

Environmental and ecological changes influence lifetime trends of reproduction, stress, and stable isotopes reconstructed from female yelloweye rockfish opercula

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Climate change threatens fisheries health through changing ecosystem dynamics; however, the impacts on the physiology and ecology of commercial fish populations are unclear. Here, annually deposited growth increments of female yelloweye rockfish (*Sebastes ruberrimus*) opercula collected in the Gulf of Alaska were used to successfully reconstruct lifetime (~1-year resolution) steroid hormone, stable isotope, spawning, and stress data. We assessed how hormone profiles, spawning and distress frequencies related to sea surface temperature (SST), chlorophyll a concentrations as well as climate indices. Further, we assessed whether incorporating indicators of foraging depth and diet, stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), would improve model interpretations. Progesterone and estradiol concentrations decreased with increasing SST, suggesting that increasing SSTs may negatively impact juvenile and subadult females' reproductive development. Spawning frequency was positively linked to changes in the North Pacific Gyre Oscillation (NPGO) index, potentially timed with favorable conditions for larval survival. This was supported by juveniles having a lower probability of a distress event during positive NPGO years compared to negative NPGO years. While relationships among environmental data and yelloweye rockfish physiology were weak, this study provides insight into the environmental impacts on the lifetime reproduction and stress of a commercially important teleost species.

Keywords: biochronology, biomarkers, climate change, fish reproduction.

Introduction

The yelloweye rockfish (*Sebastes ruberrimus*) is a targeted species for commercial, subsistence, and recreational fisheries in the Gulf of Alaska (GOA; Olson *et al.*, 2018). Overfishing of large, adult yelloweye rockfish has led to populations of smaller adults, truncated age classes, decreased biomass, and recent fishery closures (Wood *et al.*, 2021). Further, the genetically distinct “Puget Sound/Georgia Basin” yelloweye rockfish population segment located in Washington State was classified as “Threatened” on the Endangered Species List in 2010 due to overfishing (NOAA, 2018). Given that their long and complex life history makes them especially susceptible to fishing pressure as well as difficult to manage, it is important to understand how environmental stressors such as climate change may impact yelloweye physiology if conservation efforts are to be effective.

Yelloweye and other rockfish species exhibit unique life-history characteristics relative to other teleosts, including slow growth, older ages of maturity, and longer lifespans (>100 years) (Love *et al.*, 2002). The annual viviparous reproductive cycle of a female rockfish, including yelloweye, is dependent on seasonal changes and is timed with events that may support larval success (e.g. increases in primary productivity; Echeverria, 1988; Arthur, 2020). Although the long lifespan of yelloweye potentially allows for reproductive plasticity (e.g. skip spawning and senescence) to compensate for changing environmental conditions (Harvey *et al.*, 2011; Charapata *et al.*, 2022), their dependency on seasonal cues for reproductive success and sedentary lifestyle may make them susceptible to local environmental change. However, no studies have

assessed individual rockfish reproductive and stress physiology across different life-history periods in response to environmental changes.

Anthropogenic climate change, including rising sea surface temperatures (SST) caused by increased CO₂ emissions, has altered ecosystem dynamics including fish recruitment and productivity (Hoegh-Guldberg *et al.*, 2007; Pörtner and Peck, 2010; Litzow *et al.*, 2020a; IPCC, 2022). Long-term (interdecadal) environmental indices derived from SST and sea level pressure changes (Pacific Decadal Oscillation, PDO), wind-driven and horizontal upwelling atmospheric processes (North Pacific Gyre Oscillation, NPGO), or multivariate signals of the environment (Multivariate El Niño-Southern Oscillation Index, MEI) have been used to explain variability in North Pacific ecosystems (Wolter and Timlin, 1993; Mantua *et al.*, 1997; Di Lorenzo *et al.*, 2008). Because several of these climate indices have been correlated to fish production in the North Pacific Ocean (Mantua *et al.*, 1997; Di Lorenzo *et al.*, 2008; Doyle *et al.*, 2009), productivity has been used to assess population resiliency to warming trends (Pörtner and Peck, 2010). Recent advances in the analysis of incrementally grown tissues (e.g. operculum) (Charapata *et al.*, 2022) may be beneficial for obtaining temporal data to assess the physiological responses of teleosts to short-term [SST, chlorophyll a (chl-a) concentrations] and long-term (PDO, NPGO, MEI) environmental variability.

The teleost operculum is an incrementally grown bone that accrues annual light and dark growth increments (GIs), which contain physiological and ecological biomarkers (Panfili *et al.*, 2002; Charapata *et al.*, 2022), including steroid hormones

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(progesterone, estradiol, and cortisol) that help regulate female rockfish reproduction. Progesterone aids in gestation (Xu *et al.*, 2022) and is a precursor to the maturation-inducing hormones (e.g. 17 α , 20 β -Dihydroxy-4-pregnen-3-one) that are responsible for the final maturation of oocytes and stimulating ovulation (Nagahama *et al.*, 1991; Nagahama and Yamashita, 2008). Estradiol activates vitellogenesis within the liver resulting in the production of vitellogenin, a protein that supports growing oocytes (Miura *et al.*, 2007; Nagahama and Yamashita, 2008). Cortisol is associated with the stress response of teleosts (Schreck and Tort, 2016), which releases energetic stores to fulfil increased metabolic demands during reproduction (Schreck, 2009). Reproductive (progesterone and estradiol) and stress-related (cortisol) steroid hormones have been measured in female yelloweye rockfish opercula GIs to reconstruct novel lifetime hormone profiles and estimate age-specific reproductive parameters such as the onset of sexual maturity, spawning frequency, and distress event frequency (Charapata *et al.*, 2022). Similarly, carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope values measured in fish tissues have been used to assess relative foraging area (e.g. pelagic/surface or benthic) and trophic level, respectively (Fuller *et al.*, 2012; Trueman *et al.*, 2014). When paired, these biomarkers provide an opportunity to investigate age-specific impacts of environmental conditions on reproductive activities, stress, and life history patterns. The large size, long lifespan, and non-migratory lifestyle of yelloweye rockfish make them a desirable model species for biomarker analysis in their opercula and the subsequent assessment of how environmental changes impact their physiology and ecology throughout ontogeny.

The objectives of this study are to reconstruct individual lifetime steroid hormone and isotope profiles from female yelloweye rockfish opercula and to (1) estimate life history events and (2) determine the relationships among isotope and environmental data to hormone, reproductive, and stress data. Specifically, we assess how steroid hormone concentrations, spawning frequency, and distress event frequency data are related to SST, chl-a, NPGO, PDO, and MEI environmental data. Secondarily, we assess the feasibility of extracting stable isotopes from opercula, evaluate how steroid hormone profiles relate to paired $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, assess $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with age, and discuss fishery management implications from our results. This study provides vital life history information for those tasked with developing sound fishery management plans for this valuable fish and provides a framework for conducting similar analysis for other long-lived, vulnerable fish species.

Methods

Opercula collection and sampling

Female yelloweye rockfish ($N = 34$) and their opercula were collected in June and July during the 2017 and 2018 NOAA longline surveys in the GOA (Figure 1), and ovary status was assessed in a subset of these fish ($N = 18$) using maturity codes in Hannah *et al.* (2009). Methods for obtaining ages and sampling opercula GIs have been previously published in Charapata *et al.* (2022). Briefly, we used a break and burn technique to highlight the GIs (annuli) of the left otolith and counted annuli to obtain estimated ages (MacLellan, 1997;

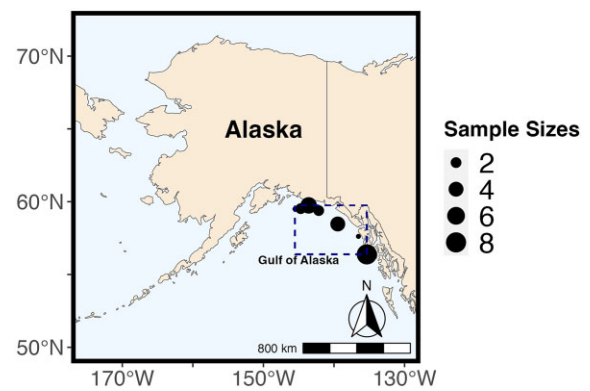


Figure 1. A map showing fish collection sites (black points) during the 2017 and 2018 NOAA longline surveys in the GOA. The size of points indicates the number of fish collected from that location. The rectangle (dashed blue lines) indicates the maximum ranges of latitude and longitude of all fish collection sites and the area where SST and chlorophyll a data were averaged for linear mixed models. Latitude and longitude were unavailable for 11 of 34 individuals and not included in the map.

Andrews *et al.*, 2002; Kerr *et al.*, 2004). We utilized high-resolution photographs of opercula paired with otolith-based age estimates to count and annotate GIs to assist in sampling opercula.

Visible GIs (paired regions of one light + one dark layer) were individually sampled using stainless steel scissors [$n = 536$, 55% of total GIs sampled ($n = 974$)]. The GIs in opercula from some older females were occasionally obscured by yellow substrate, so a protocol was developed to standardize material collection in these circumstances ($n = 438$, 45% of total, Charapata *et al.*, 2022). Briefly, tissue in obscured areas where GIs corresponded to ages that were ≤ 19 years were sampled in 1.0 mm increments, which approximated the average width of an annual visible GI during these years. For GIs representing ages > 19 years, material was sampled in 0.5 mm increments (Supplementary Figure S1). In general, this protocol resulted in a number of GI samples that agreed with otolith age estimates, although it did tend to under-sample older individuals (> 40 years) causing some degree of GI averaging (Charapata *et al.*, 2022).

Steroid hormone and stable isotope analyses

Steroid hormones from individual GIs were extracted with 2:1 chloroform:methanol using a Soxtec (FOSS, Soxtec ST 2043) (Charapata *et al.*, 2022). Detailed extraction protocols and lipid correction factors are included in the Supplementary Material.

Progesterone, estradiol, and cortisol were measured in methanol extracts using previously validated enzyme-linked immunoassay kits (Enzo Life Sciences, Catalog #: ADI-900-011, ADI-900-174, ADI-900-071, respectively) (Charapata *et al.*, 2022). We measured progesterone, estradiol, and cortisol concentrations from $N = 34$ female yelloweye rockfish opercula (age range 15–90 years), for a total of $n = 974$ GIs (Table 1). We added an additional standard to the standard curves for all three hormone assay kits to increase sensitivity of the kits (Hudson *et al.*, 2021). There were still a small number of GIs that had below detectable limits of the cortisol ($n = 1$) and estradiol ($n = 6$) assays. These data were included in analy-

Table 1. Data for individual female yelloweye rockfish opercula sampled including: age, number of GIs sampled from respective opercula, ovary stage at time of capture, length, weight, and whether paired stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) was performed for that individual (Y = "yes").

Sample ID	Age	Number of GIs sampled (<i>n</i>)	Age range of GIs (years)	Ovary stage	Fork length (mm)	Weight (g)	Paired $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$?
17ADU-01-04	19	15	5–19	–	500	2650	–
17NMFS~1(1)	35	33	2–33	–	650	5560	–
17NMFS~1(2)	25	24	1–25	–	419	2760	Y
17NMFS~1(3)	30	25	3.5–30	Resting	570	4240	Y
17NMFS~1(4)	22	22	1–22	–	457	2870	–
17NMFS~1(5)	20	20	1–20	Resting	511	2640	–
17NMFS~1(6)	30	29	1–30	Resting	575	4180	Y
17NMFS~1(7)	29	27	1–29	Maturing/developing	480	2090	Y
17NMFS~1(8)	35	34	1.5–35	Resting	604	4890	–
17NMFS~1(9)	32	29	1–32	Resting	570	3780	–
17NMFS~1(10)	33	32	4.5–33	Resting	626	4530	–
17NMFS~1(11)	48	48	1–48	Resting	670	4970	–
17NMFS~1(12)	51	46	1.5–51	Resting	680	5900	–
17NMFS~1(13)	18	18	1–18	–	545	2840	–
17NMFS~1(14)	42	38	2–42	–	654	5450	–
17NMFS~1(15)	44	42	1–44	–	660	5890	–
17NMFS~1(16)	35*	34	1.5–35	–	580	3930	Y
17NMFS~1(17)	21	21	1–21	–	500	2270	–
17NMFS~1(18)	19	19	1–19	–	412	1300	–
17NMFS~1(19)	17	17	1–17	–	410	1220	–
17NMFS~1(20)	18	17	1–18	–	410	1400	–
18NMFS~1(3)	20	21	1–20	Mature	370	1080	Y
18NMFS~1(4)	20	19	1–20	–	380	–	Y
18NMFS~1(5)	18	20	1–18	Mature	400	1210	Y
18NMFS~1(6)	16	16	1–16	–	360	730	Y
18NMFS~1(7)	15	14	1.5–15	Maturing/juvenile	325	640	Y
18NMFS~1(8)	17	17	1–17	–	395	1190	Y
18NMFS~1(12)	17	17	1–17	Mature	370	910	Y
18NMFS~1(14)	22	20	1–22	–	340	–	Y
18NMFS~1(15)	59	52	1.5–59	Mature	650	5030	Y
18NMFS~1(16)	90	62	1.5–90	Mature	880	6500	–
18NMFS~1(17)	48	47	1–48	Mature	640	4500	–
18NMFS~1(18)	55	51	1–55	Mature	670	6900	–
18NMFS~1(19)	37	28	1.5–37	Mature	635	5160	–

“–” indicates data were not recorded.

*Operculum age estimate was older than otolith (otolith ~30 years, operculum ~35 years) for this fish and the older age was assigned based on the large size and greater number of sampled GIs in the operculum ($n = 34$) compared to otolith age estimate.

sis by assigning half the detection limit [28.36 pg/ml (cortisol) and 7.00 pg/ml (estradiol)] of the respective assay reported by the manufacturer (Charapata *et al.*, 2018). Manufacturer reported inter-assay coefficients of variation were <17% for all assays. Intraassay % coefficients of variation (mean \pm standard deviation) were $4.7 \pm 4.1\%$ (progesterone), $7.3 \pm 7.7\%$ (estradiol), and $6.1 \pm 7.7\%$ (cortisol). All samples were run in duplicate with assays containing standard curves, positive and negative controls, blanks, total activity, non-specific binding, and B_0 wells. All hormone data obtained from assays were lipid corrected and reported as pg/mg lipid.

Following hormone extraction, GIs from the opercula of a subset of samples (14 females, 319 GIs) were retained to perform collagen extractions and obtain $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values. Collagen was extracted following the protocol in Smith *et al.* (2020); the detailed protocol is included in the Supplementary Material.

Stable isotope analysis was conducted at the Baylor University Stable Isotope Facility using an Elemental Analyzer Costech 4010 Elemental Combustion System paired with a Conflow IV interphase (Thermo Scientific) and Thermo Delta V advantage continuous flow Isotope ratio mass spectrometer. Bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are reported as the ratio of the heavy to light isotope relative to recognized inter-

national standards; Vienna Pee Dee Belemnite and atmospheric nitrogen, respectively, using the equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] * 1000,$$

where X is the carbon or nitrogen isotope ratio expressed in delta notation (δ) with units of ‰, R_{sample} is the sample's isotopic ratio of heavy to light isotopes ($^{13}/^{12}\text{C}$ or $^{15}/^{14}\text{N}$), and R_{standard} is the standard's isotopic ratio of heavy to light isotopes. To ensure accuracy and precision, we included an acetanilide standard ($\delta^{13}\text{C}$: -29.53 ± 0.01 ‰; $\delta^{15}\text{N}$: 1.18 ± 0.02 ‰) between approximately every 10 samples. All carbon isotope values were Seuss corrected to account for human depletion of atmospheric carbon isotope values following the Industrial Revolution by using the {SeussR} Shiny App and specifying GOA region (Clark *et al.*, 2021).

Acceptable atomic C:N ratios from studies involving fish bone collagen range from 3.00 to 3.30 (Guiry and Szpak, 2020). The mean atomic C:N ratio of samples from this study was 3.10 ± 0.28 (SD, $n = 319$ GIs). However, a small subset of samples had atomic C:N ratios > 3.30 ($n = 37$) (Supplementary Figure S2), of which, one ($n = 1$) sample had an unusually depleted $\delta^{13}\text{C}$ value and atomic C:N ratio > 3.30 and was removed from further statisti-

cal analysis (Supplementary Figure S2). There is no significant effect of lipid extraction, specifically using a 2:1 chloroform:methanol solvent, on fish bone collagen $\delta^{15}\text{N}$ values (Guiry *et al.*, 2016). Since opercula are bones (Panfili *et al.*, 2002), we assumed our lipid extraction did not alter $\delta^{15}\text{N}$ values.

Assigning age of sexual maturity, potential spawning events, and potential distress events to GIs

Maturity Z-scores were used to identify significant age-specific changes in progesterone, estradiol, and cortisol hormone concentrations (Charapata *et al.*, 2022). *Maturity Z-scores* were calculated for progesterone, estradiol, and cortisol hormones, which standardized measured concentrations in all GIs to known years of female yelloweye rockfish immaturity (1–8.9 years) (Hannah *et al.*, 2009; Charapata *et al.*, 2022) using the equation:

$$\text{Maturity } Z - \text{Score} = (\text{Hormone Conc}_{\text{age } i} - \text{Hormone Conc. Average}_{(\text{ages } 1-8.9)}) / \text{StdDeviation}_{(\text{ages } 1-8.9)}, \quad (1)$$

where “Hormone Conc_{age i}” is the hormone concentrations correlated to each GI at age *i*, “Hormone Conc. Average_(ages 1–8.9)” is the mean hormone concentrations from ages 1 to 8.9, and “Std Deviation_(ages 1–8.9)” is the standard deviations of hormone concentrations from ages 1 to 8.9. Age of sexual maturity was assigned to the first GI with simultaneous peaks (*maturity Z-scores* > 0) in progesterone and estradiol that corresponded to age 8 or above. Spawning events were assigned to subsequent GIs after age of sexual maturity if there were simultaneous peaks in progesterone and estradiol (*maturity Z-scores* > 0), and GIs were marked as being a reproductive (“Y”) or non-reproductive (“N”) GI (Charapata *et al.*, 2022). Estimates where cortisol *maturity Z-scores* were >0 while paired progesterone and estradiol *maturity Z-scores* were negative, were labelled as distress events that resulted in no spawning (Charapata *et al.*, 2022).

Environmental and chlorophyll a data

Monthly environmental and surface chl-a data were acquired for years relevant to this study (1928–2018) to compare with hormone, spawning, and distress event data. Monthly Hadley Centre Sea Surface Temperature data were averaged over the range where fish were collected (59.747 °N, –145.53 °W to 56.383 °N, –135.35 °W, Figure 1, Rayner *et al.*, 2003) from NOAA ERDDAP (<https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdHadISST.html>). MEI data from 1979 to 2018 (Chin *et al.*, 2017) were acquired from NOAA Physical Laboratories (<https://psl.noaa.gov/enso/mei/>). We acquired NPGO data from 1950 to 2018 from Di Lorenzo *et al.* (2008) (<http://www.o3d.org/npgo/npgo.php>). PDO data from 1928 to 2018 (Mantua *et al.*, 1997) were acquired from the NOAA National Centers for Environmental Information (<https://www.ncdc.noaa.gov/teleconnections/pdo/>).

We focused on months relevant to the spring phytoplankton blooms in the GOA (March–June) (Waite and Mueter, 2013) when comparing surface chl-a concentrations with yelloweye rockfish physiology. Thus, we acquired monthly (March, April, May, and June) mean chl-a (mg/m³) concentrations during 2003–2018 from L3 images (9 km resolution) from the National Aeronautics and Space Administration (NASA)

Earthdata OceanColor website (<https://oceancolor.gsfc.nasa.gov/l3/>) using the SeaDAS programme (v7.5.3, <https://seadas.gsfc.nasa.gov/>). Images were given a range in a location like SST, where we restricted averaging of chl-a over locations where fish were caught (59.747 °N, –145.53 °W to 56.383 °N, –135.35 °W, Figure 1).

All monthly environmental data were assigned to GIs based on year of growth, and if there was GI averaging, then environmental data were averaged across respective years. GI averaging is when more tissue than needed was sampled for the targeted 1-year resolution. For example, if we were sampling the GI that correlated to age 9 at 1.0 mm increments according to our sampling paradigm (Supplementary Figure S1), and we sampled 2.0 mm due to human error, this would result in an average hormone signal across ages 9 (our targeted age) and age 8. Thus, we would average any environmental data associated with years 8 and 9 of that individual to match the averaged hormone signal.

Statistical analysis

Linear and general linear mixed modeling of reproductive and stress data with environmental variables and stable isotope values

Prior to constructing linear or generalized linear mixed models (LMMs and GLMMs, respectively), environmental data were refined to include in candidate models by adapting an approach in Matta *et al.* (2018) that assessed similar environmental data (SST and PDO) with growth of an Alaska rockfish derived from otolith GI widths. Specifically, we ran repeated measure correlations using the *rncorr* package in R Studio (Bakdash and Marusich, 2017; RStudio Team, 2020) for each hormone (log₁₀ transformed and minimum *N* = 7 females per age and year, *n* = 680 total GIs) with monthly environmental and chl-a data. Month(s) of environmental variables (SST, MEI, NPGO, and PDO) and chl-a concentrations that were significantly correlated with a hormone, were averaged together to obtain a multi-month index to include in LMMs and GLMMs, respectively (Matta *et al.*, 2018). The results of the repeated measure correlation analyses for all hormones are presented in Supplementary Figure S3 and Supplementary Table S1. Chl-a data were only correlated with log₁₀ transformed estradiol data for the month of March and contained less available years (2003–2018) compared to other environmental variables (1979–2018). Thus, it was not included in LMMs or GLMMs described below. Specifics on the formulation and validation of all full and selected LMMs/GLMMs are provided in the Supplementary Material. LMMs and GLMMs with full random effect structures and varying biologically relevant fixed effect combinations were constructed and compared using AICc (Supplementary Tables S2 and S3) and selected model had the lowest AICc and highest AIC wt (Bolker *et al.*, 2009).

LMMs were used to assess the relationships of steroid hormones with environmental data. Hormone data were log₁₀ transformed to achieve approximate normality. Additionally, a minimum of seven individuals per age and year were included in the model to reduce outlier influence and maximize potential model fit of observed data. This resulted in retaining hormone data during 1979–2018, including female ages ranging from 1 to 42 years on an approximate yearly resolution (*n* = 680 GIs). If “Age” (a continuous numeric variable

in LMMs/GLMMs) was selected as a fixed effect, we classified estimated ages assigned to GIs as “juvenile” for ages 1–7 years (Charapata *et al.*, 2022). The average age of sexual maturity was ~11 years in our sample group, but the estimated functional age of sexual maturity in female yelloweye rockfish is ~17 years based on steroid hormone analysis (Charapata *et al.*, 2022). Thus, we broke up adult years into “subadult” (8–17 years) and “adult” (≥ 18 years) to assess trends in hormones during different life stages (juvenile, subadult, and adult) of female yelloweye rockfish.

LMMs were used to assess relationships of steroid hormones with paired $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Since a reduced number of GIs were analysed for stable isotopes, we retained samples where there was a minimum of four individuals per age ($n = 260$ GIs) (Charapata *et al.*, 2022) and also performed repeated measure correlations of \log_{10} transformed hormones with all $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from 14 female rockfish ($n = 318$ GIs).

GLMMs with a binomial distribution (link = “logit”) were used to model the probability of spawning and distressed events across environmental variables (Brown, 2021). For spawning probability models, only reproductive years (i.e. GIs deposited post-sexual maturity assignment) with a minimum of seven individuals ($n = 418$ GIs) per age (9–42) and year (1992–2018) and only environmental variables that were in the candidate progesterone and estradiol models were used (Supplementary Table S1). Spawning frequencies throughout the time series (1992–2018) were qualitatively compared to spawning frequencies in 2014–2018, years in which anomalously warm ocean temperatures occurred in the GOA (Litzow *et al.*, 2020a). For distress probability models, all years with a minimum of seven unique fish per age and year ($n = 680$ GIs) were included, and environmental variables in the candidate steroid hormone LMMs were assessed (Supplementary Table S1).

While our criteria for distress events centred around suppressing potential spawning activity reserved for mature adults, we did include juvenile ages (1–7 years) in the distress GLMMs described above, because distress events detected during juvenile years significantly delayed the onset of sexual maturity. Specifically, we grouped females into two groups; those that did not experience a distress event prior to sexual maturity ($N = 18$) and those that did ($N = 16$), and compared their median ages of sexual maturity. We found females with a documented distress event prior to maturity took ~1 year longer to reach maturity, had a greater distribution towards older ages of maturity (Supplementary Figure S4) and had the oldest age of sexual maturity [median \pm interquartile range (IQR), min–max, 9.3 ± 3.25 , 8–32 years] compared to females who did not experience a distress event prior to maturity (8.5 ± 1 , 8–19.5 years). The difference in median age of sexual maturity between distressed (9.3 years) and non-distressed (8.5 years) was significant (one-sided Wilcoxon rank sum test, $W = 91.5$, $p = 0.03$).

Stable isotope values with location and age

Temporal changes in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were analysed by testing if estimated marginal mean (EMM) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were different among age classes (juveniles, subadults, and adults) using LMMs where “Age Class” was a fixed effect and a random intercept per individual fish was included ($N = 14$ females, $n = 318$ GIs). Type II analysis of variance

(ANOVAs) with post-hoc Tukey Tests was used to analyse EMM for all stable isotope data among age classes using the package *emmeans* (Lenth *et al.*, 2018). General additive models (GAMs) using package *mgcv* (Wood, 2011, 2017) with random effect of sample ID and restricted maximum likelihood were used to investigate nonlinear trends across age and location. Diagnostic plots were developed using the package *gratia* (Simpson Gavin, 2022). However, adding location (Figure 1) as a factor into GAMs did not pass diagnostics, so assessment was qualitatively determined for potential location effects with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. This was due to low sample sizes with location and stable isotope data [$n = 3$ stations (Figure 1) with $N = 1$ fish each analysed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and $n = 1$ station with $N = 8$ fish]. An alpha of 0.05 was used to assess significance among relevant statistical analyses.

Results

Steroid hormone associations with environmental and chlorophyll a data

All steroid hormones had significant, albeit weak, correlations with environmental variables, except for MEI (i.e. SST, PDO, and NPGO; Supplementary Figure S3). Progesterone and estradiol had significant negative correlations with winter and summer SST data, respectively (repeated measures correlations, $r = -0.08$; progesterone, $r = -0.08$; estradiol, $p < 0.05$ for both hormones, Supplementary Figures S3, S5, and S6), while cortisol had significant positive correlations with May and June SST data ($r = 0.08$, $p < 0.05$, Supplementary Figures S3 and S7). The range of significant negative correlations for progesterone and estradiol with PDO monthly indices was -0.08 to -0.13 ($p < 0.05$, Supplementary Figure S3). Progesterone and estradiol were significantly positively correlated with NPGO monthly indices resulting in coefficients ranging from 0.08 to 0.11 ($p < 0.05$, Supplementary Figure S3). Estradiol was the only hormone to have a significant negative correlation with March chl-a concentration ($r = -0.10$, $p = 0.04$).

LMM results—steroid hormone relationships with environmental variables and stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) values

The LMM results for progesterone and estradiol retained age and SST in the top model based on the lowest AICc and highest AIC weight (Table 2). Both hormones increased with age and decreased with increases in SST (Table 2). These negative relationships between progesterone and estradiol and SST occurred during different months; progesterone related to winter temperatures (i.e. January, Supplementary Table S1, Table 2, and Figure 2), and estradiol with summer months (July and August, Supplementary Table S1, Table 2, and Figure 2). Females who became sexually mature between 8 and 11 years ($N = 21$) had progesterone and estradiol concentrations within the 95% confidence intervals of LMM predictions during juvenile, subadult, and adult ages (Figure 2). However, there was evidence that some adult females had a positive relationship of progesterone and estradiol with increasing SSTs (Supplementary Figure S8).

The selected cortisol LMM only retained “Age” as a fixed effect, which had a positive relationship with cortisol concentrations (Table 2). Observed cortisol concentrations increased as females aged (Figure 3), supporting the LMM results.

Table 2. Selected linear and generalized linear mixed models (bolded LMM and GLMM, respectively) for each dependent variable (progesterone, estradiol, cortisol, spawning frequency, and distress event frequency) based on AICc selection criteria and respective fixed effect estimates and std. errors.

Variable	Formula	K	AICc	Δ AICc	AICc wt	Total wt	Fixed effects	Estimate	Std. error
Progesterone	Log10(Pro)~ Age + SST + (Age Sample ID)	7	-76.64	0.00	0.56	0.56	(Intercept)	2.36	0.09
							Age	0.007	0.002
							SST	-0.05	0.01
Estradiol	Log10(Est)~ Age + SST + (Age Sample ID)	7	89.18	0.00	0.37	0.37	(Intercept)	2.17	0.14
	Log10(Est)~ Age + NPGO + (Age Sample ID)	7	90.35	1.17	0.20	0.57	Age	0.006	0.003
	Log10(Est)~ Age + SST + PDO + (Age Sample ID)	8	90.78	1.60	0.17	0.74	SST	-0.03	0.01
Cortisol	Log10(Cort)~ Age + (Age Sample ID) + (1 Year)	7	8.90	0.00	0.72	0.72	(Intercept)	1.89	0.052
	Log10(Cort)~ Age + SST + (Age Sample ID) + (1 Year)	8	10.88	1.98	0.27	0.99	Age	0.008	0.002
Spawning frequency	Spawning Event ("Y" or "N") ~ NPGO + (Age Sample ID)	5	480.59	0.00	0.30	0.30	(Intercept)	0.32	0.34
	Spawning Event ("Y" or "N") ~ Age + NPGO + (Age Sample ID)	6	482.46	1.87	0.12	0.42	NPGO	0.22	0.11
	Spawning Event ("Y" or "N") ~ SST + (Age Sample ID)	5	482.53	1.94	0.12	0.54			
Distress event frequency	Distress Event ("0", "1") ~ Age + NPGO + (1 Sample ID)	4	277.35	0.00	0.23	0.23	(Intercept)	-2.20	0.35
	Distress Event ("0", "1") ~ Age + SST + (1 Sample ID)	4	278.22	0.87	0.15	0.39	Age	-0.05	0.02
	Distress Event ("0", "1") ~ Age + PDO + (1 Sample ID)	4	278.45	1.10	0.14	0.52	NPGO	-0.40	0.16

The selected (bolded) and next two competitive models' (within 2 AICc) formulas, and AICc information [number of parameters (*K*), Akaike information criteria for small sample sizes (AICc), change in AICc from top selected model (Δ AICc), proportion of predictive power compared to candidate model set (AICc wt), and cumulative predictive power (Total wt)] information are provided for each variable.

Note: No other model was within 2 AICc for progesterone.

There were no selected hormone LMMs that retained $\delta^{15}\text{N}$ and/or $\delta^{13}\text{C}$ values as fixed effects (Table 3). Only progesterone was significantly positively correlated with $\delta^{13}\text{C}$ values (repeated measure correlations, $r = 0.19$, $p = 0.003$, Supplementary Figure S9). Mean collagen yield from opercula GIs was $19.69 \pm 6.89\%$ (1.75–40.00%, min–max, respectively, $n = 242$ GIs).

GLMM results—spawning and distress event frequencies' relationships with environmental variables

Spawning frequency, the percentage chance a female spawned in any year, had a positive relationship with the NPGO index based on the GLMM with the lowest AICc and highest AICc weight (Table 2). Specifically, females had $\sim 1.25\times$ greater odds of spawning when the NPGO index increased by 1 (exponentiated $\beta = 1.25 \pm 1.11$ odds ratio, Table 2). This equated to mean predicted probabilities increasing from ~ 45 to 67% chance of spawning over the complete range of negative to positive NPGO indices assessed in this study (Figure 4). Predicted mean $\pm 95\%$ CI spawning frequencies from the GLMM captured the general increasing spawning frequency trend observed with increases in the NPGO index (Figure 4), but did not explain most of the variability in spawning frequency based on the model's AIC wt (Table 2). There was a qualitatively modest decrease in spawning frequency during

years with anomalously high SSTs from 63% in 2014 to 50% in 2018 (Figure 5).

Distress event frequencies were partly explained by differences in age and the NPGO index (Table 2). Distress event frequency had a lower chance of occurring as females aged and a more positive NPGO index (Table 2). This translated into predicted exponential decreases in frequencies of distress events (keeping NPGO at a constant positive value of 1.05) with age from a mean 6.56% (2.91–11.11%, 95% CI) at ~ 1 year to 1.00% (0.18–2.63%) at 42 years (Figure 6). When the NPGO index was held at a negative value of -0.92 , distress event occurrence decreased with age, but mean frequency of distress events at age 1 was relatively high at a mean 13.24% (6.70–22.97%, 95% CI) occurrence before decreasing to 2.10% (0.47–5.40%) at ~ 42 years (Figure 6). Like spawning frequency, differences in age and NPGO index explained significant, but a small amount of variability in distress frequency based on the model's AIC wt (Table 2).

Stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) associations with age and location

EMM $\delta^{13}\text{C}$ values were significantly different among age classes (ANOVA, $p < 0.001$). Adults had significantly higher $\delta^{13}\text{C}$ values compared to juveniles (Tukey, $p = 0.001$; juvenile), but not subadults ($p = 0.56$). There were no significant

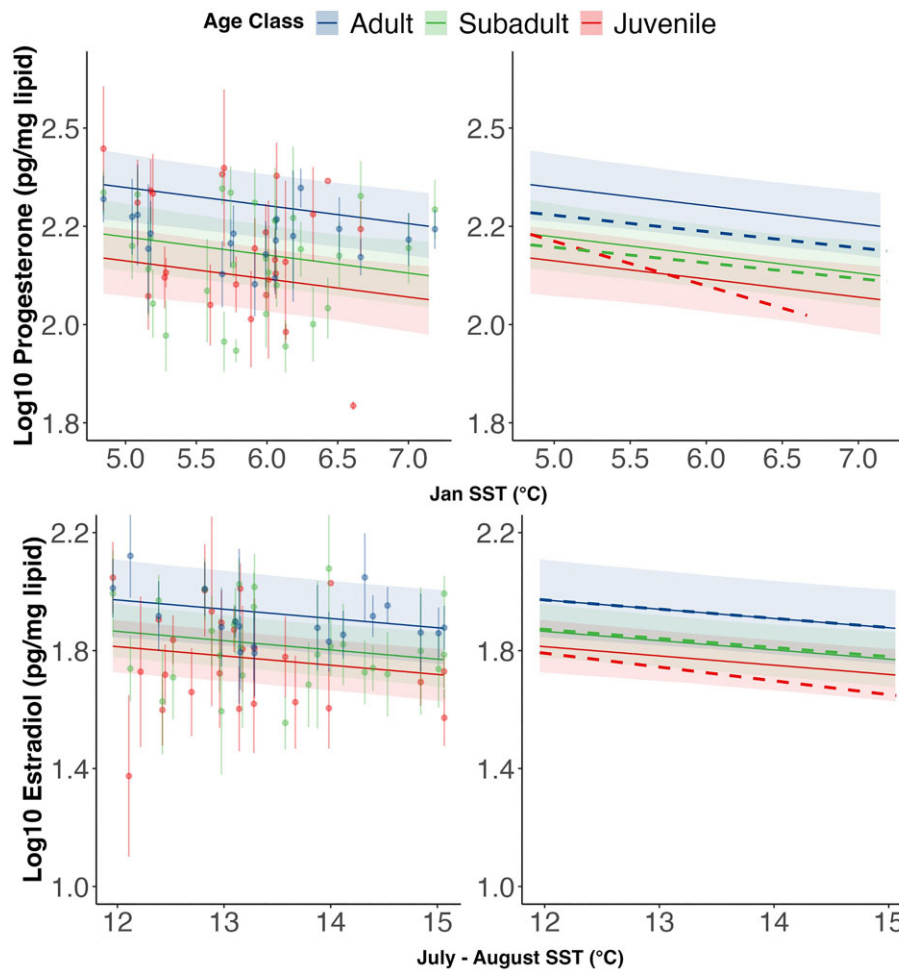


Figure 2. Mean \pm SE of log₁₀ transformed progesterone (top panels) and estradiol (bottom panels) concentrations (pg/mg lipid) measured in female yelloweye rockfish opercula GIs plotted by January (progesterone) and averaged July–August (estradiol) SST ($^{\circ}$ C) and coloured by age class (left panels). Juveniles were classified as ages 1–7 years (red points), subadults 8–17 years (green points), and adults \geq 18 years (blue points). Solid lines represent predictions from selected linear mixed models (LMMs), and shaded ribbons represent the 95% confidence intervals of fitted values for each respective age class. The linear trend of observed data among different age classes (dashed lines) was also plotted with model predictions (right panels) for a clearer visualization of overall trends. Observed data include only females that reached sexual maturity between ages 8 and 11 years ($N = 21$).

nonlinear trends in $\delta^{13}\text{C}$ across age (GAM, $p > 0.05$, Figure 7).

EMM $\delta^{15}\text{N}$ values were not significantly different among age classes ($\delta^{15}\text{N} = 14.8 \pm 0.15$ (SE) ‰; juveniles, 14.7 ± 0.15 ‰; subadults, and 14.8 ± 0.16 ‰; adults, ANOVA, $p = 0.31$). However, there were significant nonlinear trends in $\delta^{15}\text{N}$ values with age (GAM, $p < 0.001$). $\delta^{15}\text{N}$ values of ages with a minimum of four individuals (~ 1 –29 years) did increase with age, but the variation in $\delta^{15}\text{N}$ values within this age range was small 14.56–15.06 ‰ (Figure 7). Sample sizes were limited in later years, but $\delta^{15}\text{N}$ values increased once fish reached ~ 24 years (Figure 7). Visual increases of $\delta^{15}\text{N}$ after 29 years (max $\delta^{15}\text{N} = 17.87$ ‰ at ~ 37 years) were driven by 1–2 individuals (Figure 7).

Location differences in stable isotope values were assessed qualitatively due to low sample sizes, but there were visual differences in distributions and mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among catch locations (Figure 8).

Discussion

Understanding changes in species-specific reproduction and stress becomes crucial as marine environments continue to change, so that management and conservation efforts are informed and effective. In this study, we reconstructed and determined the associations among lifetime reproductive and stress data obtained from female yelloweye rockfish opercula with accompanying environmental and ecological data to fill knowledge gaps in this species. We found that reproductive hormones in females negatively correlated with increasing SST. Additionally, we found reproductive success increased and distress events decreased during environmental conditions associated with a positive NPGO. These novel results provide insight into the impact of various environmental changes on the lifetime reproductive and stress physiology of female yelloweye rockfish, which may help future management/conservation decisions.

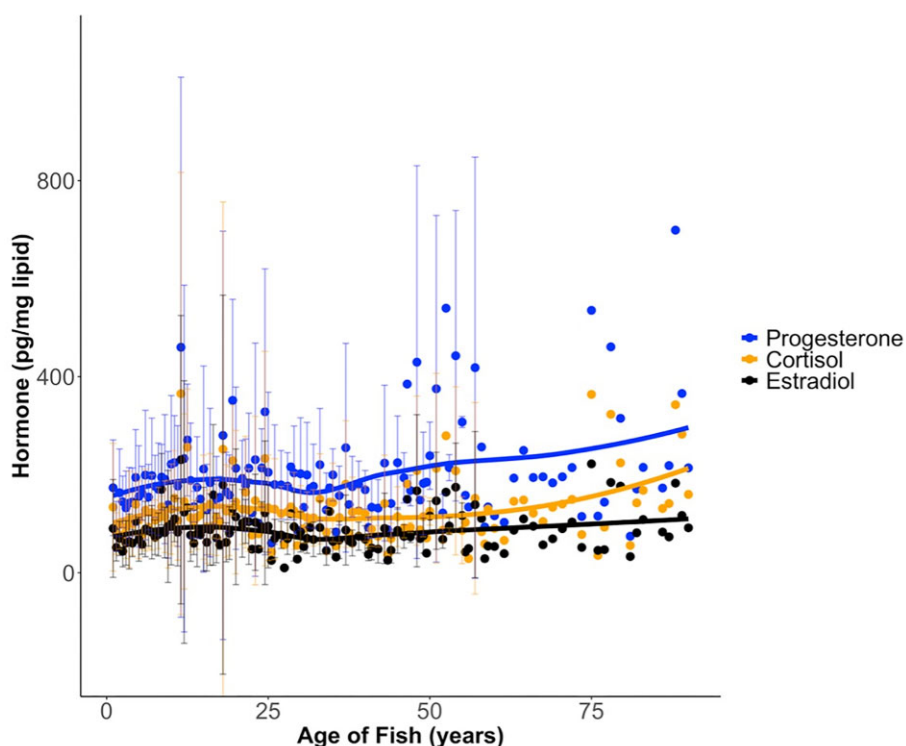


Figure 3. Overview of steroid hormone concentrations (pg/mg lipid) by age of female yelloweye rockfish. Mean progesterone (blue), cortisol (orange), and estradiol (black) concentrations (pg/mg lipid) measured in female yelloweye rockfish ($N = 34$ individuals) opercula GIs ($n = 974$) that correspond to their respective age. Points without error bars had a $N = 1$ female for those ages. Trendlines were generated using loess smoothing method.

Table 3 . Selected linear mixed models for each hormone assessing relationships with paired $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and age as fixed effects (see Supplementary Table S3) based on AICc selection criteria and respective fixed effect estimates and std. errors.

Variable	Formula	K	AICc	ΔAICc	AICc wt	Total wt	Fixed effects	Estimate	Std. error
Progesterone	Log10(Progesterone)~ Age + (1 Sample ID) + (1 Age)	5	-0.29	0.00	0.39	0.39	(Intercept)	2.13	0.06
	Log10(Progesterone)~Age + $\delta^{13}\text{C}$ + (1 Sample ID) + (1 Age)	6	0.60	0.89	0.25	0.65	Age	0.01	0.00
	Log10(Progesterone)~Age + $\delta^{15}\text{N}$ + (1 Sample ID) + (1 Age)	6	0.91	1.21	0.22	0.86			
Estradiol	Log10(Estradiol)~ Age + (Age Sample ID)	6	135.47	0.00	0.28	0.28	(Intercept)	1.75	0.08
	Log10(Estradiol)~ 1 + (Age Sample ID)	5	135.71	0.24	0.25	0.53	Age	0.010	0.006
	Log10(Estradiol)~ Age + $\delta^{15}\text{N}$ + (Age Sample ID)	7	137.28	1.82	0.11	0.64			
Cortisol	Log10(Cortisol)~ Age + (Age Sample ID)	6	58.52	0.00	0.41	0.41	(Intercept)	1.98	0.06
							Age	0.010	0.004

Bolded model number indicates the top-selected model for that hormone and the subsequent formula and AICc information [number of parameters (K), Akaike information criteria for small sample sizes (AICc), change in AICc from top-selected model (ΔAICc), proportion of predictive power compared to candidate model set (AICc weight), and cumulative predictive power (Total wt)]. The fixed effects' coefficient estimate and std. error are included for the selected model in bold. Models within 2 AICc of selected model are presented for reference.

Steroid hormone relationships with environmental variables and age

Juvenile female teleosts maintain circadian rhythm of reproductive hormones, including progesterone and estradiol (Atteke *et al.*, 2003; Min *et al.*, 2018). Functions of reproductive hormones during immaturity, not related to reproduction,

may be activating a part of the stress response (Baker and Katsu, 2020), help regulate the immune system (Yamaguchi *et al.*, 2001), or a host of other functions (reviewed in Tokarz *et al.*, 2015). Overall, reproductive hormones play important physiological roles in immature teleosts in addition to sexual development and do not remain stable during immaturity (1–7

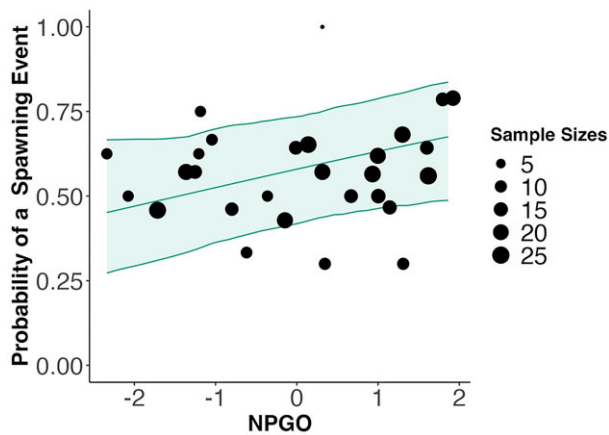


Figure 4. Probability of a spawning event at different NPGO indices. Points represent the proportions of females that had a potential spawning event with the size representing how many females were sampled at each NPGO value. The solid green line is the predicted probabilities of a spawning event from the selected linear mixed model given NPGO values in our dataset. Shaded green regions represent the 95% CI of the fitted values from the linear mixed model.

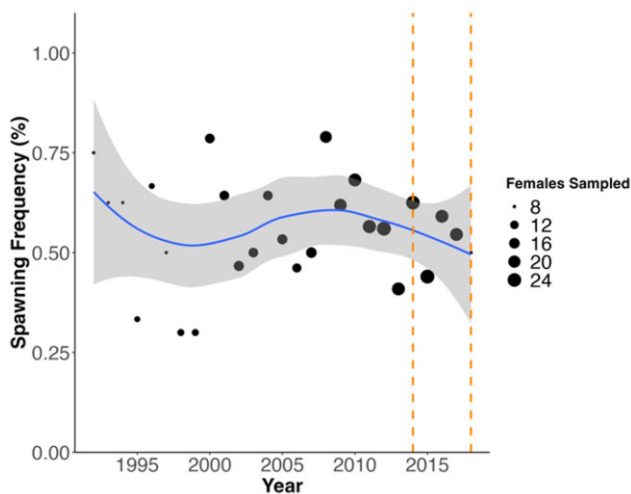


Figure 5. Temporal changes in spawning frequency for female yelloweye rockfish during years with adequate sample sizes ($N \geq 7$ females per year, $n = 418$ GIs; 1992–2018). Points represent the spawning frequency by year with size relating to the total number of females sampled that year. The general trend was plotted using the loess smoothing method (blue line) with 95% CI (grey shaded areas). Years with documented anomalously high SSTs (2014–2018) (Litzow *et al.*, 2020a) are bracketed with orange dashed lines.

years) based on the high hormone variability observed during these ages (Figure 3). Thus, monitoring steroid hormone production during immaturity helps determine juvenile resiliency to changes in their environment.

We identified a relationship between progesterone and estradiol concentrations and SST; however, the magnitude of the relationship was dependent on the age of the fish and time of year. This asynchronous timing effect of SST with reproductive hormones was not expected; however, previous studies have shown temperature to have seasonal effects on different reproductive stages in sablefish (*Anoplopoma fimbria*) (Tolimieri *et al.*, 2018). Progesterone and estradiol concentrations

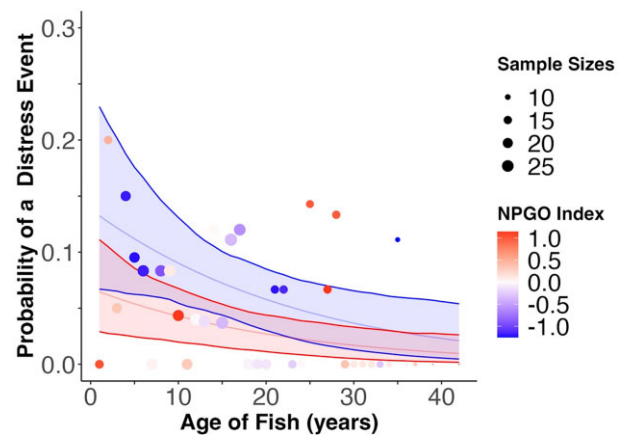


Figure 6. Probability of a distress event occurring in female yelloweye rockfish from approximate ages 1 to 42 years coloured by the strength of the NPGO. Each circle represents the proportion of females that met the criteria for a distress event at different ages. The colour represents the average strength of the NPGO index at each respective age when distress events occurred (dark red being strong positive NPGO values, while dark blue being strong negative NPGO values). The size of the points represents how many females were sampled at each age (minimum seven females per age). The solid blue line is the predicted probabilities a distress event would occur from ages 1 to 42 years keeping the NPGO index a constant negative value of -0.92 (mean negative index value in our dataset), and the shaded blue areas represent the respective 95% CI. The solid red line represents the predicted probabilities a distress event would occur from ages 1 to 42 years, while NPGO stayed a constant positive value of 1.05 (mean positive index value in our dataset), and the shaded red regions represent the respective 95% CI.

declined with increases in SST aligning with model predictions; conversely, there was evidence adults had increased reproductive hormone production during warmer water temperatures (Figure 2 and Supplementary Figure S8). Progesterone increases during rockfish final oocyte maturation (Shi *et al.*, 2011) and gestation (Xu *et al.*, 2022), which begin around January (final oocyte maturation) and February (gestation) for yelloweye in the GOA (Arthur, 2020). Since temperature helps regulate timing of ovulation (Pankhurst and Porter, 2003), possibly the warmer winter temperatures may alter or delay the final ovulation and subsequent gestation reproductive activities. Other studies assessing the effects of increasing SST on juvenile yelloweye rockfish suggest that fish grow faster (Black *et al.*, 2008), have greater mass at age 1 compared to other rockfish species, and reach sexual maturity quicker when temperature increased by $\sim 3^\circ\text{C}$ from baseline conditions (Harvey, 2009). Growing faster and maturing quicker for yelloweye and other rockfish results in relatively smaller adults (Trippel, 1995) and lower fecundity (Arthur *et al.*, 2022). The lower production of reproductive hormones in juvenile and subadult females in relatively warmer waters is possibly due to being smaller at maturity compared to similarly aged females living in cooler waters (Figures 2 and 3). However, previous studies revealed rockfish species in GOA can maintain fecundity over time despite decreases in size (length) at maturity and warmer temperatures (Beyer *et al.*, 2021; Conrath and Hulson, 2021). This may be the case for progesterone, whose temperature effects occurred during the winter where temperatures fluctuate within natural ranges, but estradiol decreased during higher

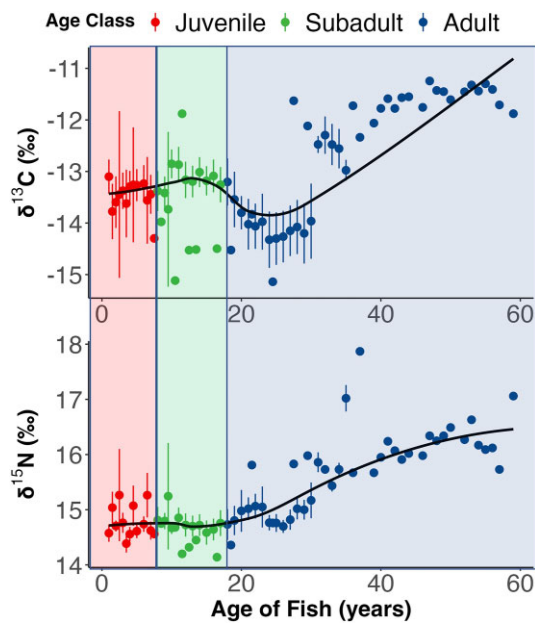


Figure 7. Mean \pm SE $\delta^{13}\text{C}$ (top panel) and $\delta^{15}\text{N}$ (bottom panel) values were measured in female yelloweye opercula GIs across age that material was deposited. Points and rectangles are coloured by age class (juvenile = red, subadult = green, adult = blue). Datum points with no error bars represent a single $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ for that age. Note: approximately ages 1–29 contain a minimum of four individuals, excluding singular datum points. Approximate ages >29 are presented for reference. The loess trendline is plotted for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (black lines).

temperatures in the summer (Table 2 and Supplementary Table S1).

Elevated temperatures outside the range of natural variability of fish could indicate thermal stress and inhibit estradiol production in juveniles and subadult female yelloweye rockfish (Pankhurst, 2016). Cortisol concentrations in female yelloweye rockfish were positively correlated with SST during May and June, preceding the negative correlations between estradiol and SST during July–August (Supplementary Figure S3). While these correlations were weak, summer SSTs exhibited significant negative relationships with estradiol based on LMM results (Table 2). Recently, the GOA has experienced the warmest years on record (2014–2019), which correlated with elevated SST anomalies outside preindustrial variability (Litzow *et al.*, 2020a). With evidence of anomalously high SST in GOA and the trends in cortisol and estradiol among juveniles and subadults, younger females (<17 years) may be more susceptible to thermal stress compared to adults (e.g. Supplementary Figure S8) resulting in reduced estradiol concentrations and reproductive activity (Figures 2 and 5). Similar decreases in estradiol, along with vitellogenin and maternal investment, were found in Atlantic salmon (*Salmo salar*) held at elevated summer temperatures (22°C) during vitellogenesis compared to those at lower temperatures (14°C and 18°C) (King *et al.*, 2003). The proposed mechanism was disruption in the aromatization of testosterone to estradiol leading to irregular final oocyte maturation (King *et al.*, 2003). Cool waters cue captive white sturgeon (*Acipenser transmontanus*) ovarian development, while those reared in warmer waters had a shorter spawning season and lower estradiol concentrations (Webb *et al.*, 2001). It is suggested that yelloweye rockfish optimal

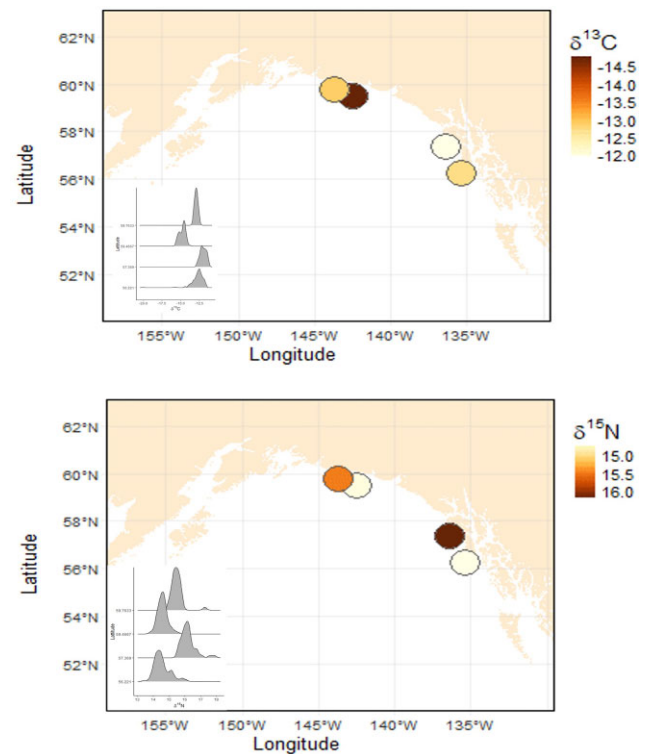


Figure 8. Map showing the mean $\delta^{13}\text{C}$ (top panel) and $\delta^{15}\text{N}$ (bottom panel) values of fish caught at different locations ($N = 11$ fish, $n = 263$ GIs). Inset maps depict the density distributions of the $\delta^{13}\text{C}$ (top panel—inset plot) and $\delta^{15}\text{N}$ (bottom panel—inset plot) values depicted on the main map ordered by latitude (north to south).

water temperatures range from 4.1°C to 12.2°C (Wood *et al.*, 2021), and vitellogenesis occurs during summer months for yelloweye in GOA (Blain and Sutton, 2016). We provide some evidence that warming summer SST ($>15^\circ\text{C}$) in GOA may be approaching the natural SST limit for normal estradiol production in younger female yelloweye rockfish (Figure 2) and may result in delayed maturity or a decrease in spawning activity of mature young females.

Models predicted a similar response for adults of decreasing progesterone and estradiol with increasing SST, which was supported by most females in our dataset ($N = 21$, females sexually mature between 8 and 11 years); however, when assessing all females in our study, there was evidence reproductive hormone production may increase with warmer temperatures during adult years (Figure 2 and Supplementary Figure S8). Although previous work documented a decline in spawning frequency during specific adult years (Charapata *et al.*, 2022), an increase in adult progesterone and estradiol with increasing SST may be based on adult yelloweye rockfish preferred habitat; at depth in colder waters compared to juveniles (O'Connell and Carlile, 1993), resulting in the dissimilar relationship compared to juveniles and subadults. Since adults can devote more energy towards reproduction instead of growth (Barneche *et al.*, 2018; Matta *et al.*, 2018), increasing temperatures may raise adult female metabolic rate and possibly elevate progesterone and estradiol production resulting in a quicker time to parturition (Beyer *et al.*, 2021) as long as temperatures do not exceed physiological ranges.

Steroid hormone relationships with stable isotope values and age

Progesterone concentrations, $\delta^{13}\text{C}$ values, and age were positively correlated in female yelloweye rockfish (Figures 3 and 7, and Supplementary Figure S9). As adults aged and migrated to greater depths (O'Connell and Carlile, 1993), $\delta^{13}\text{C}$ values increased (Trueman *et al.*, 2014), while progesterone also increased with age due to growth and reproductive processes (e.g. maturation and spawning activity; Charapata *et al.*, 2022). Thus, the progesterone and $\delta^{13}\text{C}$ correlation may be an indirect relationship due to age-related physiological and ecological processes.

We identified significant differences in $\delta^{13}\text{C}$ values among age classes, which may indicate ontogenetic changes in yelloweye rockfish foraging location and behaviour. Ages 1–11 years had relatively high $\delta^{13}\text{C}$ values suggesting young rockfish may be residing closer to shore, possibly in more productive GOA waters during periods of rapid growth (Carlson and Strarty, 1981; Kline Jr, 2007; Matta *et al.*, 2018). Decreasing $\delta^{13}\text{C}$ values during ages 11–29 years suggest females may be vertically migrating and feeding on prey in deeper meso-pelagic waters (O'Connell and Carlile, 1993; Trueman *et al.*, 2014). Data are limited post 29 years (<4 individuals per age), but the gradual increasing $\delta^{13}\text{C}$ after 29 years could signal females transitioning from meso-pelagic to deeper benthic waters where they may forage on benthic prey with a higher $\delta^{13}\text{C}$ signature (Trueman *et al.*, 2014; Olson *et al.*, 2020).

$\delta^{15}\text{N}$ values revealed possible age-related prey availability or changes in development in prey-capturing abilities for female yelloweye rockfish. Annual mean $\delta^{15}\text{N}$ values from GIs revealed relatively stable trends from ages 1 to 20 years, before beginning to increase with age (Figure 7). Yelloweye rockfish trophic level is correlated with length and gape width; thus, females cannot feed on larger prey until they are capable predators of suitable size (Olson *et al.*, 2020). In a more southern part of yelloweye rockfish's range (British Columbia), yelloweye rockfish consistently fed on lower trophic level prey (e.g. euphausiids and shrimp) until they reached 40–50 cm, before feeding on higher trophic level prey such as fish (Olson *et al.*, 2020). In northern GOA, female yelloweye rockfish length at 50% maturity is ~ 47 cm equating to ~ 16 years (Arthur, 2020). Taken together, the stable $\delta^{15}\text{N}$ values from our study during ages ~ 1 –20 years indicate these females may not have attained the size and gape width required to forage on higher trophic level prey (Figure 7). $\delta^{15}\text{N}$ increased after females reached 20 years (Figure 7), most likely signalling females reached the required size and gape width to feed on larger and higher trophic-level prey (Olson *et al.*, 2020).

While general trends in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with age suggest possible ontogenetic trends among female yelloweye rockfish in the GOA, there is still high intra and interindividual variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with age (Supplementary Figures S10 and S11). Analysing the relationships of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with environmental data was not possible due to limited sample sizes; however, environmental changes contribute to changes in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in teleosts and their prey (Canseco *et al.*, 2022) and could help explain the variability observed in our samples (Figure 7, Supplementary Figures S10 and S11). Fish were also collected in different areas of the GOA (Figure 8), which could also contribute to the high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variability. Sample sizes with location and stable iso-

topes were limited, but there were qualitative differences in means and distributions of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Figure 8). Future studies with additional samples of all ages with location data would greatly clarify ontogenetic stable isotope ratio trends in female yelloweye rockfish.

Spawning frequency and environmental variables

Spawning frequency was related to the NPGO index, which may indicate selection towards conditions conducive for larval survival. The NPGO index is a summary of wind-driven and horizontal advection variation originating from strengthening or weakening of the North Pacific Oscillation, which helps explain variability in sea surface height anomalies along with salinity, nutrients (e.g. NO_3), and chl-*a* concentrations in the GOA (Di Lorenzo *et al.*, 2008). During positive NPGO years, there are generally cooler waters and a stronger Alaska Current in the GOA (Di Lorenzo *et al.*, 2008, 2013) resulting in greater productivity (i.e. number of mature recruits per spawner) in certain salmon species in the GOA (Malick *et al.*, 2017). The mechanistic link between positive NPGO indices and fish production is unclear, but possibly positive NPGO years are associated with greater juvenile survival based on sufficient food sources (Malick *et al.*, 2017). We found approximately a 20% increase in spawning frequency when females experienced NPGO-positive years compared to NPGO-negative years (Figure 4). This could be attributed to favourable conditions (e.g. increased prey availability) for spawned larvae and greater chances of survival (Malick *et al.*, 2017). Reproductive success of other rockfish species in more southern areas (e.g. Central California) had little to no correlation with the NPGO index (Ralston *et al.*, 2013); however, it has been shown that yelloweye rockfish in the GOA and California respond differently to ocean-basin oceanographic variables (NPO, PDO, Black *et al.*, 2008), making direct comparisons difficult. This also highlights the necessity to perform this type of study among different population segments with a robust sample size to assess how other populations of yelloweye rockfish may respond to climate change-related stressors (Charapata *et al.*, 2022).

We found evidence that short-term (SST) and long-term (NPGO) environmental changes impact different aspects of yelloweye rockfish physiology. Steroid hormone production is directly related to changes in SST, similar to SST effects on reproductive physiology of other teleosts (Pankhurst, 2016), but their spawning frequency may be a function of their long reproductive lifespan and more dependent on low-frequency patterns in oceanographic variables (temperature and salinity) expressed in the NPGO index (Figures 2 and 4). Yelloweye rockfish have long reproductive lifespans and can omit spawning over multiple years during potentially poor environmental conditions (Harvey *et al.*, 2011; Charapata *et al.*, 2022). Thus, long-term trends in oceanography that affect larval survival (i.e. NPGO index), may have more impact on whether female spawning behaviour is stimulated and completed (Figure 4). This hypothesis is supported by documenting only $\sim 13\%$ decrease in spawning frequency during years with uncharacteristically warm SSTs (2014–2018) (Litzow *et al.*, 2020a) in the GOA (Figure 5). However, this is a limited dataset of 4 years, and additional future samples would help strengthen this interpretation.

Many other influences including prey availability, prey composition, body condition, and size most likely influence female yelloweye rockfish reproduction (Harvey, 2005; Beyer *et al.*, 2015, 2021; Conrath, 2017; Arthur, 2020). Additional research assessing the influence these variables have on reproduction with changes in the environment is warranted. We did assess the influence of age, a proxy for size, but that was not chosen as a predictor of spawning frequency (Table 3). This was likely due to the limited sample sizes for reproductive years (9–42 years) compared to maximum yelloweye rockfish reproductive lifespan >100 years (Frid *et al.*, 2016). While the number of samples for the older age ranges of yelloweye rockfish was limited in this study, steroid hormones increased with age, which may result in greater spawning frequency in older females (>42 years) and a greater contribution to the population (Arthur *et al.*, 2022; Charapata *et al.*, 2022).

Distress frequency with age and environmental variables

Young yelloweye rockfish (e.g. at age 1) were approximately two times less stressed during positive NPGO events than during negative events (Figure 6). The positive NPGO index in GOA is associated with greater diatom and zooplankton abundances and an increase in SST later in the spring, excluding anomalously warm years (e.g. 2014–2015) (Batten *et al.*, 2018). The peak in diatom abundances may be better timed with the start of adults giving birth during the late spring in May (Arthur, 2020). Since positive NPGO years have greater prey abundances, such as diatoms and zooplankton, for juvenile larvae (Budge *et al.*, 2022), the lower probability of experiencing a distress event is most likely connected to greater prey availability. Similar results were found with rockfish recruitment in the California Current Ecosystem, where juvenile abundances were higher with cooler, oxygenated, water compared to years with warmer, less-oxygenated, water (Schroeder *et al.*, 2019). Schroeder *et al.* (2019) suggested a similar mechanism, where cooler waters resulted in greater prey availability, but also suggested cooler water conditions could have also advected juveniles to suitable habitat.

Our model suggests adult female yelloweye rockfish may have exhibited physiological resiliency in response to environmental stressors. We found the probability of a stress event was predicted to decline with age to a mean of 1.00–2.10%, holding constant mean positive and negative NPGO conditions, respectively (Figure 6). Adult female yelloweye and other rockfish species have exhibited physiological resiliency to other stressors such as barotrauma and recompression events (Pribyl *et al.*, 2012; Blain and Sutton, 2016). Pairing those results with the low occurrence of distress events, adults display physiological resiliency to environmental stressors. Overall, our findings show that older and larger individuals may be more resilient to stressors, and their reproduction may be tied to longer-term climate trends, supporting the importance of large, adult rockfish conservation for the success of populations and recovery efforts (Magnuson-Ford *et al.*, 2009).

Implications for fishery management

Understanding how targeted stocks fair with changes to their environment is mandatory for managing populations. Yellow-

eye rockfish are the main rockfish species in the “Demersal Rockfish” and, to a lesser extent, a component of the “Other Rockfish” stocks in the GOA (Tribuzio *et al.*, 2021; Wood *et al.*, 2021), and therefore, it is imperative to develop harvesting regulations that are robust to fluctuating environmental variables (Lynch *et al.*, 2018). Currently, the “Demersal” stock of yelloweye rockfish is scored as having “substantially increased concerns” resulting in recommendations to set acceptable biological catch limits at a lower number than the current maximum allowable limit, but assesses their “environmental/ecosystem considerations” as “normal” due to having little or no information on how environmental changes would affect yelloweye rockfish (Tribuzio *et al.*, 2021). We found that warming summer SST (>15°C) would likely impact younger females’ reproductive activity, specifically, cause decreases in estradiol production (Figure 2). Additionally, younger females (1–7 years) are more susceptible to distress events associated with long-term climate patterns (NPGO index) that resulted in delayed sexual maturity by ~1 year (Figure 6 and Supplementary Figure S4). Understanding how the age of maturity will be affected by warming temperatures is imperative for informing fisheries catch, spawning biomass, and stock assessment models (Fournier and Archibald, 1982; Rodgveller *et al.*, 2015; Wood *et al.*, 2021). The GOA has gone through recent years of abnormally high SST (2014–2019, including a marine heatwave during 2014–2016) and is slow to recover to pre-heatwave conditions (Suryan *et al.*, 2021). Marine heatwaves are predicted to increase in frequency in the future for the GOA (Suryan *et al.*, 2021), and these results will provide management valuable insight into how resilient yelloweye rockfish are to environmental changes.

Adult female yelloweye, specifically ≥18 years old, exhibit tolerance to environmental changes, which is crucial for long-term sustainable fisheries. While adults expressed in reproductive hormones similar to younger females, they maintained higher overall mean concentrations (Figure 2). Additionally, adults >30 years old did not exhibit physiological stress compared to younger females, even with unfavourable environmental conditions (Figure 6). Adults live in deep waters (>100 m) (O’Connell and Carlile, 1993) and therefore may be insulated from SST warming, although warmer subsurface temperatures (~+1.5°C above mean) were observed during the marine heatwave of 2014–2016 (Barbeaux *et al.*, 2020). We qualitatively documented a decrease in spawning activity during these warmer ocean conditions (Figure 5), which indicates an increased number of females possibly skipped spawning to conserve resources during the marine heatwave with inadequate prey resources (von Biela *et al.*, 2019; Barbeaux *et al.*, 2020; Suryan *et al.*, 2021). Older (~89 years) and larger female yelloweye do not exhibit complete reproductive senescence, and they disproportionately contribute more larvae to the population than younger females, which is essential for their sustainable fisheries (Cailliet and Andrews, 2008; Arthur *et al.*, 2022; Charapata *et al.*, 2022). The current threat for yelloweye rockfish is overfishing (Magnuson-Ford *et al.*, 2009), however, if the climate (SST) continues to warm, a higher metabolism may result in decreased energy allotment towards reproduction. Incorporating or simulating future environmental conditions with possible reductions in spawning frequency in fish population models may be warranted to accurately assess these stocks in the future.

Considerations and broad conclusions

Our results provide insight into the reproductive and stress physiology throughout the lifespan of female yelloweye rockfish with varying environmental conditions; however, there are considerations to the interpretations of our results. We were only able to statistically analyse reproduction, stress, and stable isotopes in females ages 1–42 years (max = 29 years for stable isotopes) while providing empirical insights for older ages. Thus, it would be beneficial to acquire opercula from older females (>42 years) to better understand the impact of environmental conditions on their physiology and ecology. We provided data that distress events have residual effects on individuals, such as delaying sexual maturity (Supplementary Figure S4), but it would be beneficial to follow-up with a study focused on the effects of environmental change at an individual level compared to the population level presented in this study. Finally, selected GLMMs or LMMs for spawning and distress frequency and estradiol concentrations explained significant, but a minority amount of variation indicating weak relationships among these variables (Table 2). Climate indices like the NPGO and PDO may not consistently correlate with their dependent climate variables over time (Litzow *et al.*, 2020b), possibly leading to unexplained variability in selected spawning frequency and distress models. Future studies should explore other covariates (e.g. metabolic rate, lipid stores, body condition) in relation to lifetime reproduction and stress of female rockfish.

This novel study elucidates, how different environmental variables influence the lifetime physiology and ecology in female yelloweye rockfish. Juvenile and subadult (<18 years) females are most susceptible to thermal stress based on decreases in reproductive hormones and increased cortisol concentrations with GOA-SST. However, adult females are most likely minimally exposed to thermal stressors based on their movement to deep benthic habitats inferred from $\delta^{13}\text{C}$ values. Our results suggest female spawning frequency is linked to favourable environmental conditions (i.e. positive NPGO indices) that benefit larval survival based on low distress event frequency during juvenile years. Similarly, distress events decreased with age and during NPGO-positive years, providing evidence of physiological resilience in adult females. Relationships among yelloweye rockfish physiology and environmental changes were weak; however, these data may help management assess the risk of targeted yelloweye populations to changes in their environment and potentially inform accuracy in population models (Charapata *et al.*, 2022). Further, these methods for extracting lifetime reproductive and stress data from opercula can be applied across species and provide researchers data for understanding the impacts of environmental changes to the health of human-targeted teleost species.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author contributions

PC: Conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review & editing, ST: Conceptualization, data curation, funding acquisition, methodology, project administration, resources, supervision, writing—review and editing.

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Conflict of interest

The authors declare there are no competing interests.

Data availability

All finalized and corrected hormone (pg/mg lipid) and stable isotope data used in this study are deposited in this project's North Pacific Research Board data repository found here (<https://projects.nprb.org/#metadata/a43a2bbe-58e6-4792-b67f-40626c02e37b/project>).

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