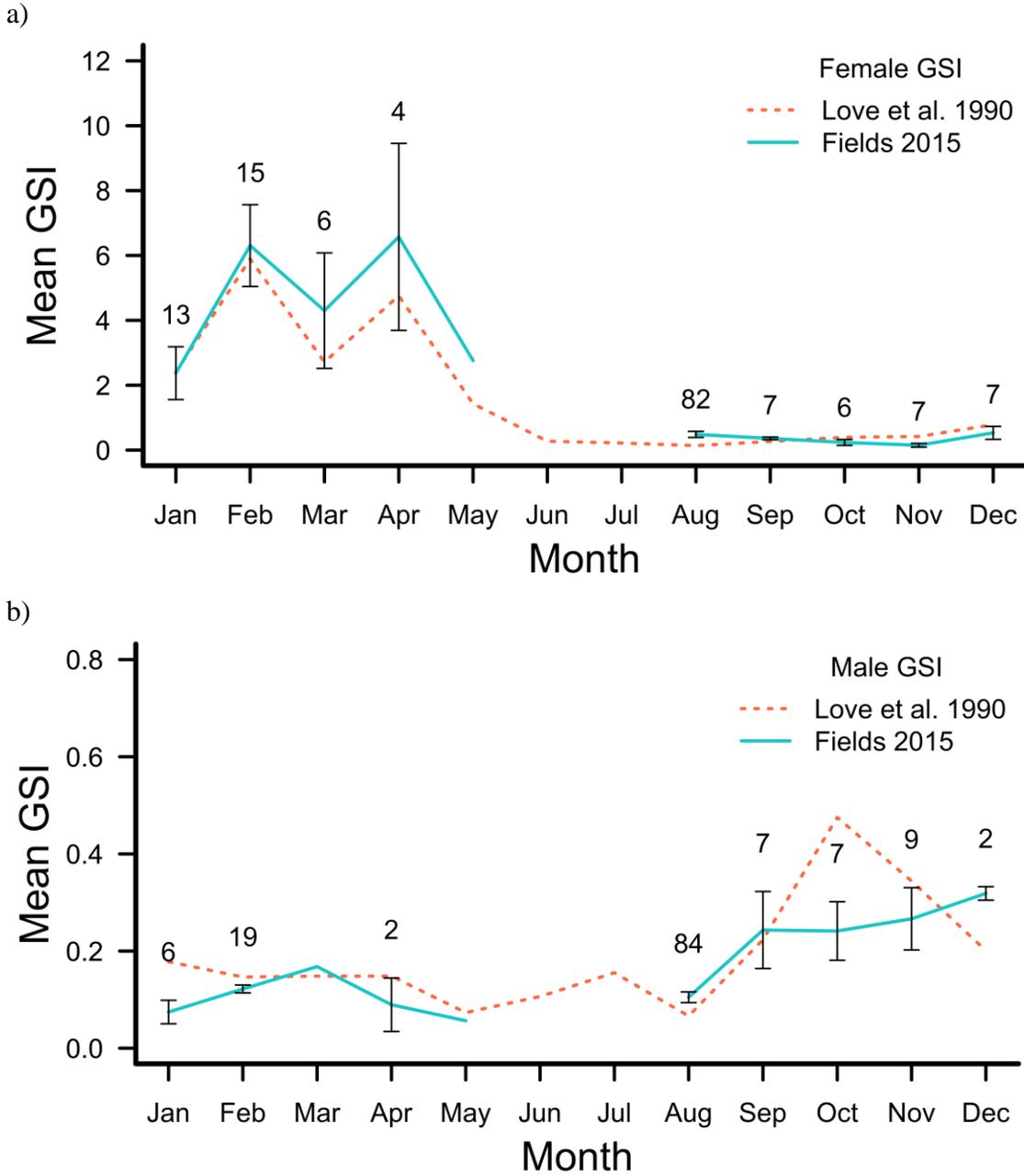


Figure 14. Mean GSI (\pm SE) for (a) female and (b) male Rosy Rockfish. Sample sizes from present study are displayed for each month. Note: Rosy Rockfish in Love et al. (1990) were collected in southern California, whereas Fields (2016) samples were collected in central California.

Length at Maturity

Maturity status (mature vs. immature) of 338 central California Rosy Rockfish were available for logistic regression and age and length-at-maturity analysis. One hundred fifty-four female and 149 male Rosy Rockfish were used in the analysis of length vs maturity (Table 7). The largest immature female was 171 mm fork length (FL), whereas the smallest mature female was 166 mm FL. The largest immature male was 211 mm FL, and the smallest mature male was 170 mm FL. Females were 50% mature at 166.8 mm FL whereas males were 50% mature at 177.1 mm FL (Table 8). Ninety-five percent confidence intervals overlapped between the sexes indicating that male and female Rosy Rockfish mature at the same size (Figure 15a). Combined, length at 50% maturity was 170.9 mm FL.

Table 7. Rosy Rockfish logistic regression coefficients a and b for fork length (mm) at maturity with standard error (SE). All r^2 values are Mcfadden's pseudo- r^2 .

	N	a	SE	b	SE	r^2	p-value
Female	154	-90.70	41.65	0.54	0.25	0.93	0.029
Male	149	-21.86	4.68	0.12	0.02	0.69	< 0.001
Combined	303	-24.34	3.81	0.14	0.02	0.74	<0.001

Table 8. Fork length at 1st, 50% and 100% maturity across three studies. Confidence intervals were unavailable from previous studies. Logistic regression was used for Fields' 2016 estimates and may not be directly comparable with previous studies.

		Love et al. 1990	Wyllie- Escheveria 1987		Fields 2016	
		FL (mm)	FL (mm)	FL (mm)	Lower 95% CI	Upper 95% CI
Male	1st	140	160	139.8	108.6	153.6
	50%	150	200	177.1	168.3	183.0
	100%	190	250	214.3	204.2	236.2
Female	1st	120	150	158.3	76.1	162.7
	50%	150	200	166.8	161.4	174.0
	100%	180	250	175.2	170.7	261.2

Age at Maturity

Age at maturity data were only available from samples collected during the 2012-14 RCA Project, as the NMFS annual Hook and Line survey in southern California does not record maturity status. One hundred forty-one female and 131 male Rosy Rockfish were used in the maturity logistic regression (Table 9). The youngest mature male and female Rosy Rockfish were 4 and 5 yr respectively. The oldest immature male and female Rosy Rockfish were 10 and 13 yr respectively, although it is likely that these individuals were in the resting phase, which makes it difficult to identify their true maturity status. Age at 50% maturity for both sexes was 8 yr and 95% confidence intervals overlapped, indicating no sex-specific differences (Fig. 15b, Table 10). The shapes of the maturity curves were similar between the sexes, indicating both sexes quickly transition into maturity.

Table 9. Rosy Rockfish logistic regression coefficients for age (yr) at maturity. All r^2 values are Mcfadden's pseudo- r^2 values calculated in JMP.

	N	<i>a</i>	SE	<i>b</i>	SE	r^2	p-value
Female	141	-7.11	1.41	0.94	0.17	0.72	<0.001
Male	131	-8.59	2.08	1.07	0.24	0.80	<0.001
Combined	172	-7.64	1.16	0.98	0.14	0.76	<0.001

Table 10. Age at 1st, 50% and 100% maturity across three studies. Confidence intervals were unavailable from previous studies. Logistic regression was used for Fields' 2016 estimates and may not be directly comparable with previous studies.

		Love et al. 1990	Wyllie- Escheveria 1987	Fields 2016		
		Age (yr)	Age (yr)	Age (yr)	Upper 95% CI	Lower 95% CI
Male	1st	–	4	4	-0.2	5.4
	50%	–	6	8	6.8	9.0
	100%	–	8	12	10.9	15.5
Female	1st	–	4	3	-0.4	4.3
	50%	–	6	8	6.6	8.5
	100%	–	8	12	11	15.2

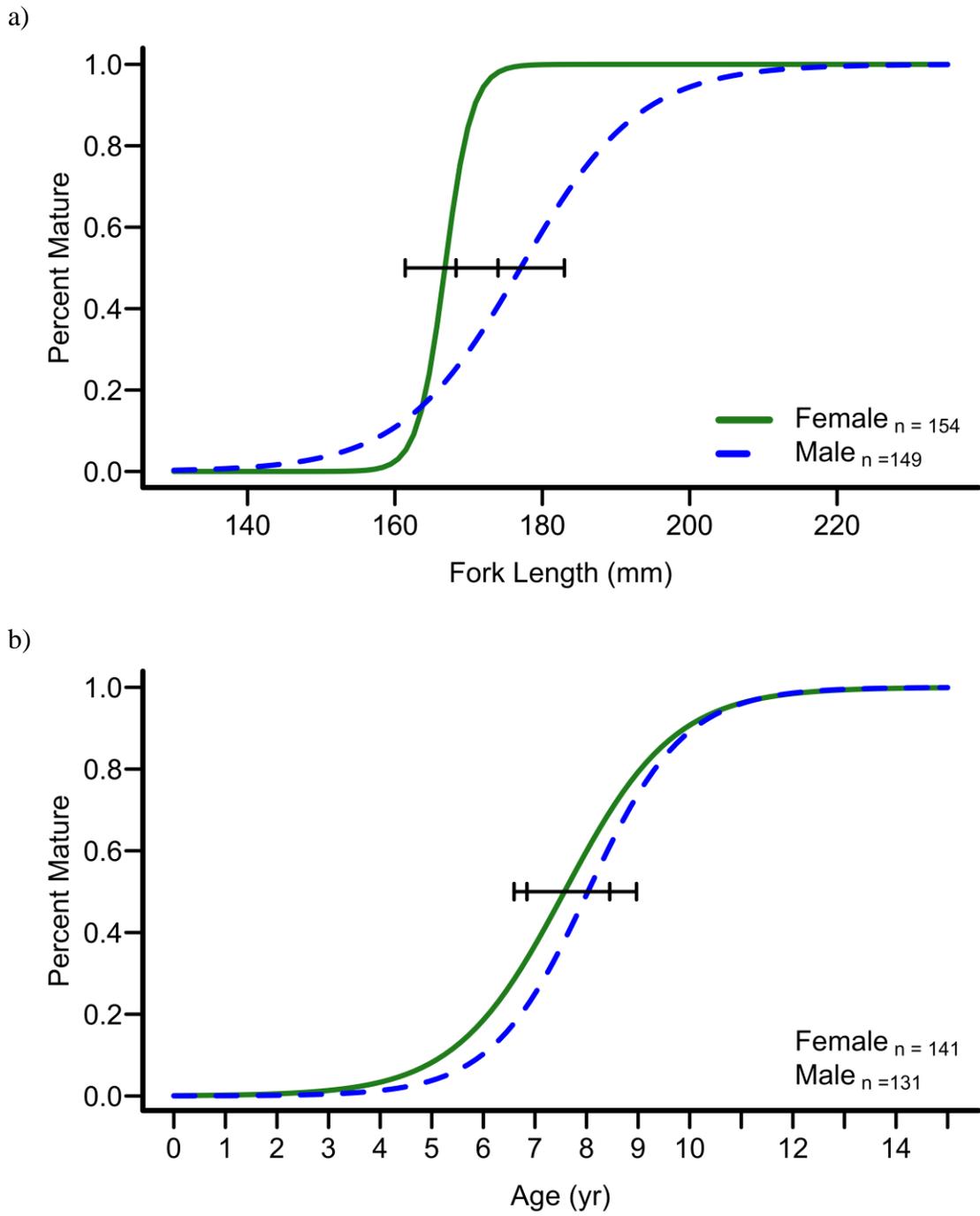


Figure 15. Rosy Rockfish (a) fork length (mm) and (b) age at maturity with 95% confidence intervals at 50% maturity.

Spatial Comparison

Length frequency distributions differed significantly between central and southern California, excluding small Monterey Rosy Rockfish ($D = 0.176$, $p = 0.004$, Fig. 16) Mean lengths, however, were not significantly between central and southern California Rosy Rockfish samples (Welch $t_{397.6} = -1.78$, $p = 0.08$).

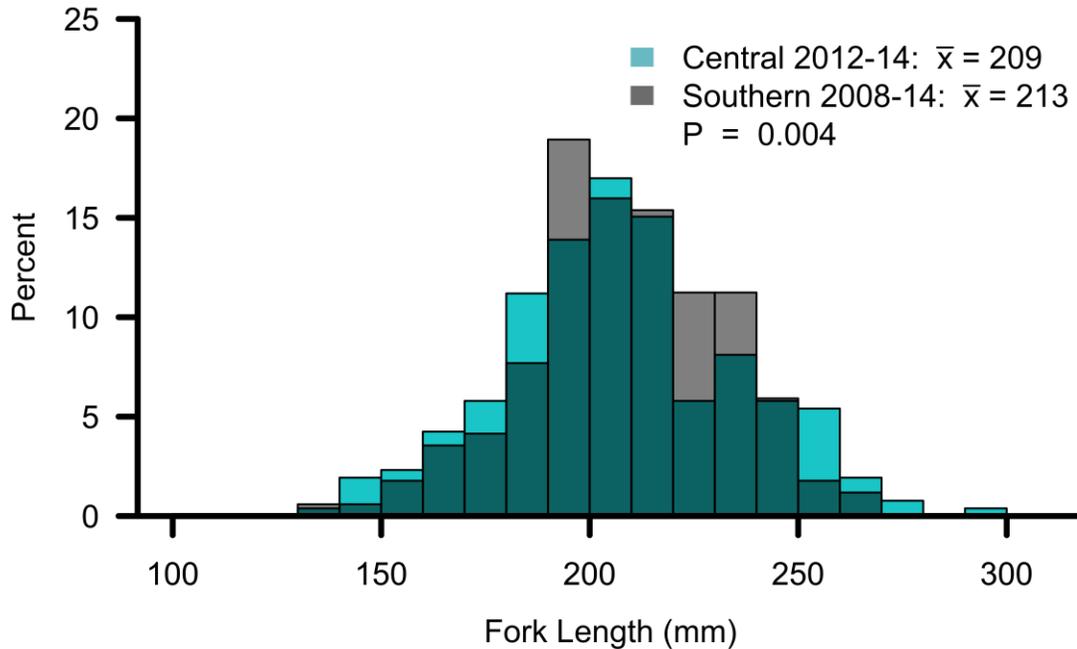


Figure 16. Length frequency distribution shown for central and southern California Rosy Rockfish used in age and growth analysis. P-value corresponds with KS-test result.

Growth

Rosy Rockfish exhibited significant variation in VBGF growth parameters between central and southern California collections (Fig 17 a-b, Table 11). Using random-effects modeling, the theoretical average maximum size, L_{inf} , was 225.0 mm (± 3.01 SD) in central California, and 231.9 mm (SD ± 2.93) in southern California. Growth coefficient K , was 0.221 (SD ± 0.01) in central California and 0.280 (SD ± 0.02) in southern California. 95% confidence intervals did not overlap between these two groups, indicating the lifetime growth

curves differ significantly between central and southern California populations, with a smaller K and larger L_{inf} in southern California. Sensitivity analysis suggested that the difference in growth coefficient K was likely due to the presence of smaller, younger Rosy Rockfish in central California, but the difference in L_{inf} remained stable.

Central California subregions exhibited unique VBGF parameters, suggesting small-scale spatial structure in life history traits (Fig. 18 a-b, Table 12). The Farallon Islands, Half Moon Bay and Santa Cruz all exhibited significantly different growth parameters of L_{inf} and K , as the 95% confidence intervals did not overlap. L_{inf} increased slightly with latitude from Santa Cruz to the Farallon Islands, however, growth coefficient K showed no such trend. L_{inf} was greatest at the Farallon Islands, whereas K was greatest at Half Moon Bay.

Table 11. Rosy Rockfish VBGF parameters L_{inf} , K , and t_0 and standard deviation (SD) in central and southern California.

Area	Year	N	L_{inf} (\pm SD)	K (\pm SD)	CV_{Age}
Central California	2012-14	296	225.0 (3.010)	0.221 (0.010)	0.12
Southern California	2008-14	170	231.9 (2.930)	0.280 (0.016)	0.15

Table 12. Rosy Rockfish VBGF parameters L_{inf} , K , and t_0 and standard deviation (SD) within central California subregions.

Area	Year	N	L_{inf} (\pm SD)	K (\pm SD)	CV_{age}
Santa Cruz	2001-05	98	233.3 (4.23)	0.187 (.014)	0.09
Half Moon Bay	2012-14	138	208.6 (1.84)	0.313 (.018)	0.11
Farallon Islands	2012-14	89	238.5 (6.64)	0.252 (.033)	0.11

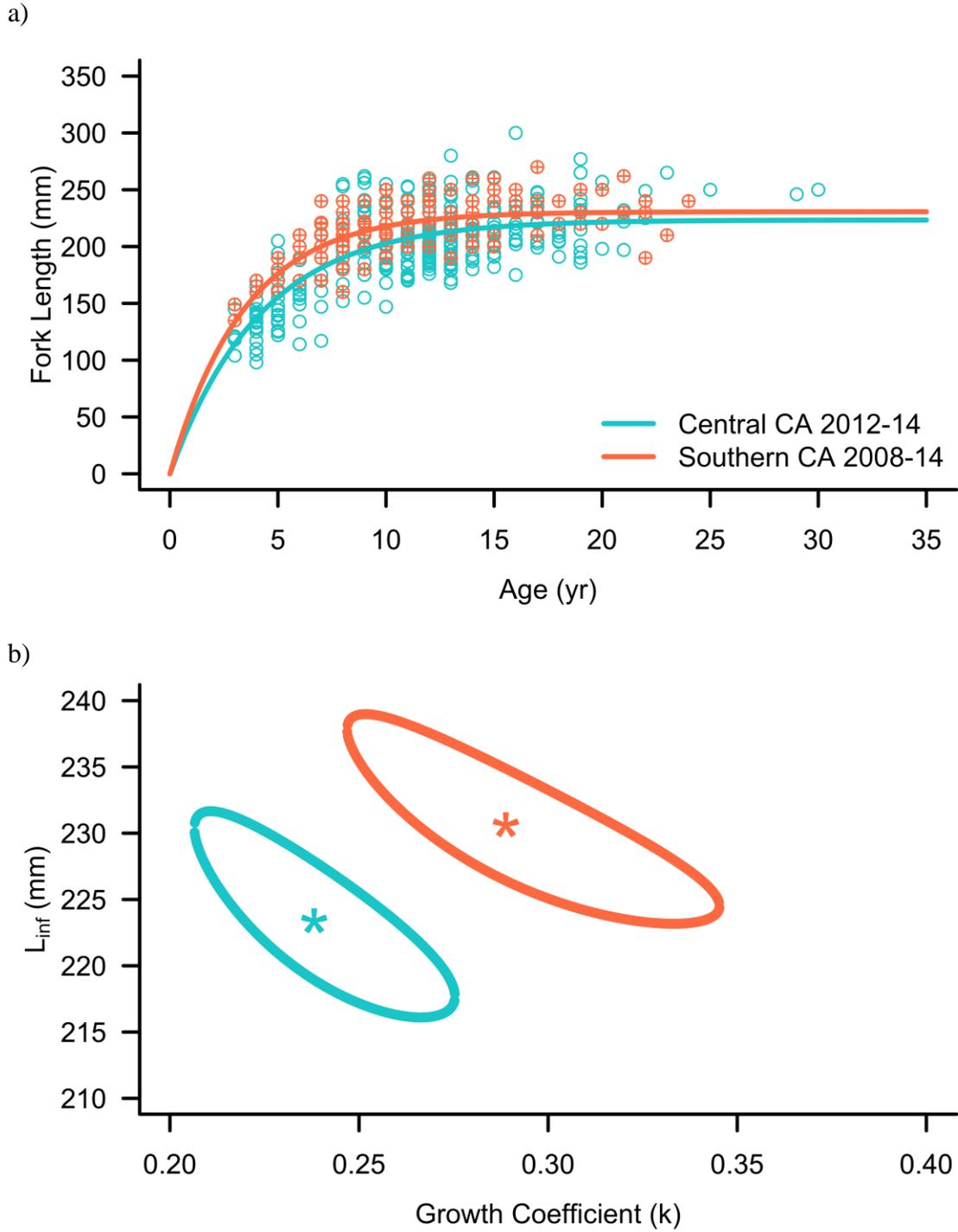
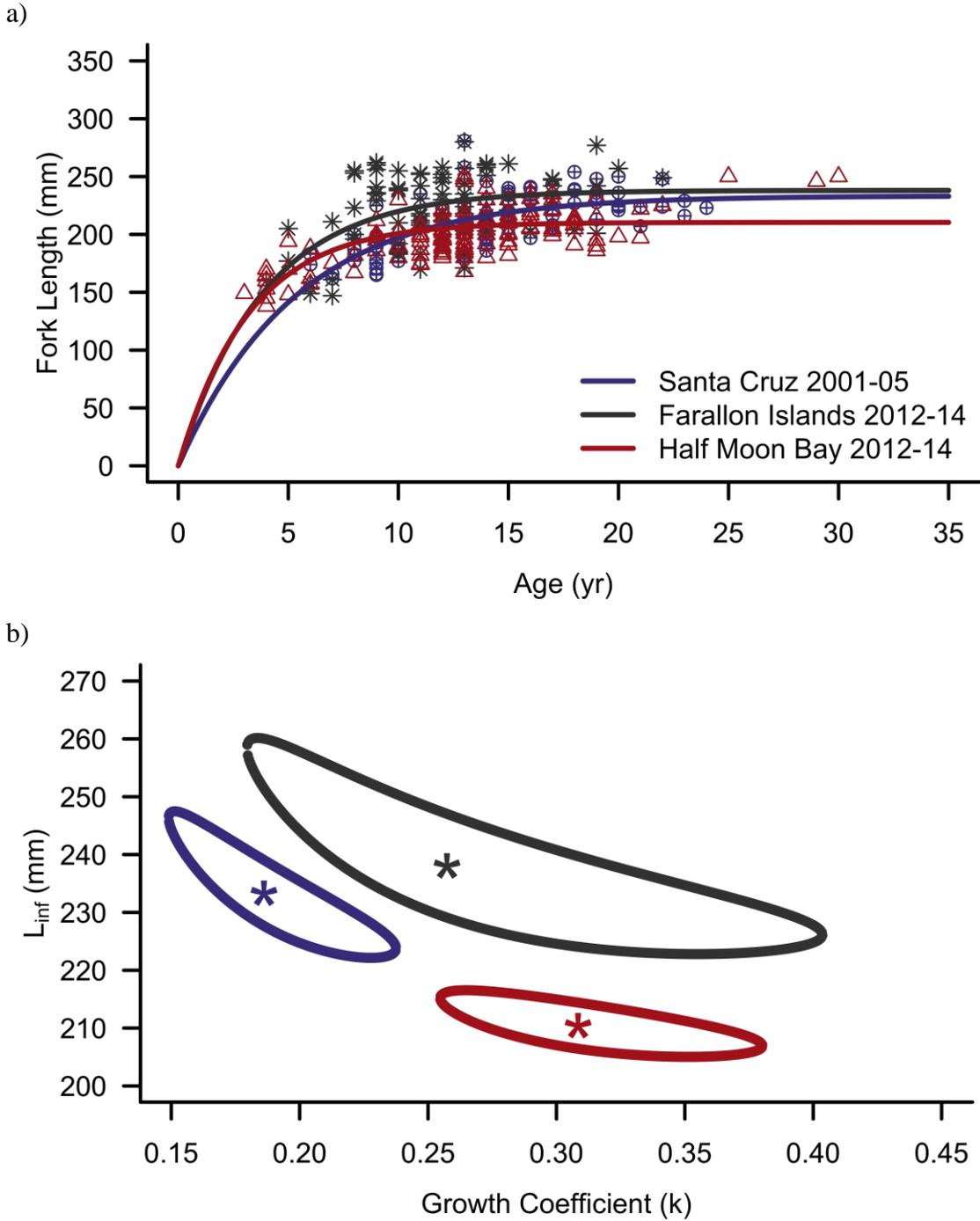


Figure 17. Central and southern California Rosy Rockfish: a) estimated age vs. fork length (mm). b) 95% confidence intervals around VBGF estimates for L_{inf} and growth coefficient K (Kimura 1980).



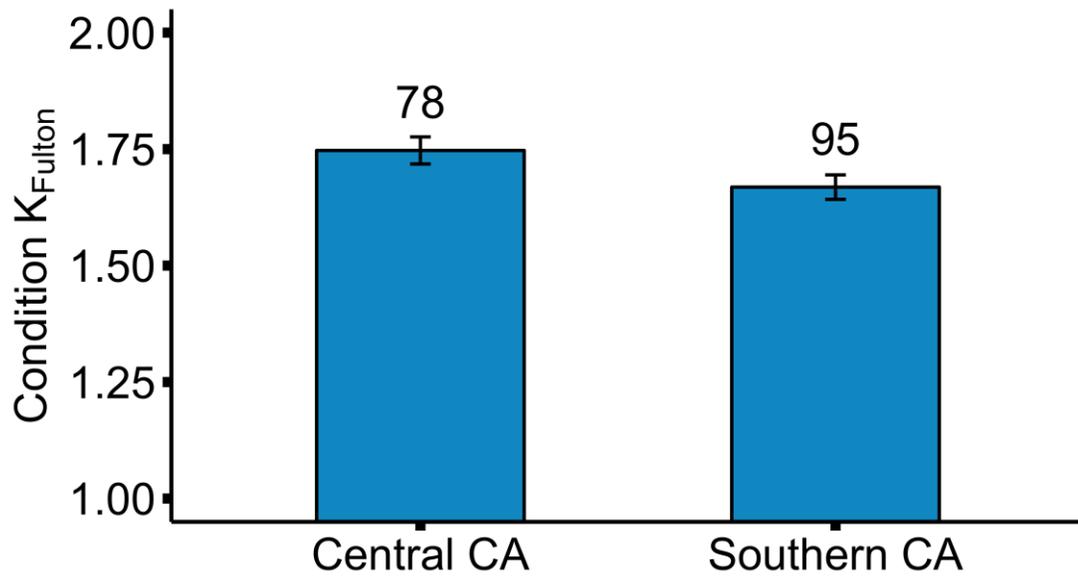


Figure 19. Fulton's condition K_{Fulton} with standard error (SE) between Rosy Rockfish in central and southern California. Samples were restricted to the months of September – November and the years 2011-2012 to control for season and year effects.

Condition, Longevity, and Survivorship

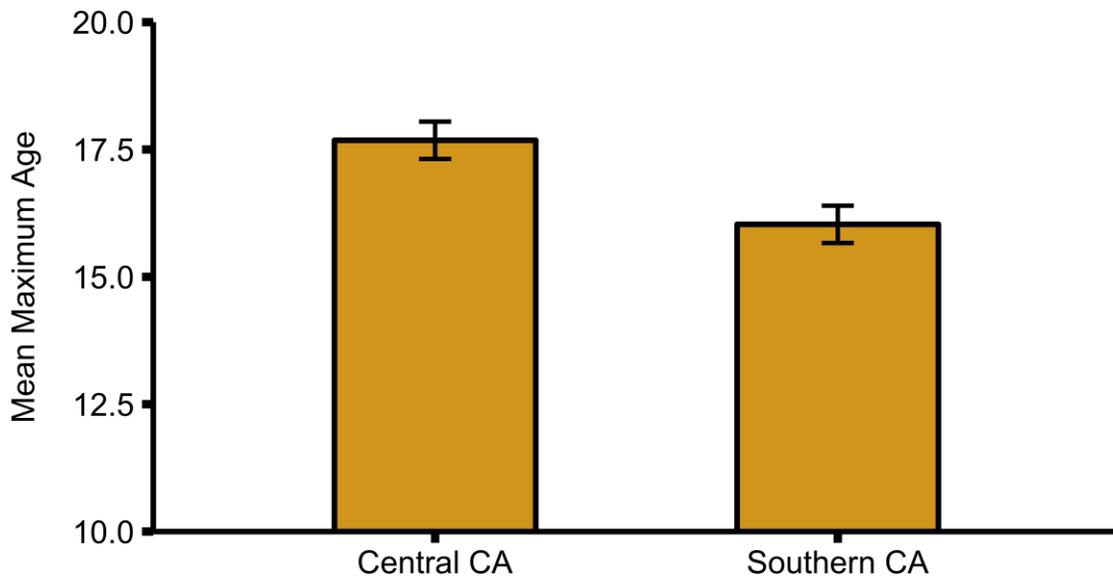
Fulton's condition, K_{Fulton} , was significantly lower in southern California compared to central California after controlling for possible season and year effects (Welch $t_{164.3} = 2.01$, $p = 0.046$, Fig. 19). Rosy Rockfish in central California exhibited greater longevity of 17.7 yr (± 0.37 SE) compared to southern California Rosy Rockfish (16.0 yr ± 0.37 SE, Welch $t_{131} = -3.18$, $p < 0.002$, Fig. 20a). Maximum age for central California 2012-14 was 30 yr, whereas in southern California the maximum age was 24 yr, despite similar sample sizes and sampling techniques. Total mortality was reduced and survivorship was greater in southern California compared with central California (ANCOVA: Age, $F_{1,22} = 240.50$, $p < 0.001$; Area, $F_{1,22} = 33.05$, $p < 0.001$; Age*Area, $F_{1,22} = 13.57$, $p = 0.001$; Fig. 20b).

Within central California subregions, there were also significant differences in mean longevity. Rosy Rockfish from the Farallon Islands had a longevity of 15.2 yr (± 0.45 SE), compared to 17.7 yr (± 0.49 SE) at Half Moon Bay and 19.3 yr (± 0.38 SE) in Santa Cruz – all three subregions were significantly different from one another (ANOVA, Subregion, $F_{2,105} = 17.1, p < 0.001$). Mean maximum age of Rosy Rockfish was 6.5 yr (± 0.30 SE) in Monterey Bay; however, these samples were not directly compared with other sites because sampling gear targeted smaller size and age classes. Rosy Rockfish from Cordell Bank were excluded from this analysis due to low sample size. There were no clear patterns or significant differences in survivorship and total mortality within central California subregions (ANCOVA: Age, $F_{1,29} = 83.37, p < 0.001$; Area, $F_{2,29} = 8.28, p = 0.001$; Age*Area, $F_{2,29} = 2.87, p = 0.073$; Table 13).

Table 13. Survivorship (S) and total mortality (Z) estimates within central California.

Region	Years	Z	S
Santa Cruz	2001-05	0.23	0.79
Half Moon Bay	2012-14	0.30	0.75
Farallon Islands	2012-14	0.26	0.77

a)



b)

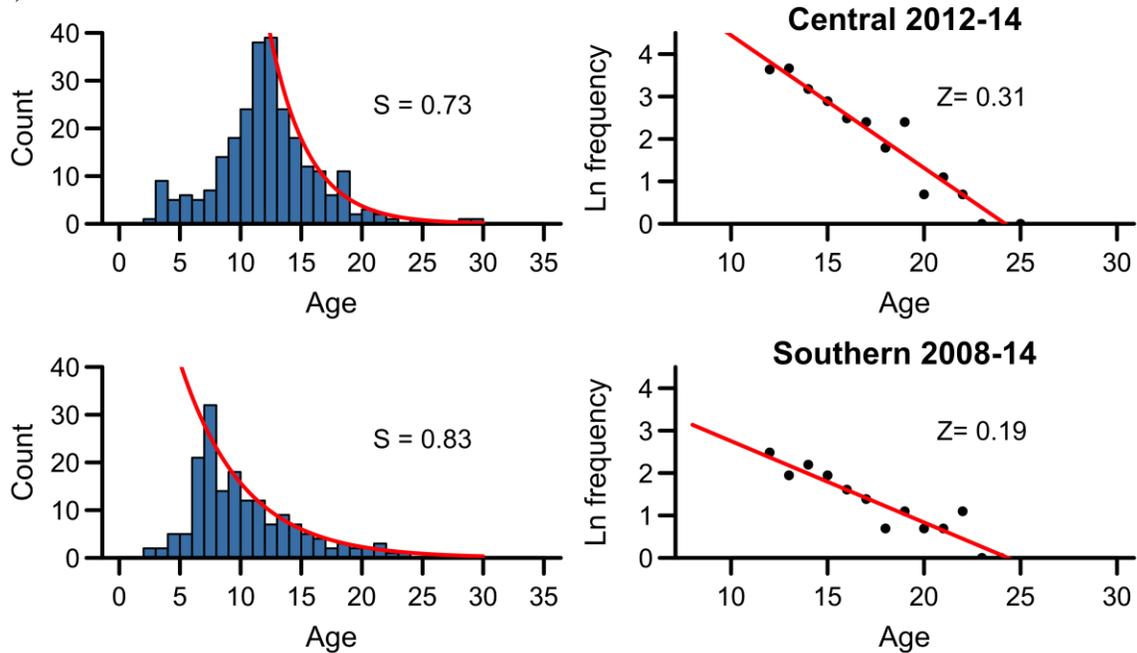


Figure 20. a) Central and southern California Rosy Rockfish mean maximum age (\pm SE). b) Log-transformed counts of age estimates fitted with linear regression where slope is the instantaneous estimate of total mortality (Z) and survivorship (S).

DISCUSSION

Ageing Rosy Rockfish

The use of bony structures to age fish has been a critical component of life history studies and fisheries management since the early twentieth century (Taylor 1914, Thompson 1916). Some of the earliest age estimation techniques, which included the use of scales and surface ageing of whole otoliths, led to an underestimation of fish ages, resulting in stock assessment models that were overly optimistic about the status of fish populations. Stock assessments that underestimated ages of fish caused an overestimate of total mortality and incorrectly estimated yield and production for long-lived fishes (Wilson and Boehlert 1990, Reeves 2003, Henríquez et al. 2016). For the past 30 years, surface ageing techniques have largely been retired in long-lived species in favor of more accurate otolith sectioning techniques (Beamish 1979, Chilton and Beamish 1982, Boehlert 1985, Leaman and Nagtegaal 1987). Nevertheless, validation of the annual periodicity in growth increments and the development of age estimation criteria continues to be a leading focus in otolith research (Campana 2005). Age estimates derived from accurate ageing techniques are therefore critical to meeting long-term sustainability objectives.

Surface-ageing of Rosy Rockfish otoliths indicated an average maximum age of 13 yr in this study, whereas the maximum age derived from the break and burn technique was 32 yr. The former age estimate is in agreement with previous studies which estimated Rosy Rockfish maximum age to be 13 yr in southern California and 14 yr in central California (Chen 1971, Lea et al. 1999). Both of these previous studies used whole otoliths to estimate ages and noted that Rosy Rockfish were a difficult species to estimate beyond age seven.

Lea et al. (1999) reported Rosy Rockfish attained $L_{inf} = 319$ mm fork length (FL) within central California between 1978-1985. From southern California, Chen (1971) reported $L_{inf} = 237$ mm FL, although his sampling was limited to Tanner Bank near the Channel Islands. Using the break and burn technique, I obtained smaller estimates of L_{inf} than when I used whole otoliths to estimate Rosy Rockfish age. A recent age and growth study of North Atlantic Wreckfish (*Polyprion americanus*) reported ages twice as old and L_{inf} estimates significantly lower than previous studies using thin sectioned otoliths (Lytton et al. 2015). Therefore, it is likely that the difference between my 1980s L_{inf} estimates compared to Lea et al. (1999) is partially due to the difference in ageing techniques.

Thin-sectioning can provide additional clarity in the interpretation of annuli for some species of fish (Beamish and Mcfarlane 2000, Stransky et al. 2005); however, break and burn remains the preferred production-ageing technique for groundfish species (MacLellan 1997, Matta and Kimura 2012). Within this study, thin sections did not improve precision among age estimates over the break and burn technique and age estimates were slightly younger using the break and burn technique; this is consistent with results reported by Stransky (2005) describing age and growth of two species of Atlantic rockfish (*S. marinus* and *S. mantilla*). It is likely that the differences in age estimates between break and burn and thin sectioning in my study were the result of being overly conservative in the presence of additional marks using thin sections.

Since the 1980s, it was accepted that sectioned otoliths yielded much older age estimates in long-lived species and validation of the annual periodicity in otolith growth increments was considered a critical step for accurate age estimates (Chilton and Beamish 1982, Campana 2001, Andrews et al. 2002, 2007). However, validation studies are often cost prohibitive and logistically difficult (Campana 2001). As a result, validation of annual

growth formation and strict ageing criteria have not been developed for Rosy Rockfish, although we assumed that annuli in this species represent similar growth increments as other validated species of rockfish. Rosy Rockfish are a difficult species to age and, until Rosy Rockfish age estimates can be formally validated and more rigorous ageing criteria developed, I decided to use the break and burn method to approximate Rosy Rockfish ages.

Detailed ageing criteria were recently published for Bocaccio (*Sebastes paucispinis*), another species of rockfish with notoriously difficult otolith growth patterns (Pearson et al. 2015). In that report, validation of the first annulus was well documented with detailed guidelines for consistently identifying checks and annuli during production ageing. However, even with strict ageing criteria, between-reader age estimates varied greatly within the oldest age classes, indicating that some species' age estimates have high levels of imprecision (Pearson 2004, Pearson et al. 2015).

Stricter ageing guidelines may increase Rosy Rockfish age estimate precision between multiple readers and make additional age-class analysis possible for this species. The increased number of potential growth marks seen in thin sections leaves open the possibility that validation will reveal Rosy Rockfish attain even older ages than estimated in my study. Nonetheless, the updated growth parameters and maximum age estimates from my study will likely prove valuable in future stock assessments for Rosy Rockfish and data poor management techniques such as productivity-susceptibility analysis.

Temporal Differences in Growth, Longevity, and Mortality

Temporal variability in fish life history traits due to shifts in oceanographic conditions, fishing intensity, and density-dependent interactions have been documented in numerous studies and occur over time scales of years to decades (Ricker 1981, Reznick 1990,

Ajiad et al. 1999, Law 2000). Understanding the nature and scale of temporal life history trait shifts is critical for effective fisheries management that relies on stock assessment model outputs to reconstruct historical fishing removals and estimate sustainable catch limits (Gertseva and Cope 2011). While some studies described temporal variability in life history traits for schooling or deep-shelf rockfish species (Boehlert 1989, Pearson 1991, Malecha et al. 2007, Schmidt 2014), few focused on shallow slope species like the Rosy Rockfish.

My work revealed that substantial declines in mean length, length frequency distribution, longevity, L_{inf} , and survivorship of Rosy Rockfish occurred over a 30-year period between the 1980s and 2010s. Pearson and Hightower (1990) reported significant interannual variation in Widow Rockfish (*S. entomelas*) growth, but cautioned that this pattern might be a sampling artifact due to spatial patterns of the fishing fleet. The declines in Rosy Rockfish mean length between 1980s and 2010s are not likely due to spatial differences between collection periods because I specifically targeted areas in 2012-2014 that were fished in the 1980s. The decline I observed is consistent with a coast-wide reduction in Rosy Rockfish mean lengths between 1978-1999 reported by Pearson (2000) and reduced mean lengths of many other rockfish species in central California over the same time period (Mason 1998). Similarly, reductions in L_{inf} were reported recently in central California Blue Rockfish (Schmidt 2014), which may indicate common ecological drivers acting on life history traits among species.

Size and age at 50% maturity are also important parameters for stock assessment models and are used to estimate spawning potential of a population (Ajiad et al. 1999). Shifts in size or age at 50% maturity can be indicative of overfishing, which is predicted to select for earlier maturing individuals (Echeverria 1987, Schmidt 2014). It is therefore necessary to investigate temporal variability in these life history traits for exploited species. Central

California Rosy Rockfish collected from 2012-14 were smaller by 30 mm and older by 2 years compared to Echeverria's 1987 central California study; however, I used a different statistical technique to estimate age at 50% maturity (logistic regression vs. proportions mature in sample) and results may not be directly comparable. While a reduction in size at maturity is consistent with increased fishing pressure, predation, or competition (Reznick et al. 1990, Ajiad et al. 1999, Law 2000, Reznick and Ghalambor 2005, Schmidt 2014), an increase in the size or age at 50% maturity might also be explained by the use of break and burn or different statistical techniques.

Sex Differences in Growth, Longevity and Mortality

Many species that attain asymptotic size after maturation exhibit strong sexual dimorphism in life history traits (Stamps 1993). For those species, variability in size is often dependent on the timing of maturation, environmental conditions, habitat and food availability, foraging behavior, and differences in removal rates between sexes (Stamps 1993). Sex-specific estimates of life history traits are important in many stock assessments (Cope et al. 2013), provide valuable spawning-potential information (Ajiad et al. 1999), and are useful in explaining the underlying ecological processes leading to sexual dimorphism (Hanson and Courtenay 1997, Hussy et al. 2012).

There were few discernable differences between male and female Rosy Rockfish size and growth parameters in my study (consistent with results reported in Echeverria 1987 and Love 1990). There were no consistent spatial or temporal patterns in mean length and growth parameter differences between Rosy Rockfish sexes. KS-tests of samples collected within the central California population from 2012-14 indicated differences in male and female length frequency distributions; however, these differences seemed to be driven by collections from

Half Moon Bay, where males were significantly larger than females, but only by an average of 10 mm. Among many groundfish species, females often attain larger sizes than males (Hanson and Courtenay 1997, Jiménez et al. 2001, Laidig et al. 2003, Gertseva et al. 2010, Hussy et al. 2012, Keller et al. 2012); although exceptions to this pattern exist (Kelly et al. 1999). The lack of clear sexual differences in mean length among other central California sample sites, within southern California, and within the 1980-83 samples indicates that the difference in Half Moon Bay was likely a sampling artifact.

Male Rosy Rockfish had greater longevity and increased survivorship than female Rosy Rockfish. Greater female mortality was reported in several other rockfish species including Yellowtail (*Sebastes flavidus*), Black (*S. melanops*) and Canary Rockfish (*S. pinniger*) (Tagart 1993, Wallace and Han-Lin 2004, Wallace et al. 2006, Wallace and Cope 2011). There is ongoing debate as to whether the lack of older females is due to increased mortality or if trawl fishing gear and sampling schemes exclude old females (Wallace and Han-Lin 2004, Wallace and Cope 2011). Tagart (1993) argued that there was no evidence that older females exist and advocated that stock assessments should precede with a ‘senescent female mortality’ hypothesis that assumes increased female mortality with age. NMFS primarily relies on trawl gear for its fisheries dependent and independent data sources (Wallace and Han-Lin 2004, Wallace and Cope 2011) and may not adequately sample suitable habitat for all species of interest (Keller et al. 2014, Marks et al. 2015). The sex specific variability in life histories observed in my study are unlikely due to distributional differences because Rosy Rockfish sex ratios remained similar across depths and areas sampled.

For many fish species that exhibit strong sexual dimorphism in size, males generally mature earlier than females and attain smaller sizes (Hanson and Courtenay 1997, Jiménez

et al. 2001, Hussy et al. 2012). I found little evidence for sexually dimorphic differences in Rosy Rockfish size or age at 50% maturity. This was consistent with previous studies from central and southern California which also found male and female Rosy Rockfish mature at similar sizes and ages (Echeverria 1987, Love 1990). However, the shape of the female Rosy Rockfish logistic curve was steeper than males, indicating that females may transition more quickly into maturity.

A species' relative reproductive energy investment, as estimated by the gonadosomatic index (GSI, de Vlaming 1982), can be used to track energy investment throughout a reproductive season (see Barnes et al. 2015). GSI analysis indicated reproductive output for both sexes of Rosy Rockfish peaked once during the year in central California. Male GSI peaked earlier than females and may indicate that female Rosy Rockfish delay fertilization and parturition until early spring. I was unable to compare reproductive characteristics of Rosy Rockfish from central and southern California because contemporary reproductive timing and GSI data for southern California were unavailable. However, trends between sexes in the central California (2012-14) data matched closely with Love et al.'s (1990) southern California GSI monthly estimates. In both central and southern California, female Rosy Rockfish GSI peaked between the months of February and March, whereas male GSI peaked in the fall between October and December. This difference in timing of peak GSI between females and males would be expected if female Rosy Rockfish are storing sperm internally controlling the timing of parturition – a phenomenon reported for multiple species of rockfish (Munoz et al. 2002, Sogard et al. 2008, Gray et al. 2015). This could result in the single, broad GSI peak observed in my samples.

In ongoing laboratory studies at NMFS SWFSC in Santa Cruz, Rosy Rockfish released up to four broods of larvae (Sue Sogard, *pers. comm.* Fisheries Ecology Division,

Southwest Fisheries Science Center, NOAA, 110 Shaffer Rd., Santa Cruz, CA 95060, USA), indicating the potential for multiple broods within a single reproductive season. Lea et al. (1999) also suggested that Rosy Rockfish might release larvae multiple times throughout the reproductive season. The results of my study do not conclusively indicate or exclude the possibility of multiple brooding in central California Rosy Rockfish. GSI may not be sensitive enough to detect multiple broods if energetic investment is reduced throughout the reproductive season. Increased sampling of Rosy Rockfish fecundity throughout the reproductive period and histological sampling would help to test *in situ* multiple brooding of Rosy Rockfish.

Spatial Differences in Growth, Longevity, and Mortality

Many fish stocks are comprised of metapopulations containing distinct life history traits across their geographic range (Ruttenberg et al. 2005, Trip et al. 2008, Keller et al. 2012). Differences in oceanographic conditions, prey availability, predator abundance, and level of fishing intensity are all factors that may drive such spatial variation in life histories (Caselle et al. 2011, Ruttenberg et al. 2011, Taylor 2014). Along the West Coast, there is evidence for limited dispersal (as little as 1- 40 km) of some nearshore rocky-reef fish larvae, leading to genetic isolation among populations (Buonaccorsi 2002, Buonaccorsi et al. 2003, Miller and Shanks 2004). As a result, there is growing concern that fisheries management practices today do not account for these small-scale variabilities in life histories (Gunderson et al. 2008, Hamilton et al. 2011b, Wilson et al. 2012). There are great challenges and costs associated with identifying, managing, and monitoring rocky reef fish populations at the appropriate small scale. However, in order to achieve sustainability objectives on both coast-

wide and regional spatial scales, it is necessary to understand the drivers of life history variation and their spatial scale.

It came as a surprise that L_{inf} was greater for Rosy Rockfish in southern California than central California, although the difference was less than 10 mm and may not have biological significance. Many other species of rockfish exhibit a positive correlation between L_{inf} and latitude (Fraidenburg 1980, Wilkins 1980, Love et al. 2002, Malecha 2007, Gertseva et al. 2010, Keller et al. 2012). However, one study by Keller (2012) found that across the Point Conception break, Greenstripe Rockfish (*Sebastes elongatus*) had greater L_{inf} in southern California compared to central California, but the growth coefficient K was greater in central California – the latter was attributed to higher productivity in central California.

Longevity and survivorship can be used to infer relative resource availability for a species, as well as fishing mortality and life history tradeoffs between growth and reproduction (Robertson et al. 2005, Ruttenberg et al. 2005, Trip 2008). Rosy Rockfish attained older ages in central California compared to specimens collected south of Point Conception. Interestingly, estimates of survivorship rates were lower in central California (even after controlling for younger modal age in southern California), suggesting that within central California there is a steeper decline of age classes from the modal age even if Rosy Rockfish ultimately attain older age with latitude. These patterns in asymptotic size, and survivorship are counter to past studies that reported negative correlation between both survivorship and growth with temperature (Robertson 2005, Ruttenberg 2005). Alternatively, Caselle (2011) reported positive correlation with temperature and growth, longevity, and survivorship of California Sheephead– a result that possibly indicates that the relative contribution of fishing mortality or density-dependent mortality may be more critical in shaping population demography than local environment. Variation in Rosy Rockfish

asymptotic size and longevity between Half Moon Bay, the Farallon Islands, and Santa Cruz may reflect small-scale differences in habitat quality, selected prey, or differential fishing intensity among these locations (Hamilton 2011a, Caselle 2011, Schmidt 2014).

Drivers of Life History Change

The variability in Rosy Rockfish life histories I observed may be due to large-scale drivers including: spatial and temporal variability in environmental conditions, fishing intensity, density-dependent factors such as competition and predation, or wide-spread temporal shifts in community structure along the coast of California. The cumulative weight of these factors, as well as corroborating evidence from other surveys, indicate that stochastic variability alone is insufficient to explain the differences I observed in Rosy Rockfish life histories.

Environmental

Both temporal and spatial variability in oceanographic conditions across the range of a species can alter life history traits (Robertson 2005, Ruttenberg et al. 2005, Hamilton 2011a). Large-scale climatic events such as the PDO, the North Pacific Gyre Oscillation (NPGO) and the El Niño Southern Oscillation (ENSO) are manifested on time scales ranging from several years to decades and are thought to control the inter-annual reproductive success of many west coast groundfish species, leading to high synchrony in recruitment (Sakuma et al. 2006, Ralston et al. 2013). The use of otolith cross-dating techniques has also linked long-term shifts in PDO and ENSO explicitly with changes in rockfish growth rates (Black et al. 2005, 2008, Thompson and Hannah 2010). Zooplankton comprise the majority of prey items for pelagic juvenile rockfishes and their species composition and biomass are

significantly altered by shifts in PDO and ENSO (Reilly et al. 1992, Peterson and Schwing 2003).

The West Coast experienced a large ENSO event from 1982-83 that reduced fish growth rates (Woodbury 1999); however, this is unlikely to have affected the fish in this study because they grew up in cooler years prior to the 1977 PDO shift. Although oceanographic conditions between the years 1980 and 1998 were warmer and less favorable to rockfish recruitment (Hare and Mantua 2000, Ralston et al. 2013), there were relatively small differences in the ENSO and PDO indices between 1967-1980 and 1999-2012, the years that a majority of individuals I sampled were developing. Other studies reported that, since 1999, ocean conditions have been cooler and generally favorable for recruitment and growth of rockfish (Sakuma et al. 2006, Ralston et al. 2013). Unless severe lagged effects exist from the positive PDO anomalies in the mid-1980s to mid-1990s, it is unlikely that the sustained reduction in Rosy Rockfish mean length, growth, and longevity that I observed in the 2010s collection compared to the 1980s was due to temporal shifts in oceanographic conditions.

Regional variations in local community structure and life history traits are often driven by bottom-up processes that influence production, prey-availability, and trade-offs between longevity and reproduction across the range of a species (Ruttenberg et al. 2005, Hamilton 2011a). Point Conception is one of the most important biogeographical breaks along California's coastline (Blanchette et al. 2007). Waters north of Point Conception are generally cooler, more productive, and influenced by strong seasonal upwelling; whereas waters south of Point Conception are characterized by warmer, less productive waters and weaker upwelling events throughout the year (Hickey 1998, Blanchette et al. 2007). A greater Fulton's condition factor and increased longevity in my central California samples

may be indicative of increased productivity north of Point Conception. Small Rosy Rockfish were difficult to obtain from southern California and greater sampling from these young size and age classes might provide the resolution necessary to evaluate the link between primary productivity and Rosy Rockfish growth across the Point Conception biogeographical break. In one recent study, over 1000 Greenstriped Rockfish from central and southern California were aged to detect variability in the growth coefficient between the two regions (Keller 2012), indicating that larger sample sizes may be necessary to detect regional subtle differences in growth for some species.

Spatial patterns in reproduction are also driven by oceanographic variability. Rosy Rockfish in my study were 30 mm larger at the mean length of 50% maturity in central California compared with Rosy Rockfish from southern California in Love's 1990 study. However, caution is warranted when comparing the two studies because we used different statistical techniques. Other studies reported central California rockfish typically mature at greater sizes and ages than southern California (Echeverria 1987, Love 2002).

Love (1990) reported evidence for multiple brooding in southern California Rosy Rockfish and speculated that reduced food availability during egg production in southern California may lead females to develop smaller batches of larvae in multiple broods. Rosy Rockfish collected in central California during 2012-14 exhibited similar seasonal patterns in GSI than Rosy Rockfish from southern California in the 1980s (Love 1990). This was unexpected because reproductive timing of fishes in central California often lags behind southern California fishes (Echeverria 1987, Love 1990, 2011, Barnes et al. 2015), which may be a result of differences in water temperature, seasonality of productivity, and prey availability.

Increased preferred prey availability, temperature, differences in habitat type, and tradeoffs between reproduction and growth along environmental gradients drive population demography and life history trait differences over both broad and narrow spatial scales (Ruttenberg et al. 2005, Trip et al. 2008, Hamilton et al. 2011). Differences in preferred Rosy Rockfish habitat may exist among the sites sampled at Half Moon Bay, the Farallon Islands, and Cordell Bank, though I did not have data to compare fine-scale, habitat, oceanographic variables, or prey availability at these sites. Cordell Bank and the Farallon Islands are both located near the continental shelf break and are characterized by constant strong upwelling and high productivity (Fontana 2013). The geographic distances between Half Moon Bay, the Farallon Islands, and Cordell Bank are relatively small (~55-75 km); making it likely that life history differences are caused by plastic rather than adaptive responses. High productivity and food availability may explain why larger Rosy Rockfish were encountered at the Farallon Islands and Cordell Bank than at Half Moon Bay sample sites. Productivity is often inversely related to temperature along the California coast (Hickey 1998, Blanchette et al. 2007), and satellite SST data confirmed the Farallon Islands and Cordell Bank sites to be significantly cooler than Half Moon Bay and Monterey.

Taylor (2014) reported that broad-scale patterns in Bullethead Parrotfish (*Chlorurus spilurus*) demography – specifically length at sex change – were driven primarily by differences in island type, habitat, and other oceanographic variables, rather than fishing pressure. Fisheries-induced changes to life history traits were detected at the island level for Bullethead Parrotfish only after controlling for differences in reef structure (Taylor 2014). Similarly, a separate study of Striated Surgeonfish (*Ctenochaetus striatus*) reported that environmental variables were better predictors of demographical differences than relative fishing pressure and more importantly noted that localized differences in growth between two

habitats on a single reef were nearly as great as the largest latitudinal gradients in growth (Trip 2008). This suggests that some anthropogenic drivers of demographic change may be obscured at large spatial scales by underlying natural variability in habitat and oceanographic conditions and further highlights the management needs in improving our understanding the species-specific scales at which life histories vary.

Fishing

Fishing is often highly selective, removing the largest, oldest members from a population while selecting for smaller, slower growing, earlier maturing individuals that reproduce before recruiting to the fishery (Law 2000, Conover and Munch 2002, Reznick and Ghalambor 2005, Taylor 2014, Mollet et al. 2015). Rockfish populations were heavily fished along the West Coast in the 1980s and 1990s. Levin et al. (2006) reported broad changes in groundfish assemblages attributed to fishing pressure. Some species such as Canary and Bocaccio Rockfish declined as much as 85% and 96% between 1977 and 2001 and the mean weight of rockfish decreased by 35% over the same time period (Levin et al. 2006). Additionally, smaller species such as Pygmy (*Sebastes wilsoni*) and Squarespot Rockfish (*Sebastes hopkinsi*) increased in abundance and relative importance to the recreational fishery after the depletion of larger species (Love 1998). The sharp declines in rockfish populations lead to the creation of Rockfish Conservation Areas (RCAs); large area closures along the West Coast primarily designed to protect and rebuild several overfished species of rockfish from commercial and recreational exploitation (Levin et al. 2006, PFMC 2011). Recreational catches declined steadily through the 1990s (Parker et al. 2000), and remained relatively low compared to peak catches in the 1980s (RecFIN 2015). The CPFV

fleet has been significantly reduced in California since it peaked in the early 1990s (Leos 2014), contributing to reductions in catch.

Intense fishing selectivity and increased mortality may result in adaptive life history trait shifts which can ultimately drive evolutionary changes within populations (Law 2000, 2007, Reznick and Ghalambor 2005). These adaptive shifts in fish life history traits were reported in numerous studies and collectively termed ‘Fisheries Induced Evolution’ (Law 2000). A study of Pacific Salmon (*Oncorhynchus* spp.) gillnet fisheries reported that average size declined for several species since the early to mid-1900s – likely the result of decades of intense and size-selective gillnet fishing (Ricker 1981). Sharp reductions in North Sea Plaice (*Pleuronectes platessa* L.) asymptotic length and continued shift towards earlier maturation were attributed to heavy fishing pressure since 1900 (Rijnsdorp 1993, Mollet et al. 2015). Fisheries induced evolution was also recently implicated in a study of Blue Rockfish (*Sebastes mystinus*), which reported that the species now matures at significantly younger ages and smaller sizes than in the 1960s and 1980s – the latter was a period of intense overfishing (Schmidt 2014).

Reznick (2005) estimated that size and age at maturity of a Trinidadian guppy (*Poecilia reticulata*) population changed by 5-15% after 7-12 generations of selective predation pressure and speculated that rates of evolution might be similar or faster under intense fishing. It was also noted that the reduction of predation or fishing mortality may not lead to quick recoveries in life history traits in the absence of strong selection for larger sizes and delayed maturity (Reznick and Ghalambor 2005). A rough extrapolation of 7-12 Rosy Rockfish generations would be 56 to 96 yr, indicating that fisheries induced evolution is unlikely because Rosy Rockfish is a bycatch species and the heaviest removals lasted for only about 20 yr in the 1980s and 1990s.

In the absence of robust population abundance estimates, it is difficult to assess how historic levels of fishing directly impacted Rosy Rockfish population demography. Within Monterey Bay, Mason (1998) reported significant declines in mean lengths for many larger species of rockfish attributed to the recreational fishery. Species such as Bocaccio (*Sebastes paucispinis*), Canary Rockfish (*S. pinniger*), and Chilipepper Rockfish (*S. goodei*) experienced significant declines in mean length between 1960 and 1996. Rosy Rockfish mean lengths were relatively stable and declined only slightly in the Monterey Bay fishery between 1983 and 1994 (Mason 1998); however, a separate report suggested coast wide declines in Rosy Rockfish mean lengths over the same time period (Pearson 2000). Mason (1998) also suggested that discard rates for Rosy Rockfish might have been greater than the 7-16% observed and, because Rosy Rockfish experience high mortality rates due to barotrauma, the true historical impact of recreational fishing pressure on Rosy Rockfish populations is likely unknown.

Historically, recreational fisheries landings have been greater in southern California than central California, which may explain the reduced longevity within southern California populations (RecFIN 2015). Caselle (2011) and Hamilton (2011) both noted that spatial variation in California Sheephead longevity may be driven by differences in historical fishing between sites. NMFS selects sites for the annual southern California hook-and-line survey to represent a range of historical harvest levels (Harms et al. 2008); however, for this study, estimates of site-specific historical fishing pressure were not available in southern California and were only available after 1987 in central California (Wilson-Vandenberg and Reilly 2000). Historical fishing pressure may have differed between Rosy Rockfish collection sites in southern and central California.

The temporal shifts I observed towards smaller sizes and increased mortality are consistent with predicted life history changes in response to intense fishing pressure (Ricker 1981, Gust et al. 2002, Reznick and Ghalambor 2005, Law 2007, Hamilton et al. 2007). However, given that fishing pressure was severely reduced and environmental conditions were generally favorable for rockfish recruitment and growth over the past 15 years, it is less clear why the patterns of decreased length, growth, and survivorship persisted into the 2010s. Seventy-five percent of Rosy Rockfish collected during 2012-14 in central California were estimated to have been born in 1998 or later and developed in cooler oceanographic regimes with reduced fishing pressure. In addition, two-thirds of the central California Rosy Rockfish I collected during 2012-14 were taken inside the boundaries of the RCA and would have experienced full protection from recreational fishing mortality (assuming limited movements and relatively small home ranges).

Though originally intended to be a temporary management strategy, the RCAs have been established long enough to result in large increases in abundance of many rockfish relative to nearby reference sites (Marks et al. 2015). Globally, marine reserves on average increase density, biomass, size, and species richness within tropical and temperate environments (Lester et al. 2009). Reserve effects can be highly dependent upon the species investigated and are sometimes confounded by small-scale regional differences in population life histories (Lester et al. 2009, Caselle et al. 2015, Starr et al. 2015). Marine reserves within the California Current are expected to require decades to accrue substantial benefits because many fish within the central California Current are slow growing, long lived, and late to mature (Marks et al. 2015, Starr et al. 2015). However, recent studies have shown that fish populations, both inside and outside of reserves, increased appreciably in relative abundance

and species targeted by fishing activities showed the greatest positive changes (Caselle et al. 2015, Marks et al. 2015).

Marks et al. (2015) found that, in addition to Rosy Rockfish, relative abundance of many large species increased in at Half Moon Bay, the Farallon Islands, and Cordell Bank since 1995-98 including Yellowtail Rockfish, Canary Rockfish, Widow Rockfish, and Lingcod. Additionally, several species exhibited site-specific increases in mean length, indicating that small scale variability in habitat and ecology may differentially influence the expected response of fish populations to reduced fishing pressure (Marks et al. 2015). Some species such as Canary Rockfish and Lingcod had reduced mean lengths in 2012-14 compared with the 1995-98 period, despite significant increases in relative abundance; a difference interpreted as indicative of increased recruitment and younger age classes for these species (Marks et al. 2015). While Marks et al. (2015) was unable to conclusively attribute overall increases in abundance to either coast-wide recruitment or reserve spillover effects, their findings were consistent with other studies that showed widespread increases in rockfish abundance along the West Coast (Cope et al. 2013, Keller et al. 2014). Despite significant increases in relative abundance across the locations sampled, Rosy Rockfish mean length did not change since 1998 among sites sampled at Half Moon Bay, the Farallon Islands, and Cordell Bank (Marks et al. 2015), indicating either lagged effects from fishing mortality or, more likely, that density-dependent factors including predation and competition were responsible for suppressing size and growth in Rosy Rockfish populations over the past 15 years.

Predation and Competition

The presence of predators in an ecosystem can profoundly impact community structure, demography, and life histories of lower trophic level prey species (Rodd and Reznick 1997, Reznick et al. 2001, DeMartini et al. 2008, Ruttenberg et al. 2011, Handelsman et al. 2013). Relative risk from predation varies across the distribution of a species and changes through time in response to fluctuations in predator abundance (Reznick et al. 1990, Hixon and Beets 1993, Beaudreau and Essington 2007). Manipulations of predator levels showed that high predation on Trinidadian guppy (*Poecilia reticulata*) populations led to heritable traits of smaller sizes, earlier maturation, and greater reproductive investment (Reznick et al. 1990, Reznick 1997, Rodd and Reznick 1997). Similar results were reported in natural studies of coral reef systems. Gust (2002) suggested that greater mortality of Great Barrier Reef parrotfish and surgeonfish due to predation may explain the decreased longevity and asymptotic sizes observed on outer reef populations when compared with inner reefs.

The removal of top predators can also have significant effects on lower trophic level community structure (DeMartini et al. 2008, Ruttenberg et al. 2011). Strong spatial variation in prey-species' size distributions and biomass among Northwest Hawaiian Island atolls were attributed to differences in predator density between sites – differences partially established by removals of top predators prior to 1992 (DeMartini et al. 2005). In a similar study at the Northern Line Islands, researchers reported that human removal of large piscivorous fish from coral reefs, such as reef sharks and snappers, significantly affected reef fish structure leading to increases in herbivorous species biomass across the spatial gradient of fishing pressure (DeMartini et al. 2008, Ruttenberg et al. 2011).

The life history changes I observed were opposite to what would be expected if they were driven by a reduction in rocky reef fishes and predator abundances. Rather, the declines in asymptotic size, size distribution, longevity, and survivorship of Rosy Rockfish over the past four decades were consistent with increased predation mortality. Several possible predators of Rosy Rockfish include larger species of rockfish, other piscivores such as Lingcod, and marine mammals, especially pinnipeds, which all experienced significant increases in population abundance over the past 20 years (Love et al. 2002, Beaudreau and Essington 2007, Weise and Harvey 2008). Rockfish species commonly feed on smaller fishes and adults have been known to prey upon young-of-the-year (YOY) rockfish (Love 2002). While direct predation of Rosy Rockfish by other rockfish has not been directly observed, the rapid and substantial increases in rockfish communities along the West Coast increases the possibility of predation mortality, especially on YOY and juvenile size classes.

Harbor Seals, California Sea Lions, and other pinnipeds also experienced substantial population increases since the 1970s (NMFS 2014a, 2014b). Pinnipeds are top predators in California's coastal ecosystems (Lowry et al. 1991, Weise and Harvey 2008, Gible and Harvey 2015). A quantitative discussion on relative predation from harbor seals or sea lions upon Rosy Rockfish is precluded by lack of direct observations or data; however, California Sea Lion diet was comprised of nearly 30% rockfish by biomass in one Monterey Bay study (Weise and Harvey 2008). Weise and Harvey (2008) also reported California Sea Lion diet compositions varied significantly with fluxuations in oceanographic conditions and certain prey species' availabilities. It is therefore possible that relative impacts of these top predators on rockfish populations could shift with changing ocean climates.

Lingcod are large, voracious, piscivorous fish with considerable habitat overlap with Rosy Rockfish (Love 2011). Lingcod diets in Puget Sound, Washington were reported to

consist of up to 24% rockfish by biomass; rockfish up to 240 mm standard length were common (Beaudreau and Essington 2007). Lingcod spawning stock biomass (SSB) was estimated to be below 10% of virgin biomass in 1997 due to overfishing but the population has since recovered above 70% virgin biomass as a result of the RCA closures that protected SSB and a series of strong recruitment years (Hamel et al. 2009). Lingcod relative abundance was significantly greater in 2012-14 at Half Moon Bay, the Farallon Islands, and Cordell Bank sample sites compared with relative abundance estimates from 1995-98 (Marks et al. 2015). Over the same time period, Lingcod were generally smaller during 2012-14 than in 1995-98, possibly indicating that there have been strong recruitment events since 1999 (Hamel et al. 2009, Marks et al. 2015). Future Lingcod diet studies in central California could help estimate potential top-down pressures exerted by this predator upon local rocky reef communities.

Competition is another density-dependant factor that may be driving the observed shifts in Rosy Rockfish life history traits. The increase in relative abundance of small rockfish species after the heavy exploitation of the 1980s and 1990s may have led to increased competition and reduced growth for Rosy Rockfish. Ecosystem-based modeling in the California Current suggested that there are relatively few interspecific interactions among adult populations of large groundfish species such as rockfish (Field et al. 2006). However, Hallacher and Roberts' (1985) study suggests that food could be a limiting factor for central California rockfish during less productive periods of the year. Predation upon recruits and competition during earlier life stages could also be an important factor in determining population demography and establishing year class strength (Hallacher and Roberts 1985, Hobson et al. 2001).

Several life history studies of adult rockfish species suggested that density-dependent responses might explain observed increases in growth and asymptotic size through time (Boehlert et al. 1989, Malecha et al. 2007). Researchers speculated that intense fishing for species like Pacific Ocean Perch in the Gulf of Alaska or Canary Rockfish and Splitnose Rockfish along the West Coast alleviated competition for limited food resources and led to increased growth for the remaining individuals (Boehlert et al. 1989, Malecha et al. 2007). Conversely, the trends of decreased growth and survivorship I observed in Rosy Rockfish life history traits appeared to be consistent with the opposite effect: increased competition over the past four decades due to increases in rocky reef fish community abundances. The relative contribution of predation versus competition towards total density-dependent mortality can be highly variable and difficult to quantify (Hixon 2005); it is notoriously difficult to demonstrate competition in the wild (Link and Auster 2013). Many rockfish species live at great depth, which presents a unique challenge in experimentally deciphering the contribution of either predation or competition on rockfish life histories.

In conclusion, I observed strong temporal and spatial variation in Rosy Rockfish life history traits. Eighty percent of Rosy Rockfish collected for my study during 2012-14 developed during years with generally favorable oceanographic conditions along the west coast. The cooler and more productive oceanographic conditions were expected to increase growth and mean length for Rosy Rockfish, yet the trends observed were opposite. Similarly, recreational fishing removals of Rosy Rockfish have been significantly reduced since the mid 1990s. The absence of increased mortality from fishing would be expected to benefit Rosy Rockfish growth, mean size, longevity, and survivorship. However, contemporary central California Rosy Rockfish had smaller mean lengths, reduced asymptotic size, reduced longevity and survivorship, and increased mortality compared with

Rosy Rockfish collected in the early 1980s. The most likely candidate for these observed life history differences were the significant, wide-scale changes to rockfish assemblages and rocky reef community structures experienced over the past four decades.

Conclusion and Management Recommendations

My study is the first to use break and burn technique to estimate Rosy Rockfish age, longevity, and survivorship along the California coast. Results indicate that Rosy Rockfish attained ages at least twice as old as previously reported. Rosy Rockfish were difficult to age and a formal validation study of annual periodicity of growth increments using Bomb-¹⁴C radiometric dating is recommended (Campana 2001). A relatively small number of otolith pairs from the NMFS 1980s collection could be used to validate Rosy Rockfish age to ~25 yr, since some of these fish were likely alive before nuclear testing in the 1960s (Kerr et al. 2005, Dwyer et al. 2016). Alternatively, a recent study showed that ¹⁸O inclusion into the otolith can validate younger age classes (Kastelle et al. 2016). Validation of age structures could lead to increased accuracy and precision of age estimates and allow for the use of age-structured data in stock assessment models.

Rosy Rockfish growth and longevity reduced over the past four decades. Examination of available evidence suggests that fishing pressure and climate shifts in the mid-1980s to mid-1990s explain initial declines in mean size of Rosy Rockfish; though samples were not available to test for changes in growth parameters or longevity in the 1990s. However, fishing effort for rockfish species declined dramatically towards the end of the 1990s because several species were declared overfished and fisheries managers closed broad regions of California's coast to commercial and recreational fishing. In addition, oceanographic conditions shifted towards generally cooler, more productive waters favorable for many groundfish species' recruitment and growth. Therefore, the continued depression of Rosy Rockfish mean length and reduction in asymptotic size and longevity are difficult to explain, but may be the result of interactions with other species and top predators which experienced dramatic population recoveries since 2000.

The federal declaration of several key rockfish species as overfished, combined with increased biological understanding of rockfish life history traits, led to more conservative management of California's groundfish stocks than in the 1980s (Parker et al. 2000). Increasingly, Ecosystem Based Fisheries Management (EBFM) approaches consider interactions and energy flow throughout the entire food web, climate variability, and life history variation through space and time (Mangel and Levin 2005, Field and Francis 2006). Current EBFM models are complicated and incomplete, yet can improve on single species models by explicitly accounting for variations in life history traits, species interactions with geography, and shifts in climate (Field and Francis 2006). Fishing has directly altered abundances of larger species along the California Coast and indirectly led to increases in smaller species (Levin et al. 2006). The increased abundance in smaller species of rockfish may prevent or slow the recovery of larger, slow growing, overfished species by eating and competing with new recruits (Levin et al. 2006). These types of interactions could be modeled in an EBFM framework. My study indicates that even small species like Rosy Rockfish can be impacted by direct and indirect fishing efforts that alter community structure and highlights the need for continual development of EBFM approaches that account for such interactions.

Differences in life history traits among geographic regions, both within central California and between central and southern California, may be a result of genetic population structure or a plastic response to local environmental or ecological conditions. Regional differences in size and age structure are relatively small and may represent stochastic processes; however genetic techniques could be used to describe the connectivity of central California sites as well as populations on either side of the Point Conception biogeographical break. Other studies have shown that rockfish exhibit strong genetic structure even over short

geographical distances possibly indicating larval dispersal is sometimes limited. Better genetic understanding of California's rockfish populations would allow for management at smaller spatial scales.

Because Rosy Rockfish are managed within a complex and only caught incidentally in the recreational fishery, current regulations and bag limits are likely sufficient for the long-term health of their populations within California. Rosy Rockfish probably experience high discard mortality as fishermen high-grade their catch for larger fishes. Stronger enforcement of regulations and better outreach regarding the use of descending devices could help mitigate the recreational fishing removals of Rosy Rockfish.

Rosy Rockfish have yet to be formally assessed (Cope et al. 2011) and data-poor methods, including Productivity-Susceptibility Analysis (PSA), categorized Rosy Rockfish as a shallow-shelf species at medium risk of over exploitation given the basic known life history traits (Cope et al. 2011). PSA outputs for Rosy Rockfish should be updated with new longevity and growth parameter estimates. However, without abundance estimates it is difficult to determine reference points for allowable catch and it is possible that Rosy Rockfish population levels were depleted further than previously thought.

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