



# Evaluating drivers of spatial variability in lingcod, *Ophiodon elongatus*, reproduction along the US West Coast

Melissa A. Head · Aimee A. Keller ·  
Laurel S. Lam

Received: 23 May 2023 / Accepted: 1 December 2023

This is a U.S. Government work and not under copyright protection in the US; foreign copyright protection may apply 2023

**Abstract** Examining variation in reproduction (estimates of maturity and adult skip spawning) over time and space provides vital information on stock structure for managing coast-wide species; however, it is equally important to identify the drivers of variability, i.e., fishing pressure, genetics, and oceanographic conditions. The 2021 lingcod, *Ophiodon elongatus*, stock assessments used separate population models, north and south of 40°10' N, based on evidence of distinct population clusters and historical fishery trends. We collected 1035 lingcod ovaries along the US West Coast over seven years (2013–2019) to evaluate trends in reproduction and inform stock management decisions. We estimated biological (physiological maturity) and functional (potential spawners) length ( $L_{50}$ ) and age ( $A_{50}$ ) at 50% maturity across eight regions: coast-wide, between management areas (north and south of 40°10' N), genetic stocks (north

and south of 38°17' N), and among important biogeographic regions including Cape Mendocino, California (north of 40°10' N), the Central coast (40°10'–34°26' N), and Pt. Conception, California (south of 34°26' N). Regional biological  $L_{50}$  and  $A_{50}$  maturity estimates (43.36–52.75 cm and 1.66–2.88 years) were smaller than functional maturity (46.31–56.65 cm and 1.89–3.23 years). Overall, regional analyses showed a decline in size and age at 50% maturity with decreasing latitude, with females south of Pt. Conception reaching maturity at much smaller sizes and younger ages than their northern counterparts. These regional estimates of maturity add to the growing body of literature that seeks to determine the best spatial management plan for lingcod sub-populations.

**Keywords** Groundfish · Reproductive biology · Sustainable fisheries management · *Ophiodon elongatus* · Maturity · Skip spawning

---

M. A. Head (✉) · A. A. Keller  
Fishery Resource Analysis and Monitoring Division,  
Northwest Fisheries Science Center, National Marine  
Fisheries Service, National Oceanic and Atmospheric  
Administration, 2725 Montlake Blvd East, Seattle,  
WA 98112, USA  
e-mail: melissa.head@noaa.gov

L. S. Lam  
Pacific States Marine Fisheries Commission,  
Northwest Fisheries Science Center, National Marine  
Fisheries Service, National Oceanic and Atmospheric  
Administration, 2725 Montlake Blvd East, Seattle,  
WA 98112, USA

## Introduction

Sustainable fisheries management along the US West Coast relies on long-term monitoring of species abundance and trends, genetic population structure, as well as biological data collection, i.e., length, weight, age, reproductive capability, and diet information. Fisheries managers use population dynamic models that incorporate these data to estimate population abundance and set harvest limits for spatially explicit

management units that are determined by a multitude of factors, such as genetics, depth, oceanographic conditions, and historic fishing pressure. Growth and reproductive parameters essential to management models, such as length and/or age at maturity and rate of skip spawning (sexually mature adults who forego spawning), are imperative in estimating spawning stock biomass and implementing minimum size restrictions. These parameters change over space and time (Head et al. 2014; Jørgensen 1990; McBride et al. 2013; Sharpe and Hendry 2009); thus, there is a need to advance the study of reproductive biology by tracking spatio-temporal changes in maturity schedules and skip spawning (mature adults failing to spawn), identifying the drivers of variability in spawning, and developing methods that capture these features when modeling spawning output.

Life history strategies of marine fishes may vary spatially and temporally as a result of differing environmental conditions, fishing intensity, and stock structure (Gertseva et al. 2017; Keller et al. 2012; Rose et al. 2001; Sharpe and Hendry 2009). This is especially true for groundfish species in the northeast Pacific that occupy broad latitudinal ranges, e.g., greenstriped rockfish, sablefish, splitnose rockfish, aurora rockfish (Gertseva et al. 2017; Head et al. 2014; Head et al. 2020; Keller et al. 2012). Spatial variability in growth and maturity may be correlated to geographic landmarks along the US West Coast (i.e., Cape Blanco, Cape Mendocino, Pt. Conception) where physical features, the California Current System and seasonal upwelling and downwelling can create oceanographically distinct regions (Cope 2004; Head et al. 2014; Keller et al. 2012). Specifically, the geography and oceanography south of Pt. Conception leads to weaker seasonal upwelling, lower productivity, smaller growth coefficients and sizes at maturity for a variety of groundfish species (Gertseva et al. 2010; Gertseva et al. 2017; Head et al. 2014; Head et al. 2020; Keller et al. 2012; Lam et al. 2021). Furthermore, oceanographic conditions can vary from year to year and throughout the year. Thus, identifying temporal relationships in reproduction can help link biological changes to oceanographic regimes and increase managers ability to forecast trends in spawning output for a given year (Lowerre-Barbieri et al. 2011).

In addition to understanding the spatial-temporal relationships between the environment and biological

processes, it is also essential to evaluate the influence of stock structure on life history variability. The discovery of genetically distinct sub-populations in several West Coast groundfish species has highlighted the need to re-evaluate the biology and spatial distribution for these sub-stocks separately (Cope 2004; Hyde et al. 2008; Keller et al. 2022); failing to do so can result in management decisions that ensure the sustainability of one subpopulation while potentially neglecting to protect the other. Accounting for variability in recruitment, growth, and spawning biomass between genetically distinct stocks is vital to fisheries managers as they determine how best to assess spatially structured populations, set appropriate harvest limits, and ensure sustainable fisheries management (Cope 2004). Over time, as management measures become more intricate and spatially explicit data becomes increasingly available, there is an effort to incorporate and manage coast-wide populations in accordance with biological and genetic differences.

The groundfish fishery along the US West Coast is comprised of over 90 species of economic importance. Among them, few have been studied as extensively as lingcod, an ecologically important species that is commercially and recreationally harvested coast-wide. Lingcod, *Ophiodon elongatus*, a member of the greenling family, occur in the northeast Pacific Ocean from the Gulf of Alaska to Baja, Mexico (Hart 1973) in waters 3–400 m in depth but are generally found between 10 and 100 m (Cass et al. 1990). They have limited home ranges (<8 km) (Starr et al. 2005) and are opportunistic top predators, feeding on species of ecological importance, such as herring, juvenile rockfish, Pacific hake, and flatfish, and thus are defined as an important ecosystem species (Beaudreau and Essington 2007; Miller and Geibel 1973).

As with many other marine fishes, lingcod are sexually dimorphic with females growing faster and attaining larger sizes (up to 120 cm) than males (up to 80 cm). Previous studies have consistently found that females reach maturity at larger sizes and older ages than males (Cass et al. 1990; Miller and Geibel 1973) though these studies are outdated and/or spatially limited. Females are batch spawners, releasing several discrete batches over a prolonged spawning season. Batch spawning species are characterized by having asynchronous oocyte development, often with several developmental stages present (Brown-Peterson et al. 2011).

Lingcod have a unique spawning strategy, with males playing a significant role in survival of young (Crow et al. 1997). During spawning season (October–March), males arrive at spawning sites first to select optimal nesting sites (rocky outcroppings in high current areas) before the arrival of females. Females migrate to shallow rocky reef habitats (10–40 m) to spawn from December through March (Jagiello et al. 1996; Tolimieri et al. 2009). Once females have released all batches of eggs, they migrate back to deeper depths, leaving males to guard the nests for 6–8 weeks until they hatch (Low and Beamish 1978; Withler et al. 2004). Males tend to return to the same nesting sites year after year, while females have low nesting site fidelity (King and Withler 2005). These behavioral factors unique to lingcod (e.g., limited movements, nesting site fidelity, and spawning in shallow waters) may contribute to the population stock structure recently confirmed in the 2021 lingcod stock assessment, providing additional evidence for the need to investigate reproductive output and maturity schedules more thoroughly.

Lingcod are among the few groundfish species that are assessed based on genetic population structure. In the 2021 lingcod stock assessment (Johnson et al. 2021; Taylor et al. 2021), the coast-wide population was divided into two management units based on updated genetic (Longo et al. 2020) and biological information (Lam et al. 2021) both of which were inextricably linked to latitude and biogeographic features. Two distinct genetic clusters in the West Coast population were identified, north and south of 38°17' N, corresponding to a biogeographic landmark at Point Reyes, California (CA) (Longo et al. 2020). Additionally, lingcod were found to exhibit a latitudinal gradient in growth, maturity, and longevity that was significantly linked to sea surface temperature and productivity, where lingcod in the northern extent of their range grew faster, lived longer and matured at larger sizes than their southern counterparts (Lam et al. 2021). Findings from these two studies, along with historic fishery landings information, were instrumental in determining the most recent management stock boundary, north and south of 40°10' N (Cape Mendocino, California) used in the 2021 US West Coast northern and southern lingcod stock assessments (Johnson et al. 2021; Taylor et al. 2021).

Variation in lingcod life history has been extensively researched in the past; however, these studies

are often outdated, regionally constrained, or both (Cass et al. 1990; Miller and Geibel 1973; Richards et al. 1990). While size and age of maturity was estimated spatially in the Lam et al. (2021) study, this was done using macroscopic evaluation which can be limiting and lead to an underestimation of size and age at maturity. Histological analysis provides a higher level of certainty in maturity determinations and can accurately estimate rates of adult skip spawning, atresia (cellular breakdown and reabsorption of oocytes), and when juveniles abort spawning and reabsorb maturing oocytes (abortive maturation) (Head et al. 2020; Min et al. 2022). Accurate maturity schedules that reflect newly defined stock structure are vital to sustainable fisheries management, especially for lingcod as they have been subject to overfishing previously (Haltuch et al. 2018).

In this study, we use histological analysis of gonad tissues to examine how spatial variability in reproduction relates to genetic and management boundaries to better inform future management decisions. Specifically, we evaluated size and age at maturity across several regions of interest: (1) coast-wide, (2) north and south of Point Reyes (38°17' N, genetic break point), (3) north and south of Cape Mendocino (40°10' N, management regions), and (4) the Central coast (40°10'–34°26' N), north and south of Pt. Conception to the Mexico border (34°26'–32°00' N). We also examined spatial trends in the annual reproductive cycle, skip spawning, and timing and location of spawning within these regional groupings to determine if other trends in lingcod reproduction are present. Overall, this study provides valuable information to fisheries managers as they seek to ensure sustainable fishing practices.

## Methods

### Sampling methodology

#### *West Coast Groundfish Bottom Trawl—survey design, field collections*

The Northwest Fisheries Science Center (NWFS) conducts an annual West Coast Groundfish Bottom Trawl (WCGBT) survey to obtain fisheries-independent data on 90+ Fishery Management Plan (FMP) species, including lingcod, along with environmental

data and data on numerous other species that are not part of the FMP, to manage and monitor trends in groundfish stocks. The survey utilizes four chartered West Coast trawl fishing vessels using a random depth-stratified sampling design of ~750 sites each year. The survey conducts two passes along the coast: mid-May–late July (pass 1) and mid-August–late October (pass 2) from the USA/Canada to the USA/Mexico borders (48°10′–32°30′N) at depths of 55 to 1280 m (Bradburn et al. 2011; Keller et al. 2017).

After completion of a successful tow, all invertebrates and vertebrates are sorted and weighed using a motion compensated scale (Marel, Reykjavik, Iceland). A subsample of up to 100 lingcod are randomly selected for sex determination, fork length (FL,  $\pm 0.5$ cm), and weight ( $\pm 0.01$ kg). Up to five individuals from this subsample are randomly selected for fin ray extraction for age determination. Fin rays collected by all sampling platforms were analyzed for age determination following methods adapted by the NWFSC's Cooperative Aging Laboratory from Chilton and Beamish (1982), which have high level of accuracy and low reader bias (Beamish and Chilton 1977; Taylor et al. 2021). Ovaries were collected from a subsample of female lingcod selected for ageing using a stratified sampling method based on length bins to prevent over or under sampling of size ranges. Ovaries were stored in individual cloth bags and placed in 10% neutral buffered formalin.

#### *Hook and line—survey design, field collections*

In addition to the fisheries independent trawl survey, the annual NWFSC Southern California Bight shelf rockfish hook and line (H&L) survey monitors groundfishes over untrawlable habitats from Point Arguello (~34°30′ N) to the USA/Mexico border (~32°00′ N) using rod and reel fishing gear (Harms et al. 2010). Sampling occurs in late September through early October aboard three chartered commercial passenger fishing vessels. The H&L survey has annually sampled 121 reefs and hard-bottom habitat sites deemed important to groundfishes since 2004, and was expanded to include sites within the Cowcod Conservation Areas (an additional 75 sites) in 2014 (Keller et al. 2019). At each site, three deckhands conducted five drops using rod and reel gear with a five hook gangion consisting of shrimp flies baited with squid (Keller et al. 2019). A maximum

of 75 fish could be sampled at each site, if all hooks and drops were full. All captured fish are identified, counted, sexed, measured (FL,  $\pm 0.5$ cm), and weighed ( $\pm 0.01$ kg) using the same instruments as the WCGBT survey. A subsample of FMP groundfish species were sampled for age information based on fisheries management needs. In 2014, ovaries were collected opportunistically from female lingcod as part of a pilot project. Then from 2016 to 2019 ovaries were collected from all females when possible. Starting in 2017, fin rays were extracted from these fish, and frozen on board for age determination. Ovaries were stored in individual cloth bags in 10% neutral buffered formalin.

#### *Oregon and Washington Department of Fish and Wildlife—field collections*

Lingcod ovarian tissue samples were collected through the Commercial Finfish Sampling Program by the Oregon Department of Fish and Wildlife (ODFW) (2014–2018) and the Washington Department of Fish and Wildlife (WDFW) (2016–2019). As this sampling relies on commercial landings, the number of samples varied seasonally. Random samples of up to 30 lingcod per landing were measured (to the nearest centimeter), weighed (to the nearest tenth of a pound), and sexed. Vessel logbook and port sampler data were provided for each sample taken, including area fished, vessel, port sampled, date of collection, individual fish data (length, weight, and sex), fish ticket number, and port sampler. Occasionally depth information was also available for individual samples.

#### *Histological analysis*

Ovarian tissue samples collected from lingcod were embedded in paraffin, thin sectioned to 4- $\mu$ m, mounted on slides, and stained with hematoxylin and eosin (Sheehan and Hrapchak 1980). We examined ovaries using a Leica DM1000 binocular microscope at  $\times 40$ – $\times 400$  magnification with a Leica DFC295 camera and imaging software (Leica Microsystem LAS EX 4.4). We histologically determined the maturity of ovaries based on a guide we specifically developed for lingcod (Table 1, Fig. 1), similar to methods outlined for other batch spawning species (Brown-Peterson et al. 2011). We recorded the

**Table 1** Maturity stages with abbreviations (1 to 8), key histological descriptions and corresponding developmental phases (1 to 12) for female lingcod, *Ophiodon elongatus*

Maturity stage	Histological description	Developmental phase
Stage 1: Immature (IM)	Oocytes small with a large nucleolus. Nucleoli begin to develop around the periphery of the nucleus.	Early perinucleus, 1
Stage 1: Immature (IM)	Larger rounder oocytes, with numerous nucleoli that move within the nucleus.	Late perinucleus, 2
Stage 2: Developing (DEV)	Follicle wall thickens and contains granulosa cells. Oil droplets and cortical vesicles form in the cytoplasm and appear white. Nucleus staining is pink and cytoplasm is dark purple.	Oil droplet formation, 3
Stage 3: Early vitellogenesis (EV)	Cortical vesicles increase along the periphery of the cytoplasm alongside yolk granules. Granules transition to globules and occupy < 25% of the cytoplasm.	Initial yolk formation, 4.1
Stage 3: Early vitellogenesis (EV)	Yolk granules continue to coalesce into globules and increase in size, occupying 25–50% of the cytoplasm.	Yolk accumulation, 4.2
Stage 4: Late vitellogenesis (LV)	Large oocytes with > 50% of cytoplasm area occupied by yolk globules. Yolk globules and oil continue to merge. Zona radiata begins to thicken.	Late vitellogenesis, 5
Stage 4: Migratory nucleus (MN)	Nuclear membrane dissolves and nuclear material is not centrally located. Yolk platelets begin to form from yolk globules. Oil droplets and yolk fuse. Zona radiata thick.	Migratory nucleus, 6
Stage 5: Hydration (HYD)	Yolk globules coalesce forming dark pink stained yolk masses.	Early hydration, 7
S Stage 5: Hydration (HYD)	Yolk coalesces into a central mass in the cell; Zona radiata very thick. Close to spawning release.	Late hydration, 8
Stage 6: Spawning (SPAWN)	Fully coalesced yolk, eggs release from zone radiata. Overlap of stage 9 and post ovulatory follicles (POFs) possible. Spawning was occurring at the time of capture.	Fully formed, 9
Stage 6: Batch spent (SPAWN)	Presence of POFs and possibly residual stage 9s from recent batch spawning event. Presence of another mature batch progressing toward spawning. Spawning not completed for the season.	Batch spent, 10
Stage 7: Spent (SPENT)	POFs present and that may be in the resorption process. Residual stage 9s may be present, along with atretic material. Immature and developing oocytes present as well, and possibly EV1 and EV2 oocytes.	Spent, 11
Stage 8: Skip spawner (SKIP)	Mass atresia indicated by >25% of oocytes in atresia. No indicators of earlier spawn event including POFs and residual stage 9s.	Skip spawning, 12

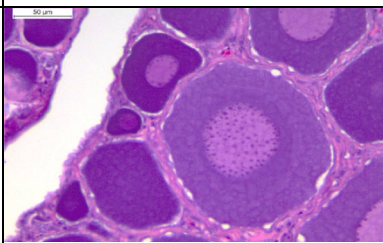
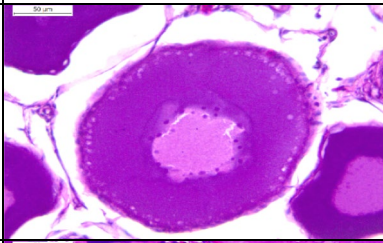
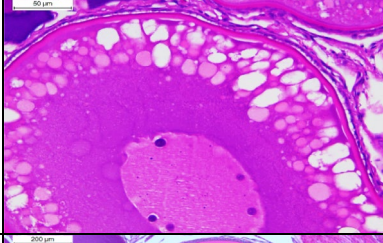
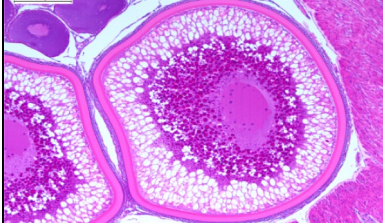
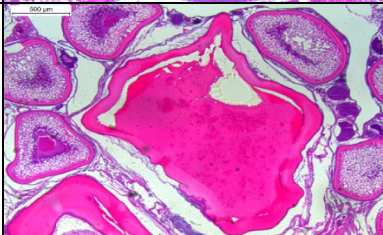
presence/absence of twelve oocyte developmental phases, which corresponded to eight maturity stages (Table 1). Two developmental phases were used to describe post-spawning events: batch spent and spent. Batch spent stage indicated that a recent batch spawning event had occurred, but there were additional batches present to be spawned. While spent females had spawned all viable batches, which signified the end of the spawning season. We visually estimated the percentage of developing and maturing oocytes in atresia across the entire sample (cellular breakdown and reabsorption of oocytes). Mass atresia, frequently indicating skip spawning or abortive maturation, was defined as  $\geq 25\%$  of stage 3+ oocytes in atresia (Frey

et al. 2015; Head et al. 2020; Rideout et al. 2000; Rideout et al. 2006).

Two estimations of maturity were recorded: biological (physiological) and functional maturity. These maturity classifications help separate fish with physiological maturity markers (i.e., presence of vitellogenic and more advanced maturity stages) that may not spawn from fish that will spawn (i.e., functional maturity) in a given year. Classifications are based on level of oocyte development, proportion of developing and maturing oocytes in atresia as defined for black, yelloweye, and aurora rockfishes (Cope et al. 2016; Gertseva and Cope 2017; Head et al. 2020). Maturity stage 3 and oocyte



**Fig. 1** Visual histology guide showing maturity stages 1–5 and corresponding oocyte developmental stage for lingcod

Maturity and Oocyte Stages	Histological Image
<p><b>Maturity Stage 1: Immature</b> Oocyte stage 1 and 2: Perinuclear</p> <p>Small oocytes with large nucleolus. Nucleoli begin to develop around the periphery of the nucleus.</p>	
<p><b>Maturity Stage 2: Developing</b> Oocyte Stage 3: Oil droplet/Cortical alveoli formation</p> <p>Follicle wall thickens. Oil droplets and cortical alveoli (stain white) form along the periphery of the cytoplasm.</p>	
<p><b>Maturity Stage 3 Early Vitellogenesis</b> Oocyte stage 4.2: Yolk accumulation</p> <p>Cortical vesicles increase along the periphery of the cytoplasm alongside yolk granules. Yolk granules coalesce into globules and increase in size, occupying 25 - 50% of the cytoplasm</p>	
<p><b>Maturity Stage 4: Late Vitellogenesis</b> Oocyte stage 5: Late Vitellogenesis</p> <p>Large oocytes with &gt; 50% of cytoplasm area occupied by yolk globules. Yolk globules and oil continue to merge. Zona radiata begins to thicken.</p>	
<p><b>Maturity Stage 5: Hydration</b> Oocyte stage 8: Late Hydration</p> <p>Yolk coalesces into a central mass in the cell, very thick zona radiata. Close to spawning and release.</p>	

developmental phase 4.1 or higher were defined as biologically mature. Biologically mature samples exhibiting mass atresia were identified as functionally immature since their overall contribution to spawning biomass would be minimal. Functional maturity defined fish that contain physiological maturity markers but did not exhibit abortive maturation or skip spawning (presence of mass atresia). Thus, we defined functional maturity as fish with

oocyte developmental stages greater than 4.2 and minimal rates of atresia (<25%).

We recorded certainty (1 or 0) of maturity determination for each sample. Uncertainty in maturity determinations were possible if flaws in sample preparation or timing of collection made it too difficult to assess if spawning had occurred or would occur later in the year (often recovering/resting and spent fish). The recovering stage was not recorded because of difficulty

separating reabsorption of oocytes aborted following failure to spawn from post-spawning markers, i.e., post ovulatory follicles (POFs), residual embryos, and mature oocytes in a late atretic state. We excluded all uncertain samples from the maturity analysis.

### Logistic estimation of maturity

Maturity ogives are commonly generated by applying a logistic model to maturity data. We used a logistic model to fit an asymptotic curve to the proportion of mature female fish at each given 1-cm length bin as:

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

where  $P$  is the proportion mature at length or age  $x$ , and parameters  $\alpha$  and  $\beta$  define the shape and location of the fitted sigmoid curve. The logistic parameters were estimated by fitting a generalized linear model (GLM) to the data (marked as mature or immature) using R ver. 4.0.1 (Core Team R 2020). Length and age at 50% maturity ( $L_{50}$ ,  $A_{50}$ ) were calculated using the estimates of  $\alpha$  and  $\beta$  from the logistic model:

$$L_{50} \text{ or } A_{50} = -\alpha/\beta \quad (2)$$

### 95% confidence intervals for significance testing

To evaluate the statistical significance of maturity estimates we used the Delta Method. This allows for estimates of variance and 95% confidence intervals (CI) (Seber 1982).

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

where  $S^2(L_{50}, A_{50})$  is the variance of  $L_{50}$  or  $A_{50}$ ,  $\hat{\alpha}$  and  $\hat{\beta}$  are estimates of parameters  $\alpha$  and  $\beta$  generated by the GLM model,  $S(\hat{\alpha})$  and  $S(\hat{\beta})$  are the standard errors of  $\hat{\alpha}$  and  $\hat{\beta}$ , and  $r$  is the correlation coefficient between length and/or age at maturity. If  $\pm 95\%$  CI overlap, then results are not considered significantly different.

### Spatial and seasonal analysis of reproductive patterns

We focused on assessing length and age at biological and functional maturity across eight regions that are

bounded by genetic, management, and biogeographic breakpoints of interest. Cape Mendocino and Pt. Conception (34°26' N) represent important biogeographic references along the West Coast and demarcate pronounced differences in geographic features, upwelling patterns, and sea surface temperature (Broitman et al. 2008; Head et al. 2020). Because of these factors we also evaluated all females north of Pt. Conception to the U.S./Canada border to compare to the eight studied regions. Separation along these major breaks allowed us to evaluate how oceanographic variability impacts reproduction in this species.

To assess trends in spawning duration and timing of spawning we evaluated the annual reproductive cycle by plotting the frequency of maturity stages as defined in Table 1, by month. We focused this analysis on three regions of interest based on management needs and availability of data: coast-wide, north and south of 40°10' N. Biologically and functionally immature fishes were excluded from the analysis to focus on development of mature individuals during the months of collection. We pooled data for all years for this analysis, as we had insufficient data to evaluate yearly differences in the month-to-month analysis. Differences in sampling capabilities by month in the north and south also confounded our ability to determine the reproductive cycle across an entire year in the southern regions; thus, this analysis encompassed June through October. In addition, we evaluated spatial distribution of samples identified as “spawning,” “batch spent,” and “spent” to identify relationships between depth, latitude, and spawning locations. We only used samples with complete location information for this analysis, which include all ovaries collected from WCGBT and H&L surveys and a subsample of WDFW ovaries. Samples collected by ODFW did not include exact location, and thus were not used in the spatial analysis of spawning and post spawning females.

## Results

### Summary of field collections

From 2013 to 2019, we utilized four sampling platforms to collect 1035 ovary samples from lingcod across the contiguous US West Coast (48° 23' N to 32° 23' N) (Table 2, Fig. 2). The number of

samples collected by each platform varied year to year (Table 2). Combining ovary collections across years, we were able to obtain samples for each month, but the frequency of monthly samples was likewise inconsistent. Thus, we are unable to evaluate seasonal trends by year. Lingcod from the WCGBT and H&L surveys were generally collected at depths from 43 to 408 m, with a median depth of 140 m ( $n = 816$ ) and a single outlier at 675 m, which was removed from this analysis. Depth information was often not available for samples collected by ODFW and WDFW.

Coast-wide fork lengths ranged from 19 to 109 cm, with a median length of 67 cm. A total of 661 lingcod fin rays were aged, of these 649 corresponded to certain maturity determinations and were used in age at maturity analyses. Ages ranged from 0 to 15 years (years), with a median age of 5 years. Female weights ranged from 0.04 to 21.4 kg, with a median weight of 2.7 kg. Range of fish lengths, weights, and ages were similar north (19–109 cm; 2.68 kg; 0–15 years) and south (21–103 cm; 2.74 kg; 0–15 years) of 40°10' N. Female lingcod weighed between 0.04–21.4 kg north of 40°10' N and 0.06–12.00 kg in the south.

### Histological observations

Histological analysis was highly certain for 97% of maturity recordings (1005 out 1035). The majority of uncertain samples appeared to be either recovering from spawning (resting) or contained high rates of atresia (> 25%) which may have indicated skip spawning. In addition, samples in early yolk development (maturity stage 3), represented 60% of uncertain maturity determinations (18 out of 30). The most frequently observed maturity stage was batch spent (28.4% or 285 out of 1005) (Maturity Stage 6, Table 1). This maturity stage was present every

month of collection with the exception of April, though April was also the least sampled month ( $n = 8$ , Fig. 3a). Only 24 fish with Maturity Stage 6 were in full spawning condition at the time of capture. The remainder batch spawned just prior to capture and had remaining batches present for later release. Fish in late vitellogenesis and migratory nucleus stage (Maturity Stage 4, Table 1) were present at a similar frequency, 27.8% (279 out of 1005), but occurred more frequently from May to October (Fig. 3a).

Skip spawning fish were encountered infrequently ( $n = 25$ ), representing only 2.5% of all maturity samples. Skip spawners were observed primarily in September ( $n = 14$ ) (Fig. 3a), across almost the entire latitudinal range sampled (47°36'–33° 42' N) within depths of 60–267 m. However, they were most frequently encountered in November ( $n = 3$ ), but this was due to the reduced sampling in this month ( $n = 28$ ). These fish ranged in size from 51 to 77 cm. Females at the lower end of the size range with mass atresia were in abortive maturation, which is when juveniles reaching maturity for the first-time abort spawning and reabsorb maturing oocytes. Of these skip and abortive spawners, 76% (19 out of 25) had more than 50% of oocytes in atresia and 60% (15 out of 25) had 75% or more of oocytes in atresia. Spent fish also represented a small percentage of the maturity stages observed (4.8%) with 46 observed in the December–April period (96% of spent observations).

### Biological and functional maturity

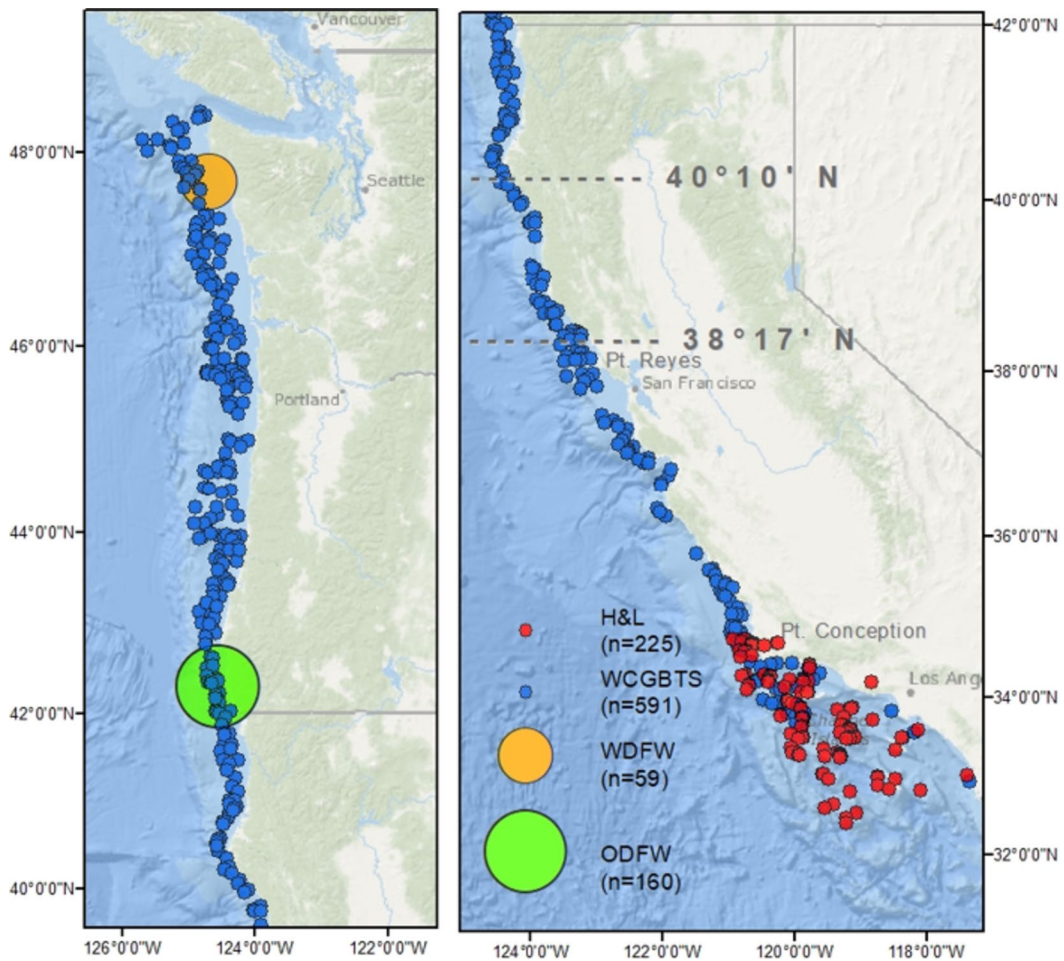
We only used maturity analyses assessed with certainty ( $n = 1005$ ) to estimate length at biological and functional maturity. Of these, 778 were biologically mature (oocyte developmental stage 4.1 or higher) and 720 were functionally mature (oocyte

**Table 2** Summary of lingcod ovaries ( $N$ ) collected from 2013 to 2019 by the NWFSC's West Coast Groundfish Bottom Trawl (WCGBT) and Hook and Line (H&L) surveys, and

	2013	2014	2015	2016	2017	2018	2019	Total
WCGBT	132	--	78	144	147	90	--	591
H&L	--	11	--	64	55	67	28	225
ODFW	--	29	31	50	29	21	--	160
WDFW	--	--	--	26	17	4	12	59
Total	132	40	109	284	248	182	40	1035

port samplers from Oregon Department of Fish and Wildlife (ODFW) and Washington Department of Fish and Wildlife (WDFW)





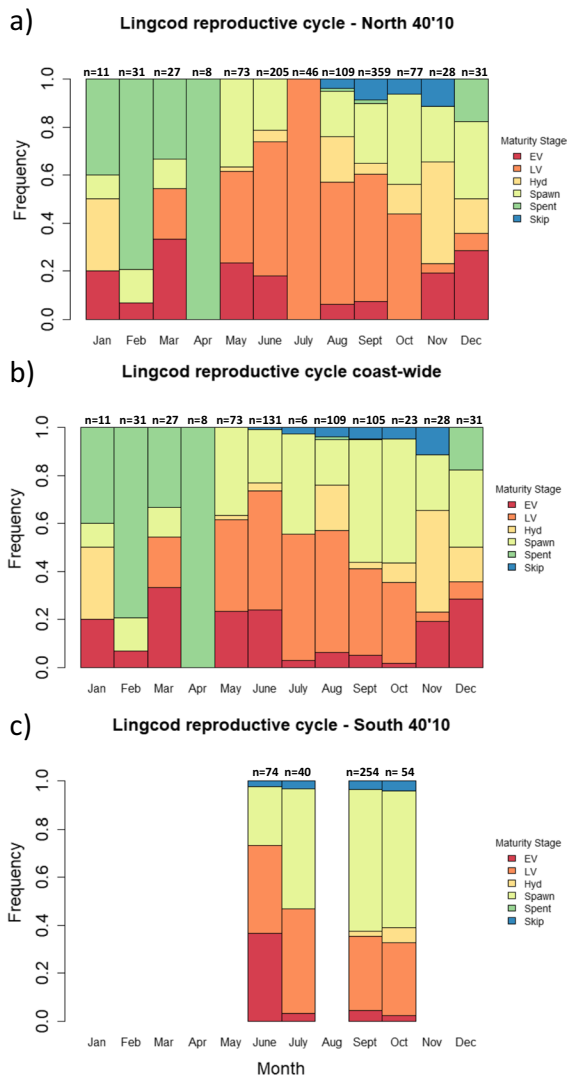
**Fig. 2** Location of lingcod ovary samples collected by the Hook & Line (H&L) (red), West Coast Groundfish Bottom Trawl survey (WCGBTS) (blue), Washington Department of Fish and Wildlife (WDFW) port samplers (orange), and Oregon Department of Fish and Wildlife (ODFW) port sampler (green) along the U.S. West Coast. The spatial break North and

South of 40°10' N and 38°17' N are denoted by dashed grey lines. Total number of samples by sampling platform, scaled by sample size, are shown in the figure legend in the bottom of the right panel. Note that WDFW and ODFW data did not have exact latitudinal location and were pooled by general state fishing areas

developmental stage 4.2 or higher, and less than 25% of oocytes in atresia). The coast-wide  $L_{50}$  difference between biological and functional maturity was significantly different ( $50.59 \pm 0.53$  and  $54.58 \pm 0.48$  cm) (Table 3).

The range of biological and functional  $L_{50}$  maturity estimates across all eight regions was 43.36–52.75 and 46.31–56.65 cm (Table 3, Fig. 4a and b). Between management regions (north and south of 40°10' N), lingcod reached biological and functional maturity at larger sizes in the north, by an average of 5.65 ( $52.75 \pm 1.01$  and  $47.10 \pm 1.21$ ) and 5.08 cm ( $56.65$

$\pm 0.87$  and  $51.57 \pm 1.08$  cm) respectively (Table 3, Fig. 4a and b). Biological maturity estimates for  $L_{50}$  between genetic stocks (north and south of 38°17' N) varied by 4.86 cm ( $51.78 \pm 0.83$  and  $46.92 \pm 1.55$  cm). However, there was a greater disparity in functional maturity ( $L_{50}$ ) between genetic stocks, by 6.79 cm ( $56.42 \pm 0.76$  and  $49.63 \pm 1.28$ ) (Table 3, Fig. 4b). The difference in biological and functional maturity between the northern management and the northern genetic stock regions were not significantly different. Similarly, there was minimal difference in  $L_{50}$  for biological maturity between southern management and



**Fig. 3 a–c** Reproductive development of mature females by month sampled **a** coast-wide, **b** north of 40°10', and **c** south of 40°10'. Frequency of samples by maturity stage shown: early vitellogenesis (EV, in red), late vitellogenesis (LV, in orange), hydration (Hyd, in sunflower yellow), spawning and batch spawned (spawn, in yellow-green), spent (in green), and skip spawning (skip, in blue). Number of samples (*n*) collected by month shown at the top of each figure

southern genetic stock regions (0.18 cm); functional maturity varied slightly (1.94 cm) between the two regions but the difference was not significant.

Biogeographic regions of study produced the largest and smallest  $L_{50}$  results for biological and functional maturity (Table 3). Results generally showed a decrease in size of maturity with decreasing latitude,

but CI also increased due to reduced samples sizes for a three region analysis. Females north of Cape Mendocino to the USA/Canada border reached length at 50% maturity at significantly larger sizes (biological:  $52.75 \pm 1.01$ , functional:  $56.65 \pm 0.87$ ) compared to the central and southern biogeographic regions. Females in the central portion of the coast (Cape Mendocino to Pt. Conception) reached biological and functional maturity at  $47.42 (\pm 2.20)$  and  $52.63 (\pm 2.05)$  cm, while females south of Pt. Conception to the USA/Mexico border produced the smallest  $L_{50}$  estimates of  $43.36 (\pm 2.86)$  and  $46.31 (\pm 2.70)$  cm for biological and functional maturity. We also looked at results north of Pt. Conception to the USA/Canada border to determine if females south of Conception were driving the differences in  $L_{50}$  along the coast. Females north of Pt. Conception reached biological and functional maturity ( $50.91 \pm 0.66$  and  $55.22 \pm 0.60$  cm) at similar sizes as fish coast-wide, north of 40°10' N and north of 38°17' N (Table 3, Fig. 4a–b). Complete results with model parameters,  $L_{50}$  maturity estimates, and corresponding 95% CI are available in Table 3.

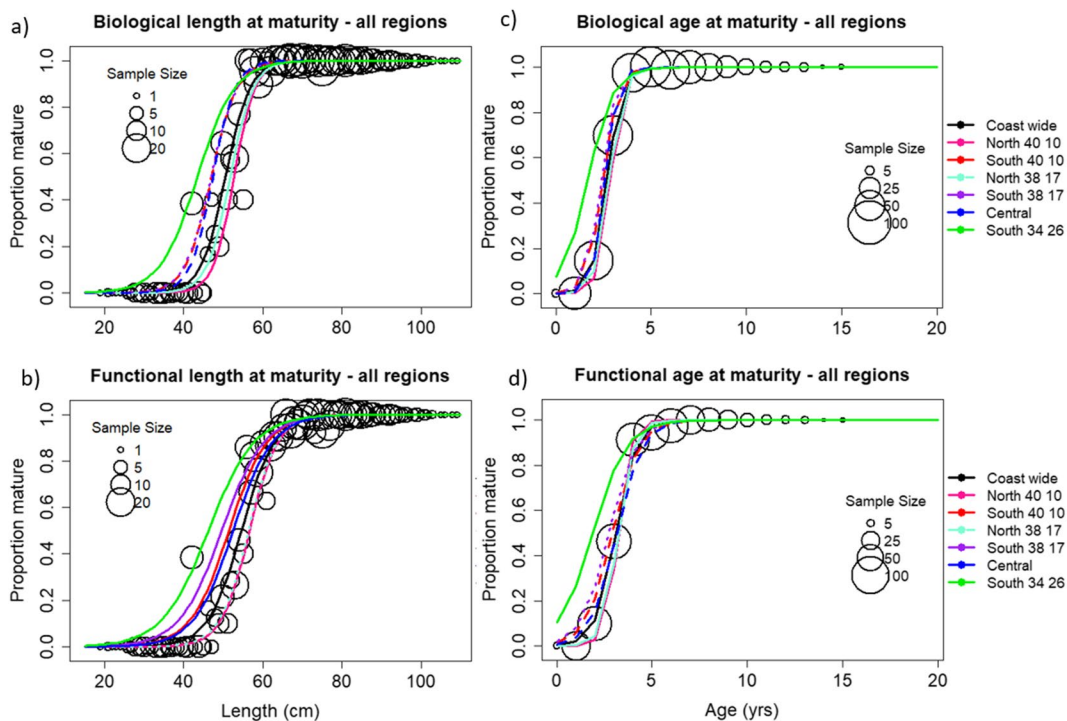
Age at 50% maturity ( $A_{50}$ ) estimates produced similar trends as  $L_{50}$  analyses, with fish reaching functional maturity at older ages than for biological maturity and a similarly latitudinal decrease in  $A_{50}$  (Table 4, Fig. 4 c–d). Coast-wide differences in  $A_{50}$  for biological ( $2.69 \pm 0.04$ ) and functional ( $3.10 \pm 0.04$ ) maturity were statistically significant. Biological and functional  $A_{50}$  results were similar between the two northern regions (north of 40°10' N and 38°17' N) (Table 4). Similarly, females south of 40°10' N and south of 38°17' N exhibited comparable results for biological ( $2.46 \pm 0.07$ ,  $2.38 \pm 0.10$ ) and functional ( $2.92 \pm 0.07$ ,  $2.74 \pm 0.09$ ) maturity (Table 4). However, results were significantly different between the north and south for both management areas and genetically defined regions.

As with  $L_{50}$ , biogeographic regions produced the most variable differences in  $A_{50}$ ; however, here female lingcod from northern and central biogeographic regions reached functional maturity at similar ages, and females south of Pt. Conception reached biological and functional maturity at significantly younger ages compared to both the central and northern biogeographic regions (Table 4). Females south of Pt. Conception reached biological ( $1.66 \pm 0.16$ ) and functional ( $1.89 \pm 0.16$ )  $A_{50}$  about a year younger

**Table 3** Number of lingcod samples (*n*) within the contiguous US West Coast used in length at 50% biological ( $L_{50\text{Bio}}$ ) and functional ( $L_{50\text{Fn}}$ ) maturity (cm) estimates with 95% confidence intervals (CI) and parameter estimates ( $\alpha$ ,  $\beta$ ) by regions: coast-wide, management boundaries north and south

Region	N	$L_{50\text{Bio}}$ ( $\pm 95\%$ CI), $\alpha$ , $\beta$	$L_{50\text{Fn}}$ ( $\pm 95\%$ CI), $\alpha$ , $\beta$
Coast-wide	1005	50.59 ( $\pm 0.53$ ), -16.337, 0.323	54.58 ( $\pm 0.48$ ), -13.000, 0.238
Management boundary			
North of Mendocino	583	52.75 ( $\pm 1.01$ ), -19.995, 0.379	56.65 ( $\pm 0.87$ ), -15.806, 0.279
South of Mendocino	422	47.10 ( $\pm 1.21$ ), -14.483, 0.308	51.57 ( $\pm 1.08$ ), -10.649, 0.207
Genetic boundary			
North of 38°17' N	653	51.78 ( $\pm 0.83$ ), -17.604, 0.340	56.42 ( $\pm 0.76$ ), -15.514, 0.275
South of 38°17' N	352	46.92 ( $\pm 1.55$ ), -14.218, 0.303	49.63 ( $\pm 1.28$ ), -9.281, 0.187
Biogeographic regions			
Mendocino to Pt Conception	196	47.42 ( $\pm 2.20$ ), -16.727, 0.353	52.63 ( $\pm 2.05$ ), -10.554, 0.201
South of Pt Conception	226	43.36 ( $\pm 2.86$ ), -9.219, 0.212	46.31 ( $\pm 2.70$ ), -7.957, 0.172
North of Pt Conception	779	50.91 ( $\pm 0.66$ ), -17.034, 0.335	55.22 ( $\pm 0.60$ ), -13.243, 0.240

of Cape Mendocino (40°10' N), genetic boundaries north and south of 38°17' N, Central coast Cape Mendocino to Pt Conception (40°10'–34°26' N), north of Pt Conception (34°26' N), and south of Pt Conception to the USA-Mexico border (34°26' N–32°00' N)



**Fig. 4 a–d** Female lingcod **a** length at biological maturity, **b** length at functional maturity, **c** age at biological maturity, and **d** age at functional maturity for the eight regions studied: coast-wide (black solid line), north (pink dashed line), and south (red solid line) of 40°10' N, North (light blue dashed

line) and South (purple solid line) of 38°17' N, Central coast (40° 10'–34° 26' N) (blue solid line), and South of Pt. Conception (34° 26' N) (green solid line). The size of the bubbles indicates the number of samples collected at each bin (length or age)

**Table 4** Number of lingcod samples (*n*) within the contiguous US West Coast used in age at 50% biological ( $A_{50Bio}$ ) and functional ( $A_{50Fxn}$ ) maturity (cm) estimates with 95% confidence intervals (CI) and parameter estimates ( $\alpha$ ,  $\beta$ ) by regions: coast-wide, management boundaries north and south of Cape

Mendocino (40°10' N), genetic boundaries north and south of 38°17' N, Central coast Cape Mendocino to Pt Conception (40°10'–34°26' N), north of Pt Conception (34°26' N), and south of Pt Conception to the USA-Mexico border (34°26' N–32°00' N)

Region	<i>N</i>	$A_{50Bio}$ ( $\pm 95\%$ CI), $\alpha$ , $\beta$	$A_{50Fxn}$ ( $\pm 95\%$ CI), $\alpha$ , $\beta$
Coast-wide	649	2.69 ( $\pm 0.04$ ), -6.849, 2.547	3.10 ( $\pm 0.04$ ), -5.753, 1.857
Management boundary			
North of Mendocino	327	2.88 ( $\pm 0.09$ ), -8.610, 2.987	3.23 ( $\pm 0.09$ ), -9.497, 2.942
South of Mendocino	322	2.46 ( $\pm 0.07$ ), -5.937, 2.411	2.92 ( $\pm 0.07$ ), -4.246, 1.453
Genetic boundary			
North of 38°17' N	387	2.82 ( $\pm 0.07$ ), -7.544, 2.676	3.23 ( $\pm 0.07$ ), -8.047, 2.493
South of 38°17' N	262	2.38 ( $\pm 0.10$ ), -6.188, 2.602	2.74 ( $\pm 0.09$ ), -3.836, 1.399
Biogeographic regions			
Mendocino to Pt Conception	164	2.59 ( $\pm 0.13$ ), -8.028, 3.105	3.15 ( $\pm 0.14$ ), -4.744, 1.507
South of Pt Conception	158	1.66 ( $\pm 0.16$ ), -2.515, 1.512	1.89 ( $\pm 0.16$ ), -2.150, 1.140
North of Pt Conception	491	2.76 ( $\pm 0.05$ ), -8.110, 2.937	3.19 ( $\pm 0.05$ ), -6.608, 2.075

than their counterparts in the north (Table 4). Results north of Pt. Conception were similar to other northern regions for both biological and functional maturity.

#### Spatial and seasonal patterns in reproduction

The number of skip and abortive spawners was small ( $n = 25$ ) and similar north (13 out of 25) and south (12 out of 25) of 40°10' N. We observed slightly more females in mass atresia north of 38°17' N (16 out of 25) than in the south (9 out of 25). These samples were present in all years sampled except 2014, the least sampled year (Table 2). The largest proportion of skip spawning fish was observed in 2016 (36% of skip spawners).

We pooled samples across years to evaluate the annual reproductive cycle and to determine if the duration and timing of spawning varied north and south of 40°10' (Fig. 3 a–c). Using this approach, we were able to evaluate monthly changes across all years, but could not investigate potential interannual shifts in the maturity schedule. Coast-wide spawning or recently batch spawned (maturity stage = Spawn) females were observed every month except April. Spent/post spawning lingcod were primarily observed from December–April and only collected north of 40°10' (mean fish length of 78.4 cm). However, sampling did not occur in the south during this time which biased our analysis of spatial trends in post spawning females. We were unable to pinpoint

the timing of peak spawning because of the presence of batch spawning events throughout the year. Coast-wide we found the largest proportion of spawning fish in September and October, both representing 42% of all maturity stages observed during those months.

Disentangling regional differences in the reproductive cycle is confounded by unequal seasonal sampling effort in the north and south. Samples north of 40°10' N were collected year round by the WCGBT survey and the WDFW and ODFW port samplers, while samples south of 40°10' N were collected by WCGBT and H&L surveys, operating in the summer and fall months only. Thus, we could only evaluate the reproductive cycle for four months in the south: June, July, August, and September (Fig. 3c). We observed a high number of spawning fish in September (72% of observations) in the south. Monthly distribution of maturity stages in the north were similar to the coast-wide annual cycle, except that only the late vitellogenesis maturity stage was observed in July. In addition, there was an observed decrease in spawning fish in September and October in the north (Fig. 3b).

We found mature (48° 23'– 32° 23' N) and immature (48° 22'–33° 37' N) fish along the entire coast. Mature fish occurred across a range of depths 42.8–408 m, with a median depth of 149.8 m. We found immature fish from 59.7 to 317.4 m at a median depth of 124.2 m. We also evaluated the spatial distribution of spawning, recent batch spawned, and spent



fish by latitude and depth (Fig. 5). We restricted samples to those with complete location information for this analysis, which reduced the number of samples available in the winter for analysis ( $n = 8$ ).

Females in spawning condition ( $n = 20$ ) were found  $48^{\circ}7' - 32^{\circ} 23' N$  and depths of 78.5–368.6 m. Based on this analysis, 75% of spawning fish were south of  $40^{\circ}10' N$  (Fig. 5). Very few samples in spent condition had complete location information ( $n = 8$ ), so we were unable to evaluate location trends of post spawning females. However, we observed all post spawning fish north of  $40^{\circ}10' N$  within a narrow depth range of 106.7–229.4 m. Fish in spawning/batch spent condition (Maturity Stage 6) were frequently encountered ( $n = 285$ ) along the entire coast  $48^{\circ} 7' - 32^{\circ} 27' N$  (Fig. 5). A larger proportion (65%) of these occurred in the southern management region (south of  $40^{\circ}10' N$ ); with the majority of batch spent fish found in the southern genetic stock region (south of  $38^{\circ}17' N$ ) (96% or 176 out of 184).

### Discussion

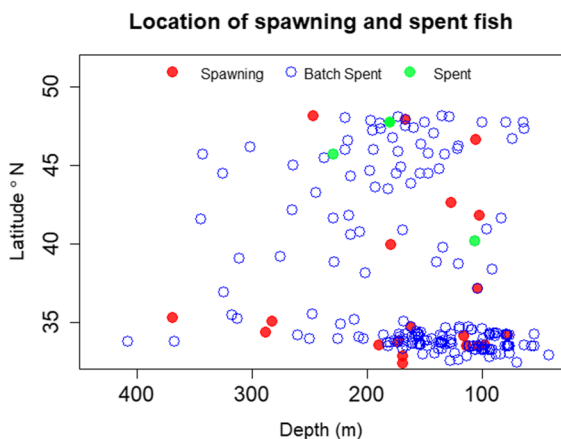
Our research offers updated histological estimates of size and age at maturity across multiple regions along the US West Coast. Previous research on lingcod estimated size and/or age at maturity as well, but

in general, these studies focused on isolated regions and/or used macroscopic maturity techniques for analysis (Cass et al. 1990; Jagielo et al. 1996; Lam et al. 2021; Miller and Geibel 1973). Research based on macroscopic analysis often fails to identify several maturity stages; including resting, skip spawning, and early developing (Saborido-Rey and Junquera 1998; Tomkiewicz et al. 2003; Costa 2009; Min et al. 2022). In addition, macroscopic misidentification has a tendency to skew toward labeling immature individuals as mature, leading to an underestimation of size and age at maturity and an overestimation of stock productivity (Min et al. 2022). For example, 30% of immature female horse mackerel, *Trachurus trachurus*, were macroscopically misidentified as mature (Costa 2009), and in Southern flounder, *Paralichthys lethostigma*, 39% of developing fish were macroscopically classified incorrectly and led to underestimation of size and age at maturity (Midway and Scharf 2012). In Kattegat cod, *Gadus morhua*, the use of macroscopic estimations of maturity could have overestimated spawning biomass by up to 35% (Vitale et al. 2006).

Overall, histological analysis is a more robust method for estimating maturity as it correctly allows researchers to identify post spawning/recovering fish through the detection of POFs, atresia, and developing oocytes that would otherwise be overlooked if using macroscopic analysis alone. This higher resolution of maturity analysis allows us to estimate rates of skip spawning and abortive maturation, an essential component of determining spawning capability and/or identifying reproductive stressors in a population. This highlights the importance of accurate estimates of maturity for use in population dynamic models, as erroneous values can lead to poor estimates of spawning biomass (TenBrink and Wilderbuer 2015; Vitale et al. 2006).

### Differentiation between current study and previous research

Previous studies on lingcod size and age at maturity on the US West Coast reported a wide range of regional estimates, ranging from 49.8 to 55.7 cm (2.8–5 years) in California (CA) (Lam et al. 2021; Miller and Geibel 1973; Silberberg et al. 2001). More recent macroscopic maturity analysis excluded the region south of Pt. Conception and reported a decline



**Fig. 5** Location of lingcod females observed in a spawning (red filled circles), spent (green filled circles), and recently batch spent (blue open circles) maturity stages collected on the West Coast Groundfish Bottom Trawl and Hook & Line surveys. Depth (m) shown on the x-axis and latitude (°N) on the y-axis



in size at maturity from Washington (WA) (50.1 cm) to Central CA (45.4 cm), but not in age at maturity (2.6 years for both regions) (Lam et al. 2021). Our results found a similar trend with female lingcod reaching larger sizes at functional maturity (56.65 cm) north of 40°10' N relative to fish south of 40°10' N (51.57 cm). Lam et al. (2021) coast-wide estimates of size and age at maturity (50.1 cm, 2.6 years) were comparable to biological  $L_{50}$  and  $A_{50}$  estimates from the current study (50.59 cm, 2.69 years); however, their estimates were smaller than our functional  $L_{50}$  and  $A_{50}$  estimates (54.58 cm, 3.1 years) by 4.48 cm and 0.5 years. This is expected since Lam et al. (2021) used macroscopic maturity determinations, which cannot account for skip spawning and abortive maturation. For comparison, the 2005 and 2009 lingcod stock assessments incorporated  $L_{50}$  estimates of 68 cm in the north (WA and Oregon (OR)) and 60 cm in the south (CA) (Hamel et al. 2009; Jagielo and Wallace 2005).

Functional maturity provides a more accurate estimate of potential spawners in a given year for use in population dynamic models (Head et al. 2020). This approach accounts for both abortive maturation by juveniles and skipped spawning by adults perhaps related to poor oceanographic conditions, limited nutrient availability, and/or other factors that negatively influence a species fitness (Head et al. 2020; Rideout et al. 2000; Rideout et al. 2006; Rideout and Rose 2006). Skipped spawning is a strategy utilized by marine fishes to move energy reserves from spawning to other processes such as growth and survival during reproductively unfavorable years, and to increase future reproductive output when conditions improve (Jørgensen et al. 2006; McBride et al. 2013; Rideout et al. 2006). Rates of skip spawning may consequently vary both spatially and temporally.

#### Spatial trends in the annual reproductive cycle

Coast-wide, we observed low rates of skip spawning in lingcod (2.5%), which impacted our ability to evaluate spatial trends. However, we found a higher proportion of skip spawners in the northern genetic stock (64% of total skip spawners), and very few observed south of Pt. Conception (2.5%). Similarly, we observed variable rates of skip spawning between years, with the largest rate occurring in 2016 which coincided with a strong El Niño in 2015–2016 and

the “warm blob” of 2014–2016 (Peterson et al. 2015, 2017). This abnormally warm period brought a northward shift in many marine species ranges, notably lipid-poor southern copepods species and gelatinous zooplankton (*Pyrosoma atlanticum*) that can influence the nutrient quality within coastal marine food webs (Brodeur et al. 2021; Peterson et al. 2017), particularly in lower trophic prey items typically consumed by lingcod. It is possible that female lingcod chose to forego spawning in northern regions, where *P. atlanticum* were most prevalent (Brodeur et al. 2021), compared to females in southern regions; however, more research and additional samples are needed to disentangle interannual patterns in skip spawning rates and how they can directly or indirectly relate to variability in oceanic regimes and prey availability.

The high frequency of post spawning (spent) samples in northern regions from December through April indicates lingcod spawning ends in early spring, confirming past studies investigating lingcod nesting behavior (Low and Beamish 1978; O'Connell 1993). However, we encountered spawning or recently spawned fish in the north every month except April and July, implying that mature females in northern waters are spawning capable throughout most of the year. Because we pooled data across years to evaluate monthly trends in development, it is possible that the timing and duration of spawning varied slightly from year to year and confounded our ability to determine the exact spawning season throughout the study area. In addition, due to the seasonality of each sampling method, particularly south of the OR/CA border, there may be fine scale regional impacts on the timing and duration of spawning that we did not detect; thus, we cannot conclude if timing of spawning is uniform along the entire coast. Nevertheless, our findings help to illustrate the complexities within the annual lingcod reproductive cycle and demonstrate that contrary to previous studies estimating that spawning occurs from December to March (Low and Beamish 1978; Withler et al. 2004), female lingcod are in spawning condition (spawning a batch or recently spawned a batch) throughout the majority of the year and likely have a greater reproductive potential than previously reported.

Additional samples are needed to pinpoint localized differences in the duration and timing of spawning in the southern stock. We did not encounter spent

fish during June, July, September, and October perhaps suggesting that the spawning season ends in the early winter through late spring in the south, similar to what we observed further north. In addition, compared to the northern region, we encountered a higher frequency of recently batch spawned females and a lower frequency of females in early vitellogenesis in the southern region in all overlapping months, particularly July. This is a strong indicator that regional differences exist, which influence the timing of and duration of spawning. Future studies on the annual reproductive cycle should consider the importance of standardizing sample collections by month, region of interest, and across multiple years. Evaluating inter-annual trends in the timing and duration of spawning would be useful in determining the drivers of reproductive success in this species. If data were available across multiple years along the entire coast, it would be possible to evaluate the influence of different oceanographic regimes as well as determine if genetic stock structure influences these processes.

#### Spatio-temporal patterns and drivers of life history

Our research results provide strong evidence that timing of lingcod maturity and duration of reproductive output is regionally distinct and potentially driven by oceanographic and environmental factors along the coast. This adds to the recent findings of genetically distinct clusters in the lingcod population north and south of Point Reyes, CA (Longo et al. 2020) and latitudinal driven differences in life history traits such as growth, longevity, and mortality coast-wide (Lam et al. 2021). We investigated timing of maturity for multiple regional groupings to identify regions where differences in  $L_{50}$  and  $A_{50}$  were most prominent. There did not appear to be substantial differences in timing of maturity between the management and genetic boundaries. However, our study demonstrates that variability in oceanographic and environmental conditions between biogeographic regions, especially the region south of Pt. Conception, are significant drivers of lingcod reproduction and this relationship should be studied in more depth to inform management models.

Our findings aligned with results from previous studies which also reported a latitudinal decline in size and age at maturity in female lingcod. The central biogeographic region (Cape Mendocino to Pt.

Conception) appears to represent a transitional region and broadly overlaps with the genetic breakpoint near Point Reyes and the management boundary at 40°10' N. However, age at maturity was not significantly different between the central and northern biogeographic regions of study. Variability in age at maturity was statistically significant between females found north and south of Pt. Conception. Differences in length at maturity among biogeographic regions showed a downward gradient in size at maturity with latitude, with females south of Pt. Conception producing the smallest  $L_{50}$  estimates. Previous studies did not report genetic or biological differences north and south of Pt. Conception (Lam et al. 2021; Longo et al. 2020), while our study found significant differences between these two regions.

Understanding how and if changes in oceanographic conditions impact biological processes is important for fisheries assessments, and can have impacts on how coast-wide stocks are managed. The biogeographic regions analyzed in this study reflect major oceanographic boundaries within the California Current Large Marine Ecosystem (CCLME), located at Cape Mendocino and Point Conception and are areas of interest when evaluating spatial differences in growth and maturity of coast-wide species (Cope 2004; Gertseva et al. 2017; Head et al. 2014; Head et al. 2020; Keller et al. 2012).

The CCLME is characterized by seasonal upwelling and downwelling (Huyer 1983; Juan-Jordá et al. 2009), which influences spatio-temporal variability in nutrient availability, biological processes, and primary productivity within biogeographic regions (Cope 2004; Gertseva et al. 2017; Juan-Jordá et al. 2009; Parrish et al. 1981). Similar to lingcod, several rockfish species, including splitnose, green-striped, and aurora rockfishes, are reported to be larger at age and live longer in the northern regions of the CCLME (Gertseva et al. 2010; Gertseva et al. 2017; Keller et al. 2012; Lam et al. 2021). Sablefish mature at younger ages and grow faster in the north (Head et al. 2014), while aurora rockfish reach maturity at a larger size with higher rates of skipped spawning north of Cape Mendocino (Head et al. 2020). These studies demonstrate that oceanographic conditions play an important role in shaping biological processes and can influence spawning behavior in West Coast groundfish species. Understanding and quantifying the observed spatial-temporal variability

in maturity and reproduction is vital for fisheries managers to appropriately capture population trends in management models.

### Fishery considerations

While significant research has been completed on lingcod, which has enabled fisheries managers to designate boundaries using genetically/biologically relevant population information, this is not the case for the majority of groundfish species along the West Coast. Multiple management scenarios must be accounted for even when spatial structure is known, including fishing intensity, historic landings, state borders, and localized depletion. There has been concern around lingcod sub-stock boundaries for many years, especially following the overfished declaration in 1999. The 2009 and 2017 stock assessments highlighted this issue and the level of uncertainty in the spatial structure utilized by managers (Haltuch et al. 2018; Hamel et al. 2009). While these assessments incorporated some degree of spatial structure with a northern (WA and OR) and southern stock (CA), this designation was based on historical catch reconstruction data, not biological information reflective of the lingcod population. Using newly available data from Longo et al. (2020) and Lam et al. (2021), the 2021 lingcod assessments reconciled a boundary for a two stock assessment that best accounts for both genetic and growth-based differences while minimizing model uncertainty. Findings from the current study can aid in differentiating reproductive potential between the newly designated northern and southern stocks. The southern stock in particular has had greater uncertainty and lower productivity than the northern stock since 2000, and faces an increased risk for localized depletion as landings in CA are at a magnitude higher than in northern regions (Haltuch et al. 2018). Results from this study not only help to quantify the difference in spawning potential, but can increase the predictability of spawning duration on a regional scale.

In addition to direct management applications of this study, updated biological and functional maturity estimates can serve as an important baseline for observing fishing effects on maturity and reproduction. Fishery removals tend to target reproductively large and old females, which is known to alter life history traits on the level of the individual (e.g.,

increased growth rates, earlier timing of maturity) and population (e.g., smaller size classes, decreased fecundity, reduced egg and larvae survival) (Conover and Munch 2002; Hixon et al. 2014; Ricker 1981). Therefore it can be difficult to disentangle spatial variability in maturity and reproduction without considering regional differences in fishing pressure. The difference in historic landings and current fishing pressure between northern and southern stocks could be a significant driver in observed results, though it is difficult to distinguish fishing effects from environmental effects on fish populations. However, previous studies dating back several decades (Cass et al. 1990; Miller and Geibel 1973; Richards et al. 1990; Silberberg et al. 2001) have similarly found a latitudinal trend in lingcod maturity, with fish from southern waters maturing earlier at smaller sizes than fish from northern waters. Because the southern lingcod population is more vulnerable and experiences higher fishing rates in recent decades, we can generalize that earlier timing of maturity in southern latitudes may be further exacerbated by increased fishing pressure.

### Additional research needs

Overall, there is a paucity of data describing lingcod reproduction in southern regions, and areas outside of the contiguous US West Coast. Determining regional differences in the timing and duration of spawning can provide insight into stock structure, though we were unable to estimate regional differences in the timing and duration of spawning due to the lack of consistency in sampling by month and region. A future study should focus on monthly coast-wide sampling across multiple years to determine how maturity schedules vary spatially and temporally, with an emphasis on southernmost regions and waters not explicitly investigated in this study: Alaska, inland waters of the Salish Sea, Canada, and Mexico. In addition, a more comprehensive study could detect small regional differences in size and age at maturity and give insight on life history processes outside the influence of the CCLME. Overall, we found a striking decrease in size at maturity (~5–10 cm difference) and age at maturity (~1 year difference) with latitude. We hypothesize that a decrease of this magnitude would impact spawning biomass estimates for stocks in the north versus the south regardless if stock boundaries occur at 40°10' or 38°17' N, as size and age at maturity

results did not vary much between these two northern regions. Fine-scale research focused on differences between the genetically distinct and admixed clusters between Stewarts Point and Point Reyes is also needed (Longo et al. 2020). Specifically, additional samples should be collected to evaluate this area as a distinct region separate from the northern and southern clusters. This would help identify if this admixed population should be managed separately.

A detailed study of reproduction in males in relation to female maturity schedules is also needed. A study similar to ours with additional samples from males and females along the entire coast by month would help to identify regional trends in the effectiveness of batch spawning events. We observed high frequency batch spawning events throughout the annual reproductive cycle, but it is unknown if these batch events are successful since mature males in spawning condition must be present concurrently. There have been several studies on male reproduction, but none that identified regional trends in relation to female maturity schedules. Males reach maturity at smaller sizes and ages than females (Lam et al. 2021; Miller and Geibel 1973), but the annual reproductive cycle in males has not been reported. In general, past studies indicated that nest guarding by male lingcod occurred from December to March (King and Withler 2005; Miller and Geibel 1973), which overlaps with the majority of post-spawning (spent) months found in this study. During nest guarding, male lingcod undergo a period of starvation while defending egg masses from fish and invertebrate predators (O'Connell 1993), rendering them vulnerable to a variety of stressors, including fishers (Miller and Geibel 1973), predation by marine mammals (Schwarz et al. 2018), and parasites (Wood et al. 2021). The energetic and/or reproductive tradeoff between males and females with respect to nest guarding is yet unquantified. Though population dynamic models are driven by female reproductive capacity, male reproductive potential may be as important to understand as females, and their polygynous mating habits further reinforce the need for information on male reproductive patterns.

#### Management Implications and Recommendations

The 2017 lingcod stock assessment was spatially structured, but boundaries between the northern and

southern stocks were based on state borders, which do not necessarily correlate with biological, genetic, or environmental patterns observed in lingcod. The 2021 stock assessments were also spatially structured north and south of 40°10' N. Our study found differences in size at maturity of ~5 cm between these two regions. These findings support the need for assessment scientists to incorporate sub-populations in the management of this coast-wide stock. However, it should be noted that differences in size at maturity north and south of 38°17' N were ~7 cm. An evaluation of size and age at maturity north of Cape Mendocino and south of Pt. Conception found a difference of almost 10 cm and over 1 year in age, indicating a continual decrease in size and age at maturity at lower latitudes. This may support the need for management of three separate sub-stocks.

In general, lingcod is a concern to managers because of their overfished history, but the southern stock is of particular interest. Lingcod in the southern regions are susceptible to overfishing and slower recovery possibly due to weaker upwelling and lower nutrient availability in southern CA. This, in combination with historically high harvest rates of large fish, leads to lower reproductive potential in the southern population (Haltuch et al. 2018). The 2021 assessments estimated the southern stock spawning biomass to be 39.4% of unfished levels, similar to the target reference point (40.0%), and the northern stock to be above the target (64.2%). Trends in overexploitation combined with known spatial differences of growth and reproduction indicate that spatially structured stock management in lingcod should be considered for sustainability and genetic diversity of this species.

**Acknowledgements** We would like to thank the vessel and scientific crews of the West Coast Groundfish Bottomtrawl and Southern California Bight shelf rockfish hook and line surveys, as well as the port samplers for Oregon and Washington Department of Fish and Wildlife, for all their help obtaining samples for this project. A special thank you to Peter Frey of the NWFSC for creating a map of sample collection. We would also like to thank Curt Whitmire and James Fellows for data quality control and support. Finally, we would like to thank Ian Taylor for his thoughtful comments while reviewing this manuscript.

**Data availability** The datasets and analysis generated for this study are available from the corresponding author on reasonable request. Data collected by NOAA's West Coast Groundfish Bottomtrawl and Southern California Bight shelf rockfish

hook and line surveys can be accessed via: <https://www.webap.ps.nwfsc.noaa.gov/data/map>.

### Declarations

Fish sampled in our study were collected as part of National Oceanic and Atmospheric Administration's (NOAA) Fisheries surveys and through ongoing sampling and monitoring of commercial fish landings conducted by the Oregon and Washington Department of Fish and Wildlife (ODFW and WDFW). Therefore, fish were not collected solely for this project. Monitoring by NOAA surveys and state port samplers provide data for stock assessments used to manage marine fisheries. All permitting requirements were completed and a Scientific Research Permit was granted for both the WCGBT and H&L surveys. Prior to submitting to the journal, this manuscript was reviewed internally by a NWFSC employee and approved for submission in NOAA's Research Publication Tracking System.

**Conflict of interest** The authors declare no competing interests.

### References

- Beamish RJ, Chilton D (1977) Age determination of Lingcod (*Ophiodon elongatus*) using dorsal fin rays and scales. *J Fish Res Board Can* 34(9):1305–1313
- Beaudreau AH, Essington TE (2007) Spatial, temporal, and ontogenetic patterns of predation on rockfishes by Lingcod. *Trans Am Fish Soc* 136:1438–1452. <https://doi.org/10.1577/T06-236.1>
- Bradburn M, Keller AA, Horness BH (2011) The 2003 to 2008 U.S. West Coast bottom trawl surveys of groundfish resources off Washington, Oregon, and California: estimates of distribution, abundance, length and age composition. U.S. Dept Commer NOAA Tech Memo NMFS-NWFSC-114
- Brodeur RD, Buckley TW, Lang GM, Draper DL, Buchanan JC, Hibshman RE (2021) Demersal fish predators of gelatinous zooplankton in the Northeast Pacific Ocean. *Mar Ecol Prog Ser* 658:89–104
- Broitman BR, Blanchette CA, Menge BA, Lubchenco J, Krenz C, Foley M, Raimondi PT, Lohse D, Gaines SD (2008) Spatial and temporal patterns of invertebrate recruitment along the West Coast of the United States. *Ecol Monogr* 78:403–421
- Brown-Peterson NJ, Wyanski DM, Saborido-Rey F, Macewicz BJ, Lowerre-Barbieri SK (2011) A standardized terminology for describing reproductive development in fishes. *Mar Coast Fish* 3(1):52–70. <https://doi.org/10.1080/19425120.2011.555724>
- Cass AJ, Beamish RJ, McFarlane GA (1990) Lingcod (*Ophiodon elongatus*). *Can J Spec Publ Fish Aquat Sci* 109:1–40
- Chilton DE, Beamish RJ (1982) Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. *Can J Spec Publ Fish Aquat Sci* 60:34–38
- Conover DO, Munch SB (2002) Sustaining fisheries yields over evolutionary time scales. *Science* 297(5578):94–96
- Cope JM (2004) Population genetics and phylogeography of the blue rockfish (*Sebastes mystinus*) from Washington to California. *Can J Fish Aquat Sci* 61:332–342. <https://doi.org/10.1139/f04-008>
- Cope JM, Sampson D, Stephens A, Key M, Mirick PP, Strachura M, Tsou T, Weyland P, Berger A, Buell T, Council E, Dick EJ, Fenske KH, Monk M, Rodomsky B (2016) Assessments of California, Oregon and Washington stocks of black rockfish (*Sebastes melanops*) in 2015. In: Stock assessment and fishery evaluation. Pacific Fisheries Management Council, Portland, Oregon
- Core Team R (2020) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Costa AM (2009) Macroscopic vs. microscopic identification of the maturity stages of female horse mackerel. *ICES J Mar Sci* 66:509–516. <https://doi.org/10.1093/icesjms/fsn216>
- Crow KD, Powers DA, Bernardi G (1997) Evidence for multiple maternal contributors in nests of Kelp Greenling (*Hexagrammos decagrammus*, Hexagrammidae). *Copeia* 1:9–15. <https://doi.org/10.2307/1447834>
- Frey PH, Head MA, Keller AA (2015) Maturity and growth of darkblotched rockfish, *Sebastes crameri*, along the U.S. west coast. *Environ Biol Fish* 98:2353–2365. <https://doi.org/10.1007/s10641-015-0441-1>
- Gertseva V, Cope J (2017) Stock assessment of the yelloweye rockfish (*Sebastes ruberrimus*) in state and federal waters off California, Oregon and Washington. Pacific Fisheries Management Council, Portland, Oregon
- Gertseva V, Cope J, Matson S (2010) Growth variability in the splitnose rockfish *Sebastes diploproa* of the northeast Pacific Ocean: pattern revisited. *Mar Ecol Prog Ser* 413:125–136. <https://doi.org/10.3354/meps08719>
- Gertseva V, Matson SE, Cope J (2017) Spatial growth variability in marine fish: example from Northeast Pacific groundfish. *ICES J Mar Sci* 74(6):1602–1613. <https://doi.org/10.1093/icesjms/fsx016>
- Haltuch MA, Wallace J, Akselrud CA, Nowlis J, Lewis AK, Valero JL, Lam L (2018) 2017 Lingcod stock assessment. Pacific Fisheries Management Council, Portland, Oregon
- 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 Fisheries Management Council, Portland, Oregon
- Harms JH, Wallace JR, Stewart IJ (2010) Analysis of fishery-independent hook and line-based data for use in the stock assessment of bocaccio rockfish (*Sebastes paucispinis*). *Fish Res* 106:298–309. <https://doi.org/10.1016/j.fishres.2010.08.010>
- Hart JL (1973) Pacific fishes of Canada. *Fish Res Board Can Bull* 180, Ottawa, ON
- Head MA, Cope JM, Wulfinck SH (2020) Applying a flexible spline model to estimate functional maturity and spatio-temporal variability in aurora rockfish (*Sebastes aurora*). *Environ Biol Fish* 103:1199–1216. <https://doi.org/10.1007/s10641-020-01014-2>
- Head MA, Keller A, Bradburn M (2014) Maturity and growth of sablefish, *Anoplopoma fimbria*, along the U.S. West Coast. *Fish Res* 159:56–67. <https://doi.org/10.1016/J.FISHRES.2014.05.007>



- 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(8):2171–2185
- Huyer A (1983) Coastal upwelling in the California current system. *Prog Oceanogr* 12:259–284. [https://doi.org/10.1016/0079-6611\(83\)90010-1](https://doi.org/10.1016/0079-6611(83)90010-1)
- Hyde JR, Kimbrell CA, Budrick JE, Lynn EA, Vetter RD (2008) Cryptic speciation in the vermilion rockfish (*Sebastes miniatus*) and the role of bathymetry in the speciation process. *Mol Ecol* 17:1122–1136. <https://doi.org/10.1111/j.1365-294X.2007.03653.x>
- Jagiello T, Leclair LL, Vorderstrasse BA (1996) Genetic variation and population structure of lingcod. *Trans Am Fish Soc* 125(3):372–386
- Jagiello TH, Wallace FR (2005) Assessment of Lingcod (*Ophiodon elongatus*) for the Pacific Fishery Management Council. Pacific Fisheries Management Council, Portland, Oregon
- Johnson KF, Taylor IG, Langseth BJ, Stephens A, Lam LS, Monk MH, Budrick JE, Haltuch MA (2021) Status of lingcod (*Ophiodon elongatus*) along the southern U.S. west coast in 2021. Pacific Fisheries Management Council, Portland, Oregon
- Jørgensen C, Ernande B, Fiksen Ø, Dieckmann U (2006) The logic of skipped spawning in fish. *Can J Fish Aquat Sci* 63:200–211
- Jørgensen T (1990) Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *ICES J Mar Sci* 46:235–248
- Juan-Jordá MJ, Barth JA, Clarke ME, Wakefield WW (2009) Groundfish species associations with distinct oceanographic habitats in the Northern California Current. *Fish Oceanogr* 18:1–19. <https://doi.org/10.1111/j.1365-2419.2008.00489.x>
- Keller A, Harms J, Wallace J, Jones C, Benante J, Chappell A (2019) Changes in long-lived rockfishes after more than a decade of protection within California's largest marine reserve. *Mar Ecol Prog Ser* 623:175–193. <https://doi.org/10.3354/meps13019>
- Keller AA, Harms JH, Elz A, Wallace JR, Benante JA, Chappell A (2022) A tale of two species: Vermilion and sunset rockfish in the Southern California Bight. *Fish Res* 250:106275. <https://doi.org/10.1016/j.fishres.2022.106275>
- Keller AA, Molton KJ, Hicks AC, Haltuch M, Wetzel C (2012) Variation in age and growth of greenstriped rockfish (*Sebastes elongatus*) along the U.S. west coast (Washington to California). *Fish Res* 119:80–88. <https://doi.org/10.1016/j.fishres.2011.12.012>
- Keller AA, Wallace JR, Methot RD (2017) The Northwest Fisheries Science Center's West Coast Groundfish Bottom Trawl Survey: history, design, and description. U.S. Dept Commer NOAA Tech Memo NMFS-NWFSC-136
- King JR, Withler RE (2005) Male nest site fidelity and female serial polyandry in lingcod (*Ophiodon elongatus*, Hexagrammidae). *Mol Ecol* 14(2):653–660
- Lam LS, Basnett B, Haltuch M, Cope J, Andrews K, Nichols K, Longo G, Samhour J, Hamilton S (2021) Geographic variability in lingcod (*Ophiodon elongatus*) life-history and demography along the US West Coast: oceanographic drivers and management implications. *Mar Ecol Prog Ser* 670:203–222. <https://doi.org/10.3354/meps13750>
- Longo GC, Lam L, Basnett B, Samhour J, Hamilton S, Andrews K, Williams G, Goetz G, McClure M, Nichols KM (2020) Strong population differentiation in lingcod (*Ophiodon elongatus*) is driven by a small portion of the genome. *Evol Appl* 13:2536–2554. <https://doi.org/10.1111/eva.13037>
- Low CJ, Beamish RJ (1978) A study of the nesting behavior of lingcod (*Ophiodon elongatus*) in the Strait of Georgia, British Columbia. *Fish Mar Serv Tech Rep*, p 843
- Lowerre-Barbieri SK, Ganius K, Saborido-Rey F, Murua H, Hunter JR (2011) Reproductive timing in marine fishes: variability, temporal scales, and methods. *Mar Coast Fish* 3:71–91. <https://doi.org/10.1080/19425120.2011.556932>
- McBride RS, Wuenschel MJ, Nitschke P, Thornton G, King JR (2013) Latitudinal and stock-specific variation in size- and age -maturity of females winter flounder, *Pseudopleuronectes americanus*, as determined with gonad histology. *J Sea Res* 75:41–51
- Midway SR, Scharf FS (2012) Histological analysis reveals larger size at maturity for Southern Flounder with implications for biological reference points. *Mar Coast Fish* 4:628–638. <https://doi.org/10.1080/19425120.2012.717524>
- 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. *Cal Dep Fish Game Bull*, p 158
- Min MA, Head MA, Cope JM, Hastie JD, Flores SM (2022) Limitations and applications of macroscopic maturity analyses: a comparison of histological and visual maturity for three west coast groundfish species. *Environ Biol Fish* 105:193–211. <https://doi.org/10.1007/s10641-021-01208-2>
- O'Connell VM (1993) Submersible observations on lingcod, *Ophiodon elongatus*, nesting below 30 m off Sitka, Alaska. *Mar Fish Rev* 55(1):19–24
- Parrish RH, Nelson CS, Bakun A (1981) Transport mechanisms and reproductive success of fishes in the California Current. *Biol Oceanogr* 1(2):175–203
- 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
- Peterson WT, Robert M, Bond N (2015) The warm Blob conditions in the northeastern Pacific Ocean. *PICES Press* 23(1):36–38
- Richards LJ, Schnute JT, Hand CM (1990) A multivariate maturity model with a comparative analysis of three lingcod (*Ophiodon elongatus*) stocks. *Can J Fish Aquat Sci* 47:24–40. <https://doi.org/10.1139/f90-109>
- Ricker WE (1981) Changes in the average size and average age of Pacific salmon. *Can J Fish Aquat Sci* 38:1636–1656
- Rideout RM, Burton MPM, Rose GA (2000) Observations on mass atresia and skipped spawning in northern Atlantic cod, from Smith Sound, Newfoundland. *J Fish Biol* 57:1429–1440. <https://doi.org/10.1111/j.1095-8649.2000.tb02222.x>
- Rideout RM, Morgan MJ, Lilly GR (2006) Variation in the frequency of skipped spawning in Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador. *ICES J Mar Sci*

- 63:1101–1110. <https://doi.org/10.1016/j.icesjms.2006.04.014>
- Rideout RM, Rose GA (2006) Suppression of reproduction in Atlantic cod (*Gadus morhua* L.). *Mar Ecol Prog Ser* 320:267–277
- Rose KA, Cowan JH Jr, Winemiller KO, Myers RA, Hilborn R (2001) Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish Fish* 2:293–327
- Saborido-Rey F, Junquera S (1998) Histological assessment of variations in sexual maturity of cod (*Gadus morhua* L.) at the Flemish Cap (north-west Atlantic). *ICES J Mar Sci* 55:515–521. <https://doi.org/10.1006/jmsc.1997.0344>
- Schwarz D, Spitzer SM, Thomas AC, Kohnert CM, Keates TR, Acevedo-Gutiérrez A (2018) Large-scale molecular diet analysis in a generalist marine mammal reveals male preference for prey of conservation concern. *Ecol Evol* 8(19):9889–9905
- Seber GAF (1982) The estimation of animal abundance and related parameters. Blackburn Press, New Jersey
- Sharpe DMT, Hendry AP (2009) Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evol Appl* 2:260–275. <https://doi.org/10.1111/j.1752-4571.2009.00080.x>
- Sheehan DC, Hrapchak BB (1980) Theory and practice of histotechnology, 2nd edn. Battelle Press, Columbus, OH
- Silberberg KR, Laidig TE, Adams PB, Albin D (2001) Analysis of maturity in lingcod, *Ophiodon elongatus*. *Calif Fish Game* 87(4):139–152
- 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
- Taylor IG, Johnson KF, Langseth BJ, Stephens A, Lam LS, Monk MH, Whitman AD, Haltuch MA (2021) Status of lingcod (*Ophiodon elongatus*) along the northern U.S. west coast in 2021. Pacific Fisheries Management Council, Portland, Oregon
- TenBrink TT, Wilderbuer TK (2015) Updated maturity estimates for flatfishes (Pleuronectidae) in the Eastern Bering Sea, with implications for fisheries management. *Mar Coast Fish Dynam Manag Ecosys Sci* 7:474–482. <https://doi.org/10.1080/19425120.2015.1091411>
- 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
- Tomkiewicz J, Tybjerg L, Jespersen Å (2003) Micro- and macroscopic characteristics to stage gonadal maturation of female Baltic cod. *J Fish Biol* 62:253–275. <https://doi.org/10.1046/j.1095-8649.2003.00001.x>
- Vitale F, Svedäng H, Cardinale M (2006) Histological analysis invalidates macroscopically determined maturity ogives of the Kattegat cod (*Gadus morhua*) and suggests new proxies for estimating maturity status of individual fish. *ICES J Mar Sci* 63:485–492. <https://doi.org/10.1016/j.icesjms.2005.09.001>
- Withler RE, King JR, Marliave JB, Beauth B, Li S, Supernault KJ, Miller KM (2004) Polygamous mating and high levels of genetic variation in lingcod, *Ophiodon elongatus*, of the Strait of Georgia, British Columbia. *Environ Biol Fish* 69(1–4):345–357
- Wood CL, Leslie KL, Greene A, Lam LS, Basnett B, Hamilton SL, Samhuri JF (2021) The weaker sex: male lingcod (*Ophiodon elongatus*) with blue color polymorphism are more burdened by parasites than are other sex–color combinations. *PLoS One* 16(12):e0261202. <https://doi.org/10.1371/journal.pone.0261202>

**Publisher’s note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.