



Geographic variability in lingcod *Ophiodon elongatus* life history and demography along the US West Coast: oceanographic drivers and management implications

Laurel S. Lam^{1,2,*}, Bonnie L. Basnett², Melissa A. Haltuch³, Jason Cope³,
Kelly Andrews⁴, Krista M. Nichols⁴, Gary C. Longo⁵, Jameal F. Samhouri⁴,
Scott L. Hamilton²

¹Pacific States Marine Fisheries Commission, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA 98112, USA

²Moss Landing Marine Laboratories, San Jose State University, Moss Landing, CA 95039, USA

³Fishery Research Analysis and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA 98112, USA

⁴Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA 98112, USA

⁵NRC Research Associateship Program, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA 98112, USA

ABSTRACT: Understanding the environmental and anthropogenic drivers of spatial patterns in life history variation for exploited fish populations is important when making management decisions and designating stock boundaries. These considerations are especially germane for stocks that are overfished or recently rebuilt, such as lingcod *Ophiodon elongatus*, a commercially and recreationally valuable species of groundfish along the West Coast of North America. Between 2015 and 2017, we collected 2189 lingcod from 24 port locations, spanning 28° of latitude from southeast Alaska (60° N) to southern California (32° N), to investigate latitudinal patterns in size- and age-structure, growth, timing of maturity, condition, and mortality, as well as to identify biologically relevant population breakpoints along the coast. We found strong latitudinal patterns in these life history and demographic traits consistent with Bergmann's rule: lingcod from colder, northern waters were larger-at-age, lived longer, matured at larger sizes, and had lower natural mortality rates than lingcod from warmer, southern waters. Female lingcod were larger-at-age, lived longer, and matured at larger sizes compared to males within each examined region. In addition, we found evidence for strong associations between lingcod life history traits and the oceanographic variables of sea surface temperature and chlorophyll a. Cluster analysis using life history traits indicated that central Oregon is a biologically relevant breakpoint for lingcod along the US West Coast. This breakpoint based on life history traits, in conjunction with a recently identified population genetic breakpoint between central and northern California, highlights the need for future lingcod stock assessments to consider multiple sources of information to best inform management of this trans-boundary stock.

KEY WORDS: Spatial variability · Life history · Lingcod · Biogeography · Growth · Northeast Pacific

— Resale or republication not permitted without written consent of the publisher —

1. INTRODUCTION

Coastal marine fishes are exposed to unique, fluctuating environments that are affected by oceanographic

variability, habitat complexity, and human-induced impacts. These factors can affect the demography and life history of broadly ranging species in a variety of ways, from altering population structure to

*Corresponding author: laurel.lam@noaa.gov

shifting patterns of growth, reproduction, and mortality (Robertson et al. 2005a,b, Hamilton et al. 2011). The influence of changing latitudes and the environmental gradients associated with them on life history variation has been repeatedly documented in marine environments (Boehlert & Kappenman 1980, Gertseva et al. 2017, Kapur et al. 2020), often showing that organisms from colder regions are larger-at-age, have increased longevity, and mature earlier at smaller sizes compared to conspecifics residing in warmer locales (Bergmann 1847, Ray 1960, for an exception see Conover & Present 1990). This phenomenon, referred to as Bergmann's rule, is generally attributed to temperature-driven energetic trade-offs between somatic growth and reproduction, and regional variability in food availability and metabolism (Atkinson & Sibly 1997, Munch & Salinas 2009).

Fishing pressure can also have substantial effects on population structure and the life history of fish stocks over time. 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) that can have short- and long-term repercussions on recruitment, reproductive output, stock resilience, and overall economic yield (Hixon et al. 2014), where overfished populations are left in a particularly vulnerable state in the face of changing climate conditions. In species with broad distributions, the degree of exploitation can be spatially and temporally inconsistent; therefore, historic and current fishing trends must not be overlooked when disentangling drivers of observed trait variation.

Despite these known spatial and temporal influences on life history traits, fisheries management methods often make the simplifying assumption of spatial uniformity across broad regions, segments of a population, or the entire stock. As a result, a mismatch between spatial scales of management and local fish demographics can exist when detailed information is not available (Cope & Punt 2011). Past studies have demonstrated that incorporating spatially explicit sources of population variation into harvest models can reduce the risk of localized depletion (Okamoto et al. 2020) and improve stock assessment performance (Cope & Punt 2011). Likewise, accounting for life history differences when implementing management regulations in the form of catch quotas and minimum size limits has the potential to maximize overall yield and sustainability (Hamilton et al. 2011, Wilson et al. 2012, Okamoto et al. 2020). Methods of defining stock structure based on biological and/or genetic information for management purposes

has advanced considerably in the past decade (Spies & Punt 2015, Andrews et al. 2018, Kapur et al. 2020); however, the key to producing spatially structured assessments ultimately depends on the data used to inform them. Such data are often outdated, regionally constrained, or lacking altogether (Maunder & Piner 2015).

The groundfishes of the Northeast Pacific along the US West Coast would especially benefit from the use of spatially structured assessments as they are long-lived, widely distributed, have relatively small home ranges as adults (Love et al. 2002), and thus have the potential for life history variability associated with geographic features and environmental conditions. High-latitude waters near southeast Alaska (57° N) are generally cooler and more productive than low-latitude regions south of Point Conception, California (32° N); however, the strength of upwelling and productivity is largely dependent on interactions among the California Current System (CCS), seasonal wind forcing, and physical features (i.e. capes, points, submarine canyons, and islands) (Ware & Thomson 2005, Checkley & Barth 2009). Over 300 species of groundfishes inhabit this stretch of coast, including 100+ economically valuable species managed under the groundfish fishery management plan that contributes \$70 million in ex-vessel revenue annually (PFMC 2019). Despite their importance, spatial variability in life history and demographic traits and the relationships between these traits and environmental gradients remain to be explored for the majority of groundfishes (for exceptions, see Rooper 2008, Wilson et al. 2008, Laidig 2010).

In this study, we examined the life history and demography of lingcod *Ophiodon elongatus* Girard, 1854, a commercially valuable groundfish and key sportfish prized by recreational anglers on the West Coast of North America (NMFS 2018). Lingcod contribute close to 7.5% of total recreational groundfish landings and \$1.4 million in ex-vessel revenue in the commercial sector (PFMC 2019). Past studies have indicated that lingcod exhibit geographic variability in body size, spatial separation between sexes, and have limited adult home ranges (Starr et al. 2005, Tolimieri et al. 2009, Bassett et al. 2018), suggesting the potential for substantial variation in demography and life history traits throughout their range. Despite this potential, current lingcod stock assessment regions are structured around state regulatory and fishery management considerations, and only grossly capture latitudinal biological patterns seen in the population. In addition, until quite recently, lingcod stock assessments lacked fishery-independent data

from all habitat types and stressed major uncertainty regarding the proper break points for stocks and sub-stocks and stock-specific length-at-age data (Hamel et al. 2009, Haltuch et al. 2018), indicating the need for consistent monitoring so that a robust time-series can be established.

Our goal in this study was to determine how lingcod demography and life history traits vary across its US range and to examine how oceanographic factors may influence this geographic variability. We predicted that lingcod in cooler, northern waters with higher primary productivity will be larger-at-age, longer lived, later to mature, and in better condition than lingcod from warmer, southern latitudes where waters are relatively nutrient-poor. Our objectives were (1) to quantify and compare life history and demographic traits (growth, longevity, size- and age-at-maturity, somatic condition, and mortality) of lingcod in 7 regions along the US West Coast; (2) to investigate associations between life history parameters and oceanographic indicators; and (3) to determine whether distinct clusters occurred within the West Coast lingcod population based on similarities in life history traits, to determine biologically relevant breakpoints in the lingcod stock.

2. MATERIALS AND METHODS

2.1. Species natural history

Lingcod (Family Hexagrammidae) range from Kodiak Island, Alaska, to Baja California, Mexico (Wilby 1937, Miller & Lea 1972). They are opportunistic top predators, feeding on a variety of taxa including octopus and squid, herring, rockfishes, and flatfishes (Beaudreau & Essington 2011, B. L. Basnett unpubl. data). Genetic studies using allozyme or mitochondrial DNA markers reported that lingcod are genetically similar throughout their coastal range (Marko et al. 2007); however, results using thousands of genome-wide markers generated with restriction site associated DNA sequencing (RADseq) suggest evidence for 2 distinct genetic clusters, with a northern and southern lingcod group separated offshore of Point Reyes, California (Longo et al. 2020).

Previous studies of lingcod life history are decades old, geographically limited, and vary in collection methods; additionally, there has not been a comprehensive study conducted for lingcod across the entirety of its range. It is important to emphasize that past climate and anthropogenic factors likely influence extant patterns in life history, underscoring the

necessity of conducting regular studies on harvested populations. In specific regions where detailed studies have been conducted, lingcod were found to be sexually dimorphic, with females typically growing faster and attaining larger asymptotic sizes than males (Miller & Geibel 1973, Cass et al. 1990). During spawning season (December–February), females move from deeper offshore areas (100–200 m) to shallow (10–40 m) rocky habitats to deposit eggs at favorable nesting sites, pre-chosen and guarded by mature males (Cass et al. 1990). After the eggs are deposited, female lingcod will return to depth and leave the male to guard the eggs until they hatch (Low & Beamish 1978). Upon hatching, the larvae are pelagic for several months before settling to soft-bottom habitats. Juvenile lingcod often remain on soft-bottom habitats until attaining a size of ~35 cm (1–2 yr of age) before moving into high-relief rocky habitats, potentially for protection from larger predators (Petrie & Ryer 2006, Bassett et al. 2018).

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 (Starr et al. 2005, Greenley et al. 2016). During non-spawning months, males and females exhibit spatial segregation by depth and habitat type, where a higher proportion of female lingcod are caught in the commercial fishery by trawl gear in low relief, deep, offshore habitats, and a higher proportion of male lingcod are caught in the recreational fishery by divers and party-boat anglers in comparatively shallow, nearshore habitats (Miller & Geibel 1973, Jagielo 1999).

2.2. Study location and collection methods

Lingcod were collected from 7 regions along the US West Coast between 2015 and 2017: Southeast Alaska (54° 30' N–59° 48' N), Puget Sound, coastal Washington (46° 16' N–49° N), Oregon (42° N–46° 16' N), northern California (38° 2' N–42° N), central California (34° 30' N–38° 2' N), and southern California (32° 2' N–34° 30' N) (Fig. 1). These regions were initially selected based on major biogeographic features (Point Conception, Cape Mendocino, Columbia River, Puget Sound) with potential for pronounced influence on groundfish life history, as well as certain federal/jurisdictional boundaries (US–Canadian border, Oregon–California border, US–Mexican border). Lingcod were caught using hook-and-line fishing gear on commercial passen-

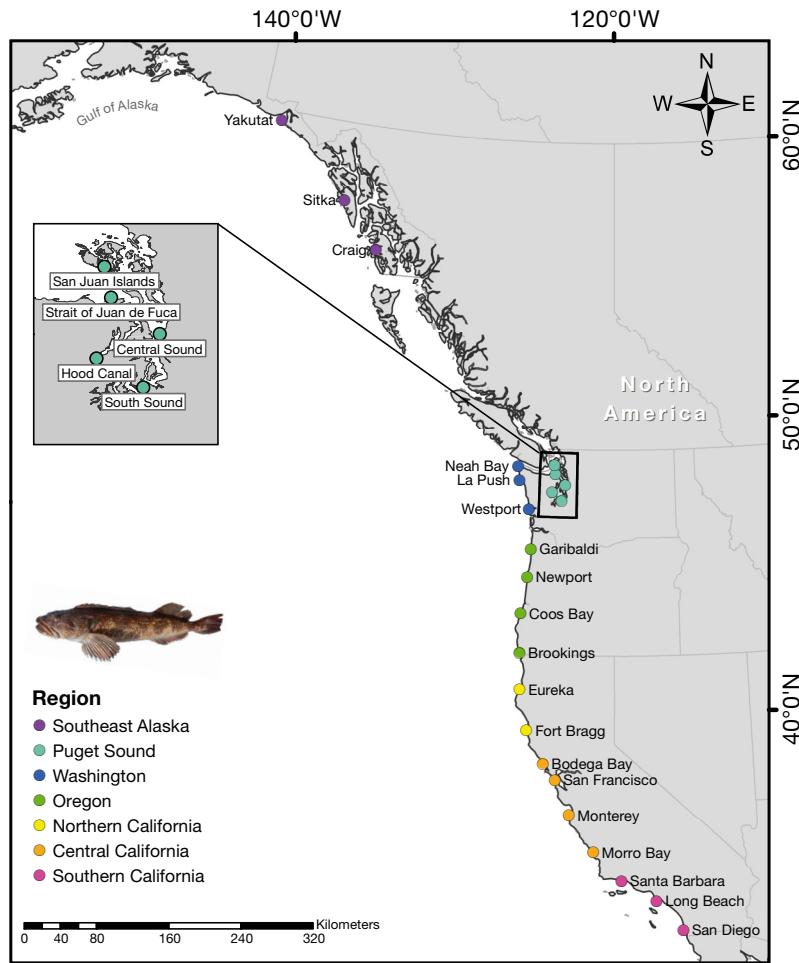


Fig. 1. Study area. Ports are color-coded by region; 2 to 5 ports were chosen per region based on commercial passenger fishing vessel availability and accessibility

ger fishing vessels (CPFVs) year-round, though the majority of samples (83.3%) were collected from March–October (non-spawning months). Three to 4 fishing ports were selected per region ($n = 24$ 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 availability and accessibility of CPFVs. We worked closely with CPFV captains and local volunteer anglers to identify appropriate fishing grounds and to ensure that lingcod landed from one port did not overlap with lingcod landed from an adjacent port. On average, we fished for 2.5 d out of each port to obtain the targeted sample size of 75–100 lingcod per port. 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 near each port were sampled for an equal amount of time. Lingcod can be targeted using weighted bars, jigs, swim baits, and live bait, which

greatly reduces incidental catch of other bottomfish species (i.e. *Sebastodes* spp.). Similar terminal tackle types were used by recreational anglers coastwide to ensure that gear selectivity did not bias collections. Both small and large lingcod were caught from all ports, indicating that the bulk of the size range was targeted effectively. Because lingcod are known to recruit to rocky substrate at around 35 cm total length (Miller & Geibel 1973), it is unlikely that smaller size classes were excluded by this mode of fishing in rocky habitats. Additional samples were provided by the Alaska commercial longline fishery, the Northwest Fisheries Science Center (NWFSC) Rockfish Bycatch Study in Puget Sound (Andrews et al. 2018), the Oregon Department of Fish and Wildlife Marine Reserves Program (Huntington et al. 2014), and the California Collaborative Fisheries Research Program (Wendt & Starr 2009).

Total length (cm), weight (kg), sex, and body coloration were recorded immediately after lingcod were landed, then fish were frozen or put on ice until dissection. Lingcod were euthanized per the Institutional Animal Care and Use Committee (Protocol #964) at San Jose State University. Catch and

location information (e.g. latitude, longitude, depth, relief, and fishing duration) were collected at the start and stop for each drift, though for the purposes of this study lingcod were grouped and analyzed by landed port or region. Gill tissue was collected and stored in 95% ethanol, a subset of which ($n = 548$) was used for genetics (Longo et al. 2020). Male and female gonads were weighed (g) and macroscopically inspected to assess maturity stage according to Washington Department of Fish and Wildlife (WDFW) standards (Table S1 in the Supplement at www.int-res.com/articles/suppl/m670p203_supp.pdf) (Silberberg et al. 2001). While macroscopic assessment of maturity is not a reliable determinant of functional maturity, it is an adequate method for demonstrating biological maturity for the purposes of this study (M. Head, NWFSC, pers. comm.).

To evaluate growth rates (length-at-age), age-at-maturity, and longevity, lingcod were aged using the fin-ray method (Chilton & Beamish 1982), which

has the highest accuracy, readability, and minimal between-reader bias when compared to other ageing structures (Beamish & Chilton 1977, Cass & Beamish 1983) (Fig. S1). Fin rays 4–8 on the second dorsal fin were removed at the base joint and frozen. Fin rays collected in Washington were processed and aged by the WDFW ageing lab then sent to Moss Landing Marine Laboratories (MLML) where cross-lab ageing validation was established (Table S2, Fig. S2). All other fin rays were processed and aged at MLML following the fin ray preparation protocol and ageing methods described by Chilton & Beamish (1982) and currently employed by WDFW (R. LeGoff, WDFW, pers. comm.).

2.3. Life history and demographic analysis

We used the computing platform R version 3.5.1 and JMP Pro version 14 for all analyses, and an alpha level of 0.05 for statistical tests. Sex ratios were assessed across all regions using Pearson's chi-squared test. We compared size- and age-frequency distributions among regions and between sexes using the multiple sample nonparametric Kruskal-Wallis test and the 2-sample Kolmogorov-Smirnov test, respectively, allowing us to detect differences in cumulative frequency distributions among groups. Due to the seasonality of the depth distribution for male and female fish, lingcod caught within spawning months November–February were excluded from this analysis. The Steel-Dwass method was used for pairwise comparisons between regions. We used residual analysis to account for the covariate of depth as a confounding factor when comparing lingcod size and age 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 regressions on depth versus size and depth versus age were extracted and used in the nonparametric comparisons by region and sex.

We examined differences in growth rate by fitting von Bertalanffy growth functions (VBGF) to length-at-age data for each region and sex or each port (depending on the analysis) using maximum likelihood parameter estimates (Kimura 1980) and the following equation:

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

where L_t equals the estimated length at age t , L_{inf} is the predicted maximum asymptotic length, k is the growth coefficient, and t_0 is the theoretical time

when length equals 0. The t_0 parameter was not estimated but fixed to 0, which we deemed biologically appropriate as larval lingcod are only 12 mm upon hatching (Petrie & Ryer 2006), and young-of-the-year lingcod (important for anchoring the VBGF curve) were not collected in this study. We used a 2 parameter estimation for generating maximum likelihood VBGF curves. Confidence intervals (95%) were calculated around least squares estimates of L_{inf} and k for each subpopulation using bootstrap methods (Kimura 1980). Longevity (T_{max}) is presented as the maximum sampled age per region (Beverton 1992). We also calculated the average oldest age using the mean of the upper quartile of ages (Choat & Robertson 2002) to provide a more robust and conservative estimate for comparing T_{max} . The average oldest age was derived per port and compared among regions using ANOVA. We assessed timing at 50% maturity using logistic regression based on macroscopic assessment of gonad stage (mature vs. immature fish). Confidence intervals (95%) were estimated using bootstrapping and compared among regions; significant differences in the timing of maturity occurred when confidence intervals did not overlap. No estimate for length or age at 50% maturity was derived for lingcod in southern California due to small sample size of immature individuals ($n = 1$).

Natural mortality rate (M) was estimated using a weighted composite of several well-known empirical methods (Cope 2017), using growth and T_{max} estimates as parameter inputs. We chose to use L_{inf} , k , and T_{max} to generate the composites as there was the least amount of variability associated with these parameters. Estimates of M were weighed so that the contribution of empirical methods using overlapping parameter inputs totaled 1. A lognormal error distribution with a CV of 0.2 was included to incorporate uncertainty for point estimates and to create a prior distribution plot of M values per port. Then we used an ANOVA to identify differences in M among regions. We estimated total mortality (Z) using the Chapman-Robson method of cross-sectional catch-curve analysis (Chapman & Robson 1960) with a correction factor for variance inflation (Smith et al. 2012). The Chapman-Robson method is based on maximizing a likelihood function on a geometric distribution for catch at age. Fish younger than the modal age were excluded from the regression (Beverton & Holt 1959, Chapman & Robson 1960, Robson & Chapman 1961, Ricker 1975). Fishing mortality (F) was derived using the formula $F = Z - M$.

Finally, we examined and compared lingcod condition using morphometric and physiological indices:

Fulton's K condition factor was used to assess general health of individual lingcod, where the weight is proportional to the cube of its length:

$$K = (\text{body weight} / \text{total length}^3) \times 100 \quad (2)$$

(Fulton 1902, Bolger & Connolly 1989). High K values signify that a fish is heavier, and potentially healthier, for a given length. The hepatosomatic index (HSI):

$$\text{HSI} = (\text{liver weight} / \text{body weight}) \times 100 \quad (3)$$

calculates the ratio of the liver weight to overall body weight and measures the energy reserve status of a fish, where high HSI indicates healthier condition with more energy reserved in the liver (Htun-Han 1978, Bolger & Connolly 1989). To account for the effect of seasonality on body condition, lingcod caught during pre-spawning and spawning months were again excluded from the analysis. Total length was positively correlated with Fulton's K ($\beta = 0.002$, $r^2 = 0.04$, $F_{1,2117} = 96.5$, $p < 0.0001$) and HSI ($\beta = 0.01$, $r^2 = 0.04$, $F_{1,2108} = 80.1$, $p < 0.0001$); therefore, residuals from linear regressions were extracted and used in the subsequent ANOVA among regions to eliminate the confounding effect of body size.

2.4. Multivariate analysis and population clustering

We conducted a series of multivariate analyses to identify potential breaks, or geographic boundaries, where similarities in lingcod life histories can be grouped using life history estimates on the port-scale as opposed to the *a priori* defined regions. We used an agglomerative hierarchical cluster analysis among all sampled ports to identify data-defined clusters with no prior specifications based on region. Non-metric multidimensional scaling (nMDS) was used to visualize and ordinate the data-driven clusters in 2-dimensional space, and a permutational multivariate analysis of variance (PERMANOVA) was run to test if identified clusters were significantly different from one another. Euclidean distances were calculated among ports using normalized size- and age-based life history parameters: L_{inf} , k , mean size, T_{max} , size at 50% maturity, and M . The average silhouette method was used as a means of statistical clustering validation to compute the optimal number of port clusters (Everitt et al. 2001, Rencher 2002), and the complete linkage agglomerative clustering method was used to identify similar ports within those clusters. Homogeneity of group variances was tested using a multivariate analogue of Levene's test.

Finally, a principal component analysis (PCA) was used to determine the spatial association among coastwide lingcod life history traits and to further explore the association between long-term mean oceanographic factors (sea surface temperature [SST] and chlorophyll a [chl a] concentration) and observed latitudinal trends in life history. Here, we used chl a as a proxy for ecosystem productivity since areas with high concentrations of chl a are able to support higher secondary production of prey types typically consumed by lingcod (Worm et al. 2002). Life history parameters of L_{inf} and k , mean length, T_{max} , M , Fulton's K , and HSI were derived on the port-level data 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 the analysis. Mean SST and chl a data were obtained from the Giovanni online data system, developed and maintained by the NASA Goddard Earth Sciences Data and Information Services Center (<https://giovanni.gsfc.nasa.gov>). SST ($^{\circ}\text{C}$) and chl a (mg m^{-3}) data are 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 fished locations were isolated per port and averaged over a 12 yr period (2005–2017) that encompassed the ages of lingcod in the data set. Principal components (PCs) with eigenvalues > 1 (Girden 2001) were saved and used in a linear regression with mean SST and chl a, respectively.

3. RESULTS

3.1. Geographic variability in life history

Lingcod ($n = 2189$) were collected coastwide from rocky habitats between 2015 and 2017 (Table 1). Within regions, male and female lingcod were caught in significantly different proportions across all regions ($\chi^2_6 = 239.66$, $p < 0.0001$); however, the majority of this difference was driven by lingcod from Washington, which was female-dominated. This difference is likely due to the greater shelf width and reduced rocky habitat off the coast of Washington; in all other regions, males were more common. Upon removing Washington-caught lingcod 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 39.8% females to 60.2% males. Lingcod were caught from depths of 7–170 m (mean \pm SE: 59.8 ± 0.82 m). After accounting for the confounding factors of depth and seasonality,

Table 1. Lingcod catch summary by region. Number of ports were chosen based on commercial passenger fishing vessel location and availability. Each port was fished for an average of 2.5 d. Sample size of unsexed, female, and male lingcod, and percent female per region are shown (total n = 2189). TL: total length

	No. of ports	Days fished	Female (n)	Male (n)	Unsexed (n)	Percent female	Max. TL (cm)	Min. TL (cm)
Total	24	58	1036	1153	2	0.47	127	16.7
Alaska	3	11	105	169	0	0.38	127	41.5
Washington	3	6	318	68	0	0.82	112	39.0
Puget Sound	5	10	62	60	1	0.51	108	20.0
Oregon	4	10	146	211	0	0.41	111	33.8
N. California	2	4	82	118	0	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	0.35	97.0	40.2

median lengths differed across all sampled regions (Kruskal-Wallis test, $\chi^2_6 = 350.2$, $p < 0.0001$) and followed a latitudinal trend where lingcod decreased in size in southern latitudes (Fig. 2A). On top of the latitudinal trends in body size, female lingcod were larger than male lingcod in all regions sampled (Fig. S3). Median ages also differed significantly across regions (Kruskal-Wallis test, $\chi^2_6 = 148.9$, $p < 0.0001$), and tended to decline from north to south; however, regions south of Oregon were statistically indistinguishable (Fig. 2B). There was no significant difference in the average oldest age among regions (Fig. 2C); however, lingcod from Alaska were older than lingcod from central California based on Tukey's post hoc test. T_{\max} generally declined with latitude (Table 2). Median female lingcod sizes and ages were larger and older, respectively, than male lingcod within each region with the exception of northern California where there was no difference in male and female age frequency (Fig. S3). Based on average oldest age, female lingcod consistently lived longer than males by a mean of 1.4 ± 0.33 yr (Table 2).

Lingcod growth parameters L_{inf} and k were inversely related and exhibited a strong latitudinal cline across all regions (Table 2, Fig. 3A). Non-overlapping 95% confidence intervals indicated there were 4 major subgroups with statistically different growth patterns: Alaska and Washington; Puget Sound; Oregon and northern California; and central and southern California (Fig. 3B). These subgroups followed a latitudinal trend with decreasing maximum sizes and increasing k from north to south, with the exception of Puget Sound which had the highest k . Within each region, female lingcod attained levels of L_{inf} that were on average ($\pm \text{SD}$) 22.1 ± 3.12 cm larger than male lingcod, although it took them longer to attain this body size (Table 2, Fig. S4).

Size at 50% maturity decreased with decreasing latitude, with the exception of Puget Sound (Table 2, Fig. 4A). We did not observe a latitudinal trend for age at 50% maturity (Fig. 4B), indicating that differences in length at maturity are likely in response to the latitudinal differences in growth. Within each region, female lingcod matured an average ($\pm \text{SD}$) of 10.2 ± 7.17 cm larger and 0.9 ± 0.81 yr older than male lingcod (Fig. S5). There was no significant difference in lingcod M among regions, although we observed a trend of decreasing M with increasing latitude. Z and F also decreased with increasing latitude, except in lingcod from Washington which, along with lingcod from southern California, had the highest Z and F values (Table 2). In Puget Sound, the calculated value for M was greater than Z , resulting in a negative F . Male lingcod consistently exhibited higher M than females across all regions, with the exception of lingcod from central California. There was no consistent pattern in Z and F between sexes, but male lingcod had higher Z in Puget Sound, Oregon, northern California, and central California (Table 2).

Condition was analyzed for lingcod caught in non-spawning months only. After accounting for the positive relationship between condition and lingcod size, we found no consistent latitudinal trend in Fulton's K among regions (Fig. 5A, Table S3). Lingcod in the southern California region had the highest mean ($\pm \text{SE}$) Fulton's K (1.07 ± 0.008) and were thus heavier for a given length than fish from all other regions. HSI exhibited a latitudinal trend, indicating liver energy stores increased as latitude decreased from north to south (Fig. 5B). Similar to Fulton's K , individuals from southern California had the greatest mean HSI (2.18 ± 0.045) compared to other regions. Regardless of size, male lingcod were found to have a significantly higher mean Fulton's K than female

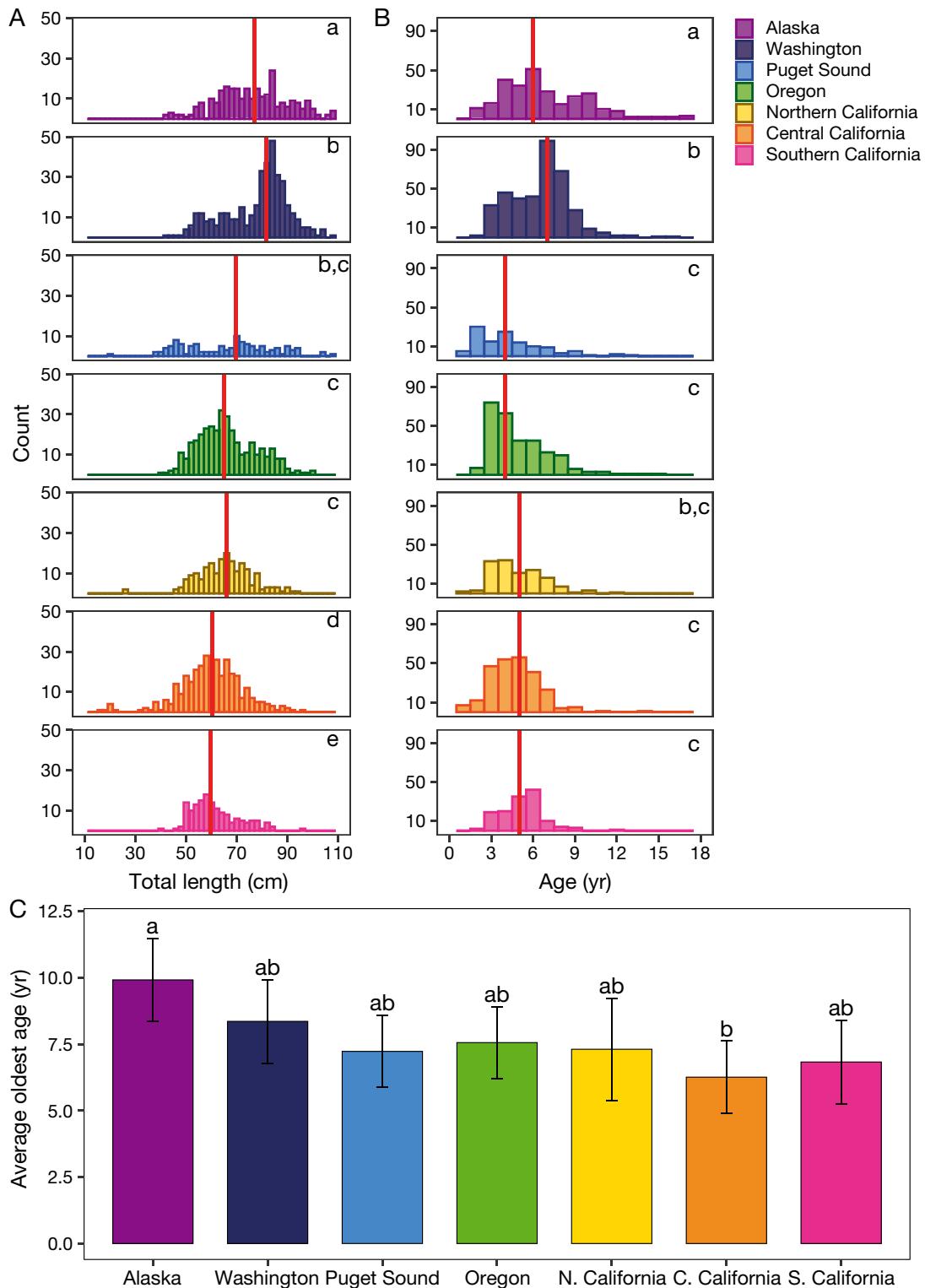


Fig. 2. (A) Size- and (B) age-frequency of lingcod by region (sexes pooled) in order of decreasing latitude. Red vertical line: median size and age per region. Regions were compared using the nonparametric Kruskal-Wallis test; nonparametric pairwise comparisons were conducted using Steel-Dwass All Pairs, where non-overlapping letters indicate significant difference ($\alpha = 0.05$). Note that nonparametric analysis was performed on extracted residuals from the linear regression between length and depth. (C) Average oldest age was calculated using the mean of the upper quartile of ages. Error bars were calculated using ± 2 SE. Statistical significance is noted by the lack of overlapping letters above error bars

Table 2. Von Bertalanffy growth function (VBGF) parameters (L_{inf} and k), average oldest age, and maximum sampled age (T_{max}) are shown for each sampled region by sex. Average oldest age was calculated using the mean upper quartile of observed ages. Size and age ranges at 50% maturity were derived from bootstrapped upper and lower confidence intervals (95%). Timing of maturity could not be established for certain region-sex combinations, particularly in southern California, due to small sample size of immature individuals. Total mortality (Z), natural mortality (M), and fishing mortality (F) were estimated for each region by sex. F was derived as: $F = Z - M$. In some instances, F resulted in zero or a negative value and is not shown.

	L_{inf} (SE)	k (SE)	Age of top quartile (SE)	T_{max}	Size, age at 50% maturity (cm, yr)	Size range	Age range	Z (SE)	M (SE)	F
Coastwide	93.4 (0.84)	0.266 (0.006)	7.9 (0.07)	18	43.1, 2.3	41.3–44.8	2.1–2.5	0.56 (0.02)	0.3 (0.0001)	0.26
Female only	100.3 (0.99)	0.25 (0.006)	8.3 (0.09)	17	50.1, 2.6	47.6–52.4	2.3–2.8	0.57 (0.04)	0.31 (0.0001)	0.26
Male only	74.8 (0.68)	0.358 (0.010)	7.2 (0.10)	18	41.6, 2.2	39.0–43.5	2–2.4	0.44 (0.06)	0.32 (0.0002)	0.12
Alaska	98.2 (1.70)	0.265 (0.012)	10.9 (0.25)	18	53.1, 2.9	46.9–56.7	2–3.4	0.32 (0.04)	0.3 (0.0001)	0.02
Female	106.7 (2.36)	0.27 (0.02)	12 (0.47)	17	68.3, 4.2	63.4–73.6	3.6–4.7	0.32 (0.09)	0.31 (0.0001)	0.01
Male	85.76 (1.19)	0.33 (0.01)	10.3 (0.31)	18	51.7, 2.5	46.4–55.1	1.2–3.1	0.32 (0.07)	0.31 (0.0002)	0.01
Washington	98.4 (1.38)	0.265 (0.010)	8.8 (0.13)	16	48.2, 2.5	44.5–51.4	2.1–2.8	0.79 (0.07)	0.32 (0.0001)	0.47
Female	96.73 (1.15)	0.29 (0.01)	8.8 (0.14)	16	53.7, 2.8	47–57.9	2.1–3.2	0.79 (0.08)	0.33 (0.0001)	0.46
Male	68.78 (1.99)	0.5 (0.05)	6.3 (0.35)	9	51, 2.8	45.3–54.3	1.7–3.3	0.59 (0.12)	0.5 (0.0002)	0.09
Puget Sound	91.9 (2.17)	0.370 (0.022)	7.7 (0.34)	13	43.2, 1.5	35.7–48.7	0.6–2.1	0.35 (0.08)	0.41 (0.0002)	–
Female	100.21 (3.07)	0.34 (0.03)	7.5 (0.38)	12	56.2, 2.4	51.1–61.9	1.5–3	0.44 (0.05)	0.42 (0.0002)	0.02
Male	80.56 (1.87)	0.44 (0.03)	7 (0.54)	13	39, 1	26.7–43.5	0–2	0.36 (0.05)	0.42 (0.0002)	–
Oregon	88.8 (1.53)	0.305 (0.012)	7.5 (0.19)	15	48.8, 2.5	44.6–51.8	2–2.9	0.42 (0.03)	0.35 (0.0001)	0.07
Female	97.35 (1.97)	0.27 (0.01)	8.6 (0.33)	15	56.4, 3	54.2–58.4	2.5–3.4	0.35 (0.08)	0.34 (0.0001)	0.02
Male	73.1 (1.21)	0.45 (0.02)	6.2 (0.17)	10	49, 2.7	47.1–50.7	2.4–2.9	0.56 (0.05)	0.51 (0.0002)	0.05
N. California	81.8 (1.97)	0.364 (0.024)	7.0 (0.18)	12	47.7, 2.1	42.4–50.5	1.4–2.9	0.53 (0.1)	0.43 (0.0002)	0.1
Female	92.24 (2.57)	0.31 (0.02)	7.1 (0.25)	10	54.2, 3	51.2–57.7	2.9–3	0.48 (0.12)	0.47 (0.0002)	0.02
Male	69.63 (1.33)	0.49 (0.03)	6.8 (0.27)	12	34.9, 1.2	28–43.7	0–2	0.49 (0.08)	0.46 (0.0002)	0.03
C. California	81.3 (1.55)	0.308 (0.013)	6.7 (0.11)	14	41.6, 2.5	39.3–43.4	2.3–2.7	0.54 (0.11)	0.37 (0.0001)	0.17
Female	89.22 (2.29)	0.28 (0.02)	6.7 (0.11)	9	45.4, 2.6	42.7–47.8	2.2–2.9	0.49 (0.14)	0.49 (0.0002)	–
Male	70.23 (1.25)	0.39 (0.02)	5.8 (0.13)	14	40.8, 2.4	38–42.9	2.1–2.7	0.59 (0.12)	0.39 (0.0002)	0.2
S. California	75.3 (1.86)	0.356 (0.027)	6.6 (0.09)	12	–	–	–	0.87 (0.18)	0.43 (0.0002)	0.44
Female	87.49 (2.8)	0.31 (0.03)	8 (0.29)	12	–	–	–	0.64 (0.13)	0.41 (0.0001)	0.23
Male	66.94 (1.1)	0.42 (0.03)	6.4 (0.09)	12	–	–	–	0.59 (0.12)	0.44 (0.0002)	0.15

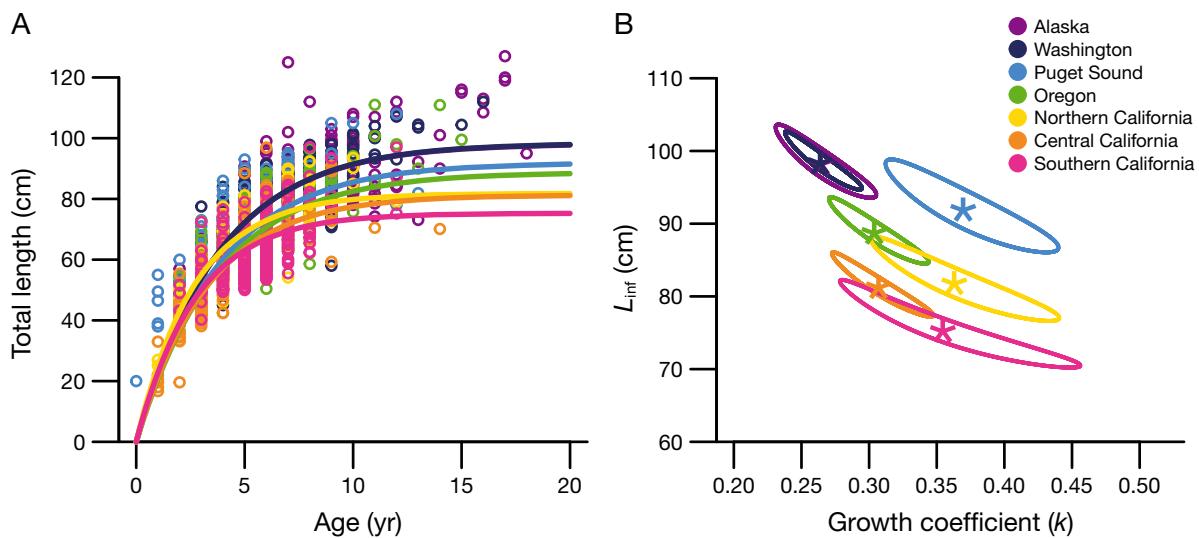


Fig. 3. (A) Spatial variation in lingcod von Bertalanffy growth curves across 7 sampled regions and (B) 95 % confidence intervals for predicted maximum asymptotic length (L_{inf}) and growth coefficients (k) for each region. Overlapping intervals indicate no difference in growth. Note that the growth curves for lingcod from Alaska and Washington overlap

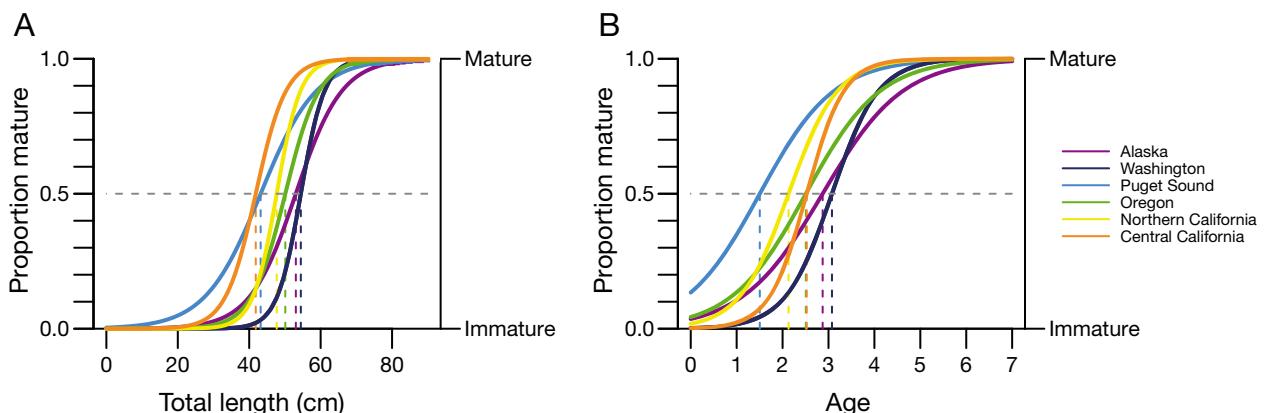


Fig. 4. Logistic regression estimating (A) total length at 50 % maturity and (B) age at 50 % maturity for lingcod from each sampled region along the US West Coast. Horizontal dashed line: time when 50 % of the population is mature; vertical dashed lines: size and age at 50 % maturity for each region. Maturity of lingcod from southern California could not be estimated due to small sample size of immature individuals

lingcod in all regions south of Oregon (Table S3). Male lingcod also had higher HSI than females within all California regions, but a lower HSI than females in Washington.

3.2. Multivariate analysis and oceanographic indicators

We found evidence for 2 clusters of lingcod along the US West Coast based on the suite of life history and demographic traits we analyzed. Sampled ports were generally separated into northern (Alaska, Washington, and northern Oregon) and southern

(southern Oregon, northern California, central California, and southern California) clusters (Fig. 6A), which were significantly different from each other in life history traits (PERMANOVA: $F_{1,18} = 16.02$, $p < 0.001$). The magnitude and direction of the vectors indicate that the formation of the 2 clusters is driven by differences in growth, size, and T_{max} , where lingcod from the northern cluster are larger and older than lingcod from the southern cluster. Lingcod from the southern cluster have higher M rates and obtain maximum sizes more quickly (larger k value) (Fig. 6B).

Principal component 1 (PC 1) and principal component 2 (PC 2) together comprised up to 76.0 % of

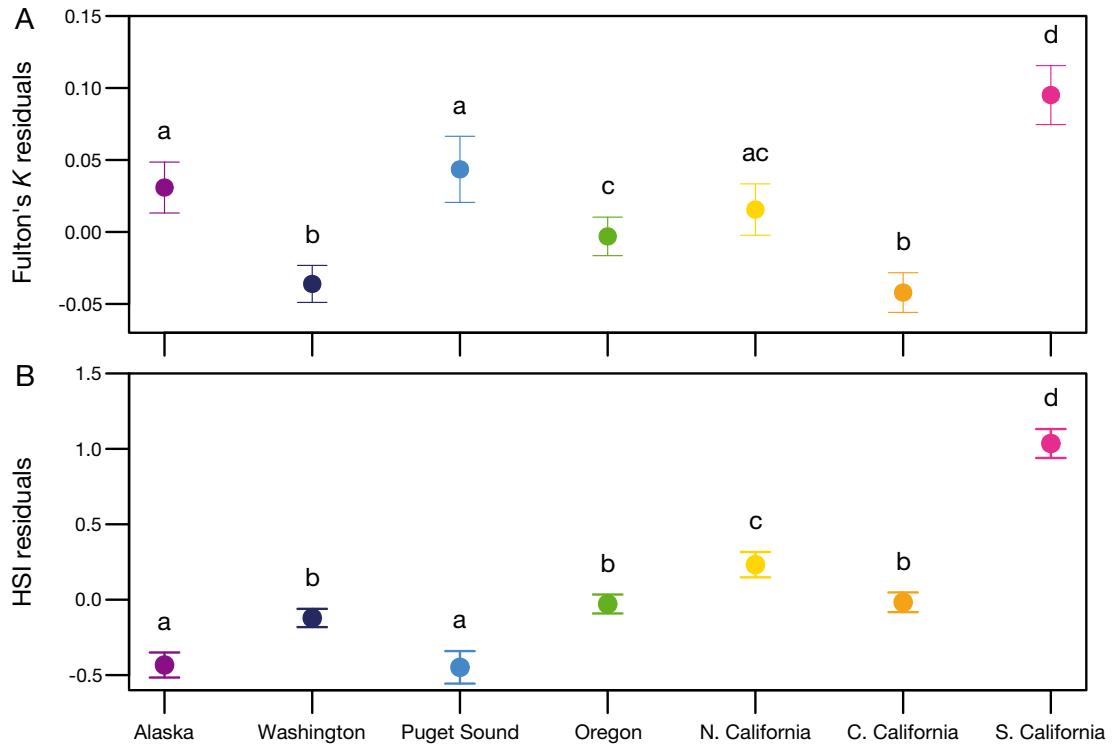


Fig. 5. (A) Fulton's K condition index residuals and (B) hepatosomatic index (HSI) residuals by region with 95 % confidence intervals shown as error bars. Overlapping letters indicate no regional difference in Fulton's K or HSI based on Tukey's HSD pairwise analysis

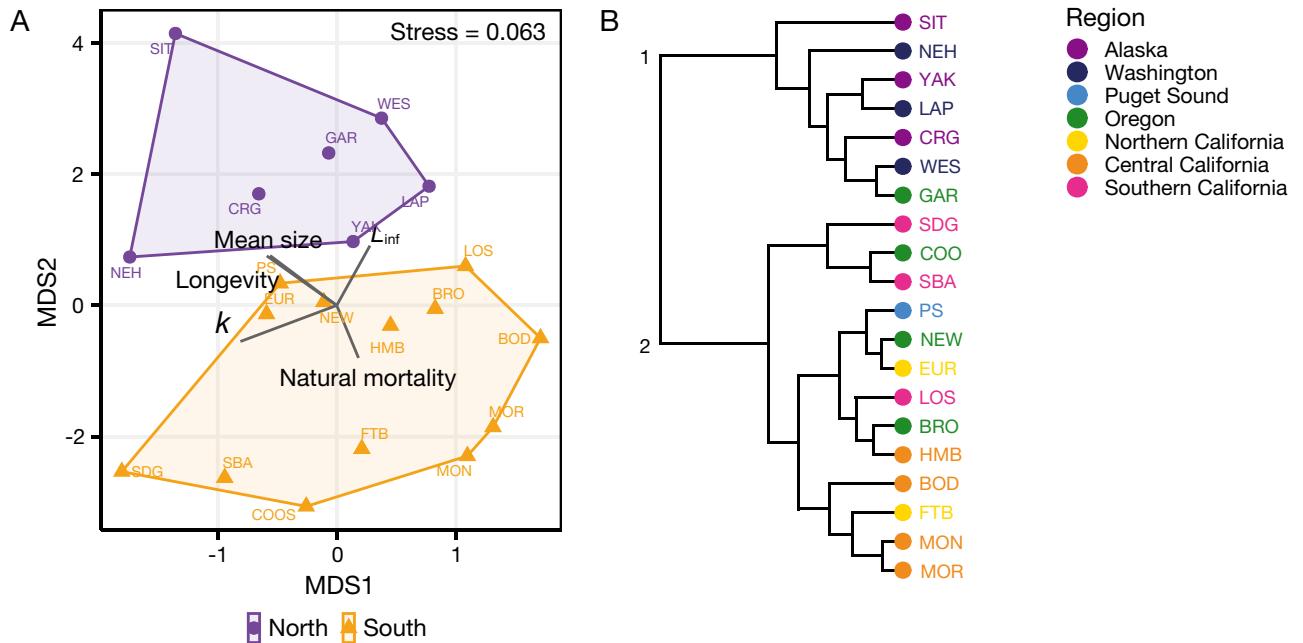


Fig. 6. Spatial variation in coastwide lingcod population as influenced by growth-based life history traits (growth coefficient [k], predicted maximum asymptotic length [L_{inf}], longevity, mean size, and natural mortality). Three-letter port codes correspond to sampled ports, as shown in Fig. 1, and are colored according to region. Note that ports for Puget Sound (PS) were pooled due to small sample size. (A) Non-metric multidimensional scaling (nMDS) plot maps each ports in multivariate space to visualize how clusters were identified based on life history traits, where the direction and magnitude of the life history vectors indicate how influential each trait is in creating the northern and southern clusters. (B) Dendrogram of sampled ports indicates 2 clusters: northern (containing ports from Alaska to central Oregon) and southern (containing ports from central Oregon to southern California)

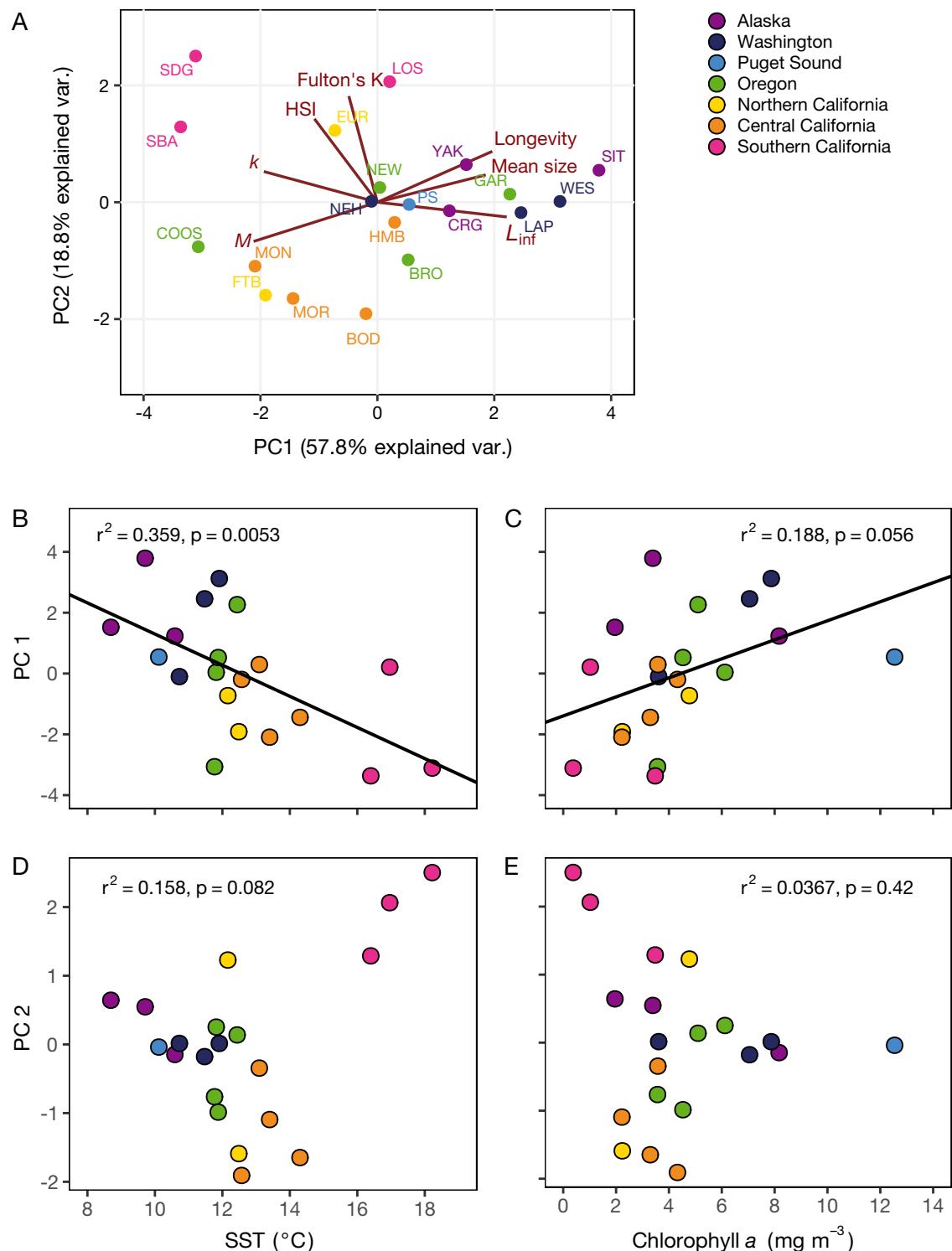


Fig. 7. (A) Principal component analysis was used to determine the spatial association of coastwide lingcod life history traits and to examine the influence of long-term mean oceanographic factors. Each point represents a port and is color-coded by region, with the exception of Puget Sound, which represents all Puget Sound ports pooled due to small sample size per port. Principal components (PC) 1 and 2 together comprise 76% of the variance seen in the data set. PC 1 is an indicator of growth and longevity (T_{\max}) while PC 2 is associated with health, or condition. Linear regression between (B) PC 1 and sea surface temperature (SST), (C) PC 1 and chl a, (D) PC 2 and SST, and (E) PC 2 and chl a. PC 1 is strongly and significantly correlated with SST and chl a; PC 2 also exhibits a slight relationship between SST and chl a, but the trend is not significant.

the variation seen in the port-level life history data (Fig. 7). 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 was driven primarily by factors related to size and growth, where positive values of PC 1 were correlated with L_{inf} , T_{max} , and mean size, and negative values of PC 1 were correlated with k and M . PC 2 accounted for 20.2% of the variation and was composed of condition indices, HSI and Fulton's K , on the positive scale. PC 1 showed a significant negative relationship with mean SST and a significant positive relationship with chl a (Fig. 7A,B), such that lingcod obtain larger sizes, live longer, and experience higher survivorship as temperatures decline and primary productivity increases. PC 2 showed no relationship with SST or chl a (Fig. 7C,D).

4. DISCUSSION

Predictably, biogeographic variability in demography and life history traits in commercially important marine fishes is potentially high where latitudinal environmental gradients are pronounced (Pörtner et al. 2008). Despite the importance of such spatially structured biological variation for increasing the accuracy of stock assessments and the sustainability of fisheries management practices, most exploited species have not been studied with the sufficient spatial and temporal resolution needed to better inform assessments. Here, we closed the information gap on geographic variability in life history and demographic trait variation for lingcod, demonstrating that, in accordance with Bergmann's Rule, individuals from colder, high latitude regions along the US West Coast are generally larger-at-age, grow slower, live longer, and reach maturity at larger sizes than individuals from warmer, low latitude regions. These patterns are mirrored by gradients in SST and ecosystem productivity, suggesting the potential for a causal connection; however, we discuss several external factors likely influencing this outcome. This study adds to a growing body of literature (Keller et al. 2012, 2018, Gertseva et al. 2010, 2017, Kapur et al. 2020) on shelf and slope groundfish species that defy common assumptions about the lack of population structure and uniformity in biological traits over broad spatial scales and underscores the importance of these considerations for generating accurate scientific advice for fisheries management.

Similar coastwide latitudinal trends in size and growth have been reported in shelf (greenstriped rockfish *Sebastodes elongatus*, widow rockfish *S. ento-*

melas), shelf-slope (sablefish *Anoplopoma fimbria*), and slope groundfish species (splitnose rockfish *S. diplopis*, aurora rockfish *S. aurora*, Dover sole *Microstomus pacificus*) (Keller et al. 2012, Gertseva et al. 2017, Kapur et al. 2020). Like lingcod, these species tended to reach larger maximum sizes in northern latitudes, while k mirrored upwelling patterns and was greater near Cape Mendocino, California, the area with the highest levels of primary productivity within the CCS (Checkley & Barth 2009). This peak in k near Cape Mendocino was also seen in growth rates for canary rockfish *S. pinniger*, petrale sole *Eopsetta jordani*, and darkblotched rockfish *S. crameri*, though a latitudinal pattern in L_{inf} did not exist (Gertseva et al. 2017). While it is unlikely that this kind of spatially explicit life history information will be available in the near-term for the >90 species managed formally under the Pacific Fisheries Management Council's Groundfish Fishery Management Plan (PFMC 2019), accumulating evidence suggests that geographic variability in life history and demographic traits may be the rule rather than the exception.

Lingcod are included in the federal nearshore and shelf groundfish complexes and may therefore be influenced by coastal upwelling patterns similarly to other shelf species, though it is evident that lingcod share similarities with deeper dwelling shelf-slope and slope species as well. Lingcod occupy a broad depth range and are at times spatially segregated based on sex and size class, but they can also be relatively more mobile than other demersal rockfish species when foraging and migrating from deeper depths to spawn (Starr et al. 2005, Tolimieri et al. 2009). While male lingcod are generally distributed shallower and move more frequently than females (Starr et al. 2005, Greenley et al. 2016), both sexes exhibited the same coastwide trends in L_{inf} and k . Among the previously studied species, latitudinal trends in lingcod growth are most similar to that of Dover sole (L_{inf} increases at higher latitudes while k generally declines, except in northern California); however, they differ in reproductive behavior, ecology, and spatial distribution. Notably, based on both past findings and our current results, lingcod are a comparatively productive groundfish species in the greenling family, growing faster and maturing at younger ages (2–3 yr) than many other groundfishes, and they invest heavily in reproduction as evidenced by male nest-guarding behavior. Therefore, early life stages are likely sensitive to coastal upwelling patterns that affect early growth rates, while factors like temperature and fishing pressure may have a greater influence on the L_{inf} values we observed.

The effects of fishing on the lingcod population can confound life history results and skew the size distribution of sampled individuals. Lingcod have been commercially and recreationally harvested along the US West Coast since the early 20th Century, with the vast majority (mean of 62.3 % since 2005 and up to 70.8 % since 2014) of US landings (excluding Alaska) taken by the recreational hook-and-line fishery in recent decades (Haltuch et al. 2018). From 2010–2019, the highest recreational lingcod landings in the contiguous US West Coast originated from central California (37.0 %), followed by Oregon (24.9 %), Washington (15.1 %), northern California (14.3 %), and southern California (8.7 %), respectively (PSMFC 2020). As fishing tends to remove large, older individuals from the population, it is likely that lingcod collected from our sampling efforts do not include historically old (and large) individuals that would be found in an unfished population, thereby resulting in reduced estimates of T_{\max} and elevated mortality rates. Calculating M using T_{\max} from a fished population results in values that closely resemble Z rates and an F rate near zero, as seen in some regions in this study (Table 2). While there was still a latitudinal gradient in lingcod M , we can conclude that the absolute value of our M estimates would be different had they been derived from an unfished population.

More generally, it is possible that the geographic differences in growth, age-at-maturity, and condition we observed have been influenced by long-term, regionally distinct histories of exploitation. Fishery removals typically result in truncated populations where individuals are smaller, grow faster, and reach maturity at smaller sizes (Beamish et al. 2006, Conover et al. 2009). However, there is no direct evidence available to make inferences about how regionally specific exploitation histories interact with latitudinal environmental gradients to produce the patterns we observed. Comparisons between the results of the current study and those from past studies are challenged by substantial differences in study locations, collection methods, and ageing methodologies (Table S4). With these caveats in mind, there appears to be some suggestion that lingcod from the current study may grow faster, reach smaller maximum sizes, and mature earlier at smaller sizes than lingcod from previous studies (Table S4), though more directed research is needed. Overall, the trends in life history and distribution from this study continue to show strong evidence that lingcod in northern regions are larger-at-age, live longer, and reach maturity at larger sizes compared to lingcod from southern regions. Lingcod from regions with the highest recreational

take (central California and Oregon) did not deviate from Bergmann's Rule, demonstrating that despite high harvest rates, lingcod life history traits still reflect underlying patterns in temperature and environmental factors. Important regional data gaps in lingcod life history include British Columbia, Canada, and Baja California, Mexico. Both regions experience different oceanographic conditions and fishing pressure than are characteristic of US waters and should be incorporated in future evaluations of latitudinal trends in life history variation.

We observed an exception to Bergmann's Rule in lingcod from Puget Sound, which exhibited a greater growth coefficient and earlier timing at 50 % maturity compared to adjacent regions; however, the inland waters of Puget Sound comprise a unique network of sheltered waterways and inlets and are subject to environmental forcing parameters (e.g. tidal currents, freshwater input, wind effects, and vertical stratification) that influence localized oceanographic properties to a degree that is unseen in waters on the open coast (Strickland 1983, Moore et al. 2008). This, in combination with the history of overfishing in Puget Sound throughout the mid- to late-20th Century, creates discrepancies in life history and demography in conspecifics inhabiting coastal versus enclosed waters. A past study found that quillback rockfish *S. maliger* likewise exhibited higher growth rates and lower L_{\inf} in Puget Sound compared to nearby oceanic waters (West et al. 2014); however, considering the ecological role lingcod play in nearshore ecosystems, it is likely that the interplay among local oceanography, historic fishing practices, and trophic interactions contributes to the large uncertainties associated with Puget Sound lingcod growth and maturity estimates.

4.1. Oceanographic drivers influencing life history variability

It is evident that life history traits related to growth, size, M and T_{\max} were strongly associated with coast-wide oceanographic gradients and were demonstrably more predictable, whereas traits related to lingcod health and condition were spatially and annually variable. Along the US West Coast, nutrient availability in the CCS is reliant upon coastal wind-driven upwelling and horizontal advection from the North Pacific Gyre and is directly correlated with SST (Di Lorenzo et al. 2008). Northern latitudes near southeast Alaska and Washington have the highest average chl a concentrations in the Northeast Pacific,

originating from fresh water input and a steady supply of land-derived nutrients (Ware & Thomson 2005), while the central CCS area between Cape Blanco (southern Oregon) and Point Conception (southern California) is considered the region of maximum upwelling due to strong wind forcing and along-shelf nutrient transport, with a local maximum at Cape Mendocino, northern California (Checkley & Barth 2009). In lower latitudes 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). Size- and growth-related biological parameters are indicative of long-term population characteristics, representing metrics that are integrated over a lifetime, while somatic condition is reflective of current environmental factors and can be more susceptible to localized fluctuations in resource availability and environmental variability.

Our lingcod samples were collected from 2015–2017, overlapping with the greatest anomalous marine heatwave and concurrent El Niño Southern Oscillation (ENSO) event on record (Hu & Fedorov 2019). The effects of the 2015–2016 ENSO were drastically exacerbated by a persistent, anomalous mass of warm water in the Northeast Pacific, a marine heat wave known as 'The Blob' (Bond et al. 2015, Blunden & Arndt 2016) that brought a northward shift in many marine species ranges and coincided with a variety of unusual biological events and species sightings. CCS waters typically dominated by lipid-rich, northern copepod species were replaced by lipid-poor, southern copepod species, changing the composition and nutrient quality within the coastal food web (Peterson et al. 2017). Examination of lingcod gut contents from the southern California region found that 7% of lingcod stomachs contained pelagic red crabs *Pleuroncodes planipes* (B. L. Basnett unpubl. data), a species commonly seen during previous ENSO events (McClatchie 2016). This anomalous pulse of prey resources may be correlated with high body condition of lingcod from southern California, while likewise shifting typical prey availability and nutrient profiles in northern waters, producing northern lingcod in poorer condition. These effects could result in several cohorts of southern California lingcod with faster early growth; however, rapid growth does not necessarily translate into increased survival or productivity later in life, when the effects of the anomalous event have passed. In a study investigating black rockfish *S. melanops* early life history during the Blob years, individuals exhibiting the fastest early growth had decreased survival, possibly due to

the absence of suitable prey required to sustain this period of rapid growth (Fennie 2020). Unlike black rockfish, lingcod are opportunistic predators in near-shore environments and fulfill a unique ecological role and would likely respond differently to marine anomalies. The relationship between predator–prey interactions and patterns in coastal productivity (typical and atypical) remains an important area of inquiry for understanding growth patterns of multiple species; however, this endeavor remains data-limited as baseline information is needed prior to the start of environmental anomalies to truly understand short- and long-term challenges to survival and reproduction.

4.2. Sex-specific drivers influencing life history variability

Reproduction within the Hexagrammid and Cottid families is unique in that the males exhibit nest-guarding behavior during spawning months where they sit on exposed rocky reefs, undergo a period of starvation while embryos develop (Cass et al. 1990), and are left vulnerable to predation and potentially unfavorable oceanographic conditions. In contrast, female lingcod are able to feed throughout the year, potentially magnifying size-specific differences over time. Because parental nest-guarding behavior comes at considerable cost to survival and fitness (Sabat 1994, Balshine-Earn 1995), early maturation, faster growth, and small asymptotic body sizes in male lingcod may have evolved to offset the risk associated with nest-guarding and to maximize reproductive potential (Charnov & Berrigan 1991). However, observed differences between male and female lingcod life history were consistent with sex-specific differences in several other groundfish species as well, nest-guarding and otherwise (Gertseva et al. 2017). Across the majority of fish taxa, females generally have higher lipid and protein content and are in better condition than male conspecifics as it is assumed that females require more energy for egg production and brooding (Breder & Rosen 1966, Parker 1992), though this assumption may not be true for lingcod where male nest-guarding behavior is also energetically costly. We found no differences in somatic condition between sexes per region north of Oregon; however, male lingcod were consistently in better condition throughout all regions south of Oregon. This is likely due to spatial differences in prey availability as preliminary diet analyses revealed that in southern regions, male lingcod consumed a significantly greater

proportion of cephalopods by number and by weight compared to females (B. L. Basnett unpubl. data).

4.3. Management implications

The boundary we identified in central Oregon using size and growth-based life history traits does not align directly with the genetic population break reported by Longo et al. (2020) at Pt. Reyes, near the port of Bodega Bay on the boundary of northern and central California (Fig. 1). This contrast is not uncommon nor unexpected as mechanisms driving genetic differentiation do not necessarily overlap with those influencing variability in growth, T_{\max} , and maturity. Clines in genetic structure arise on evolutionary timescales and result from the non-mutually exclusive processes of random genetic drift, secondary contact between previously isolated populations, and continuous and/or discontinuous environmental conditions (Endler 1977), while spatial differences in life history can be shaped on comparatively short-term decadal scales and are influenced by a variety of external and internal drivers, as previously discussed. Phenotypic plasticity in association with Bergmann's Rule has been observed in the absence of genetic change across a variety of taxa (Husby et al. 2011, Teplitsky et al. 2008), including sablefish (Jasonowicz et al. 2017) and several rockfish species (Sivasundar & Palumbi 2010). While the mechanism behind lingcod genetic differentiation is postulated to be largely driven by differences in environmental conditions (Longo et al. 2020), there is no clear explanation as to why population boundaries based on genetics or life history traits should or should not coincide. A large majority (89.7%) of lingcod samples used by Longo et al. (2020) were supplied from the current study, therefore it can be assumed that there were no discrepancies in sampling distribution or season among studies. Research is ongoing as genetics and life history delineation methods continue to advance, but it is apparent that long-term (on evolutionary timescales) and short-term (decadal timescales) environmental changes can have lasting effects on widely ranging populations (Cope & Punt 2009), effects that can be exacerbated by external factors like fishing and changing climate regimes. Determining appropriate stock breakpoints using multiple data sources can be difficult to reconcile from a management perspective and will likely require increased interagency (state, federal, and tribal) adaptability and collaboration as new methods are discovered or conservation goals shift.

For lingcod, as with many groundfish species, life history variability is often investigated for the purpose of informing the spatial structuring of stock assessment models that more accurately capture the population dynamics of a given stock (Hamilton et al. 2011, Kapur et al. 2020). Unfortunately, regional stock assessment structure often aligns with political boundaries and the historic exploitation patterns within those boundaries when estimating stock health, rather than biologically relevant geographic breakpoints that might better reflect natural population processes (Cope et al. 2016, Haltuch et al. 2018). Several limitations exist in this study, most notably the lack of samples within international waters, effectively truncating the southern range and part of the northernmost range, and the use of *a priori* defined regions and ports to locate biological breakpoints, which contains biogeographic assumptions and biases instead of relying on data-driven analyses or models. However, best practices for parameterizing spatial models are still being explored and require refining and simulation testing across a range of scenarios (Berger et al. 2017, Okamoto et al. 2020). Based on our findings, neither the stock boundary currently used in the lingcod stock assessment (2 stocks, with a break at the California–Oregon border) nor the population genetic structure identified by Longo et al. (2020) (2 stocks, with a break at Pt. Reyes, central California) aligns with the biogeographic breakpoint we identified using life history and demographic traits (central Oregon). We found evidence of 2 regional clusters for the lingcod stock using size- and age-based life history parameters for each sampled port along the coast: a northern and southern cluster, with the break in central Oregon between the ports of Garibaldi and Newport. Although this boundary between the northern and southern clusters is not dramatically different from the current boundary used in stock assessments, it demonstrates the potential for considering alternate, biologically driven breakpoints when managing natural resources, modeling population health, and setting conservation goals.

Utilizing spatially structured stock assessments to guide management decisions can aid in preventing localized depletion and optimizing harvest potential for all groundfishes but particularly species that are, or were previously, overfished. There has always been greater uncertainty and lower productivity surrounding lingcod stock status in California than in Oregon and Washington (Haltuch et al. 2018), and within California, regional recreational fishing habits vary based on season and vessel accessibility. In

particular, lingcod in central and southern California face a greater risk for depth-based localized depletion due to high rates of recreational fishing that disproportionately targets male lingcod in shallow, nearshore habitats; depletion that may be overlooked without spatial guidance. Future modeling work accounting for spatial variability in genetics, historic fishing pressure, and/or life history-based population dynamics could reveal how best to set size regulations, seasonal closures, and catch limits that are sensitive to local harvest practices and reduce the risk of depletion (Waples et al. 2008, Spies & Punt 2015).

In conclusion, this study emphasizes the value of obtaining accurate spatial information for determining stock structure and dynamics for management purposes. Doing so for the >90 species of federally managed groundfish on the US West Coast, let alone all exploited marine fishes, is an unrealistic endeavor. However, species vary widely in allowable attainment and value and can be prioritized accordingly. Over the past several decades, fisheries management has focused on advancing ecosystem-based approaches where multispecies interactions, environmental fluctuations, and community shifts through time and space are considered throughout the decision-making process (Sainsbury et al. 2000, Link 2005, Tam et al. 2017, Link et al. 2020). Applying the approach used in this study to even a small subset of highest-priority groundfish stocks will help to tailor management approaches, including harvest and allocation decisions, to maximize long-term sustainability in an uncertain future.

Acknowledgements. We thank the volunteer anglers and the captains and crew of the following sportfishing vessels: F/V 'Chubasco', F/V 'Tigerfish', F/V 'New Sea Angler', F/V 'Hula Girl', F/V 'Malia Kai', F/V 'D&D', F/V 'Ocean Captain', F/V 'Betty Kay', F/V 'Tidewinds', F/V 'Telstar', F/V 'Samson', F/V 'Superstar', F/V 'Reel Steel', F/V 'Endeavor', F/V 'Stardust', F/V 'Toronado', F/V 'Outer Limits', F/V 'Perseverance', F/V 'Kingfisher', F/V 'Jackpot', F/V 'Sea Raven', F/V 'Fishfull Thinking II', F/V 'The Joker', and F/V 'AllStarFishing'. We thank G. Williams for coordinating lingcod sampling efforts in Puget Sound and Alaska. T. Li, B. Warren, and K. Critchlow provided assistance with field sampling and laboratory sample preparation. We extend a special thanks to R. LeGoff, S. Rosenfield, and J. Topping with the Washington Department of Fish and Wildlife and N. Atkins at the NWFSC Ageing Lab for teaching L.S.L. lingcod ageing methods and providing cross reads. Funding was provided by the NOAA National Marine Fisheries Service Habitat Assessment Improvement Plan and NOAA Cooperative Research Program under grant #NA15-NMF4550353, and the CSU COAST (Council on Ocean Affairs, Science, and Technology) graduate scholarship, International Women's Fishing Association Scholarship, the California State University Monterey Bay Under-

graduate Research Opportunities Center (UROC), Simpkins Family Scholarship, Myers Oceanographic Trust, and Loury Family Marine Science Outreach Scholarship to L.S.L. Additional fiscal assistance was provided by the Pacific States Marine Fisheries Commission. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect the views of the National Oceanic & Atmospheric Administration or the US Department of Commerce.

LITERATURE CITED

- Andrews KS, Nichols KM, Elz A, Tolimieri N and others (2018) Cooperative research sheds light on population structure and listing status of threatened and endangered rockfish species. *Conserv Genet* 19:865–878
- Atkinson D, Sibly RM (1997) Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends Ecol Evol* 12:235–239
- Balshine-Earn S (1995) The costs of parental care in Galilee St Peter's fish, *Sarotherodon galilaeus*. *Anim Behav* 50: 1–7
- Bassett M, Lindholm J, Garza C, Kvitek R, Wilson-Vandenberg D (2018) Lingcod (*Ophiodon elongatus*) habitat associations in California: implications for conservation and management. *Environ Biol Fishes* 101:203–213
- Beamish RJ, Chilton D (1977) Age determination of lingcod (*Ophiodon elongatus*) using dorsal fin rays and scales. *J Fish Res Board Can* 34:1305–1313
- Beamish RJ, McFarlane GA, Benson A (2006) Longevity overfishing. *Prog Oceanogr* 68:289–302
- Beaudreau AH, Essington TE (2011) Use of pelagic prey subsidies by demersal predators in rocky reefs: insight from movement patterns of lingcod. *Mar Biol* 158:471–483
- Berger AM, Goethel DR, Lynch PD (2017) Introduction to 'Space oddity: recent advances incorporating spatial processes in the fishery stock assessment and management interface'. *Can J Fish Aquat Sci* 74:1693–1697
- Bergmann C (1847) Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Größe. *Göttinger Studien* 3: 595–708
- Bevetton RJH (1992) Patterns of reproductive strategy parameters in some marine teleost fishes. *J Fish Biol* 41: 137–160
- Bevetton RJH, Holt SJ (1959) A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In: Wostenholme GW, O'Conner M (eds) *Ciba Foundation colloquia on ageing*, Vol 5: the lifespan of animals. J & A Churchill, London, p 142–180
- Blunden J, Arndt DS (eds) (2016) State of the climate in 2015. *Bull Am Meteorol Soc* 97:S1–S275
- Boehlert GW, Kappelman RF (1980) Variation of growth with latitude in two species of rockfish (*Sebastodes piniger* and *S. diploproa*) from the northeast Pacific Ocean. *Mar Ecol Prog Ser* 3:1–10
- Bolger T, Connolly PL (1989) The selection of suitable indices for the measurement and analysis of fish condition. *J Fish Biol* 34:171–182
- Bond NA, Cronin MF, Freeland H, Mantua N (2015) Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophys Res Lett* 42:3414–3420
- Breder CM, Rosen DE (1966) Modes of reproduction in fishes. American Museum of Natural History, Natural History Press, Garden City, NY

➤ Cass AJ, Beamish RJ (1983) First evidence of validity of the fin-ray method of age determination for marine fishes. *N Am J Fish Manage* 3:182–188

Cass AJ, Beamish RJ, McFarlane GA (1990) Lingcod (*Ophiodon elongatus*). *Can Spec Publ Fish Aquat Sci* 109:1–40

➤ Chapman D, Robson DS (1960) The analysis of a catch curve. *Biometrics* 16:354–368

➤ Charnov EL, Berrigan D (1991) Evolution of life history parameters in animals with indeterminate growth, particularly fish. *Evol Ecol* 5:63–68

➤ Checkley DM Jr, Barth JA (2009) Patterns and processes in the California Current System. *Prog Oceanogr* 83:49–64

Chilton DE, Beamish RJ (1982) Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. *Publ Spec Can Sci Halieut Aquat* 60:34–38

Choat JH, Robertson DR (2002) Age-based studies. In: Sale PF (ed) *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, CA, p 57–80

➤ Conover DO, Present TM (1990) Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia* 83:316–324

➤ Conover DO, Munch SB, Arnott SA (2009) Reversal of evolutionary downsizing caused by selective harvest of large fish. *Proc R Soc B* 276:2015–2020

➤ Cope JM (2017) The natural mortality estimator. The Barefoot Ecologists Toolbox. http://barefootecologist.com.au/shiny_m

➤ Cope JM, Punt AE (2009) Drawing the lines: resolving fishery management units with simple fisheries data. *Can J Fish Aquat Sci* 66:1256–1273

➤ Cope JM, Punt AE (2011) Reconciling stock assessment and management scales under conditions of spatially varying catch histories. *Fish Res* 107:22–38

Cope JM, Sampson D, Stephens A, Key M and others (2016) Assessments of California, Oregon, and Washington stocks of black rockfish (*Sebastodes melanops*) in 2015. Pacific Fishery Management Council, Portland, OR

➤ Cudaback CN, Washburn L, Dever E (2005) Subtidal inner-shelf circulation near Point Conception, California. *J Geophys Res C Oceans* 110:C10007

➤ Di Lorenzo E, Schneider N, Cobb KM, Franks PJS and others (2008) North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophys Res Lett* 35: L08607

Endler JA (1977) Geographic variation, speciation, and clines. *Monographs in Population Biology* No. 10. Princeton University Press, Princeton, NJ

Everitt BS, Landau S, Leese M (2001) Cluster analysis, 4th edn. Arnold, London

Fennie HW (2020) Grow fast or die young: influence of ocean conditions and larval growth on patterns of selective mortality and settlement variability of rockfishes. PhD thesis, Oregon State University, Corvallis, OR

Fulton TW (1902) Rate of growth of sea fishes. Neill & Company, Edinburgh

➤ Gertseva VV, Cope JM, Matson SE (2010) Growth variability in the splitnose rockfish *Sebastodes diploproa* of the northeast Pacific Ocean: pattern revisited. *Mar Ecol Prog Ser* 413:125–136

➤ Gertseva V, Matson SE, Cope J (2017) Spatial growth variability in marine fish: example from Northeast Pacific groundfish. *ICES J Mar Sci* 74:1602–1613

Girden ER (2001) Evaluating research articles from start to finish. Sage Publications, Thousand Oaks, CA

Greenley AP, Green K, Starr RM (2016) Season and ontogenetic movements of lingcod (*Ophiodon elongatus*) in Central California, with implications for marine protected area management. *CCOFI Rep* 57:71–88

Haltuch MA, Wallace J, Akselrud CA, Nowlis J and others (2018) 2017 Lingcod stock assessment. Pacific Fishery Management Council, Portland, OR

Hamel OS, Sethi SA, Wadsworth TF (2009) Status and future prospects for lingcod in waters off Washington, Oregon, and California as assessed in 2009. Pacific Fishery Management Council, Portland, OR

➤ Hamilton SL, Wilson JR, Ben-Horin T, Caselle JE (2011) Utilizing spatial demographic and life history variation to optimize sustainable yield of a temperate sex-changing fish. *PLOS ONE* 6:e24580

➤ Hixon MA, Johnson DW, Sogard SM (2014) BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES J Mar Sci* 71:2171–2185

➤ Htun-Han M (1978) The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: gonosomatic index, hepatosomatic index and condition factor. *J Fish Biol* 13:369–378

➤ Hu S, Fedorov AV (2019) The extreme El Niño of 2015–2016: the role of westerly and easterly wind bursts, and preconditioning by the failed 2014 event. *Clim Dyn* 52:7339–7357

Huntington BE, Watson J, Matteson K, McIntosh N and others (2014) Oregon marine reserves ecological monitoring report 2010–11. Oregon Department of Fish and Wildlife, Marine Resources Program, Newport, OR

➤ Husby A, Hille SM, Visser ME (2011) Testing mechanisms of Bergmann's Rule: phenotypic decline but no genetic change in body size in three passerine bird populations. *Am Nat* 178:202–213

➤ Jagielo TH (1999) Movement, mortality, and size selectivity of sport-and trawl-caught lingcod off Washington. *Trans Am Fish Soc* 128:31–48

➤ Jasonowicz AJ, Goetz FW, Goetz GW, Nichols KM (2017) Love the one you're with: genomic evidence of panmixia in the sablefish (*Anoplopoma fimbria*). *Can J Fish Aquat Sci* 74:377–387

➤ Kapur M, Haltuch M, Connors B, Rogers L and others (2020) Oceanographic features delineate growth zonation in Northeast Pacific sablefish. *Fish Res* 222:105414

➤ Keller AA, Molton KJ, Hicks AC, Haltuch M, Wetzel C (2012) Variation in age and growth of greenstriped rockfish (*Sebastodes elongatus*) along the US west coast (Washington to California). *Fish Res* 119–120:80–88

➤ Keller AA, Frey PH, Wallace JR, Head MA, Wetzel CR, Cope JM, Harms JH (2018) Canary rockfishes *Sebastodes piniger* return from the brink: catch, distribution and life history along the US west coast (Washington to California). *Mar Ecol Prog Ser* 599:181–200

Kimura DK (1980) Likelihood methods for the von Bertalanffy growth curve. *Fish Bull* 77:765–776

Laidig TE (2010) Influence of ocean conditions on the timing of early life history events for blue rockfish (*Sebastodes mystinus*) off California. *Fish Bull* 108:442–449

➤ Link JS (2005) Translating ecosystem indicators into decision criteria. *ICES J Mar Sci* 62:569–576

➤ Link JS, Huse G, Gaichas S, Marshak AR (2020) Changing how we approach fisheries: a first attempt at an operational framework for ecosystem approaches to fisheries management. *Fish Fish* 21:393–434

➤ Longo GC, Lam L, Basnett B, Samhouri J and others (2020) Strong population differentiation in lingcod (*Ophiodon elongatus*) is driven by a small portion of the genome. *Evol Appl* 13:2536–2554

Love MS, Yoklavich M, Thorsteinson LK (2002) The rockfishes of the northeast Pacific. University of California Press, Berkeley, CA

Low CJ, Beamish RJ (1978) A study of the nesting behavior of lingcod (*Ophiodon elongatus*) in the Strait of Georgia, British Columbia. Technical Report No. 843. Fisheries and Marine Service, Nanaimo, BC

➤ Marko PB, Rogers-Bennett L, Dennis AB (2007) MtDNA population structure and gene flow in lingcod (*Ophiodon elongatus*): limited connectivity despite long-lived pelagic larvae. *Mar Biol* 150:1301–1311

➤ Maunder MN, Piner KR (2015) Contemporary fisheries stock assessment: many issues still remain. *ICES J Mar Sci* 72: 7–18

McClatchie S (2016) State of the California Current 2015–16: comparisons with the 1997–98 El Niño. *CCOFI Rep* 57: 1–57

Miller DJ, Geibel JJ (1973) Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. *Fish Bull* 158:1–137

Miller DJ, Lea RN (1972) Guide to the coastal marine fishes of California. *Fish Bull* 157:1–249

➤ Moore SK, Mantua NJ, Kellogg JP, Newton JA (2008) Local and large-scale climate forcing of Puget Sound oceanographic properties on seasonal to interdecadal timescales. *Limnol Oceanogr* 53:1746–1758

➤ Munch SB, Salinas S (2009) Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. *Proc Natl Acad Sci USA* 106:13860–13864

National Marine Fisheries Service (2018) Fisheries economics of the United States, 2016. NOAA Tech Memo NMFS-F-SPO-187

➤ Okamoto DK, Hessing-Lewis M, Samhouri JF, Shelton AO, Stier A, Levin PS, Salomon AK (2020) Spatial variation in exploited metapopulations obscures risk of collapse. *Ecol Appl* 30:e02051

Pacific Fisheries Management Council (2019) Status of the Pacific coast groundfish fishery: stock assessment and fishery evaluation. Pacific Fishery Management Council, Portland, OR

➤ Pacific States Marine Fisheries Commission (2020) Recreational fisheries information network. <https://www.recfi.org> (accessed 9 Sept 2020)

➤ Parker GA (1992) The evolution of sexual size dimorphism in fish. *J Fish Biol* 41:1–20

➤ Peterson WT, Fisher JL, Strub PT, Du X, Risien C, Peterson J, Shaw CT (2017) The pelagic ecosystem in the Northern California Current off Oregon during the 2014–2016 warm anomalies within the context of the past 20 years. *J Geophys Res Oceans* 122:7267–7290

➤ Petrie ME, Ryer CH (2006) Hunger, light level and body size affect refuge use by post-settlement lingcod *Ophiodon elongatus*. *J Fish Biol* 69:957–969

➤ Pörtner HO, Bock C, Knust R, Lannig G, Lucassen M, Mark FC, Sartoris FJ (2008) Cod and climate in a latitudinal cline: physiological analyses of climate effects in marine fishes. *Clim Res* 37:253–270

➤ Ray C (1960) The application of Bergmann's and Allen's rules to the poikilotherms. *J Morphol* 106:85–108

Rencher AC (2002) Methods of multivariate analysis, 2nd edn. John Wiley & Sons, New York, NY

Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. *Bull Fish Res Board Can* 191:1–382

➤ Ricker WE (1981) Changes in the average size and average age of Pacific salmon. *Can J Fish Aquat Sci* 38:1636–1656

➤ Robertson DR, Ackerman JL, Choat JH, Posada JM, Pitt J (2005a) Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. *Mar Ecol Prog Ser* 295: 229–244

➤ Robertson DR, Choat JH, Posada JM, Pitt J, Ackerman JL (2005b) Ocean surgeonfish *Acanthurus bahianus*. II. Fishing effects on longevity, size and abundance? *Mar Ecol Prog Ser* 295:245–256

➤ Robson DS, Chapman DG (1961) Catch curves and mortality rates. *Trans Am Fish Soc* 90:181–189

Rooper CN (2008) An ecological analysis of rockfish (*Sebastodes* spp.) assemblages in the North Pacific Ocean along broad-scale environmental gradients. *Fish Bull* 106:1–11

➤ Sabat AM (1994) Costs and benefits of parental effort in a brood-guarding fish (*Ambloplites rupestris*, Centrarchidae). *Behav Ecol* 5:195–201

➤ Sainsbury KJ, Punt AE, Smith AD (2000) Design of operational management strategies for achieving fishery ecosystem objectives. *ICES J Mar Sci* 57:731–741

Silberberg KR, Laidig TE, Adams PB (2001) Analysis of maturity in lingcod (*Ophiodon elongatus*). *Calif Fish Game* 87:139–152

➤ Sivasundar A, Palumbi SR (2010) Life history, ecology and the biogeography of strong genetic breaks among 15 species of Pacific rockfish, *Sebastodes*. *Mar Biol* 157: 1433–1452

➤ Smith MW, Then AY, Wor C, Ralph G, Pollock KH, Hoenig JM (2012) Recommendations for catch-curve analysis. *N Am J Fish Manage* 32:956–967

➤ Spies I, Punt AE (2015) The utility of genetics in marine fisheries management: a simulation study based on Pacific cod off Alaska. *Can J Fish Aquat Sci* 72:1415–1432

➤ Starr RM, 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. *Mar Technol Soc J* 39:19–30

Strickland RM (1983) The fertile fjord: plankton in Puget Sound. University of Washington Press, Seattle, WA

➤ Tam JC, Link JS, Rossberg AG, Rogers SI and others (2017) Towards ecosystem-based management: identifying operational food-web indicators for marine ecosystems. *ICES J Mar Sci* 74:2040–2052

➤ Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merilä J (2008) Bergmann's Rule and climate change revisited: disentangling environmental and genetic responses in a wild bird population. *Proc Natl Acad Sci USA* 105: 13492–13496

➤ Tolimieri N, Andrews K, Williams G, Katz S, Levin PS (2009) Home range size and patterns of space use by lingcod, copper rockfish and quillback rockfish in relation to diel and tidal cycles. *Mar Ecol Prog Ser* 380:229–243

➤ Waples RS, Punt AE, Cope JM (2008) Integrating genetic data into management of marine resources: How can we do it better? *Fish Fish* 9:423–449

➤ Ware DM, Thomson RE (2005) Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science* 308:1280–1284

Wendt DE, Starr RM (2009) Collaborative research: an effective way to collect data for stock assessments and evaluate marine protected areas in California. *Mar Coast Fish* 1:315–324

West JE, Helser TE, O'Neill SM (2014) Variation in quillback rockfish (*Sebastodes maliger*) growth patterns from oceanic to inland waters of the Salish Sea. *Bull Mar Sci* 90: 747–761

Wilby GV (1937) The ling cod, *Ophiodon elongatus* Girard. *Bull Fish Res Board Can* 54:1–24

Wilson JR, Broitman BR, Caselle JE, Wendt DE (2008) Recruitment of coastal fishes and oceanographic variability in central California. *Estuar Coast Shelf Sci* 79:483–490

Wilson JR, Kay MC, Colgate J, Qi R, Lenihan HS (2012) Small-scale spatial variation in population dynamics and fishermen response in a coastal marine fishery. *PLOS ONE* 7:e52837

Worm B, Lotze HK, Hillebrand H, Sommer U (2002) Consumer versus resource control of species diversity and ecosystem functioning. *Nature* 417:848–851

Editorial responsibility: Konstantinos Stergiou,
Thessaloniki, Greece
Reviewed by: 3 anonymous referees

Submitted: November 17, 2020

Accepted: May 6, 2021

Proofs received from author(s): July 5, 2021