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Decade-scale spatio-temporal variability in maturity of Pacific hake, *Merluccius productus*, along the US West Coast

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Abstract Pacific hake, *Merluccius productus*, is the most abundant groundfish in the California Current Large Marine Ecosystem and plays a vital role in predator–prey dynamics. Hake population dynamics are driven by large annual fluctuations in recruitment and intense levels of harvest. The sustainability of harvests relies on stock assessment models reflecting accurate population trends and life-history parameters, such as the size or age at maturity and the rate at which mature adults fail to spawn. We evaluated biological and functional maturity of Pacific hake from 2009 to 2021 using histological samples collected along the West Coast of North America. Maturity parameters were estimated using a standard asymptotic logistic curve and a more flexible cubic spline to evaluate reductions in functional maturity at older ages. We uncovered temporal variability in maturity across years (length and age at 50% functional maturity ranging from 29.89 to 37.89 cm and 1.93 to 3.24 years). There were also significant increases in functional maturity for fish north of Pt. Conception, CA (nearly 9 cm larger and 1 year older). Pacific hake were found to spawn batches throughout the year and along the entire US West Coast, extending previous reports of spawning occurring primarily in southern California from January to February. To support sustainable fisheries management, biological collections should provide data that allow for consideration of non-stationary life history parameters in stock assessments, such as spatio-temporal differences in maturity.

Keywords Life history · Spatial and temporal variability · Ecosystem-based management · California current · Maturity · Skipped spawning

Introduction

Sustainable fisheries management relies on long-term monitoring of population trends and assessing life-history attributes, i.e., growth and reproductive capacity. Reproductive parameters including the maturity schedule by length or age and the rate

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at which sexually mature adults forego spawning (i.e., skipped spawning) are vital components of age-structured stock assessment models used to determine harvest quotas and inform regulatory management decisions. Spawning biomass models are often a critical derived quantity from stock assessments, and accurate maturity information can help to define how that is interpreted. These parameters may change over space and time, (Jørgensen 1990; Sharpe and Hendry 2009; McBride et al. 2013; Head et al. 2014, 2020; Skjæraasen et al. 2015; Williams et al. 2016) but assessment models typically assume a given stock is demographically homogenous. Thus, there is a need to better understand and integrate spatio-temporal differences in the reproductive biology of a stock into assessment models to improve the robustness of management advice that is often based on estimates of spawning stock size or output.

Life-history strategies of marine fishes often differ spatially and temporally as a result of variable environmental conditions, fishing intensity, and stock structure (Rose et al. 2001; Sharpe and Hendry 2009; Keller et al. 2012; Gertseva et al. 2017). Along the U.S. West Coast, localized oceanographic conditions and productivity within the California Current Large Marine Ecosystem (CCLME) are influenced by coastal topography, broad-scale oceanographic regimes, and seasonal upwelling and downwelling (Cope 2004; Keller et al. 2012; Head et al. 2020). Differences in growth rates, reproduction, natural mortality, and abundance commonly occur for groundfish species in the northeast Pacific region across broad geographic ranges, such as with greenstriped rockfish (*Sebastes elongatus*; Ayers 1859) (Keller et al. 2012), sablefish (*Anoplopoma fimbria*; Pallas 1814) (Head et al. 2014), splitnose rockfish (*Sebastes diploproa*; Gilbert 1890) (Gertseva et al. 2017), aurora rockfish (*Sebastes aurora*; Gilbert 1890) (Head et al. 2020), and lingcod (*Ophiodon elongatus*; Girard 1854) (Lam et al. 2021; Head et al. 2023). The timing and duration of spawning, skipped spawning, and reproductive success both within and across years 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). Spatio-temporal patterns in maturity and growth are important considerations for robust stock assessment models used for management advice (Gerritsen et al. 2003; Kapur et al. 2020).

Reproductive strategy is a defining life-history trait for understanding genetic or phenotypic stock structure (Cadrin et al. 2023). Failing to account for population heterogeneity (e.g., subpopulations) can result in management actions towards the sustainability of one subpopulation while potentially neglecting to protect the other (Cope 2004; Hyde et al. 2008; Cope and Punt 2011; Keller et al. 2022). Many species have been managed as a unit stock across their entire range, despite regional differences in population trends, stock structure, and life-history characteristics (Berger et al. 2017). In addition, data used to inform population dynamic models often come from isolated or seasonally limited studies that represent small portions of a population (Head et al. 2020). As management measures are refined to meet changing fisheries and ecosystem needs (e.g., climate change and blue economy), there has been increased scientific effort to develop management advice in accordance with environmental, biological, and genetic stock structure.

There are at least 18 different species of *Merluccius*, hake, found in the Atlantic and Pacific Oceans (Lloris et al. 2005). The Northeast Pacific hake, *Merluccius productus* (Ayers 1855), population is composed of three genetically distinct stocks including the coastal stock from Southern California (CA) to the Queen Charlotte Sound, Canada (25° N–55° N), the Puget Sound stock, and the Strait of Georgia stock (Iwamoto et al. 2004). A separate dwarf species (*Merluccius hernandezi*; Mathews 1985) is found off Baja, California (Vrooman and Paloma 1977; Mathews 1985; Iwamoto et al. 2004). More recent genetic analysis corroborated a single coastal stock but found some spatial differentiation (Longo et al. 2024). Thus, any coast-wide variability in life history parameters that exists are not linked to genetic structure.

Accordingly, we aim to evaluate how reproductive capacity (rates of maturity and skipped spawning) changes over space and time to inform stock management of Pacific hake, a species that is both important economically and ecologically (Phillips et al. 2023). Here we provide up-to-date coast-wide and regional estimates of maturity across multiple years. We expand upon historical studies, specifically clarifying Pacific hake's reproductive strategy which had not been fully explained previously. This work provides greater insight into shifts in reproductive behaviors under varying environmental conditions over time and thereby increases the ability to project variability in reproductive output under different scenarios.

Materials and methods

Pacific hake

Pacific hake are the most abundant groundfish in the CCLME (Edwards et al. 2022) and play a vital role in predator and prey dynamics (Ressler et al. 2007; Hicks et al. 2013). Hake are ubiquitously distributed along the West Coast of North America (Ressler et al. 2007; Hamel et al. 2015), supporting a large commercial fishery with an annual average catch of 241,467 tons over the past 50 + years (Edwards et al. 2022).

Pacific hake are highly migratory, moving annually in the fall from feeding grounds north of Cape Mendocino, CA to southern California (localized between Cape Mendocino and Pt. Conception, CA) for spawning in the winter (Alverson and Larkins 1969; Bailey 1981, 1982; Bailey et al. 1982; McFarlane and Saunders 1997). Following spawning, adults migrate north every spring and summer, typically as far as Vancouver Island, Canada but there are records off Alaska as well. Locating spawning aggregations has been challenging. Early work, based on egg and larval surveys off California (Bailey et al. 1982), showed latitudinal variability in spawning location, with spawning in higher latitudes occurring during warmer years (Bailey et al. 1982; Hollowed 1992).

Historical studies also indicated that timing of spawning and maturity vary as well (Bailey et al 1982). Larvae were found from December to May (Bailey et al. 1982), suggesting a protracted spawning season, with egg and larval data signifying peak spawning in January and February. Females were reported to mature between the ages of 3 and 4 and at a length of 34 to 40 cm (Best 1963; MacGregor 1966, 1971; Dorn and Saunders 1997), and a latitudinal cline in maturity along the West Coast has been hypothesized (MacGregor 1971).

Sampling methodology

West coast groundfish bottom trawl survey

The Northwest Fisheries Science Center (NWFSC) conducts an annual West Coast Groundfish Bottom Trawl ("trawl") survey to obtain fisheries-independent data on 90 + Fishery Management Plan species, including Pacific hake, for managing and monitoring trends in groundfish stocks. The trawl survey utilizes four chartered West Coast commercial trawl vessels that follow a random depth-stratified sampling design to collectively sample approximately 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 US/Canada to the US/Mexico borders (48° 10′–32° 30′ N) at depths of 55 to 1280 m. A standard Aberdeen-style trawl net with a 3.8 cm (stretched) mesh liner codend, 25.9 m headrope, and 31.7 m footrope is used for all bottom trawling fishing operations (Bradburn et al. 2011; Keller et al. 2017).

After completion of a successful tow, all invertebrates and vertebrates were sorted and weighed using a motion compensated scale (Marel, Reykjavik, Iceland). A subsample of up to 20 Pacific hake were randomly selected for sex determination and fork length (FL, ± 0.5 cm) and mass (± 0.01 kg) measurements. Up to two individuals from this subsample were randomly selected for otolith extraction and subsequent age determination. Otoliths were aged (Chilton and Beamish 1982) by the NWFSC's Cooperative Aging Laboratory with a relatively high level of precision (mean CV of 0.13 across ages) (Edwards et al. 2022). In 2009, and 2012 through 2019, ovaries were collected from a subsample of the female Pacific hake that were selected for ageing, using a stratified sampling method based on length bins to prevent over or under sampling of size ranges.

Joint US-canada integrated ecosystem and pacific hake acoustic-trawl survey

The Integrated Pacific Hake Ecosystem and Acoustic-Trawl ("acoustic") survey is the primary fishery-independent method used to assess the abundance and distribution of hake along the West Coast of the USA and Canada (Clemons et al. 2024). The acoustic survey, which covers the primary extent of the stock, is conducted biennially from approximately mid-June to mid-September by the NWFSC and the Department of Fisheries and Oceans of Canada. An Aleutian Wing Trawl 24/20 mid-water trawl net with a 32 mm codend liner was used for daytime trawling operations. In interim years, acoustic research cruises are completed that also result in trawl-caught Pacific hake, though spatial coverage is not as extensive. During typical trawl operations, trawling speed averages about three knots, with durations lasting only long enough to ensure that an adequate sample is obtained. Trawl locations are not predetermined prior to the survey but are conducted opportunistically and depend on the occurrence and pattern of backscattering layers observed. Trawling can occur from the US-Mexico border up to Dixon Entrance, AK, but typically spans from Point Conception, CA to the Canadian/Alaskan boarder.

In 2016 and 2017, fishery-independent winter surveys (January–February) were conducted to evaluate the feasibility of completing a winter spawning survey and to collect biological samples during the winter months. Acoustic transects on this winter survey spanned from approximately Newport, OR to San Diego, CA, with trawls conducted opportunistically following the same protocols as the standard summer acoustic survey.

Catch was sorted and weighed using a motion compensated scale (Marel, Reykjavik, Iceland) and a random subsample of hake was selected for sex determination, fork length (FL, ± 0.5 cm) and mass (± 0.01 kg) measurements, otolith extraction, visual maturity determination, and diet composition. Ovaries were collected from a subsample of those fish selected for ageing using a stratified sampling method based on length bins in 2012, 2013, 2015–2019, and 2021.

At-sea hake observer program

The NWFSC's At-Sea Hake Observer Program ("observer program") deploys trained fisheries observers on vessels that catch and process at-sea (catcher processor and mothership fleets) targeting Pacific hake from May to December off the coasts of Washington, Oregon, and northern California. Each vessel carries two observers to ensure round-the-clock sampling of hauls for every fishing day. Observers record fishing effort including date, time, location, and total catch. All catch is weighed on a NOAA-certified motion compensated flow scale and observers collect randomized samples to determine catch composition. Random subsamples of Pacific hake are collected for sex determination, fork length (FL, ± 0.5 cm), individual mass (± 0.01 kg), and otolith extraction. Ovaries were excised from a random subsample of hake selected for ageing from 2013 to 2017.

Histological analysis

Ovary samples were placed in 10% neutral buffered formalin immediately after collection for tissue fixation. A subsection, generally from the middle section, of the ovary was cut and then stored in microcassettes for slide preparation. Tissue was embedded in paraffin, thin sectioned to 4 µm, mounted on slides, and stained with hematoxylin and eosin (Sheehan and Hrapchak 1980). Ovary histology was assessed using a Leica DM1000 binocular microscope at 40–400 × magnification with imaging software (Leica Microsystems LAS EX 4.7) to identify reproductive status. We developed a reproductive staging guide after reviewing Pacific hake female gonad tissue slides (Table 1), which followed similar methods outlined for other batch spawning species (Hunter and Macewicz 1985; Murua and Motos 2006; Brown-Peterson et al. 2011; Head et al. 2023) that develop multiple modes of eggs asynchronously (Supplementary Image 1) to be spawned at different times.

Histological analysis included recording the presence/absence of thirteen reproductive phases, corresponding to ten maturity stages (Table 1). We visually estimated the percentage of developing and maturing oocytes in atresia (cellular breakdown and reabsorption of oocytes). Mass atresia, frequently indicating skipped spawning or abortive maturation, is generally defined as ≥ 25% of stage 3 + oocytes in atresia (Rideout et al. 2000; Rideout and Rose 2006; Head et al. 2020). However, Pacific hake were observed aborting whole developing batches of oocytes, while simultaneously recruiting healthy new batches for spawning. This does not necessarily indicate skipped spawning but a reduction in spawning output through aborted partial batches. A female was determined to be a skipped spawner if all mature batches present in the ovary sample were in a state of mass atresia. If there was no indication of previous spawning and only one mature batch was present in mass atresia, we equated this with skipped spawning or abortive maturation as well.

We recorded maturity state according to the following two classifications: biological and functional maturity. Biological maturity (i.e., physiological maturity) identified fish that exhibited maturity

Table 1 Maturity and oocyte development stages for Pacific hake, *Merluccius productus*, with histological descriptions

Maturity stage Oocyte developmental stage	Histological description
Stage 1: Immature (IM) Stage 1: Early perinucleus	Oocytes small with a large nucleolus. Nucleoli begin to develop around the periphery of the nucleus
Stage 1: Immature (IM) Stage 2: Late perinucleus	Larger rounder oocytes, with numerous nucleoli that move within the nucleus
Stage 2: Developing (DEV) Stage 3: Oil droplet formation	Follicle wall thickens and contains granulosa cells. Oil droplets form in the cytoplasm and appear white. Nucleus staining is pink and cytoplasm is dark purple
Stage 3: Early vitellogenesis (EV1) Stage 4.1: Initial yolk formation	Cortical vesicles increase along the periphery of the cytoplasm alongside yolk granules. Granules transition to globules and occupy < 25% of the cytoplasm
Stage 3: Early vitellogenesis (EV2) Stage 4.2: Yolk accumulation	Yolk granules continue to coalesce into globules and increase in size, occupying 25–50% of the cytoplasm
Stage 4: Late vitellogenesis (LV) Stage 5: Late vitellogenesis	Large oocytes with > 50% of cytoplasm area occupied by yolk globules. Yolk globules and oil continue to merge. Zona radiata begins to thicken
Stage 4: Migratory nucleus (MN) Stage 6: Migratory nucleus	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
Stage 5: Hydration (HYD) Stage 7: Early hydration	Yolk globules coalesce forming dark pink stained masses. Yolk masses occupy less than 50% of oocyte
Stage 5: Hydration (HYD) Stage 8: Late hydration	Yolk coalesces into a central mass in the cell; Zona radiata very thick. Close to spawning release
Stage 6: Spawning (SPAWN) Stage 9: Full developed, spawning	Fully coalesced yolk, eggs release from zone radiata. Overlap of stage 9 oocytes and POFs possible. Spawning was occurring at the time of capture
Stage 7: Batch spent (SPAWN) Stage 10: Batch spent	Presence of post ovulatory follicles and possibly residual stage 8 and 9 s from recent batch spawning event. Presence of another mature batch progressing towards spawning. Spawning is not completed for the season
Stage 8: Spent Stage 11: Post spawning/Spent	POFs present and that may be in the resorption process. Residual stage 9 s may be present, along with atretic material. Immature and developing oocytes are present as well, and possibly EV1 and EV2 oocytes
Stage 9: Skipped spawning (SKIP) Stage 12: Skipped spawning	Greater than 25% of oocytes in mature batches in atresia. No indicators of earlier spawning events including POFs and residual hydrated oocytes
Stage 10: Senescence Stage 13: Senescence	Ovarian tissue is inactive, decaying, lacking oogonia or primary oocytes. Degenerating oocytes could be present with misshapen vacuoles. The ovary is reduced in size and becomes translucent

markers (presence of vitellogenic oocytes and more advanced maturity stages), whereas functional maturity additionally took into account fish that biologically could spawn but may not in a given year (Lefebvre and Field 2015; Min et al. 2022; Head et al. 2023). The development of cortical alveoli vesicles is not a strong indicator of maturity in Pacific hake. These generally co-occur with early vitellogenic oocytes and are seen in the highest abundance during the resting/regressing stage of development. Similar trends have been reported in petrale sole (*Eopsetta jordani*) (Lockington 1879) and other species of hake (Lefebvre et al. 2019; Carbonara et al. 2019; Candelma et al. 2021). Thus, maturity stage 3 and oocyte developmental phase 4.1 (early vitellogenesis) or higher were defined as biologically mature. Biologically mature samples exhibiting mass atresia of all maturing batches were identified as functionally immature because their overall contribution to spawning biomass for that year is minimal to non-existent. Functional maturity was defined as fish that contained maturity markers (yolked oocytes and/or post spawning markers) and were not exhibiting juvenile abortive maturation, skipped spawning, or senescence in adults. Therefore, functional maturity was defined as fish with batches in oocyte developmental stages greater than 4.1 and not in mass atresia.

A measure of certainty (1 or 0) was recorded for maturity assignments to reduce the potential for providing inaccurate determinations. Uncertain maturity determinations were possible if flaws in sample preparation impacted the ability to determine maturity status or if timing of collection made it too difficult to assess if spawning had occurred or would occur later in the year indicative of recovering/regenerating fish. The regenerating stage was not recorded because of difficulty separating post-spawning recovering females from late stage mass atresia that can occur in skipped spawners. All uncertain samples were excluded from the maturity analysis.

Because of the frequency of batch spawning events observed in Pacific hake, a category for batch spent (maturity stage 7, Table 1) was also recorded. This helped to separate females that were spent, indicating all batches had been spawned for the season, from individuals that were actively still spawning batches. Batch spent is defined by residuals from a previous batch spawning event, i.e., post ovulatory follicles and residual mature oocytes in atresia, and the presence of other mature batches progressing toward spawning. The final stage in the reproductive cycle, senescence (maturity stage 10, Table 1), was defined as the end of reproductive capability in a fish's life, which can occur in older females. The ovary appeared shrunken and translucent, with the majority of the ovarian tissue inactive, decaying, and lacking oocytes.

Maturity models

Two methods were used to estimate Pacific hake length- and age-based maturity ogives, a logistic model and a cubic spline model. The logistic model fits an asymptotic curve to the proportion of mature female fish at each given 1 cm length or year bin as $P_x = \frac{1}{1+e^{-(\alpha+\beta x)}}$,

where P_x is the proportion mature at length or age x and parameters α and β define the shape and location of the fitted sigmoid curve. The logistic parameters were estimated by fitting a generalized linear model (GLM) to the length or aged fish marked as mature or immature using R (RStudio Team 2023). Length and age at 50% functional or biological maturity (L_{FXN50}, A_{FXN50}, L_{BIO50}, A_{BIO50}) were calculated using the estimates of α and β from the logistic model, where the following example is for age at 50% functional maturity but is generalizable for all length and age calculations: $A_{FXN50} = -\alpha/\beta$.

The cubic spline model allowed for additional flexibility in the maturity ogive and, thus, can capture changes in sexually mature adults that fail to spawn in a given year (Head et al. 2020). This method uses piecewise polynomials to interpolate values between points (Venables and Dichmont 2004), which differs from the logistical S-shaped relationship that assumes constant maturity once 100% maturity is initially reached (i.e., the population continues to be functionally mature for all sizes and ages above the asymptotic point). The number of inflection points in the cubic spline model indicating where some adults fail to spawn was limited by the number of allowable "knots" (see https://github.com/shcaba/Maturity_spline for specific details).

The Delta Method was used to estimate variance and 95% confidence intervals (Seber 1982) associated with size and age at maturity following:

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

where S^2 (L or A_{50}) is the variance at 50% maturity, $\hat{\alpha}$ and $\hat{\beta}$ are parameter estimates of α and β, respectively. $S\left(\hat{\alpha}\right)$ and $S\left(\hat{\beta}\right)$ are the standard errors of $\hat{\alpha}$ and $\hat{\beta}$, respectively, and r is the correlation coefficient of length or age at maturity.

Spatiotemporal analysis of reproductive patterns

We assessed biological and functional maturity size and age across regions of interest based on both management and biogeographic breakpoints. We evaluated size and age at maturity coast-wide (Regions 1–3), north of Cape Mendocino, CA ("Region 1," 40° 10′ N), between Cape Mendocino and Pt. Conception, CA ("Region 2," 40° 10′–34° 26′ N), and South of Pt. Conception to the US/Mexico border ("Region 3," 34° 26′–32° 38′ N) to determine if there was a latitudinal gradient in maturity (Fig. 1). We focused analysis on differences north (Regions 1 and 2) and south of Pt. Conception, CA (Region 3) because initial research on this species found differences in maturity between these regions. Interannual variability in size and age at maturity was estimated for Regions 1–3 and Regions 1 and 2. Data were insufficient for Region 3 across all years of sampling to estimate maturity annually.

We evaluated the reproductive development cycle by examining the frequency of the highest maturity stage present by month across all years because

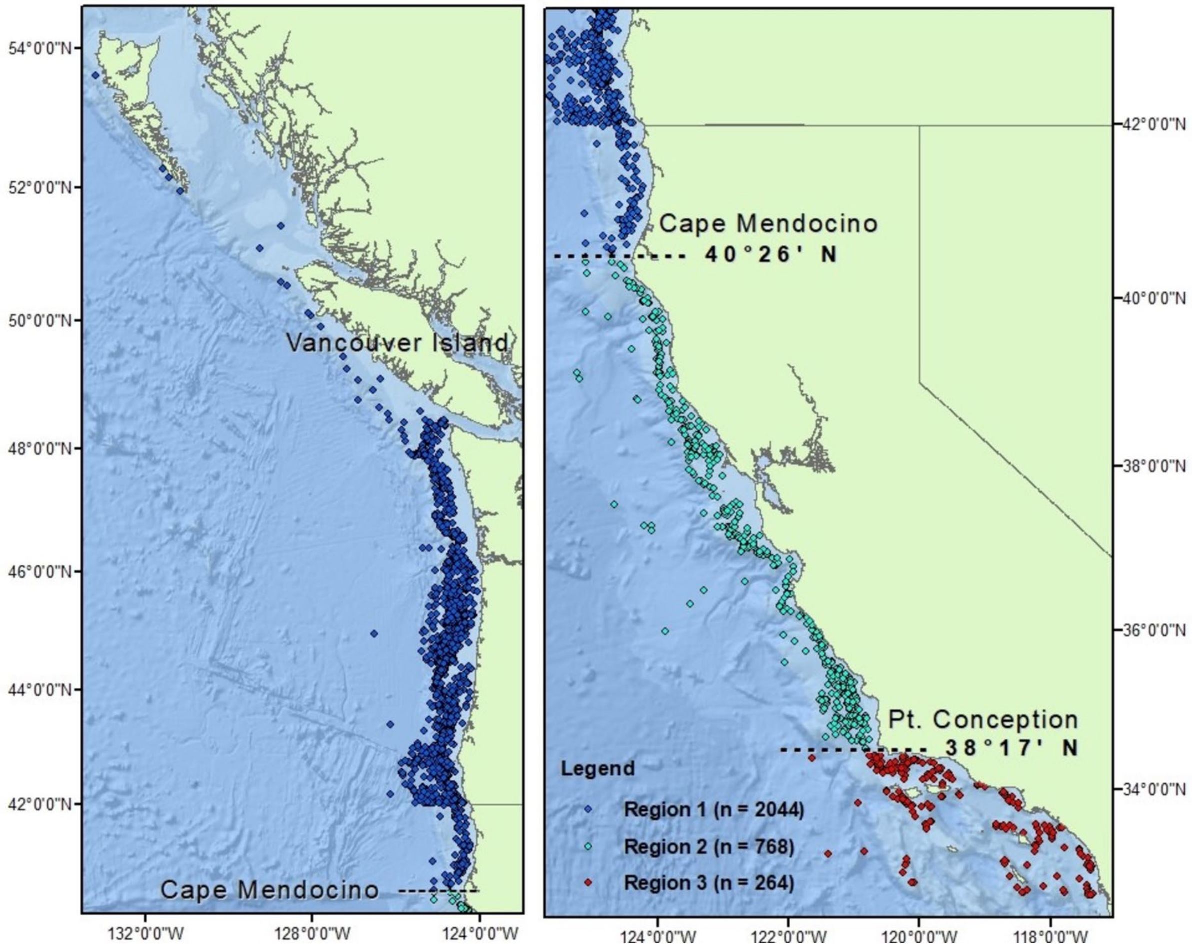


Fig. 1 Distribution of samples collected across Region 1 (shown in blue), Region 2 (shown in cyan), and Region 3 (shown in red). The biogeographic break points for regions are also shown: Cape Mendocino, CA and Pt. Conception, CA. Sample sizes for each region are reported in the figure legend

there were insufficient monthly data when evaluated by year. We excluded stage 1 immature samples from this analysis to focus on the development of maturing individuals during the months of collection. Limited monthly data were available in Region 3, so the analysis was restricted to the months of January, February, June, July, and October.

The start date to delineate seasons was standardized using the fall equinox (09/22), winter solstice (12/21), spring equinox (3/20), and summer solstice (6/21); thus allowing for the evaluation of seasonal changes in the frequency of maturity stages 6–7 ("spawning") and maturity stage 8 ("post spawning"). We evaluated seasonal changes in spawning between and amongst samples north and south of Pt. Conception where data were available. Only samples with complete location information (latitude and bottom depth) were used for this analysis, thus samples collected by the observer program were not used to evaluate the location of spawning and post spawning fish because bottom depth was unknown. Many of the samples collected in the late fall in the northern region were from observers.

Results

Summary of sample collections

We collected Pacific hake, *Merluccius productus*, ovaries in 2009 and then annually from 2012 to

2021, with the exception of 2020 due to the SARS covid-19 pandemic's impact on survey operations (Table 2). The observer program, and the trawl and acoustic surveys collected ovary samples, but consistency between these groups varied from year to year (Table 2). A total of 3470 hake ovaries were available for histological analysis from samples collected from fishery-independent (acoustic and trawl surveys) and fishery-dependent (observer program) sources. The geographic area of samples collected ranged from 53° 37′–32° 38′ N, with 72 samples collected North of the US/Canada border (Fig. 1). Female mass ranged from 0.02 to 3.54 kg, with an average mass of 0.54 kg. The average mass of functionally mature females was 0.66 kg and ranged from 0.08 to 3.54 kg. For reference, the mean weight of age 15–20-year-old Pacific hake was estimated to be 1.031 kg (Edwards et al. 2022). Interannual differences in the mean age (range of mean age, 4.4–5.4; $n=3290$) and length (range of mean length, 40.0–43.6 cm; $n=3470$) of fish sampled suggested that strong year classes did not bias the results of this study, as the mean length and age of females was similar between years (Table 3). Overall, a full complement of population sizes (16–79 cm) and ages (1–21 years) were reflected in available samples.

Analysis of histological observations

Maturity status was determined with 100% certainty for 3076 samples (88% of total samples collected), of these 2908 samples had corresponding age information. Females with uncertain maturity determination had a mean age of 4.3 years and a size of 41.2 cm. Months with the highest level of uncertain maturity determinations were May ($n=130$), June ($n=114$), and July ($n=71$), where uncertainty was largely related to difficulty in determining if a fish was post spawning/regressing or recovering from skipped spawning. In addition, 8% ($n=31$) of uncertain samples were in a mass atretic stage (>25% of oocytes in atresia) creating difficulty in determining whether skipped spawning or partial reabsorption of a batch had occurred.

Skipped spawning in Pacific hake (i.e., all batches in mass atresia) was infrequent (1.3%; $n=40$). These females had a median age of 6 years old, and primarily occurred in Regions 1 and 2 ($n=38$). Skipped spawning females were observed in every sampling year with the exception of 2021, though there was reduced sampling effort during this year (Table 2). Nearly 43% ($n=17$) of skipped spawning females had > 75% of oocytes in atresia (Supplementary Images 2), indicating the potential for complete reproductive failure. Five of these fish were older than 10 years of age. Two females, ages 14 and 16, found near the border of Washington/Canada (47° 49′ N) and just over the border in Canada (51° 57′ N) were senescent (Supplementary Images 3).

Spatio-temporal analysis of size and age at maturity

Of the 3076 ovaries analyzed for biological and functional maturity, 77% ($n=2371$) were biologically mature and 75% ($n=2308$) were functionally mature. Coast-wide (Regions 1–3) biological and functional age at 50% maturity for all years sampled were similar at 2.39 (±0.01) and 2.47 (±0.01) years, respectively. Coast-wide biological and functional length at 50% maturity were 33.96 (±0.09) and 34.33 (±0.09) cm, respectively (Table 3).

Estimates of length at 50% functional maturity between Region 1 (36.38 ± 0.16 cm), Region 2 (36.04 ± 0.34 cm), and Region 1 and 2 (36.09 ± 0.10 cm) were statistically similar, while length at maturity in Region 3 (27.00 ± 0.79 cm) was considerably smaller and statistically different than for the other

Table 2 Summary of Pacific hake ovaries collected by the West Coast Groundfish Bottom Trawl Survey (Trawl), the Integrated Pacific Hake Ecosystem and Acoustic-Trawl (Acoustic), and the At-Sea Hake Observer Program (Observer) from 2009 to 2021

Source	2009	2012	2013	2014	2015	2016	2017	2018	2019	2021	Total
Trawl	263	71	70	271	279	74	107	115	59	0	1309
Acoustic	0	197	257	0	196	131	65	62	66	68	1042
Observer	0	0	206	246	208	258	201	0	0	0	1119
Total	263	268	533	517	683	463	373	177	125	68	3470

Table 3 Pacific hake length (cm) and age (years) at 50% biological (L_{BIO50} or A_{BIO50}) and functional (L_{FXN50} or A_{FXN50}) maturity with ± 95% confidence intervals shown in parenthesis. Several regions of interest with corresponding sample sizes (n) were explored: Coast-wide (Regions 1–3), Canada to Cape Mendocino, CA (Region 1), Mendocino–Pt. Conception (Region 2), south Pt. Conception, CA (Region 3), and north of Pt. Conception, CA (Regions 1 and 2). The range (R) and mean ($\bar{x}$) ages (year) and lengths (cm) sampled by year and region are provided as well

Year	*N*	Age R,$\bar{x}$	A_{BIO50}	A_{FXN50}	*n*	Length R and $\bar{x}$	L_{BIO50}	L_{FXN50}
2009								
Regions 1–3	244	1–13, 4.9	1.84 (0.07)	2.02 (0.09)	246	16–77, 42.0	28.78 (0.96)	29.89 (0.90)
Regions 1 and 2	197	1–13, 5.3	2.62 (0.14)	3.07 (0.12)	199	16–77, 44.0	34.16 (1.65)	35.45 (1.30)
2012								
Regions 1–3	245	1–16, 5.3	2.89 (0.10)	3.24 (0.11)	247	24–74, 42.8	36.99 (1.33)	37.89 (1.23)
Regions 1 and 2	237	1–16, 5.3	2.93 (0.11)	3.29 (0.11)	237	24–74, 43.0	37.26 (0.89)	38.24 (1.46)
2013								
Regions 1–3	423	1–18, 5.1	2.39 (0.06)	2.39 (0.06)	429	22–77, 42.8	35.56 (0.77)	36.02 (0.75)
Regions 1 and 2	416	1–18, 5.1	2.39 (0.07)	2.39 (0.07)	422	22–77, 43.0	35.97 (0.81)	36.39 (0.79)
2014								
Regions 1–3	393	1–16, 5.3	2.00 (0.05)	2.08 (0.05)	451	19–79, 43.6	31.28 (0.64)	32.00 (0.63)
Regions 1 and 2	0	NA	NA	NA	393	22–79, 44.7	34.49 (0.96)	34.99 (0.96)
2015								
Regions 1–3	537	1–17, 5.2	2.26 (0.03)	2.48 (0.04)	607	16–73, 41.1	31.66 (0.40)	32.40 (0.40)
Regions 1 and 2	527	1–17, 5.2	2.22 (0.04)	2.55 (0.04)	554	19–73, 42.4	33.13 (0.49)	34.03 (0.50)
2016								
Regions 1–3	391	1–17, 4.7	2.54 (0.07)	3.01 (0.06)	403	18–69, 40.0	36.26 (0.65)	36.82 (0.65)
Regions 1 and 2	373	1–17, 4.7	2.58 (0.08)	3.06 (0.06)	385	18–69, 40.0	36.77 (0.84)	37.40 (0.70)
2017								
Regions 1–3	339	1–15, 5.2	2.00 (0.06)	1.93 (0.06)	339	17–69, 42.6	32.92 (0.91)	33.03 (0.88)
Regions 1 and 2	320	1–15, 5.3	2.16 (0.08)	2.04 (0.07)	320	21–69, 43.2	35.14 (1.44)	35.08 (1.30)
2018								
Regions 1–3	163	1–21, 5.1	2.27 (0.12)	2.36 (0.12)	170	20–75, 42.5	34.77 (1.49)	34.97 (1.49)
Regions 1 and 2	129	1–21, 5.4	2.03 (0.20)	2.36 (0.18)	134	21–75, 44.8	37.85 (2.61)	38.09 (2.53)
2019								
Regions 1–3	105	1–15, 5.4	2.58 (0.23)	3.17 (0.28)	116	21–76, 42.9	34.05 (2.28)	34.31 (2.72)
Regions 1 and 2	91	1–15, 5.8	2.51 (0.27)	2.86 (0.33)	100	21–76, 44.5	35.73 (2.91)	34.46 (3.47)
2021								
Regions 1–3	68	1–17, 4.4	2.28 (0.28)	2.38 (0.29)	68	22–67, 40.6	35.65 (4.52)	36.21 (4.91)
Regions 1 and 2	0	NA	NA	NA	NA	NA	NA	NA
2009–2021								
Regions 1–3	2908	1–21, 5.1	2.39 (0.01)	2.47 (0.01)	3076	16–79, 42.0	33.96 (0.09)	34.33 (0.09)
Region 1	1990	1–21, 5.4	2.41 (0.01)	2.38 (0.01)	2044	16–77, 43.6	36.60 (0.18)	36.38 (0.16)
Region 2	761	1–17, 4.6	2.65 (0.03)	2.91 (0.03)	768	18–70, 40.7	35.07 (0.35)	36.04 (0.34)
Regions 1 and 2	2751	1–21, 5.2	2.46 (0.01)	2.56 (0.01)	2812	16–79, 42.8	35.84 (0.11)	36.09 (0.10)
Region 3	157	1–14, 3.7	1.46 (0.09)	1.45 (0.09)	264	16–68, 34.0	26.79 (0.79)	27.00 (0.79)

regions (Table 3, Fig. 2). Age at 50% functional maturity was slightly larger in Region 2 than Region 1 and Region 3 (Table 3, Fig. 2). However, the most significant difference in maturity was between Region 1 and 2 pooled and Region 3, where females in Region 3 matured at almost 9 cm smaller and over a year younger than their northern counterparts (Table 3). Differences in the asymptotic relationship between

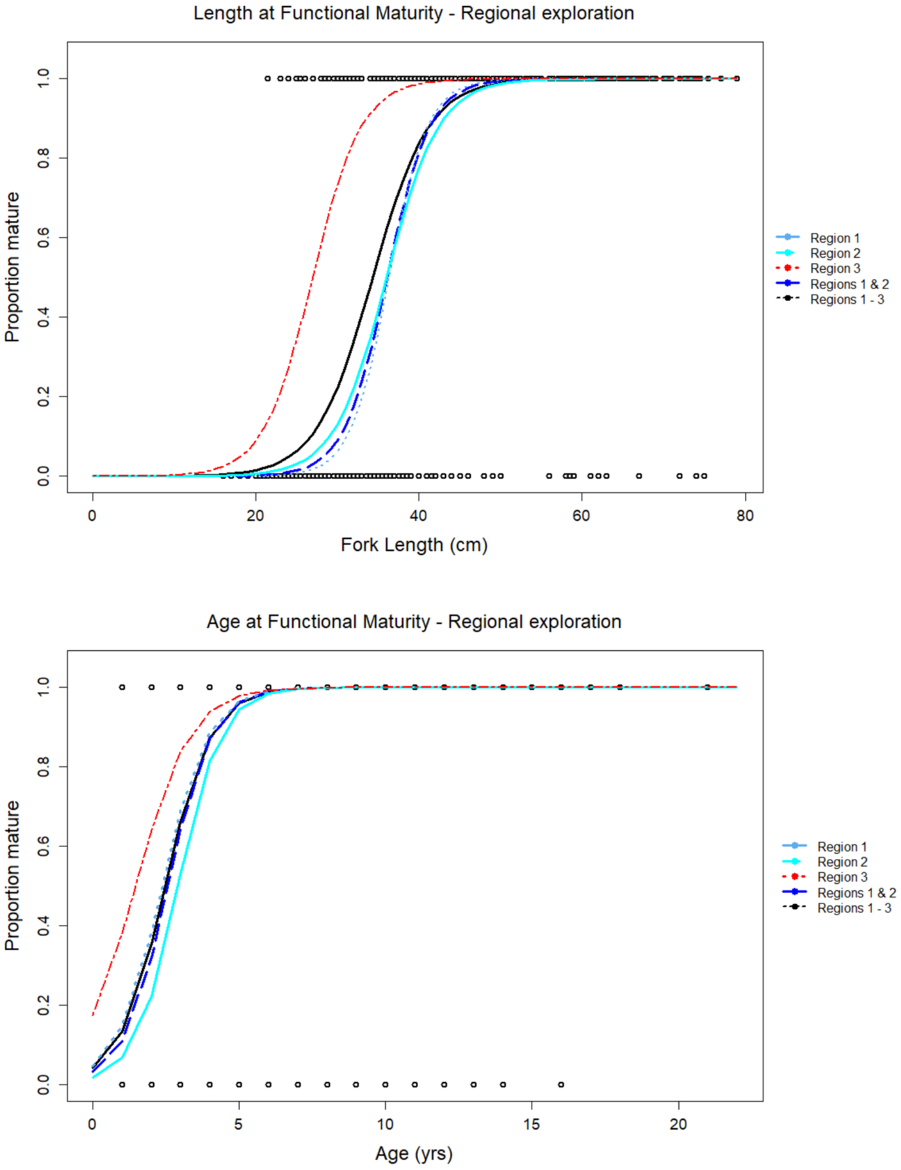


Fig. 2 Length (top panel) and age (bottom panel) at functional maturity using a logistic generalized linear model for the following regions: Region 1 (steel blue dotted line), Region 2 (cyan solid line), Region 3 (red two-dash line), Regions 1 and 2 (blue long-dash line), and Regions 1–3 (black solid line) for all years sampled. Open circles represent the lengths or ages used in analysis

Region 1 and 2 pooled and Region 3 were present when the cubic spline was fit to the data compared to the logistic curve, with minimal skipped spawning ($n = 2$) in Region 3 (Fig. 3).

We also observed interannual variability in size and age at maturity across years (Table 3, Fig. 4). Coast-wide estimates (Regions 1–3) of A_{FXN50} and L_{FXN50} ranged between 1.93–3.24 years and 29.89–37.89 cm (Table 3, Fig. 4), respectively. Some years had overlapping CI for length and age at biological and functional maturity, possibly due to the reduced sampling size when evaluating by year. Though age at biological and functional maturity was statistically different in multiple years of this study and when evaluated for all years combined (Table 3, Fig. 5). Annual estimates of A_{FXN50} and L_{FXN50} for Regions 1 and 2 ranged between 2.04–3.29 years and 34.03–38.24 cm, respectively. The highest estimates of A_{FXN50} in Regions 1 and 2 occurred in 2009, 2012, and 2016, which all had age at 50% maturity >3 years (Table 3, Fig. 5). The lowest estimates of A_{FXN50} in the north were in 2014, 2017, and 2018, which were closer to 2 years at 50% maturity (Table 3, Fig. 5).

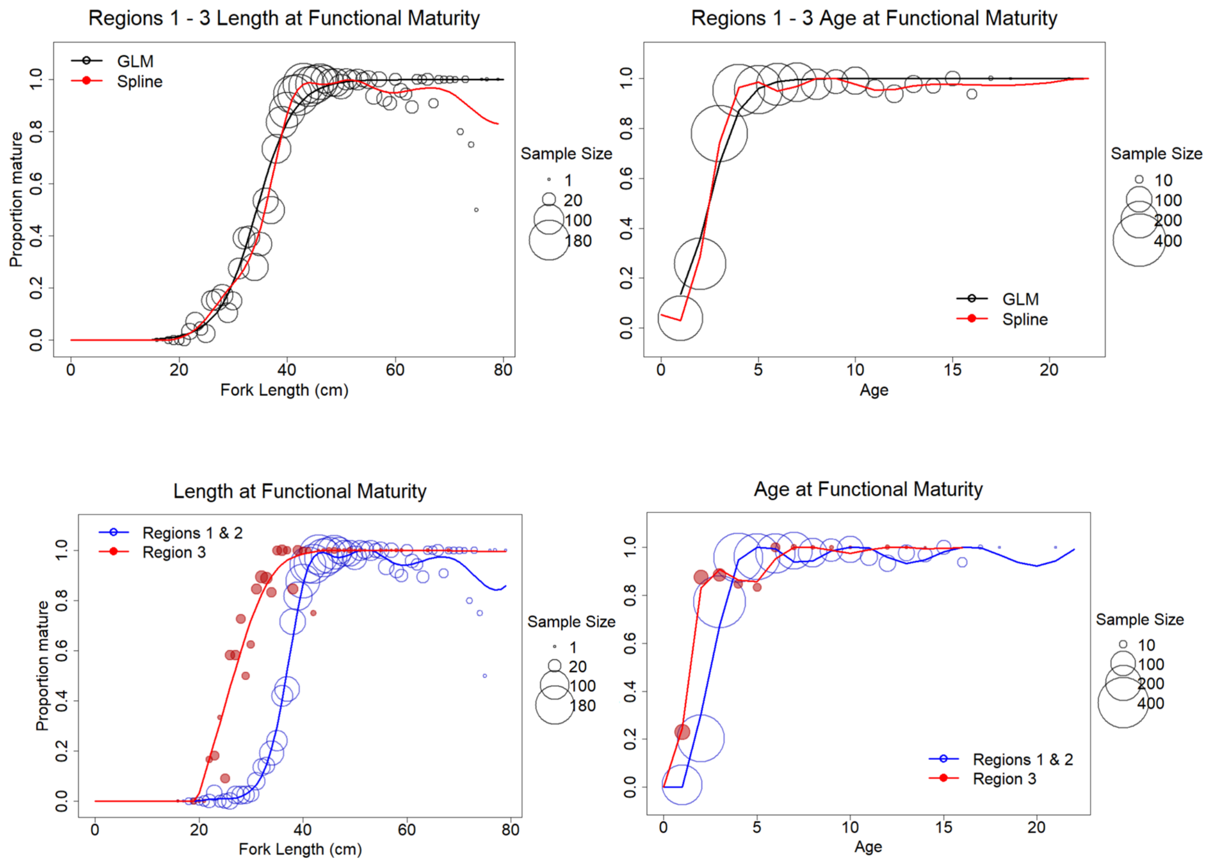
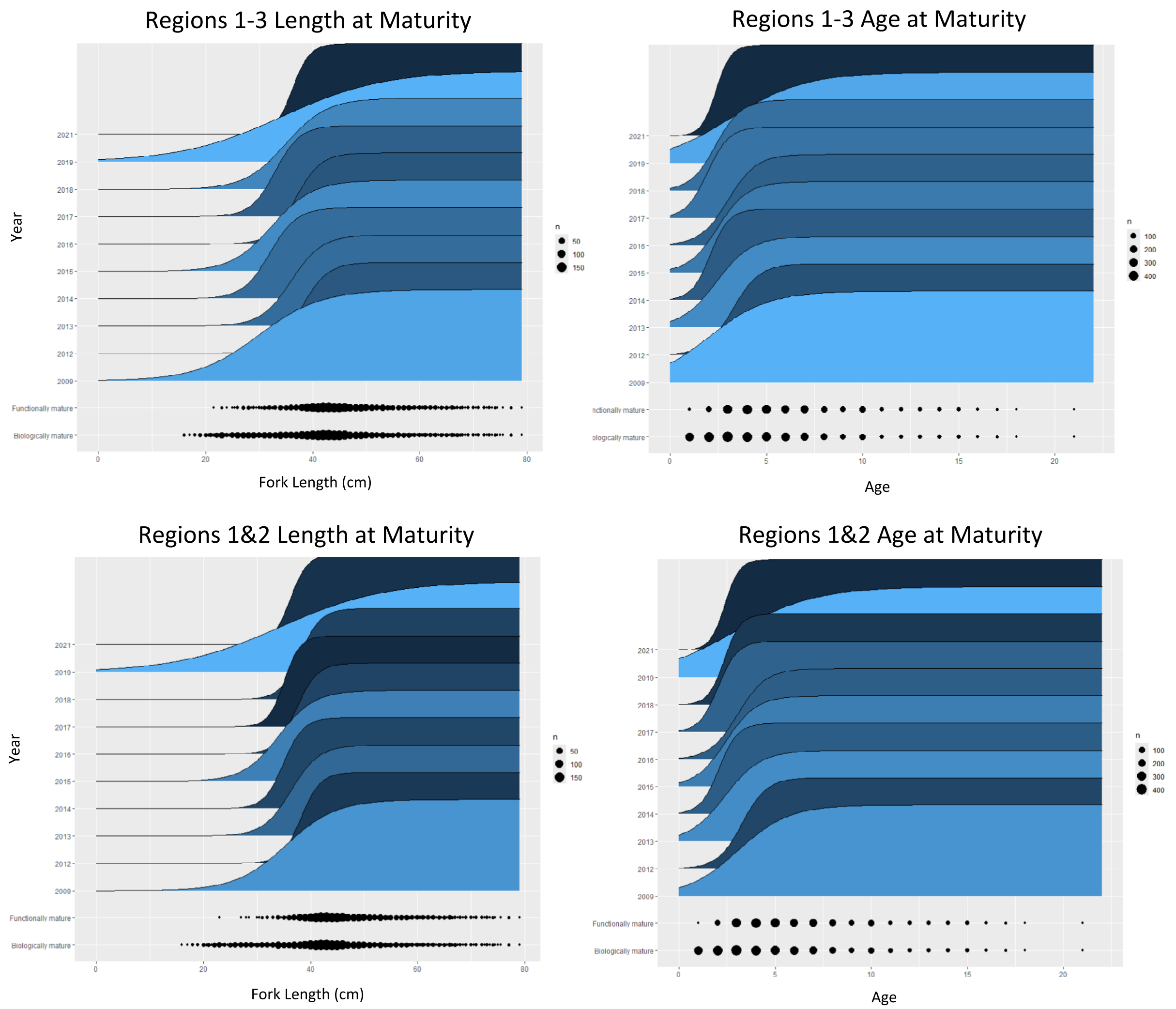


Fig. 3 Comparison of fits from generalized linear models (GLMs) and cubic splines for length (top left) and age (top right) at functional maturity for Regions 1–3 pooled. Cubic spline fits between Regions 1 and 2 (shown in blue) and Region 3 (shown in red) for functional (bottom left) and biological (bottom right) maturity. The size of the bubbles represent the number of samples collected at each length or age bin

Spatial and seasonal changes in spawning and the annual reproductive cycle

Maturity stage 7 (batch spent) was the most frequently recorded stage ($n = 624$, 20.3%; Fig. 6). Defining the end of the spawning season in Pacific hake was challenging, because the next batch initiates quickly thereafter. Batch-spent fish were most often encountered from June to September, representing 78.7% ($n = 491$) of recordings for this stage (Figs. 6 and 7). We observed completely spent fish, indicating the end of the spawning season, 357 times (11.6% of all certain maturity recordings). The highest proportions of spent/post spawning females were observed in May and June (33.3%, $n = 119$ and 39.5%, $n = 141$; Fig. 6). The average size and age of spent females were 48.3 cm and 7.8 years old, respectively. Only five post spawning fish were found in Region 3, and all of those occurred in July (Figs. 6 and 7) from three different years. However, there were zero samples collected in Region 3 during May–June, thus 99% of post spawning fish were found in Regions 1 and 2. Females in full spawning condition ($n = 61$) were present from 52° 16′ N to 32° 39′ N and were most frequently reported in May ($n = 14$) and June ($n = 15$). Spawning fish were observed at an average depth of 311 m (Fig. 7). There was a higher frequency of post spawning females in the spring and summer, and spawning females in Region 1 and 2 were more frequent in the winter (Supplementary Fig. 1).



Regions 1-3 Length at Maturity

Regions 1-3 Age at Maturity

Regions 1&2 Length at Maturity

Regions 1&2 Age at Maturity

Fig. 4 Fork length (left) and age (right) at functional maturity for Regions 1–3 (top panels) and Regions 1 and 2 (bottom panels) regions across years of sampling (2009, 2012–2019, 2021). The color of the ridges represents similarity between years. Number of biologically mature and functionally mature samples at each bin are provided above the *x*-axis, where the size of the dot is indicative of sample size

Discussion

Spatio-temporal estimates of maturity—how does it compare to historical estimates?

We used histological analysis to estimate maturity in Pacific hake, a highly precise method for determining maturity status (West 1990; Hunter and Macewicz 2003). Historical life-history studies on Pacific hake that assessed maturity and spawning were valuable for informing management models but often utilized macroscopic maturity identification (visual inspection of the ovary; Best 1963; MacGregor 1971; Dorn and Saunders 1997; McFarlane and Saunders 1997), were from a limited portion of the stock's geographic range, and/or did not span multiple years (Alverson and Larkins 1969; Ermakov 1982). We evaluated these differences to determine how comparable our results are to earlier studies.

In some historical studies, it was difficult to determine how maturity was estimated (Alverson and Larkins 1969; Ermakov 1982), but estimates of 50% maturity were around 3–4 years and 37–40 cm and generally appear to be based on macroscopic maturity

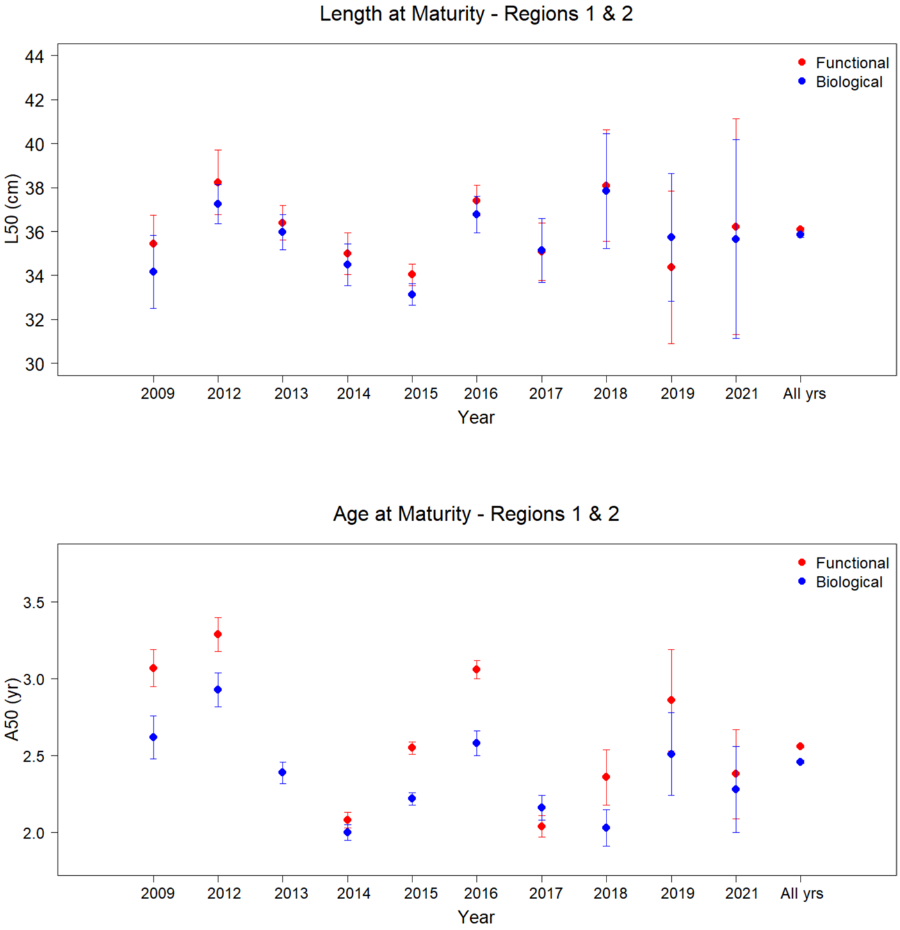


Fig. 5 Length (L_{50}, top panel) and age (A_{50}, bottom panel) at 50% functional (red) and biological (blue) maturity for Regions 1 and 2 across years of sampling (2009, 2012–2019, 2021) with 95% confidence intervals (bars)

(most likely representing biological maturity) (Best 1963; Alverson and Larkins 1969; Ermakov 1982; Bailey et al. 1982; Dorn and Saunders 1997). Macroscopic analysis is widely reported to misidentify maturity stages; including regenerating/resting, skipped spawning, and early developing stages (Saborido-Rey and Junquera 1998; Tomkiewicz et al. 2003; Costa 2009; Min et al. 2022). Failures to account for mass atresia events (skipped spawning) can lead to an overestimation of spawning capacity. Our results indicate historical estimates overestimated maturity and/or size and age at maturity have decreased over time. In our review of historical maturity studies, we found Dorn and Saunders's (1997) 1990–1992 analysis was the most thorough conducted along the US West Coast, which utilized at-sea fishery observers' macroscopic maturity recordings for 1062 females. They estimated 50% maturity at about 3 years and 37 to 38 cm, while our coast-wide functional maturity estimates represent a decrease in maturity at 2.5 years and 34 cm. Though, these macroscopic readings are more likely to represent biological maturity, which we estimated at 2.4 years and 34 cm.

Spatio-temporal trends in maturity

Our study spanned the entire US West Coast, while previous studies were more limited in scope due to reduced coastal survey extent (Bailey et al. 1982; McFarlane and Saunders 1997) or because they were collected from commercial fishing vessel observations (Dorn and Saunders 1997). There did not appear to be a consistent latitudinal gradient in maturity across the spatial extent of the population but rather a more abrupt phenotypic cline in size and age at maturity around Pt. Conception, California. Earlier studies suspected a latitudinal decrease in length at maturity

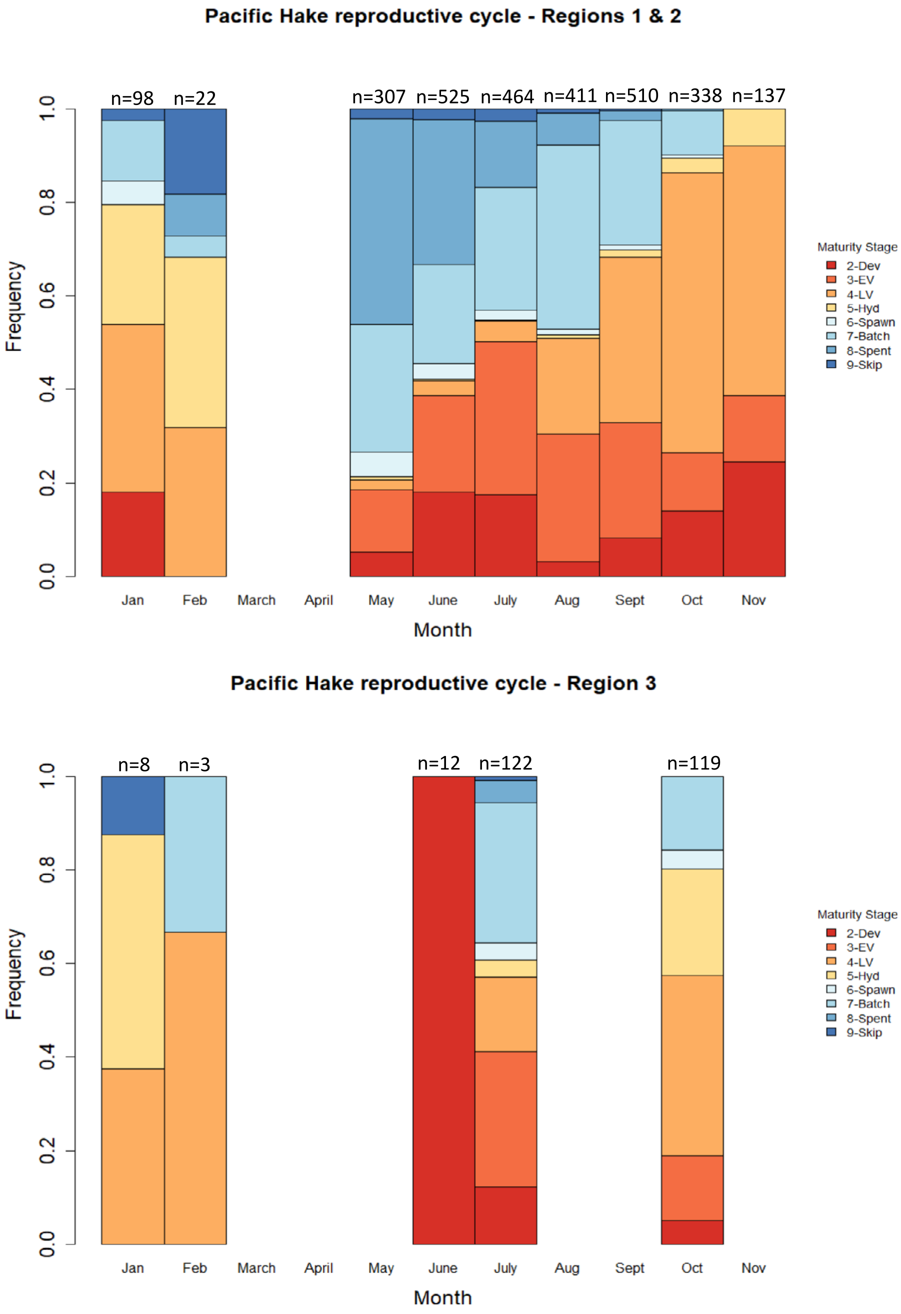


Fig. 6 The annual reproductive cycle by month (January–February, May–November) and region, Regions 1 and 2 (upper panel) and Region 3 (lower panel). Note samples were not collected in March, April, and December. Immature (Stage 1) and senescent (Stage 10) females were removed from this analysis to focus on evaluating developing and mature fish. The number of samples (*n*) collected each month is provided at the top of each bar

with decreasing latitude and reported smaller sizes at maturity (34.0 cm) in Southern California (MacGregor 1966) and Baja California (MacGregor 1971). MacGregor (1971) also reported mature females as small as 22.2 cm off Baja California, but this dwarf hake stock, *Merluccius hernandezi*, was later determined to be a genetically separate species (Iwamoto et al. 2004). It is unknown if the smaller sizes at maturity South of Pt. Conception we found is related to different methodologies for estimating maturity from earlier studies or representative of plasticity in growth and maturity as a response to different environmental conditions.

Many of these earlier studies were constrained to sampling during limited time frames and/or when fishing was occurring. Our study utilized both

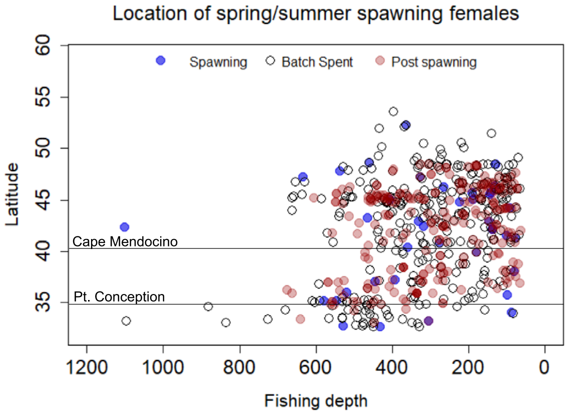


Fig. 7 Location of spawning (blue filled circles), post spawning (red filled circles), and recent batch spent (open black circles) versus fishing depth (m) for Pacific hake females across all years sampled during the spring and summer months (March 20th–September 20th). Latitudinal location of Cape Mendocino and Pt. Conception, CA are shown using horizontal lines

fishery-independent and fishery-dependent sources of information to sample as frequently as possible across multiple seasons over a decade to better track trends in maturity and spawning. This allowed us to refine behaviors of Pacific hake reproductive biology that were not available in earlier studies, i.e., interannual and spatial variability, reproductive strategy, batch spawning success, and timing and length of spawning season. We found interannual variability in size and age at maturity in the coast-wide and in the northern regions at levels up to 8 cm and 1.25 years, which translates to a considerable redefinition of spawning individuals used in population assessments. Piecing together multiple sources of data we were able to evaluate the annual reproductive cycle, but we lacked samples in December, March, and April. These months may provide valuable information about the timing of peak spawning. Unfortunately, there was not consistent annual sampling in Region 3. Thus, we were unable to evaluate interannual changes in maturity or effectively compare the reproductive cycle between Regions 1 and 2 pooled and Region 3. This would be valuable information to pursue in future studies to compare maturity and spawning capabilities between regions.

The mechanisms behind variability could be related to multiple factors including annual and seasonal changes in oceanic conditions, interannual migratory patterns of females south of Pt. Conception and/or fishing-induced selection resulting in decreased age or size at maturity. Further, changes in size and age at maturity are impacted by oceanic conditions in the previous years, as growth rates are influenced by environmental conditions (Neuheimer and Grønkjaer 2012), potentially creating a time lag in the influence on size and age at maturity. Average sea surface temperature (SST) in the CCLME was cooler than usual in 2009 and 2012, while 2016 started off warmer and transitioned to cooler over the year (Fiedler and Mantua 2017; Capotondi et al. 2019), all years that corresponded to high estimates of age at maturity North of Pt. Conception, CA. Our lowest estimates of age at maturity were in 2014 and 2017coinciding with above-average SST in the CCLME (Fiedler and Mantua 2017; Capotondi et al. 2019; NOAA Fisheries 2022). An anomalous multiyear warming trend in the Pacific Northwest (the "Blob") began in 2014 and was amplified by the 2015–2016 El Niño (Bond et al. 2015; Capotondi et al. 2019). Thus, the warmer than usual 2014–2016 conditions may be drivers of the smaller age at maturity in 2017 and the much larger than average sizes at maturity in 2016.

Pacific hake spawning location, recruitment, larval distribution and survival, and distribution of mature individuals are influenced by environmental conditions such as water temperature, upwelling/downwelling, and current velocity (Bailey 1981; Hollowed 1992; Agostini et al. 2006; Hamel et al. 2015; Malick et al. 2020). It is highly possible that interannual variability in rates of maturity are related to an increase in northward latitudinal migration of the portion of the population in Southern California because these fish reach maturity at smaller sizes and ages. There is evidence that Pacific hake move further North in warmer years (Dorn 1995; McFarlane and Saunders 1997; King et al. 2011; Malick et al. 2020), and thus, the fish in Region 3 may migrate further North of Conception in warmer years reducing maturity estimates in Regions 1 and 2. Furthermore, increased rates of length at maturity did not necessarily reflect the same level of increase in age at maturity in our annual estimates. This may be an indicator of fluctuations in growth and/or rates of mortality between years. A more detailed analysis is needed to understand how environmental drivers can impact rates of maturity, spawning, and growth.

The decreased size and age at maturity we observed could be related to differences in methods used to estimate maturity relative to historical studies, an evolutionary response to fishing pressure, and/or changes in environmental conditions. Shifts in size and age at maturity have occurred in heavily exploited species, e.g., North Sea Plaice (*Pleuronectes platessa*; Linnaeus 1758), Atlantic cod, and North Sea cod stock (*Gadus morhua*; Linnaeus 1758) (Rijnsdorp 1993; Trippel 1995; Rowell 1993). This evolutionary response increases a fish's chance of reproducing before fishing mortality can occur (Trippel 1995; Kuparinen and Merilä 2007; Heino et al. 2015). Decreases in size and age at maturity can negatively impact a population's reproductive potential because larger, older individuals are thought to contribute more to spawning biomass (Kuparinen and Merilä 2007). Pacific hake are a heavily targeted species, with peak catches of 440,000 t reported in 2017 (Edwards et al. 2022). It is possible that prolonged fishing pressure, or even intense fishing over a few years, could drive a reduction in age and length at maturity. However phenotypic plasticity caused by changes in the environment could also play a role in decreasing rates of maturity, thus it is challenging to link which variables, e.g., methods, fishing pressure, and changing environmental conditions, are influencing variability in Pacific hake maturity.

Clarifying knowledge of Pacific hake's reproductive biology

When and where are hake spawning?

Historically, Pacific hake were thought to spawn from January to April, with peak spawning in January and February (MacGregor 1971; Bailey 1981, 1982; McFarlane and Saunders 1997). These conclusions were based on observations of spawning females during winter months (McFarlane and Saunders 1997), as well as egg and larvae data from the California Cooperative Oceanic Fisheries Investigations (CALCOFI) ichthyoplankton surveys. It was later demonstrated that CALCOFI surveys were insufficient for sampling Pacific hake, specifically because of inadequate gear design and a reduction in geographic range over time (Hollowed 1989; Ressler et al. 2007).

Our study elucidated the reproductive patterns of Pacific hake over a decadal time frame and along the full geographic extent of the US West Coast. We determined that Pacific hake have a prolonged spawning season that occurs for most of the year, but there may be interannual variability in the length of the spawning season. We were unable to evaluate interannual variability by month of development because of differences in sampling effort between years. In addition, we were unable to obtain samples in December, March, and April. These are months of an expected increase in hydration of eggs and spawning. A more robust study that samples annually by month along the entire coast would be needed to detect potential changes in the spawning season and further describe the annual reproductive cycle. We had a high level of uncertainty in maturity determinations in the months of May through July. Many of these samples may have been post spawning/resting, but the level of tissue degradation made it difficult to determine with certainty. This information is still valuable even if it can not be used for maturity determinations, as it suggests that these months may indicate the end of the spawning season. In addition, females in full spawning condition most frequently occurred in May through June, and post spawning fish were frequently encountered in May through July. Most likely the spawning season is generally wrapping up in July or August, but then there is a quick transition to the next season as we observe females spawning in the fall and winter seasons as well. Other species of hake have also been observed spawning throughout the year, i.e., *Merluccius hubbsi* (Marini 1933), *M. paradoxus* (Franca 1960), *M. capensis* (Castelnau 1861), and *M. merluccius* (Linnaeus 1758) (Osborne et al. 1999; Murua and Motos 2006; Macchi et al. 2018). Interestingly, we observed high rates of the batch spent stage from May to September. It is feasible that a portion of the population spawns for longer time periods, or that remaining batches present during these months were later aborted. In addition, it may be difficult to determine when hake are fully spent, and there could be some overlap in the spent and batch spent stage.

It has long been believed that Pacific hake conduct an annual migration from summer feeding grounds in Northern latitudes to spawning grounds in the winter South of Cape Mendocino, with South of Pt. Conception, CA thought of as the primary spawning location for the coastal stock (Alverson and Larkins 1969; Bailey 1981, 1982; Bailey et al. 1982; McFarlane and Saunders 1997). Our study indicates that spawning is occurring outside of the winter months and across the entire US West Coast. Thus, the reported annual migration may be unrelated to spawning behaviors in Pacific hake and may be correlated to other factors, e.g., prey availability and environmental conditions. In addition, there were earlier reports of a northward increase in spawning location over time (Hollowed 1992; Horne and Smith 1997; Sanders and McFarlane 1997) and, during the 1982 to 1983 El Niño, hake eggs were found off Oregon and Washington (Hollowed 1992). Through the 1990s Pacific hake's range was extended to more northerly waters, which may have been related to warmer surface waters and a reduction in upwelling (King 2005; Ressler et al. 2007). It is unknown if the results of our study are an indicator of change in the annual timing and location of spawning or if earlier studies were not sampling across the full spatial and temporal range of spawning.

What is hake's reproductive strategy?

Previous work concluded that Pacific hake spawned once a year (MacGregor 1966, 1971), but there were some reports of multimodal development of oocytes indicating the potential for multiple batches (MacGregor 1971; Foucher and Beamish 1980; Ermakov 1982; Smith 1995; McFarlane and Saunders 1997) or remaining batches were reabsorbed following spawning (MacGregor 1971). Our results indicate that Pacific hake are indeterminate batch spawners (Hunter and Macewicz 1985), with multimodal asynchronous oocyte development. This reproductive strategy has been confirmed in other species of hake as well (Osborne et al. 1999; Murua et al. 1998; Murua and Motos 2006; Macchi et al. 2018). This is an important clarification for Pacific hake biology, as it could relate to the boom and bust recruitment dynamics of this species. The frequency of batch spawning events and number of eggs spawned will be variable between different environmental regimes for indeterminate batch spawners (Hunter et al.1985; Murua and Motos 2006).

Pacific hake reproductive behaviors appear to be dynamic, with females able to mobilize gametes quickly. It is challenging to discriminate between skipped spawning and temporary down regulation of spawning output in this species. We observed atresia frequently but only confirmed that about 1.3% of fish exhibited mass atresia indicative of complete spawning failure in a given year. Almost all skip spawners were found north of Pt. Conception (Regions 1 and 2) even though the south of Pt. Conception is generally characterized by lower productivity, weaker upwelling, and higher sea surface temperatures (Checkley and Barth 2009). For many groundfish species along the US West Coast, this results in slower growth rates and smaller sizes at maturity (Keller et al. 2012; Head et al. 2023).

Finally, one of the most interesting biological phenomena we observed was reproductive senescence in old females. Senescence is rarely documented in wild fish populations, but is common in other taxa (Reznick et al. 2005; Benoît et al. 2020). However, these fish represent a small portion of the population and would rarely be encountered because of fishing harvest and natural mortality (Benoît et al. 2020). In addition, we observed females over the age of 10 years with catastrophic rates of atresia, which may also indicate a decline in spawning potential as fish age. Senescence has been documented in other fast-growing batch spawning species, i.e., anchovies and herring (Benoît et al. 2018, 2020; Uriarte et al. 2016). Accounting for senescence, which represents an age-specific decline in fecundity, would enhance spawning output models that generally assume older females have higher contribution to spawning biomass.

Capturing biological and functional maturity in management models

Failing to account for non-spawning adults in the maturity ogive and the spatial–temporal dynamics of spawning behavior can result in biased estimates of spawning stock biomass and status relative to biological reference points (Morgan and Brattey 2005; Head et al. 2020). We found minimal change to the length and age at 50% maturity estimates between Regions 1 and 2 and Region 3 for biological maturity, but we found a significant difference in the functional maturity asymptote indicating failures to spawn in the mature population in Regions 1 and 2. The age-at-functional-maturity asymptote was less variable after reaching the initial 100% maturity than the length at functional maturity, which decreased for mature lengths. While females aged 15 and older were infrequently encountered, increased sampling of this age group might reveal a decrease in maturity over the lifespan of Pacific hake because of the presence of senescence and mass atresia events in older females. Overall, the flexibility in the maturity ogive afforded by the cubic spline better represents this species' reproductive dynamics, i.e., skipped spawning and senescence.

Management implications and recommendations

The 2022 Pacific hake stock assessment utilized an age at 50% maturity between 2 and 3 years (Edwards et al. 2022). These estimates came from a subset of the data used in this analysis but did not incorporate the change in asymptote observed in results from the cubic spline model or interannual variability in the maturity ogive. However, uncertainty in the drivers of variability needs to be addressed to make informed assumptions about historical estimates of age and size at maturity. Our lowest age and length at maturity results by year often occurred during warmer years, when Pacific hake are known to move further north (Dorn 1995; McFarlane and Saunders1997; King et al. 2011; Malick et al. 2020), which could be helpful information for reconstructing maturity based on temperature for years without available samples. We were unable to evaluate interannual changes in maturity between Regions 1 and 2 and Region 3 because of unequal sampling in these regions between years. More robust annual sampling in Region 3 is needed to compare regional and interannual differences in maturity.

Currently only maturity information north of Pt. Conception (Regions 1 and 2) is incorporated into the stock assessment, but the Southern portion of the stock (Region 3) may influence life history dynamics in the North. It is unknown how many fish in the southern region move to the northern region and at what level they are exploited in the fishery. Additional research is needed on Pacific hake migratory patterns to understand how the northern and southern portion of this population interact with each other. Generally, the acoustic survey samples from Canada to Pt. Conception biannually during the summer months. It may be beneficial for this survey to sample the US/Mexico border to fully understand the coastal stock biomass, as well as in different months to capture trends in movement and spawning capability.

Fecundity was input as a function of mass-at-age in the 2022 stock assessment (Edwards et al. 2022) but Pacific hake are indeterminate batch spawners and skipped spawning can occur in larger, older fish. Thus, mass-at-age fecundity is not an effective method to capture Pacific hake spawning potential, and a batch fecundity study is needed to understand the spawning output relationship. Because the maturity ogive is variable over time and space, as well as across age, it will be essential to determine how these variables impact spawning output as well. In Argentine hake (*Merluccius hubbsi*), the number of spawning events was related to temperature while batch fecundity was correlated to fish condition (Macchi et al. 2018). We would expect a similar relationship in Pacific hake.

Overall, we believe this research identified needs and suggestions to help ensure sustainable management of the most ecologically important species in the CCLME. In the face of changing oceans, it is pertinent that variability in life history biology, and abundance is accurately tracked and reflected in management models. To do this, long-term monitoring is needed to track trends across changing environmental conditions. This will allow better forecasting of species' response to fishing pressure and environmental stressors. This study elucidated the plasticity of Pacific hake's reproductive biology and the need to incorporate these dynamics in management models.

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Data availability The data and analysis generated for this manuscript are available from the corresponding author on reasonable request. Data collected by NOAA's West Coast Groundfish Bottom Trawl Survey can be accessed through the data warehouse: https://www.webapps.nwfsc.noaa.gov/data/map.

Declarations

Ethical approval Fish sampled in our study were collected as part of the National Oceanic and Atmospheric Administration's (NOAA) Fisheries surveys. Therefore fish were not collected solely for this project. Monitoring by NOAA surveys provides data for stock assessments used to manage marine fisheries. All permitting requirements were completed and a Scientific Research Permit was grated for both surveys. This manuscript was reviewed internally by a NOAA employee and approved for submission in NOAA's Research Publication Tracking System.

Conflict of interest The authors declare no competing interests.

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