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Geographic and Habitat-Based Variation in Lingcod (*Ophiodon Elongatus*) Demography and Life-History Along the U.S. West Coast

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**GEOGRAPHIC AND HABITAT-BASED VARIATION IN LINGCOD (*OPHIODON*
ELONGATUS) DEMOGRAPHY AND LIFE-HISTORY 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
Laurel Szeche Lam

Fall 2019

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

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ELONGATUS*) DEMOGRAPHY AND LIFE-HISTORY ALONG THE
U.S. WEST COAST**

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by

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DEDICATION

This thesis is dedicated to all of the boat captains who made this thesis possible:

Captain Steve on the Hula Girl, Captain Mike “Jambo” on the Malia Kai, Captain Rob on the D&D, Captain Noah on the Ocean Captain, Captain Kurt on the Betty Kay, Captain Kyle on the Superstar, Captain Randy on the Telstar, Captain Tim on the Reel Steel, Captain Rick on the New Sea Angler, Captain Allen on the Tigerfish, Captain Brian on the Chubasco, Captain Brad on the Endeavor, Captain Dane on the Stardust, Captain Ray on the Toronado, Captain Paul on the Outer Limits, Captain Chuck with Kingfisher Charters, and Captain Geoff with Sea Raven Charters.

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CHAPTER I

GEOGRAPHIC VARIABILITY IN LINGCOD (*OPHIODON ELONGATUS*) DEMOGRAPHY AND LIFE HISTORY ALONG THE U.S. WEST COAST: OCEANOGRAPHIC DRIVERS AND MANAGEMENT IMPLICATIONS

Abstract

Fish populations exhibit variation in life-history and demography based on a variety of biological, environmental, and anthropogenic factors. Understanding the spatial patterns in life-history variability for commercially exploited fish stocks is important when making management decisions and designating stock boundaries. Between 2015 and 2017, 2,189 Lingcod were collected from seven geographically distinct regions along the West Coast to investigate latitudinal patterns in population distribution, growth, timing of maturity, condition, and natural and fishing mortality. Life history parameters of growth, maturity, longevity, condition, and natural and total mortality were calculated and compared for Lingcod in each region and by sex. A principle components analysis was used to relate trends in life-history parameters to coastwide environmental patterns in sea surface temperature and productivity. Non-metric multidimensional scaling ordination plot and PERMANOVA were used to identify biologically relevant breakpoint(s) for Lingcod along the U.S. West Coast. The results from this study demonstrate that Lingcod exhibit strong latitudinal patterns in life history that is consistent with Bergmann's Rule, where Lingcod from colder, northern waters grow faster and larger, live longer, mature at larger sizes, and have lower natural mortality rates than Lingcod from warmer, southern waters. Lingcod total mortality rates did not follow a latitudinal trend but were highest in Washington and Southern California regions, which is consistent with historic fishing practices, current fishing pressure, and local patterns of productivity within those regions. Between sexes, female Lingcod were found to grow faster and larger, live longer, mature at larger sizes, and were in worse condition than male conspecifics. These findings suggest that while Lingcod life-history traits related to age, growth, and condition are strongly influenced by localized patterns of temperature and oceanography along the coast, there can be considerable variation based on a regions' history of exploitation. A biologically relevant breakpoint for Lingcod along the U.S. West Coast was identified at the central Oregon coast, dividing the Lingcod stock into northern and southern substocks. The coastwide Lingcod population and fishery may benefit by using this boundary as a biologically appropriate break point when conducting future stock assessments. Implications for applying these findings to other federally managed groundfish species and stock assessment models are discussed.

Introduction

Marine fishes are exposed to unique, constantly fluctuating environments that are affected by oceanographic variability, habitat complexity, and human-induced impacts. These factors have been shown to affect demography and life history of broadly ranging species in a variety of ways, from altering population structure to shifting patterns of growth, maturity, and mortality (Robertson et al. 2005*a*, Robertson et al. 2005*b*, Keller et al. 2011, Hamilton et al. 2011). For economically important fish stocks, this can have considerable consequences on fisheries management and stock assessment methods (Hilborn et al. 2003, King and McFarlane 2003, Maunder and Piner 2015).

Modern fishery management strategies along the U.S. West Coast rely on species-specific stock assessment models, which are based on quantifiable life-history parameters (e.g., recruitment, growth, size and age at maturity, fecundity, natural mortality), estimates of stock biomass, and the history of exploitation (Hilborn 2003, Hilborn et al. 2003*a*, Worm et al. 2009). Stock assessment models often assume that life history parameters are stable and unchanging across a species' range or the management area of interest (Cope et al. 2011, Dichmont et al. 2016). Thus, most fish stocks are managed over broad geographic areas with catch limits, minimum size limits, or other regulations applying equally in all places (Fahrig 1993, Punt 2003). Past studies indicate that the assumption of spatial uniformity in stock status can be inaccurate and lead to errors in fisheries management; therefore, it is essential to include data on regional life-history variability to guide future stock assessment efforts (Hilborn et al. 2003*b*, Hilborn 2003, Gunderson et al. 2008, Cope and Punt 2011).

Demography and life-history of fish species are often influenced by latitude (Boehlert and Kappenman 1980, Gertseva et al. 2010, Keller et al. 2012, Gertseva et al. 2017, Keller et al. 2018) and the environmental factors associated with it. Typically, organisms in higher latitudes exhibit slower growth rates, increased longevity, and attain larger adult sizes compared to organisms residing in lower, warmer latitudes (Bergmann 1847, Allee and Schmidt 1951, Ray 1960, Atkinson 1994, Atkinson and Sibly 1997, for an exception, see Conover and Present 1990). This can be due to numerous ecological factors but is generally attributed to temperature-driven energetic tradeoffs between somatic growth and reproduction, and regional variability in food availability and metabolism (Boyce 1978, Choat and Robertson 2002, Munch and Salinas 2009).

Latitudinal variation in life history and demography of fishes has been reported in both temperate (Boehlert and Kappenman 1980, Brodziak and Mikus 2009, Keller et al. 2012, Gertseva et al. 2017) and tropical (Robertson et al. 2005a, Robertson et al. 2005b) marine environments and can influence fisheries management methods. Two economically important groundfish species from the Channel Islands in Southern California, California sheephead (*Semicossyphus pulcher*) and grass rockfish (*Sebastes rastrelliger*), display geographic variation in life-history traits that appear to be linked to environmental gradients in temperature, productivity, and historic fishing pressure (Hamilton et al. 2011, Wilson et al. 2012). Wilson et al. (2012) found that even subtle changes in life-history and demographic rates can translate to large differences in spawning potential in the Grass rockfish population. Additionally, Hamilton et al. (2011) demonstrated that by dividing the Channel Islands region into spatially explicit management zones based on oceanographic patterns of productivity, total yield of the

California sheephead fishery could be maximized while the population is maintained at sustainable levels.

GROUNDFISHES OF THE NORTHEAST PACIFIC

In the Northeast Pacific along the U.S. West Coast, a large gradient in oceanographic conditions occurs due to interactions between the California Current System (CCS) and seasonal and annual wind forcing, influencing sea surface temperatures and upwelling events in nearshore environments. These factors control many of the transport mechanisms necessary for nutrient supply and larval dispersal and survival (Checkley and Barth 2009). Physical features such as capes, points, submarine canyons and islands play an important role in determining the intensity of upwelling events, which in turn directly influences regional fish productivity (Ware and Thomson 2005). There are several natural breaks in the biogeography of the Pacific coastline where many species range endpoints occur: Cape Blanco in Oregon, Cape Mendocino in northern California, and Point Conception in southern California (Blanchette et al. 2008, Checkley and Barth 2009). The regions between these break points exhibit localized oceanographic patterns in sea surface temperature, primary productivity, and trophic interactions (Foster and Schiel 1985, Love et al. 2002, Ware and Thomson 2005), resulting in marked disparities in the demography and structure of nearshore fish communities.

The groundfishes that inhabit the Northeast Pacific are diverse, wide-ranging, long-lived, have a strong association with the seafloor (Archibald et al. 1981, Love et al. 1990, Love et al. 2002) and include over 90 species of rockfishes, roundfishes, flatfishes,

sharks, skates and others (PFMC 2014). While 70% of assessed groundfish stocks are found to be at or above the management target of 40% of virgin biomass, only 30% of groundfish species within the U.S. West Coast groundfish fishery complex are assessed on a regular basis. Additionally, many of these commercially important stocks experienced severe overfishing through the 1980s and 1990s due to misinformation (e.g. unreported catch, overestimation of stock productivity) and mismanagement (e.g. unregulated sectors, overcalculated annual catch limits) (NMFS 2009). With over 8,000 miles of coastline (NOAA 2016), the U.S. West Coast encompasses a wide range of habitats and environmental conditions; this diversity of conditions can result in regional differences in life-history parameters and population structure of many groundfishes. Incorporating data on regional life-history variability into assessments of stock status and health may prevent future stock collapses and lead to improved sustainability of fisheries.

Lingcod (*Ophiodon elongatus*, Girard 1883) are an ideal species to use in examining variability in life history and demography. Lingcod are members of the groundfish complex, are broad ranging and ubiquitous along the U.S. West Coast and are opportunistic top predators in the nearshore demersal ecosystem (Wilby 1937, Miller and Lea 1972, Hart 1973). Lingcod exhibit geographic variability in body size, spatial separation between sexes and have limited home ranges, suggesting that they may have the potential for substantial variation in demography and life-history traits across their range.

The Lingcod stock along the U.S. West Coast is assessed for the Pacific Fishery Management Council on a regular basis, however several limitations exist that can lead to uncertainty in assessment models (Jagiello and Wallace 2005, Hamel et al. 2009).

Lingcod are currently modeled as having a northern (Washington and Oregon) and southern (California) stock, where biological and catch information are grouped in each region (Jagiello et al. 1997, Adams et al. 1999). Historically, there has been higher uncertainty regarding Lingcod stock status for the southern area relative to the northern area since early landings information in the south was much sparser and sample sizes used for growth, maturity, and mortality estimates were considerably smaller (Jagiello et al. 2003). When the coastwide Lingcod stock was considered rebuilt in 2005 to 64% of its unfished biomass, the northern and southern areas were rebuilt to significantly different levels, with the northern region recovering to 87% of the unfished biomass and the southern region recovering to only 24% of the unfished biomass (Jagiello and Wallace 2005). This validates the previous decision to manage Lingcod as multiple stocks; however, it may also indicate that managing Lingcod by more than two region specific sub-stocks may be necessary to ensure that estimates of Lingcod stock productivity are accurate and to prevent the potential for overharvesting on localized scales. The 2009 Lingcod stock assessment (Hamel et al. 2009) stressed major uncertainty regarding the proper break points for stocks and sub-stocks, and stock-specific length-at-age data. These issues remain unaddressed in the 2017 Lingcod stock assessment (Haltuch et al. 2017). In addition, ageing validity and ageing bias have affected estimates of age and size at maturity of Lingcod in past stock assessments due to inconsistent ageing methods (Chatwin 1956, Miller and Geibel 1973, Beamish and Chilton 1977). While Lingcod have been aged throughout their range, ageing has focused on limited regional scales, small sample sizes, or specific size classes; there has not been a comprehensive Lingcod

ageing study across its range among all size classes (Chilton and Beamish 1982, Cass and Beamish 1983, Laidig et al. 2001, Silberberg et al. 2001).

My goal in this chapter was to determine how Lingcod demography and life history vary across its coastwide range in correlation to oceanographic indicators. My research objectives were (1) to quantify and compare sex-specific population structure and life-history (growth rates, longevity, size and age at maturity, somatic condition, and mortality rates) of Lingcod in seven regions along the U.S. West Coast; (2) to investigate potentially correlated associations between life-history parameters and oceanographic indicators; (3) to identify distinct groups within the coastwide Lingcod population based on similarities in life-history so as to determine biologically relevant breakpoints in the Lingcod stock; and (4) to suggest management implications of these findings for Lingcod and other commercially important groundfish species.

Based on past studies on Lingcod life-history and Bergmann's rule, I predicted that among coastwide regions, Lingcod at higher latitudes will have larger median and asymptotic sizes, live longer, grow faster, reach maturity at larger sizes, and have lower natural mortality compared to Lingcod from lower latitudes (Bergmann 1847, Echeverria 1987, Haldorson and Love 1991). Furthermore, I expected Lingcod at high latitudes to be in better condition than Lingcod from lower latitudes because colder waters in the northern CCS are more productive than warmer southern waters. I expect that Lingcod life history parameters will be directly related to environmental correlates (sea surface temperature and productivity) and predict that biologically driven breaks in the Lingcod population to occur at major biogeographic locations (i.e. Cape Blanco, Cape Mendocino, and/or Point Conception) along the coast.

Methods

SPECIES NATURAL HISTORY

Lingcod are in the greenling family (Hexagrammidae) and range from Kodiak Island, Alaska to Baja California, Mexico (Wilby 1937, Miller and Lea 1972, Hart 1973). They are opportunistic top predators, feeding on a variety of taxa, including octopus and squid (Cephalopoda), herring (*Clupea sp.*), rockfishes (*Sebastes sp.*), and flatfishes (Pleuronectiformes) (Miller and Geibel 1973, Beaudreau and Essington 2011). Genetic studies using a mitochondrial DNA marker found that Lingcod are genetically similar throughout their coastal range, suggesting extensive gene flow among populations throughout the West Coast (Jagiello et al. 1997, Marko et al. 2007).

Like other groundfish species, Lingcod are sexually dimorphic, with females typically growing faster and attaining larger asymptotic sizes. Females also reach maturity at larger sizes, between 3-5 years of age, whereas males are smaller but reach maturity earlier at 2 years of age (Miller and Geibel 1973, Cass et al. 1990). Spawning typically begins in early December and peaks from January to March. Mature females move from deeper offshore areas (100-200 m) to shallow (10-40 m) rocky habitats to deposit eggs at favorable nesting sites (Wilby 1937, Jewell 1968, Low and Beamish 1978). Mature males will initially select and guard optimal nesting areas, crevices or rocky outcrops with high water flow, before the arrival of spawning females. After eggs are deposited, female Lingcod will return to depth and leave the male to guard the eggs until they hatch, usually between 5-7 weeks (Low and Beamish 1978, Miller and Geibel 1973). Nest guarding by males protects developing embryos from predation by

opportunistic fish and invertebrate predators (Jewell 1968, Low and Beamish 1978).

Upon hatching, the larvae are approximately 12 mm in total length and stay pelagic until they reach about 70 mm, at which point they typically settle to soft-bottom habitats.

Juvenile Lingcod often remain on soft-bottom habitats until attaining a size of 350 mm (1-2 years of age) before moving into high-relief rocky habitat, potentially for protection from larger predators (Petrie and Ryer 2006).

Adult Lingcod display a high degree of site fidelity with an established location of residence (< 8 km home range), but frequently leave for brief periods of time over short distances, presumably to feed (Jagiello 1990, Jagiello 1999, Starr et al. 2005, Greenley 2009,). Residence times vary by sex, size, season, and habitat of residence (Greenley et al. 2016, Stahl et al. 2014). Due to this, males and females exhibit slight spatial segregation by depth and habitat type. More females are caught in the commercial fishery by trawl gear in low relief, deep, offshore habitats (62.4% females, 37.6% males), and more males caught in the recreational fishery by divers and party boat anglers in shallow, nearshore areas with high relief rocky habitat (66.3% males, 33.7% females) (Miller and Geibel 1973).

SAMPLING AREA AND COLLECTION PROTOCOL

Lingcod were collected from seven geographically distinct regions along the U.S. West Coast and Alaska; Southeast Alaska (54°30'N to 59°48'N), Puget Sound, coastal Washington (46°16'N-49°N), Oregon (42°N - 46°16'N), northern California (38°02'N - 42°N), central California (34°30'N - 38°02'N), and southern California (32°32'N - 34°30'N) (Fig. 1). The selection of these regions was made to evenly distribute sampling

effort across a broad latitudinal scale; the precise locations of life-history break points were determined post data-collection.

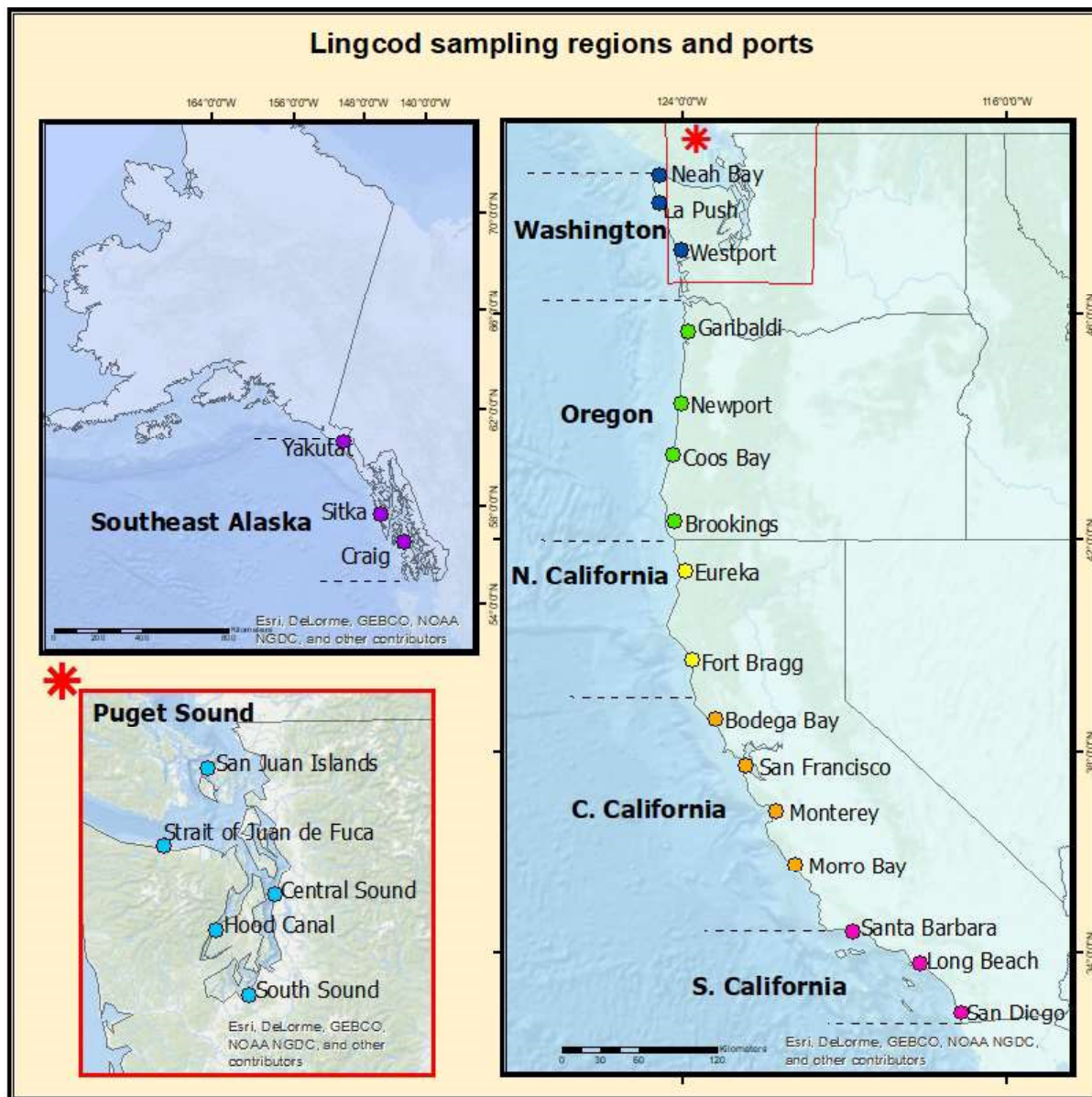


Figure 1: Map of study site showing sampling ports per region

Lingcod were caught using hook-and-line fishing gear across all seven regions on chartered fishing boats. Three to four fishing ports were selected per region ($n=23$ ports total), with the goal that selected ports were evenly distributed within each region and across the entire study area (Fig. 1), depending upon the geographic location of the ports and the availability and accessibility of recreational party boats (or Commercial Passenger Fishing Vessels [CPFVs]). CPFVs were chartered at each port for a half- to full-day of fishing, depending on weather and the number of Lingcod collected. We worked closely with CPFV captains, deckhands and local volunteer anglers to identify appropriate fishing grounds in order to collect 100 Lingcod per port using hook-and-line fishing gear. To ensure a thorough collection of Lingcod across a wide range of age and size classes, shallow (<60 m) and deep (60-170 m) nearshore and offshore rocky reefs were sampled equally. Lingcod can be targeted using weighted bars, jigs, swim baits, and live bait, which greatly reduces incidental catch of other bottomfish species (i.e. *Sebastes* spp). Because Lingcod are known to recruit to rocky substrate around 35 cm total length (Miller and Geibel 1973), it is unlikely that smaller size classes are excluded by this mode of fishing in rocky habitats.

All incidentally caught species were measured and released. Species suffering from barotrauma were descended and released at depth using a descending device (SeaQualizer®) to reduce mortality. Catch information, such as location, depth, relief, and catch per unit effort, was collected for each drift. Landed individuals were euthanized per the Institutional Animal Care and Use Committee protocol (Permit Number: 964), as approved by San Jose State University. Total length (cm), weight (kg), sex, and color status were collected immediately after the Lingcod was landed. Fresh gill tissue was also

collected during onboard sampling and preserved in 95% ethanol to be used for future genetic analyses. The Lingcod were then frozen or put on ice until dissection.

LAB DISSECTIONS

Standard morphometrics were collected during the lab dissection process: Total length (cm), standard length (cm), whole weight (kg), gape (mm), and body depth (mm). Additionally, liver weight (g) was measured for condition, the weights of whole stomachs (g) were measured, and stomach contents were stored in 95% ethanol to be used in future Lingcod diet studies. Male and female gonads were weighed (g) and visually inspected for maturity according to WDFW standards (Table 1; Silberberg et al. 2001). Muscle tissues samples were collected in 1.8 mL cryogenic vials and frozen for future fatty acid and stable isotope analysis. Fin rays 4-8 on the second dorsal fin were removed at the base joint and kept frozen until ready to be aged. Fin rays collected in Washington were sent to WDFW to be processed and aged by their ageing lab then returned to MLML where cross-lab ageing validation was established. All other fin rays were processed and aged at MLML. Sagittal otoliths were removed, cleaned, and stored dry for potential age validation studies. Otoliths were only retained in California because age validation work is regularly done in Oregon, Washington and Alaska.

AGEING

To evaluate geographic variation in age frequencies and growth rates (length-at-age curves, see below), I aged 75 to 100 Lingcod from each port following the Lingcod fin ray preparation protocol described by Chilton and Beamish (1982) and currently used

by the WDFW (R. LeGoff, WDFW, *personal communication*). Lingcod were aged using rays 4-8 on their second dorsal fin, which has been found to have the highest accuracy, readability, and minimal between-reader bias when compared to other ageing structures (Chilton and Beamish 1977, Cass and Beamish 1983, Claiborne et al. 2016). After cutting off the appropriate dorsal fin section, I dried the rays so that they lay perpendicular to the cut base by using a wire frame cage to hold the rays in place. The fins were dried for up to three days, then hardened with two coats of a medium thickness Cyanoacrylate (CA) glue, set with CA accelerator, and left to dry completely for one to two days. Using a PACE Pico high-speed saw, 1-2 mm wide sections (depending on fin size) were cut beginning from the fin base joint, producing 5-6 readable ray sections. The sections were then oriented in the order that they were cut and mounted on a microscope slide using two coats of medium viscosity Cytoseal™ 60 mounting fluid. After the slides completely dried, the sections were aged and stored in slide boxes.

Ages were determined by counting the number of annuli, the translucent zones that form once a year during winter growth. Annuli are often distinct along all growth axes of each fin ray section (Fig. 2). The opaque summer growth zone forms during the spring and summer months, during periods of fast growth. Fine, translucent rings called “checks” can form during summer growth zones, making it difficult to distinguish between actual annuli, potentially resulting in over-ageing error. Additionally, fin ray sections closer to the fin base may contain “occlusions”, or holes caused by resorption of the center of the fin ray in older Lingcod, obscuring early annulus rings and leading to error by under-ageing. However, error can be minimized using known mean annular radii measurements for the first, second, and third annuli. I used the established mean annular

radii measurements found by Beamish and Chilton (1977), later validated by McFarlane and King (2001), for Lingcod collected in their northern range, and the mean annular radii measurements validated by Laidig et al. (2001) for Lingcod in their southern range. All samples were read using a compound microscope at 30x to 50x using transmitted light. The imaging software Image Pro Plus 7.0 was used to measure the annular radii of one to three optimal fin ray sections per fish to verify the location of the first three annuli. The NWFSC Cooperative Ageing Project (CAP) laboratory and WDFW aged 509 Lingcod collected from Washington waters; I aged the remaining 1,681 Lingcod caught in all other regions. I conducted a blind double-read of a subsample of 219 fish to test my own ageing bias and precision, while a subsample of 386 and 196 slides were exchanged with the WDFW ageing lab and the CAP lab, respectively, to be cross read for accuracy and precision.

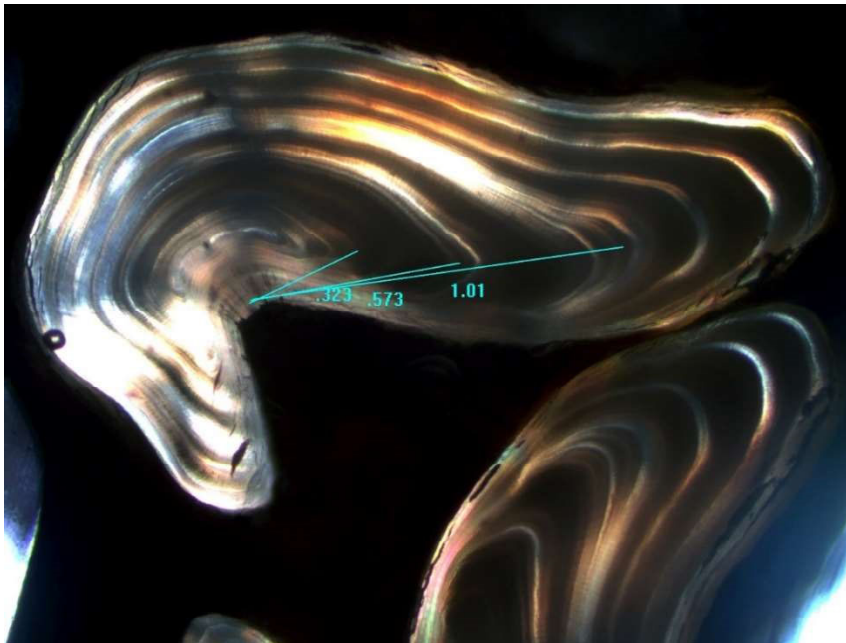


Figure 2: Lingcod fin-ray section with radii measurements on the first three annuli (in mm). The winter growth increments can be seen in white.

MATURITY ASSESSMENTS

Maturity status was assessed through visual inspection of gonads using the maturity stages defined by the WDFW for male and female Lingcod (Table 1). Five stages were described for female maturity (immature, maturing, mature, spent, and transitional) and three stages (immature, mature, and transitional) for males. However, for the purpose of fitting maturity curves for age and length at 50% maturity, only the stages of mature and immature gonads were used.

Table 1: Lingcod maturity stages as defined by the Washington Department of Fish and Wildlife (WDFW) (Silberberg et al. 2001).

	Stages	Description
Female	Immature	Ovaries are small (1.5-2.0 cm). Color ranges from translucent pink to red. Multiple-veined in appearance. No distinguishable eggs present.
	Maturing	Eggs are visible and opaque. Ovaries are swelling with an orange colored egg mass. The ovary wall may or may not be thickened.
	Mature	Ovaries are swollen with large, pale, sticky egg mass. The ovaries will appear thickened.
	Spent	Thick-walled ovaries are empty and flaccid. They may appear bloodshot. There may be residual eggs inside the ovary.
	Transitional	Ovaries are thick-walled and firming in early stage, progressing to thinner-walled, multi-veined condition similar to advanced immature ovaries. Eggs are not distinguishable.
Male	Immature	Testes are small, round to thin ribbon in shape. Color may range from translucent to white.
	Transitional	Moderate sized testes, firm and compact. The color ranges from brown to mottled white. Flowing sperm is not present.
	Ripe	Testes moderate to large, softening and white. Flowing sperm should be detectable by pressure or visible in cut cross-section.

Data Analysis

Analyses were conducted using the statistical computing platform R version 3.5.1 and JMP Pro version 14. To account for the potential confounding effects of depth of collection on the analysis, linear regression was used to test the relationship between depth and size, and depth and latitude. If a significant effect of depth was discovered, samples were stratified and subdivided as needed to control for these factors throughout the analyses.

AGEING ERROR

Several sources of error are associated with the age determination of calcified structures. Accuracy error accounts for how close the estimated age is to the true age, and precision error is a measure of the reproducibility of measurements on a given structure (Chang 1982, Campana 2001). The coefficient of variation ($CV = SD/\text{mean}$) has been shown to be a robust measure of precision, (Kimura and Lyons 1991, Campana et al. 1995, Campana 2001) and can be written as:

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

Where CV_j is the age precision estimate for a single fish (the j th fish). X_{ij} is the i th age determination of the j th fish, X_j is the mean age estimate for the j th fish, and R is the number of times the fish is aged. This equation can be averaged across fish to produce an average coefficient of variation (ACV). While there is no universally accepted target

level of precision for ageing studies, an ACV of 5% to 7.6% serves as a comparable reference point (Campana 2001).

To ensure accuracy and to reduce reader bias, age bias plots were evaluated as a method of quality control (Campana et al. 1995) (Fig. 3). Age readings of ager y are presented as mean ages with 95% confidence intervals corresponding to each of the age categories reported by ager x (Campana et al. 1995). Age bias plots allow for visual assessment of potential differences in paired age estimates. The use of age bias plots is the only method of age comparison that allows clear visual detection of systematic age differences, or nonlinear relationships (i.e. diverging agreement as the lower or upper range is approached) between ager x and ager y. The ACV between L. Lam, and L. Lam and WDFW are below Campana's maximum reference point of 7.6% (6.0% and 6.6%, respectively). The ACV between myself and the CAP lab exceeds the reference point (8.2%) but the relationship between the agers is linear and has a 97% agreement within 2 years (Table 2). The intent of the confidence intervals is not necessarily to assign statistical significance to the comparison, but to allow informed interpretation of any differences between the observed line and the equivalence line (Campana 2001). Overall, my age reads have no apparent systematic bias with respect to ages read by WDFW and the CAP lab.

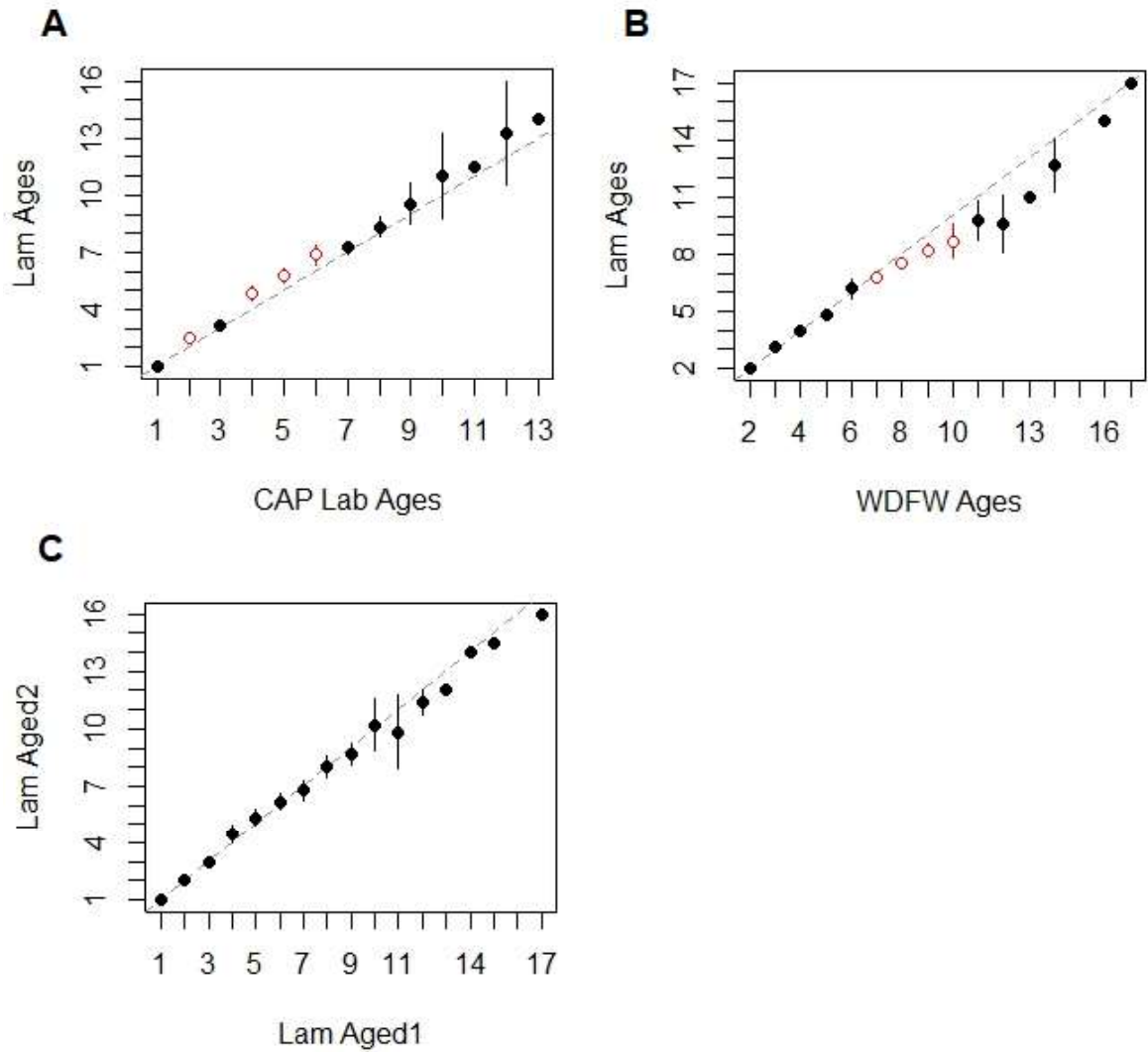


Figure 3: Age-agreement plots between A.) Lam and CAP Lab, B.) Lam and WDFW age reads and C.) Lam to Lam age reads. The dashed 1:1 agreement line is shown for comparative purposes. Significantly different ages between age readers are shown in red ($\alpha=0.05$).

Table 2: Average coefficient of variation (ACV), average percent error (APE), and percent agreement between 3 agers: L. Lam, the NWFSC Cooperative Ageing Project (CAP) lab, and the Washington Department of Fish and Wildlife (WDFW) ageing lab.

	ACV	APE	% agreement	+/- 1 yr	+/- 2 yr
L. Lam: CAP lab	8.2	5.9	55%	87%	97%
L. Lam: WDFW	6.6	4.7	52%	89%	98%
L. Lam: L. Lam	6.0	4.2	61%	90%	98%

AGE- AND SIZE-STRUCTURE

The nonparametric Kruskal-Wallis test was used to compare age and size distributions among all regions, followed by the Steel-Dwass method for pairwise comparisons between regions. The Kolmogorov-Smirnov test was used to compare size-frequency distributions between sexes.

GROWTH CURVES AND LONGEVITY

To examine differences in growth rates, I fit sex-specific von Bertalanffy growth functions (VBGF) to size at age data for male and female Lingcod from each region using maximum likelihood parameter estimates (Kimura 1980). The following equation was used:

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

Where L_t equals the estimated length at age, L_{inf} is the predicted maximum asymptotic length, k is the growth coefficient, t is the age, and t_0 is the theoretical time when length equals 0. The t_0 parameter is largely a modelling artifact, not a biological parameter, and is included to adjust for initial sizes in the VBGF (Beverton 1954, Schnute and Fournier 1980). I anchored t_0 to 0, which is biologically appropriate since larval Lingcod are

known to be only 12 mm upon hatching (Petrie and Ryer 2006). I used a two-parameter estimation for generating maximum likelihood VBGF curves. 95% confidence regions were calculated around least squares estimates of L_{inf} and k for each subpopulation using bootstrap methods (Kimura 1980). Longevity was calculated based on the mean of the upper quartile of ages for each region by sex and habitat (Robertson and Choat 2002). VBGF parameters and longevity estimates were considered significantly different if confidence regions did not overlap.

MATURATION CURVES

Logistic regression (mature vs. immature fish) was used to determine size and age at 50% maturation for Lingcod by region and sex. Sex-specific differences in age at maturation were determined using the logistic regression equation:

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

Where P_x is the proportion of fish mature at age x , a is the intercept, and b is the coefficient describing the rate at which the proportion of mature fish increases with age. Length at maturity was calculated similarly. 95% confidence intervals were estimated using bootstrapping and compared among regions. The timing of maturity was considered statistically different if the 95% confidence intervals did not overlap.

CONDITION

Several indices were used to examine condition of collected Lingcod samples. To assess general health of individual Lingcod, I used the Fulton's K condition factor [$K = 100 \cdot (W/L^3)$], where the whole weight (W) is proportional to the cube of its length (L)

(Fulton 1902, Bolger and Connolly 1989). High K values signify that a fish is heavier, and potentially healthier, for a given length. The hepatosomatic index ($HSI = 100 * (\text{liver mass (g)} / \text{body mass (g)})$) was also used as an index of condition. 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 (higher liver weight to body weight ratio) (Htun-Han 1978, Bolger and Connolly 1989). I used a general linear model (GLM) was used to investigate the influence of the continuous variable of size, and the categorical variables of region, sex, and season on Lingcod condition. The interaction between size and region, and size and sex, were included in the model. The full model containing all predictor variables was compared to all combinations of nested models using the Akaike Information Criterion (AIC), where the model with the lowest AIC indicates the best fit model. To control for possible season and year effects, only Lingcod caught in 2015-2017 between the months of March through October were used. I used residual analysis to control for the confounding effect of size on condition when comparing among regions and between sexes, but not in the GLM because size was included in the GLM as a covariate.

MORTALITY

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} since it is assumed that if an individual in a population had a high mortality rate, it would not survive long enough to reach old age (Hoenig 1963). I used the updated Hoenig non-linear least squares estimator (Hoenig 1983) developed by Then et al. (2015), as it performs better

than other commonly used empirical methods (Alverson and Carney 1975, Pauly 1980, Jensen 1996) across a broad range of fish species:

$$M_{Hoenig} = (4.899)A_{max}^{-0.916}$$

Where A_{max} is the maximum observed age. Following recommendations from Hamel (2015), the Hoenig A_{max} model was fit under a log-log transformation so the slope is forced to be -1 in the transformed space, such that the point estimate for M is:

$$M_{Hamel} = 5.4/A_{max}$$

This formula was used by Haltuch et al. (2017) in the 2017 Lingcod stock assessment to estimate a prior on M .

Total mortality (Z) was calculated using the Chapman-Robson method of cross-sectional catch-curve analysis (Chapman and Robson 1960) with a correction factor for variance inflation (Smith et al. 2012). Z was obtained from each region for both sexes. Each substock follows the assumptions that the population is closed, has constant mortality and recruitment rates, constant vulnerability, and that the sample is unbiased. Fish younger than the modal age were excluded from the regression (Beverton and Holt 1959, Chapman and Robson 1960, Robson and Chapman 1961, Ricker 1975). The Chapman-Robson estimator is based on mean age (\bar{a}) above the recruitment age and the sample size, n :

$$Z = \log ([1 + \bar{a} - 1/n]/\bar{a})$$

This estimator is considered a minimum variance unbiased estimator (Chapman and Robson 1960), with variance approximated by:

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

By solving for natural mortality, M , and total mortality, Z , fishing mortality, F , can then be calculated using the equation $F = Z - M$.

MULTIVARIATE ANALYSES OF SPATIAL STRUCTURE IN LIFE HISTORY

A principle components analysis (PCA) was used to determine the spatial association of coastwide Lingcod life history traits and to examine the influence of long-term mean oceanographic factors (Sea surface temperature and chlorophyll a concentration) on those life history traits. Here, chlorophyll a will be used as a proxy for ecosystem productivity since areas with high concentrations of chlorophyll a are able to support higher secondary production of prey types typically consumed by Lingcod. Life-history parameters of L_{inf} and k , mean size, longevity, natural mortality, Fulton's K , and HSI were derived on the port level and normalized for the PCA. Factors (size at 50% maturity, age at 50% maturity, maximum age) containing missing values from a subset of ports were excluded from analysis. Mean sea surface temperature (SST) and chlorophyll a data was obtained from the Giovanni Visualization data portal through NASA Earthdata EODIS (2018). SST ($^{\circ}\text{C}$) and chlorophyll a (mg/m^3) data is collected at a spatial resolution of 4 km using moderate-resolution imaging spectroradiometer (MODIS) Aqua satellites. SST and chl a data in closest proximity to our fishing sites were isolated and averaged over a 12-year period (2005 to 2017) per port. Principle components (PCs) with eigenvalues >1 (Girden 2001) were saved and used in a linear regression with mean SST and chlorophyll a , respectively.

To identify potential Lingcod subpopulations based on life-history similarities along the coast, an agglomerative hierarchical cluster analysis was performed among all

sampled ports. Euclidean distances were calculated among ports using normalized growth-based life-history parameters that are typically used in stock assessment models: L_{inf} , k , mean size, longevity, size at 50% maturity, and natural mortality. The average silhouette method was used as a means of statistical clustering validation to compute the optimal number of clusters, k , where the highest average silhouette width indicates the best k option (Everitt et al. 2001, Rencher 2002). The complete linkage agglomeration clustering method was used to group the ports into k clusters. A non-metric multi-dimensional scaling (nMDS) ordination plot was generated to preserve the order of relationships between ports and to visualize how the clusters were identified and the relative dissimilarity of clusters in multivariate space based on life-history traits. Vectors were used to demonstrate the influence of each life-history trait in creating the clusters. A permutational multivariate analysis of variance (PERMANOVA) was run to determine whether the variance in port clusters can 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

2,189 Lingcod were collected from rocky habitats between 2016-2017 (Table 3). On average, we fished for 2.5 days out of each port to obtain the targeted sample size of 75-100 Lingcod per port. Additional samples were provided by the Alaska commercial longline fishery, the NWFSC Rockfish Bycatch Study in Puget Sound, the Oregon

Department of Fish and Wildlife Marine Reserves Program, and the California Collaborative Fisheries Research Program. All Lingcod were caught from depths of 7 to 170 ft (mean: 59.8, SD±38.3) Averaged across regions, collected Lingcod exhibited a relatively even distribution of females and males (47% female) (Table 3). Among regions, there were significantly different sex-ratios ($\chi^2_6=253.56$, $p<0.0001$), however this may be due to Lingcod from Washington regions being heavily skewed towards females. Within all other regions, males were more common. Upon removing the Washington region from the sex-ratio analysis, there was no significant difference in sex ratios ($\chi^2_5=8.98$, $p=0.1100$), and the average sex-ratio among all regions was 41% females to 59% males.

Table 3: Catch summary by region. Number of ports were chosen based on CPFV location and availability. Each port was fished in for an average of 2.5 days. Maximum and minimum total length (TL) were recorded in cm, and number of unsexed, female, and male Lingcod.

	Number of ports	Days fished	Female, N	Male, N	Unsexed, N	Percent female	Max TL (cm)	Min TL (cm)
(N = 2,189)	23	58	1036	1153	2	0.47	-	-
Alaska	3	11	105	169	-	0.38	127	41.5
Washington	3	6	318	68	-	0.82	112	39
Puget Sound	4	10	62	60	1	0.51	108	20
Oregon	4	10	146	211	-	0.41	111	33.8
N. California	2	4	82	118	-	0.41	93.5	25.1
C. California	4	9	224	347	1	0.39	96.9	16.7
S. California	3	8	99	180	-	0.35	97	40.2

GEOGRAPHIC DIFFERENCES IN POPULATION STRUCTURE AND LIFE HISTORY

Due to the differences in depth range sampled, I used residual analysis to account for the covariate of depth as a confounding factor when comparing Lingcod size distributions. There was a significantly positive linear relationship between depth and size ($\beta=0.048$, $r^2=0.17$, $F_{1,1822}=457.8$, $p<0.0001$) and depth and age ($\beta=0.005$, $r^2=0.10$, $F_{1,1575}=170.9$, $p<0.0001$). Residuals from the linear regression were saved and used in the subsequent comparisons by region.

Lingcod length frequency distributions across all sampled regions were significantly different (Kruskal-Wallis test, $\chi^2_6=453.6$, $p<0.0001$). Using the Steel-Dwass method for nonparametric pairwise comparisons, I found Lingcod size frequency distributions to follow a latitudinal trend where median Lingcod size decreases with decreasing latitude (Fig. 4A). All regions were significantly different from one another with the exception of the mid-regions (Northern California, Oregon, and Puget Sound).

Lingcod age distributions were also significantly different across all regions (Kruskal-Wallis test, $\chi^2_6=182.3$, $p<0.0001$). Using pairwise comparisons between each region, I found Lingcod from Alaska to have the oldest median age, followed by Lingcod from Washington. Lingcod from all regions south of Washington were statistically similar (Fig. 4B).

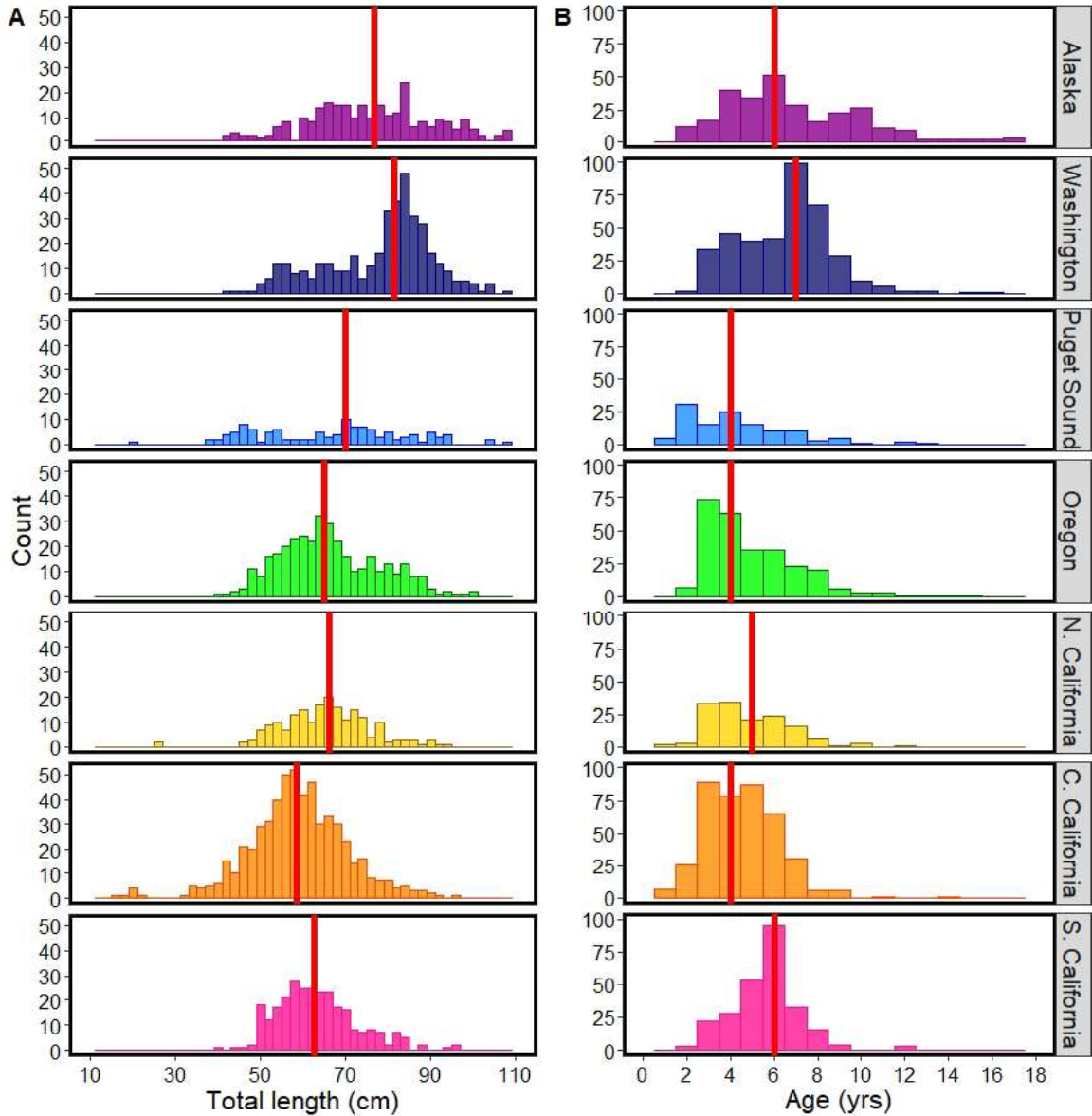


Figure 4: A) Size- and B) age-frequency of Lingcod by region (sexes pooled) in order of decreasing latitude. The red vertical line indicates median size or age per region.

Lingcod growth parameters L_{inf} and k are inversely related (Pilling et al. 2002) and exhibit a strong latitudinal cline across all regions (Table 4, Fig. 5A). Large L_{inf} and small k values were found in northern regions, and small L_{inf} and larger k values were observed in southern regions. Non-overlapping 95% confidence intervals indicate there were four major subgroups with significantly different growth patterns: Alaska and

Washington; Puget Sound; Oregon and northern California; and central and southern California. These subgroups follow a latitudinal trend with decreasing L_{inf} and increasing k values from north to south (Fig. 5B). Longevity decreased consistently as a function of latitude across all sampled regions (Table 4).

Table 4: Von Bertalanffy growth function (VBGF) parameters, L_{inf} and k , and longevity (T_{max}) values by region with sexes and habitats pooled. Standard deviation (SD) for L_{inf} , k , and standard error (SE) for T_{max} estimates are included. T_{max} among regions is considered statistically different if 95% confidence intervals do not overlap.

	$L_{inf}(SD)$	$k (SD)$	$T_{max} (SE)$
Coastwide	93.4 (1.69)	0.266 (0.01)	7.9 (0.07)
<i>Female only</i>	100.3 (1.97)	0.25 (0.01)	8.3 (0.09)
<i>Male only</i>	74.8 (1.36)	0.358 (0.02)	7.2 (0.1)
Alaska	98.2 (3.39)	0.265 (0.02)	10.9 (0.25)
Washington	91.9 (4.35)	0.37 (0.04)	8.8 (0.13)
Puget Sound	98.4 (2.76)	0.265 (0.02)	7.7 (0.34)
Oregon	88.8 (3.06)	0.305 (0.02)	7.5 (0.19)
Northern California	81.8 (3.94)	0.364 (0.05)	7.0 (0.18)
Central California	81.3 (3.11)	0.308 (0.03)	6.7 (0.11)
Southern California	75.3 (3.73)	0.356 (0.05)	6.6 (0.09)

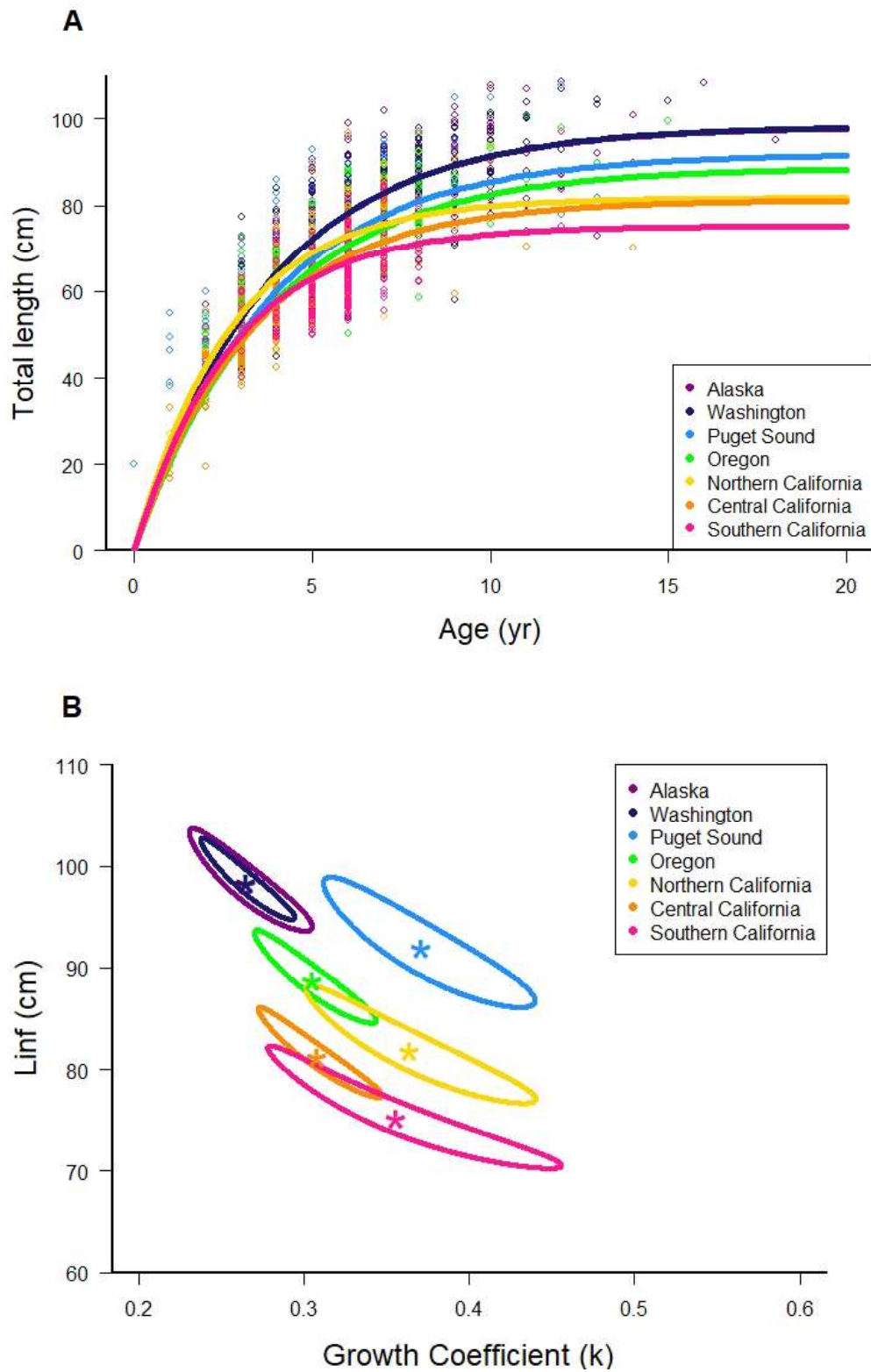


Figure 5: A) Spatial variation in *Lingcod* lifetime growth curves across 7 sampled regions with habitats and sexes pooled, and B) 95% confidence intervals for L_{inf} and k for each region. Overlapping intervals indicate no difference in growth.

Length and age at 50% maturity were derived using logistic regression to compare the timing of maturity across regions. There was a latitudinal trend in which size at 50% maturity decreased as latitude declined, with the exception of Puget Sound (Table 5, Fig. 6A). I did not observe a latitudinal trend for age at 50% maturity (Fig. 6B). No estimate for length or age at 50% maturity was derived for Lingcod in southern California due to small sample size of immature individuals ($N=1$) (Table 5).

Table 5: Lingcod size- and age- at 50% maturity using logistic regression by region (sexes pooled) with bootstrapped lower confidence intervals (LCI) and upper confidence intervals (UCI). No immature individuals were aged in southern California hence size and age at 50% could not be determined.

Region	Size at 50% maturity (cm)	LCI	UCI	Age at 50% maturity (yr)	LCI	UCI
Alaska	53.1	46.9	56.7	2.9	2.0	3.4
Washington	48.2	44.5	51.4	2.5	2.1	2.8
Puget Sound	43.2	35.7	48.7	1.5	0.6	2.1
Oregon	48.8	44.6	51.8	2.5	2	2.9
Northern California	47.7	42.4	50.5	2.1	1.4	2.9
Central California	41.6	39.3	43.4	2.5	2.3	2.7
Southern California	-	-	-	-	-	-

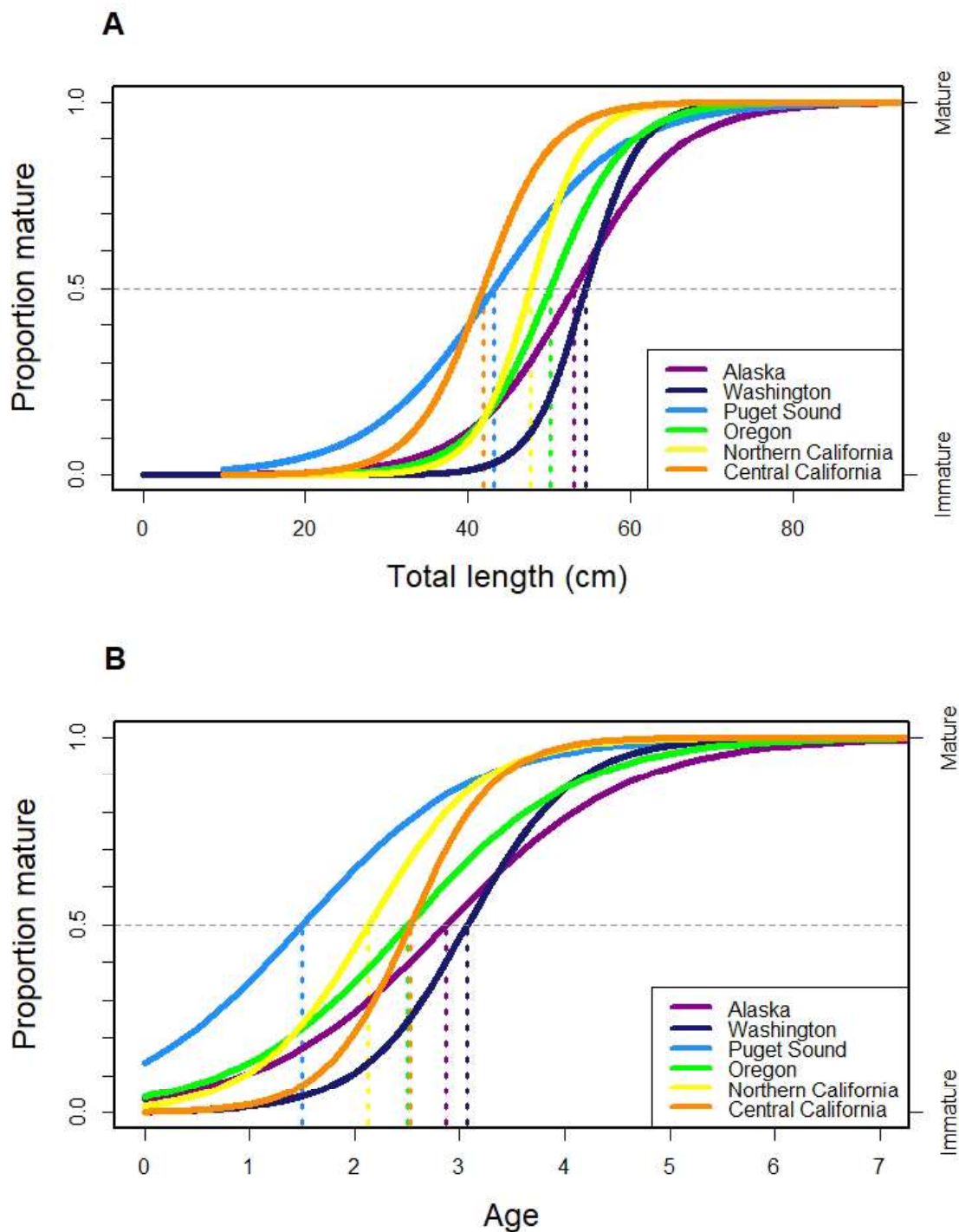
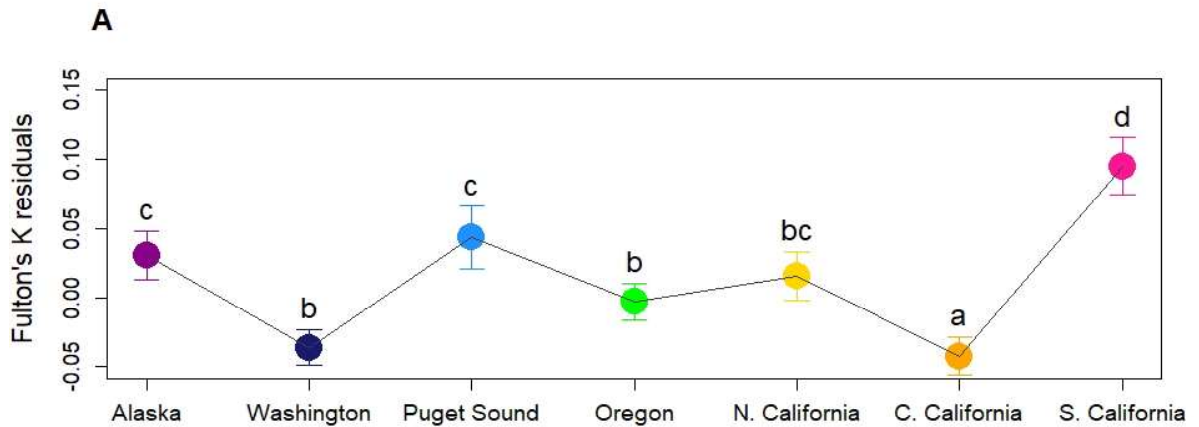


Figure 6: Logistic regression of A) total length at 50% maturity and B) age at 50% maturity for Lingcod from each sampled region along the U.S. West Coast. The horizontal dashed line represents the time when 50% of the population is mature. Size and age at 50% is indicated by the vertical dashed lines. Size and age of maturity for Lingcod from Southern California could not be calculated due to small sample size of immature individuals.

Condition was analyzed using morphometric (Fulton's K) and physiological (Hepatosomatic, HSI) indices. There was a positive relationship between Fulton's K and length ($\beta=0.002$, $r^2=0.04$, $F_{1,2117}=96.5$, $p<0.0001$), and HSI and length ($\beta=0.01$, $r^2=0.04$, $F_{1,2108}=80.1$, $p<0.0001$), therefore residuals were used in the subsequent condition comparisons among regions.

Across regions with sexes pooled, there was no latitudinal trend in Fulton's K condition factor (Fig. 7A). Lingcod in the southern California region consistently had the highest mean Fulton's K (1.07, SD ± 0.13) and were thus heavier on average than fish from the other regions. HSI exhibited a latitudinal trend and increases as latitude decreases (Fig. 7B). Similar to Fulton's K index, individuals from southern California had the greatest mean HSI (2.18, SD ± 0.76) compared to other regions.



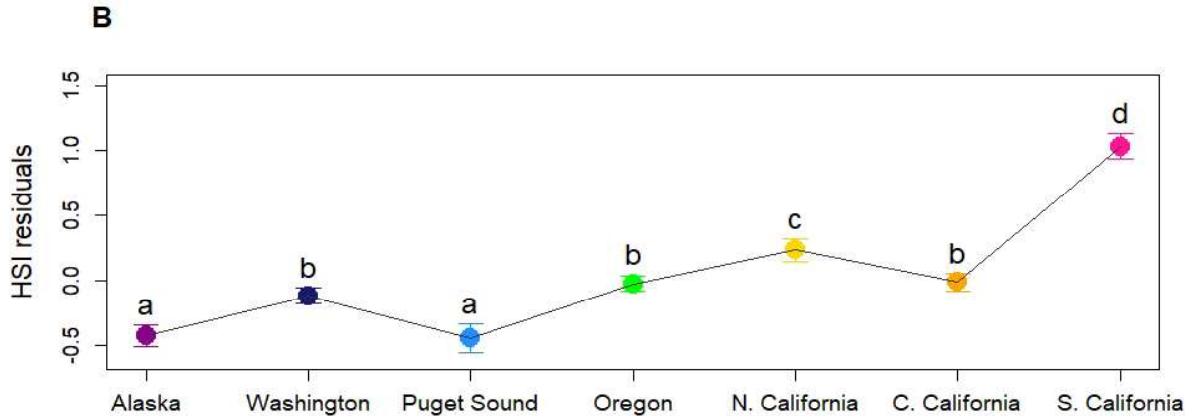


Figure 7: A) Fulton's K condition index residuals and B) hepatosomatic index (HSI) residuals by region with 95% upper and lower confidence intervals shown as error bars. Overlapping letters indicate no regional difference in Fulton's K or HSI based on Tukey's HSD pairwise analysis.

A GLM was used to investigate the influence of the continuous variable of size, and the categorical variables of region, sex, and season on Lingcod condition. The interaction between size and region, and size and sex were included in the model. Fulton's K indices for Lingcod were most strongly influenced by size ($F_{1,2104}=207.56$, $p<.0001$), region ($F_{6,2104}=23.13$, $p<.0001$), sex ($F_{1,2104}=79.37$, $p<.0001$), and season ($F_{3,2104}=14.05$, $p<.0001$). The interaction between sex*size ($F_{1,2104}=7.47$, $p=0.0063$) was also significant. Lingcod with higher Fulton's K condition indices tended to be larger males from southern regions that were caught during winter. Overall, the six effects accounted for 20.4% of variance in Lingcod Fulton's K. The effects of size, region, sex, and season contributed the most to determining Fulton's K.

In order of importance, size ($F_{1,2092}=173.71$, $p<.0001$), season ($F_{3,2092}=47.41$, $p<.0001$), region ($F_{6,2092}=24.48$, $p<.0001$), and region*size ($F_{6,2092}=5.76$, $p<.0001$) were significant predictors that accounted for 27.0% of the variation in HSI. The effect of sex

and the interaction between sex*size was not a significant contributor. Lingcod with high HSI were typically larger individuals from southern regions that were caught in the fall. For both condition indices, size, region, and seasonality appear to be the most significant drivers behind Lingcod condition, while the effects of sex are variable.

Natural mortality (M) was calculated using the Chapman-Robson method of catch-curve analysis. Lingcod M was higher in southern end of their range and lower in the northern end, with high variability in the mid-range regions (Table 6). Total mortality rate, Z , similarly exhibited a slight latitudinal trend, with the exception of Lingcod from Washington. Z rates of Lingcod were highest in Washington and southern California.

Fishing mortality, F , was derived using the formula $F = Z - M$ (Table 6). There is no trend in F across regions, however, F is greatest in Lingcod from southern California and from Washington, which parallels the pattern seen in Z . In some instances, M was calculated to be greater than Z , resulting in a negative F .

Table 6: Total (Z), natural (M), and fishing (F) mortality rates for each region where F is calculated as $F = Z - M$. F was left blank in cases where M exceeds Z (resulting in a negative F). Standard error (SE) from Z calculations are shown in parentheses.

	Z (SE)	M	F
Alaska	0.32 (0.04)	0.30	0.02
Washington	0.79 (0.07)	0.34	0.45
Puget Sound	0.35 (0.08)	0.42	-
Oregon	0.42 (0.03)	0.36	0.06
Northern California	0.53 (0.1)	0.45	0.08
Central California	0.54 (0.11)	0.39	0.15
Southern California	0.87 (0.18)	0.45	0.42

SEX-BASED DIFFERENCES IN POPULATION STRUCTURE AND LIFE HISTORY

There were significant differences between male and female Lingcod length frequency distributions coastwide ($D=0.517$, $p<0.0001$) as well as within each region analyzed separately (Fig.8). Female median sizes were consistently larger than male median sizes. Unsexed individuals (U) were excluded from analysis.

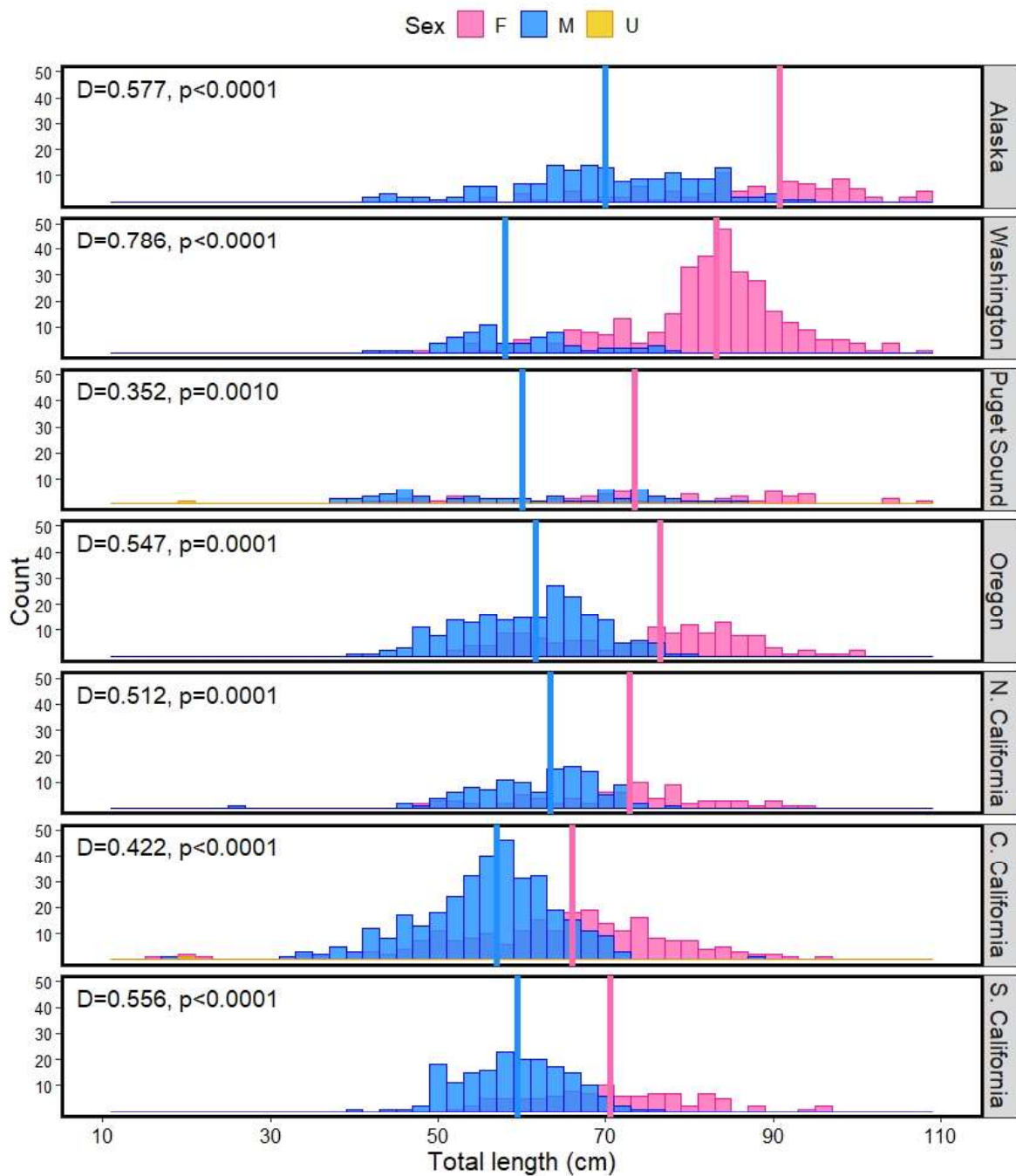
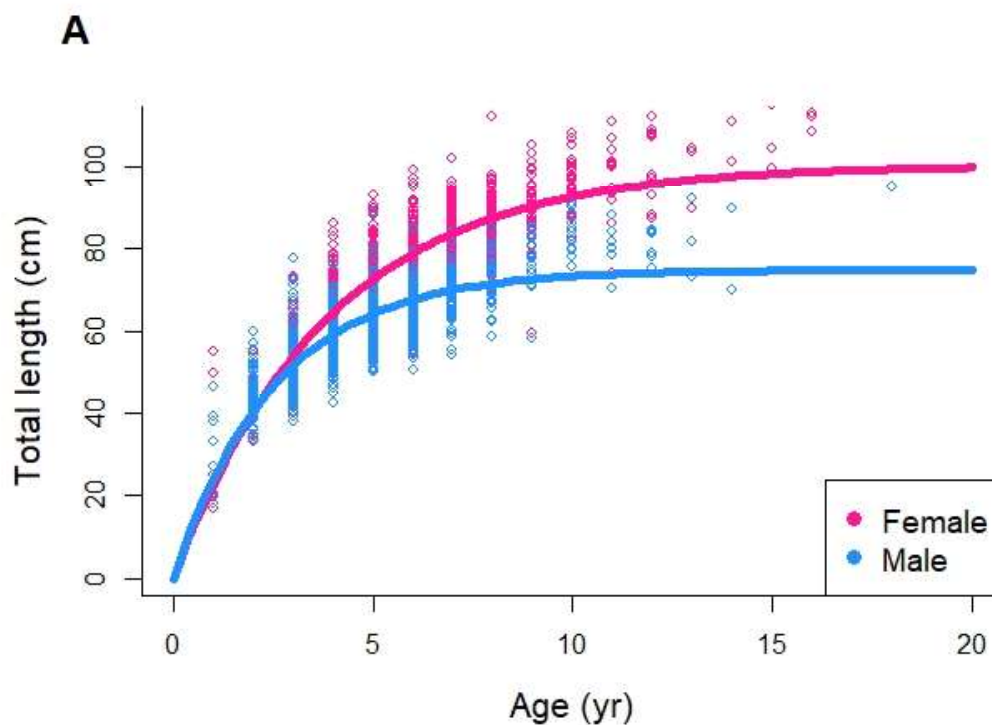


Figure 8: Length frequency distribution of Lingcod per region by sex (female, male, and unsexed). The pink and blue lines represent the median total length for female and male Lingcod, respectively. Female median sizes were consistently smaller than male median sizes across all regions.

Comparing growth rates between sexes, female Lingcod attained larger maximum size ($L_{inf} = 100.3$, $SD \pm 1.97$ cm) than males ($L_{inf} = 74.8$, $SD \pm 1.36$ cm) (Fig. 9A, Table 7). However, male Lingcod reach asymptotic size faster ($k = 0.358$, $SD \pm 0.02$) than females ($k = 0.25$, $SD \pm 0.01$) (Fig. 9B, Table 7). In addition, female Lingcod live significantly longer (8.3 years, $SE \pm 0.09$) than males (7.2 years, $SE \pm 0.1$).

Table 7: Von Bertalanffy growth function (VBGF) parameters L_{inf} , k , and longevity (T_{max}) values by sex. Standard deviation (SD) for L_{inf} , k , and standard error (SE) for T_{max} estimates are included. T_{max} among regions is considered statistically different if 95% confidence intervals do not overlap.

	L_{inf} (SD)	k (SD)	T_{max} (SE)
Female	100.3 (1.97)	0.26 (0.01)	8.3 (0.09)
Male	74.8 (1.36)	0.358 (0.02)	7.2 (0.1)



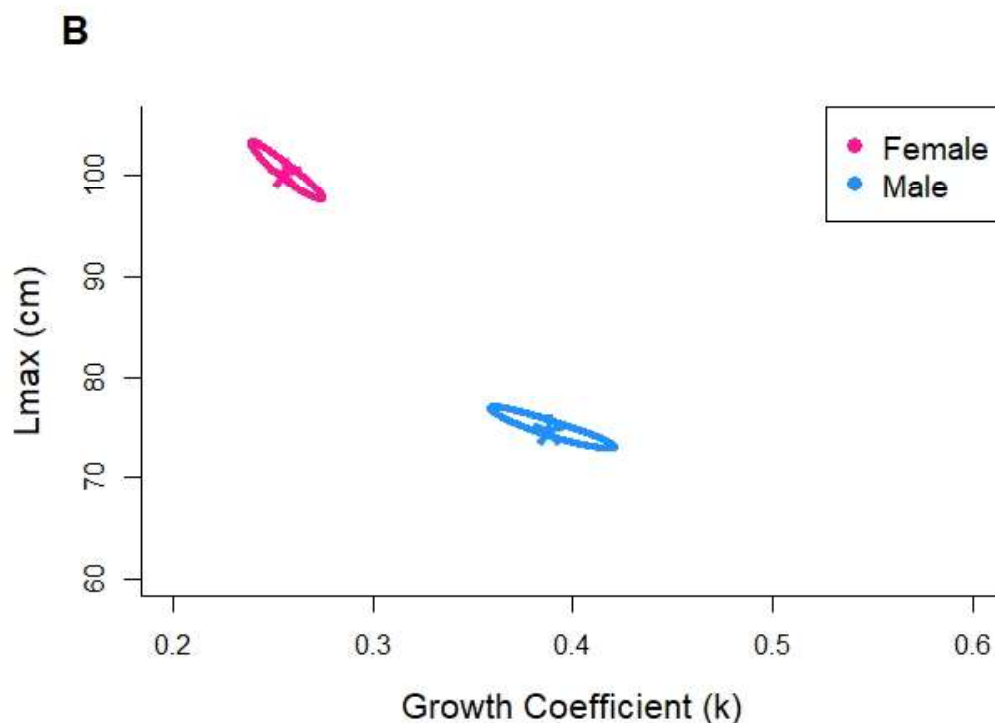


Figure 9: A) Variation in lifetime growth curves for male and female Lingcod (regions pooled) and B) 95% confidence intervals for best fit L_{inf} and k parameters for male and female Lingcod. Overlapping confidence intervals indicate no difference in growth rates.

Coastwide, female Lingcod size and age at 50% maturity (50.1 cm, 2.6 years) were significantly greater than that of male Lingcod (41.6 cm, 2.2 years) (Table 8, Fig. 10). Size at 50% maturity was significantly different between sexes, but there was no difference in age at 50% maturity. Immature females ranged in size from 16.7 cm to 79.0 cm (1-6 years), whereas the smallest mature female was 30.5 cm (1 year old). Immature males ranged in size from 17.5 cm to 62.3 cm (0-4 years), with the smallest mature male being 27.2 cm in length (1 year old). However, because Lingcod are batch spawners, it can be difficult to macroscopically determine maturity stages accurately. Gonads of larger and older individuals characterized as immature may be misidentified if captured outside of spawning season (Melissa Head, NWFSC, *personal communication*).

Table 8: Female and male Lingcod size and age at 50% maturity with upper and lower confidence intervals (UCI, LCI, respectively). Size at 50% maturity is significantly different between sexes, but there is no difference in age at 50% maturity.

Sex	Size at 50% maturity	LCI	UCI	Age at 50%	LCI	UCI
Female	50.1	47.6	52.4	2.6	2.3	2.8
Male	41.6	39.0	43.5	2.2	2.0	2.4

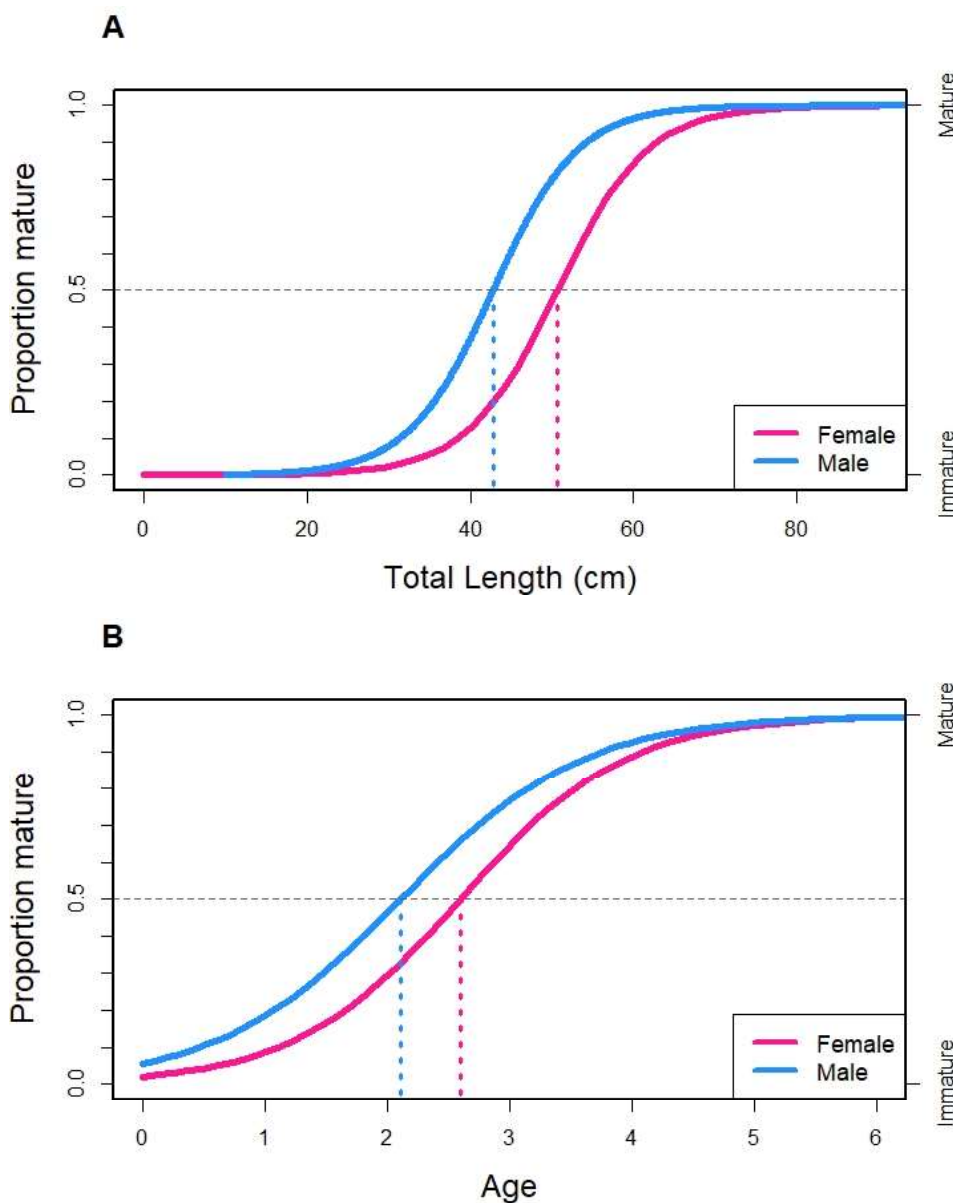


Figure 10: Logistic regression of A) size (cm) and B) age at 50% maturity for both sexes with regions pooled. The horizontal dashed line represents the time when 50% of the population is mature and the vertical dashed lines represent size and age at 50% maturity, respectively.

Welch's t-tests assuming unequal variances were used to test for significant differences between the mean residuals of Fulton's K and HSI as a function of sex. Males were found to be in better condition than females, with a significantly higher mean Fulton's K (Welch's $t_{1743} = 7.62, p < 0.0001$) and HSI (Welch's $t_{1733} = -3.30, p = 0.0010$).

Females had higher natural mortality rates compared to males as well as higher total mortality rates, however the difference was not significant (Table 9). Fishing mortality was also higher in female Lingcod than in male Lingcod.

Table 9: Total (Z), natural (M), and fishing (F) mortality rates for each sex (all regions pooled) where F is calculated as $F = Z - M$. Standard error (SE) for Z is shown in parentheses.

	Z (SE)	M	F
Female	0.57 (0.04)	0.32	0.25
Male	0.44 (0.06)	0.30	0.14

PCA BETWEEN OCEANOGRAPHIC INDICATORS AND LIFE HISTORY TRAITS

Principle component 1 (PC 1) and principle component 2 (PC 2) together comprised up to 76.0% of the variation seen in the port-level life-history data subset (Fig. 11). Only PC 1 and PC 2 had eigenvalues > 1 (3.91 and 1.41, respectively). PC 1 accounted for 55.8% of the variation in the data and is driven primarily by factors related to size and growth, where positive values of PC 1 are correlated with L_{inf} , longevity, and mean size, and negative values of PC 1 are correlated with k , and natural mortality, M . PC 2 accounted for 20.2% of variation and is comprised of condition indices, HSI and Fulton's K, on the positive scale.

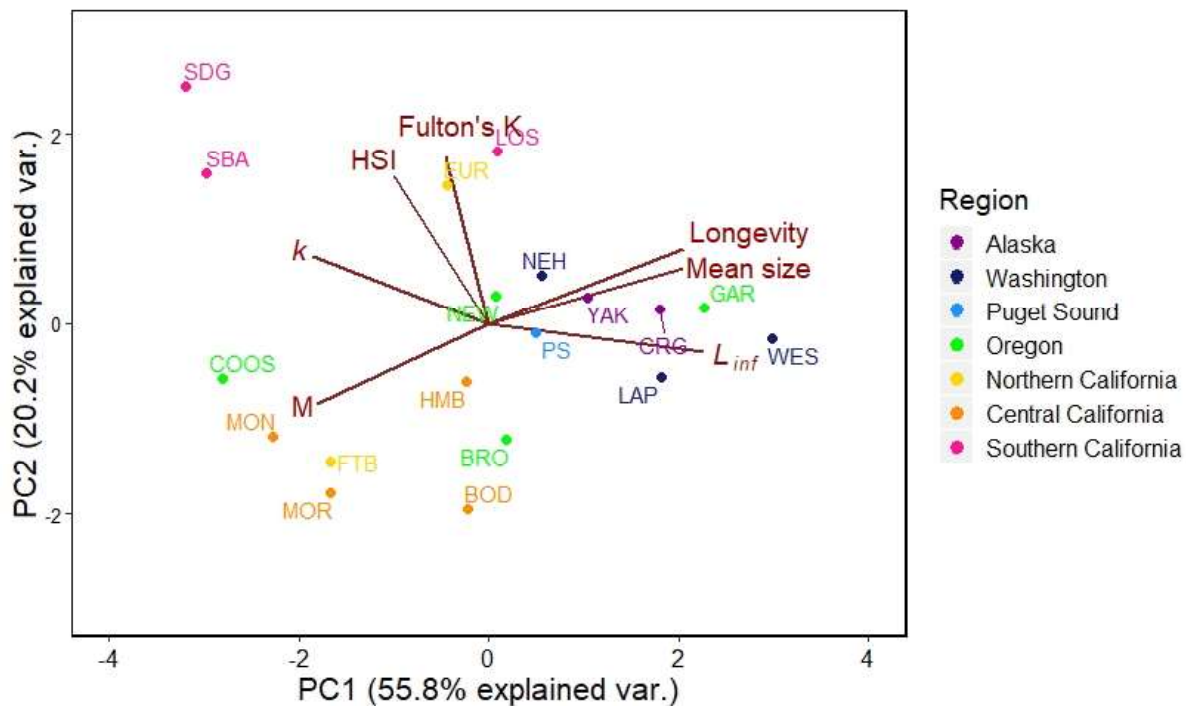


Figure 11: Principle components analysis (PCA) factor loadings for 7 life-history traits on the port-level. Principle components (PC) 1 and 2 together comprise 76% of the variance seen in the dataset. PC 1 is an indicator of health and longevity while PC 2 represents overall condition

PC 1 showed a significant negative relationship with mean SST and a significant positive relationship with chlorophyll *a* (Fig. 12A and 12B). PC 2 exhibited a positive relationship with SST and a slight negative relationship with chlorophyll *a*, however neither of the interactions are significant (Fig. 12C and 12D).

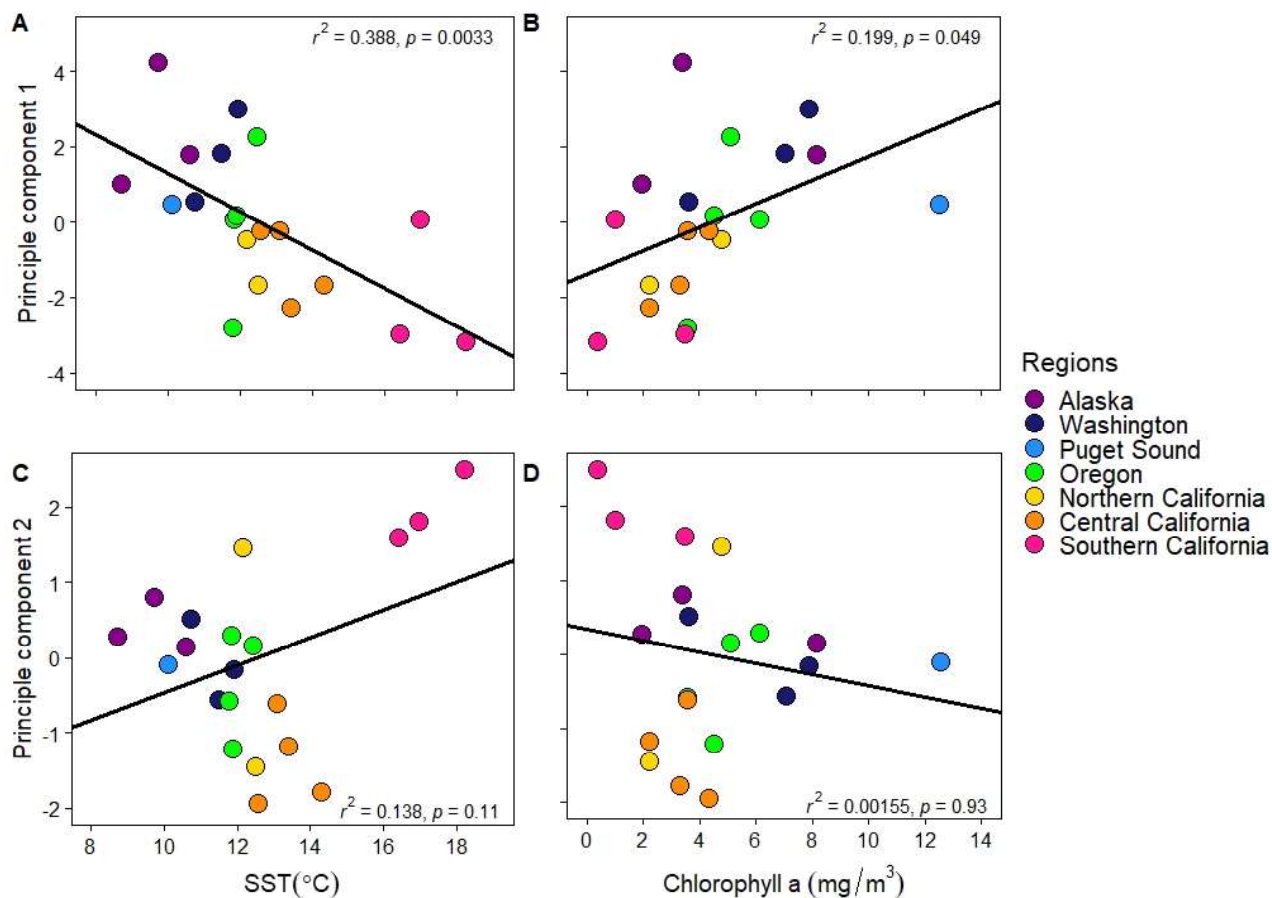


Figure 12: Linear regression between A.) PC 1 and sea surface temperature (SST), B.) PC 1 and chlorophyll a, C.) PC 2 and SST, and D.) PC 2 and chlorophyll a. Each point represents a port and is color coded by region. PC 1 is a measure of growth and longevity while PC 2 is an indicator of overall condition.

CLUSTER ANALYSIS AND nMDS BY PORT

The average silhouette width analysis identified two clusters as being the optimal number of groupings for Lingcod along the U.S. West Coast. Sampled ports are generally separated into a northern (Alaska, Washington, and Oregon) and southern (Oregon, northern California, central California, and southern California) cluster (Fig. 13). The two clusters are significantly different (PERMANOVA: $F_{1,18}=16.022, p<0.001$). The

magnitude and direction of the vectors indicate that the formation of the two clusters is driven by differences in growth, size, and longevity, where Lingcod from the northern cluster are larger and older than Lingcod from the southern cluster. Inversely, Lingcod from southern clusters have higher natural mortality rates and reach maximum sizes faster (larger k value) (Fig. 14)

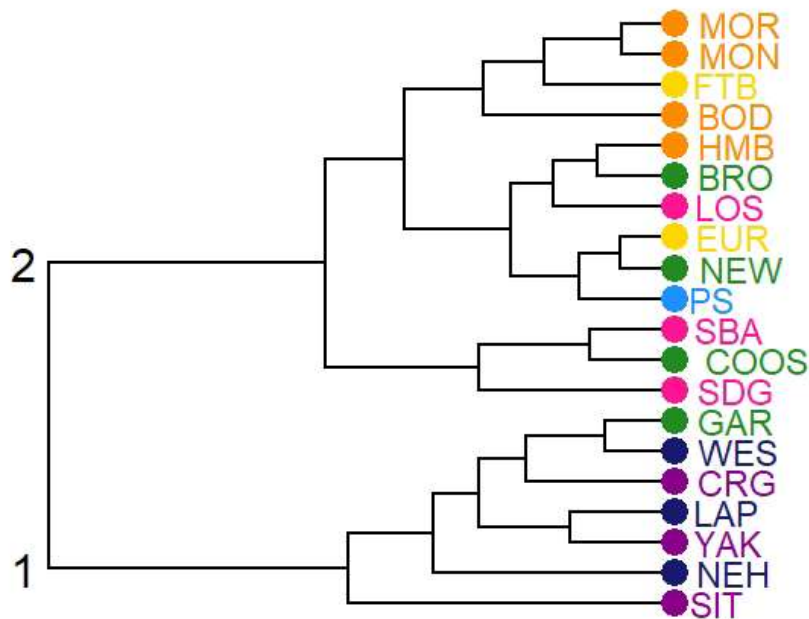


Figure 13: Dendrogram of all sampled ports, clustered by growth-based life-history traits (k , L_{inf} , longevity, mean size, and natural mortality) using the complete linkage agglomerative clustering method. Two clusters were identified as being optimal using the average silhouette width. Ports are colored according to region.

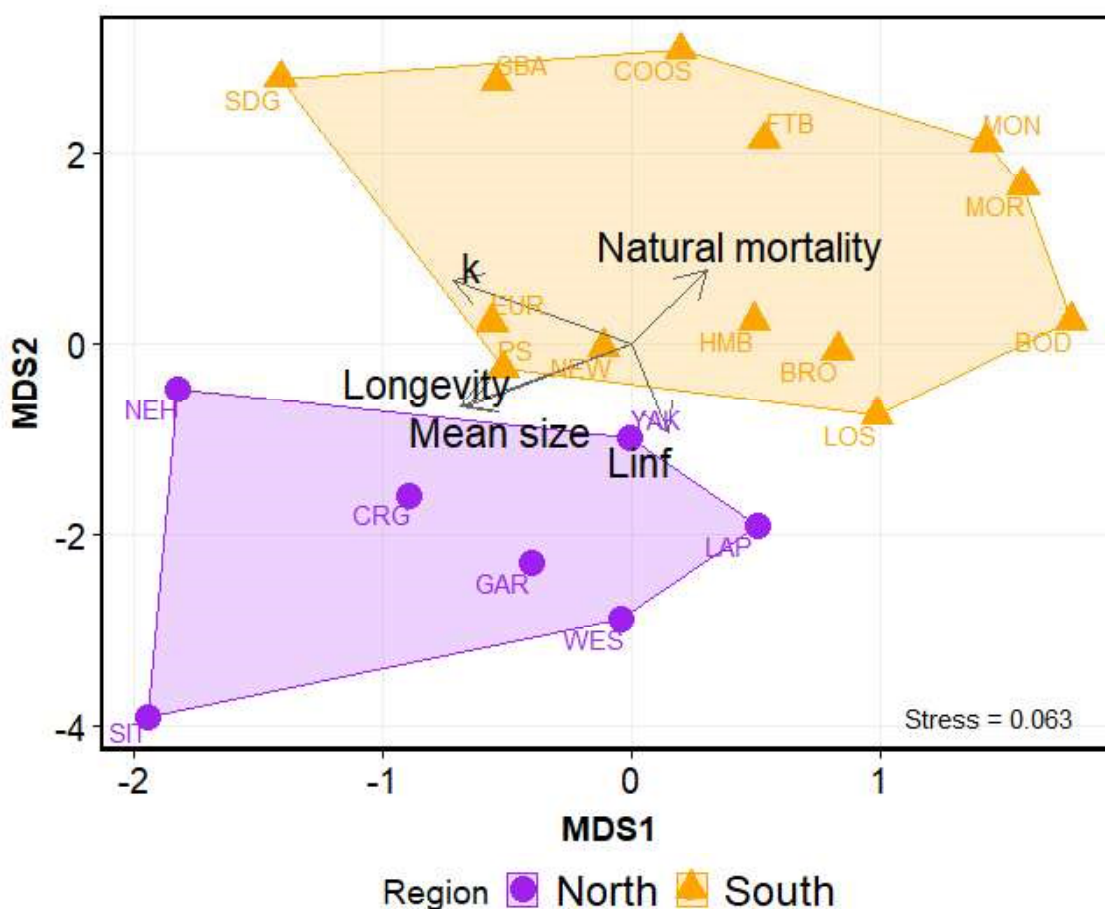


Figure 14: Nonmetric multidimensional scaling (nMDS) plot showing the differences between the northern and southern cluster. The direction and magnitude of the life-history vectors indicate how influential each life-history trait is in creating the clusters.

Discussion

In this study, latitudinal variability in Lingcod life-history was investigated to determine biologically appropriate management units and breakpoints for the Lingcod stock along the U.S. West Coast. Past studies have found that neglecting to account for spatially-specific patterns in life-history and demography of natural populations can lead to mismanagement and can be detrimental to long-term sustainability of a population (Hilborn et al. 2003, King and McFarlane 2003, Maunder and Piner 2015).

VARIABILITY IN LINGCOD DEMOGRAPHY AND LIFE-HISTORY

Spatial differences in life-history have been investigated in many shelf and slope groundfish species: Splitnose rockfish (Boehlert and Kappenman 1980, Gertseva et al. 2010), Canary rockfish (Boehlert and Kappenman 1980, Keller et al. 2018), Dover sole (Brodziak and Mikus 2000, Gertseva et al. 2017), California sheephead (Hamilton et al. 2011, Caselle et al. 2011), Greenstriped rockfish (Keller et al. 2012), Grass rockfish (Wilson et al. 2012), California halibut (Barnes et al. 2015), and Rosy rockfish (Fields 2016). In those studies, consistent with Bergmann's Rule, individuals from northern, colder, nutrient rich waters generally grew faster, attained larger maximum sizes, and lived longer than those from southern, warmer waters (Exceptions: Canary rockfish, California halibut, Rosy rockfish). Those studies also demonstrated that variability in latitudinal patterns of growth, maturity, and mortality, can be due to a combination of oceanographic conditions, biogeographic features, species interactions, and historic fishing pressure. As a result, it is difficult to attribute life-history differences to any one factor without considering the combination of possibilities on a regional scale.

I found that Lingcod exhibit latitudinal patterns in growth and maturity, with individuals from high latitude regions reaching larger maximum sizes, living longer, growing faster and reaching maturity at larger sizes than individuals from low latitude regions. As there was no significant difference in age at 50% maturity among regions, the variability seen in size at 50% maturity is most likely due to faster growth rates at higher latitudes rather than differences in timing or age of maturity. As demonstrated in the PCA, environmental factors of SST and productivity (as measured by chlorophyll *a*) play a significant role in influencing growth, longevity, and body size of Lingcod throughout

the California Current System (CCS) as trends in one are closely mirrored by trends in the other. While Lingcod are not planktivorous, patterns in chlorophyll *a* are closely linked to Lingcod productivity since areas with higher chlorophyll *a* concentrations are able to support higher secondary production of prey types consumed by Lingcod. Patterns in chlorophyll *a* are therefore reflective of spatial differences in Lingcod prey type, abundance, and quality. Colder latitudes near Southeast Alaska and northern Washington have the highest average chlorophyll *a* concentrations in the Pacific Northeast, originating from fresh water input and a steady supply of land-derived nutrients (Hickey and Banas 2003, Ware and Thomson 2005). The central area between the Cape Blanco and Point Conception is considered the region of maximum upwelling (Parrish et al. 1981, Strub et al. 1990, Checkley and Barth 2009) due to strong wind forcing and along-shelf nutrient transport. South of Point Conception, a major biogeographic and oceanographic boundary, wind stress decreases, reducing offshore transport and is therefore comparatively nutrient poor (Cudaback et al. 2005). As shown by the relationship between SST and productivity across all sampled ports, as well as in previous studies, these two oceanographic factors are inextricably linked (Chavez et al. 2010, Feng et al. 2015) and are the primary drivers behind the latitudinal patterns seen in Lingcod size and growth along the U.S. West Coast.

Fish condition is an important measure of energy reserves and can have a large influence on growth, survival, and reproductive success (Love 1974, Lambert and Dutil 1997, Adams 1999, Shulman and Love 1999) as well as serve as an important indicator of habitat productivity and ecosystem health (Lloret et al. 2002, Lloret and Planes 2003). Also, temperature has been assumed to play an important role in determining fish

condition (Ratz and Lloret 2003) where fish living in colder, northern waters tend to be in better condition than those from warmer southern waters (Keller et al. 2012, Fields 2016, Keller et al. 2018). I found the opposite to be true, with Lingcod from warmer, less productive southern California waters exhibiting the highest Fulton's K and HSI condition indices, demonstrating that Lingcod from this region are heavier for a given length and have a larger liver to body weight ratio when compared to Lingcod from other regions.

Several hypotheses could explain the spatial variation in body condition I observed. In southern regions where growth is slower, condition may be higher due to the energetic tradeoff that occurs where energy stores are conserved for later use at the expense of somatic growth (Fisher et al. 2007). In addition, pulsed resource availability in southern waters can affect short-term HSI and Fulton's K calculations. The years between 2014 and 2016 saw one of the strongest El Niño Southern Oscillation (ENSO) events on record (Blunden and Arndt 2016). Beginning in the spring of 2014, coastal sea surface temperatures in the Northeast Pacific were significantly higher than average (+2.5°C) due to the formation of an anomalous warm water mass that continued to persist through 2015-2016 (Jacox et al. 2016, Bond et al. 2015). The abnormally warm waters brought a northward shift in many marine species ranges and coincided with a variety of unusual biological events and species sightings (Bond et al. 2015). In particular, pelagic red crabs (*Pleuroncodes planipes*) were reported to be washing up along the central to southern California coast from January through October of 2015, which is consistent with the stranding patterns seen during the 1997-1998 ENSO event as well (McClatchie 2016). Preliminary examination of Lingcod diet contents from the southern California region

found about 25% of full stomachs to contain pelagic red crabs (B. Brown, *unpublished data*). This anomalous pulse of prey resources may thus explain the high body condition of southern California samples. ENSO conditions could similarly be affecting typical prey availability in northern waters, resulting in northern Lingcod with poorer condition. While past studies typically link colder temperatures with higher fish condition, it is possible that condition may in fact be following patterns of marine productivity (Ratz and Loret 2003). Therefore, prey availability and regional upwelling patterns can potentially be a stronger indicator of condition over direct temperature effects.

Lingcod did not exhibit a latitudinal pattern in total mortality and only a slight latitudinal trend in natural mortality rates; however, these two metrics are influenced by highly disparate factors. M is derived using maximum observed age, A_{max} , not longevity, T_{max} , therefore empirically calculated M values can be easily skewed by outliers and has the potential to be highly variable (Hoenig 1963, Pascual and Iribarne 1993, Maunder and Piner 2015). This variability can be seen in past Lingcod studies where different methods (tag-recapture, empirical formulas) were used to calculate M , with inconsistent results (values ranging from 0.18 to 0.8) (Forrester 1973, Jagielo 1994, Starr et al. 2005). Little research has been done to directly compare natural mortality over large geographic ranges, however, in principle, it can be assumed that in the absence of fishing, fish that live longer (i.e. fish from northern, productive, latitudes) experience higher survival and hence lower natural mortality rates. Conversely, Z is affected by both M and fishing mortality, F . F is based on historic fishing pressure and is the parameter that is set as a management target instead of one that is mathematically derived.

Lingcod from Washington and southern California showed the highest Z compared to all other regions as well as the highest F , while mid-range regions were significantly lower and exhibited no trend in Z or F . Lingcod from southern California appear more sensitive to fluctuations in fishing mortality due to the compounding effect of high historic Lingcod harvest rates that remove large, reproductive adults, and predominantly weak oceanographic conditions unfavorable to recruitment. This can result in an overall reduction in spawning stock biomass and spawning potential (Haltuch et al. 2017). Similar results were reported by Hamilton et al. (2011) and Fields (2016) when comparing total mortality of California sheephead and Rosy rockfish, respectively, across spatially distinct areas. Regions experiencing greater fishing pressure had significantly higher total mortality rates.

In the early 2000s, when the Lingcod stock was federally recognized as being overfished coastwide, harvest rates in the south (California) had already exceeded management targets for several years. Recently, harvest rates have been below management targets, however the exploitation status of Lingcod is still considerably higher in the south than it is in the north (Haltuch et al. 2017). In the case of Lingcod from Washington, although F is comparable to that of southern California Lingcod, M is lower, potentially due to greater productivity and nutrient influx in the northern CCS region creating conditions beneficial to recruitment and survival. From this it can be inferred that whereas the Lingcod stock has historically been heavily exploited coastwide, regional population performance, health, and resilience is heavily dependent on small-scale coastal dynamics.

SEX-BASED VARIABILITY IN LINGCOD DEMOGRAPHY AND LIFE-HISTORY

Sexual dimorphism is seen in both endothermic and ectothermic organisms, such that reproductive success is maximized for each sex (Shine 1979, Ghiselin 1974, Berns 2013). Sex-based differences in size and growth are generally driven by differences in energy allocation towards somatic growth versus reproduction and tradeoffs in reproductive investment (Rjinsdorp 1989, Krebs and Davies 2009). In fishes, females generally grow larger, mature later and have higher lipid and protein content than male conspecifics (Breder and Rosen 1966, Echeverria 1986, Rjinsdorp 1989, Parker 1992, Krebs and Davies 2009). However, this is dependent on mode of fertilization; in families exhibiting external fertilization, male parental care is 70% more common while the opposite is true in families using internal fertilization, where females are 86% more likely to invest in parental care (Gross and Shine 1981).

In Lingcod and others in the Hexagrammid and Cottid families, males guard nests during offspring embryonic development and heavily invest in reproduction. Parental nest guarding behavior comes at considerable risk and cost to survival and fitness by limiting the male's opportunity to forage and by increasing exposure to predation (Townshend and Wootton 1985, Sabat 1994, Balshine-Earn 1995, Lindstrom 1998). This is a potential driver behind the earlier timing of maturity and smaller sizes seen in male Lingcod; energy is diverted away from somatic growth sooner to focus on maximizing reproductive potential (Roff 1986, Charnov and Berrigan 1991*b*, Parker 1992). In addition, the higher condition and energy reserve status seen in male Lingcod may be reflective of the greater energetic cost required to successfully select a nesting site and defend egg masses against predators for 8-12 weeks during spawning season. Past studies

on species with nest-guarding males, found that reproductive success is positively related to male condition as greater energy availability translates to increased investment in reproductive effort (Knapp 1995, Lindstrom 1998). It is possible that male Lingcod are in better condition because of higher reproductive investment, however this trend is not seen in other species, nest-guarding or otherwise (Lloret et al. 2002, Lloret and Ratz 2000, Cope and MacCall 2005, Cope and Key 2009, Sogabe et al. 2012). Moreover, the same sex-based differences in size and growth seen in Lingcod are found in many other non-nest guarding rockfish, flatfish, and roundfish species as well (Boehlert and Kappenman 1980, Brodziak and Mikus 2000, Gertseva et al. 2010, Barnes et al. 2015, Gertseva et al. 2017).

The Lingcod in my study were collected using methods commonly employed by the recreational hook-and-line fishery that disproportionately targets male Lingcod from nearshore rocky habitats (Figure 3, Miller and Geibel 1973). Heavy exploitation can produce population level changes due to the tendency of the fishing industry to remove large, long-lived, reproductive individuals from the population (Ricker 1981, Levin et al. 2006). This results in fishing induced evolution, where truncated size and age distributions lead to declines in average body size, faster growth, and earlier size at maturity over time (Ricker 1981, Rjinsdorp 1993, Conover and Munch 2002, Reznick and Ghalambor 2005, Beamish et al. 2006, Schmidt 2014, Fields 2016). Energy resources that used to be directed towards somatic growth are instead diverted to hasten gonad development, leading to smaller spawners and reduced size-at-age in mature fish (Dieckmann and Heino 2007, Pardoe et al. 2009). Over the past decade, the recreational Lingcod fishery has grown substantially, almost quadrupling its total landings since 2010

(Haltuch et al. 2017). Therefore, the smaller sizes, earlier maturation, and faster growth seen in male Lingcod from this study may be a direct result of fishing induced evolution. However, it is likely a combination of fishing pressure and behavioral and energetic tradeoffs during spawning that makes sexual dimorphism in Lingcod so pronounced.

CLUSTER ANALYSIS AND MANAGEMENT IMPLICATIONS

Results from the cluster analysis and nMDS demonstrate that the boundary currently used in Lingcod stock assessments (2 stocks, with a break at the California-Oregon border) may not be the most biologically appropriate geographic breakpoint for the coastwide population. Based on estimated life-history parameters for each sampled port along the coast, I found evidence for two regional clusters for the Lingcod stock: A northern and southern cluster with the boundary in central Oregon, between the ports of Garibaldi and Newport. While this boundary between the northern and southern clusters is not dramatically different than the current boundary used in stock assessments, it is still informative and has important management implications for Lingcod and other Groundfish species along the U.S. West Coast.

The current Lingcod stock assessment boundary at the California-Oregon state line was initially chosen because it was easier to regulate and to keep track of total landings on the state level. Prior to 1997, however, the Lingcod population was assessed on the coastwide scale as a single stock. It was eventually split up into northern and southern zones in 1997 due to drastic declines in the population but even then, separate stock assessments were only conducted because the southern region was extremely data limited compared to the northern region and not because of biologically relevant

population differences. This is the same rationale used in all recent stock assessments that have been conducted on broad ranging groundfish species (Hicks et al. 2010, Hicks and Wetzel 2015, Cope et al. 2015, Cope et al. 2016, Thorson and Wetzel 2016, Gertseva and Cope 2017, Stephens and Taylor 2018). For especially data limited species (i.e. Greenstriped rockfish, Widow rockfish, Bocaccio, Brown rockfish, Stripetail rockfish, English sole, and Rex sole), a single coastwide stock is commonly used. For species with sampling data over a longer timer series and accurate landings information from both commercial and recreational fishery sectors (i.e. Canary rockfish, Yelloweye rockfish, Black rockfish, Yellowtail rockfish, China rockfish, Copper rockfish), two to three coastwide breaks are often considered, typically occurring at state lines. While life-history variability was investigated in some of the above mentioned species, for the purpose of creating a stock assessment model with high predictive power, coastwide breaks corresponding to accurate historic catch records are often used in place of biologically significant geographic boundaries (Hicks and Wetzel 2015, Cope et al. 2016).

State lines are commonly used because each state has its own unique history of fishing exploitation that is driven by fisher behavior and market demand, which affects the commercial and recreational fishing sectors in different ways. However, it is important to account for latitudinal variability in growth, maturity, longevity and mortality when modelling natural populations and setting size regulations, seasonal closures, and catch limits. Additional population breaks can be found within state lines, and considering larger states like California and Alaska, separate stock assessments may be needed on a regional level within states as well. For groundfish species that are

overfished or have been overfished in the past, spatially explicit management and assessment methods that incorporate state-specific historic fishing practices and biological population parameters could be the key to ensuring that fishery sustainability and yield can be maximized for years to come.

CONCLUSIONS AND RECOMMENDATIONS

Disentangling the mechanisms behind how fish populations change over broad latitudinal ranges can be very complex and has strong implications for the future of stock assessments and fisheries management methods. The goal of this study was to investigate the latitudinal and sex-specific factors that can have profound impacts on life-history estimates used in groundfish stock assessment models. Modelling methods are constantly advancing and adapting as new information becomes available, however, models are only as good as the data used to parameterize them (Mangel and Levin 2005, Maunder and Piner 2014), and current stock assessments can be limited by the lack of historic harvest information and insufficient or inconsistent indices of abundance.

Given the results from this study, I would recommend a detailed examination of the long-term economic trade-offs between setting size regulations and catch quotas according to regional estimates of growth, maturity, and mortality from two Lingcod groups along the U.S. West Coast with the break in central Oregon (Between the ports of Newport and Garibaldi). Total fisheries yield using central Oregon as the dividing boundary should be compared to that of using the boundary of the status quo at the California-Oregon border. Understandably, the management, assessment, and enforcement of a separate northern and southern stock for Lingcod divided at central

Oregon would require a substantial increase in state and federal involvement, funding, and monitoring; commercial and recreational landings information will need to be more spatially explicit on the port-level to capture fine scale fishery removal patterns. Risk-assessment and cost-benefit analyses should be conducted and compared to fully assess the feasibility and real-world application of this option.

Because the most significant differences in Lingcod growth, maturity, and mortality rates were driven by sex, I propose separate regulations for male and female Lingcod in the recreational fishery only. Compared to the 100% mortality rate from using commercial fixed gear fishing methods (e.g. bottom-trawl and long-line), hook-and-line gear used in the recreational fishery can have very low post-release mortality rates. Unlike rockfishes that are affected by barotrauma, Lingcod are exceptionally hardy and experience little to no hooking or deck mortality, enabling them to be safely released at the surface. Additionally, Lingcod can easily be externally sexed by the presence of a conical papillae in males. Given that male Lingcod mature earlier than females, reducing the minimum size limit and increasing the bag limit for males could increase overall fishery yield while ensuring that larger, reproductive females remain in the population. While sex-based management is not often done on finfish fisheries, the West Coast Dungeness Crab fishery has abided by sex-specific regulations for over 100 years (CDFW 2011) and is still a lucrative and sustainable fishery today. The Dungeness Crab fishery serves as a successful example of sex-specific management where the preservation of large, reproductively mature females directly increases the productivity the fishery and the population (Rasmuson 2013).

In conclusion, this study underscores the value of obtaining accurate spatial information for determining stock structure and dynamics for management purposes. Over the past several decades, fisheries management has been focusing on developing ecosystem-based management plans where multispecies interactions, environmental fluctuations, and community shifts through time and space are considered throughout the decision-making process (Jennings et al. 2001).

While it may not be economically realistic to conduct a study like this one on over 90+ groundfish species individually, there are assemblages within the groundfish complex that have been found to co-occur across spatial or temporal scales (Cope and Haltuch 2012); an indicator species within each assemblage can be identified and used to represent the larger group for more targeted research on patterns of life-history variability. Stock assessors can use this information as a baseline to understand how groundfish assemblages can shift over space and time as a result of certain management decisions so that sustainable stocks can be maintained for future needs.

References

- Adams, S. M. (1999). Ecological role of lipids in the health and success of fish populations. In *Lipids in freshwater ecosystems* (pp. 132-160). Springer, New York, NY.
- Adams, P. (1986). Status of Lingcod (*Ophiodon elongatus*) stocks off the coast of Washington, Oregon and California. *Status of the Pacific Coast groundfish fishery through 1986 and recommended biological catches for 1987*. Appendix 7, 58 p. *Pacific Fishery Management Council, Portland, Oregon*.
- Adams, P. B., Williams, E. H., Silberberg, K. R., & Laidig, T. E. (1999). Southern Lingcod stock assessment in 1999. *Appendix: status of the Pacific groundfish fishery through 1999 and recommended biological catches for 2000*. *Pacific Fishery Management Council, Portland, Oregon*.
- Allee, W. C., & Schmidt, K. P. (1951). *Ecological animal geography*. John Wiley And Sons, Inc.; London.
- Alverson, D. L., & Carney, M. J. (1975). A graphic review of the growth and decay of population cohorts. *Journal du Conseil*, 36(2), 133-143.
- Archibald, C. P., W. Shaw, and B. M. Leaman. (1981). Growth and mortality estimates of rockfishes (*Scorpaenidae*) from B.C. coastal waters 1977-1979. *Canadian Technical Report or Fisheries and Aquatic Sciences*. 1048. Nanaimo, BC: Government of Canada, Fisheries and Oceans.
- Atkinson, D. (1994). Temperature and organism size: a biological law for ectotherms? *Advances in ecological research*, 25, 1-1.
- Atkinson, D., & Sibly, R.M. (1997) Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology & Evolution*, 12:6, 235-239.
- Balshine-Earn, S. I. G. A. L. (1995). The costs of parental care in Galilee St Peter's fish, *Sarotherodon galilaeus*. *Animal Behaviour*, 50(1), 1-7.
- Barth, J. A., Pierce, S. D., & Smith, R. L. (2000). A separating coastal upwelling jet at Cape Blanco, Oregon and its connection to the California Current System. *Deep Sea Research Part II: Topical Studies in Oceanography*, 47(5-6), 783-810.
- Beamish, R. J., & Chilton, D. (1977). Age determination of Lingcod (*Ophiodon elongatus*) using dorsal fin rays and scales. *Journal of the Fisheries Board of Canada*, 34(9), 1305-1313.
- Beamish, R. J., McFarlane, G. A., & Benson, A. (2006). Longevity overfishing. *Progress in Oceanography*, 68(2-4), 289-302.
- Beaudreau, A. H., & Essington, T. E. (2007). Spatial, temporal, and ontogenetic patterns of predation on rockfishes by Lingcod. *Transactions of the American Fisheries Society*, 136(5), 1438-1452.
- Berger, A. M., Arnold, L., & Rodomsky, B. T. (2015). Status of Kelp Greenling (*Hexagrammos decagrammus*) along the Oregon Coast in 2015. *Pacific Fishery Management Council, Portland, OR*.
- Bergmann, C. (1847) Ueber die verhältnisse der wdrmeokonomie der thiere zu ihrer grosse. *Gottinger studien* (3), 595-708.

- Berns, C.M. (2013). The evolution of sexual dimorphism: understanding mechanisms of sexual shape differences. In: Moriyama H, editor. *Sexual dimorphism*. Rijeka: InTech; 2013. p. 1-16.
- Beverton, R. J. (1954). Notes on the use of theoretical models in the study of the dynamics of exploited fish populations (No. 2). U.S. Fishery Laboratory, 154 p.
- Beverton, R. J. H. (1992). Patterns of reproductive strategy parameters in some marine teleost fishes. *Journal of Fish Biology*, 41, 137-160.
- Beverton, R. J. H., & Holt, S. J. (1959). A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In *Ciba Foundation Symposium-The Lifespan of Animals (Colloquia on Ageing), Volume 5* (pp. 142-180). John Wiley & Sons, Ltd.
- Blanchette, C. A., Melissa Miner, C., Raimondi, P. T., Lohse, D., Heady, K. E., & Broitman, B. R. (2008). Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. *Journal of Biogeography*, 35(9), 1593-1607.
- Blanchette, C. A., & Gaines, S. D. (2007). Distribution, abundance, size and recruitment of the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. *Journal of Experimental Marine Biology and Ecology*, 340(2), 268-279.
- Blunden, J. and D. S. Arndt, Eds., (2016). State of the Climate in 2015. *Bulletin of the American Meteorological Society*, 97 (8), S1–S275, DOI:10.1175/2016BAMSStateoftheClimate.1
- Boehlert, G. W., & Kappenman, R. F. (1980). Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploproa*) from the northeast Pacific Ocean. *Marine Ecology Progress Series*, 3(1), 1-10.
- Bolger, T., & Connolly, P. L. (1989). The selection of suitable indices for the measurement and analysis of fish condition. *Journal of Fish Biology*, 34(2), 171-182.
- Bond, N. A., Cronin, M. F., Freeland, H., & Mantua, N. (2015). Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters*, 42(9), 3414-3420.
- Boyce, M.S. (1978). Climatic variability and body size variation in muskrats (*Ondatra zibethicus*) of North America. *Oecologia* 36:1–19.
- Breder, C. M., & Rosen, D. E. (1966). Modes of reproduction in fishes.
- Brodeur, R. D. (2001). Habitat-specific distribution of Pacific ocean perch (*Sebastes alutus*) in Pribilof Canyon, Bering Sea. *Continental Shelf Research*, 21(3), 207-224.
- Brodziak, J., & Mikus, R. (2000). Variation in life history parameters of Dover sole, *Microstomus pacificus*, off the coasts of Washington, Oregon, and northern California. *Fishery Bulletin*, 98: 661-673.
- Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: a practical information-theoretic approach*. Second edition. Springer-Verlag, New York, USA.
- Butler, J. L., Love, M. S., & Laidig, T. E. (2012). *A guide to the rockfishes, thornyheads, and scorpionfishes of the northeast Pacific*. University of California Press.

- California Department of Fish and Game (2012). Dungeness crab report from California's Living Marine Resources: A Status Report.
- Campana, S. E., Annand, M. C., & McMillan, J. I. (1995). Graphical and statistical methods for determining the consistency of age determinations. *Transactions of the American Fisheries Society*, 124(1), 131-138.
- Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*, 59(2), 197-242.
- Cass, A. J., & Beamish, R. J. (1983). First evidence of validity of the fin-ray method of age determination for marine fishes. *North American Journal of Fisheries Management*, 3(2), 182-188.2
- Cass, A.J., Beamish, R.J. and McFarlane, G.A. (1990). Lingcod (*Ophiodon elongatus*). *Canadian Special Publication of Fisheries and Aquatic Sciences*. 109, 40 p.
- Chang, W. Y. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences*, 39(8), 1208-1210.
- Charnov, E. L., & Berrigan, D. (1991). Evolution of life history parameters in animals with indeterminate growth, particularly fish. *Evolutionary Ecology*, 5(1), 63-68.
- Chapman, D., & Robson, D. S. (1960). The analysis of a catch curve. *Biometrics*, 354-368.
- Chatwin, B. M. (1956). Age and growth of Lingcod (*Ophiodon elongatus*). *Fisheries Research Board of Canadian Pacific Program Report*, 105, 22-26.
- Chatwin, B. M. (1958). Mortality rates and estimates of theoretical yield in relation to minimum commercial size of Lingcod (*Ophiodon elongatus*) from the Strait of Georgia, British Columbia. *Journal of the Fisheries Board of Canada*, 15(5), 831-849.
- Chavez, F. P., Messié, M., & Pennington, J. T. (2010). Marine primary production in relation to climate variability and change.
- Checkley Jr, D. M., & Barth, J. A. (2009). Patterns and processes in the California Current System. *Progress in Oceanography*, 83(1-4), 49-64.
- Chilton, D. E., & Beamish, R. J. (1982). Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. *Canadian Special Publication of Fisheries and Aquatic Sciences* 60: p 34-38.
- Choat, J. H., & Robertson, D. R. (2002). Age-based studies. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, California, USA, 57-80.
- Conover, D. O., & Present, T. M. (1990). Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia*, 83(3), 316-324.
- Cope, J. M., & MacCall, A. D. (2005). Status of kelp greenling (*Hexagrammos decagrammus*) in Oregon and California waters as assessed in 2005. *Pacific Fishery Management Council*, 7700, 158.
- Cope, J. M., & Key, M. (2009). *Status of Cabezon (Scorpaenichthys marmoratus) in California and Oregon waters as assessed in 2009*. Pacific Fisheries Management Council.
- Cope, J. M., & Punt, A. E. (2011). Reconciling stock assessment and management scales under conditions of spatially varying catch histories. *Fisheries Research*, 107(1), 22-38.

- Cope, J.M., Dick, E. J., MacCall, A., Monk, M., Soper, B., & Wetzel, C. (2013). Data-moderate stock assessments for brown, China, copper, sharpchin, stripetail, and yellowtail rockfishes and English and rex soles in 2013. *National Oceanic and Atmospheric Administration, National Marine Fisheries Service*.
- Cope, J.M., Sampson, D., Stephens, A., Key M., Mirick, P.P.,...& Rodomsky, B.T. (2016). Assessments of California, Oregon and Washington Stocks of Black Rockfish (*Sebastes melanops*) in 2015. *National Oceanic and Atmospheric Administration, National Marine Fisheries Service*.
- Cudaback, C. N., Washburn, L., & Dever, E. (2005). Subtidal inner-shelf circulation near Point Conception, California. *Journal of Geophysical Research: Oceans*, 110(C10).
- Dichmont, C. M., Deng, R. A., Punt, A. E., Brodziak, J., Chang, Y. J., Cope, J. M., ... & Prager, M. H. (2016). A review of stock assessment packages in the United States. *Fisheries Research*, 183, 447-460.
- Estes, J. A., Tinker, M. T., Williams, T. M., & Doak, D. F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, 282(5388), 473-476.
- Echeverria, T. W. (1987). Thirty-four species of California rockfishes: maturity and seasonality of reproduction. *Fishery Bulletin*, 85(2), 229-250.
- Fahrig, L.E. (1993). Effect of fish movement and fleet spatial behavior on management of fish substocks. *Natural Resource Modeling*, 7(1), 37-56.
- Fields, R. T. (2016). Spatial and temporal variation in rosy rockfish (*Sebastes rosaceus*) life history traits (Masters Thesis). *California State University, Monterey Bay*.
- Fisher, R., Sogard, S. M., & Berkeley, S. A. (2007). Trade-offs between size and energy reserves reflect alternative strategies for optimizing larval survival potential in rockfish. *Marine Ecology Progress Series*, 344, 257-270.
- Feng, Jianfeng, Joël Marcel Durant, Leif Chr Stige, Dag Olav Hessen, Dag Øystein Hjermann, Lin Zhu, Marcos Llope, and Nils Chr Stenseth. (2015). Contrasting correlation patterns between environmental factors and chlorophyll levels in the global ocean. *Global Biogeochemical Cycles* 29(12): 2095-2107.
- Forrester, C. R. (1973). *The Lingcod (Ophiodon elongatus) in waters off western Canada*. Pacific Biological Station.
- Foster, M. S., & Schiel, D. R. (1985). The ecology of giant kelp forests in California: a community profile. *U.S. Fish and Wildlife Service Biological Report*, 85(7.2). 152 pp.
- Fulton, T. W. (1902). *Rate of growth of sea fishes*. Neill & Company, *Edinburgh, Scotland*. p 326-439.
- Gertseva, V. V., Cope, J. M., & Matson, S. E. (2010). Growth variability in the splitnose rockfish *Sebastes diploproa* of the northeast Pacific Ocean: pattern revisited. *Marine Ecology Progress Series*, 413, 125-136.
- Gertseva, V., Matson, S. E., & Cope, J. (2017). Spatial growth variability in marine fish: example from Northeast Pacific groundfish. *ICES Journal of Marine Science*, 74(6), 1602-1613.
- Gertseva, V. and Cope, J.M. (2017). Stock assessment of the yelloweye rockfish (*Sebastes ruberrimus*) in state and Federal waters off California, Oregon and Washington. Pacific Fishery Management Council, Portland, OR. Available from <http://www.pcouncil.org/groundfish/stockassessments/>

- Ghiselin, M. T., *The Economy of Nature and the Evolution of Sex* (University of California Press, Berkeley, 1974).
- Gillooly, J. F., & Baylis, J. R. (1999). Reproductive success and the energetic cost of parental care in male smallmouth bass. *Journal of Fish Biology*, 54(3), 573-584.
- Girden, E.R. (2001). Evaluating research articles from start to finish. Thousand Oaks, CA, Sage Publications.
- Grebel, J. M., & Cailliet, G. M. (2010). Age, growth, and maturity of Cabezon (*Scorpaenichthys marmoratus*) in California. *California Fish and Game*, 96(1), 36-52.
- Greenley, A.P. (2009). Movements of Lingcod (*Ophiodon elongatus*) tagged in Carmel Bay, CA. MS Thesis San Jose State University, Moss Landing Marine Laboratories, Moss Landing, CA 95039. 81 pp.
- Greenley, A., Green, K., & Starr, R. M. (2016). Season and ontogenetic movements of Lingcod (*Ophiodon elongatus*) in Central California, with implications for Marine Protected Area management. *California Cooperative Oceanic Fisheries Investigative Reports*, 57, 71-88.
- Gunderson, D. R., Parma, A. M., Hilborn, R., Cope, J. M., Fluharty, D. L., Miller, M. L., ... & Greene, H. G. (2008). The challenge of managing nearshore rocky reef resources. *Fisheries*, 33(4): 172-179.
- Haldorson, L., & Love, M. (1991). Maturity and fecundity in the rockfishes, *Sebastes* spp., a review. *Marine Fisheries Review*, 53(2), 25-31.
- Haltuch, M.A., Wallace, J., Akselrud, C.A., Nowlis, J., Barnett, L.A.K., Valero, J.L., Tsou, T., Lam, L. 2018. 2017 Lingcod Stock Assessment. Pacific Fishery Management Council, Portland, OR. Available from <http://www.pcouncil.org/groundfish/stock-assessments/>
- Hamilton, S.L., Wilson, J.R., Ben-Horin, T., & Caselle, J.E. (2011). Utilizing spatial demographic and life history variation to optimize sustainable yield of a temperate sex-changing fish. *PLoS ONE* 6(9): e24580. doi:10.1371/journal.pone.0024580.
- Hamel, O. S., Sethi, S. A., & Wadsworth, T. F. (2009). Status and future prospects for Lingcod in waters off Washington, Oregon, and California as assessed in 2009. *Pacific Fishery Management Council, Portland, Oregon*.
- Hart, J.L. (1973). *Pacific fishes of Canada*. Fisheries Research Board of Canada, Ottawa, 740 p.
- He, X., and Field, J.C. (2017). Stock Assessment Update: Status of Bocaccio, *Sebastes paucispinis*, in the Conception, Monterey and Eureka INPFC areas for 2017. *Pacific Fishery Management Council, Portland, Oregon*.
- Hickey, B.M. (1979). The California current system – hypotheses and facts. *Progress in Oceanography*, 8, 191–279.
- Hickey, B. M., & Banas, N. S. (2003). Oceanography of the US Pacific Northwest coastal ocean and estuaries with application to coastal ecology. *Estuaries*, 26(4), 1010-1031.
- Hicks, A. C., Haltuch, M. A., & Wetzel, C. R. (2009). Status of Greenstriped Rockfish (*Sebastes elongatus*) Along the Outer Coast of California, Oregon, and Washington. *National Marine Fisheries Service, Northwest Fisheries Science Center*.
- Hicks, A. C., & Wetzel, C. R. (2015). The status of Widow Rockfish (*Sebastes entomelas*) along the US west coast in 2015. *Pacific Fishery Management Council, Portland, OR*.

- Hilborn, R. (2003). The state of the art in stock assessment: Where we are and where we are going. *Scientia Marina*, 67(1), 15-20.
- Hilborn, R., Branch, T. A., Ernst, B., Magnusson, A., Minte-Vera, C. V., Scheuerell, M. D., & Valero, J. L. (2003a). State of the world's fisheries. *Annual review of Environment and Resources*, 28(1), 359.
- Hilborn, R., Quinn, T. P., Schindler, D. E., & Rogers, D. E. (2003b). Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences*, 100(11), 6564-6568.
- Hixon, M. A., Johnson, D. W., & Sogard, S. M. (2013). BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*, 71(8), 2171-2185.
- Hoening, J. M. (1983). Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin*, 82(1), 898-903.
- Htun-Han, M. (1978). The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: gonosomatic index, hepatosomatic index and condition factor. *Journal of Fish Biology*, 13(3), 369-378.
- Jacox, M. G., Hazen, E. L., Zaba, K. D., Rudnick, D. L., Edwards, C. A., Moore, A. M., & Bograd, S. J. (2016). Impacts of the 2015–2016 El Niño on the California Current System: Early assessment and comparison to past events. *Geophysical Research Letters*, 43(13), 7072-7080.
- Jagiello, T. H. (1990). Movement of tagged Lingcod (*Ophiodon elongatus*) at Neah Bay, Washington. *Fishery Bulletin*, 88(4), 815-820.
- Jagiello, T. H. (1995). Abundance and survival of Lingcod at Cape Flattery, Washington. *Transactions of the American Fisheries Society*, 124(2), 170-183.
- Jagiello, T., Adams, P., Peoples, M., Rosenfield, S., Silberberg, K. R., & Laidig, T. E. (1997). Assessment of Lingcod in 1997. *Pacific Fishery Management Council, Portland, Oregon*.
- Jagiello, T. H. (1999). Movement, mortality, and size selectivity of sport-and trawl-caught Lingcod off Washington. *Transactions of the American Fisheries Society*, 128(1), 31-48.
- Jagiello, T. H., Wilson-Vandenberg, D., Sneva, J., Rosenfeld, S., & Wallace, F. (2000). Assessment of Lingcod (*Ophiodon elongatus*) for the Pacific Fishery Management Council in 2000. *Pacific Fishery Management Council, Portland, OR*.
- Jagiello, T. H., Wallace, F. R., & Cheng, Y. W. (2003). Assessment of Lingcod (*Ophiodon elongatus*). *Pacific Fishery Management Council, Portland, OR*.
- Jagiello, T., A. Hoffmann, J. Tagart, and M. Zimmermann. (2003). Demersal groundfish densities in trawlable and untrawlable habitats off Washington: Implications for the estimation of habitat bias in trawl surveys. *Fishery Bulletin*, 101, 545–565.
- Jagiello, T. H., & Wallace, F. R. (2005). Assessment of Lingcod. *Ophiodon elongatus*, 1-153. *Pacific Fishery Management Council, Portland, Oregon*
- Jensen, A. L. (1996). Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(4), 820-822.

- Jensen, A.L. (1997). Origin of the relation between K and L_{inf} and synthesis of relations among life history parameters. *Canadian Journal of Fisheries and Aquatic Sciences*. Sci. 54: 987-989.
- Jewell, E. D. (1968). SCUBA diving observations on Lingcod spawning at a Seattle breakwater. *Washington Department of Fisheries Research Paper*, 3, 27-36.
- Keller, A. A., Molton, K. J., Hicks, A. C., Haltuch, M., & Wetzel, C. (2012). Variation in age and growth of greenstriped rockfish (*Sebastes elongatus*) along the U.S. west coast (Washington to California). *Fisheries Research*, 119, 80-88.
- Keller, A. A., J. R. Wallace, & Methot, R. D. (2017). The Northwest Fisheries Science Center's West Coast Groundfish Bottom Trawl Survey: History, Design, and Description. *U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-136*.
- Keller, A. A., Frey, P. H., Wallace, J. R., Head, M. A., Wetzel, C. R., Cope, J. M., & Harms, J. H. (2018). Canary rockfishes *Sebastes pinniger* return from the brink: catch, distribution and life history along the US west coast (Washington to California). *Marine Ecology Progress Series*, 599, 181-200.
- Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin*, 77(4), 765-776.
- Kimura, D. K., & Lyons, J. J. (1991). Between-reader bias and variability in the age-determination process. *Fishery Bulletin*, 89(1), 53-60.
- Kimura, D. K. (2008). Extending the von Bertalanffy growth model using explanatory variables. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(9), 1879-1891.
- King, J. R., & McFarlane, G. A. (2003). Marine fish life history strategies: applications to fishery management. *Fisheries Management and Ecology*, 10(4), 249-264.
- Knapp, R. A. (1995). Influence of energy reserves on the expression of a secondary sexual trait in male bicolor damselfish, *Stegastes partitus*. *Bulletin of Marine Science*, 57(3), 672-681.
- Krebs, J. R., & Davies, N. B. (Eds.). (2009). *Behavioural ecology: an evolutionary approach*. John Wiley & Sons.
- Laidig, T.E., K.R. Silberberg, and P.B. Adams. (2001). Age validation of the first, second, and third annuli from the dorsal rays of Lingcod (*Ophiodon elongatus*). *NOAA Technical Memorandum* 306, 19 p.
- Lambert, Y., & Dutil, J. D. (1997). Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of cod (*Gadus morhua*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 54(S1), 104-112.
- Lindström, K. (1988). Male-male competition for nest sites in the sand goby, *Pomatoschistus minutus*. *Oikos*, 67-73.
- Lloret, J., Gil de Sola, L., Souplet, A., & Galzin, R. (2002). Effects of large-scale habitat variability on condition of demersal exploited fish in the north-western Mediterranean. *ICES Journal of Marine Science*, 59(6), 1215-1227.
- Lloret, J., & Planes, S. (2003). Condition, feeding and reproductive potential of white seabream *Diplodus sargus* as indicators of habitat quality and the effect of reserve protection in the northwestern Mediterranean. *Marine Ecology Progress Series*, 248, 197-208.

- Lorenzen, K. (1996). The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *Journal of Fish Biology*, 49(4), 627-642.
- Love, R.M. (1974). *The Chemical Biology of Fishes*. Academic Press, London. 547 pp.
- Love, M. S., J. E. Caselle, and K. Herbinson. (1998a). Declines in nearshore rockfish recruitment and populations in the southern California Bight as measured by impingement rates in coastal generating stations. *Fisheries Bulletin*, 96:492-501.
- Love, M.S., P. Morris, M. McCrae, and R. Collins. (1990). Life history aspects of 19 rockfish species (*Scorpaenidae: Sebastes*) from the southern California Bight. *NOAA-TR-NMFS-87, La Jolla, CA*.
- Love, M. S., Yoklavich, M., & Thorsteinson, L. K. (2002). *The rockfishes of the northeast Pacific*. University of California Press, Berkeley, California, 416 p.
- Low, C. J., & Beamish, R. J. (1978). A study of the nesting behavior of Lingcod (*Ophiodon elongatus*) in the Strait of Georgia, British Columbia. *Fisheries and Marine Service Technical Report 843*, 27p.
- Low, C. J., & Beamish, R. J. (1978). A study of the nesting behavior of Lingcod (*Ophiodon elongatus*) in the Strait of Georgia, British Columbia. *Fisheries and Marine Service Technical Report 843*, Nanaimo. British Columbia.
- Mangel, M., & Levin, P. S. (2005). Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 360(1453), 95-105.
- Marko, P. B., Rogers-Bennett, L., & Dennis, A. B. (2007). MtDNA population structure and gene flow in Lingcod (*Ophiodon elongatus*): limited connectivity despite long-lived pelagic larvae. *Marine Biology*, 150(6), 1301-1311.
- Maunder, M. N., & Piner, K. R. (2014). Contemporary fisheries stock assessment: many issues still remain. *ICES Journal of Marine Science*, 72(1), 7-18.
- McClatchie, S. (2016). State of the California Current 2015–16: Comparisons with the 1997–98 El Niño. *California cooperative oceanic fisheries investigations. Data report*, 57.
- McFarlane, G. A., & King, J. R. (2001). The validity of the fin-ray method of age determination for Lingcod (*Ophiodon elongatus*). *Fishery Bulletin*, 99(3), 459-459.
- Miller, D. J., & Geibel, J. J. (1973). Summary of blue rockfish and Lingcod life histories, a reef ecology study, and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California (Vol. 158). *State of California, Resources Agency, Department of Fish and Game*.
- Munch, S. B., & Salinas, S. (2009). Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. *Proceedings of the National Academy of Sciences*, 106(33), 13860-13864.
- NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. Moderate-resolution Imaging Spectroradiometer (MODIS) Aqua Ocean Color Data; 2014 Reprocessing. NASA OB.DAAC, Greenbelt, MD, USA. doi: 10.5067/AQUA/MODIS_OC.2014.0. Accessed on 10/8/2018
- National Marine Fisheries Service (2009). Our living oceans. Report on the status of U.S. living marine resources, 6th edition. U.S. Department of Commerce, *NOAA Technical Memo*. NMFS-F/SPO-80, 369 p.

- National Marine Fisheries Service (2014). Fisheries Economics of the United States, 2012. U.S. Department of Commerce, *NOAA Technical Memo*. NMFS-F/SPO-137, 175p. Available at: <https://www.st.nmfs.noaa.gov/st5/publication/index.html>.
- National Marine Fisheries Service (2016). Annual Report to Congress on the status of U.S. fisheries–2015. U.S. Department of Commerce, NOAA, National Marine Fisheries Service, Silver Spring, MD.
- O'Connell, V. M. (1993). Submersible observations on Lingcod, *Ophiodon elongatus*, nesting below 30 m off Sitka, Alaska. *Marine Fisheries Review*, 55(1), 19-24.
- Ogle, D. H. (2016). *Introductory fisheries analyses with R*. Chapman and Hall/CRC.
- Pacific Fisheries Management Council (PFMC), (2014). Pacific Coast Groundfish Fisheries Management Plan: For the California, Oregon and Washington Groundfish Fishery. <http://www.pcouncil.org/groundfish/fishery-managementplan/>. May 19 2014.
- Parker, G. A. (1992). The evolution of sexual size dimorphism in fish. *Journal of Fish Biology*, 41, 1-20.
- Parrish, R. H., Nelson, C. S., & Bakun, A. (1981). Transport mechanisms and reproductive success of fishes in the California Current. *Biological Oceanography*, 1(2), 175-203.
- Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil*, 39(2), 175-192.
- Petrie, M. E., & Ryer, C. H. (2006). Hunger, light level and body size affect refuge use by post-settlement Lingcod *Ophiodon elongatus*. *Journal of fish biology*, 69(4), 957-969.
- Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O, ...& Sainsbury, K.J. (2004). Ecosystem-based fishery management. *Science* 305:346-347.
- Pilling, G. M., Kirkwood, G. P., & Walker, S. G. (2002). An improved method for estimating individual growth variability in fish, and the correlation between von Bertalanffy growth parameters. *Canadian Journal of Fisheries and Aquatic Sciences*, 59(3), 424-432.
- Punt, A. E. (2003). The performance of a size-structured stock assessment method in the face of spatial heterogeneity in growth. *Fisheries Research*, 65(1), 391-409.
- Rasmuson, L. K. (2013). The biology, ecology and fishery of the Dungeness crab, *Cancer magister*. *Advances in Marine Biology*, 65: 95-148. Academic Press.
- Ray, C. (1960). The application of Bergmann's and Allen's rules to the poikilotherms. *Journal of Morphology*, 106(1), 85-108.
- Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada*, 191, 1-382.
- Rijnsdorp, A. D., & Ibelings, B. (1989). Sexual dimorphism in the energetics of reproduction and growth of North Sea plaice, *Pleuronectes platessa* L. *Journal of Fish Biology*, 35(3), 401-415.
- Rijnsdorp, A. D. (1993). Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia*, 96(3), 391-401.
- Robertson, D. R., Ackerman, J. L., Choat, J. H., Posada, J. M., & Pitt, J. (2005a). Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. *Marine Ecology Progress Series*, 295, 229-244.

- Robertson, D. R., Choat, J. H., Posada, J. M., Pitt, J., & Ackerman, J. L. (2005b). Ocean surgeonfish *Acanthurus bahianus*. II. Fishing effects on longevity, size and abundance?. *Marine Ecology Progress Series*, 295, 245-256.
- Robson, D. S., & Chapman, D. G. (1961). Catch curves and mortality rates. *Transactions of the American Fisheries Society*, 90(2), 181-189.
- Roff, D. A. (1986). Predicting body size with life history models. *BioScience*, 36(5), 316-323.
- Ruttenburg, B.I., Haupt, A.J., Chiriboga, A.I., & Warner, R.R. (2005) Patterns, causes and consequences of regional variation in the ecology and life history of a reef fish. *Oecologia*, 145: 394-403.
- Sabat, A. M. (1994). Costs and benefits of parental effort in a brood-guarding fish (*Ambloplites rupestris*, Centrarchidae). *Behavioral Ecology*, 5(2), 195-201.
- Schmidt, K. T. (2014). Life history changes in female blue rockfish, *Sebastes mystinus*, before and after overfishing, in central California (Masters Thesis). *California State University, Monterey Bay*.
- Schnute, J., & Fournier, D. (1980). A new approach to length–frequency analysis: growth structure. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(9), 1337-1351.
- Smith, B. D., McFarlane, G. A., & Cass, A. J. (1990). Movements and Mortality of Tagged Male and Female Lingcod in the Strait of Georgia, British Columbia. *Transactions of the American Fisheries Society*, 119(5), 813-824.
- Smith, W. D., Cailliet, G. M., & Melendez, E. M. (2007). Maturity and growth characteristics of a commercially exploited stingray, *Dasyatis dipterura*. *Marine and Freshwater Research*, 58(1), 54-66.
- Smith, M. W., Then, A. Y., Wor, C., Ralph, G., Pollock, K. H., & Hoenig, J. M. (2012). Recommendations for catch-curve analysis. *North American Journal of Fisheries Management*, 32(5), 956-967.
- Shulman, G. E., & Love, R. M. (1999). *The biochemical ecology of marine fishes* (Vol. 36). Academic Press.
- Shine, R. 1979. Sexual selection and sexual dimorphism in the Amphibia. *Copeia* 1979: 297-306.
- Silberberg, K. R., Laidig, T. E., Adams, P. B., & Albin, D., (2001). Analysis of maturity in Lingcod, *Ophiodon elongatus*. *California Fish and Game*, 87(4), 139-152.
- Sogabe, A., Mohri, K., & Shoji, J. (2012). Reproductive seasonality of the seaweed pipefish *Syngnathus schlegeli* (Syngnathidae) in the Seto Inland Sea, Japan. *Ichthyological research*, 59(3), 223-229.
- Stahl, J., K. Green, and Vaughn, M., (2014). Examination of Lingcod, *Ophiodon elongatus*, movements in Southeast Alaska using traditional tagging methods. Alaska Department of Fish and Game, *Fishery Data Series* No. 14-28.
- Starr, R. M., O'Connell, V., Ralston, S., & Breaker, L. (2005). Use of acoustic tags to estimate natural mortality, spillover, and movements of Lingcod (*Ophiodon elongatus*) in a marine reserve. *Marine Technology Society Journal*, 39(1), 19-30.
- Stephens A., and Taylor, I.G. (2018). Status of Yellowtail Rockfish (*Sebastes flavidus*) Along the U.S. Pacific Coast in 2017. *National Oceanic and Atmospheric Administration, National Marine Fisheries Service*.

- Strub, P. T., James, C., Thomas, A. C., & Abbott, M. R. (1990). Seasonal and nonseasonal variability of satellite-derived surface pigment concentration in the California Current. *Journal of Geophysical Research: Oceans*, 95(C7), 11501-11530.
- Then, A.Y., J.M. Honeig, N.G. Hall, D.A. Hewitt. (2015). Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES Journal of Marine Science*. 72(1); 82-92.
- Thorson, J. T., & Wetzel, C. (2015). The status of canary rockfish (*Sebastes pinniger*) in the California Current in 2015. *National Oceanic and Atmospheric Administration, National Marine Fisheries Service*.
- Townshend, T. J., & Wootton, R. J. (1985). Adjusting parental investment to changing environmental conditions: the effect of food ration on parental behaviour of the convict cichlid, *Cichlasoma nigrofasciatum*. *Animal behaviour*, 33(2), 494-501.
- United Nations Food and Agriculture Organization (2013). *The State of World Fisheries and Aquaculture 2013*. Rome: UN FAO. xiv + 142 pp.
- United States Government Accounting Office (1994) *Ecosystem management: Additional actions needed to adequately test a promising approach*.
Available: <http://archive.gao.gov/t2pbat2/152537.pdf>. Accessed 5 December 2008.
- Ware, D. M., and Thompson, R. E. (1991). Link between long-term variability in upwelling and fish production in the northeast Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 2296–2306.
- Ware, D. M., & Thomson, R. E. (2005). Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science*, 308(5726), 1280-1284.
- Wilby, G. V. (1937). The ling cod, *Ophiodon elongatus* Girard. *Bulletin of the Fisheries Research Board of Canada*, (54):1–24.
- Wilson, J. R., Kay, M. C., Colgate, J., Qi, R., & Lenihan, H. S. (2012). Small-scale spatial variation in population dynamics and fishermen response in a coastal marine fishery. *PLoS ONE*, 7(12), e52837.
- Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., ... & Jensen, O. P. (2009). Rebuilding global fisheries. *Science*, 325(5940), 578-585.
- Yoklavich, M. M., Cailliet, G. M., Greene, H. G., & Sullivan, D. (1995). Interpretation of sidescan sonar records for rockfish habitat analysis: examples from Monterey Bay. *Alaska Department of Fish and Game Special Publication*, 9, 11-14.
- Yoklavich, M. M., Greene, H. G., Cailliet, G. M., Sullivan, D. E., Lea, R. N., & Love, M. S. (2000). Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. *Fisheries Bulletin*, 98, 625-641.

CHAPTER II

HABITAT-BASED DIFFERENCES IN LINGCOD DEMOGRAPHY AND LIFE HISTORY: HOW CAN STOCK ASSESSMENTS MEET THE NEEDS OF A CHANGING FISHERY?

Abstract

Life histories of broadly ranging groundfish stocks can vary based on environment and habitat type. Neglecting to account for this variability can have consequences on management decisions and fishery sustainability. Along the U.S. West Coast, groundfish stock assessments rely on biological parameters that are obtained by the West Coast Groundfish Bottom Trawl Survey (WCGBTS). While the WCGBTS provides vital, long-term fisheries data on species abundance, distribution and life-history for over 90 groundfish species, it is inherently biased towards groundfishes occupying trawlable habitats and fails to represent fishes in untrawlable, high-relief habitats. In this chapter, life-history parameters of growth, maturity, condition and mortality from Lingcod caught over high-relief habitats were compared to those from Lingcod obtained by the WCGBTS. As predicted, Lingcod from high-relief habitats were found to grow faster, attain larger sizes, mature earlier, and be in better body condition than Lingcod from low-relief habitats. While Lingcod from high-relief areas had lower natural mortality rates, they also had significantly higher total mortality presumably due to heavier fishing pressure. Using the von Bertalanffy growth model, I evaluated the factors explaining variability in size-at-age and found that coastwide Lingcod growth is best modelled using five geographic regions, habitat, and sex. Based on these findings, I recommend the inclusion of a coastwide hook-and-line survey to target groundfishes

found over untrawlable, high-relief habitats so that biological parameters used in stock assessment models accurately represent the targeted population.

Introduction

Habitat composition and structure influence fish stocks in a variety of ways that can have consequences for their life-history, population demography, and distribution (Pacunski and Palsson 2002, Hilborn et al. 2003*b*, Lloret and Planes 2003, Cope and Punt 2011). Younger age classes benefit from complex nursery habitats that help to increase survivorship during vulnerable life stages (Sale and Dybdahl 1975, Munday et al. 1997, Risk 1997, Tolimieri 1995, Holbrook et al. 1990, Samhuri et al. 2009), whereas older age classes can exhibit strong habitat preferences, resulting in a positive relationship between habitat type and adult abundances (Larson and DeMartini 1974, Carr 1989, DeMartini and Roberts 1990, Holbrook et al. 1990). Additionally, movement among habitats can be an integral part of fish life cycles, such as during times of settlement, recruitment, and spawning. Habitat usage can vary across broad geographic scales due to differences in substrate availability, complexity and distribution (e.g. continuous versus patchy), or the abundance of predators, competitors, and prey (Gust et al. 2002, Robertson et al. 2005*a*).

Compared to low-relief, flat bottom habitats, high-relief rocky reefs can enhance the biodiversity of entire ecosystems and surrounding fish populations by providing spatial refuge from predation and supporting a higher abundance of resources and prey types, such as algae, invertebrates, and cryptic fish species (Able 1999, Yoklavich et al. 2000, Lloret et al. 2002, Lloret and Planes 2003). These differences play an important

role in producing marked geographic variation in demography, recruitment, and survivorship of various fish populations (Robertson and Kaufmann 1998, Robertson et al. 2005, Bellquist et al. 2008, Knip et al. 2011), and highlight the emerging need to use more spatially-explicit approaches to manage wide-ranging fish stocks and their associated habitats. As discussed in the previous chapter, stock assessment methods that neglect to account for population differences based on environmental or anthropogenic affects can lead to mismanagement and inaccuracies in estimates of stock productivity (Hilborn et al. 2003b, King and McFarlane 2003, Maunder and Piner 2014).

In addition, habitat type can have important implications for fishery methods and fishing behavior. Many fishing gear types (i.e. Hook-and-line, bottom trawl, purse seining, etc.) Are developed in a such a way as to maximize catch and to target high-value species from specific habitats or areas of interest (Cotter and Pilling 2007). For instance, bottom trawl gear targets fish over low-relief, flat bottomed habitats, while hook-and-line methods typically target areas with high-relief that are unfishable by other means. Because of this, habitat dictates the method by which fish populations are caught for commercial and scientific purposes. Restrictions that are enacted to protect essential fish habitats (i.e. Cordell Banks, Cowcod Conservation Areas, Davidson Seamount) do so by limiting fishing access by specific fisheries and fishing gear (Pacific Fisheries Management Council 2012).

Along the U.S. West Coast, fishery independent data for groundfish assessments are obtained from the annual NMFS West Coast Groundfish Bottom Trawl Survey (WCGBTS). The WCGBTS is the only coastwide, long-term monitoring survey that collects indices of abundance, spawning potential, and recruitment for over 90 federally

managed groundfish species over trawlable habitats since 1998 and is the primary source of biological data used in federal stock assessments (Keller et al. 2017). Many groundfish species, however, are found over both high-relief (untrawlable) and low-relief habitat types. While the WCGBTS is advantageous in modelling groundfish abundance over a long time series, it can create bias in understanding population status and trends because the biological information is collected by only one gear type (bottom-trawl). The WCGBTS can be limited in scope because it only estimates life-history parameters from fish in trawlable habitats, excluding groundfish populations that occupy non-trawlable, high relief habitats (Jagiello et al. 2003). Nearshore, untrawlable reefs are unaccounted for when inputting biological parameters of growth, maturity, and mortality into groundfish stock assessments even though they are heavily exploited coastwide. Because many groundfish species may not readily migrate between these habitats, a significant amount of biological information could be lost by overlooking this essential habitat type. The omission of rocky, high-relief areas can cause an over- or under-estimation of stock productivity that can have consequences on marine ecosystems and local fishing industries alike.

In this chapter, I will again be using Lingcod as the focal stock with which to examine variability in life-history and demography based on spatial differences. While Lingcod are caught commercially using bottom-trawl gear, the recreational fishery typically targets nearshore rocky (high-relief) untrawlable habitats in shallower depths between 6-55 m (California Department of Fish and Wildlife 2018, Oregon Department of Fish and Wildlife 2018, Washington Department of Fish and Wildlife 2018). Lingcod are known to have a high degree of site fidelity as adults (Starr et al. 2004, Starr et al.

2005, Greenley 2009, Tolimieri et al. 2009) but also exhibit ontogenetic movements and will migrate during winter spawning months. Despite this, the biological life-history parameters used to determine coastwide stock productivity in assessment models are based entirely on trawl-caught Lingcod, therefore there is a significant data gap for Lingcod living in shallow, nearshore, rocky reefs that are targeted by the recreational fishery. In recent years, the recreational Lingcod fishery has steadily grown and now far exceeds the commercial fishery in total landings (Hamel et al. 2009, Haltuch et al. 2017), therefore to be more accurate stock assessments should reflect this shift by incorporating biological information from high-relief, untrawlable habitats as well.

The goal of this chapter is to compare Lingcod population structure and life-history traits between trawlable (low-relief) and untrawlable (high-relief) habitats. My research objectives were (1) to quantify and compare population structure and life-histories (growth rates, longevity, size and age at maturity, somatic condition, and natural and total mortality rate) of Lingcod between habitats, (2) to investigate the spatial scale of life history variability along the coast between habitats, regions, and sexes using growth model comparisons, and (3) to suggest management implications of these findings for Lingcod and other commercially- and recreationally-important groundfish species. In comparing low-relief and high-relief habitats, I predicted that because high-relief areas typically have higher species abundances (Stein et al. 1992, Carlson and Straty 1981, Yoklavich et al. 1995, Yoklavich et al. 2000, Love et al. 2002) and hence prey availability, an opportunistic predator like the Lingcod inhabiting these areas would attain larger sizes, higher longevity, faster growth, lower natural mortality, and improved body condition than Lingcod inhabiting areas of low-relief. However, due to current patterns of

exploitation in the Lingcod fishery, I expected Lingcod from high-relief habitats to have greater total mortality than Lingcod from low-relief habitats.

Methods

SAMPLING AREA AND COLLECTION PROTOCOL

Lingcod were collected over high-relief, rocky reefs and low-relief, flat bottom habitats from five geographically distinct regions along the contiguous U.S. West Coast: coastal Washington ($46^{\circ}16'N - 49^{\circ}N$), Oregon ($42^{\circ}N - 46^{\circ}16'N$), northern California ($38^{\circ}02'N - 42^{\circ}N$), central California ($34^{\circ}30'N - 38^{\circ}02'N$), and southern California ($32^{\circ}32'N - 34^{\circ}30'N$) (Fig. 15). These five regions correspond to well-known breakpoints for a variety of marine species (Dawson 2001, Buonaccorsi et al. 2002, Williams and Ralston 2002, Cope 2004, Blanchette et al. 2008, Sivasundar and Palumbi 2010).



Figure 15: Map of study site showing sampling ports per region.

Two fishing methods were used to collect Lingcod and are intended to be indicative of the two habitat types of interest. Lingcod from low-relief habitats were obtained using bottom trawl gear; Lingcod from high-relief habitats were caught via hook-and-line fishing gear. There are several fundamental differences between the sampling gear types regarding selectivity and catchability that will be discussed, however

due to the nature of the fishing gear and the methods described below, it is reasonable to associate all trawl caught Lingcod with low-relief habitats that are often targeted by the commercial fishery, and all hook-and-line caught Lingcod with rocky habitats utilized by the recreational fishery. Therefore, each method is reflective of both habitat and fishery. Throughout my subsequent analyses, results, and discussion, I will be referring to the two fishing methods as proxies for the differences between low-relief and high-relief habitats.

Trawl caught Lingcod were acquired through collaboration with the NOAA NWFSC West Coast Groundfish Bottom Trawl Survey (WCGBTS) between 2014 and 2016. The survey is the primary source of fishery-independent information for West Coast stock assessments, collecting biological data from federally important groundfish species and estimating relative abundance and distribution of groundfish populations over areas of low-relief. The WCGBTS targets the upper continental slope and shelf at depths of 55 to 1,280 meters from the U.S.-Canada border to the U.S.-Mexico border using a random stratified sampling design with standardized trawl fishing gear (Keller et al. 2017). Through this collaboration, 2,095 Lingcod from low-relief habitats were retained from the survey between 2015 and 2016. The associated catch location information (depth, longitude, and latitude) was obtained for each individual from the NWFSC data manager.

Lingcod were caught using hook-and-line fishing gear on chartered recreational fishing boats from northern Washington to southern California. This area was divided into five primary sampling regions: Washington, Oregon, northern California, central California, and southern California. Two to four fishing ports were selected per region ($n=16$ ports total), with the goal that selected ports were evenly distributed within each

region and across the entire study area, depending upon the geographic location of the ports and the availability and accessibility of recreational party boats (or Commercial Passenger Fishing Vessels [CPFVs]). CPFVs were chartered at each port for a half- to full-day of fishing, depending on weather and the number of Lingcod collected. We worked closely with CPFV captains, deckhands and local volunteer anglers to identify appropriate fishing grounds in order to collect 300 Lingcod per region using hook-and-line fishing gear. To ensure a thorough collection of Lingcod across a wide range of age and size classes, shallow (<60 m) and deep (60-170 m) nearshore and offshore rocky reefs were targeted equally by our fishing efforts. Lingcod can be targeted using weighted Lingcod bars, jigs, swim baits, and live bait, which greatly reduces incidental catch of other bottomfish species (i.e. *Sebastes* spp). Because Lingcod are known to settle primarily in soft bottom habitats and move ontogenetically to rocky substrate around 35 cm total length (Miller and Geibel 1973, Bassett et al. 2018), it is unlikely that Lingcod smaller than 35 cm would be encountered in rocky habitats.

All incidentally caught species were measured and released. Species suffering from barotrauma were descended and released at depth using a descending device (Seaqualizer®) to reduce mortality. Catch information, such as location, depth, relief, and catch per unit effort, was collected for each drift. Landed individuals were euthanized per the Institutional Animal Care and Use Committee protocol (Permit Number: 964), as approved by San Jose State University. Total length (cm), weight (kg), sex, and color status were collected immediately after the Lingcod was landed. The Lingcod were then frozen or put on ice until dissection.

LAB PROCEDURES

As in Chapter 1, standard morphometrics, tissue samples, and maturity information were collected during the lab dissection process. Hook-and-line caught Lingcod from each port (n=75-100) were aged following the Lingcod fin ray preparation protocol described by Chilton and Beamish (1982) and currently used by the WDFW (R. LeGoff, WDFW, *personal communication*). Trawl caught samples were prepared and aged by the NWFSC ageing lab. Ages were determined by counting the number of annuli, the translucent zones that form once a year during winter growth. Annuli are often distinct along all growth axes of each fin ray section. Ageing accuracy can be improved using known mean annular radii measurements for the first, second, and third annuli, as measured in Figure 2.

DATA ANALYSIS

Analyses were conducted using the statistical computing platform R version 3.5.1 and JMP Pro version 14 (SAS Institute, Inc., Cary, NC). To account for depth differences between the sampling methods, only data generated from depth ranges shallower than 170 m were used in subsequent analyses.

SEX-RATIO COMPARISONS

Male to female sex-ratios between habitats were compared using a contingency table and the chi-squared test. Due to differences in sampled depths between high-relief and low-relief habitats, sex ratios were examined across regions for each habitat separately

LIFE-HISTORY ANALYSES

The following life-history analyses are similar to those performed in Chapter 1. Size- and age-frequency distributions were compared between the two habitat types using the nonparametric two-sample Kolmogorov-Smirnov test, which compares the two cumulative frequency distributions. The von Bertalanffy growth function (VBGF) was fit to size-at-age data for Lingcod from both habitat types using maximum likelihood parameter estimates (Kimura 1980). Longevity was calculated based on the mean of the upper quartile of ages for each region by habitat (Choat and Robertson 2002). Logistic regression (Mature vs. Immature fish) was used to determine size and age at 50% maturation for Lingcod by habitat. Fulton's K condition factor and the hepatosomatic index (HSI) were used to examine differences in body condition and energy storage, respectively. To control for possible season and year effects, only Lingcod caught in 2015-2017 between the months of March through October were used. I used residual analysis to control for the confounding effect of size on condition when comparing between habitats. A GLM was used to investigate the influence of the continuous variable of size, and the categorical variables of region, sex, and habitat on Lingcod condition. Natural mortality, M , was estimated using the non-linear least squares Hoenig estimator based on maximum age, A_{max} (Hoenig 1983). Total mortality (Z) was estimated using the Chapman-Robson method of cross-sectional catch-curve analysis (Chapman and Robson 1960) with a correction factor for variance inflation (Smith et al. 2012). With this method, fishing mortality, F , is calculated using the equation $F = Z - M$.

VON BERTALANFFY GROWTH FUNCTION MODEL FITTING

To investigate the spatial scale of growth variability along the coast between habitats and sexes, variability in Lingcod growth parameters was explored using a model comparison approach. Growth was chosen as the focus of this model comparison approach as variability in individual size and size-at-age can translate into profound differences in other life-history parameters. The null hypothesis assumes that covariates (sex: male and female, habitat: low-relief or high-relief, and latitude or region) have no effect on growth. Seven latitude-based subdivisions were compared based on biogeographic breaks, state line boundaries, past stock assessments, and commonly accepted management divisions (Fig. 16). VBGF models were fit to one 2-region option using a northern and southern boundary used by the most recent Lingcod stock assessment (North: Washington and Oregon, South: California); three 3-region options, with breaks occurring by state line (Washington, Oregon, California), by splitting California at Point Conception (Washington-Oregon combined, California North, California South), and by biogeographic boundaries (North: U.S.-Canada border to Cape Mendocino, Central: Cape Mendocino to Point Conception, South: Point Conception to U.S.-Mexico border). Two 5-region models were also explored according to the five predetermined regions used in this study (5-Pre: Washington, Oregon, northern California, central California, and southern California) and the five INPFC management areas used in past and current groundfish assessments (Vancouver, Columbia, Eureka, Monterey, and Conception) (Fig. 16).

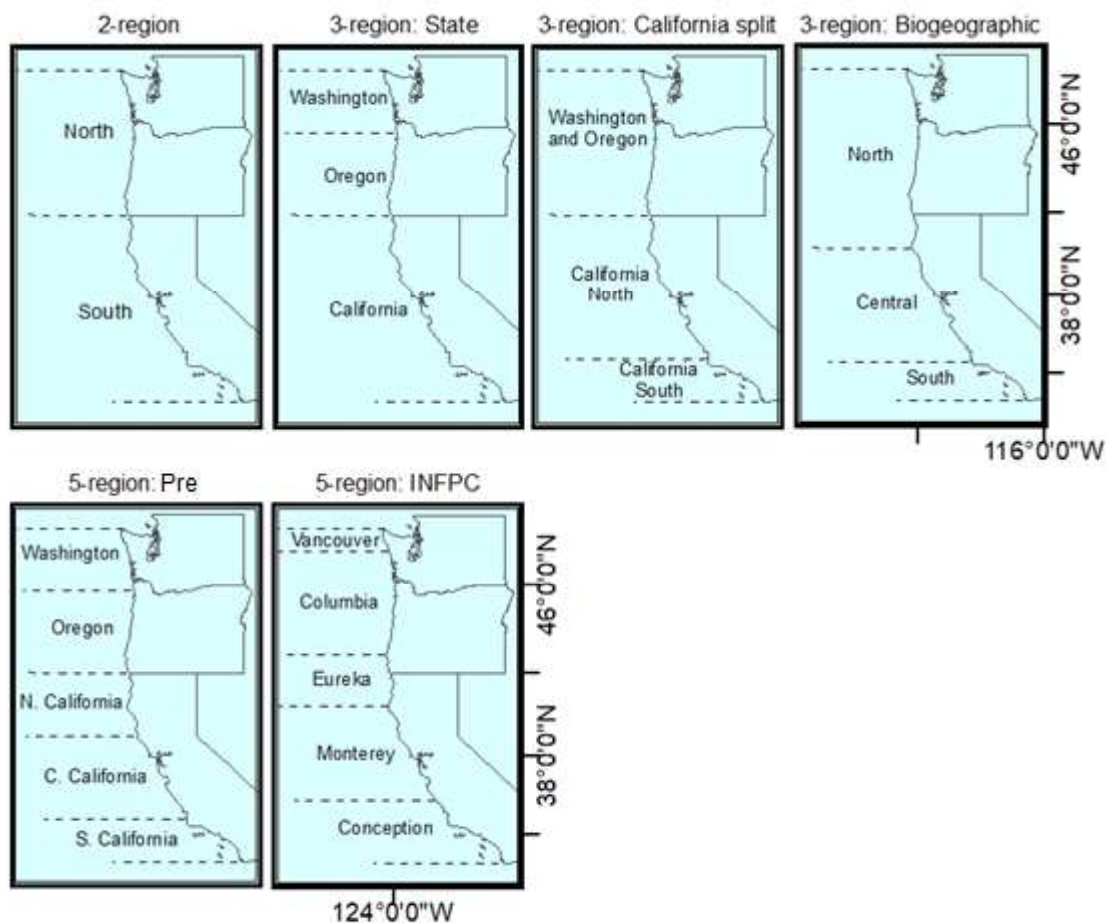


Figure 16: Map of 2-, 3-, and 5-region growth modelling options. The 2-region option was considered based on the past two lingcod stock assessment areas. The 3-region options are based on state line, on splitting California at Point Conception, and on biogeographic boundaries. The 5-region options are based on the sub-regions used in this study and on INPFC regions.

Models were fit in stages starting with the simplest growth model (assumes no variation due to sex, habitat, or region) followed by adding the effect of sex, habitat, and geographic area in order of complexity. Standard nonlinear least squares and associated likelihood methods were used to estimate parameters for these models (Kimura 2008). All combinations of explanatory variables (region, habitat, and sex) were evaluated using Akaike's information criterion with correction for small sample bias (AIC_c) to select the

best-fit model, where the model with the lowest AIC_c is the most parsimonious. ΔAIC_c (the difference between AIC_c and the minimum AIC_c value) was used to determine relative support among competing models. The best model is defined as having a $\Delta AIC_c = 0$, and models with a $\Delta AIC_c < 2$ are considered to fit the data as well as the best-fit model (Burnham and Anderson 2002).

Results

CATCH SUMMARY

1,794 Lingcod were collected from rocky, high-relief habitats between 2016-2017. Data from 2,095 Lingcod occupying low-relief habitats were obtained from the NWFSC WCG BTS between 2014-2016 (Table 10). To ensure that both sampled habitats were comparable across regions, Lingcod collected from depths over 170 m were excluded from Table 10 and subsequent analyses. For the high-relief caught Lingcod, on average each port was fished between 1 to 5 days to obtain the targeted sample size of 75-100 Lingcod per port. Additional samples were provided by the Oregon Department of Fish and Wildlife Marine Reserves Program and the California Collaborative Fisheries Research Program.

Sex ratios were compared among regions and habitats. Because each habitat sampled occurred within different depth substrata (Welch's $t_{3462.3} = 47.92$, $p < 0.0001$), sex ratios were examined across regions for each habitat separately. Lingcod from high-relief habitats were caught in shallower waters, between 7.6 to 170 m (Mean: 59.8, $SD \pm 125.7$) whereas Lingcod from low-relief trawlable habitats were captured at deeper depths, between 57.0 to 170 m (Mean: 113.4, $SD \pm 28.6$). Averaged across regions, the majority

of Lingcod caught in low-relief habitats were females (58%) while individuals in high-relief habitats exhibited a relatively even distribution of females and males (48% female) (Table 10). Within the low-relief habitats, there were no regional differences in sex ratio ($X^2(4)=5.71$, $p=0.2219$) and consistently more females were sampled than males. Sex-ratios of high-relief caught Lingcod were significantly different among regions ($X^2(4)=243.01$, $p<0.0001$), however this was due to Lingcod from Washington regions being heavily skewed towards females. Within all other regions, males were more common. Upon removing the Washington region from the sex-ratio analysis, there was no significant difference in sex ratios among regions in the hook-and-line samples ($X^2(3)=2.34$, $p=0.506$), and the average sex-ratio among all hook-and-line regions was 39% females to 61% males.

Table 10: Catch summary by habitat. Number of ports and days fished are not indicated for trawl fished regions due to the sampling method used by the West Coast Groundfish Bottom Trawl Survey (WCGBTS). Maximum and minimum total length (cm), and number of unsexed female and male Lingcod were recorded for all sampled regions.

	Number of ports	Days fished	Female, <i>N</i>	Male, <i>N</i>	Unsexed, <i>N</i>	Percent female	Max TL (cm)	Min TL (cm)
High-relief (N = 1,794)	16	37	869	924	1	0.48	-	-
Washington	3	6	318	68	-	0.82	112	39
Oregon	4	10	146	211	-	0.41	111	33.8
Northern California	2	4	82	118	-	0.41	93.5	25.1
Central California	4	9	224	347	1	0.39	96.9	16.7
Southern California	3	8	99	180	-	0.35	97	40.2
Low-relief (N = 2,095)			1152	819	124	0.58	-	-
Washington	-	-	185	113	-	0.62	98	28
Oregon	-	-	346	266	16	0.57	92	13.2
Northern California	-	-	158	122	8	0.56	88	14.8
Central California	-	-	368	267	92	0.58	89	10
Southern California	-	-	95	51	8	0.65	78	18
Grand Total			2,021	1,743	125	0.54		

HABITAT-BASED DIFFERENCES IN POPULATION STRUCTURE AND LIFE-HISTORY

Across all regions combined, Lingcod median sizes were larger (Figure 17A: $D=0.59$, $p<0.0001$) and median ages were older (Fig. 17B: $D=0.61$, $p<0.0001$) in high-relief habitats than Lingcod from low-relief habitats. This trend was also observed when size- and age- residuals between habitats were compared within each region separately.

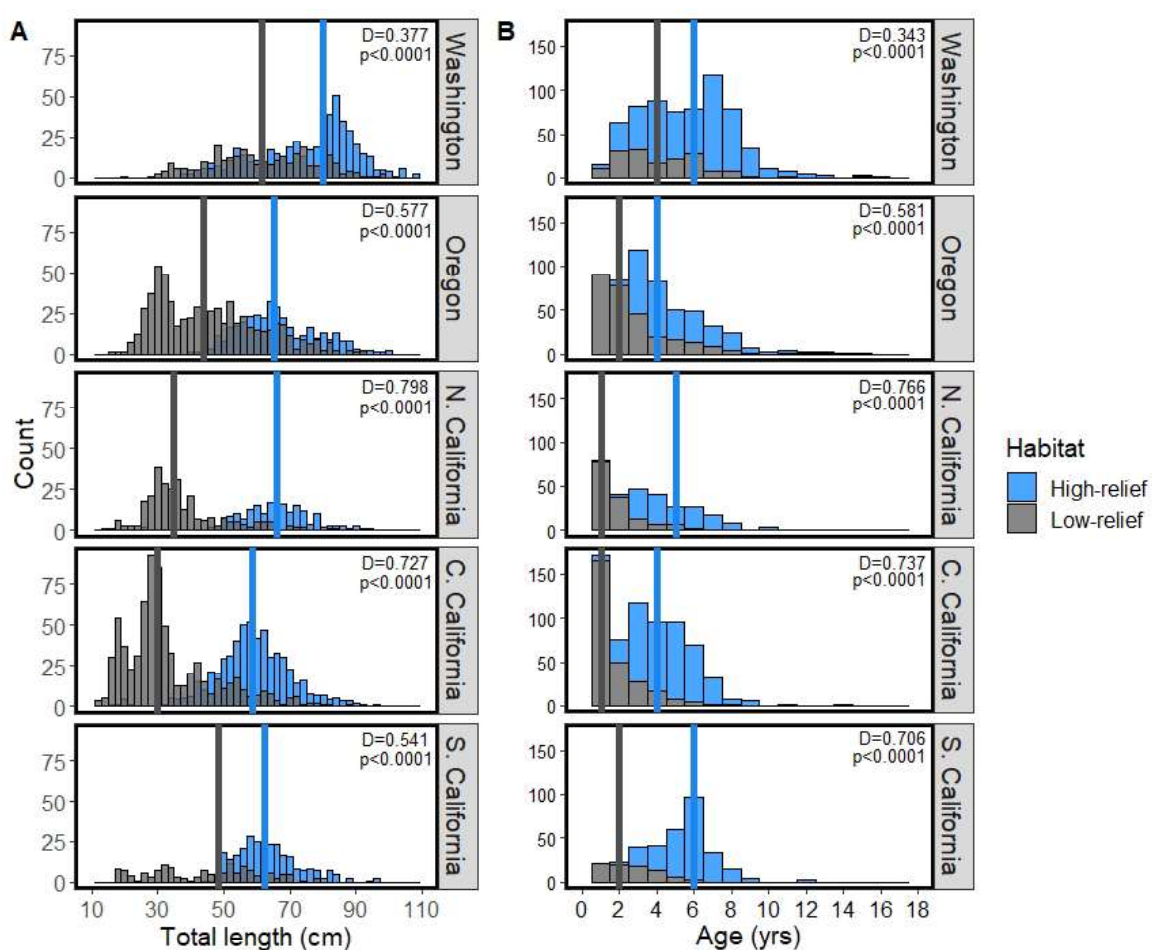


Figure 17: A) Length and B) age frequency of Lingcod by habitat per region (Sexes pooled). The blue and grey vertical lines indicate the median size of Lingcod from high-relief and low-relief habitats, respectively.

Lingcod caught in high-relief habitats achieved significantly larger asymptotic sizes (L_{inf}) than Lingcod from low-relief habitats coastwide (Table 11, Fig. 18A). This trend was also found when males and females were analyzed from each habitat independently, as well as when comparing between habitats within each region individually. The k parameter of the VBGF is elevated in Lingcod from low-relief habitats, indicating faster initial growth as asymptotic size is reached (Fig. 18B), however, k and L_{inf} are non-independent so this result is expected. In addition, Lingcod caught in high-relief habitats attain older ages and have a significantly greater longevity than Lingcod in low-relief habitats (Welch's $t_{634} = 522.0$, $p < 0.0001$) (Table 11).

Table 11: Von Bertalanffy growth function (VBGF) parameters L_{inf} and k , and estimates of longevity (T_{max}) for Lingcod sampled coastwide, by sex, region and habitat. Standard deviation for the L_{inf} , k , and standard error for T_{max} estimates are shown.

	High-relief			Low-relief		
	L_{inf} (SD)	k (SD)	T_{max} (SE)	L_{inf} (SD)	k (SD)	T_{max} (SE)
Coastwide	93.4 (1.69)	0.266 (0.01)	7.9 (0.07)	77.1 (1.94)	0.433 (0.02)	4.6 (0.1)
<i>Female only</i>	100.3 (1.97)	0.25 (0.01)	8.3 (0.09)	84.6 (2.65)	0.377 (0.02)	5.8 (0.18)
<i>Male only</i>	74.8 (1.36)	0.358 (0.02)	7.2 (0.1)	66.3 (1.91)	0.558 (0.04)	4.3 (0.11)
Washington	91.9 (4.35)	0.37 (0.04)	8.8 (0.13)	84.8 (2.9)	0.38 (0.03)	7.1 (0.3)
Oregon	88.8 (3.06)	0.305 (0.02)	7.5 (0.19)	75.9 (2.82)	0.445 (0.03)	4.6 (0.19)
N. California	81.8 (3.94)	0.364 (0.05)	7.0 (0.18)	64.7 (4.4)	0.586 (0.08)	3.0 (0.17)
C. California	81.3 (3.11)	0.308 (0.03)	6.7 (0.11)	66.2 (4.62)	0.542 (0.07)	3.1 (0.12)
S. California	75.3 (3.73)	0.356 (0.05)	6.6 (0.09)	64.7 (6.64)	0.6 (0.15)	3.8 (0.14)

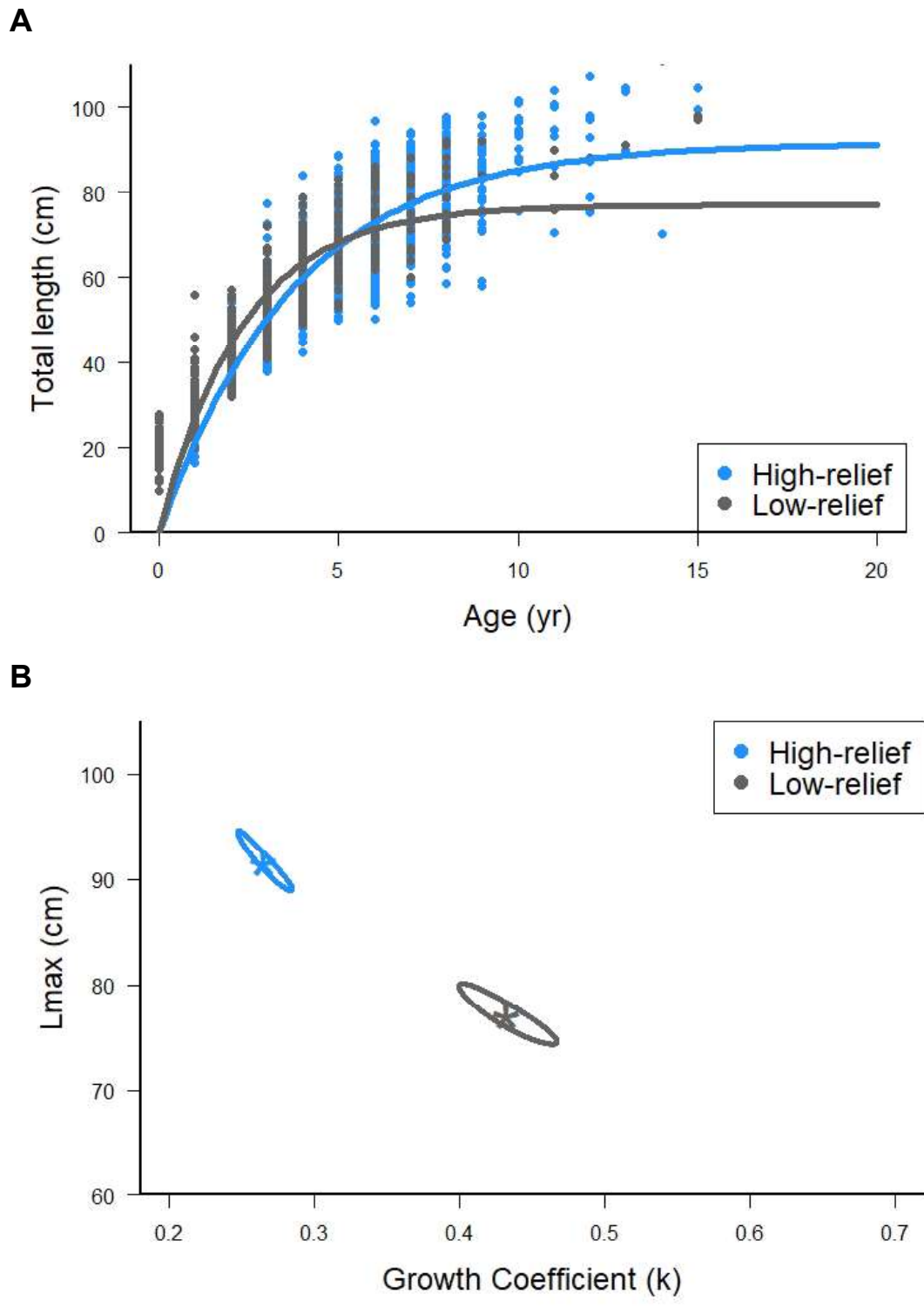


Figure 18: A) Variation in lifetime growth curves from Lingcod in high-relief versus low-relief habitats (region and sexes pooled) and B) 95% confidence intervals for best fit L_{inf} and k parameters both habitats. Overlapping ranges indicate no difference in growth.

Lingcod occupying high-relief habitats reached maturity at significantly smaller sizes (non-overlap of 95% CI) than Lingcod caught in low-relief habitats (Table 12, Fig. 19A). There was also a non-significant trend for Lingcod to mature at earlier ages in high-relief habitats (Fig. 19B). Analyzing each sex separately, female Lingcod from high- and low-relief habitats reached 50% maturity at similar sizes and ages; male Lingcod from high-relief habitats reached maturity at significantly smaller sizes than male Lingcod from low-relief habitats (Table 12). Age-at-maturity for male Lingcod in trawlable habitats was unable to be calculated.

Table 12: Size (cm) and age (years) at 50% maturity comparison by habitat and sex. Upper and lower confidence intervals (UCI and LCI, respectively) were estimated using bootstrapping.

	Size at 50% maturity	LCI	UCI	Age at 50% maturity	LCI	UCI
High-relief:	43.7	41.7	45.3	2.3	2.1	2.5
Female	50.1	47.6	52.4	2.6	2.3	2.8
Male	41.6	39.0	43.5	2.2	2.0	2.4
Low-relief:	49.2	47.3	51.3	2.6	2.2	3.0
Female	51.6	47.6	52.4	2.6	2.0	3.0
Male	44.9	41.4	48.2	-	-	-

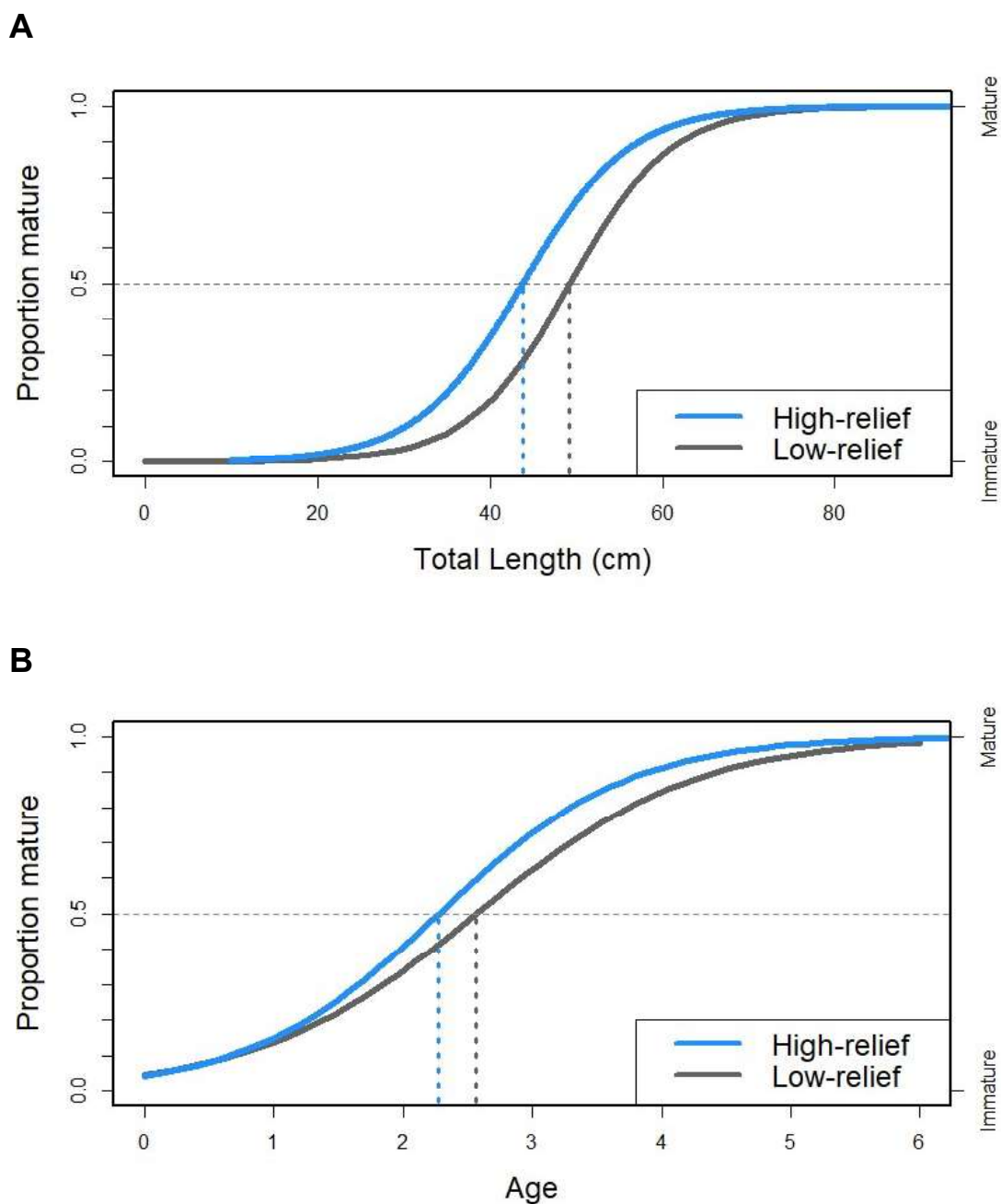


Figure 19: Logistic regression for A) length (cm) and B) age at 50% maturity for *Lingcod* caught from high-relief and low-relief habitats. The horizontal dashed line represents the time when 50% of the population is mature and the vertical dashed lines represent size and age at 50% maturity, respectively.

Welch's t-tests assuming unequal variances were used to test for significant differences between the mean residuals of Fulton's K and HSI as a function of habitat.

With sexes pooled, Lingcod from high-relief habitats were generally in better body condition, with a higher mean Fulton's K (i.e., heavier for a given length) (0.96 ± 0.003) than Lingcod in low-relief habitats (0.85 ± 0.005) (Welch's $t_{1873.5} = -6.42, p < 0.0001$). Individuals from high-relief areas also had higher mean energy stores in the liver (1.46 ± 0.02), measured as the hepatosomatic index (HSI), than individuals from low-relief areas (1.29 ± 0.02), however the difference was not statistically significant (Welch's $t_{357.6} = 1.36, p = 0.17$). When sexes were analyzed separately between habitats, I found that female Lingcod did not exhibit differences in HSI or Fulton's K between habitats, while male Lingcod showed a significant difference in Fulton's K only (Welch's $t_{126.7} = -3.84, p < 0.0001$). A GLM was used on residual values to investigate the influence of habitat, sex, and region on Lingcod condition. Region was the only significant indicator of HSI ($F_{4,1637} = 113.1, p < 0.0001$). In order of importance, region ($F_{4,2226} = 36.8, p < 0.0001$), sex ($F_{1,2226} = 121.8, p < 0.0001$), and habitat ($F_{1,2226} = 13.9, p = 0.0002$) were significant predictors of Fulton's K.

Lingcod from low-relief areas had significantly higher natural mortality rates (M) compared to those from high-relief areas (Welch's $t_{2643} = -14.9, p < 0.0001$) (Table 13). This is consistent with the size-structure analysis that found smaller, younger individuals in low-relief habitats. The opposite was found regarding total mortality rates (Z); Lingcod from high relief areas have greater total mortality than Lingcod from low-relief, trawlable habitats. Fishing mortality, F was left blank in cases where M is greater than Z , resulting in a negative F value (Table 13). Between sexes, female Lingcod had a higher Z than male Lingcod in high-relief habitats, but a lower Z in low-relief habitats.

Table 13: Total (Z), natural (M), and fishing (F) mortality rates per habitat where F is calculated as $F=Z-M$. In instances where a negative value was calculated (when M is greater than Z), F was left blank. Standard errors (SE) for Z and M are shown in parentheses.

	Z (SE)	M (SE)	F
High-relief:	0.61 (0.04)	0.40 (0.001)	0.16
Female	0.69 (0.03)	0.46 (0.004)	0.23
Male	0.43 (0.07)	0.49 (0.003)	-
Low-relief:	0.48 (0.03)	0.61 (0.01)	-
Female	0.44 (0.02)	0.61 (0.01)	-
Male	0.53 (0.03)	0.77 (0.01)	-

MODELLING THE SPATIAL SCALE OF LINGCOD GROWTH VARIABILITY

Thirty-three possible growth-model hypotheses were tested in order of increasing complexity. The 2-region divide was selected based on the most recent stock assessment, which consisted of a northern region (Washington and Oregon) and a southern region (California). Three 3-region options were explored using boundaries based on state line (State: Washington, Oregon, and California), by splitting California at Point Conception and combining Washington and Oregon (CA split), and by biogeographic boundaries (Biogeographic: U.S.-Canada border to Cape Mendocino, Cape Mendocino to Point Conception, and Point Conception to the U.S.-Mexico border) (Fig. 16). The two 5-region options considered incorporated INPFC areas (INPFC: Vancouver, Columbia, Eureka, Monterey, and Conception) and the 5 predetermined regions used in this study (5-Pre: Washington, Oregon, northern California, central California, and southern California) (Fig. 16).

Results from this analysis indicate that model fits of growth variability improved with the addition of further information (Table 14). The best-fit model for Lingcod growth occurred with the inclusion of five predetermined regions (5-Pre), sex, and habitat, and was far and away the best model). This was followed by the model including 5-INPFC regions, sex, and habitat. Within the 3-region options alone (without sex and method), the model using boundaries denoted by state line fit better than alternatives using 3-biogeographic boundaries or by dividing California, however the 3-biogeographic regions fit much better when the parameter of sex was included. Between sex and habitat effects, sex had a greater influence on Lingcod growth variability as the inclusion of sex consistently improved model fit more than the inclusion of habitat. Models incorporating both habitat and sex outperformed models with each effect separately.

Table 14: Degrees of freedom (*df*), number of parameters (*p*), corrected Akaike's Information Criterion (*AIC_c*), and ΔAIC_c (the difference between the *AIC_c* and the minimum *AIC_c* value) for each von Bertalanffy growth model combination. Model fit improves with the addition of information. The best-fit model for describing Lingcod growth along the U.S. West Coast incorporates 5-regions using predetermined divisions used in this study, and the effects of sex and habitat (shown in bold).

Model description	df	p	AIC _c	BIC	ΔAIC_c
Length only	3	2	17104.15	17121.52	1490.47
With sex	5	4	16035.19	16064.14	421.51
With habitat	5	4	16910.08	16939.02	1296.4
Habitat and sex	9	8	15921.51	15973.58	307.83
With 2 regions	5	4	16622.64	16651.59	1008.96
With sex	9	8	15801.2	15853.27	187.52
With habitat	9	8	16452.22	16504.29	838.54
With habitat and sex	17	16	15676.49	15774.73	62.81
With 3 regions					
State	7	6	16546.47	16586.99	932.79
Biogeographic	7	6	16602.68	16643.19	989
CA split	7	6	16613.95	16654.47	1000.27
With 5 regions					
INPFC	11	10	16548.05	16611.67	934.37
Pre	11	10	16499.55	16563.17	885.87
With 3 regions and sex					
State + sex	13	12	15797.67	15872.84	183.99
Biogeographic + sex	13	12	15754.94	15830.11	141.26
CA split + sex	13	12	15803.35	15878.52	189.67
With 3 regions and habitat					
State + habitat	13	12	16398.1	16473.27	784.42
Biogeographic + habitat	13	12	16426.16	16501.34	812.48
CA split + habitat	13	12	16430.55	16505.73	816.87
With 5 regions and sex					
INPFC + sex	21	20	15750	15871.29	136.32
Pre + sex	21	20	15751.73	15873.02	138.05
With 5 regions and habitat					
INPFC + habitat	21	20	16362.67	16483.96	748.99
Pre + habitat	21	20	16336.77	16458.06	723.09
With 3 regions, sex, and habitat					
State + sex + habitat	25	24	15667.51	15811.81	53.83
Biogeographic + sex + habitat	25	24	15634.75	15779.06	21.07
CA split + sex + habitat	25	24	15674.08	15818.39	60.4
With 5 regions, sex, and habitat					
INPFC + sex + habitat	41	40	15622.84	15858.94	9.16
Pre + sex + habitat	41	40	15613.7	15849.8	0

Discussion

Differences in habitat type and structure have been shown to influence population distribution, growth, maturity, energy reserves and behavior in terrestrial and aquatic species (Myers and Parker 1965, Lagory 1986, Pacunski and Palsson 2001, Lloret et al. 2002, Lombardi et al. 2003, Vinagre et al. 2008). To ensure that natural populations are being managed properly across broad areas, habitat type needs to be considered when proposing size regulations, gear restrictions, and harvest quotas. Past studies have found that neglecting to account for spatially-specific patterns in life-history and demography of natural populations can lead to mismanagement and can be detrimental to long-term sustainability of a population (Hilborn et al. 2003, King and McFarlane 2003, Maunder and Piner 2015).

In this study, west coast commercial and recreational fishing methods (bottom trawl versus hook-and-line) were used as a proxy for habitat. When using bottom-trawl fishing gear, low-relief habitats are targeted to maximize efficiency and reduce net snags on boulders and pinnacles. Alternatively, anglers using hook-and-line methods typically focus on high-relief habitats when targeting Lingcod and other rockfish species since adults of legal size are known to associate with nearshore rocky reefs.

DRIVERS BEHIND HABITAT-BASED VARIABILITY IN LINGCOD LIFE-HISTORY

Lingcod from high-relief habitats were larger at a given age indicating faster average lifetime growth, however individuals caught in low-relief habitats exhibited faster initial growth, as seen by the greater k value during early ages before maturity is reached (<5 years). This is possibly an artifact of the nonlinear Von Bertalanffy growth

equation where the lack of young individuals (0 and 1 year olds) caught in high-relief areas can inflate the difference in k between habitats. However, habitat-based behavioral differences in juvenile Lingcod can affect early growth as well. Lingcod have been shown to alter their foraging behavior depending on refuge availability, where juvenile Lingcod in structured habitats spend more time hiding than foraging while juvenile Lingcod in low-relief, open environments forage for longer periods of time at greater risk and energetic tradeoff (Petrie and Ryer 2006). Additionally, foraging return may be greater in open areas as rocky or biogenic structures can interfere with prey detection and capture success rate (Ryer 1988). Therefore, it may benefit juvenile Lingcod to remain in areas with minimal structure in order to maximize foraging opportunities and growth until a certain size is reached before moving into high-relief habitats with more refuge. As marine fish mature, energy becomes increasingly focused on reproduction versus somatic growth and survival becomes a greater priority (Krebs and Davis 2009). Lingcod from both habitat types reach 50% maturity at generally the same age but at difference sizes due to this discrepancy in early growth.

Lingcod in trawlable habitats were typically smaller and younger than Lingcod caught in untrawlable habitats. A strong recruitment pulse of young-of-the-year Lingcod can be seen in the mid-regions of Oregon, Northern California and Central California, which is consistent with the pattern of high productivity in this area. As discussed in Chapter 1, the stretch of coast between Cape Blanco and Point Conception is considered an area of maximum upwelling (Parrish et al. 1981, Strub et al. 1990, Checkley and Barth 2009) and is less prominent in southern California and Washington, indicating the potential for spatial variability in recruitment strength coastwide. To control for the effect

of the recruitment pulse on skewing size- and age-frequency comparisons, smaller sizes were truncated (<30 cm), reexamined, and resulted in similar findings to the original analysis.

Gear selectivity can also influence observed Lingcod sizes. Commercial trawl methods capture Lingcod from all size classes whereas recreational hook-and-line fishing gear may be biased towards larger fish, excluding smaller sizes (Chatwin 1958, Ralston 1990). Given that juvenile Lingcod do not typically recruit to rocky habitats until they reach about 35 cm (Miller and Geibel 1973), it is unlikely that a significant portion of size classes <35 cm were excluded by hook-and-line fishing gear in my study. Larger Lingcod can potentially outcompete smaller individuals when striking fishing lures or bait and skew the size of captured individuals (Ricker 1969, Gotz et al. 2007, Etienne et al. 2010), however this behavior is expected regardless of terminal tackle from a predatory species like Lingcod. Both methods are equally selective at the upper end of the size distribution, therefore, the resulting difference in size and age frequency between low-relief and high-relief habitats is likely an accurate representation of the Lingcod population caught by commercial and recreational fisheries, respectively.

Differences in habitat quality between trawlable and untrawlable areas can affect Lingcod health and survivability across multiple life stages. High-relief habitats provide spatial refuge from predators and sufficient prey resources that can maximize growth, reproduction and condition, while enhancing the biodiversity of whole communities (Able 1999, Yoklavich et al. 2000, Lloret et al. 2002, Lloret and Planes 2003). Lingcod, like other rockfishes, utilize high-relief habitats as a means of refuge, reproduction, and food, though this is dependent on seasonality and sex (Greenley et al. 2016, Starr et al.

2005, Beaudreau and Essington 2011). Lingcod caught from rocky reefs were in better condition, matured at smaller sizes, and had lower natural mortality than Lingcod in low-relief habitats, suggesting greater energy reserves and potentially higher reproductive output and survivability (Lloret et al. 2002, Lloret and Planes 2003), however, many of these initial differences appeared to be driven by sex as there was a higher proportion of male Lingcod (61%) in high-relief habitats. Between the two habitats, female Lingcod did not vary significantly in condition (Fulton's K and HSI) or timing of maturity but male Lingcod did. The GLM also indicated that sex was a stronger factor influencing condition over habitat effects. As nest-guarders, male Lingcod may mature earlier and be in better condition in order to maximize reproductive potential and success in high-relief habitats (Knapp 1995, Lindstrom 1998). In addition, male Lingcod show greater site fidelity while female Lingcod tend to be more migratory, moving farther distances away from rocky habitats for longer periods of time (Starr et al. 2005, Greenley et al. 2016). Therefore, in addition to energetic tradeoffs due to nest-guarding behavior, long term habitat effects on maturity and condition may be reduced in female Lingcod while having a greater impact on sedentary males.

Total mortality between habitats behaved as expected considering the history of the Lingcod fishery along the U.S. West Coast. Lingcod from high-relief habitats had a significantly higher total mortality (Z) than trawl caught Lingcod, which mirrors the increase in popularity of the recreational fishery and the concurrent decline of the commercial groundfish trawl fishery in the past few decades (Hamel et al. 2009, Haltuch et al. 2017). In the past, landings from the commercial trawl fishery far exceeded that of the recreational hook-and-line fishery, however, since 2014, Lingcod landings from both

the northern (Washington and Oregon) and southern (California) recreational sectors have been greater than their respective commercial sectors (Fig. 20). Coastwide, the recreational fishery surpassed the commercial fishery by an average of 642.2 metric tons per year since 2014 (Haltuch et al. 2017).

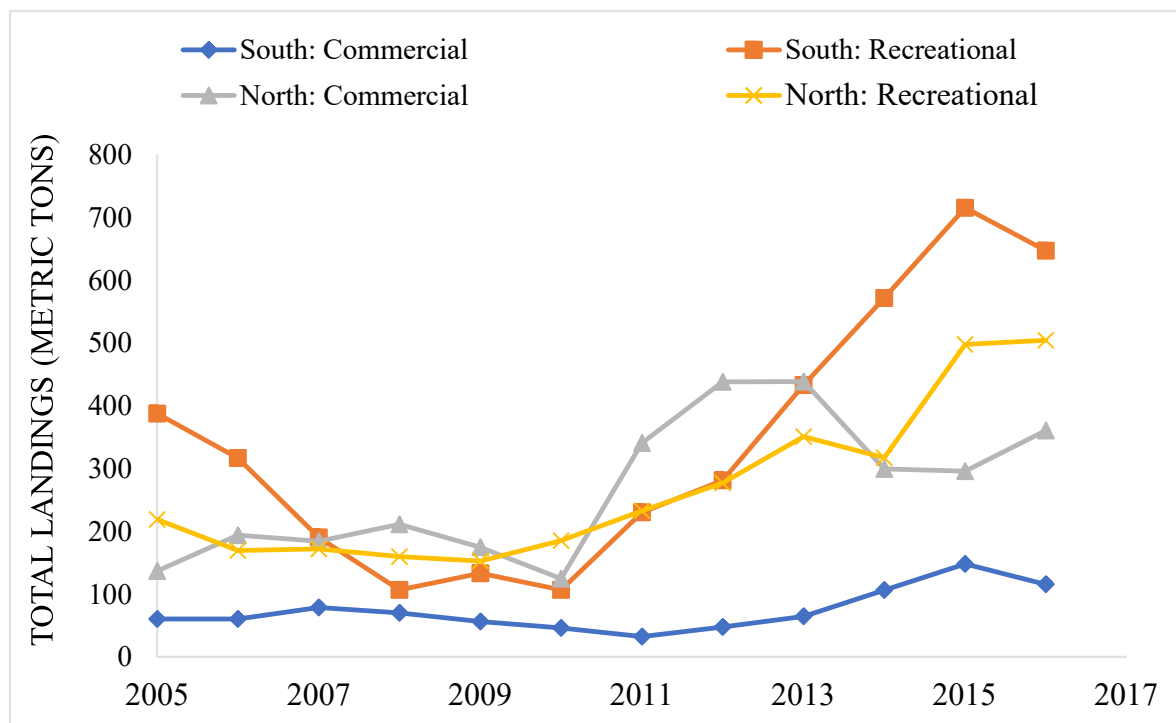


Figure 20: Commercial and recreational Lingcod landings in metric tons from the Northern (Washington and Oregon) and Southern (California) stock assessment regions (Hamel et al. 2009, Haltuch et al. 2017).

The shift seen between fishery sectors is primarily driven by population decline and changes in fishing regulations and catch quotas. While commercial Lingcod landings had been steadily declining since its peak in the early 1980s, total allowable catch in the commercial sector was dramatically reduced by over 80% in 2000 when the Lingcod fishery was deemed overfished coastwide (Hamel et al. 2009). Since 2000, landings from

the recreational hook-and-line sector have grown in both the Northern and Southern stock assessment regions, indicating that Lingcod found over high-relief habitats are being increasingly targeted compared to Lingcod from low-relief, trawlable habitats. This can have lasting effects on the coastwide Lingcod population due to the fishing industry's tendency to disproportionately remove large individuals and the connectivity between habitats (Jagiello 1990). Spillover effects can in turn influence populations from low-relief habitats and the commercial trawl sector. Understanding how shifts in a fishery, such as fishing method or location, fisher behavior, and market demand, can have long term population-level effects on broad-ranging fish stocks is necessary when considering management options. Stock assessments using life-history parameters from only one fishing sector or habitat type might not be representative of the population as a whole. This oversight could lead to errors in models of population growth and harvest, resulting in mismanagement and under- or over-harvest of regional stocks.

SPATIAL PATTERNS OF LINGCOD GROWTH ALONG THE U.S. WEST COAST

The best fit Von Bertalanffy model describing Lingcod growth along the West Coast contained the most complex combination of parameters: 5 regions, 2 habitats, and 2 sexes. From a management standpoint, this information gives us insight on how the coastwide Lingcod population could potentially be divided for management into 5 regional subpopulations, with different regulations for each sex and habitat. However, there are obvious limitations in the management of a single species in terms of economic and regulatory feasibility. Overall, it can be seen that the inclusion of sex alone improves

the growth model fit much more than including habitat, and the addition of both sex and habitat vastly improves the model fit over using geographic divisions.

The current Lingcod stock assessment model is conducted as two separate assessments (northern and southern regions) and uses unique biological parameters for trawl-caught male and female Lingcod for each region (Haltuch et al. 2017). As evidenced by the results shown in this study, making a relatively small change by adopting habitat-specific growth, maturity, and mortality parameters into the current stock assessment model can help to increase the accuracy of future assessments for Lingcod. This also supports the implementation of separate size limits for male and female Lingcod within the commercial and recreational fisheries as size at maturity can be variable. Ultimately, more analyses are needed to quantify the degree to which the model can benefit compared to the cost of increased enforcement and data collection. Accounting for habitat-specific life history differences can be especially relevant to an industry that has undergone dramatic changes like the Lingcod fishery. The shift from being primarily a commercial fishery to a recreational fishery within several decades can be a significant driver of population-level change, therefore, stock monitoring and managing efforts need to be adaptive and reflective of those changes.

CONCLUSIONS AND RECOMMENDATIONS

The goal of this study was to demonstrate how habitat-based factors can have profound impacts on life-history estimates used in groundfish stock assessment models. While the groundfish Fisheries Management Plan has made identifying essential fish habitat (EFH) a priority for spatial management, there is still much research to be

conducted on how habitat effects can directly and indirectly influence fish growth, maturity, longevity, mortality, and condition on a species by species basis. Groundfish stock assessment models are constantly advancing and adapting as new information becomes available, however, they are currently limited to using biological information derived from fisheries-independent trawl surveys.

Given the results from this study, I recommend the inclusion of habitat considerations when estimating life-history parameters for Lingcod and other groundfish species that occupy both trawlable and untrawlable habitats. The FRAM Hook-and-Line Survey in the Southern California Bight has been collecting distribution and abundance information from rockfishes in untrawlable habitats since 2004, however this is only done in the southern California area. Because a significant proportion of total Lingcod landings come from the recreational hook-and-line sector, it is necessary to implement a coastwide fisheries-independent hook-and-line survey when collecting vital stock assessment information. The WCG BTS 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. A comparable, long-term survey should be conducted over untrawlable habitats along the contiguous U.S. West Coast so that stock assessments are more accurate in representing the demography and biology of targeted populations vulnerable to recreational fishing.

References

- Able, K. W. (1999). Measures of Juvenile Fish Habitat Quality: Examples from. In *American Fisheries Society Symposium* (Vol. 22, pp. 134-147).
- Bassett, M., Lindholm, J., Garza, C., Kvitek, R., & Wilson-Vandenberg, D. (2018). Lingcod (*Ophiodon elongatus*) habitat associations in California: implications for conservation and management. *Environmental biology of fishes*, *101*(1), 203-213.
- Bellquist, L. F., Lowe, C. G., & Caselle, J. E. (2008). Fine-scale movement patterns, site fidelity, and habitat selection of ocean whitefish (*Caulolatilus princeps*). *Fisheries Research*, *91*(2-3), 325-335.
- Beaudreau, A. H., & Essington, T. E. (2011). Use of pelagic prey subsidies by demersal predators in rocky reefs: insight from movement patterns of Lingcod. *Marine biology*, *158*(2), 471-483.
- Blanchette, C. A., Melissa Miner, C., Raimondi, P. T., Lohse, D., Heady, K. E., & Broitman, B. R. (2008). Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. *Journal of Biogeography*, *35*(9), 1593-1607.
- Buonaccorsi, V. P., Kimbrell, C. A., Lynn, E. A., & Vetter, R. D. (2002). Population structure of copper rockfish (*Sebastes caurinus*) reflects postglacial colonization and contemporary patterns of larval dispersal. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(8), 1374-1384.
- Burnham, K. P., & Anderson, D. R. (2003). Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, USA.
- Carlson, H. R., & Straty, R. R. (1981). Habitat and nursery grounds of Pacific rockfish, *Sebastes* spp., in rocky coastal areas of southeastern Alaska. *Marine Fisheries Review*, *43*(7), 13-19.
- Carr, M. H. (1989). Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology*, *126*(1), 59-76.
- Cass, A.J., Beamish, R.J. and McFarlane, G.A. (1990). Lingcod (*Ophiodon elongatus*). *Canadian Special Publication of Fisheries and Aquatic Sciences*. *109*, 40 p.
- Chapman, D., & Robson, D. S. (1960). The analysis of a catch curve. *Biometrics*, 354-368.
- Chatwin, B. M. (1958). Mortality rates and estimates of theoretical yield in relation to minimum commercial size of Lingcod (*Ophiodon elongatus*) from the Strait of Georgia, British Columbia. *Journal of the Fisheries Board of Canada*, *15*(5), 831-849.
- Checkley Jr, D. M., & Barth, J. A. (2009). Patterns and processes in the California Current System. *Progress in Oceanography*, *83*(1-4), 49-64.
- Chilton, D. E., & Beamish, R. J. (1982). Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. *Canadian Special Publication of Fisheries and Aquatic Sciences* *60*: p 34-38.
- Choat, J. H., & Robertson, D. R. (2002). Age-based studies. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, California, USA, 57-80.
- Cope, J. M. (2004). Population genetics and phylogeography of the blue rockfish (*Sebastes mystinus*) from Washington to California. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(3), 332-342.

- Cope, J. M., & Punt, A. E. (2011). Reconciling stock assessment and management scales under conditions of spatially varying catch histories. *Fisheries Research*, 107(1), 22-38.
- Cotter, A. J. R., & Pilling, G. M. (2007). Landings, logbooks and observer surveys: improving the protocols for sampling commercial fisheries. *Fish and Fisheries*, 8(2), 123-152.
- Dawson, M. N. (2001). Phylogeography in coastal marine animals: a solution from California?. *Journal of Biogeography*, 28(6), 723-736.
- DeMartini, E. E., & Roberts, D. A. (1990). Effects of Giant Kelp (*Macrocystis*) on the density and abundance of fishes in a cobble-bottom kelp forest. *Bulletin of Marine Science*, 46(2), 287-300.
- Etienne, M.P., Obradovich, S., Yamanaka, L., and Mcallister, M. 2010. May 6. Extracting abundance indices from longline surveys: method to account for hook competition and unbaited hooks.
- Everitt, B.S., Landau, S., and Leese, M. (2001). Cluster Analysis, Fourth edition, Arnold.
- Götz, A., Kerwath, S.E., and Attwood, C.G. 2007. Comparison of the effects of different line fishing methods on catch composition and capture mortality of South African temperate reef fish. *African Journal or Marine Science* 29(2): 177–185.
- Gust, N., Choat, J., & Ackerman, J. (2002) Demographic plasticity in tropical reef fishes. *Marine Biology* 140: 1039–1051.
- Greenley, A. P. (2009). Movements of Lingcod (*Ophiodon elongatus*) tagged in Carmel Bay, CA (Doctoral dissertation, San Jose State University).
- Greenley, A. P., Green, K., & Starr, R.M. (2016). “Seasonal and ontogenetic movements of Lingcod (*Ophiodon elongatus*) in central California, with implications for marine protected area management”. CalCOFI Rep., Vol. 57, 2016.
- Haltuch, M.A., Wallace, J., Akselrud, C.A., Nowlis, J., Barnett, L.A.K., Valero, J.L., Tsou, T., Lam, L. (2017). 2017 Lingcod Stock Assessment. Pacific Fishery Management Council, Portland, OR. Available from <http://www.pcouncil.org/groundfish/stock-assessments/>
- Hamel, O. S., Sethi, S. A., & Wadsworth, T. F. (2009). Status and future prospects for Lingcod in waters off Washington, Oregon, and California as assessed in 2009. *Pacific Fishery Management Council, Portland, Oregon*.
- Hilborn, R. (2003). The state of the art in stock assessment: Where we are and where we are going. *Scientia Marina*, 67(1), 15-20.
- Hilborn, R., Quinn, T. P., Schindler, D. E., & Rogers, D. E. (2003b). Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences*, 100(11), 6564-6568.
- Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. U.S. National Marine Fisheries Service Fishery Bulletin 82:898–903.
- Holbrook, S.J., Carr, M.H., Schmitt, R.J., & Coyer, J.A. (1990) Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. *Bulletin of Marine Science* 47:104– 114.
- Jagiello, T. H. (1990). Movement of tagged Lingcod (*Ophiodon elongatus*) at Neah Bay, Washington. *Fishery Bulletin*, 88(4), 815-820.
- Jagiello, T., Hoffmann, A., Tagart, J., & Zimmermann, M. (2003). Demersal groundfish densities in trawlable and untrawlable habitats off Washington: implications for the estimation of habitat bias in trawl surveys. *Fishery Bulletin*, 101(3), 545-565.

- JMP[®], Version 14. SAS Institute Inc., Cary, NC, 1989-2019.
- Keller, A. A., J. R. Wallace, & Methot, R. D. (2017). The Northwest Fisheries Science Center's West Coast Groundfish Bottom Trawl Survey: History, Design, and Description. *U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-136*.
- King, J. R., & McFarlane, G. A. (2003). Marine fish life history strategies: applications to fishery management. *Fisheries Management and Ecology*, *10*(4), 249-264
- Krebs, J. R., & Davies, N. B. (Eds.). (2009). *Behavioural ecology: an evolutionary approach*. John Wiley & Sons.
- Knapp, R. A. (1995). Influence of energy reserves on the expression of a secondary sexual trait in male bicolor damselfish, *Stegastes partitus*. *Bulletin of Marine Science*, *57*(3), 672-681.
- Knip, D. M., Heupel, M. R., Simpfendorfer, C. A., Tobin, A. J., & Moloney, J. (2011). Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks, *Carcharhinus amboinensis*, in a tropical nearshore region. *Marine Ecology Progress Series*, *425*, 233-246.
- Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin*, *77*(4), 765-776.
- Lagory, K. E. (1986). Habitat, group size, and the behaviour of white-tailed deer. *Behaviour*, *98*(1-4), 168-179.
- Larson, R. J., & DeMartini, E. E. (1984). Abundance and vertical distribution of fishes in a cobble-bottom kelp forest off San Onofre, California. *Fisheries Bulletin*, *82*(1), 37-53.
- Lindström, K. (1988). Male-male competition for nest sites in the sand goby, *Pomatoschistus minutus*. *Oikos*, 67-73.
- Lloret, J., Gil de Sola, L., Souplet, A., & Galzin, R. (2002). Effects of large-scale habitat variability on condition of demersal exploited fish in the north-western Mediterranean. *ICES Journal of Marine Science*, *59*(6), 1215-1227.
- Lloret, J., & Planes, S. (2003). Condition, feeding and reproductive potential of white seabream *Diplodus sargus* as indicators of habitat quality and the effect of reserve protection in the northwestern Mediterranean. *Marine ecology. Progress series*, *248*, 197-208.
- Lombardi, L., Fernández, N., Moreno, S., & Villafuerte, R. (2003). Habitat-related differences in rabbit (*Oryctolagus cuniculus*) abundance, distribution, and activity. *Journal of Mammalogy*, *84*(1), 26-36.
- Lombardi, L., Fernández, N., & Moreno, S. (2007). Habitat use and spatial behaviour in the European rabbit in three Mediterranean environments. *Basic and Applied Ecology*, *8*(5), 453-463.
- Love, M. S., Yoklavich, M., & Thorsteinson, L. K. (2002). The rockfishes of the northeast Pacific. University of California Press, Berkeley, California, 416 p.
- Maunder, M. N., & Piner, K. R. (2014). Contemporary fisheries stock assessment: many issues still remain. *ICES Journal of Marine Science*, *72*(1), 7-18.
- Miller, D. J., & Geibel, J. J. (1973). Summary of blue rockfish and Lingcod life histories, a reef ecology study, and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California (Vol. 158). *State of California, Resources Agency, Department of Fish and Game*.

- Munday P.L., Jones G.P., & Caley M.J. (1997) Habitat specialisation and the distribution and abundance of coral-dwelling gobies. *Marine Ecology Progress Series*, 152:227–239.
- Myers, K., & Parker, B. S. (1965). A study of the biology of the wild rabbit in climatically different regions in eastern Australia. I. Patterns of distribution. *CSIRO Wildlife Research*, 10(1), 1-32.
- Pacific Fishery Management Council (2012). Pacific coast groundfish 5-year review of essential fish habitat. Report to Pacific Fishery Management Council. Phase 1: New information, September 2012. Portland, OR. 416 p.
- Pacunski, R. E., & Palsson, W. A. (2001). Macro-and micro-habitat relationships of adult and sub-adult rockfish, Lingcod and kelp greenling in Puget Sound. *Puget Sound Research* (Vol. 1).
- Parrish, R. H., Nelson, C. S., & Bakun, A. (1981). Transport mechanisms and reproductive success of fishes in the California Current. *Biological Oceanography*, 1(2), 175-203.
- Petrie, M. E., & Ryer, C. H. (2006). Hunger, light level and body size affect refuge use by post-settlement Lingcod *Ophiodon elongatus*. *Journal of fish biology*, 69(4), 957-969.
- Ralston, S. (1990). Size selection of snappers (Lutjanidae) by hook and line gear. *Canadian Journal of Fisheries and Aquatic Sciences*, 47(4), 696-700.
- Rencher, A.C. (2002). *Methods of Multivariate Analysis*, Second edition, Wiley.
- Ricker, W.E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. *J. Fish. Res. Bd. Can.* 26(3): 479–541.
- Risk, A. (1997). Effects of habitat on the settlement and post-settlement success of the ocean surgeonfish *Acanthurus bahianus*. *Marine Ecology Progress Series*, 161, 51-59.
- Robertson, D., & Kaufmann, K. W. (1998). Assessing early recruitment dynamics and its demographic consequences among tropical reef fishes: Accommodating variation in recruitment seasonally and longevity. *Austral Ecology*, 23(3), 226-233.
- Robertson, D. R., Ackerman, J. L., Choat, J. H., Posada, J. M., & Pitt, J. (2005a). Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. *Marine Ecology Progress Series*, 295, 229-244.
- Robertson, D. R., Choat, J. H., Posada, J. M., Pitt, J., & Ackerman, J. L. (2005b). Ocean surgeonfish *Acanthurus bahianus*. II. Fishing effects on longevity, size and abundance?. *Marine Ecology Progress Series*, 295, 245-256.
- Ryer, C. H. (1988). Pipefish foraging: effects of fish size, prey size and altered habitat complexity. *Marine Ecology Progress Series*, 48, 37.
- Sale P.F., & Dybdahl, R. (1975). Determinants of community structure for coral reef fishes in an experimental habitat. *Ecology*, 56: 1343–1355.
- Samhuri, J. F., Vance, R. R., Forrester, G. E., & Steele, M. A. (2009). Musical chairs mortality functions: density-dependent deaths caused by competition for unguarded refuges. *Oecologia*, 160(2), 257-265.
- Sivasundar, A., & Palumbi, S. R. (2010). Life history, ecology and the biogeography of strong genetic breaks among 15 species of Pacific rockfish, *Sebastes*. *Marine biology*, 157(7), 1433-1452.

- Smith, M. W., Then, A. Y., Wor, C., Ralph, G., Pollock, K. H., & Hoenig, J. M. (2012). Recommendations for catch-curve analysis. *North American Journal of Fisheries Management*, 32(5), 956-967.
- Starr, R. M., O'Connell, V., & Ralston, S. (2004). Movements of Lingcod (*Ophiodon elongatus*) in southeast Alaska: potential for increased conservation and yield from marine reserves. *Canadian Journal of Fisheries and Aquatic Sciences*, 61(7), 1083-1094.
- Starr, R. M., O'Connell, V., Ralston, S., & Breaker, L. (2005). Use of acoustic tags to estimate natural mortality, spillover, and movements of Lingcod (*Ophiodon elongatus*) in a marine reserve. *Marine Technology Society Journal*, 39(1), 19-30.
- Strub, P. T., James, C., Thomas, A. C., & Abbott, M. R. (1990). Seasonal and nonseasonal variability of satellite-derived surface pigment concentration in the California Current. *Journal of Geophysical Research: Oceans*, 95(C7), 11501-11530.
- Stein, D. L., B. N. Tissot, M.A. Hixon, and W. Barss (1992). Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. *Fishery Bulletin*. 90:540-551.
- Tolimieri, N. (1995) Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. *Oecologia* 102:52-63.
- Tolimieri, N., Andrews, K., Williams, G., Katz, S., & Levin, P. S. (2009). Home range size and patterns of space use by Lingcod, copper rockfish and quillback rockfish in relation to diel and tidal cycles. *Marine Ecology Progress Series*, 380, 229-243.
- Vinagre, C., Amara, R., Maia, A., & Cabral, H. N. (2008). Latitudinal comparison of spawning season and growth of 0-group sole, *Solea solea* (L.). *Estuarine, Coastal and Shelf Science*, 78(3), 521-528.
- Williams, E. H., & Ralston, S. (2002). Distribution and co-occurrence of rockfishes (family: Sebastidae) over trawlable shelf and slope habitats of California and southern Oregon. *Fishery Bulletin*, 100(4), 836-855.
- Yoklavich, M. M., Cailliet, G. M., Greene, H. G., & Sullivan, D. (1995). Interpretation of sidescan sonar records for rockfish habitat analysis: examples from Monterey Bay. *Alaska Department of Fish and Game Special Publication*, 9, 11-14.
- Yoklavich, M. M., Greene, H. G., Cailliet, G. M., Sullivan, D. E., Lea, R. N., & Love, M. S. (2000). Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. *Fisheries Bulletin*, 98, 625-641.