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Rachel O. Brooks

California State University, Monterey Bay

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**GEOGRAPHIC VARIABILITY IN THE LIFE HISTORY AND DEMOGRAPHY OF
CANARY ROCKFISH, *SEBASTES PINNIGER*, ALONG THE U.S. WEST COAST**

A Thesis

Presented to the

Faculty of

Moss Landing Marine Laboratories

California State University Monterey Bay

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Marine Science

by

Rachel O. Brooks

Summer 2021

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

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CANARY ROCKFISH, *SEBASTES PINNIGER*, ALONG THE U.S. WEST COAST



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by

Rachel O. Brooks

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DEDICATION

This thesis is dedicated to all of the captains, crew, and volunteer anglers who helped make this dissertation possible.

ABSTRACT

Geographic Variability in the Life History and Demography of Canary Rockfish, *Sebastodes pinniger*, Along the U.S. West Coast

by

Rachel O. Brooks

Master of Science in Marine Science

California State University Monterey Bay, 2021

Marine fishes that persist across broad geographic ranges experience gradients in environmental and oceanographic conditions, anthropogenic stressors, and ecological factors that influence their population dynamics. Understanding the spatial- and temporal-scale at which life history characteristics and demographic patterns vary is essential for successful management and long-term sustainability of marine fisheries. The Canary Rockfish is a commercially and recreationally valuable groundfish species along the West Coast of North America. After being declared overfished in 2000, several restrictions were put in place to constrain commercial and recreational fishing opportunities. These restrictions coupled with favorable ocean conditions led to the recovery of the Canary Rockfish stock to a rebuilt status of 40% unfished biomass in 2015. Despite being an important species in the management of U.S. West Coast fisheries, the life history of Canary Rockfish across untrawlable habitats have rarely been described, including latitudinal patterns in life history traits and population demography. From 2017 through 2019, 1,567 Canary Rockfish were collected from 13 port locations along the U.S. West Coast, to investigate latitudinal patterns in size- and age-structure, growth, maturity, condition, and mortality, as well as to identify biologically relevant population breakpoints along the coast. Sex-specific differences in life history parameters were also investigated coastwide. Canary Rockfish exhibited strong latitudinal patterns in life history parameters; Canary Rockfish from colder, northern port locations exhibited larger sizes-at-age, lived longer, had variable condition, matured at larger sizes and older ages, and had lower mortality rates than Canary Rockfish from warmer, southern port locations. Male Canary Rockfish exhibited smaller sizes-at-age, lived longer, were in similar condition and matured at similar sizes in comparison to female conspecifics. Trends in life history parameters related to size, age and maturity were negatively correlated with coastwide patterns in sea surface temperature and positively correlated with coastwide patterns in primary productivity (chlorophyll *a*). Cluster analysis using life history traits indicated central Oregon as a biologically relevant break point for Canary Rockfish populations along the U.S. West Coast and should be considered in future stock assessment models. Further research should explore stock structure through genetic analysis and compare hook-and-line data from untrawlable habitats with fishery-independent bottom trawl surveys to assess habitat-based differences in Canary Rockfish life history and demography.

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INTRODUCTION

Marine fishes that persist across broad geographic ranges experience gradients in oceanographic, ecological, and anthropogenic factors (e.g., temperature, primary production, habitat structure, predator and prey interactions, fishing, pollution, climate change) that influence their population dynamics. For an increasing number of species, these factors have been shown to affect intraspecific variability in life history and demography, often resulting in altered population structure and latitudinal shifts in size and age structure (Robertson *et al.*, 2005; DeMartini *et al.*, 2008), growth (Gertseva *et al.*, 2005; Keller *et al.*, 2012), maturity (Haldorson and Love, 1991; Lombardi-Carlson *et al.*, 2003), and mortality (Robertson *et al.*, 2005; Hamilton *et al.*, 2011). An understanding of the spatial- and temporal-scales at which life history characteristics and demographic patterns vary is essential for successful management and long-term sustainability of marine resources (Gunderson *et al.*, 2008; Lorenzen *et al.*, 2010; Prince, 2010; Hamilton *et al.*, 2011; Wilson *et al.*, 2012).

Studies of fished and unfished species have documented geographic variation in demography and life history, often associated with latitudinal gradients in environmental conditions. Generally, organisms inhabiting northern latitudes exhibit later reproductive timing, increased longevity and larger sizes compared to organisms of the same species inhabiting lower latitudes (Bergmann, 1847 – quoted in James, 1970; Atkinson, 1994; Atkinson and Sibly, 1997; Angilletta and Dunham, 2003). This pattern in life history variability can often be explained by several ecological factors but is generally attributed to temperature-mediated tradeoffs between somatic growth and reproduction, as well as regional variability in food availability and metabolism (Robertson *et al.*, 2005a; Ruttenberg *et al.*, 2005; Munch and Salinas, 2009). Studies of countergradient variation in growth have revealed that some species are genetically adapted to seasonal differences in prey availability and length of the growing season, and therefore show greater growth potential in colder regimes, possibly owing to greater food conversion efficiencies (Conover and Present, 1990; Conover *et al.*, 2009). In a study that isolated temperature effects by controlling for latitudinal differences, Ruttenberg *et al.* (2005) showed that growth, longevity, and reproductive output in the damselfish *Stegastes beebei* was strongly related to regional differences in temperature, productivity (chlorophyll *a*) and food availability of preferred algal prey. Caselle *et al.* (2011) reported strong negative relationships between temperature and the size at sex change and growth to asymptotic size of California Sheephead

(*Semicossyphus pulcher*) across a major portion of the species range along the eastern Pacific, after controlling for the effects of population density.

Ecological factors have also been shown to influence patterns in demography and life history of fishes. The presence, or absence through removal, of large predators in an ecosystem can greatly influence the demographics of lower trophic level prey species. Where predators are more abundant, prey fishes often exhibit reduced longevity, smaller sizes at age, and earlier reproductive timing (DeMartini *et al.*, 2008; Ruttenberg *et al.*, 2011). In locations where the abundance of conspecifics are elevated and intraspecific competition is intense, fish grow slower, attain smaller sizes, and mature earlier compared to locations with a lower abundance of conspecifics (Gust, 2004; Samhouri, 2009; Caselle *et al.*, 2011). This was demonstrated by Caselle *et al.* (2011), who found strong density-dependent patterns at the population level of California Sheephead across a substantial portion of their geographic range. In locations with elevated densities of California Sheephead, fish are smaller in size, have lower reproductive output, and change sex at smaller sizes and younger ages. They attributed these density-dependent effects on life histories to resource competition and differences in prey quantity and quality among populations. There is also growing evidence of ontogenetic changes in habitat utilization by demersal fishes (e.g., Auster *et al.*, 2003, Bassett *et al.*, 2017), which can influence demography at smaller scales, within latitudinal zones.

Fishing pressure is known to directly affect life history characteristics and can drive demographic changes. Industrial fishing pressure from commercial and recreational fleets provides one of the greatest sources of change in the growth of fishes globally (Myers and Worm, 2003). Moreover, fishing pressure is often selective and can lead to size-selective mortality by removing the largest, oldest, and most fecund individuals, thereby causing the size distribution of populations to shift downwards (Jennings *et al.*, 1999; Conover and Munch, 2002; Hamilton *et al.*, 2007; Law, 2007). Additionally, selective fishing practices favor slow growing, early maturing individuals who reproduce prior to recruiting into the fishery (Ricker, 1981; Rijnsdorp, 1993; Conover and Munch, 2002; Hamilton *et al.*, 2007). These trait changes are called fisheries-induced evolution (FIE), a process in which phenotypic traits belonging to non-selected organisms (i.e., smaller individuals) are preserved through survival and become more dominant in frequency within the gene pool (Conover and Munch, 2002). The selective removal

can induce changes in life histories and has been shown to decrease age and size at sexual maturity (Jørgensen, 1990; Rijnsdorp, 1993; Olsen *et al.*, 2004, 2005; Schmidt, 2014), reduce mean size (Ricker, 1981; Hamilton *et al.*, 2007), affect growth rates (Millner and Whiting, 1996; Sinclair *et al.*, 2002; Fields, 2016), and alter community composition and top predator abundance (DeMartini *et al.*, 2008). Conversely, fishing pressure may have the opposite effect in that fishery removals can reduce intraspecific density-dependent competition, leading to greater food availability and resulting in faster growth and earlier maturation (Law, 2000).

On top of geographic variation, males and females can exhibit variability in life history traits within a region. Variability in size between sexes is often dependent upon the timing of maturation, removal rates as well as environmental conditions (Stamps, 1993). Sex-based differences in maturation are frequently observed in animals with asymptotic growth after maturity (Stamps, 1993). In fishes, secondary sexual dimorphism is often associated with species that have internal fertilization or protection of the eggs or young by a parent (Breder and Rosen, 1966). Often, sex-based differences in size and growth are generally driven by tradeoffs between allocating energy towards reproduction or somatic growth (Rijnsdorp, 1989; Stearns, 1989). For many fish species that exhibit strong sexual dimorphism, females tend to attain larger sizes and mature later than male conspecifics (Breder and Rosen, 1966; Parker, 1992). In some species, males and females are known to segregate by depth and/or habitat type and those factors can lead to differences between sexes (Haraldstad and Jonsson, 1983; Jagielo, 1990; Gordon, 1994; Langan *et al.*, 2019).

Along the U.S. West Coast, stock assessments are the primary method by which fish stocks are monitored and used to inform resource managers. Stock assessments use models that are built upon estimates of stock biomass, exploitation rates (e.g., commercial and recreational fleets) and quantifiable life history parameters (e.g., recruitment, growth, size and age at maturity, fecundity, natural mortality), providing scientific advice to inform fisheries managers (Hilborn and Walters, 1992; Hilborn, 2003; Hilborn *et al.*, 2003; Worm *et al.*, 2009). Often due to data limitations, these models assume life history parameters are uniform across a species' geographic range or management region (Cope and Punt, 2011). Mounting evidence suggests that averaging life-history information across a species geographic range can potentially lead to over- or under-harvesting on a regional basis and can have considerable consequences for

fisheries management (Hilborn, 2003; Hilborn *et al.*, 2003; Gunderson *et al.*, 2008; Cope and Punt, 2011). Additionally, the life history and demographic information used in assessments are often entirely absent or sorely outdated. As a result, strong assumptions that influence stock assessment outputs and subsequent harvest recommendations are made. Therefore, it is essential to provide resource managers with updated life history parameters and account for regional estimates to prevent these kinds of forced decisions.

Groundfishes of the Northeast Pacific

Along the Northeast Pacific, the California Current System (CCS) provides a large gradient in oceanographic conditions. Seasonal and annual wind forcing influence sea surface temperatures and upwelling events, which ultimately impact larval dispersal, nutrification, and biological production in the nearshore environment (Checkley and Barth, 2009). Geographic and bathymetric features, such as coastal capes, bays, islands, and submarine banks and canyons play an essential role in determining the intensity of coastal upwelling events, which in turn influences regional productivity and the distribution of marine taxa (Checkley and Barth, 2009). Plumes from both the Juan de Fuca Strait and Colombia River also provide an influx of nutrients and enhance biological productivity (Hickey and Banas, 2008; Checkley and Barth, 2009; Hickey *et al.*, 2009). Major biogeographic boundaries within the CCS occur at Cape Blanco, Cape Mendocino and Point Conception, where localized patterns in sea surface temperature and productivity persist, resulting in marked disparities in demography and nearshore community structure on either side of these geographic features (Horn *et al.*, 2006; Blanchette *et al.*, 2008; Checkley and Barth, 2009; Sivasundar and Palumbi, 2010).

The Fishery Management Plan for groundfishes inhabiting the coastal waters of the Northeast Pacific Ocean formally includes approximately 90 different species, with 64 of those species being from the genus *Sebastodes* (Rockfish) (PFMC 2020). Rockfishes are among the longest-lived fishes on the planet (Andrews *et al.*, 2002, 2007; Black *et al.*, 2005; Thompson and Hannah, 2010). In a majority of rockfish species, females attain larger maximum sizes and are larger at age compared to males (Love *et al.*, 2002). Rockfishes are late to mature and are known to have variable reproductive success, with females maturing at larger sizes than males for a majority of species (Echeverria, 1987; Haldorson and Love, 1991; Berkeley *et al.*, 2004). These life history characteristics make rockfishes highly susceptible to overfishing (Parker *et al.*, 2000;

Levin *et al.*, 2006). Management decisions based on an incomplete understanding of rockfish life history and unreported catches led to the dramatic decline of 54 rockfish species in the late 1980's and early 1990's, and the resultant federal declaration of 7 species (*S. paucispinis*, *S. pinniger*, *S. levis*, *S. crameri*, *S. alutus*, *S. entomelas*, *S. ruberrimus*) being listed as overfished in the early 2000's (Love, Yoklavich and Thorsteinson, 2002; Levin *et al.*, 2006). To restore these historically low populations, harvest guidelines, quotas, trip and landing limits, gear restrictions, seasonal closures, and spatial closures such as Rockfish Conservation Areas (RCAs) were put in place by managers to constrain commercial and recreational exploitation (PFMC 2020).

Currently, the main method of monitoring groundfish stocks along the U.S. West Coast is through the Northwest Fisheries Science Center (NWFSC) bottom trawl surveys. This fishery-independent trawl survey is the only coastwide, long-term monitoring survey that collects estimates of abundance, distribution, and length and age composition for federally managed groundfish species over trawlable low-relief habitats (Bradburn *et al.*, 2011). Since 1998, the NWFSC bottom trawl survey has been one of the main sources of biological samples used to estimate life history parameters in stock assessment models (Keller *et al.*, 2017). While the NWFSC bottom trawl survey provides valuable information regarding groundfish abundance across trawlable (low-relief) habitats, it does not account for groundfishes over untrawlable (high-relief) habitats. Previous research suggests differences in groundfish size and abundance between these two habitats (Jagielo *et al.*, 2003; Starr *et al.*, 2016). Without directed sampling of all habitats, managers may be using information that does not equally represent the status of the complete stock.

Canary Rockfish

The Canary Rockfish (*Sebastodes pinniger*, Gill 1864) range from the western Gulf of Alaska, USA (south of Shelikof Strait) to northern Baja California, Mexico (Punta Colnett) (Hart, 1973; Miller and Lea, 1976; Love, *et al.*, 2002; Mecklenburg *et al.*, 2002). Although this species of rockfish has a wide distribution, they are more commonly encountered from British Columbia, Canada to central California, USA (Miller and Lea, 1976; Boehlert, 1980; Boehlert and Kappenman, 1980; Love *et al.*, 2002). Canary Rockfish are opportunistic foragers, feeding primarily on crustaceans such as planktonic euphausiids and mysids, and occasionally on small fishes such as Shortbelly Rockfish (*Sebastodes jordani*), myctophids, and stomiatoids (Love, 1991;

Love *et al.*, 2002), while juveniles have been recorded to feed on crustaceans (e.g., harpacticoid copepods), barnacle cyprids, and euphausiid eggs.

There exists little direct information regarding stock structure of Canary Rockfish along the U.S. West Coast. Canary Rockfish spawn in the winter, producing pelagic larvae and juveniles that remain in the upper water column for 3–4 months prior to settling nearshore (Krigsman, 2000; Love *et al.*, 2002). Limited information suggests significant movement of adult Canary Rockfishes, with distances of up to 236 kilometers between tag and recapture locations (DeMott, 1982). Hannah and Rankin (2011) utilized acoustic telemetry to study the movements of eight species of Rockfishes inhabiting Siletz Reef on the Oregon coast and concluded that Canary Rockfish showed low site fidelity and wide-ranging movements that exceeded the scale of their detection grid. Previous genetic analysis of stock structure conducted by Wishard *et al.* (1980) reported evidence that two stocks may exist for Canary Rockfish – one located off northern California and southern Oregon and the other located off northern Oregon and Washington. More recent work, using microsatellite loci and restriction site associated DNA sequencing (RAD-seq), suggest little support for Canary Rockfish stock structure along the U.S. West Coast (Gomez-Uchida *et al.*, 2003; Burdick, 2016; Andrews *et al.*, 2018).

Similar to most rockfish species, Canary Rockfish are known to undergo ontogenetic migrations, moving to deeper waters as they increase in size and age (Love *et al.*, 2002). Juvenile Canary Rockfish are commonly found in shallow subtidal and intertidal areas, while adults are commonly encountered along the continental shelf between depths of 80-200 m (Love *et al.*, 2002). Juvenile and young-of-the-year (YOY) Canary Rockfish have been observed to associate with ripple scour depressions and the rock-sand interface of shallow reefs (Love *et al.*, 2002; Hallenbeck *et al.*, 2012; Bolton, 2014). Adult and sub-adult Canary Rockfish primarily occur in and around areas of high relief such as pinnacles, boulder fields, and artificial structures (i.e., piers, oil platforms, and sunken vessels), but have also been observed near soft bottom areas adjacent to reef structures (Love, 1991; Love *et al.*, 2002; Jagielo *et al.*, 2003; Tissot *et al.*, 2007; Vestfals, 2009; Bolton, 2014). This species can be found forming loose schools above rocky substrate, while others are non-schooling, solitary individuals, leading to an extremely patchy population distribution that is reflected in both the fishery and survey encounter rates (Tissot *et al.*, 1992; Love *et al.*, 2002).

The Canary Rockfish are a commercially and recreationally important species along the U.S. West Coast. This species was lightly exploited before the early 1940s, and heavily fished thereafter, with a minimum spawning stock biomass reached in the mid-1990s (Wallace and Cope, 2011). Canary Rockfish were subsequently declared overfished in 2000, resulting in the implementation of a rebuilding plan which put into place protections including limited catch, spatial closures, and gear restrictions to reduce the bycatch in rocky habitats and shelf flatfish trawls (Bellman *et al.*, 2005; Thorson and Wetzel, 2016). These restrictions coupled with shifts towards favorable ocean conditions led to a moderate increase in Canary Rockfish biomass to the management target of 40% of unfished biomass, resulting in the Pacific Fishery Management Council declaring the stock recovered following the adoption of the 2015 stock assessment (Thorson and Wetzel, 2016).

Despite being an important species in the management of U.S. West Coast fisheries, latitudinal patterns in life history parameters and demography of Canary Rockfishes have rarely been described (Boehlert, 1980; Boehlert and Kappenman, 1980; Sampson *et al.*, 2008; Keller *et al.*, 2018). Previous studies have reported significant variation in growth curves for Canary Rockfishes between sexes (Westrheim, 1975; Six and Horton, 1977; Boehlert and Kappenman, 1980; McClure, 1982; Keller *et al.*, 2018). Recent work conducted by Keller *et al.* (2018) evaluated differences in Canary Rockfish life history characteristics among three regions separated at key biogeographic breaks across the U.S. West Coast (north of Cape Mendocino, between Cape Mendocino and Point Conception, south of Point Conception), primarily using samples from the NWFSC bottom trawl survey. They observed variation in spatial patterns (CPUE and distribution) and life history parameters combined with reduced occurrence of large/old Canary Rockfishes south of Cape Mendocino, suggesting coastwide differences that imply the existence of distinct biological stocks. There is some disagreement over the maturity schedule among several west coast studies. Prior research across southern British Columbia and northern Washington, indicated that female Canary Rockfish reach larger sizes at 50% maturity (48 cm) compared to males (41 cm) (Westrheim, 1975; Gunderson and Sample, 1980). Across Oregon, McClure (1982) reported males to reach 50% maturity at 12 years (39 cm) and females to reach 50% maturity at 10 years (43 cm), while Phillips (1964) recorded Canary Rockfish from California to reach 50% maturity around 5 to 6 years (35.6 cm) for both sexes. More recent

coastwide estimates reported females to reach 50% maturity around 11 years (43 to 46 cm) (Head *et al.*, 2016; Keller *et al.*, 2018).

The biological data used to generate Canary Rockfish life history parameters in past studies have been predominantly from trawl collected specimens (Boehlert, 1980; Boehlert and Kappenman, 1980; see Sampson *et al.*, 2008 for an exception). However, Canary Rockfish are widely known to associate with hard rocky substrate (Love *et al.*, 2002; Vestfals, 2009; Bolton, 2014) and are not frequently encountered during bottom trawl surveys (Thorson and Wetzel, 2016; Keller *et al.*, 2018). The two most recent Canary Rockfish stock assessments specifically called for an expanded assessment region and additional information about the status of stocks and sub-stocks, including improved estimates of life history traits and demography across untrawlable (high relief) habitats (Wallace and Cope, 2011; Thorson and Wetzel, 2016). In addition, another major limitation of the current assessment that has caused significant challenges is the disproportionate low abundance of adult female Canary Rockfish older than 20–30 years (Thorson and Wetzel, 2016), while many males are recorded living over 50 years. One solution to explain the lack of older females has been to assume a higher natural mortality rate for females or a dome shaped selectivity, such that older adult females are alive but residing in a habitat not sampled sufficiently to detect them (i.e., high relief rocky habitat that is not sampled by the trawl survey). The 2015 Stock Assessment (Thorson and Wetzel, 2016) indicated considerable uncertainty regarding several life history parameters for Canary Rockfish, including natural mortality rates of adults and juveniles.

To provide information regarding latitudinal patterns in the demography and life history of the recently recovered Canary Rockfish stock across high relief untrawlable habitats, I quantified and compared spatially explicit life history parameters among different latitudinal areas along the U.S. West Coast. The specific objectives in the present study were to: (1) Quantify and compare the population structure and life history parameters (size and age structure, growth, length and age at maturity, body condition, and mortality rates) of Canary Rockfish between sexes and among latitudinal areas; (2) Investigate associations of life history parameters with gradients in oceanographic conditions (temperature and productivity); (3) Identify breaks within the coastwide Canary Rockfish stock based on similarities in life history parameters; and (4) Assess sex-specific differences in the population structure and life history

parameters (size and age structure, growth, length and age at maturity, body condition, and mortality rates) of Canary Rockfish within the identified cluster regions.

METHODS

Study Area and Sample Collection

Canary Rockfish samples were collected from 2017 through 2019 out of 13 different port locations ranging from the U.S. – Canadian border ($48^{\circ} 59'N$) to just south of Point Conception ($34^{\circ} 26'N$; Fig. 1). Fishing grounds were identified by local captains, deckhands and volunteer anglers and approximately 100 Canary Rockfish samples were collected per port using hook-and-line fishing gear. Port locations were chosen depending on the geographical location and the availability and accessibility of Commercial Passenger Fishing Vessels (CPFVs).

CPFV's were chartered at each port for either full- or half-day trips, dependent on weather and proximity to fishing grounds. Timed fishing drifts were conducted where information on number of fishers, time spent fishing (min), location (GPS coordinates), depth (m), and bottom relief were recorded for each individual drift. Collections of Canary Rockfish occurred across shallow (<50 m) and deep (50-180 m) reefs with anglers using predominantly baited and non-baited shrimp flies to catch the fish. Landed Canary Rockfish were euthanized via cranial concussion. Immediately thereafter, individuals were tagged with a unique numbered T-bar tag, measured to the nearest cm (total length), and a fin clip was taken from the left pectoral fin and stored in 95% Ethanol for future population genetic studies. Canary Rockfish were stored on ice until later processing. Collections were conducted under an approved San Jose State University Institutional Animal Care and Use Committee protocol (#964), in addition to the required federal (SRP #31-2017 [2017], LOA #02-2018 [2018]), and state (CA #6477; OR #21047 [2017], #22149 [2018]; WA #17-024) permits.

All bycatch associated with Canary Rockfish collections were identified and measured to the nearest cm (total length) prior to release. Other rockfishes comprised the primary bycatch associated with Canary Rockfish collections. Rockfish showing external signs of barotrauma (i.e., stomach eversion, exophthalmia, corneal gas bubbles, subcutaneous gas bubbles, and

prolapsed cloaca) were returned to depth using a Seaqualizer® descending device. Fishes not exhibiting signs of external barotrauma were released at the surface.

Lab Dissections

Standard morphometrics were collected during dissections: total length (cm), fork length (cm), standard length (cm), body depth (cm) and whole weight (kg). Liver tissue was extracted and weighed (g) for later analysis of energy storage and condition. Male and Female gonads were extracted, weighed (g), and visually inspected based on criteria outlined in Wyllie Echeverria (1987) and Westrheim (1975) (Table 1). Seven maturity stages for females (immature, maturing, vitellogenesis, fertilization, eyed larvae, spent, resting) and 5 maturity stages for males (immature, maturing, spermatogenesis, spawning, recently spawned/resting) were macroscopically identified. Ovaries within developmental stages 1-2 were considered immature and ovaries within stages 3-7 were considered mature. Testes within developmental stages 1-2 were considered immature and testes within stages 3-5 were considered mature. Gonads were preserved in 10% Buffered formalin for later histological examination. Weights of intact stomachs (g) were measured and contents were fixed in 10% buffered formalin and later transferred to 95% Ethanol for long term storage to be used in future Canary Rockfish diet studies. Intact stomachs refer to individuals with stomachs fully intact within the body cavity and no internal signs of barotrauma. In addition, a muscle tissue sample was removed below the anterior portion of the dorsal fin and stored frozen in a 1.8 mL cryogenic vial for later stable isotope analysis. Finally, sagittal otoliths were removed, cleaned, and stored dry for ageing at Moss Manding Marine Laboratories (MLML).

Age Determination

Canary Rockfish aging followed protocols outlined by Chilton and Beamish (1982), and currently used by the NWFSC Cooperative Aging Project (CAP) Laboratory in Newport, OR (B. Kamikawa). The break and burn technique as outlined by Chilton and Beamish (1982) has proven to be the most efficient and reliable method for aging Canary Rockfish and is the methodology of choice by current stock assessment biologists. This technique involves splitting the otolith in half across the nucleus and burning the exposed edge over an ethanol flame to increase the contrast between the translucent and opaque bands of each annuli. Due to the robust size of Canary Rockfish otoliths, a Pace® PICO155 low speed precision saw was used to split

otoliths in half, in a more precise and controlled fashion. Six hundred grit grinding paper was used to remove etches caused by the blade prior to burning. Burned otoliths were set in clay, brushed with a thin coat of mineral oil and viewed under a Leica® S6 E stereo vision microscope (6.3x – 40x).

Canary Rockfish ages were determined by counting the number of annuli, the translucent zones that form once a year during winter growth (Fig. 2). Opaque zones are laid down during spring/summer months and are associated with periods of fast growth, while translucent (hyaline) zones are formed over winter months during periods of slow growth (Baskin, 1987). These alternating opaque and translucent annuli are often interpreted as annual growth bands (Chilton and Beamish, 1982; Baskin, 1987) and have been validated through bomb radiocarbon (^{14}C) techniques for Canary Rockfish (Piner *et al.*, 2005). Otoliths were initially viewed at a three-quarter angle to the microscope lens, in order to identify the first few years of growth using the burnt surface (B. Kamikawa, *personal communication*). Once the first few years were identified, counts were conducted along the dorsal side of the broken surface, approximately half-way to the sulcus or along the sulcus margin and were confirmed using the ventral surface of the otolith (Chilton and Beamish, 1982; B. Kamikawa, *personal communication*). A blind read of 446 Canary Rockfish otoliths was conducted to test aging bias and precision and a subsample of 534 otoliths were exchanged with the NWFSC CAP Laboratory to be cross read for accuracy and precision.

Age Precision

Several sources of error are associated with age determination of fishes. Precision error measures the reproducibility of measurements for a given structure of a fish, while accuracy error refers to how close the estimated age is to the true age (Beamish and Fournier, 1981; Chang, 1982; Campana, 2001). The coefficient of variation has been shown to provide a robust measure of precision and can be expressed as the ratio of the standard deviation over the mean (Kimura and Lyons, 1991; Campana *et al.*, 1995; Campana, 2001):

$$CV_j = 100\% \times \sqrt{\frac{\sum_{i=1}^R (X_{ij} - X_j)^2}{R - 1}} / X_j$$

Where CV_j is the age precision estimates for the j^{th} fish; X_{ij} is the i^{th} age determination of the j^{th} fish; X_j is the mean age estimate of the j^{th} fish and R is the number of times each fish was aged. This equation can be averaged across fish to generate an average coefficient of variation (ACV). There is no *a priori* value of precision which can be designated as a target level for aging studies since precision is highly influenced by the species and the nature of the structure. On the basis of reviewed literature by Campana (2001), many aging studies can be carried out with a CV of less than 7.6%, corresponding to an average percent error (APE) of 5.5%. The ACV between R. Brooks, and R. Brooks and NWFSC CAP Lab are below Campana's maximum reference point (2.1% and 6.0%, respectively; Table 2).

Age bias plots were employed as a method of quality control to diagnose systematic differences between two sets of age determinations ensure accuracy and reduced reader bias (Campana, Annand and McMillan, 1995) (Fig. 3). Age readings for ager X are displayed as mean ages with 95% confidence intervals corresponding to ages reported by ager Y (Campana, Annand and McMillan, 1995). These plots allow for visualization of the deviation of ages from reader to reader along a hypothetical 1:1 line and allows for clear visual detection of systematic age bias (Campana, Annand and McMillan, 1995; Matta and Kimura, 2012). The age bias plots revealed a negative bias for ages past 20 years (Fig. 3). However, for ages lower than 20 years, the bias is never less than -2 years relative to the true age.

DATA ANALYSIS

Age- and Size-Structure

Age and size distribution among ports were compared using the non-parametric Kruskall-Wallis test followed by the Steel-Dwass method for pairwise comparison between ports. The Kolmogorov-Smirnov test was used to compare size-frequency distributions between sexes. Maximum sampled age (T_{\max}) is presented as the oldest observed individual per port and sex, respectively (Beverton 1992). For a more robust and conservative estimate, average oldest age was calculated using the mean of the upper quartile of ages (Choat & Robertson 2002). The average oldest age was derived for each port and compared using ANOVA. The coastwide sex-specific average oldest age estimates were considered significantly different if 95% confidence intervals did not overlap.

Growth Curves

Spatial differences in lifetime growth trajectories were compared by fitting the Von Bertalanffy growth function (VBGF) to the length-at-age data from each focal population using least squares techniques and the following equation:

$$L_t = L_{\text{inf}}(1 - e^{-k(t-t_0)})$$

Where, L_t is the estimated length at age t , L_{inf} is the estimated maximum length, k is the estimated coefficient of growth (or how quickly individuals approach the asymptotic length), t equals age, and t_0 is the theoretical time at which fish in age zero. Maximum likelihood techniques were used to estimate the 95% confidence bounds around the best fit VBGF parameter following Kimura (1980) and Hamilton *et al.* (2011) in R (R Development Team 2009). If confidence intervals did not overlap, the populations were considered significantly different.

Maturity

To assess differences in timing at maturity of Canary Rockfish among ports and between sexes, a logistic regression was fit to length and age data using the following equation:

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

Where P_x is the proportion of fish mature at a given age, a is the intercept, and b is the coefficient describing the rate at which the proportion of mature fish increase with age. Length at maturity was also calculated and compared among ports and between sexes. The age (A_{50}) and length (L_{50}) at which 50% of the population matured was considered significantly different if the 95% confidence intervals did not overlap.

Condition

Fulton's condition factor (Fulton's K) was used to assess general fish health whereby the whole fish weight is proportional to the cube of its length (Fulton, 1902; Bolger and Connolly, 1989):

$$\text{Fulton's K} = 100 \times \frac{\text{Total Weight (g)}}{\text{Total Length}^3 (\text{cm})}$$

Larger Fulton's K values indicate better condition (i.e., heavier in weight for a given length), while lower Fulton's K suggests poor condition. Given that there were significant differences in Fulton's K among ports, a 2-way ANOVA with the factors of port, sex and their interaction was used to assess differences between male and female Canary Rockfish condition. The hepatosomatic index (HSI) was also used as an index of condition:

$$\text{HSI} = 100 \times \frac{\text{Liver Mass (g)}}{\text{Body Mass (g)}}$$

In contrast to Fulton's K, HSI measures the energy reserve status of a fish, where high HSI indicates healthier condition with more energy reserved in the liver (i.e., higher liver weight to body weight ratio) (Htun-Han, 1978; Bolger and Connolly, 1989). Because HSI was also found to be significantly different among ports, a 2-way ANOVA accounting for port and sex as factors, and their interaction was used to assess differences between sexes.

Mortality

Several mortality rates were estimated for Canary Rockfish: total mortality (Z), fishing mortality (F) and natural mortality (M). The natural mortality rate (M) was estimated using the non-linear least squares Hoenig estimator based on maximum age (A_{\max}). M is inversely related to A_{\max} as it is assumed that an individual associated with a population that has a high mortality rate will not survive long enough to reach an old age (Hoenig, 1983). The updated Hoenig estimator developed by Then *et al.* (2014) was used, since it performs better than other commonly used empirical methods (Alverson and Carney, 1975; Pauly, 1980; Jensen, 1996):

$$M = (4.899)A_{\max}^{-0.916}$$

Where A_{\max} is the maximum age observed. Following recommendations from Hamel (2015) and the 2016 Canary Rockfish stock assessment, the Hoenig A_{\max} model was fit under a log-log regression transformation with the slope forced to -1, such that the point estimate for M is:

$$M = \frac{4.374}{A_{\max}}$$

M was calculated for each sampling port and for both sexes.

Total mortality (Z) was calculated using the Chapman-Robson method of cross-sectional catch-curve analysis with a correction factor for variance inflation (Chapman and Robson, 1960; Smith *et al.*, 2012). Following standard fisheries methods of catch-curve analysis, individuals younger than the modal age were excluded from the analysis (Robertson, Ackerman, *et al.*, 2005). The Chapman-Robson Z estimator is:

$$Z = \log \left[\frac{1 + T - \frac{1}{n}}{T} \right]$$

Where n is the total number of fish observed on the descending limb and of the catch curve and (T) is the mean recorded age of fish on the descending limb of the catch curve. Z was calculated for each sampling port and for both sexes. The catch curve method follows the assumptions that a population is closed, recruitment is constant among years, mortality is constant, catchability is constant across ages and the sample is not biased. The Chapman Robson estimator is considered a minimum variance unbiased estimator with variance approximated as follows:

$$VAR(Z) \approx \frac{(1 - e^{-Z})^2}{ne^{-Z}}$$

After solving for natural mortality (M) and total mortality (Z), fishing mortality (F) was derived using the following equation:

$$F = Z - M$$

Multivariate Analysis of Life History Parameters and Oceanographic Indicators

A principal components analysis (PCA) was used to determine the spatial associations of coastwide Canary Rockfish life history traits. The port level life-history traits used for the PCA analysis included the VBGF parameters L_{inf} and k, length at 50% maturity (L_{50}), age at 50% maturity (A_{50}), Fulton's K, average oldest age, and natural mortality (M). To examine the relative influence of long-term oceanographic conditions on life history traits, principal components with eigenvalues greater than 1 were saved to be used in a linear regression analysis with mean chlorophyll *a* as a proxy for productivity and sea surface temperature (SST), respectively. Chlorophyll *a* (mg/m^3) and SST ($^{\circ}\text{C}$) data were obtained through the Giovanni online data system, developed and maintained by NASA Goddard Earth Sciences Data and

Information Service Center (GES DISC) (Acker and Leptoukh, 2007). SST and chlorophyll *a* data were extracted from a 4 x 4 km box in closest proximity to fishing locations and were averaged across a 12-year period (2005-2017) for each port.

An agglomerative hierarchical cluster analysis was used to identify Canary Rockfish subpopulations based on similarities in life history traits among ports. Euclidian distances were calculated among ports using normalized life-history traits: VBGF parameters L_{inf} and k , length at 50% maturity (L_{50}), age at 50% maturity (A_{50}), Fulton's K , average oldest age, and natural mortality (M). The average silhouette width was used as a means of statistical clustering validation to determine the optimal number of clusters. The highest average silhouette width indicates the best cluster (Everitt *et al.* 2001, Rencher 2002). A permutational multivariate analysis of variance (PERMANOVA) was used to determine whether the variance in port clusters could be attributed to growth-based life history predictors. Homogeneity of group variances was tested using a multivariate analogue of Levene's test.

RESULTS

Catch Summary

A total of 1,567 Canary Rockfish were collected from high relief, untrawlable habitats between 2017-2019 (Table 3). On average, it took 3 days of fishing from each port to obtain the desired sample size of 75-100 Canary Rockfish. Additional samples were provided by the Oregon Department of Fish and Wildlife Marine Reserves Program and the California Collaborative Fisheries Research Program. Coastwide, Canary Rockfish were caught from depths of 20.1 –184.7 m (Mean = 89.4 m, SD \pm 39.0 m).

Across ports, Canary Rockfish exhibited an even distribution of females and males (Table 3). However, there were significantly different sex-ratios among ports ($X^2_{12}=38.97$, $p<0.0001$). Upon further examination, the difference in sex-ratios among ports resulted from skewed collections out of Neah Bay and Eureka. Neah Bay samples exhibited a greater proportion of males, while Eureka samples resulted in a greater proportion of females. Upon removing Neah Bay and Eureka from the sex-ratio analysis, there was no significant difference in sex-ratios ($X^2_{10}=14.98$, $p=0.1329$) and the average sex-ratio among ports was 49.1% females and 50.9% males. Individuals where sex could not be determined (unknown) made up a small

proportion of samples and were excluded from further analysis of sex-based differences in life history.

Coastwide analysis revealed a positive linear relationship between depth and length ($r^2=0.52$, $F_{1,1565}=1707.5$, $p<0.0001$) as well as depth and age ($r^2=0.39$, $F_{1,1550}=990.4$, $p<0.0001$). To account for the covariate of depth as a confounding factor when comparing Canary Rockfish length and age distributions across ports, residual values from the linear regressions were saved and used in subsequent comparisons.

Sex Specific Differences in Population Structure and Life History

Canary Rockfish population structures varied considerably between sexes coastwide. Male and female Canary Rockfish length frequency distributions differed coastwide with females exhibiting larger median sizes (KS Test; $D = 0.1314$, $p<0.0001$). When Canary Rockfish size distributions were analyzed separately for each sampling port, only northern and southern ports exhibited a significant difference in male and females size distributions (Westport, Garibaldi, Newport, Moss Landing, Morro Bay, and Santa Barbara; Fig. 4A). Female median sizes tended to be larger than male median sizes for all sampling ports except for Neah Bay and Half Moon Bay. Additionally, male and female Canary Rockfish age frequency distributions differed coastwide (KS Test; $D=0.0871$, $p=0.0057$). When Canary Rockfish age distributions were analyzed separately for each sampling port, only northern ports (Neah Bay and Westport) exhibited a significant difference between males and females (Fig. 4B). Male median ages tended to be greater than female median ages across Washington and northern Oregon ports. As a result, male Canary Rockfish tended to live significantly longer (average oldest age = 21.8, SE ± 0.4) than females coastwide (average oldest age = 17.2, SE ± 0.3) (Fig. 5; Table 7).

The Von Bertalanffy growth function (VBGF) was fit with coastwide length and age data to assess differences in growth (k) and theoretical maximum size (L_{inf}) between sexes. Growth parameters, L_{inf} and k , varied substantially between male and female Canary Rockfish coastwide (Fig. 11). Female Canary Rockfish attained larger maximum size ($L_{inf} = 58.3$, SE ± 0.2 cm) than males ($L_{inf} = 52.7$, SE ± 0.1 cm) (Fig. 6A; Table 4). Male Canary Rockfish reach asymptotic size faster ($k = 0.191$, SE ± 0.0001) than females ($k = 0.167$, SE ± 0.0001) (Fig. 6B; Table 4).

Coastwide, female Canary Rockfish matured at similar sizes (39.8 cm) compared to males (39.6 cm) (Figure 7A, Table 5). Male Canary Rockfish matured at similar ages (7.6 years)

compared to females (7.1 years) (Fig. 7B; Table 5). Immature females ranged from 15.9-50.5 cm in length, while the smallest mature female was 34.3 cm long (5 years old). Total lengths of immature males ranged from 19.8-48 cm, with the smallest mature male being 35 cm in length (5 years old).

Sex-specific coastwide estimates of Fulton's K and the hepatosomatic index (HSI) were calculated to assess differences between male and female Canary Rockfish somatic condition. No difference in Fulton's K was detected between male and female Canary Rockfish (2-way ANOVA; Sex: $F_{1,1539} = 0.416$, $p = 0.519$; Sampling Port: $F_{12,1539} = 13.487$, $p < 0.0001$; Sex*Sampling Port: $F_{12,1539} = 1.0496$, $p = 0.400$; Fig. 8A). Additionally, no difference in HSI was detected between males and females (2-way ANOVA; Sex: $F_{1,1517} = 0.957$, $p = 0.384$; Sampling Port: $F_{12,1517} = 35.235$, $p < 0.0001$; Sex*Sampling Port: $F_{12,1517} = 0.759$, $p = 0.734$; Fig. 8B).

Log-linear regression of age frequency data revealed female Canary Rockfish have a greater total mortality rate compared to male Canary Rockfish when comparing the coastwide population (Table 9; Fig. 9), although this was not statistically significant when assessing the differences in slope between male and female populations (ANCOVA: Age*Sex, $F_{1,62} = 0.80$, $p = 0.374$). Within ports, female Canary Rockfish exhibited greater total mortality rates compared to males, with the exception of Eureka, Moss Landing, Morro Bay, and Santa Barbara, where male Canary Rockfish exhibited greater total mortality rates. Natural mortality rates of female Canary Rockfish were greater than males when comparing the coastwide population (Table 6). Similarly, at the port level, natural mortality rates of females were greater than that of males, with the exception of Newport, Moss Landing and Morro Bay. Male and female Canary Rockfish from Newport exhibited the same natural mortality rates. Finally, the fishing mortality rate was estimated to be twice as high for female Canary Rockfish compared to males when comparing the coastwide population (Table 6).

Geographic Differences in Population Structure and Life History

Canary Rockfish population structure varied considerably among ports. Length frequency distributions of Canary Rockfish differed significantly among ports (Kruskal-Wallis test, $X^2_{12} = 340.4$, $p < 0.0001$, Fig. 10A) and followed a latitudinal trend whereby median sizes declined from Washington to southern Oregon, with a slight increase across central California. Age

frequency distributions of Canary Rockfish also differed significantly among ports (Kruskal-Wallis test, $X^2_{12}=358.9$, $p < 0.0001$; Fig. 10B). Northern ports (Neah Bay and Westport) differed from all others due to older fish being present in the samples. As a result, there were differences in the average oldest age calculated among sampling ports (ANOVA, $F_{12,427} = 98.4$, $p < 0.0001$; Fig. 11). Specifically, Canary Rockfish from northern ports (Neah Bay, Westport, Garibaldi, Newport) tended to exhibit older ages relative to Canary Rockfish from southern ports.

The Von Bertalanffy growth function (VBGF) was fit to the length and age data to assess differences in growth (k) and theoretical maximum size (L_{inf}) of Canary Rockfish among ports. Canary Rockfish exhibited variation among sampling ports in their VBGF parameters (Fig. Table 7; 12A and B). The theoretical average maximum size, L_{inf} , tended to decrease from northern to southern ports. Similarly, the growth coefficient, k , exhibited a slight latitudinal trend, but was more variable among ports. Non-overlapping 95% confidence intervals suggests that ports are significantly different from one another (Fig. 12B). Generally, VGBF parameters L_{inf} and k separated into two distinct groups. Neah Bay, Westport, Garibaldi, Newport, Coos Bay, Moss Landing, Eureka, and Santa Barbara formed one overlapping cluster, while Brookings, Fort Bragg, Bodega Bay, Half Moon Bay and Morro Bay formed the second overlapping cluster.

Length and age at 50% maturity were derived using logistic regression to compare the timing of maturity of Canary Rockfish among ports (sexes pooled). Logistic regression analysis revealed a latitudinal trend in which total length at 50% maturity generally decreased with decreasing latitude (Table 8; Fig. 13A). A relatively similar trend was observed for age at 50% maturity as well (Table 8; Fig. 13B).

Fish condition was analyzed using the morphometric index, Fulton's K, and the standardized liver weight, the hepatosomatic index (HSI). There was a significant difference in Fulton's K among ports (1-way ANOVA, $F_{12,1535} = 16.67$, $p < 0.0001$; Fig. 8A). Canary Rockfish from southern ports exhibited a higher Fulton's K value, with the exception of Westport, Newport, and Eureka. Conversely, HSI revealed the opposite pattern with larger standardized liver weights observed across northern ports, with the exception of Neah Bay and Eureka (1-way ANOVA, $F_{12,1534} = 91.76$, $p < 0.0001$; Fig. 14B).

Catch curve analyses of age-frequency data revealed substantial variation in instantaneous total mortality rates (Z) among focal ports (Table 9). Spatial differences in instantaneous total mortality rates were statistically significant when assessing the differences in the slope of catch among ports (ANCOVA: Age*Sampling Port, $F_{12,351} = 2.49$, $p = 0.004$). Generally, southern and central ports exhibited greater total mortality rates compared to ports in the northern extent of the sampling range. Natural mortality (M) exhibited a similar trend as total mortality, wherein natural mortality rates were greatest from fish caught out of southern and central ports compared to northern ports (Table 9). The natural mortality rate was highest out of Morro Bay because the maximum age (T_{max}) sampled from this port was relatively low (Morro Bay: Range = 4-10 years, Mean = 7.2 years). Fishing mortality rates (F) were derived from these two estimates and did not exhibit a trend among ports (Table 9). The highest estimated fishing mortality rates occurred out of Eureka, Fort Bragg, and Moss Landing, CA. In some instances, natural mortality was calculated to be greater than total mortality, resulting in a negative value for fishing mortality.

Association of Life History Parameters to Gradients in Oceanographic Conditions

The principal components analyses identified spatial associations of Canary Rockfish life history traits at the port level. Principal component 1 (PC1) and principal component 2 (PC2) together accounted for up to 78% of the variation seen in the life history data generated from the sampling ports (Fig. 15). PC1 accounted for 56% of the variation in the data and was driven primarily by factors related to longevity and growth, where positive values of PC1 are correlated with longevity, L_{inf} , and maturity, and negative values are correlated with growth (k) and natural mortality (M). PC2 accounted for 22% of the variation and is primarily comprised of the condition index, Fulton's K , on the positive scale.

There was a negative relationship between PC1 and mean SST ($r^2 = 0.5206$, $F_{1,11} = 11.9463$, $p = 0.0054$; Fig. 16A), indicating that fish reach larger sizes, older ages, and mature later at sites with cooler water temperatures. In contrast, there was a positive relationship between PC1 and mean chlorophyll a ($r^2 = 0.5191$ $F_{1,11} = 11.8715$, $p = 0.0055$; Fig. 16B), indicating that fish reach larger sizes, older ages, and mature later at locations with higher primary productivity. While not statistically significant, there was a slight positive trend between

PC2 and mean SST (Fig. 16C), suggesting fish were in better condition (Fulton's K) in warmer locations. There was no relationship between PC2 and mean chlorophyll *a* (Fig. 16D).

Metapopulation Analysis

An agglomerative hierarchical cluster analysis identified two clusters as being the optimal number of groupings for Canary Rockfish along the U.S. West Coast based on similarities in life history traits among ports (Avg. Silhouette Width = 0.61). Sampled ports separated into a northern and southern cluster, with a breakpoint in central Oregon between Coos Bay and Newport (PERMANOVA; $F_{1,11} = 25.74$, $p = 0.002$; Fig. 17).

Based on the results of the cluster analysis, Canary Rockfish demography and life history characteristics were subsequently quantified within these two geographic regions. Overall, female and male Canary Rockfish differed in their median age and length between regions. Median lengths and ages were greater in the northern region compared to the southern region (Fig. 18). When comparing age and length frequency distributions between sexes within the cluster-defined regions, female Canary Rockfish exhibited a larger median length than males in the northern region (KS Test; $D = 0.186$, $p < 0.0001$) and male Canary Rockfish reached an older median age than females in the northern region (KS Test; $D = 0.186$, $p < 0.0001$). Median lengths were significantly different between sexes in the southern region (KS Test; $D = 0.157$, $p < 0.0001$), but not age (KS Test; $D = 0.082$, $p = 0.104$). Additionally, Canary Rockfish exhibited greater average oldest age in the northern region compared to the southern region, with males attaining older ages than females in both regions (2-way ANOVA; Sex: $F_{1,480} = 55.8$, $p < 0.0001$; Region: $F_{1,480} = 990.7$, $P < 0.0001$; Sex*Region: $F_{1,480} = 16.3$, $p < 0.0001$; Fig. 19; Table 10). There was an interactive effect of sex and region on Canary Rockfish average oldest age due to an 18-year difference in T_{max} between males ($T_{max} = 51$) and females ($T_{max} = 33$) in the northern region compared to an 8-year difference in the southern region (Male $T_{max} = 29$; Female $T_{max} = 21$).

Overall, Canary Rockfish from the northern region reached larger maximum sizes (Females $L_{inf} = 58.6$ cm; Males $L_{inf} = 53.3$ cm) compared to the southern region (Females $L_{inf} = 54.9$ cm; Males $L_{inf} = 48.4$ cm). Within respective regions, females attained larger maximum sizes compared to males (Fig. 20A; Table 10). Comparing the VBGF parameter k between regions and sexes, Canary Rockfish attained asymptotic sizes more slowly in the northern region

(Female $k = 0.17$; Male $k = 0.20$) compared to southern region (Female $k = 0.19$; Male $k = 0.23$), while females tended to attain asymptotic sizes more slowly than males in their respective regions (Fig. 20B; Table 10).

Canary Rockfish from the northern region matured at larger sizes and older ages compared to the southern region (Fig. 21; Table 10). In the northern region, female Canary Rockfish matured at older ages and larger sizes compared to males (Female: $L_{50} = 46.1$ cm, $A_{50} = 9.1$ years; Male: $L_{50} = 43.8$ cm, $A_{50} = 8.9$ years; Fig. 21A). In the southern region, male Canary Rockfish matured at older ages and larger sizes compared to females (Female: $L_{50\%} = 38.4$ cm, $A_{50} = 6.6$ years; Male: $L_{50} = 39.0$ cm, $A_{50} = 7.4$ years; Fig. 21A).

There were few discernable trends in Fulton's K condition index among male and female Canary Rockfish for northern and southern regions (2-way ANOVA; Sex: $F_{1,1536} = 1.969$, $p = 0.162$; Region: $F_{1,1536} = 1.117$, $p = 0.291$; Sex*Region: $F_{1,1536} = 1.820$, $p = 0.178$; Fig. 22A). Conversely, the hepatosomatic index (HSI) was considerably different between northern and southern regions, with male and female Canary Rockfish exhibiting greater standardized liver weights in the north compared to the south (2-way ANOVA; Sex: $F_{1,1536} = 0.003$, $p = 0.959$; Region: $F_{1,1536} = 200.76$, $p < 0.0001$; Sex*Region: $F_{1,1536} = 0.634$, $p = 0.426$; Fig. 22B).

Catch curve analyses of age-frequency data revealed variation in total mortality rates (Z) between cluster regions (Table 10; Fig. 23), which was statistically significant for males but not for females (ANCOVA, Male: Age*Region, $F_{1,54} = 14.03$, $p = 0.0004$; Female: Age*Region, $F_{1,43} = 2.52$, $p = 0.120$). Canary Rockfish exhibited a lower estimated total mortality rate (Z) in the northern region compared to the southern region, with females having an overall greater total mortality rate compared to males within both regions (Table 10). The estimated natural mortality rate (M) showed a similar pattern, with M being higher in the southern region and females having a higher M than males in both regions. The estimated fishing mortality rate (F) was greater in the southern region and higher for females.

DISCUSSION

Sex Specific Differences in Canary Rockfish Demography and Life History

Many species that attain asymptotic size after maturation exhibit strong sex-based differences 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, 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) and can provide valuable information regarding spawning potential (Ajiad *et al.*, 1999). Coastwide, I found male Canary Rockfish exhibited smaller sizes, slower growth, greater longevity, lower mortality rates, and similar timing in maturity as females.

Sex-based differences in growth have been described for various groundfish species along the U.S. West Coast (Laidig *et al.*, 2003; Gertseva *et al.*, 2010; Keller *et al.*, 2012; Gertseva *et al.*, 2017; Lam *et al.*, *in press*). For example, Gertseva *et al.* (2017) found females to reach larger asymptotic sizes than males for eight species of groundfish along the U.S. West Coast. Laidig *et al.* (2003), Gertseva *et al.* (2010), Keller *et al.* (2012), and Lam *et al.* (*in press*) reported females to grow faster and attain a larger average asymptotic size than males for Blue Rockfish (*Sebastodes mystinus*), Splitnose Rockfish (*Sebastodes diploproa*), Greenstripe Rockfish (*Sebastodes elongatus*) and Lingcod (*Ophiodon elongatus*), respectively. I found a similar dimorphic growth pattern for Canary Rockfish and confirmed previous findings (Boehlert and Kappenman, 1980; Stanley *et al.*, 2005; Thorson and Wetzel, 2016; Keller *et al.*, 2018). The greatest divergence in growth between sexes in my study occurred around the age and size of sexual maturation and may be associated with reproductive investment. Dimorphic growth patterns are often linked with maturation, in that earlier maturation is usually associated with slower growth rates given life history trade-offs between growth and reproduction.

For many fish species that exhibit strong sexual dimorphism in size and growth, males generally mature earlier than females and attain smaller sizes (Hanson and Courtenay, 1997; Jiménez *et al.*, 2001; Hüssy *et al.*, 2012). I found little evidence for sex-based differences in coastwide Canary Rockfish size and age at 50% maturity. Moreover, the length and age at 50% maturity of females in my study was lower than prior estimates reported by Wylie Echeverria

(1978; $L_{50} = 44$ cm, $A_{50} = 9$ years), McClure (1982; $L_{50} = 43$ cm, $A_{50} = 10$ years), and Westrheim (1975; $L_{50} = 48$ cm). Possible underlying mechanisms for reduced size and age at maturity in female Canary Rockfish include fishery-induced evolution, compensatory (phenotypic) responses linked to population declines, a changing environment, or a combination of these effects (Trippel, 1995; Kuparinen and Merilä, 2007).

The high rate of fishery removals from the late 1980s to late 1990s (Thorson and Wetzel, 2016) may have exerted selective pressure for female Canary Rockfish to mature earlier in life to achieve greater reproductive success prior to harvest. Such a selective advantage for early maturing fish could alter the gene pool and result in a reduced age at 50% maturity for the population over time. Declines in the length and age at maturity of Darkblotched Rockfish (*Sebastes crameri*), North Sea Plaice (*Pleuronectes platessa*), and northwest Atlantic Cod (*Gadus morhua*) have been largely attributed to such genetic shifts (Olsen *et al.*, 2005; Rijnsdorp *et al.*, 2005; Frey *et al.* 2015). A potential confounding factor in comparing size and age at 50% maturity values from this analysis to previous studies is the variability in geographic location of sample sites. For many U.S. West Coast Rockfishes, including Canary Rockfish, past studies have suggested that length at maturity increases with latitude (Westrheim, 1975; McClure, 1982; Echeverria, 1987; Haldorson and Love, 1991). As a result, this may have led to skewed size at maturity by combining maturity estimates coastwide among respective sexes.

More recent coastwide estimates of female Canary Rockfish reported length and age at 50% maturity of females to be approximately 46 cm and 11 years, respectively (Keller *et al.*, 2018). These values were much larger than what I found. There could be several possible explanations for why my results differ from Keller *et al.* (2018), including differences in methods used to identify maturity and/or habitats surveyed. Contrary to earlier studies that based maturity assessments on visual observations (Phillips, 1957; Westrheim, 1975; Gunderson and Sample, 1980; McClure, 1982), more recent results are based on histological examination of ovaries, which is thought to be a more reliable method of maturity determination. Several studies have evaluated macroscopic versus histological maturity determinations, and found variable agreement (Costa, 2009; McBride, Vidal and Cadrin, 2013). Often disagreement in maturity determination occurs when fish are shifting from immature to mature status and those that are partially spent. Specimens for my study were taken predominantly outside of the spawning

season – making visual determination of maturity status challenging, which may have resulted in potential sources of misidentification.

A majority of the samples collected in the Keller *et al.* (2018) study were obtained through the West Coast Groundfish Bottom Trawl Survey (WCGBTS) which is inherently biased towards groundfishes occupying trawlable, low-relief habitats and fails to represent fishes in untrawlable, high-relief habitats such as I surveyed. Female Canary Rockfish inhabiting untrawlable, high-relief habitats may be maturing sooner due to a greater abundance of resources and food availability in comparison to those occupying trawlable, low relief habitats. This was demonstrated by Lam *et al.* (*in press*), who found differences in size and age at maturity of Lingcod between trawlable, low-relief and untrawlable, high-relief habitats. Lingcod inhabiting high-relief habitats were found to mature sooner compared to conspecifics inhabiting low-relief habitats. Conversely, the mean depths between these two studies were drastically different, as I surveyed much shallower depths. The mean depth for immature females from the Keller *et al.* (2018) study was 117 m, compared to the mean depth of 157 m for mature females. The mean depth of capture of immature and mature females in my study was 64 m and 107 m, respectively. Canary Rockfish are known to display ontogenetic migration; adults move into deeper waters as they mature (Love *et al.*, 2002). As a result, the decrease in estimated size and age at 50% maturity could be directly related to the overall shallower depths surveyed in my study. A combined estimate from these two studies may provide a more comprehensive understanding of true population trends in maturity.

Greater female mortality has been reported for several Rockfish species including Yellowtail Rockfish (*Sebastodes flavidus*), Black Rockfish (*Sebastodes melanops*), and Rosy Rockfish (*Sebastodes rosaceous*) (Tagart *et al.*, 2000; Wallace and Lai, 2005; Wallace *et al.*, 2008; Fields, 2016). The degree to which this pattern reflects dome shaped selectivity, such that older adult females are still alive but residing in a habitat not sampled sufficiently to detect them (i.e., high relief rocky habitat that is not sampled by the trawl survey) or physiological stress resulting from the costs of reproduction for females (i.e., senescent mortality hypothesis) has been the focus of much discussion.

Recent stock assessment models account for the deficit in older females observed in age-composition samples from bottom trawl surveys by assuming an elevated natural mortality for

female Canary Rockfish post-maturity (Thorson and Wetzel 2016). The 2015 stock assessment model estimated a “base” natural mortality rate of 0.052 for both sexes and a “ramp” natural mortality rate of 0.102 by age 14 for females. This is consistent with my study results as male Canary Rockfish exhibited greater longevity and lower mortality rates compared to females. Age frequency throughout the current study was not markedly different by sex for Canary Rockfishes younger than 20 years. However, for fishes older than 20 years, males ($n = 134$) outnumbered females ($n = 52$) by approximately 2.5 to 1. A similar decrease in females older than 20 to 25 years was observed by Stanley *et al.* (2005) in Canadian waters, and by Keller *et al.* (2018) across the U.S. West Coast. The results from my study do not support the hypothesis of fishery selectivity as I also found female Canary Rockfish to have lower longevity and greater mortality rates compared to males across untrawlable, high relief habitats. Rather, my results suggest that female Canary Rockfish mortality may be better explained by the senescent mortality hypothesis, in which females show an increasing mortality rate with age (Tagart *et al.*, 2000).

Geographic Patterns in Canary Rockfish Demography and Life History

Spatial patterns in population demography and life history have been reported in groundfishes across the Northeast Pacific and in other fishes around the world. Across the U.S. West Coast, spatial variation in population demography and life history have been reported at both a regional (Hamilton *et al.*, 2011; Wilson *et al.*, 2011; Barnes, 2015; Fields, 2016) and coastwide scale (Gertseva *et al.* 2010; Keller *et al.*, 2012; Lam *et al.*, *in press*; Gertseva *et al.* 2017). The potential causes of spatial variation in population demography and life history include differences in ocean productivity and temperature, species interactions, habitat availability, and historic fishing pressure. Regardless of the causal factors, persistent spatial differences in population demography and life history characteristics within a stock may create a need to manage meta-populations or sub-stocks of important fished species.

Variation in growth curves for Canary Rockfish were previously described in the Northeast Pacific (Boehlert, 1980; Boehlert and Kappenman, 1980; Keller *et al.*, 2018). Boehlert and Kappenman (1980) indicated that growth of Canary Rockfishes varied little with latitude, although their samples came predominantly from specimens across Washington and Oregon with ages greater than 20 years. Keller *et al.* (2018) reported growth curves of Canary Rockfish to differ among survey areas (North: $40^{\circ} 26'$ to $48^{\circ} 28'$ N, Central: $34^{\circ} 27'$ to $40^{\circ} 26'$ N, South:

32° 30' to 34° 27' N). Females exhibited larger sizes at age and reached larger asymptotic sizes south of Point Conception, while males exhibited larger sizes at age and reached larger asymptotic sizes North of Cape Mendocino. Likewise, I found Canary Rockfish to exhibit a latitudinal pattern in growth, with individuals from northern ports having greater longevity, reaching larger asymptotic sizes, and growing faster compared to southern ports.

Latitudinal patterns in growth have been reported for several groundfishes across the Northeast Pacific. For example, Greenstriped Rockfish (*Sebastodes elongatus*), Yellowtail Rockfish (*Sebastodes flavidus*), Widow Rockfish (*Sebastodes entomelas*), Sablefish (*Anoplopoma fimbria*), and Lingcod (*Ophiodon elongatus*) all exhibited a positive cline in asymptotic size with increasing latitude along the continental U.S. West Coast (Fraidenburg, 1981; Pearson and Hightower, 1991; Keller *et al.*, 2012; Head *et al.*, 2014, Lam *et al.*, *in press*), however, this was not the case for California Halibut (*Paralichthys californicus*) (Fraidenburg, 1981; Pearson and Hightower, 1991; Keller *et al.*, 2012; Head *et al.*, 2014, Barnes, 2015; Lam *et al.*, *in press*). It is suspected that differences in environmental conditions and fishing pressure may collectively or individually contribute to regional variation in growth curves (Gertseva *et al.*, 2010; West *et al.*, 2014; Keller *et al.*, 2018). As demonstrated in the PCA, I found that sea surface temperature and productivity (as measured by chlorophyll *a*) are closely linked with size, growth, and longevity of Canary Rockfish along the U.S. West Coast. Cooler temperatures and greater productivity in the northern extent of these survey regions may allow for greater efficiencies in energy transfer rates between trophic levels, and thus resulting in larger sizes up north. South of Cape Mendocino, the California Current Ecosystem is characterized by weaker upwelling and lower productivity. Smaller asymptotic size in that area could be linked to productivity. Likewise, enhanced upwelling and elevated productivity north of Cape Mendocino could support faster growth and larger body sizes in Canary Rockfish (Juan-Jordá *et al.*, 2009).

Fishing pressure is often selective in that it typically removes the largest, oldest, and most fecund individuals, thereby driving a downwards shift in size distribution of populations (Jennings *et al.*, 1999; Conover and Munch, 2002; Hamilton *et al.*, 2007; Law, 2007). Selective fishing practices favor slow growing, early maturing individuals who reproduce prior to recruiting in the fishery (Ricker, 1981; Rijnsdorp, 1993; Conover and Munch, 2002; Hamilton *et al.*, 2007). Gertseva *et al.* (2010) proposed that differences in fishing intensity may be

responsible for the cline in asymptotic sizes reported for Splitnose Rockfish (*Sebastodes diploproa*) along the U.S. West Coast. Greater fishing pressure in the south could skew the size distribution of the population in that region to smaller sizes, thus reducing the southern estimate of asymptotic size relative to the north. However, historical catch reconstruction for Canary Rockfish reported by Thorson and Wetzel (2016) does not corroborate this trend. Overall, they reported greater catch from Oregon, followed by Washington and then California for all fleets combined. This suggests that oceanographic factors may play a bigger role in comparison to historical fishing pressure in influencing size and growth of Canary Rockfish.

Previous studies suggest maturity of Canary Rockfish may differ between northern and southern areas, although geographic ranges were less expansive and locations for regional subdivisions unspecified (Phillips, 1957; Westrheim, 1975; Gunderson and Sample, 1980; McClure, 1982; Echeverria, 1987; Thorson and Wetzel, 2016; Keller *et al.*, 2018). Prior research across southern British Columbia and northern Washington, reported length at 50% maturity (L_{50}) ranging from 48.5 to 49.2 cm (Westrheim, 1975; Gunderson and Sample, 1980). Across Oregon, McClure (1982) reported somewhat smaller values for male and female L_{50} ($M = 39$ cm; $F = 43$ cm) and age at 50% maturity (A_{50}) ($M = 12$ years; $F = 10$ years), whereas Phillips (1964) recorded L_{50} at 35.6 cm and A_{50} at 5 to 6 years for Canary Rockfish (both sexes) from California. Although these previous studies were across different time scales, the observed regional variability in size and age at maturity tracked results in the current study. I found notable decreases in size at 50% maturity from north to south along the U.S. West Coast.

Increased length at 50% maturity towards higher latitudes is relatively common in North Pacific Rockfishes (Haldorson and Love, 1991) and has also been reported for North Atlantic Redfishes (*Sebastes marinus*, *S. mentella*, *S. fasciatus*; Ni and Sandeman, 1984). Female Aurora Rockfish (*S. aurora*) and Sablefish (*Anoplopoma fimbria*) were reported to exhibit regional differences in maturity, with a decrease in length at 50% maturity from north to south of Cape Mendocino (Head *et al.*, 2014; Head *et al.*, 2020). Age at 50% maturity also differed north and south of Cape Mendocino, with female Sablefish maturing at a younger age further north. Atka mackerel (*Pleurogrammus monopterygius*) also exhibited a cline in size at 50% maturity, increasing from west to east in Alaska, while no difference was detected for age at 50% maturity (Cooper, McDermott and Ianelli, 2010). Conversely, Brodziak and Mikus (2000) reported a

latitudinal cline in maturation rates of Dover Sole (*Solea solea*), where male and females matured at smaller sizes and younger ages at higher latitudes. Both Cooper *et al.* (2010) and Head *et al.* (2014) attributed differences in size at maturity among sampling areas to differences in growth rates and size at age, where regions exhibiting larger sizes at 50% maturity had faster growth rates and larger sizes at age for those populations. Since there were no significant differences in age at 50% maturity among focal ports in the current study, the variability seen in size at 50% maturity is most likely explained by faster growth rates at higher latitudes rather than differences in timing or age of maturity (Caselle *et al.*, 2011).

Countergradient variation in growth and size-selective winter mortality may provide a potential underlying mechanism to explain the patterns we see in Canary Rockfish growth, size and reproduction. Countergradient variation in growth and other demographic traits (i.e., faster growth and larger sizes at higher latitudes) have been documented in several fish species, but most famously in Atlantic Silversides (*Menidia menidia*) (Conover and Present 1990). Often, fish from colder regions are genetically adapted to shorter growing seasons, and therefore show greater growth potential, potentially owing to greater food conversion efficiency. The cooler water temperatures and shorter growing season associated with higher latitudes along the northeast Pacific, may lead to genetic selection of faster growth and larger sizes in northern populations through time. Juvenile Canary Rockfish that maximize their growth and attain larger sizes during the shorter growing season in the north, may be less susceptible to mortality from energetic deficiencies or predation as winter proceeds. Additionally, temperature effects have been found to be important for the frequency of reproduction and survival of adults (Angilletta *et al.*, 2004). Since reproduction is typically less frequent in colder environments, natural selection may favor a larger body size to maximize fecundity at each reproductive opportunity.

Fish condition is an important measure of energy reserves and can have a large influence on growth, survival and reproductive success (Love, 1970; Lambert and Dutil, 1997; Shul'man and Love, 1999). Fish condition can also serve as an important indicator of ecosystem health and habitat productivity (Lloret and Planes, 2003). Inadequate energy reserves have been implicated in the reduced reproductive success of several fish species through reduced fecundity and/or quality of eggs and larvae (Kjesbu *et al.*, 1992; Lam *et al.* bert and Dutil, 1997; Marshall and Frank, 1999). Conversely, other studies have not found any relationship between maternal

condition and egg viability (Ouellet *et al.*, 2001). Poor condition (i.e., lower available energy reserves) may also lower the chances of survival of big fish, leading to an increase of natural mortality (Love, 1970; Krivobok and Tokareva, 1972; Shul'man and Love, 1999). Starvation due to exhaustion of energy reserves, particularly in smaller individuals and during the nonfeeding periods, weakens fish and also renders them more susceptible to predation and to a variety of environmental stressors (e.g., parasites and thermal effects). Temperature has been shown to play an important role in determining fish condition. Rätz and Lloret (2003) reported Atlantic Cod (*Gadus morhua*) living in colder waters to be in poorer condition than Atlantic Cod in warmer waters. Conversely, Rosy Rockfish (*Sebastodes rosaceous*), Greenstriped Rockfish (*Sebastodes elongatus*), and Canary Rockfish (*Sebastodes pinniger*) occupying higher, colder latitudes, tended to be in better condition than those from lower latitudes along the U.S. West Coast (Keller *et al.*, 2012; Fields, 2016; Keller *et al.*, 2018). I found this to be the case for Canary Rockfish HSI but not for Fulton's K.

Across Washington and northern Oregon, land derived nutrients and freshwater inputs from the Juan de Fuca Strait and Columbia River produce some of the highest average Chlorophyll *a* concentration across the Pacific Northeast (Hickey and Banas, 2003, 2008; Ware and Thomson, 2005; Checkley and Barth, 2009; Hickey *et al.*, 2009). High chlorophyll concentrations in the northern California Current Ecosystem (CCE) are reflected in higher biomass of prey trophic levels, such as zooplankton, and other fish stocks (Landry and Lorenzen, 1989; Hickey and Banas, 2003). Preliminary examination of Canary Rockfish diet contents revealed that bony fishes made up over 50% of the diet of fishes caught from Washington ports, while krill and shrimp dominated the diet for ports across Oregon and California (J. Silva, *unpublished data*). The higher liver condition and level of lipids storage observed towards the northern extent of the sampling region may be attributed to greater food supply as a result of enhanced productivity in this region.

Surprisingly, Fulton's K did not follow this latitudinal pattern. This may be explained by the temporal variability in collections across sampling ports. Contrary to what was predicted, the highest Fulton's K values were observed across Canary Rockfish collected from southern California. Off California, Canary Rockfish spawning takes place during the winter (December–March) (Love *et al.*, 2002). Due to sampling limitation and weather restrictions, Canary Rockfish

were collected during the fall from Eureka (October), Santa Barbara (October and November), and Moss Landing (October), whereas all other collections took place during the late spring and summer. For the previously mentioned ports, I detected a greater gonad weight relative to body weight. The temporal variability in Canary Rockfish collections may explain the higher Fulton's K values observed across the southern ports as ripening gonads most likely positively skewed the observed Fulton's K values.

Canary Rockfish exhibited a slight latitudinal pattern in total mortality among ports. In general, I found total mortality rates of Canary Rockfish were lower in northern, cooler, more productive ports. Patterns in total mortality may reflect localized variability in environmental conditions as well as the history of exploitation and size-selective fishing. Lower natural mortality rates of Canary Rockfish caught near northern ports may be due to greater productivity and nutrient influx across the northern CCE creating conditions more beneficial to recruitment and survival. Alternatively, spatially variable historical fishing pressure by commercial and recreational fishing sectors likely may have influenced the higher fishing mortality rates reflected across California ports. Canary Rockfish fishing mortality peaked in the early 1990s (Thorson and Wetzel, 2016). They were federally declared overfished in 2000 and catch restrictions were put in place to reduce the fishing mortality. Recovery of Canary Rockfish began earlier across Washington, where the relative spawning output was estimated to be higher than Oregon and California (Thorson and Wetzel, 2016). The higher total mortality rate across California ports calculated in this study tracks the historical recreational landings of Canary Rockfish, with greater recreational fishing pressure experienced across California followed by Oregon and Washington (Thorson and Wetzel, 2016). Although commercial and recreational fishing opportunities for Canary Rockfish were severely restricted in the 2000s, mortality associated with these fisheries post 2000 was comprised of discard mortality (Thorson and Wetzel, 2016). The greater fishing mortality rates across California ports may reflect the higher discard rates reported for California compared to Washington and Oregon. A combination of unfavorable recruitment, predominantly weak oceanographic conditions, and greater historic removals of large, fecund, reproductive individuals across California likely translated to the higher total mortality rates observed. Similar results were reported for other groundfish species along U.S. West Coast (Hamilton *et al.*, 2011; Fields, 2016; Lam *et al.*, 2019). For example, Hamilton *et al.* (2011) reported significantly higher total mortality rates for California Sheephead from sites with

warmer water, less productivity, and higher fishing pressure when comparing spatially distinct areas throughout the southern California Bight.

Natural mortality (M) of Canary Rockfish exhibited a similar latitudinal trend as total mortality. Natural mortality is often derived from the maximum observed age, A_{max} , therefore an empirically calculated natural mortality rate can be easily skewed and has the potential to be highly variable (Hoenig, 1963; Maunder and Piner, 2015). The current stock assessment model estimates natural mortality of Canary Rockfish based on the oldest observed maximum age of 84 years (Thorson and Wetzel, 2016). Although little research has been done to examine natural mortality across large geographic scales, it can be presumed that in the absence of fishing, fish that live longer (i.e., fishes from northern regions) experience lower natural mortality. Although this trend was observed in my study, it may be confounded by the depths surveyed. Similar to many rockfish species, Canary Rockfishes display ontogenetic migrations, in which adults move into deeper waters as they mature (Love *et al.*, 2002). The variability in M values I observed may have been partially influenced by the variable maximum depths sampled in my study as fish caught from shallower maximum depths tended to have younger maximum ages and thus have greater natural mortality rates.

Cluster Analysis and Implications for Fisheries Management

Results presented in the cluster analysis suggests that the boundaries applied in the most recent Canary Rockfish stock assessment (1 stock, 3 area model) may not be the most biologically appropriate geographic breakpoints for the coastwide population. I found Canary Rockfish port-specific life history parameters to cluster into a northern and southern stock with a break occurring in central Oregon, between the ports of Newport and Coos Bay. The break determined in this study is considerably different from the current boundaries used in the stock assessment and could have important management implications for the Canary Rockfish resource as previous research has demonstrated that incorporating spatially explicit demographic variation into fisheries models can enhance fishery yield (Hamilton *et al.*, 2011; Wilson *et al.*, 2012).

Prior to the 2015 assessment, the Canary Rockfish resource was modeled as a single coastwide stock (Methot and Piner, 2001; Methot and Stewart, 2005; Stewart, 2009; Wallace and Cope, 2011). The most recent Canary Rockfish stock assessment employed a three-area model, corresponding approximately to state boundaries (CA: 32-42°, OR: 42-46°, WA: 46-49° N) to

account for spatial variation in exploitation history among strata, however, the resource is still managed as a single coastwide stock. For data limited groundfish species (i.e., Brown Rockfish, *Sebastodes auriculatus*; English Sole, *Parophrys vetulus*; Greenstriped Rockfish, *S. elongatus*; Rex Sole, *Glyptocephalus zachirus*; Stripetail Rockfish, *S. saxicola*; Sharpchin Rockfish, *S. zacentrus*; and Widow Rockfish, *S. entomelas*), a single coastwide stock is commonly used (Hicks *et al.*, 2009; Cope *et al.*, 2015; Hicks and Wetzel, 2015; Adams *et al.* 2019). As is the case with Canary Rockfish, species with accurate landings information and long-term sampling data (i.e., Black Rockfish, *Sebastodes melanops*; China Rockfish, *Sebastodes nebulosus*; Copper Rockfish, *Sebastodes caurinus*; Lingcod, *Ophiodon elongatus*; Yelloweye Rockfish, *Sebastodes ruberrimus*; Yellowtail Rockfish, *Sebastodes flavidus*) often have two to three coastwide breaks typically corresponding with state jurisdiction boundaries (Cope *et al.*, 2015, 2016; Gertseva and Cope, 2017; Haltuch *et al.*, 2018; Stephens and Taylor, 2018). While spatial variation in life history parameters have been investigated for some of the previously mentioned species, biologically relevant boundaries are rarely applied in stock assessment models as this often results in a lower predictive power in comparison to using historic catch data (Hicks and Wetzel, 2015; Cope *et al.*, 2016; Adams *et al.*, 2019).

Keller *et al.* (2018) reported geographic differences in Canary Rockfish life history and demography, however, the spatial scales at which Canary Rockfish life history varied were different from my study. I used a hierarchical clustering technique to identify subpopulations based on similarities in life history traits among focal ports and found a break in the Canary Rockfish stock to occur just north of Cape Blanco, Oregon. Keller *et al.* (2018) assessed the spatial variability of life history parameters independently and used predetermined regions separated by prominent biogeographic breakpoints (Point Conception and Cape Mendocino, California) along the U.S. West Coast. Discrepancies in the two studies could be a result of the differences in analytical techniques used to delineate stocks. Additionally, there are substantial differences in the habitats sampled in each survey. The majority of biological data collected in the Keller *et al.* (2018) study was acquired through trawl surveys on soft bottom and low-relief habitat, whereas data generated in my study were from hook-and-line sampling that focused on high-relief rocky habitat.

State boundaries are often used to designate areas in stock assessments as they tend to have their own unique history of exploitation that is driven by both fisher behavior and market demand, which affects the commercial and recreational fishing sectors in different ways. However, it is also important to consider latitudinal differences in life history parameters (i.e., longevity, growth, maturity, and mortality) when modeling natural populations and setting catch limits. Moreover, population breaks can often correspond to biogeographic boundaries that occur within state lines, as was found in my study and Keller *et al.* (2018). Therefore, spatially explicit management and assessment methods that incorporate biological population parameters in addition to state-specific historic fishing information could be the key to ensuring successful management and long-term sustainability of marine resources.

Conclusions and Recommendations

During the last few decades, fisheries management has been moving towards developing ecosystem-based management plans incorporating multispecies interactions, environmental fluctuations, and community shifts throughout time and space (Jennings *et al.*, 1999). Unraveling the mechanisms behind why fish populations change over broad latitudinal ranges can be difficult, however, and requires extensive information. The purpose of my study was to explore the latitudinal and sex-specific factors that can impact the life history estimates used in groundfish stock assessment models, as well as provide new information regarding life-history of Canary Rockfish across untrawlable, high relief rocky habitats. Although modeling methods have advanced in recent years, the models are only as good as the data available (Mangel and Levin, 2005; Maunder and Piner, 2015), and insufficient, or inconsistent, indices of abundance and lack of historical harvest information can limit current stock assessments.

Currently, groundfish stock assessment models are generally limited to using biological information derived from the fisheries-independent West Coast Groundfish Bottom Trawl Surveys (WCGBTS). The WCGBTS has served as a crucial resource to the management of groundfishes by providing an index of relative abundance over time, length-frequency distributions, and age-frequency distributions of over 90 groundfish species. However, several studies have shown that groundfish demography and life histories may differ between habitats along the U.S. West Coast (Starr *et al.*, 2016; Lam *et al.*, 2019). Therefore, I suggest a comparative study to assess differences in demography and life history traits of Canary Rockfish

between trawlable (low-relief) and untrawlable (high-relief) habitats. In addition, a comparable long-term survey should be conducted over untrawlable habitats along the U.S. West Coast so that stock assessments are more accurate in representing the demography and life history of populations across rocky reef habitats in which many groundfishes are widely known to associate.

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Table 1. Canary Rockfish maturity stages as defined by Echeverria (1987) and Westrheim (1975).

Sex	Stage	Condition	Description
Female	1	Immature	Ovary small, translucent to pink
	2	Maturing	Ovary small, yellow, translucent or opaque
	3	Vitellogenesis	Ovary large, yellow, opaque
	4	Fertilization	Ovary large, orange to yellow, translucent
	5	Eyed larvae	Ovary large, translucent yellow or gray, with black dots (embryo/larvae spots)
	6	Spent	Ovary large, flaccid, red, a few larvae may be present
	7	Resting	Ovary moderate size, firm, red-gray, some black blotches
Male	1	Immature	Testes small, threadlike, transparent to white at periphery
	2	Maturing	Testes small, ribbonlike, white and triangular
	3	Spermatogenesis	Testes white and swollen, sperm throughout testis in cross section, triangular
	4	Spawning	Testes large, soft, white – sperm flows freely when cut
	5	Recently Spawned/ Resting	Testes becoming firm and dark gray-brown

Table 2. Average coefficient of variation (AVC), average percent error (APE), and percent agreement between 2 agers: R. Brooks and the NWFSC Cooperative Aging Project (CAP) lab.

	n	ACV	APE	% Agreement
Brooks: CAP Lab	534	6.03	4.27	53%
Brooks: Brooks	446	2.06	1.45	88%

Table 3. Catch summary by port. Number of ports were chosen based on CPFV location and availability. Each port was fished an average of 3.2 days.

Port	Days Fished	Female			Percent Female			Depth (m)			Total Length (cm)		Age (years)	
		N	N	N	Mean	Min	Max	Min	Max	Min	Max	Min	Max	
Coastwide	42	761	798	8	48.6	89	20	185	15.9	63.4	2	51		
Neah Bay	8	61	108	2	36.1	91	20	137	16.2	61.9	3	51		
Westport	3	143	120	-	54.4	105	49	152	21.2	62.1	3	41		
Garibaldi	2	52	49	1	51.5	105	59	138	23.6	61.6	3	36		
Newport	3	57	65	-	46.7	143	23	185	25.2	63.4	4	31		
Coos Bay	2	32	30	-	51.6	46	28	119	23.5	57.9	3	25		
Brookings	1	52	86	2	37.7	62	28	79	18.1	51.2	3	17		
Eureka	2	66	33	2	66.7	59	29	101	20	57.5	3	22		
Fort Bragg	2	50	50	-	50.0	67	27	91	15.9	50.9	2	22		
Bodega Bay	4	50	56	-	47.2	85	22	130	18.3	53.1	3	27		
Half Moon Bay	3	50	63	-	44.2	76	36	127	28	51.1	4	29		
Moss Landing	3	46	38	-	54.8	75	22	91	23.2	53.1	3	17		
Morro Bay	5	55	45	1	55.0	86	34	102	26.9	47.9	4	10		
Santa Barbara	4	47	55	-	46.1	119	104	131	35.8	55	6	29		

Table 4. Von Bertalanffy growth function (VBGF) parameters L_{inf} and k , average oldest age, and maximum sampled age (T_{max}) of coastwide male and female Canary Rockfish, respectively. ± 1 standard error (SE) for L_{inf} , k , and average oldest age estimates denoted in parentheses.

Sex	k (SE)	L_{inf} (SE)	Age of Top Quartile (SE)	Maximum Sampled Age (T_{max})
Male	0.191 (0.0001)	52.7 (0.1)	21.8 (0.39)	51
Female	0.167 (0.0001)	58.3 (0.2)	17.2 (0.33)	33

Table 5. Coastwide male and female Canary Rockfish length (L_{50}) and age (A_{50}) at 50% maturity with lower and upper 95% confidence intervals (CI) in parentheses.

Sex	L_{50} (cm)	Lower CI	Upper CI	A_{50} (year)	Lower CI	Upper CI
Male	39.6	39.2	40.2	7.6	7.3	7.9
Female	39.8	39.2	40.4	7.1	6.8	7.3

Table 6. Total (Z), natural (M), and fishing (F) mortality rates for each region. ± 1 standard error (SE) for Z estimates denoted in parentheses.

Sex	Z (SE)	M	F
Male	0.11 (0.01)	0.09	0.02
Female	0.17 (0.01)	0.13	0.04

Table 7. Von Bertalanffy growth function (VBGF) parameters L_{inf} and k , average oldest age, and maximum sampled age (T_{max}) for Canary Rockfish collected out of each sampling port (sexes pooled). Average oldest age was calculated using the mean upper quartile of observed ages. ± 1 standard error (SE) for L_{inf} , k , and average oldest age estimates denoted in parentheses.

Port	k (SE)	L_{inf} (SE)	Age of Top Quartile (SE)	Maximum Sampled Age (T_{max})
Coastwide	0.183 (0.0060)	54.8 (0.3)	19.7 (0.28)	51
Neah Bay	0.184 (0.0002)	55.1 (0.02)	26.41 (0.78)	51
Westport	0.183 (0.0002)	56.1 (0.02)	24.40 (0.63)	41
Garibaldi	0.204 (0.0003)	54.2 (0.02)	21.26 (0.89)	36
Newport	0.198 (0.0003)	54.5 (0.02)	22.94 (0.56)	31
Coos Bay	0.242 (0.0007)	50.9 (0.06)	11.17 (1.31)	25
Brookings	0.235 (0.0007)	46.2 (0.06)	8.64 (0.41)	17
Eureka	0.187 (0.0004)	56.0 (0.06)	13.33 (0.61)	22
Fort Bragg	0.223 (0.0006)	47.6 (0.06)	9.03 (0.68)	22
Bodega Bay	0.190 (0.0004)	51.0 (0.05)	13.71 (1.01)	27
Half Moon Bay	0.263 (0.0004)	44.8 (0.06)	9.36 (0.76)	29
Moss Landing	0.222 (0.0005)	52.5 (0.05)	10.0 (0.61)	17
Morro Bay	0.216 (0.0010)	49.5 (0.09)	8.35 (0.09)	10
Santa Barbara	0.282 (0.0007)	48.6 (0.03)	13.28 (0.82)	29

Table 8. Canary Rockfish length (L_{50}) and age (A_{50}) at 50% maturity (sexes pooled) with lower and upper 95% confidence intervals (CI).

Port	L_{50} (cm)	Lower CI	Upper CI	A_{50} (years)	Lower CI	Upper CI
Coastwide	39.8	39.4	40.1	7.3	7.2	7.5
Neah Bay	44.2	42.7	45.9	8.7	7.9	9.3
Westport	44.8	43.5	46.1	9.0	8.5	10.0
Garibaldi	44.7	43.1	46.2	8.9	8.0	10.0
Newport	44.8	43.4	46.1	9.2	8.5	9.9
Coos Bay	40.8	39.5	42.3	7.3	6.3	8.9
Brookings	41.7	40.0	43.0	9.3	8.7	9.8
Eureka	38.6	38.0	39.0	6.6	6.1	7.1
Fort Bragg	36.9	36.1	38.0	6.9	6.4	7.5
Bodega Bay	41.5	40.3	42.5	8.4	7.8	9.0
Half Moon Bay	37.4	36.6	38.2	7.1	6.5	7.7
Moss Landing	36.2	34.9	37.9	5.4	5.0	5.9
Morro Bay	37.7	36.6	38.8	6.7	6.0	7.2
Santa Barbara	34.1	9.5	38.6	5.5	5.9	7.2

Table 9. Total (Z), natural (M), and fishing (F) mortality rates for each region. F was left blank in cases where M exceeds Z (resulting in a negative F). ± 1 standard error (SE) for Z estimates denoted in parentheses.

Port	Z (SE)	M	F
Coastwide	0.14 (0.01)	0.09	0.06
Neah Bay	0.12 (0.02)	0.09	0.04
Westport	0.14 (0.03)	0.11	0.04
Garibaldi	0.11 (0.04)	0.12	--
Newport	0.12 (0.02)	0.14	--
Coos Bay	0.24 (0.05)	0.17	0.07
Brookings	0.28 (0.07)	0.26	0.02
Eureka	0.30 (0.08)	0.20	0.10
Fort Bragg	0.30 (0.08)	0.20	0.10
Bodega Bay	0.19 (0.04)	0.16	0.02
Half Moon Bay	0.19 (0.04)	0.15	0.04
Moss Landing	0.36 (0.13)	0.26	0.11
Morro Bay	0.23 (0.06)	0.44	--
Santa Barbara	0.15 (0.05)	0.15	0.00

Table 10. L_{inf} , k , average oldest age, T_{max} , length at 50% maturity (L_{50}), age at 50% maturity (A_{50}), Total mortality (Z), natural mortality (M), and fishing mortality (F) estimates for male and female Canary Rockfish from northern and southern cluster regions. ± 1 standard error (SE) denoted in parentheses.

Cluster Region	Sex	k (SE)	L_{inf} (SE)	Age of Top Quartile (SE)	Maximum Sampled Age (T_{max})	L_{50} (cm)	A_{50} (years)	Z (SE)	M	F
North	Male	0.195 (0.0001)	53.3 (0.01)	25.6 (0.51)	51	43.8	8.9	0.04 (0.01)	0.09	--
	Female	0.172 (0.0001)	58.6 (0.02)	21.0 (0.42)	36	46.1	9.1	0.08 (0.02)	0.13	--
South	Male	0.225 (0.0003)	48.4 (0.02)	11.3 (0.45)	29	39.0	7.4	0.23 (0.05)	0.15	0.08
	Female	0.185 (0.0002)	54.9 (0.03)	9.9 (0.22)	21	38.4	6.6	0.38 (0.05)	0.21	0.17

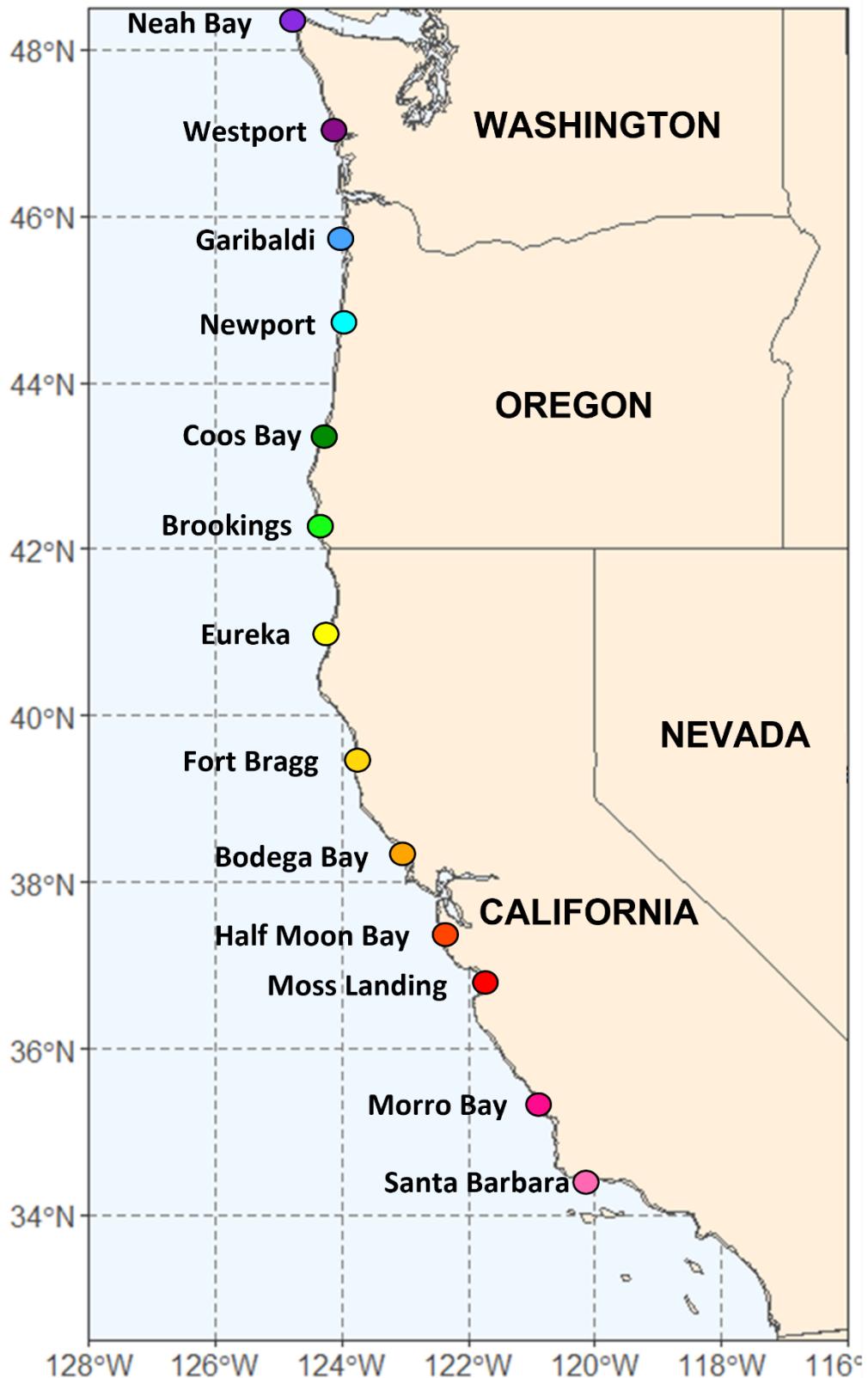


Figure 1. Map of study sites highlighting fishing ports used for collection trips to sample Canary Rockfish.

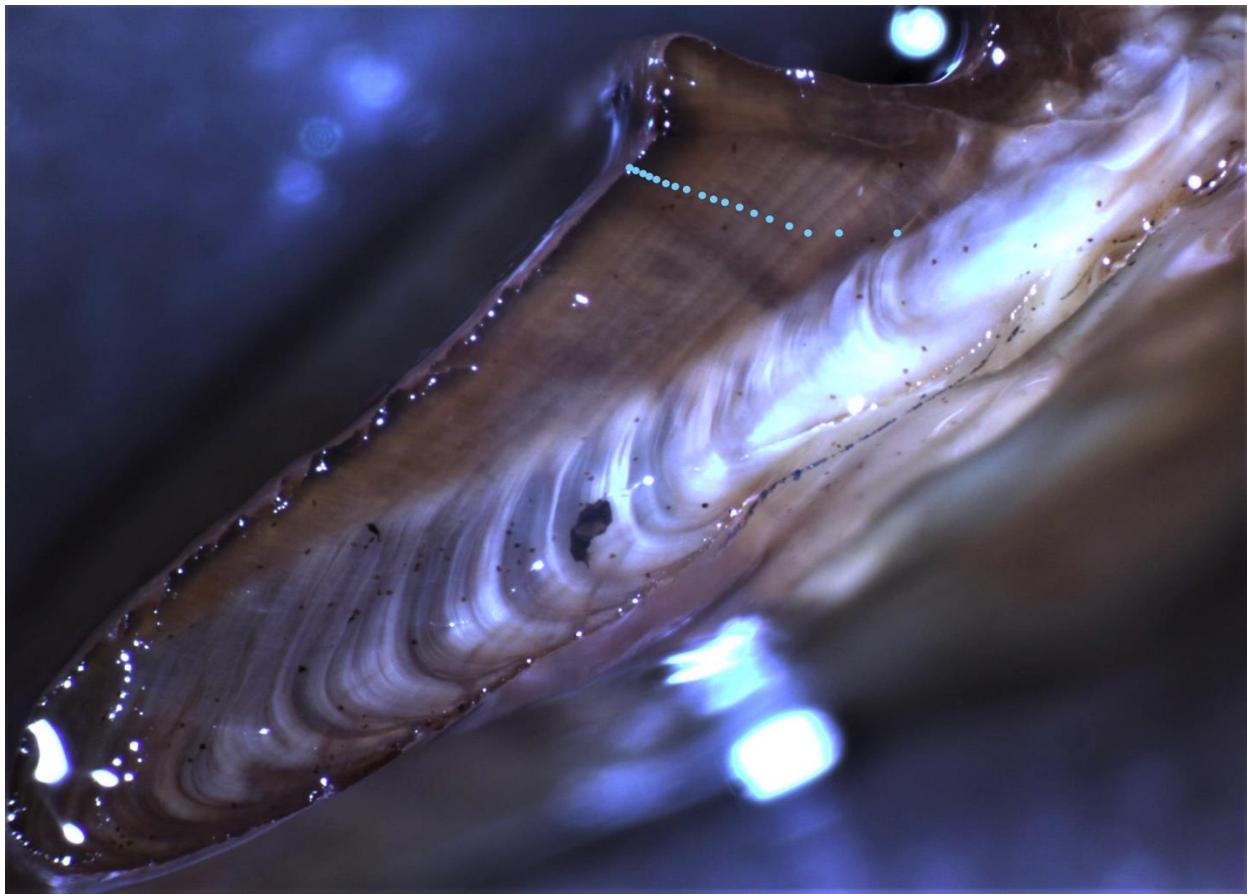


Figure 2. Transverse section of a Canary Rockfish otolith. Light blue dots indicate annual bands used to age each fish. This Canary rockfish was aged to be 18 years old.

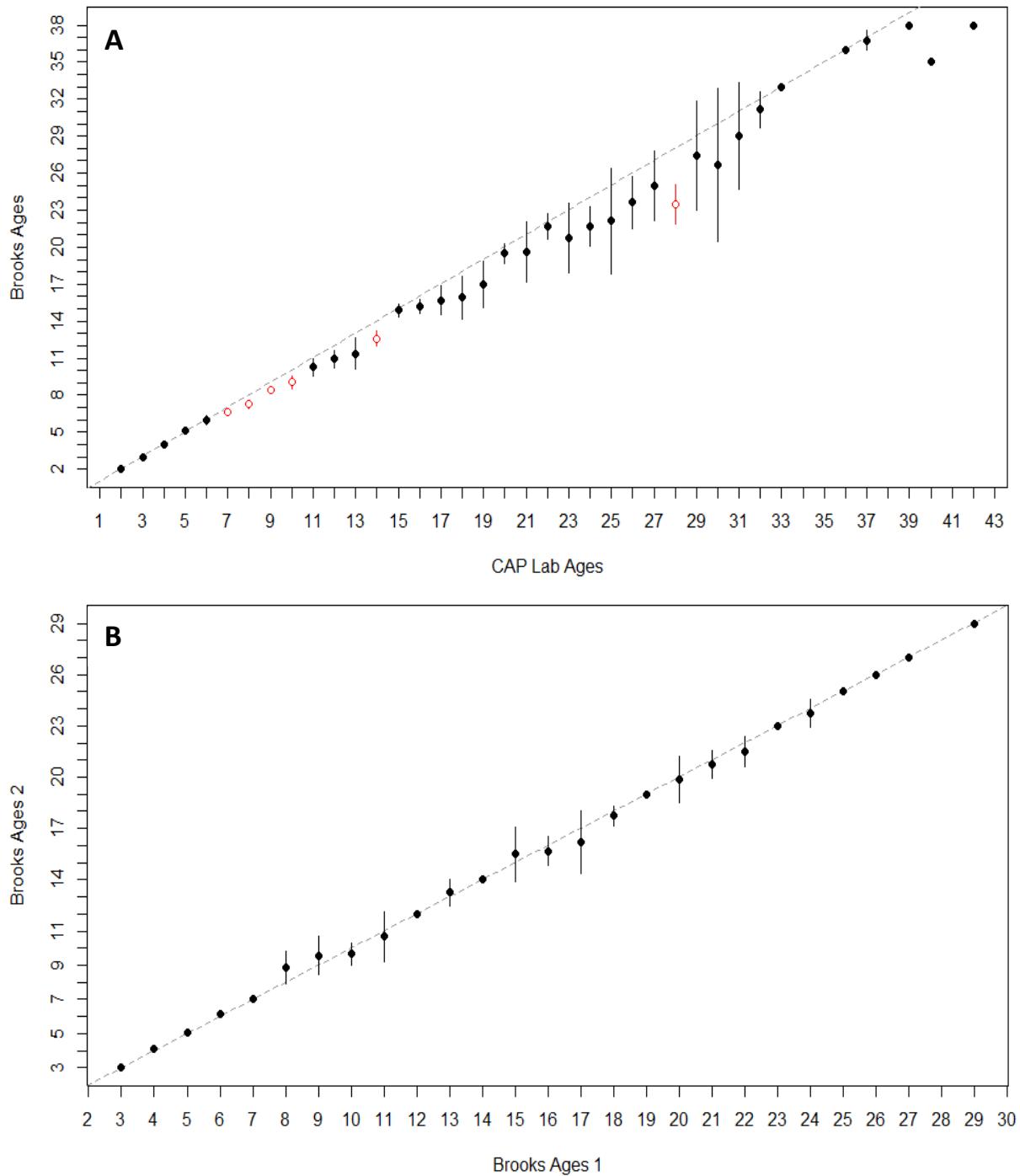


Figure 3. Age-agreement plots between (A) Brooks and CAP Lab, (B) first and second reads of the same otolith by the same reader (Brooks). The dashed 1:1 agreement line is shown for comparative purposes.

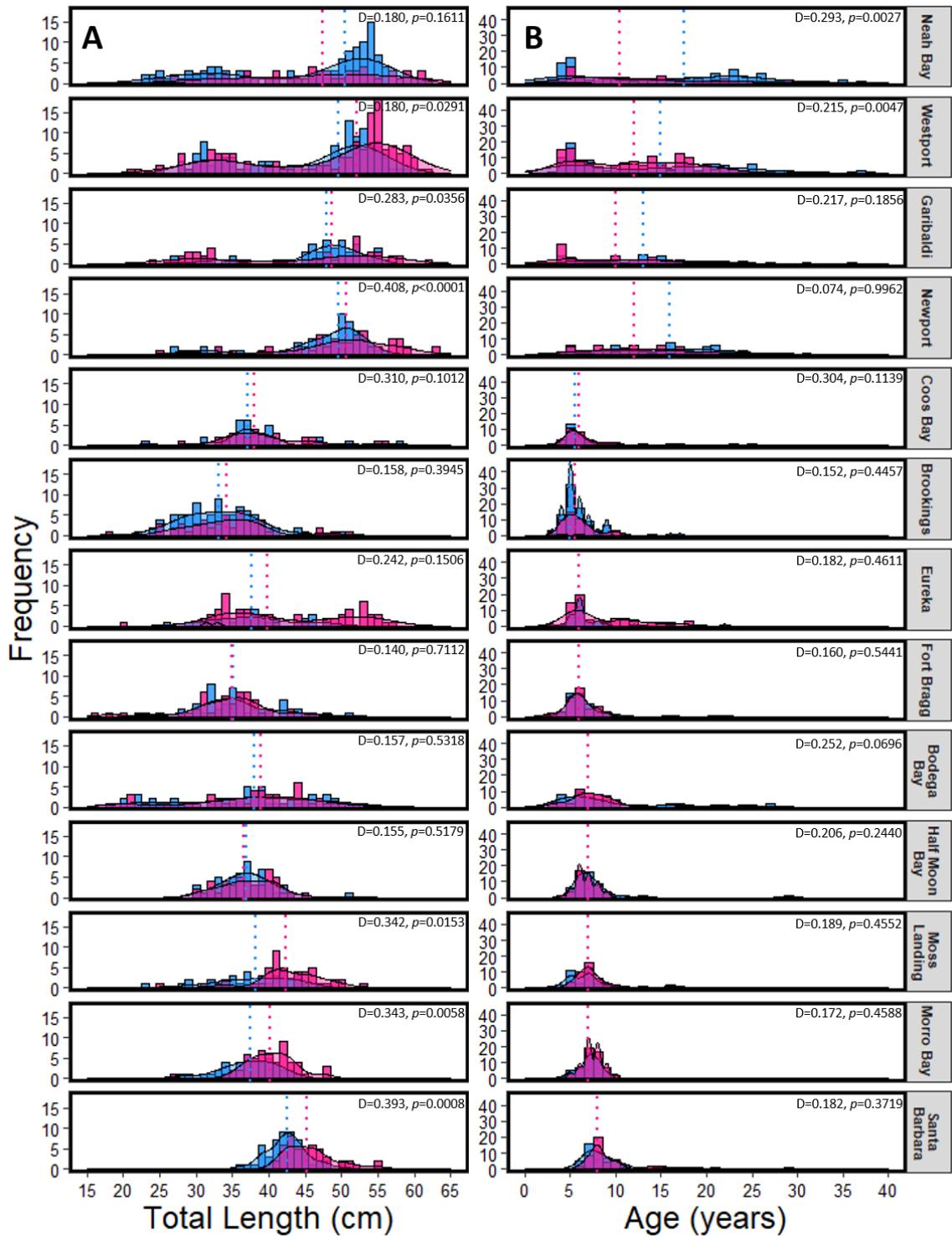


Figure 4. (A) Length and (B) age frequency distribution for male (blue) and female (pink) Canary Rockfish. Ports are arranged by decreasing latitude. Blue and Pink dashed vertical lines indicate median size for each sex.

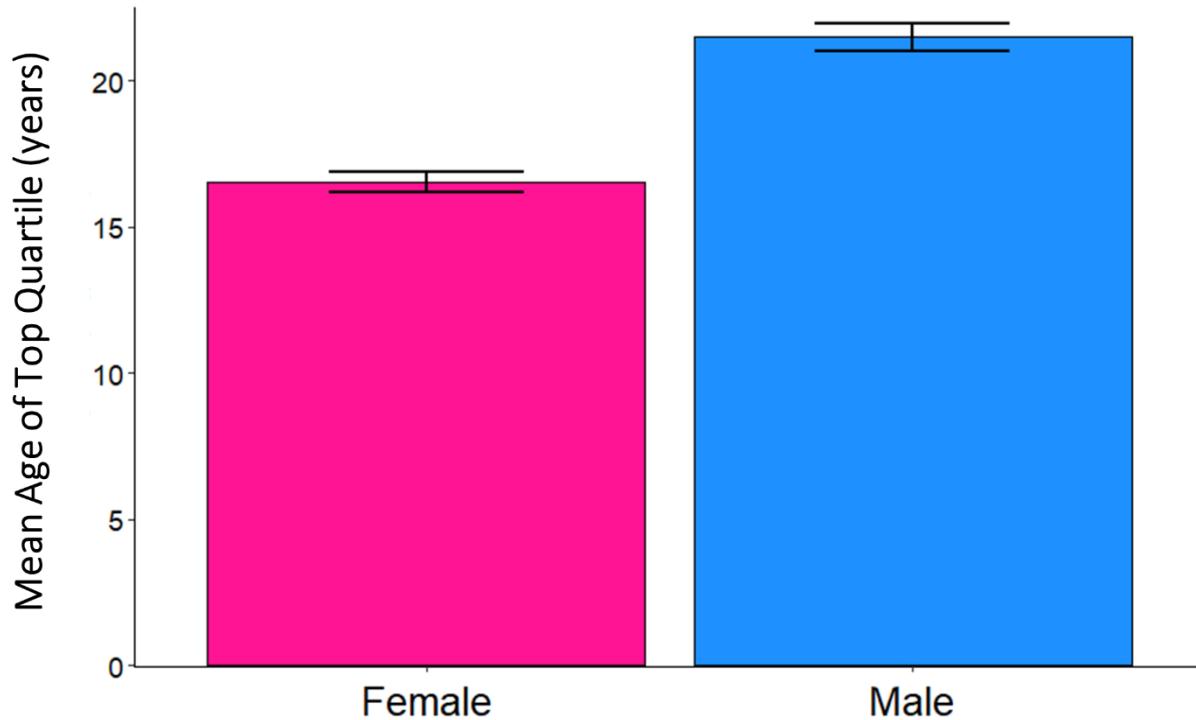


Figure 5. Average oldest age of male and female Canary Rockfish. Error bars indicate ± 1 standard error.

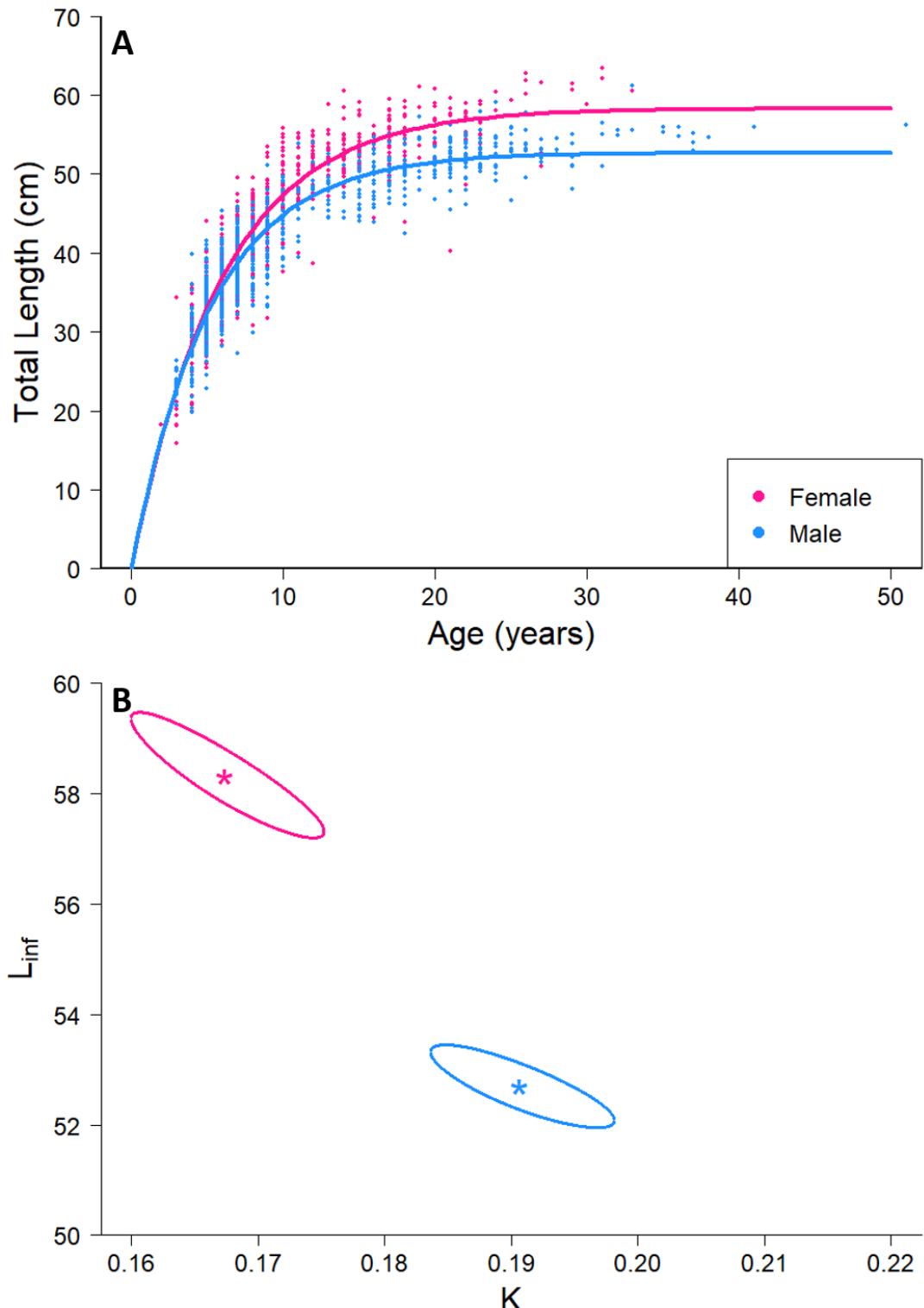


Figure 6. Coastwide male and female Canary Rockfish (A) lifetime growth curves, and (B) 95% confidence ellipses of L_{inf} and k growth parameters. Overlapping ellipses indicate no difference in k and L_{inf} .

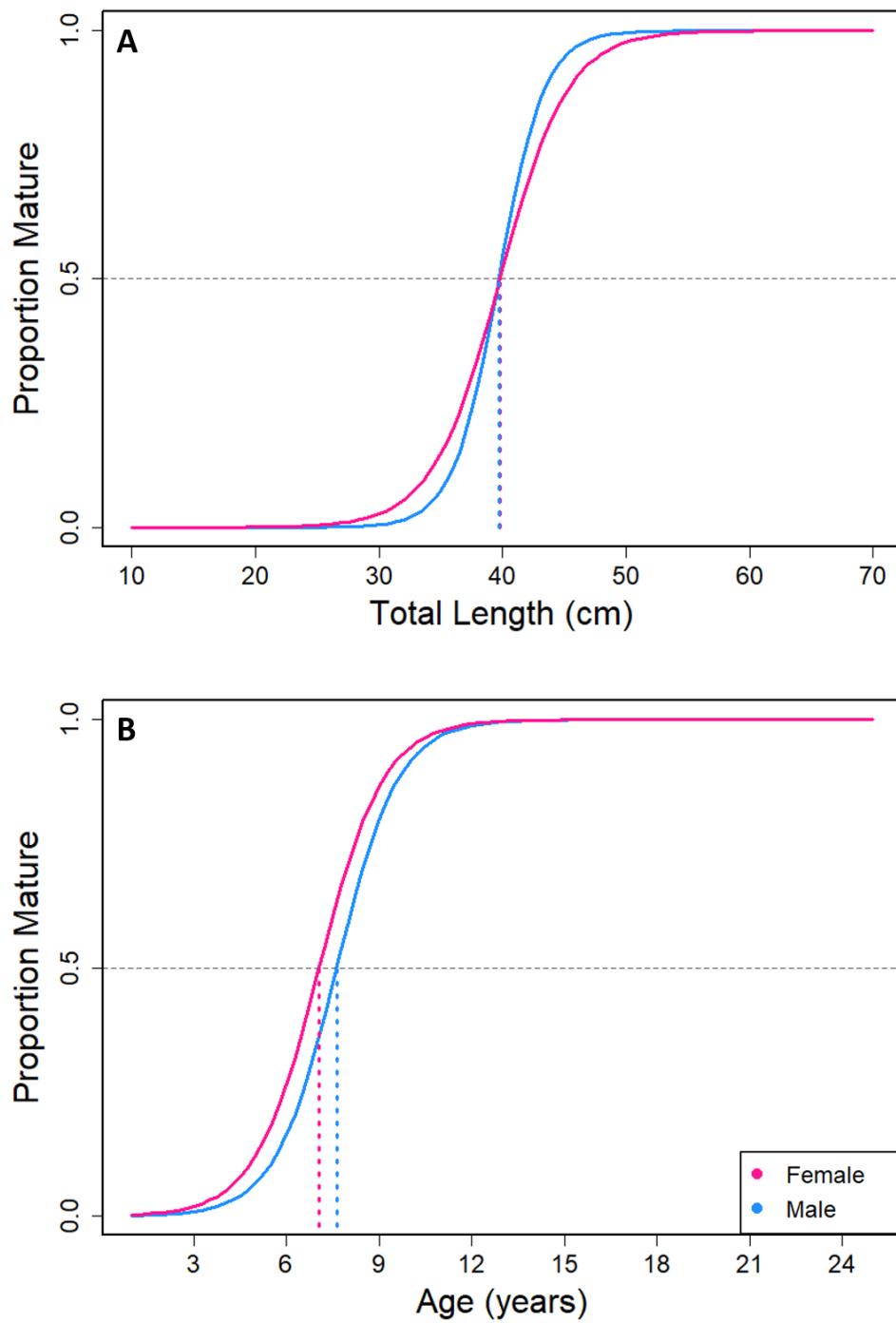


Figure 7. Maturity curves fitted to (A) total length (cm) and (B) age (years) for male (blue) and female (pink) Canary Rockfish collected coastwide. Black horizontal dashed lines indicate the threshold for identifying when 50% of the population is mature. Dashed vertical lines indicate size or age at 50% maturity for males and females.

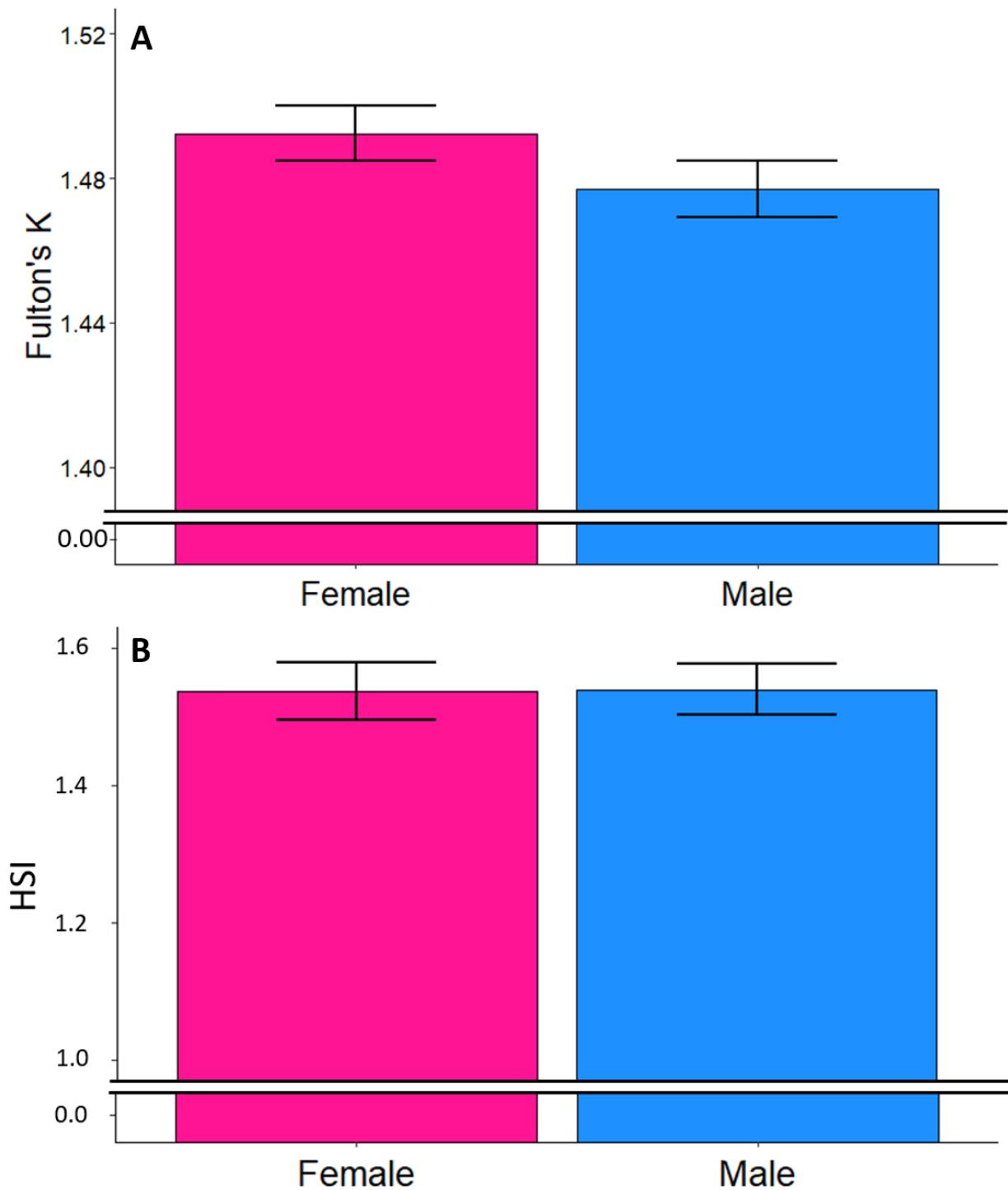


Figure 8. Mean (A) Fulton's K condition index and (B) hepatosomatic index (HSI) for coastwide male and female Canary Rockfish, respectively. Error bars indicate ± 1 standard error.

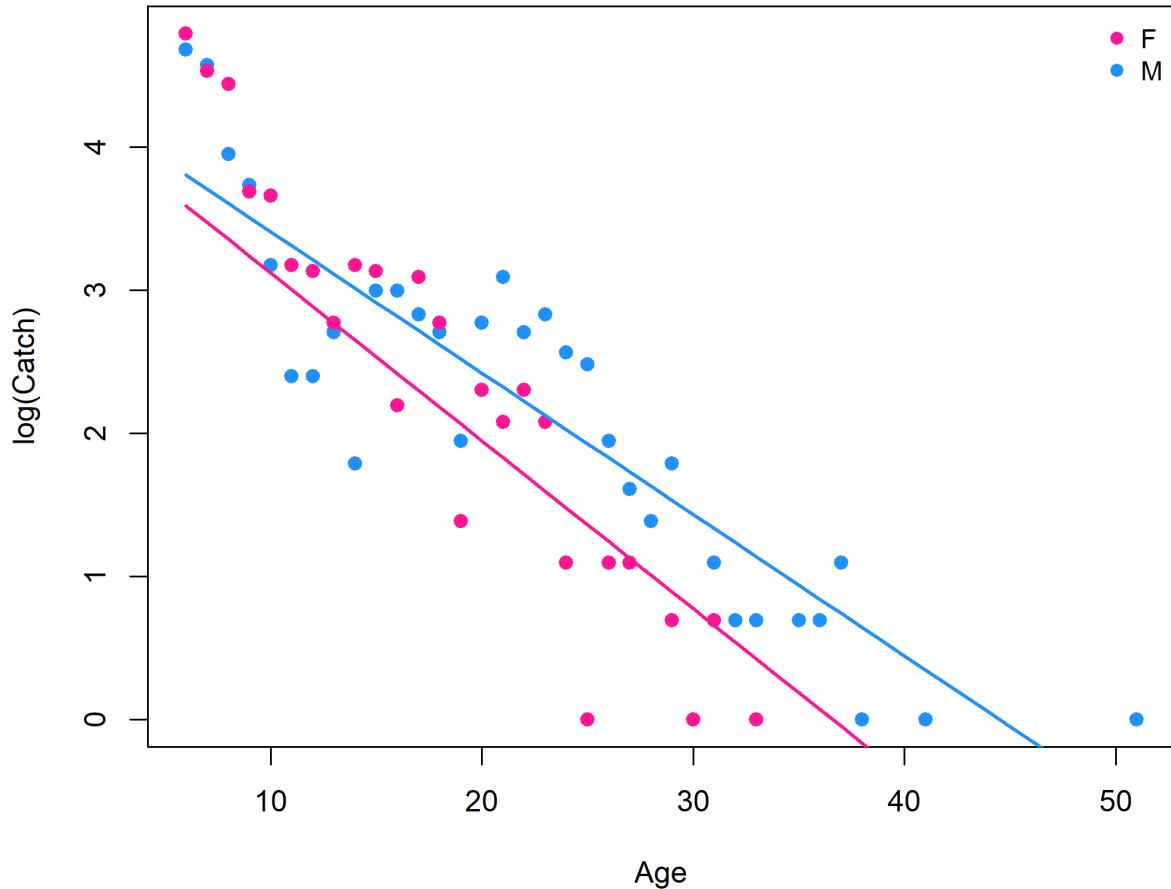


Figure 9. Age based catch curve estimates of annual mortality rates from log-linear regression of age frequency data for male and female Canary Rockfish.

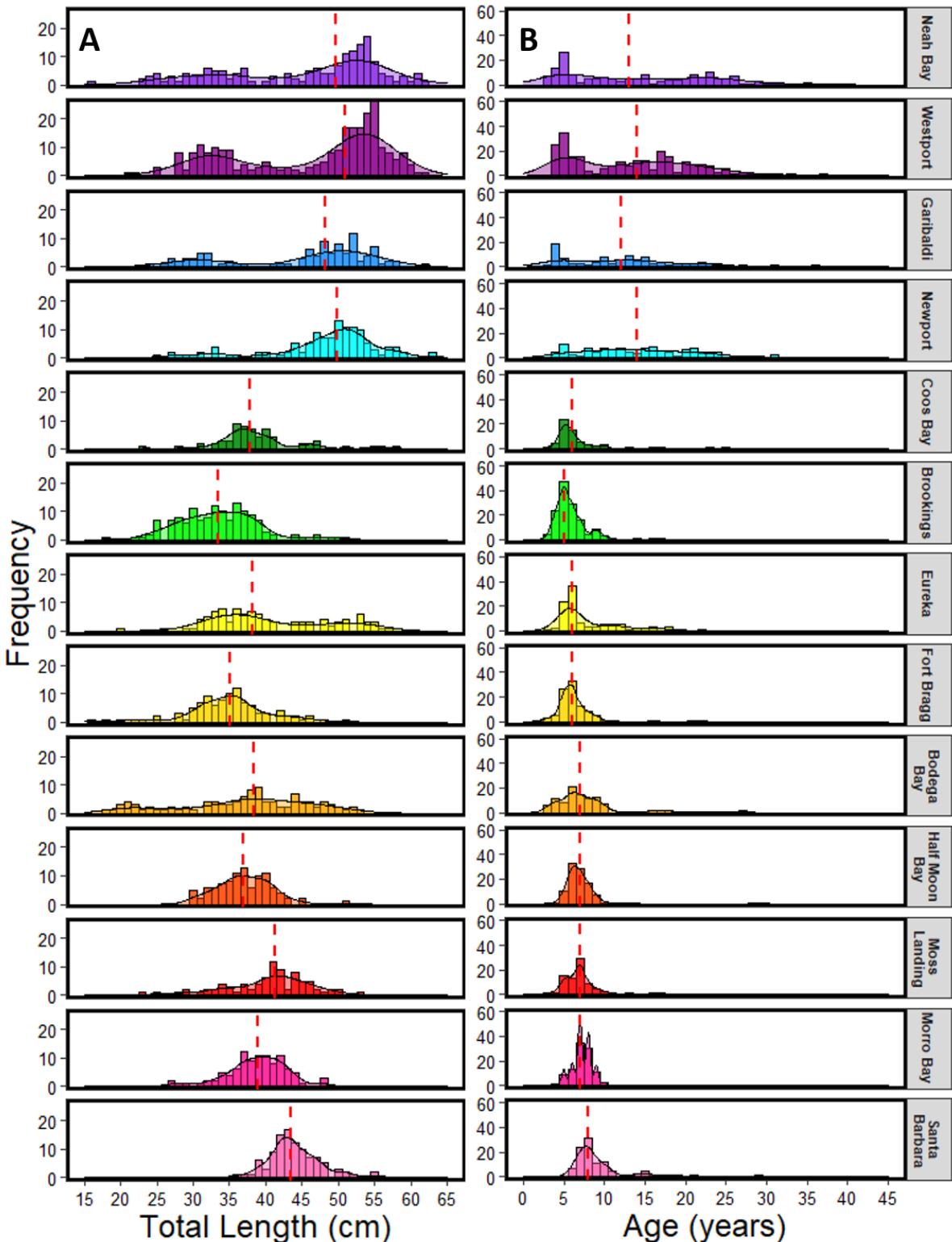


Figure 10. (A) Length and (B) age frequency distributions for Canary Rockfish from each sampling port (sexes pooled). Ports are arranged by decreasing latitude. Red dashed vertical lines indicate median size.

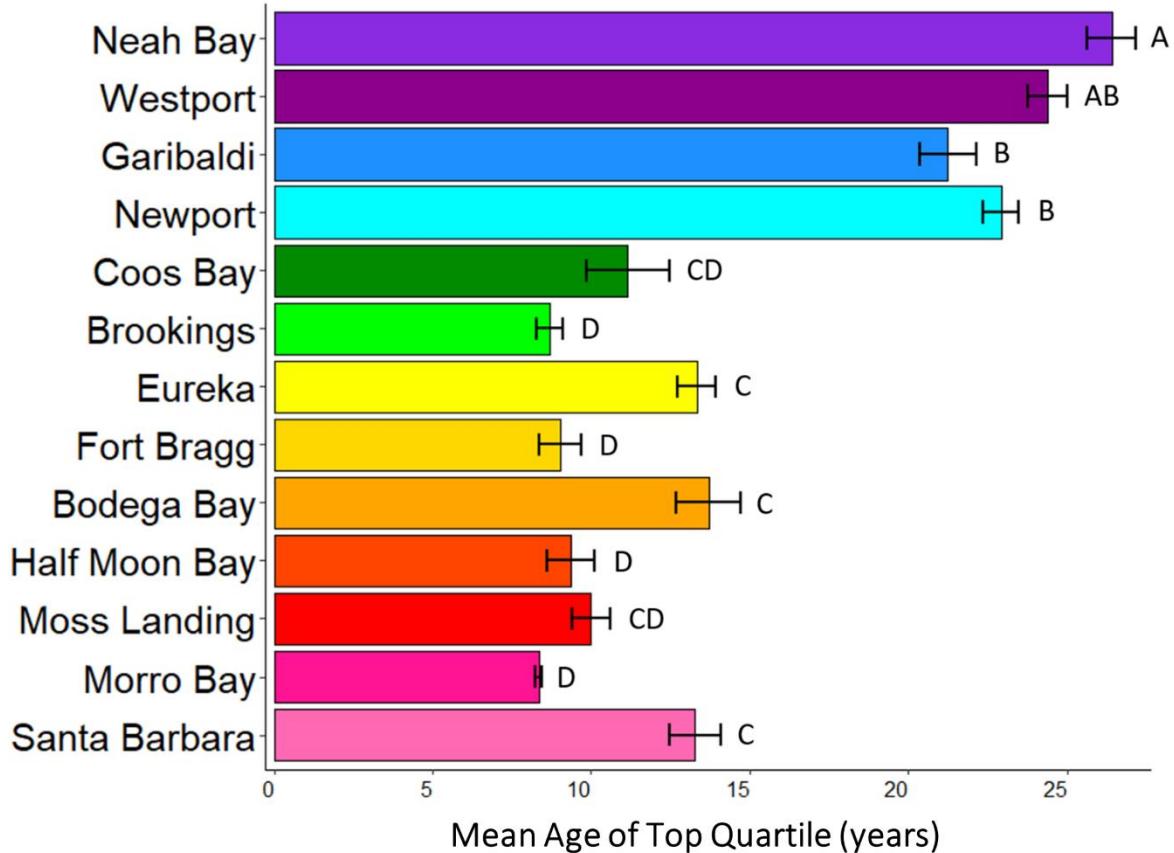


Figure 11. Average oldest age of Canary Rockfish collected from each port. Error bars indicate ± 1 standard error. Letters above bars denote significantly different ports as determined by Tukey's HSD tests.

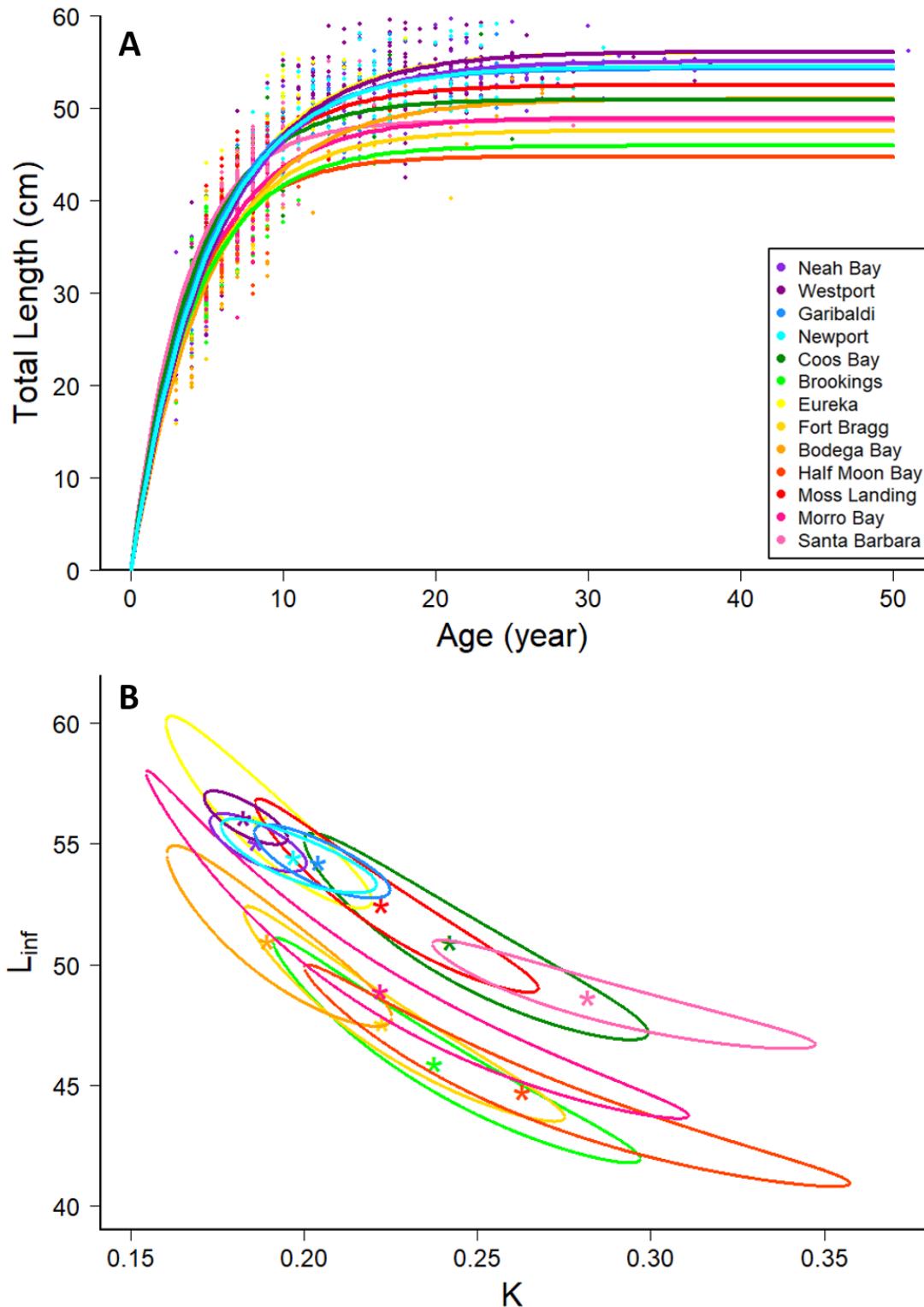


Figure 12. (A) Canary Rockfish lifetime growth curves across 13 different sampling ports with sexes pooled, and (B) 95% confidence intervals from L_{inf} and k for each sampling port. Overlapping intervals indicate no difference in k and L_{inf} .

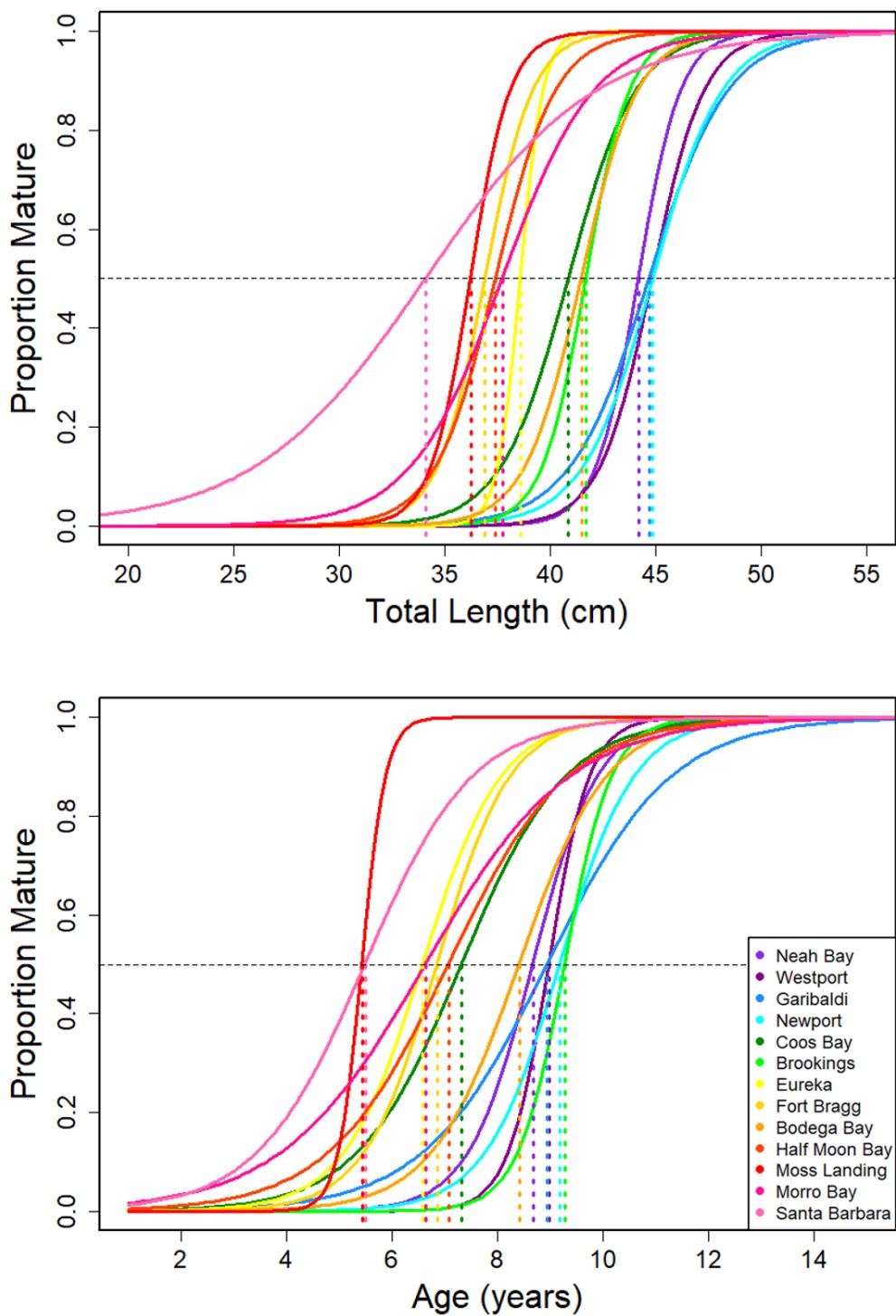


Figure 13. Maturity curves fitted to (A) total length (cm) and (B) age (years) for Canary Rockfish (sexes pooled) collected from their respective sampling port. Black horizontal dashed line indicates the threshold for identifying when 50% of the population is mature. The size and age at 50% maturity for respective ports is indicated by vertical dashed lines.

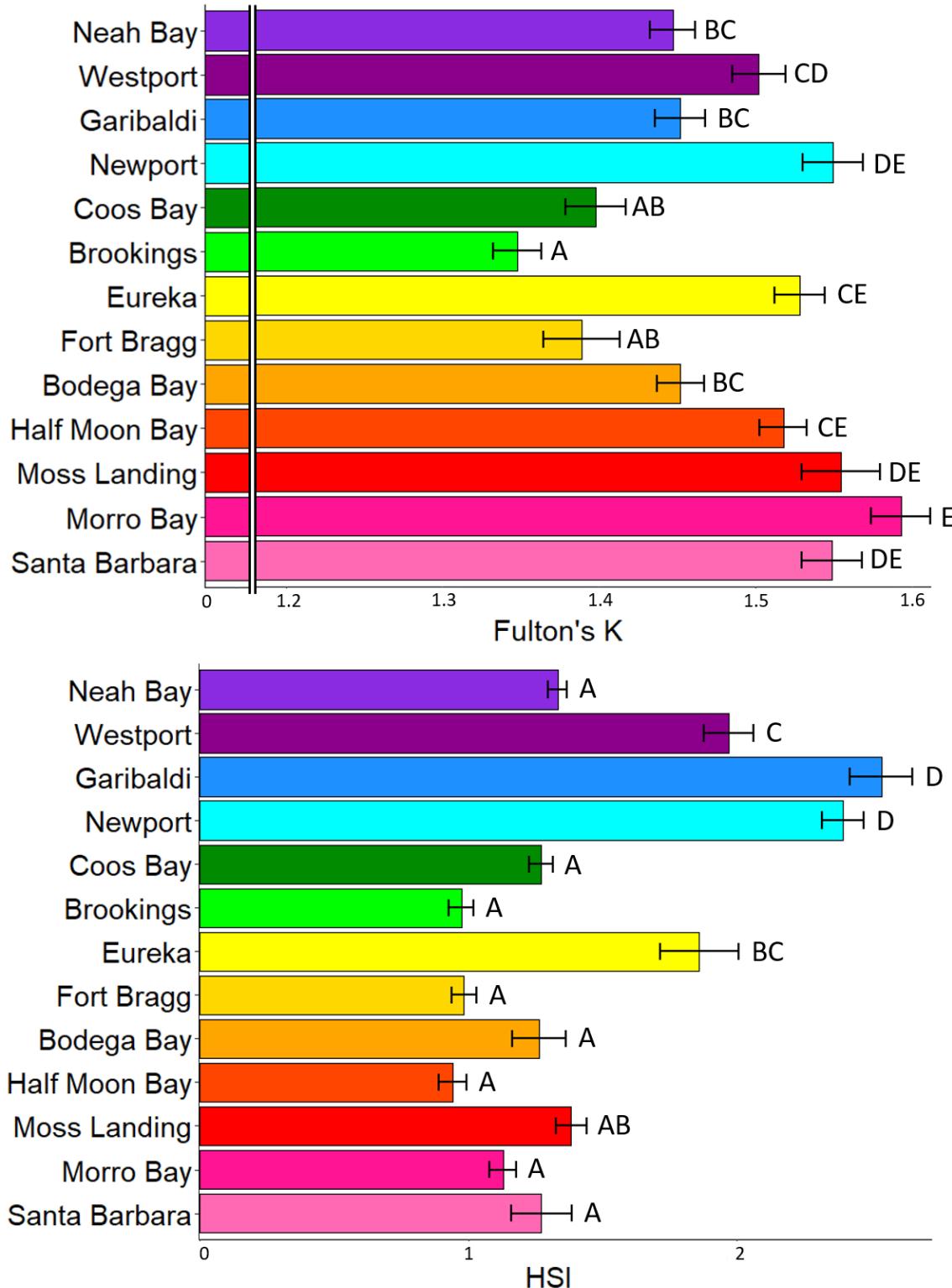


Figure 14. Mean (A) Fulton's K condition index and (B) hepatosomatic index (HSI) for each port. Error bars indicate ± 1 standard error. Letters above bars denote significantly different groups as determined by Tukey's HSD post hoc tests.

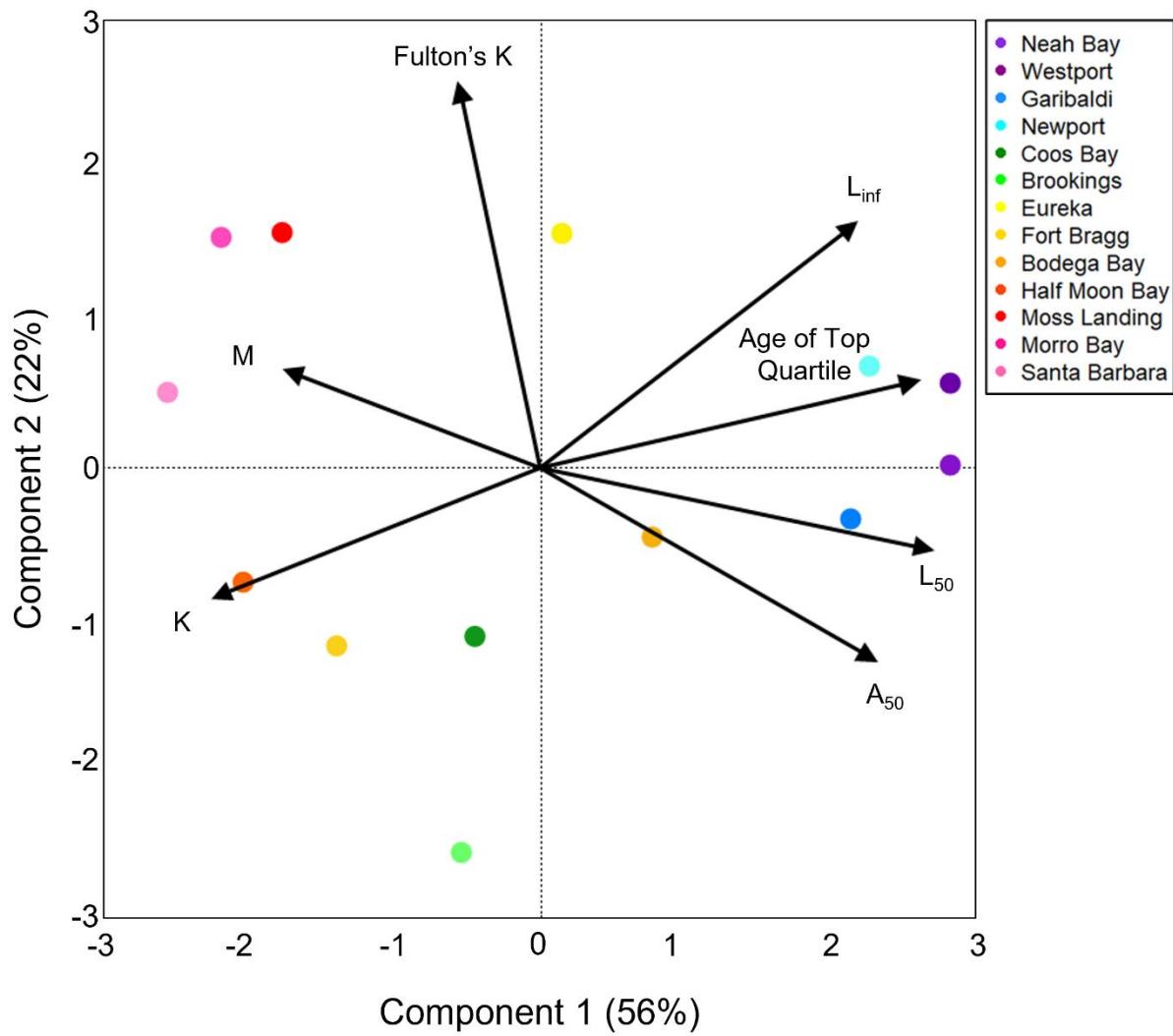


Figure 15. Principal components analysis (PCA) factor loadings for 7 life-history traits calculated for each sampling port. Principal component (PC) 1 and 2 together comprise 78% of the variance seen in the dataset.

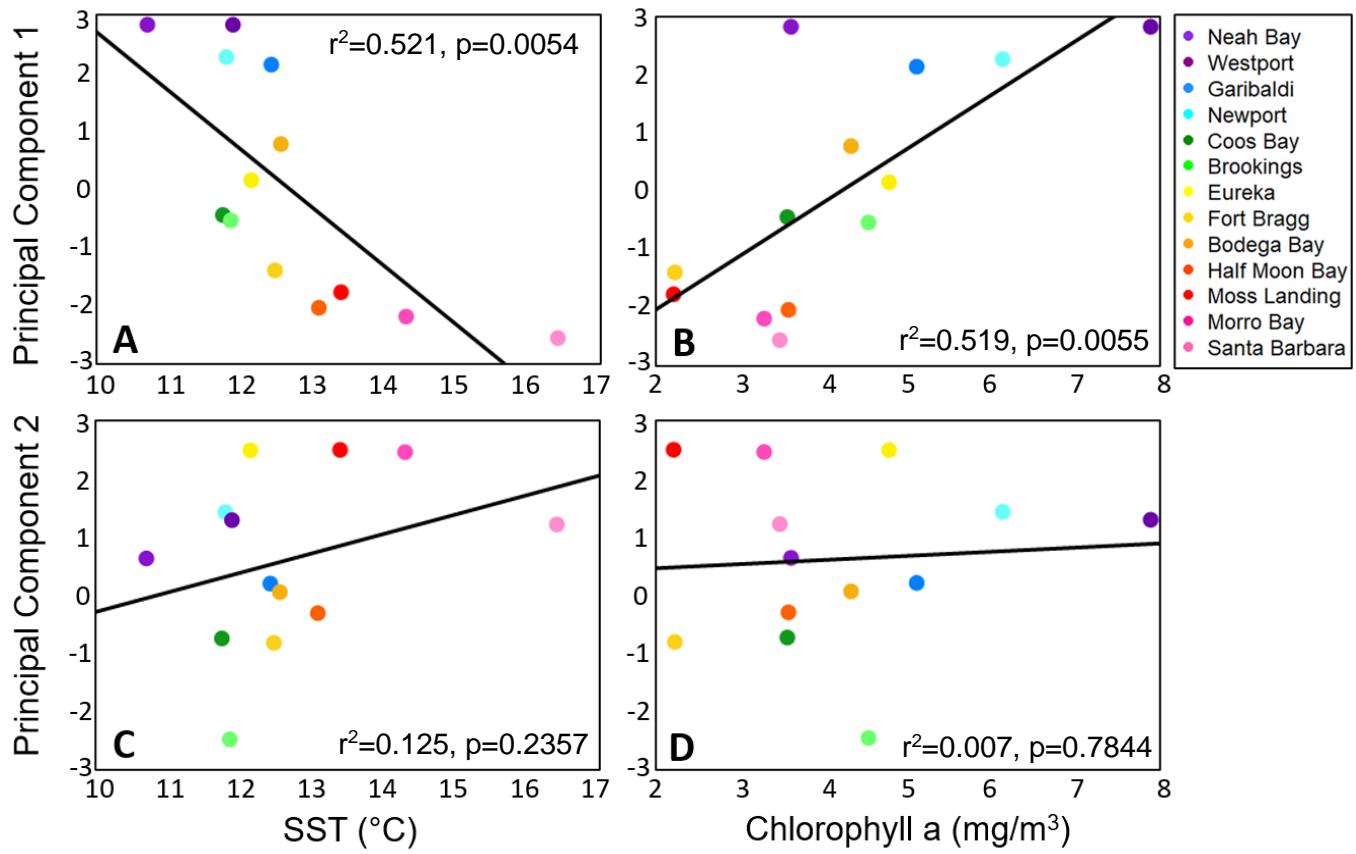


Figure 16. Linear regression between (A) PC1 and sea surface temperature (SST), (B) PC1 and chlorophyll *a*, (C) PC2 and SST, and (D) PC2 and chlorophyll *a*. PC1 is a measure of size, age, and maturity, where positive values of PC1 are correlated with increased ages, larger size, and later maturity. Negative values of PC1 are correlated with decreased VBGF parameter *k* and natural mortality rates (*M*). PC2 is an indicator of overall condition, where positive values of PC2 correlate with greater Fulton's *K*.

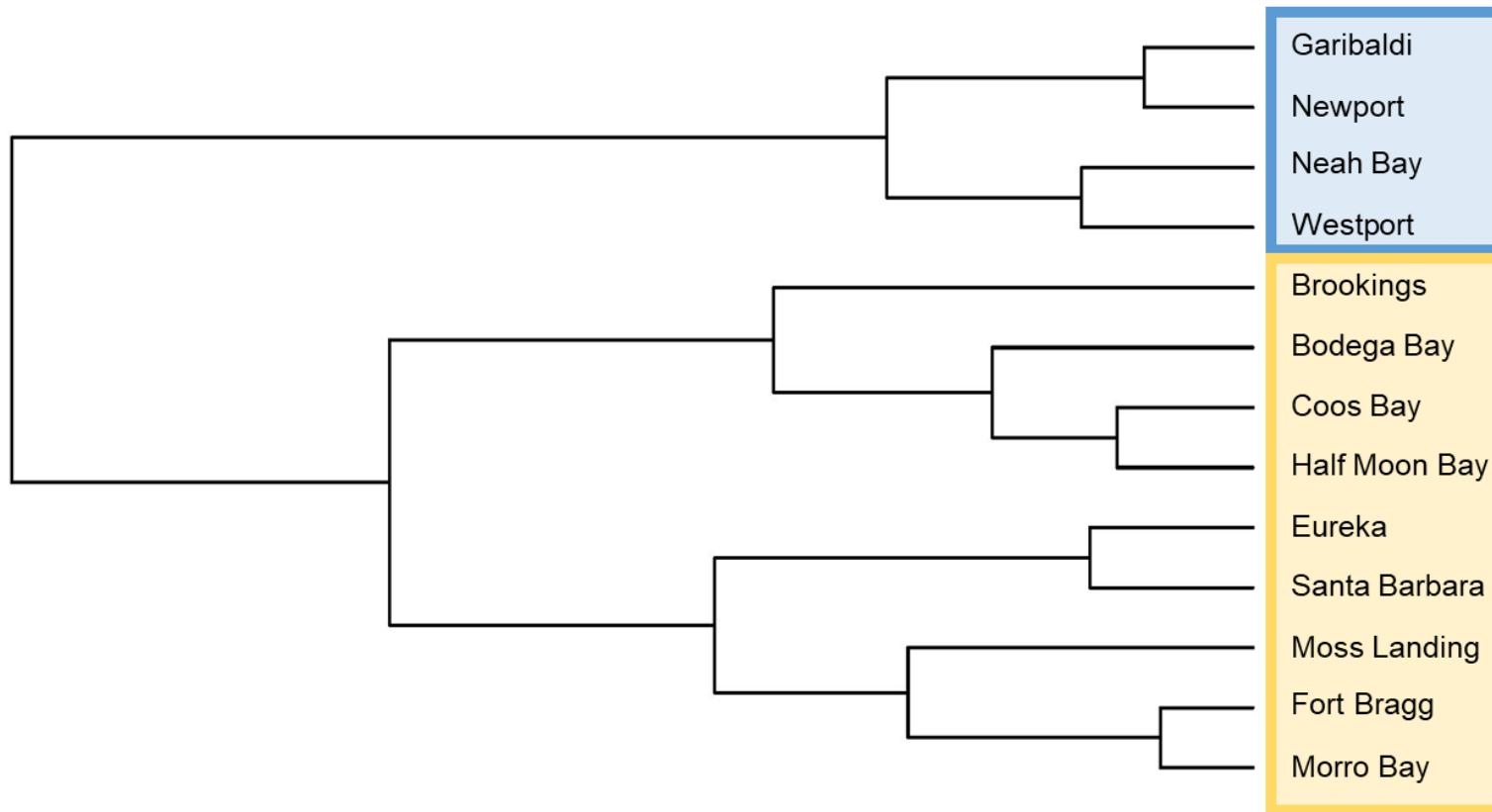


Figure 17. Dendrogram depicting results from agglomerative cluster analysis. Euclidian distances were calculated among ports using normalized life-history traits: VBGF parameters L_{inf} and k , length at 50% maturity (L_{50}), age at 50% maturity (A_{50}), Fulton's K , average oldest age, and natural mortality (M) and clustered using complete-linkage techniques. Two clusters (southern cluster highlighted in orange and northern cluster highlighted in blue) were identified using the average silhouette width.

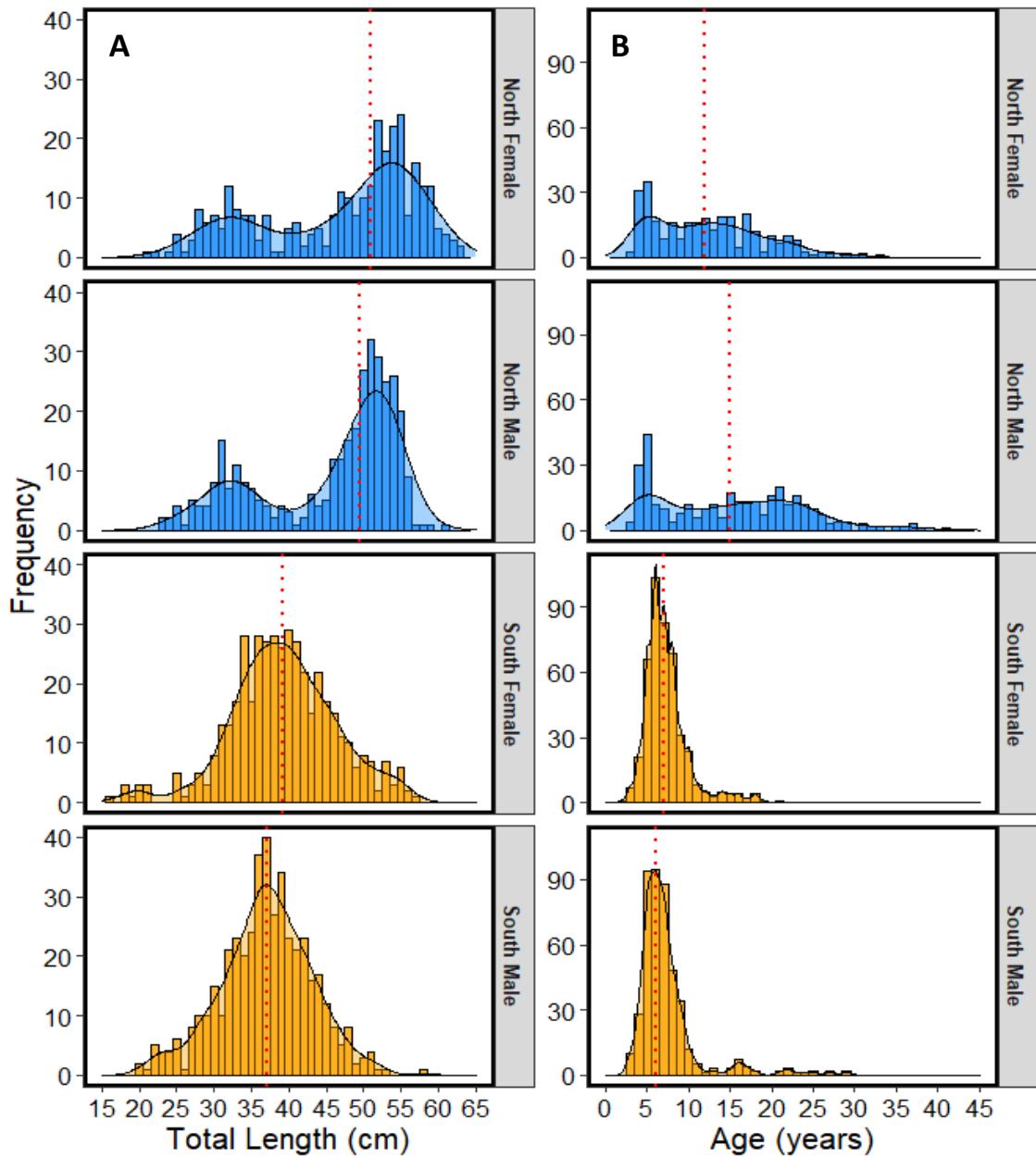


Figure 18. (A) Length and (B) age frequency distribution for male and female Canary Rockfish in northern (blue) and southern (orange) cluster regions. Red dashed vertical lines indicate median size.

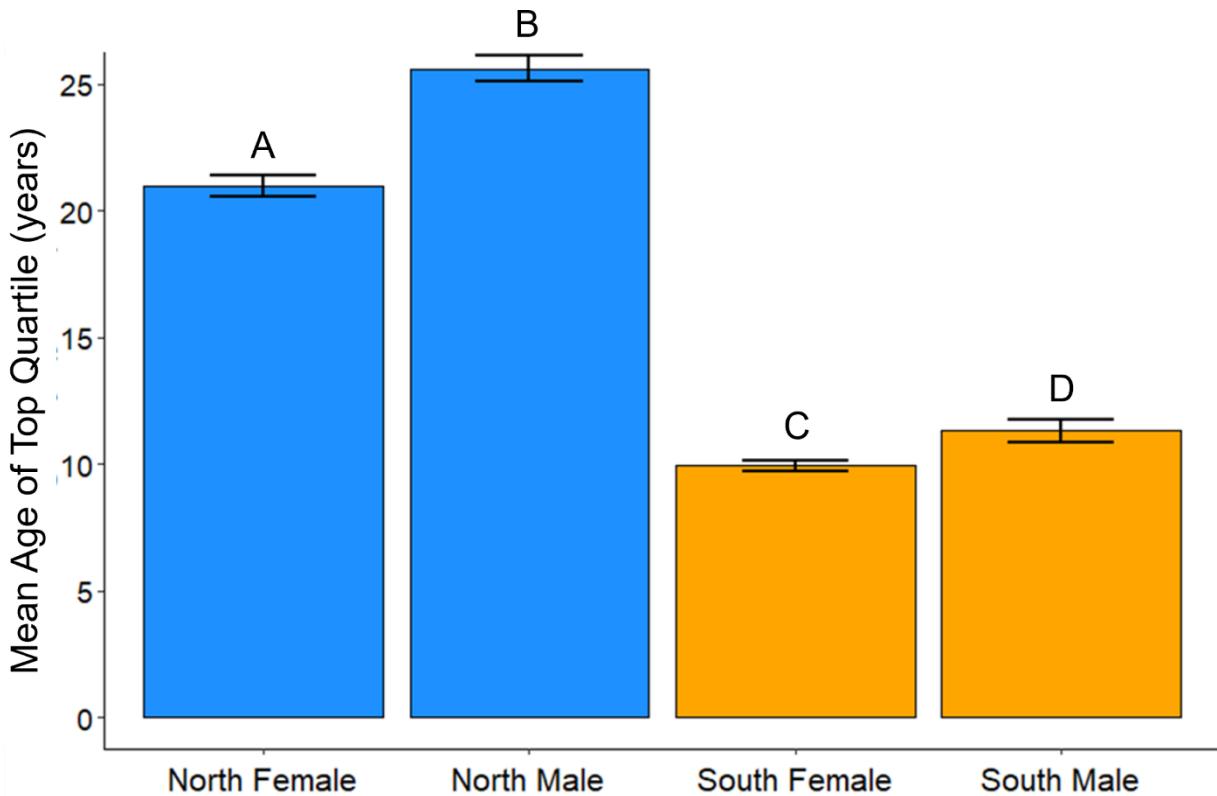


Figure 19. Average oldest age for male and female Canary Rockfish in northern and southern cluster regions. Error bars indicate ± 1 standard error.

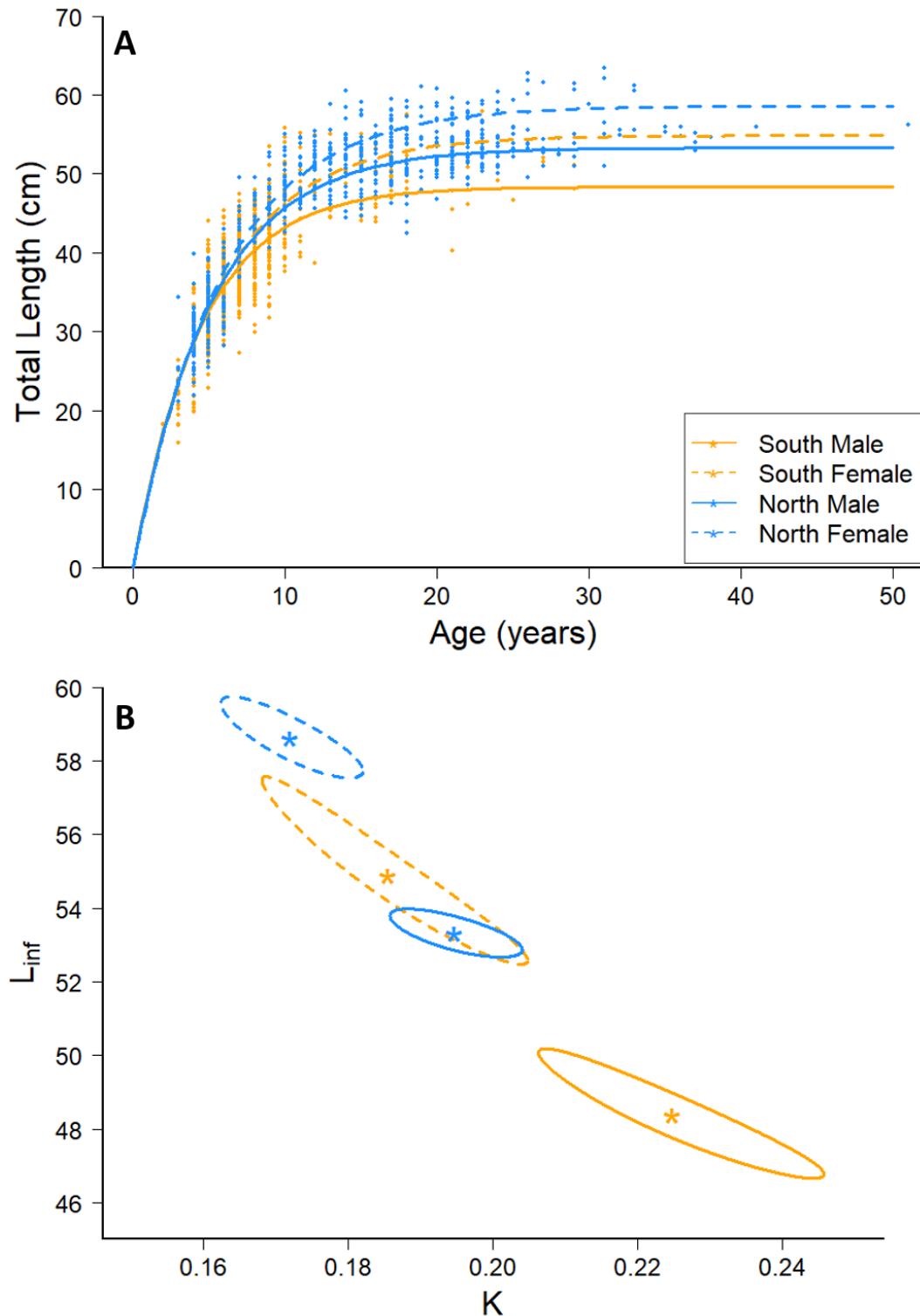


Figure 20. Canary Rockfish male and female (A) lifetime growth curves for northern and southern cluster regions, and (B) 95% confidence intervals from L_{inf} and k for northern and southern clusters. Overlapping intervals indicate no difference in k and L_{inf} .

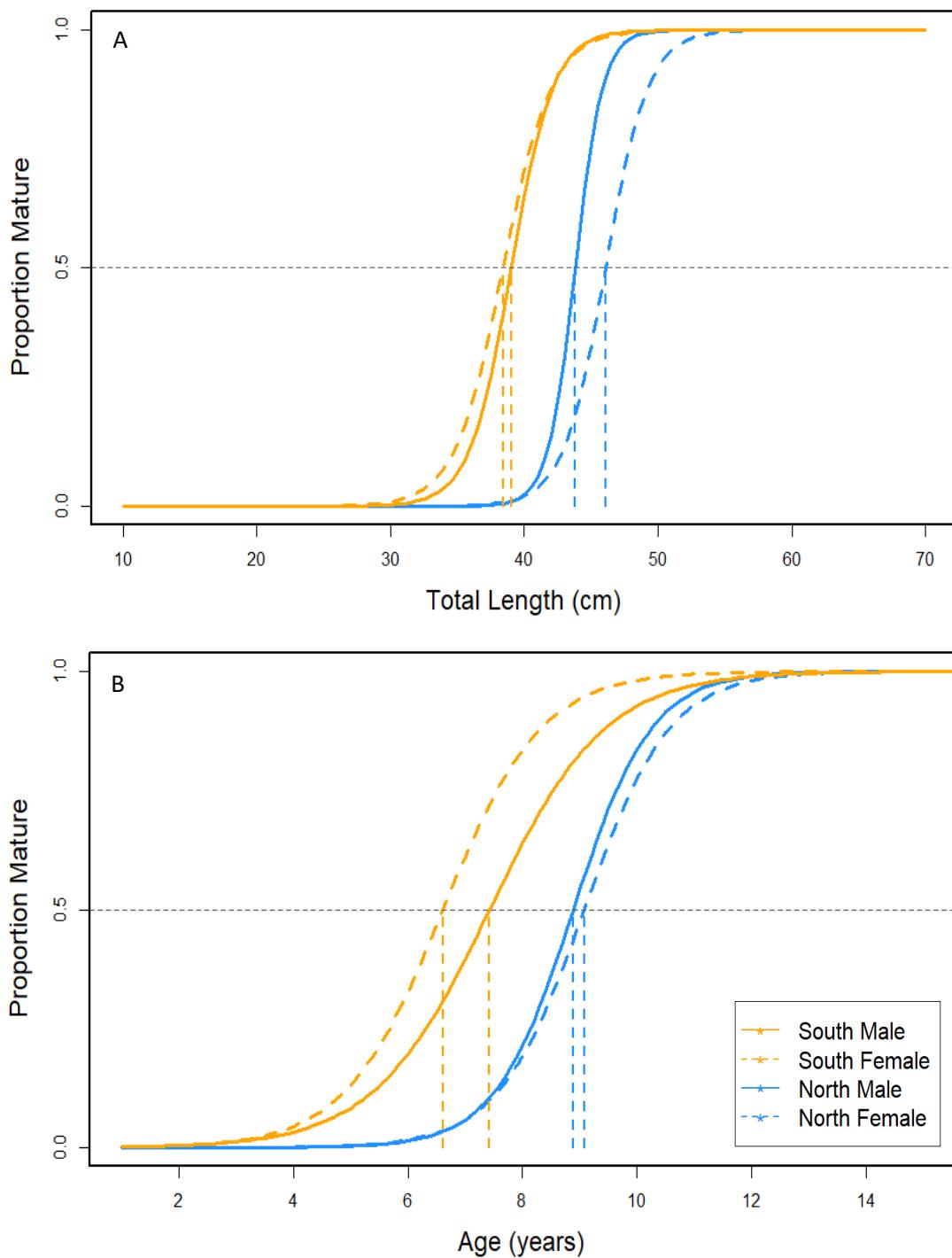


Figure 21. Maturity curves fitted to (A) total length (cm) and (B) age (years) for male and female Canary Rockfish for northern (blue) and southern (orange) cluster regions. Black horizontal dashed line signifies the threshold where 50% of the population is mature. Size and age at 50% maturity for respective regions and sexes is indicated by vertical dashed lines.

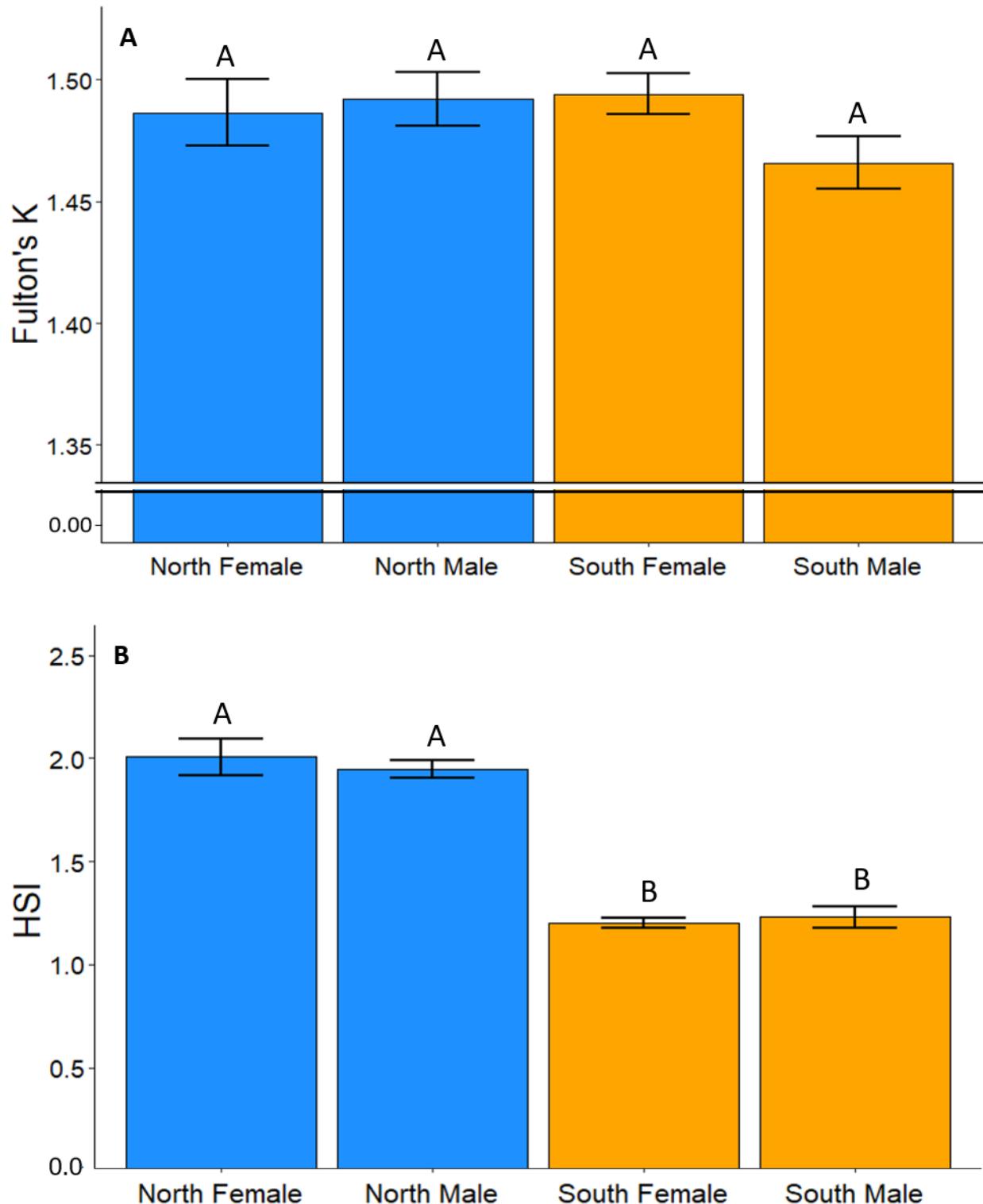


Figure 22. Mean (A) Fulton's K condition index and (B) hepatosomatic index (HSI) for male and female Canary Rockfish for northern and southern cluster regions. Error bars indicate ± 1 standard error.

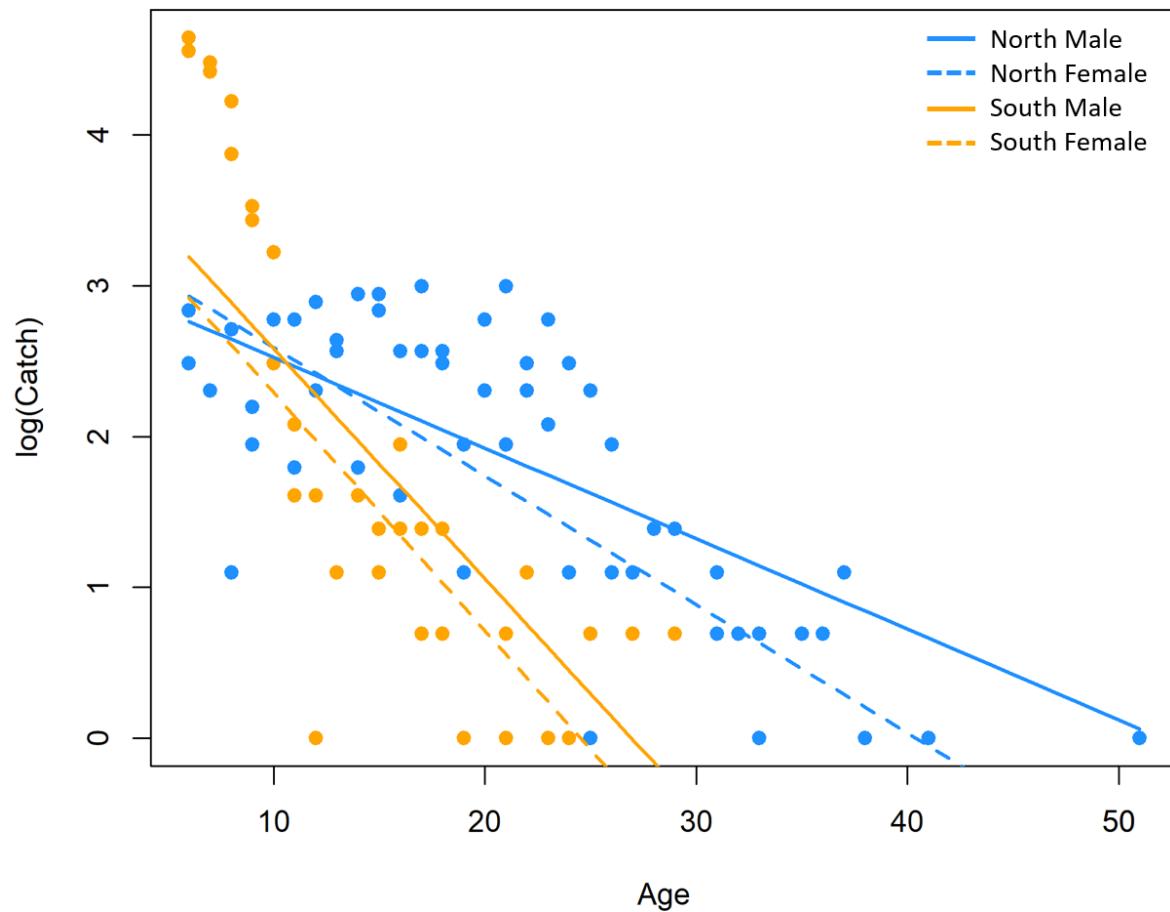


Figure 23. Age based catch curve estimates of annual mortality rates from log-linear regression of age frequency data for male and female Canary Rockfish for northern (blue) and southern (orange) cluster regions.