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ARTICLE

Elevated fish growth yet postponed maturation during intense marine heatwaves

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Abstract

In the last decade, the northeast Pacific Ocean has experienced new climatic extremes with the occurrence of several marine heatwaves (MHWs), prolonged periods of warmer-than-normal ocean temperatures, likely as a result of anthropogenic climate change. The temperature-size rule is used to contextualize the impacts of climate change on fish maturity and growth, and predicts earlier maturation, faster growth of juveniles, and smaller adult body sizes with increasing temperatures. We investigated the temporal dynamics of fish reproductive development, maturity, and growth from 2014 to 2021, during intense and less intense MHW conditions. We estimated length and age at 50% maturity with histological sections of ovarian tissue samples collected from 644 female Black Rockfish (*Sebastes melanops*) caught off the Pacific Coast of the United States (42° N–49° N) and estimated von Bertalanffy growth function parameters with length-at-age data for a subset of 302 females. During intense MHWs, maturation was postponed, reproductive success was lower by a third, and parasite prevalence in ovaries was nominally higher. Younger females were larger at age during intense MHWs, and throughout the last decade, growth rate coefficients were higher than what is typically expected for slower-growing fishes, like rockfishes. The increase in juvenile growth during intense MHW conditions may be explained by the temperature-size rule, but our observation of postponed maturation contradicts theoretical predictions. Our work reveals that MHWs can induce shifts in fish growth and maturation, but that the temperature-size rule may not provide an adequate framework to predict how increasing temperatures associated with climate change may influence reproductive development and maturity for fishes with complex reproductive strategies. An understanding of how anomalous environmental conditions interact with fish life histories may help predict population vulnerability, which will be critical for future fisheries management under climate change.

KEYWORDS
climate change, fisheries, life history, reproductive biology, rockfishes (*Sebastes*), temperature-size rule

INTRODUCTION

Global climate change has generated novel and extreme ocean conditions that have impacted fisheries worldwide (Brander, 2010; IPCC, 2023; Sumaila et al., 2011). In the last decade, the northeast Pacific Ocean has experienced new climatic extremes and increased variability (Harvey et al., 2023), with marine heatwaves (MHWs), prolonged periods of anomalously warm ocean temperatures, occurring with increasing frequency, intensity, and duration (Barkhordarian et al., 2022; Laufkötter et al., 2020). Recent MHW events are likely caused by anthropogenic climate forcing (Barkhordarian et al., 2022; Oliver et al., 2018). At the time of this publication, the 2014–2016 MHW that occurred in the northeast Pacific Ocean (moniker: “the blob”) was the most intense and longest MHW in the last 40 years (Bond et al., 2015; Free et al., 2023; Laufkötter et al., 2020; Peterson et al., 2015). MHWs are predicted to occur with increased severity and frequency in the future (Frölicher et al., 2018; IPCC, 2019; Oliver et al., 2019).

Globally, the characteristics (e.g., geographic center, intensity, rate of onset, and duration) of recent MHWs have varied, and so too have the biological impacts (Free et al., 2023; Hobday et al., 2018). Recent MHWs in the northeast Pacific Ocean have induced extreme shifts in ecosystem dynamics, including lower primary productivity (Whitney, 2015), changes in zooplankton community composition (Ashlock et al., 2021; Brodeur et al., 2019; Nielsen et al., 2021; Peterson et al., 2017), mass mortality events in seabirds (Jones et al., 2018) and marine mammals (Di Lorenzo & Mantua, 2016), and decreased productivity of fish and invertebrate populations (Laurel & Rogers, 2020; PFMC, 2019a, 2019b; Rogers et al., 2021; Rogers-Bennett & Catton, 2019; Shanks et al., 2020). Important fisheries were forced to close or were severely restricted due to population crashes (Barbeaux et al., 2021; PFMC, 2019a, 2019b; Rogers-Bennett & Catton, 2019) or unexpected species interactions (Free et al., 2023; Santora et al., 2020). While many populations experienced declines or decreased productivity, a few fisheries benefitted from MHW conditions due to resulting species range shifts and expansions (Chasco et al., 2022; Costello et al., 2020; Runcie et al., 2019) or enhanced recruitment (Starr & Haigh, 2022; Schroeder et al., 2019).

Life history strategy is an evolutionary response to the characteristics of an ambient environment (Mangel et al., 2007) and life history traits and reaction norms influence individuals’ capacity to acclimate or adapt to novel or extreme conditions (McClure et al., 2023; Pacifici et al., 2017). Physiology and fitness, and thus adaptive capacity, are linked through life history tradeoffs that result in resource allocation decisions between growth, reproduction, and long-term survival (Mangel et al., 2007; Stearns, 1989). The metabolic theory of ecology (Brown et al., 2004) and the temperature-size rule (Atkinson, 1994; Kingsolver & Huey, 2008) predict that ocean warming will result in elevated juvenile growth rates as a consequence of temperature-dependent processes, yet earlier maturation and smaller adult body sizes because of trade-offs between growth and reproduction across temperatures (Kindsvater et al., 2024; Kingsolver & Huey, 2008; Wootton et al., 2022). Species from a diversity of taxa experienced changes in growth and reproduction under MHW conditions (Barlow et al., 2023; Fennie et al., 2023; Minuti et al., 2022; Oke et al., 2022; Piatt et al., 2020; Shanks et al., 2020; Wild et al., 2019), with physiological responses to MHWs varying based on previous exposure, life history stage, and life history strategy (Fennie et al., 2023; Smith et al., 2023).

Rockfishes (genus *Sebastes*) are a diverse assemblage with more than 60 species ubiquitously distributed in the northeast Pacific Ocean, and comprise an important component of commercial and recreational fisheries on the Pacific Coast of North America (Love et al., 2002). While rockfishes have a life history strategy that maximizes reproductive success in dynamic ecosystems over their lifespans (Bobko & Berkeley, 2004; Mangel et al., 2007; Thorson et al., 2023), this same suite of adaptations may increase their vulnerability to climate change due to their complex reproductive strategies and slow population growth (McClure et al., 2023). Understanding the reproductive ecology of fish populations is key to managing the long-term viability of fisheries (Hilborn & Walters, 1992; Hjort, 1914), particularly for rockfishes, which have highly episodic recruitment (Ralston et al., 2013; Wheeler et al., 2017; Zabel et al., 2011). Stressors, like climate change, that impact fish life history traits, like growth or reproduction, create new challenges for maintaining sustainable fisheries (Leaman, 1991; McClure et al., 2023).

Fishes with complex reproductive strategies, like rockfishes, can reallocate energy from reproduction when conditions are poor (Hannah & Parker, 2007; Jørgensen et al., 2006; Lefebvre & Field, 2015; Rideout et al., 2005). Rockfishes have the ability to break down and reabsorb developing oocytes (future eggs) as a form of energy reallocation, a process called atresia. Mass atresia during the spawning season implies reduced reproductive output or spawning omission (Conrath, 2017; Frey et al., 2015; Head et al., 2020; McDermott, 1994; Rideout et al., 2000). Mass atresia is observed both when younger, smaller fish postpone participating in a reproductive event for the first time, called immature cycling or abortive maturation (Hannah & Parker, 2007) and when older, larger, mature individuals forgo spawning, called skipped spawning (Rideout et al., 2005; Rideout & Tomkiewicz, 2011).

Biological maturity identifies individuals that are physiologically mature, in which initial energy investment into reproduction occurs (as evidenced by yolk development; Head et al., 2020). Functional maturity is a more stringent definition of biological maturity that also accounts for events of abortive maturation and skipped spawning, and thus identifies individuals that not only invested energy into reproduction but will also likely spawn in a given year (Conrath, 2017; Frey et al., 2015; Head et al., 2020; McDermott, 1994; Pacicco et al., 2023; Reed et al., 2023; Rideout et al., 2000).

In this study, we investigate the temporal dynamics of female Black Rockfish (*Sebastes melanops*) reproductive development, maturity, and growth from 2014 to 2021, in years with intense MHWs and years that were closer to the climatic average. Black Rockfish are an important component of fisheries (Cope et al., 2016, 2023) and food webs in nearshore habitat in the northern California Current (Brodeur et al., 2014; Doran, 2020; Gladics et al., 2014; Mills et al., 2007; Schwartzkopf & Heppell, 2020). Black Rockfish are one of the seven species of rockfish identified as highly vulnerable to climate change in the California Current large marine ecosystem (CCLME) due to both high biological sensitivity and high climate exposure risk (McClure et al., 2023), yet there is no formal inclusion of environmental drivers in the assessment and management of this species (Cope et al., 2016, 2023). Here, we (1) describe their reproductive development cycle, (2) estimate maturity-at-length and -age relationships for both biological and functional classifications of maturity, (3) explore the impacts of varying intensities of MHWs on reproductive development cycles and maturity schedules, and (4) estimate length-at-age relationships and growth rate coefficients during intense and less intense MHW conditions.

METHODS

All statistical analyses and visualizations of the data (Rosemond et al., 2024) and results were conducted in R version 4.3.0 (R Core Team, 2023).

Sample collection

Project scientists, Oregon Department of Fish and Wildlife biologists, and Washington Department of Fish and Wildlife biologists sampled Black Rockfish caught in recreational fisheries from 2014 to 2021 in the northeast Pacific Ocean (42° N–49° N; Figure 1). The catch date was recorded, and fish were randomly selected from the catch. Selected fish were sexed macroscopically, and fork length or total length was measured to the nearest millimeter. Total length, when measured, was converted to fork length using the following equation:

$$\mathrm{FL} = -1.421 + 0.983 \times \mathrm{TL} \tag{1}$$

where FL is the fork length (in millimeters) and TL is the total length (in millimeters) (Cope et al., 2016; Echeverria & Lenarz, 1984; Love et al., 2002).

For those fish identified as female, ovarian tissue and both sagittal otoliths were removed for maturity and age determination, respectively. Ovaries were stored in 10% neutral buffered formalin and otoliths were stored in 50% ethanol. The Oregon Department of Fish and Wildlife Marine Resources Program Fish Aging Project determined ages for a subsample of females by counting otolith annuli using the break-and-burn method (CARE, 2006). Black Rockfish ages have been validated for this method (Terwilliger et al., 2023). Only samples collected from September through April were utilized in this study, as this period captures peak female reproductive development toward spawning and parturition (Bobko & Berkeley, 2004; Cope et al., 2016).

Categorizing ocean conditions

The CCLME on the eastern boundary of the North Pacific Ocean is highly dynamic, with variable conditions driven by seasonal upwelling, regional oceanography, and broad-scale climate patterns (Harvey et al., 2023). Recent MHWs have been identified as important drivers of ecosystem dynamics in the CCLME (Harvey et al., 2023). We explored the influence of MHWs on Black Rockfish maturity and growth. The NOAA National Data Buoy Center maintains historic and real-time climatic data collected at buoy stations off the coast of central Oregon (USA) (45° N, where many of our samples were collected and an approximate mid-point of our study area; Figure 1). Using hourly sea surface temperature (SST) data recorded at Station 46050 (Stonewall Bank, ~40 km from the coast, timeseries beginning in 1991) and Station 46097 (Newport Shelf, ~20 km from the coast, time series beginning in 2016), we calculated daily mean SST (averaged between both timeseries when they overlapped) to identify and categorize MHW events in our study area. We identified MHW events as prolonged periods ($\geq$5 days) during which SST was warmer than the 90th percentile of seasonal climatology based on the 30-year baseline period of 1991–2021 (Hobday et al., 2016, 2018). Seasonal climatology, threshold climatology, and MHW events were identified using the "heatwaveR" R package (Schlegel & Smit, 2018). We calculated cumulative MHW intensity as the cumulative mean daily SST anomalies

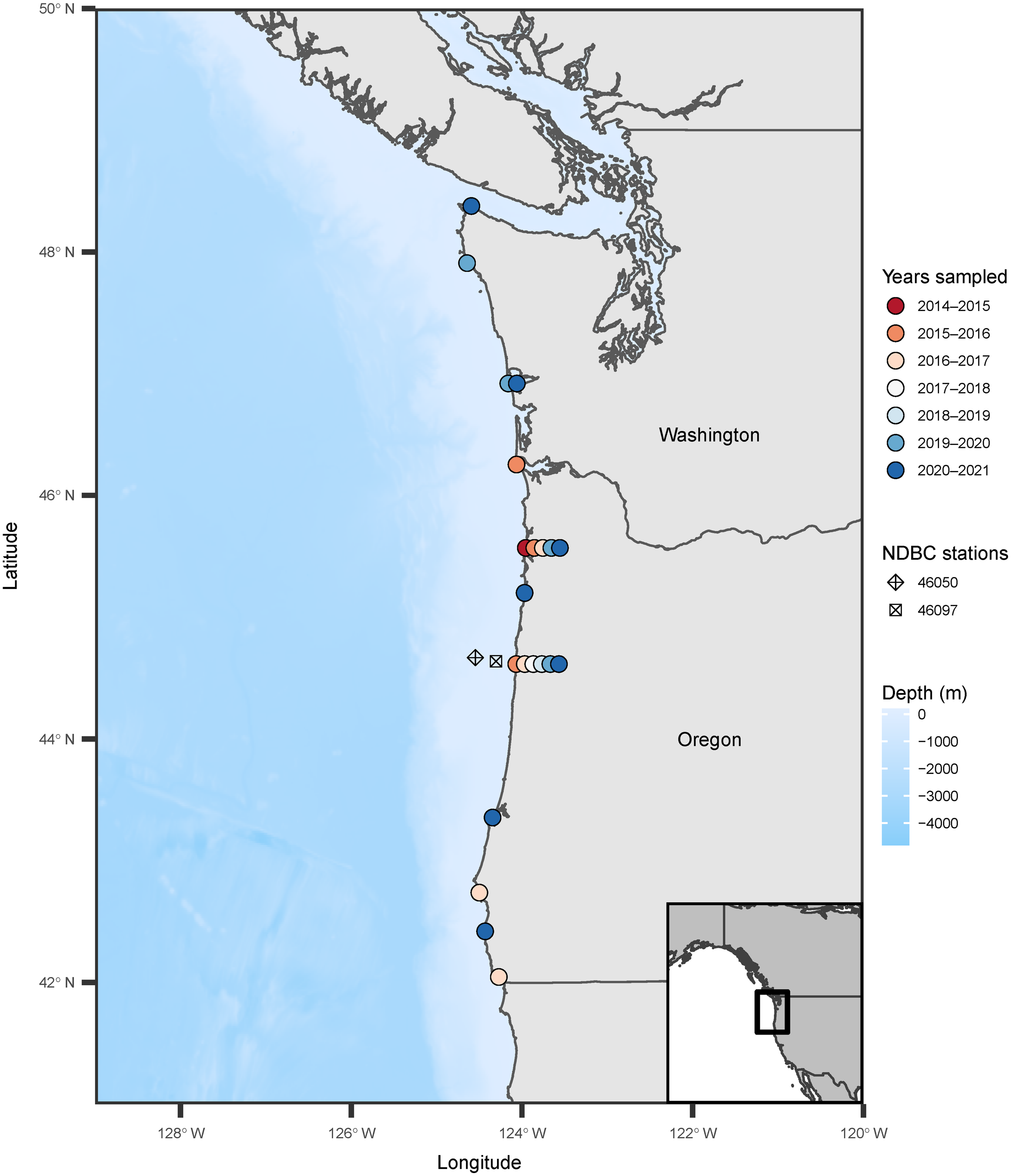

FIGURE 1 Map of the port locations in Oregon and Washington, USA, where female Black Rockfish maturity samples were collected from 2014 to 2021 (circles color-coded by year sampled, jittered if sampled in multiple years). The locations of the National Data Buoy Center (NDBC) stations where temperature data were collected are depicted by the diamond and square. The bathymetry (depth gradient) highlights the nearshore shelf. The inset of the northeast Pacific Ocean and the Pacific Coast of North America highlights the study area in the black rectangle. Map lines delineate study areas and do not necessarily depict accepted national boundaries. Map created using "raster" (Hijmans, 2020), "sf" (Pebesma, 2018), and "marmap" (Pante & Simon-Bouhet, 2013) R packages and visualized using the "ggplot2" R package (Wickham, 2016).

associated with MHW events using the following equation:

$$\text{Cumulative MHW intensity} = \sum\nolimits_{i=1}^{n} \text{SST}_i - \text{Threshold SST}_i \quad (2)$$

where n is the total number of days, SST_i is the mean daily SST for day i, and Threshold SST_i is the value of the threshold SST (>90th percentile of seasonal climatology) for day i. We then used the magnitude of the cumulative MHW intensity from September through April to categorize MHW intensity during peak female reproductive development each year.

Daily SST, seasonal climatology, threshold climatology, and MHW events were visualized using the "ggplot2" R package (Wickham, 2016).

Reproductive development and maturity

Ovarian tissue samples were dehydrated, processed, and embedded in paraffin wax and thin sectioned to 4 μm. Thin sections were mounted on slides and stained with hematoxylin and eosin (H&E; Sheehan & Hrapckak, 1980). To determine maturity status and stage of reproductive development, we examined ovarian histological tissue samples using a compound microscope at 40×–400× magnification that was equipped with a camera and imaging software, following methods consistent with those used for other rockfish species (Conrath, 2017, 2019; Conrath & Knoth, 2013; Frey et al., 2015; Head et al., 2020; Lefebvre & Field, 2015; McDermott, 1994; Shaw et al., 2012). We recorded 11 stages of oocyte development and seven corresponding stages of reproductive development (Appendix S1: Figure S1a–e; Appendix S1: Table S1). We visually estimated the percentage of oocytes in atresia for each sample, which we then categorized into five levels of atresia (level 1: <5%; level 2: ≥5% <25%; level 3: ≥25% <50%; level 4: ≥50% <75%; and level 5: ≥75%). We defined mass atresia as ≥25% of oocytes at stage ≥4.1 in atresia, which indicates the breakdown and resorption of advancing oocytes and thus implies failure to advance toward spawning (Conrath, 2017; Frey et al., 2015; Head et al., 2020; McDermott, 1994; Rideout et al., 2000). We also recorded the presence or absence of parasites in each sample and attempted to identify parasites into broad taxonomic groups.

We identified the most advanced oocyte development stage for each sample and then compared the proportion of each maximum stage by month during peak reproductive development to describe the phenology of the female reproductive cycle (Head et al., 2020). We included only oocytes at stage ≥3 in this analysis. We then investigated whether MHW intensity influenced the phenology of the reproductive development cycle by evaluating the progression of reproductive development during intense and less intense MHWs. Reproductive development cycles were visualized as the proportion of females in each development stage by month using the "ggplot2" R package (Wickham, 2016).

We histologically determined both the biological and functional maturity status for each female. We used only ovary samples collected during peak reproductive development (September through April) to avoid wrongly identifying resting or recovering females as immature (and vice versa) because of uncertainty in identifying spawning outcome in early developmental stages (Head et al., 2016). We recorded reader uncertainty in maturity status assignments and only used the samples that we recorded as "certain" in our maturity-at-length and -age analyses. For biological maturity, females were identified as mature based on the presence of physiological markers of maturity (e.g., yolk development, oocyte stage ≥4.1) and if post-ovulatory follicles (POFs) from a recent spawning event were present. Mass atresia of advancing oocytes was not considered when assigning biological maturity status but was a criterion for assigning functional maturity status. Females were classified as functionally mature if maximum oocyte stage was ≥4.2 in September and October or oocyte stage was ≥5 in November through April (which is when we would expect more advanced physiological development relative to the timing of spawning and parturition; Bobko & Berkeley, 2004; Cope et al., 2016), and if the atresia level was <3, or if POFs were present.

Maturity-at-length and -age analysis

The body length (or age) at which 50% of females in a population reach maturity, L_{50} (or A_{50}), is a parameter used in fish stock assessment models to capture the maturity-at-length (or -age) relationship to estimate spawning output, which in turn is used to set management targets (King & McFarlane, 2003; Mangel et al., 2010).

Biological and functional maturity status observations (0 = immature and 1 = mature) were fitted in separate logistic regression models ("glm" R function, family = binomial, link = "logit") to estimate the proportion of mature female Black Rockfish at a certain length or age using the following equation:

$$P = \frac{1}{1 + e^{-(\alpha + \beta x)}} \quad (3)$$

where P is the proportion mature at length or age x, and parameters α and β define the shape and location, respectively, of the fitted sigmoid curve. The estimated model parameters were used to define the maturity ogive and to calculate L_{50} or A_{50} (Frey et al., 2015; Head et al., 2014, 2020) using the following equation:

$$L_{50}(\text{or}\, A_{50}) = -\frac{\alpha}{\beta} \tag{4}$$

We used a bootstrapping method and the "boot" R package (Canty & Ripley, 2024) to estimate 95% CIs of L_{50} (and A_{50}) estimates.

To investigate the influence of MHWs on biological and functional maturity schedules, maturity observations were fitted in separate multiple logistic regression models ("glm" R function, family = binomial, link = "logit") that included length (or age) and a categorical variable to signify intense ($n = 200$) versus less intense ($n = 444$) MHWs. Our model set also included models with an additional term to account for the random effect of the year in which samples were collected. These models were fitted using the "glmer" R function in the "lme4" R package (Bates et al., 2015). We validated models by examining model standardized residuals. We used an information-theoretic approach (Burnham & Anderson, 2002) with Akaike information criterion (AIC; "AIC" R function) and relative differences in AIC (ΔAIC) to evaluate support for models in our a priori model set. The model with the lowest AIC score was determined to be the best model, models with $\Delta\text{AIC} < 2$ were considered competitive models, and models with $\Delta\text{AIC} > 10$ were considered unlikely to be plausible alternatives for the best model (Burnham & Anderson, 2002). We evaluated the strength of support for specific covariates by the degree to which 95% CIs of each covariate coefficient overlapped 0, with strongest support for coefficients with 95% CIs that did not overlap 0, less support for <10% overlap, and little or no support for >10% overlap (Anthony et al., 2006; Dugger et al., 2015). The model parameters from the selected models were used to define the maturity ogive and to calculate L_{50} or A_{50}. For models that included a random effect, we used a bootstrapping method and the "bootMer" R function in the "lme4" package (Bates et al., 2015) to estimate 95% CIs. We used the "ggplot2" R package (Wickham, 2016) to visualize the maturity-at-length and -age results.

Length-at-age analysis

We quantified female Black Rockfish growth dynamics during the study period (2014–2021). Our length-at-age analysis included a subsample of the females included in the maturity-at-length analysis for which we also obtained age data ($n = 302$). A growth function was fit to length-at-age data (first, all years pooled) by nonlinear regression ("nls" R function). Growth was described with the von Bertalanffy function using the following equation:

$$L_t = L_\infty\left[1 - e^{-k(t-t_0)}\right] \tag{5}$$

where L_t is the expected fork length (in centimeters) at age t, k is the growth rate coefficient (per year), L_∞ is the asymptotic average fork length (in centimeters), and t_0 is the age in years of fish at an average length of 0 cm. In this case, t_0 was fixed at 0 years, as in other Black Rockfish growth models (Cope et al., 2023).

A growth function (same equation as above) was fitted to length-at-age data collected in years with intense MHWs ($n = 108$) and a growth function (same equation as above) was fitted to length-at-age data collected in years with less intense MHWs ($n = 194$) to explore the influence of MHWs on growth dynamics. We examined model fit (residual SE) and convergence (achieved convergence tolerance). We used a bootstrapping method and the "boot" R package (Canty & Ripley, 2024) to estimate 95% CIs of model coefficients. We used the "ggplot2" R package (Wickham, 2016) to visualize length-at-age data and growth functions.

RESULTS

Sample collection

A total of 771 female Black Rockfish were sampled from September through April in Oregon and Washington waters from 2014 to 2021. After both uncertain ($n = 121$) and unreadable ($n = 6$) maturity samples were excluded, 644 samples were included in the maturity-at-length analysis and 302 samples were included in the maturity-at-age and length-at-age analyses (Table 1; Appendix S1: Table S2). Fork lengths ($n = 644$) ranged from 23 to 56 cm, with a mean (±SE) length of 40.13 (±0.94) cm. Ages ($n = 302$) ranged from 4 to 23 years, with a mean (±SE) age of 7.84 (±0.31) years.

Categorizing ocean conditions

The oceanography in the northeast Pacific Ocean was highly variable over the study period, with some environmental indices reaching new extremes between 2014 and

TABLE 1 Female Black Rockfish maturity and age samples were included in the maturity-at-length, maturity-at-age, and length-at-age analyses.

Year (Sep.–April)	*n* (length)	Size range (cm)	Mean size ± SE (cm)	*n* (age)	Age range (years)	Mean age ± SE (cm)
2014–2015	50	36–52	41.78 ± 0.50	50	5–23	7.34 ± 0.36
2015–2016	150	33–56	41.34 ± 0.36	58	4–11	7.17 ± 0.19
2016–2017	157	27–50	39.98 ± 0.36	74	4–14	7.51 ± 0.22
2017–2018	32	30–47	38.78 ± 0.75	…	…	…
2018–2019	28	30–50	39.11 ± 0.95	…	…	…
2019–2020	133	25–53	38.89 ± 0.43	50	5–18	7.90 ± 0.31
2020–2021	94	23–55	40.06 ± 0.64	70	4–18	9.07 ± 0.34
Total	644			302		

Note: Table includes sampling year, sample size (n), size and age ranges, and mean size and age ± SE.

2021 (Harvey et al., 2023). The MHW that began in the fall of 2014 and dissipated by the fall of 2016 (“the blob”) had distinct impacts on the CCLME relative to MHWs that occurred every year during the rest of the study period (Harvey et al., 2023). “The blob” MHW occurred closer to shore and at a higher intensity than the other MHWs and thus likely impacted the nearshore environment differently. The cumulative intensity of SST anomalies associated with MHW events was highest during peak reproductive development during “the blob” (2014–2015: 172.7°C and 2015–2016: 65.6°C, as measured ~20–40 km off the coast of central Oregon (USA); Figure 2; Table 2) relative to the following years. We categorized MHW events during “the blob” years as “intense MHWs.” The MHWs that occurred after “the blob” did not have as intense signatures nearshore, but still impacted the CCLME (Harvey et al., 2023), so these MHW events were classified as “less intense MHWs” (Figure 2; Table 2). Of the 644 females included in the maturity-at-length analysis, we sampled 200 during intense MHWs and 444 during less intense MHWs. Of the subsample of those females for which we also obtained age data ($n = 302$), 108 were sampled during intense MHWs and 194 were sampled during less intense MHWs.

Reproductive development and maturity

We described the phenology of the reproductive development cycle using maturity samples pooled across all years. Oocytes developed toward hydration in October through December, with parturition of larvae likely occurring in January and February. Post-parturition individuals were observed in February, March, and April (Figure 3a). During intense MHWs, a higher proportion of individuals developed more advanced stage oocytes (0.46, stage ≥4.1) earlier in the spawning season relative to what occurred during less intense MHWs (0.39, stage ≥4.1); however, as the spawning season continued, the proportion of individuals progressing toward spawning capability was lower during intense MHWs (Figure 3b,c). The overall proportion of individuals that successfully released larvae (a measure of reproductive success) was lower by a third during intense MHWs (0.26, combining samples in March and April) than the proportion sampled during less intense MHWs (0.40, combining samples in March and April).

We did not determine whether females had successfully reproduced in prior years, so we did not explicitly separate abortive maturation from skipped spawning in the analysis; however, we did identify individuals in the upper end of the size distribution that had likely reproduced previously but, in the year in which they were sampled, exhibited mass atresia of oocytes so likely skipped spawning that year. During intense MHWs, 156 out of 200 females (78.0%) were identified as biologically mature, and 92 out of 200 (46.0%) were identified as functionally mature. Out of the biologically mature females, 14.1% were classified as functionally immature due to mass atresia of oocytes and 44.9% were classified as functionally immature based on the level of oocyte development relative to the timing of spawning and parturition. During less intense MHWs, 352 out of 444 females (79.3%) were identified as biologically mature, and 222 females (50.0%) were classified as functionally mature. Out of the biologically mature females, 13.3% were classified as functionally immature due to mass atresia of oocytes and 49.7% were classified as functionally immature based on the level of oocyte development relative to the timing of spawning and parturition.

We documented the presence of parasites in 69 out of 765 samples (9.0%; including samples of both certain and uncertain maturity determination). The percentage of

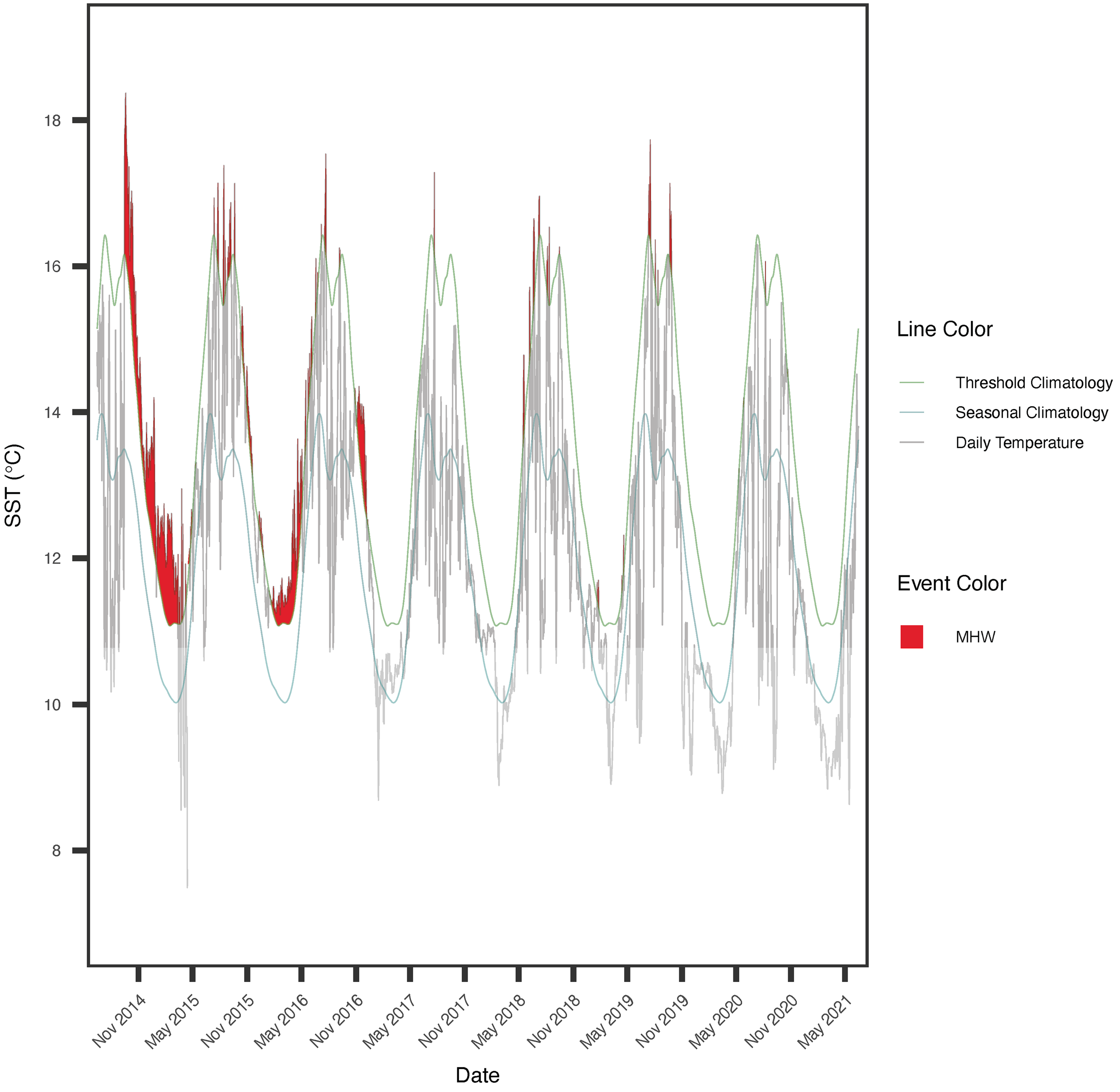

FIGURE 2 Time series of daily sea surface temperature (SST) (in degree Celsius) measured ~20–40 km off the coast of central Oregon (USA) (gray line), seasonal climatology based on a 30-year baseline period of 1991–2021 (light blue line), and threshold (90th percentile of the seasonal climatology; light green line). Warm-water anomalies were used to categorize marine heatwave (MHW) events (shown in red) during female Black Rockfish peak reproductive development from 2014 to 2021.

ovaries infected with parasites was nominally higher during intense MHWs (11.2%) than during less intense MHWs (8.1%). We identified some of the parasites as flatworms (class: Digenea) (Bruno et al., 2006) and observed evidence of encysted, degenerate parasites within the ovaries (Figure 4a,b). Parasites occurred in some samples with mass atresia and/or granulosa inflammation, which usually signals an immune system response (Blazer, 2002; Kumar & Joy, 2015) (Figure 4a,c).

Maturity-at-length and age analysis

Maturity-at-length

The overall L_{50} estimate for biological maturity across all years of the study (2014–2021) was 34.38 cm (95% CI: 33.15 cm, 35.22 cm) (Model 3, Table 3a). After classifying the same samples with the functional maturity definition (taking into account the timing of reproductive development and the level of atresia), the length at which females reached functional maturity was nearly 6 cm larger (40.36 cm [95% CI: 39.89 cm, 40.87 cm]; Model 3, Table 3b) than the biological maturity classification.

The model with MHW as an environmental covariate was selected as the best biological maturity-at-length logistic regression model with the lowest AIC (Model 1, Table 3a). Intense MHWs (MHW = +) resulted in a shift in the maturity ogive to the right (biological maturity was reached at a larger size on average). There was strong support for the influence of MHWs on biological maturity-at-length (95% CIs did not overlap 0) (Model 1, Table 3a). The variation due to the random effect of year in the random effects model was not estimable (close to 0) (Model 2, Table 3a).

The functional maturity-at-length logistic regression model with MHW as an environmental covariate and the random effect of year had the lowest AIC and was selected as the best model (Model 1, Table 3b). Intense MHWs (MHW = +) resulted in a shift in the maturity curve to the right (functional maturity was reached at a larger size on average). There was strong support for the influence of MHWs on functional maturity-at-length (95% CIs did not overlap 0) (Model 1, Table 3b).

TABLE 2 Categorical classification of marine heatwave (MHW) intensity.

Year (Sep.–April)	*n* (length)	*n* (age)	MHW (cumulative intensity;°C)
2014–2015	50	50	Intense (172.7)
2015–2016	150	58	Intense (65.6)
2016–2017	157	74	Less intense (23.9)
2017–2018	32	…	Less intense (0.0)
2018–2019	28	…	Less intense (0.0)
2019–2020	133	50	Less intense (4.6)
2020–2021	94	70	Less intense (0.0)

Note: Table includes the sample size (*n*) in each year for length and age, and MHW cumulative intensity.

We estimated L_{50} during intense and less intense MHWs using the selected best models for biological (Model 1, Table 3a) and functional (Model 1, Table 3b) maturity-at-length. During intense MHWs, biological maturity was reached at a larger size on average, with L_{50} increasing from 33.87 cm (95% CI: 32.73 cm, 34.71 cm) during less intense MHWs to 36.52 cm (95% CI: 35.06 cm, 37.73 cm) during intense MHWs (Figure 5). A similar pattern was observed for functional maturity. During intense MHWs, functional maturity was reached at a larger size on average, with L_{50} increasing from 39.74 cm (95% CI: 39.02 cm, 40.57 cm) during less intense MHWs to 42.32 cm (95% CI: 41.40 cm, 43.47 cm) during intense MHWs (Figure 5).

Maturity-at-age

The overall A_{50} estimate for biological maturity for the study period (2014–2021) was 4.40 years (95% CI: −0.54 years, 5.40 years) (Model 1, Table 4a). After classifying the same samples with the functional maturity definition, the age at which females reached maturity almost doubled ($A_{50} = 8.25$ years [95% CI: 7.86 years, 8.92 years]; Model 2, Table 4b).

Of the biological maturity-at-age logistic regression models, the model with only age as the predictor variable had the lowest AIC and was selected as the best model (Model 1, Table 4a); however, both the model with MHW as an environmental covariate and the model with MHW as a covariate plus the random effect of year were competitive models (within 2 ΔAIC of the best model). There was little support for the influence of MHWs on

TABLE 3 Statistical results of logistic regression models and selection criteria used to evaluate the influence of marine heatwaves (MHWs) on female Black Rockfish (a) biological maturity-at-length ogives and (b) functional maturity-at-length ogives.

Response variable	Model	df	Intercept (α)	Length (β)	MHW (+)	Random effect	AIC	ΔAIC
(a) Biological maturity	1	3	−11.72 ± 2.47	0.35 ± 0.07	−0.92 ± 0.49	…	500.04	0
	2	4	−11.72 ± 2.47	0.35 ± 0.07	−0.92 ± 0.49	Year (σ = not estimable)	502.04	2.00
	3	2	−10.73 ± 2.29	0.31 ± 0.06	…	…	511.33	11.29
(b) Functional maturity	1	4	−16.37 ± 2.76	0.41 ± 0.07	−1.07 ± 0.93	Year ($\sigma^2 = 0.23$)	626.25	0
	2	3	−15.99 ± 2.65	0.40 ± 0.07	−0.85 ± 0.42	…	630.29	4.04
	3	2	−15.36 ± 2.58	0.38 ± 0.06	…	…	644.78	18.53

Note: Statistical results include df, model coefficients (α = intercept, β = slope, and MHW = marine heatwave), and a random effect, if included in the model. Point estimates ± 95% CIs are reported for model coefficients and estimated variance (σ^2) is reported for the random effect of year (7 groups), if included. MHW (+) signifies the effect of intense MHW conditions relative to the reference category (less intense MHWs). Selection criteria include the Akaike information criterion (AIC) and the change in AIC (ΔAIC).

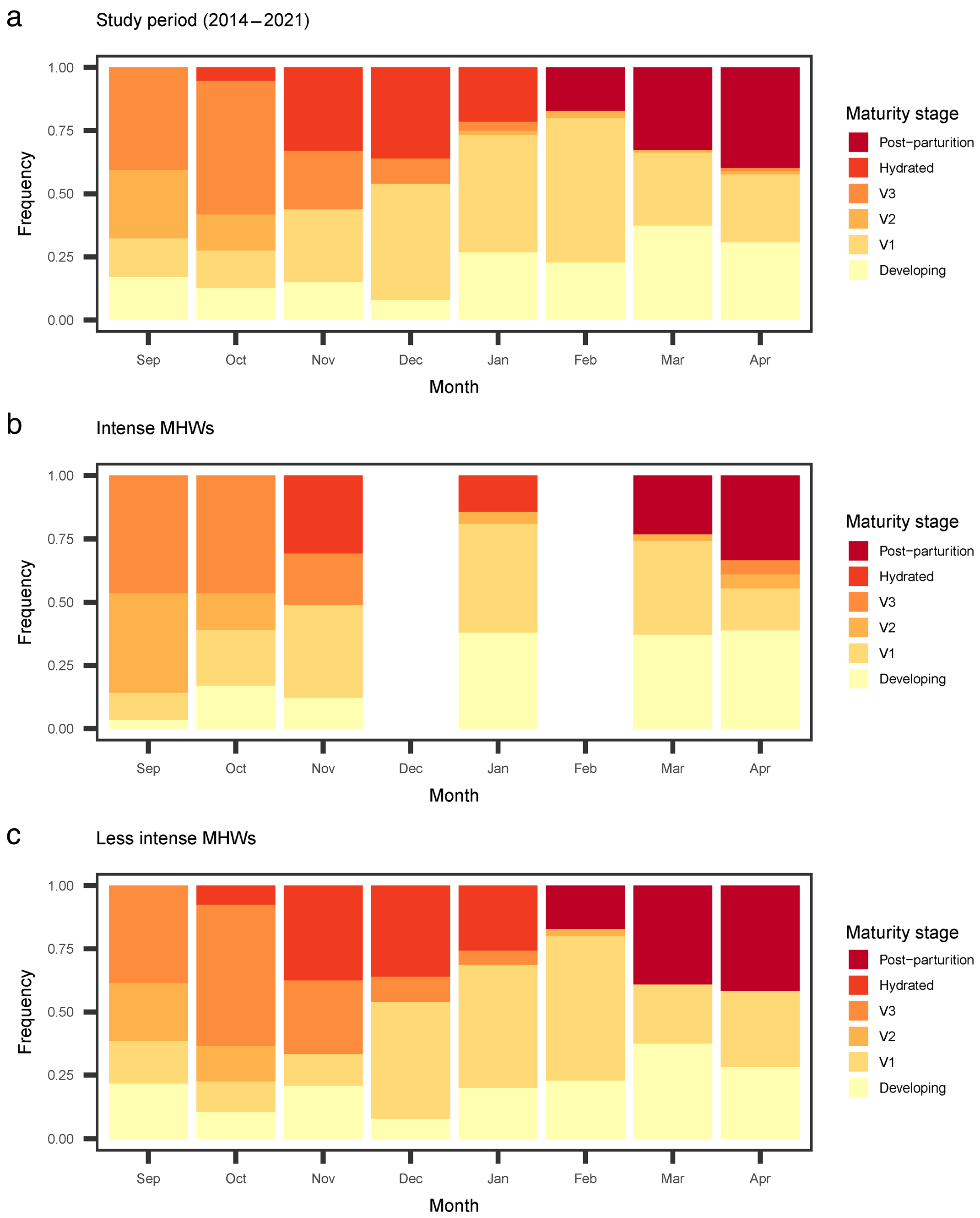

FIGURE 3 The reproductive development cycle of female Black Rockfish sampled in the northeast Pacific Ocean from 2014 to 2021. The frequency of each maturity stage is shown for each month during the period of peak reproductive development (September through April) for (a) samples combined across all years of the study, (b) during intense marine heatwaves (MHWs), and (c) during less intense MHWs. Maturity stages are (from least to most advanced): developing (oocyte Stage 3), V1 (oocyte stage 4.1), V2 (oocyte stage 4.2), V3 (oocyte stages 5 and 6), hydrated (oocyte stages 7 and 8), and post-parturition (oocyte stage 11); see also Appendix S1: Table S1.

biological maturity-at-age in any of the competitive models (95% CIs overlapped 0) (Table 4a).

Of the functional maturity-at-age logistic regression models, the model with MHW as an environmental covariate had the lowest AIC and was selected as the best model (Model 1, Table 4b), but the model with only age as the predictor variable and the model with MHW as a covariate plus the random effect of year were competitive models (within 2 ΔAIC of the best model). In the models with MHW as a covariate, intense MHWs (MHW = +) resulted in a shift in the maturity curve to the right (functional maturity was reached at an older age on average), and there was some support for the influence of MHWs on functional maturity-at-age in the best model (<10%

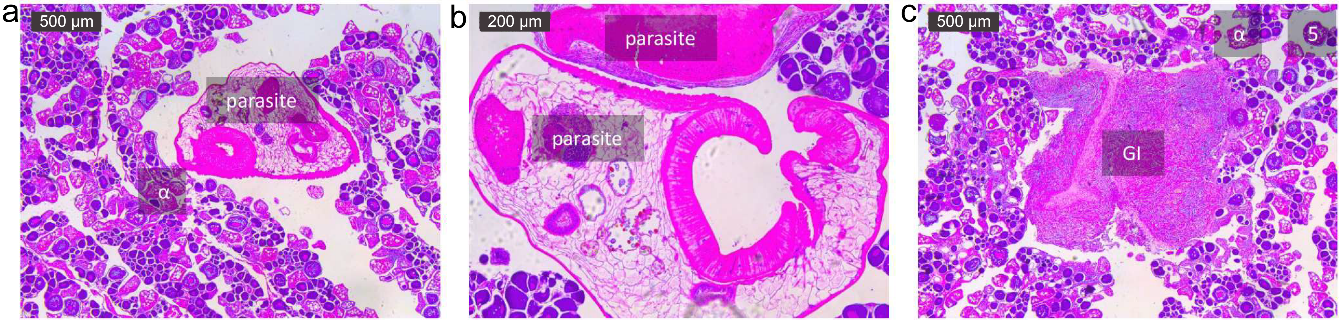

FIGURE 4 Parasites and immune response observed in female Black Rockfish ovaries include (a) vitellogenic oocytes in atresia (α) with a parasite, (b) an example of an encysted, degenerate parasite (at the top of the image) and a (recently) live parasite, and (c) granulomatous inflammation (GI) with mass atresia of early-stage oocytes and evidence of some oocyte development to stage 5. Photo credit: Melissa A. Head.

overlap of CIs with 0) (Table 4b). The variation due to the random effect of year in the random effects model was close to 0 (Model 3, Table 4b).

We estimated A_{50} during intense and less intense MHWs using the selected best models for biological (Model 2, Table 4a) and functional (Model 1, Table 4b) maturity-at-age that included MHW as a covariate. There was little difference in the estimates of biological maturity-at-age during intense and less intense MHWs (intense MHWs: 4.56 years [95% CI: 0.47 years, 5.68 years]; less intense MHWs: 4.56 years [95% CI: −0.13 years, 5.64 years]). For functional maturity-at-age, during intense MHWs, the functional maturity curve shifted to the right (functional maturity was reached at an older age on average), with A_{50} increasing from 8.01 years (95% CI: 7.57 years, 8.66 years) during less intense MHWs to 8.73 years (95% CI: 8.04 years, 9.94 years) during intense MHWs.

Length-at-age analysis

The von Bertalanffy growth function fitted with length-at-age data pooled across all years resulted in a growth rate coefficient (k) of 0.25 year^{-1} (95% CI: 0.23 year^{-1}, 0.28 year^{-1}) and asymptotic average length (L_∞) of 47.61 cm (95% CI: 46.24 cm, 49.24 cm) (Table 5). The growth function fitted with length-at-age data collected during intense MHWs resulted in an elevated growth rate coefficient ($k = 0.31\ \text{year}^{-1}$; 95% CI: 0.24 year^{-1}, 0.41 year^{-1}) compared to the growth rate coefficient in less intense MHW years ($k = 0.22\ \text{year}^{-1}$, 95% CI: 0.20 year^{-1}, 0.23 year^{-1}) (Table 5; Figure 6). The asymptotic average body size during intense MHWs was smaller on average than that estimated during less intense MHW years, but CIs overlapped (intense MHWs: $L_\infty = 46.59$ cm [95% CI: 43.43 cm, 50.61 cm]; less intense MHWs: $L_\infty = 48.91$ cm [95% CI: 47.59 cm, 50.87 cm]; Table 5; Figure 6).

DISCUSSION

During the last decade (2013–2023), numerous MHWs occurred around the globe (Frölicher et al., 2018), with MHWs reoccurring almost every year in the northeast Pacific Ocean (Harvey et al., 2023). Our work emphasizes the importance of understanding how anomalous events in marine systems influence the expression of fish life history traits with potential consequences for the long-term productivity of fish populations, and therefore, sustainable management. Rockfishes are both ecologically and economically important along the Pacific Coast of North America (Love et al., 2002) but are vulnerable to climate change because of their unique life history characteristics (McClure et al., 2023). Our study investigated the temporal dynamics of Black Rockfish maturity and growth during novel climate events and compared responses during intense versus less intense MHWs. During intense MHWs, maturation was postponed and resulted in Black Rockfish reaching biological and functional maturity at larger sizes on average. The shift in maturity-at-length schedules led to an increase in estimated L_{50} by ~2.6 cm for both biological and functional maturity. Estimates of A_{50} for functional maturity also increased during intense MHWs, and the shift in maturity-at-age schedules to older ages-at-maturity likely represents an underlying fundamental response in reproductive strategy separate from an interaction with growth dynamics. Growth rate coefficients were higher during intense MHWs than those during less intense MHWs, and both estimates were elevated relative to what is expected for the species (Cope et al., 2016, 2023). We also found that, during intense MHWs, the proportion of females that successfully released larvae decreased by a third, and the prevalence of parasites in ovaries was nominally higher. These dynamics are important to consider through the lens of climate change, especially if more extreme conditions

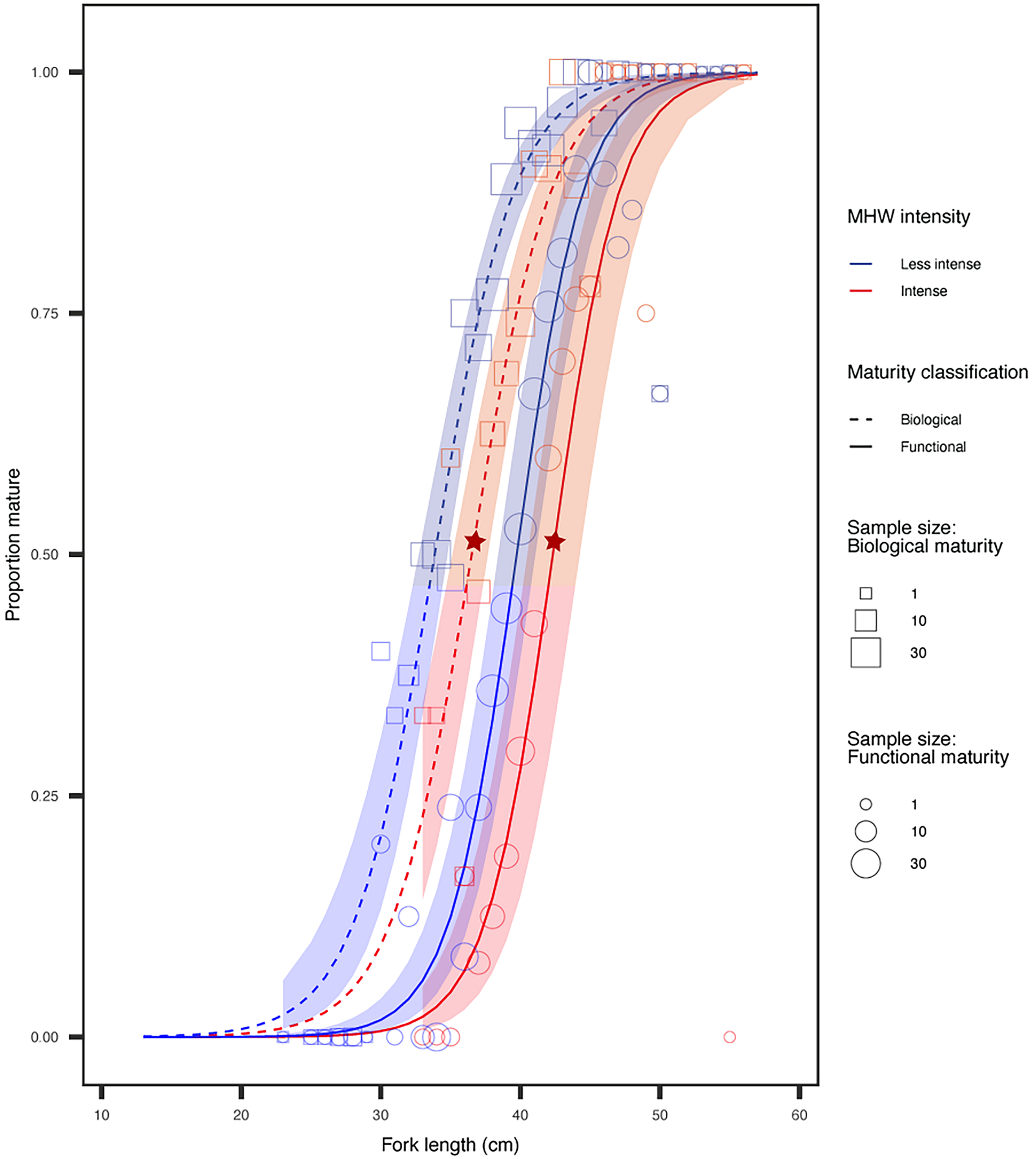

FIGURE 5 Female Black Rockfish biological and functional maturity-at-length during intense marine heatwaves (MHWs) and less intense MHWs. Predicted biological maturity ogives are represented by the dashed lines and functional maturity ogives are represented by the solid lines, with intense MHW (and 95% CIs) shown in red (and designated with a star) and less intense MHW (and 95% CIs) shown in blue. Sample size is denoted by the size of the symbols.

cause shifts in growth, maturation, reproductive success, and host–parasite interactions that may impact the future population productivity of fish populations around the world.

This decade of change provided a unique opportunity to investigate the impacts of MHWs on fish life history traits in the northeast Pacific Ocean because MHWs occurred with high frequency and differing characteristics

TABLE 4 Statistical results of logistic regression models and selection criteria used to evaluate the influence of marine heatwaves (MHWs) on female Black Rockfish (a) biological maturity-at-age ogives and (b) functional maturity-at-age ogives.

Response variable	Model	df	Intercept (α)	Age (β)	MHW (+)	Random effect	AIC	ΔAIC
(a) Biological maturity	1	2	-1.78 ± 1.32	0.40 ± 0.18	…	…	306.17	0
	2	4	-1.96 ± 1.48	0.43 ± 0.19	$-1.58 \times 10^{-4} \pm 0.89$	Year ($\sigma^2 = 0.14$)	307.57	1.40
	3	3	-1.73 ± 1.37	0.40 ± 0.18	-0.07 ± 0.57	…	308.11	1.94
(b) Functional maturity	1	3	-5.24 ± 1.50	0.65 ± 0.19	-0.47 ± 0.56	…	327.98	0
	2	2	-5.61 ± 1.45	0.68 ± 0.19	…	…	328.68	0.70
	3	4	-5.24 ± 1.50	0.65 ± 0.19	-0.47 ± 0.56	Year ($\sigma^2 = 1.22 \times 10^{-15}$)	329.98	2.00

Note: Statistical results include df, model coefficients (α = intercept, β = slope, and MHW = marine heatwave), and a random effect, if included in the model. Point estimates ± 95% CIs are reported for model coefficients, and estimated variance (σ^2) is reported for the random effect of year (5 groups), if included. MHW (+) signifies the effect of intense MHW conditions relative to the reference category (less intense MHWs). Selection criteria include the Akaike information criterion (AIC) and the change in AIC (ΔAIC).

TABLE 5 Statistical results of female Black Rockfish growth function models for the study period and during intense and less intense marine heatwaves.

Model	n	t_0 (cm)	k (year^{-1}) (95% CI)	L_∞ (cm) (95% CI)	Residual SE; df	No. iterations to convergence; achieved tolerance
Study period (2014–2021)	302	0 (fixed)	0.25 (0.23, 0.28)	47.61 (46.24, 49.24)	2.95; 300	5; 1.00×10^{-6}
Intense	108	0 (fixed)	0.31 (0.24, 0.41)	46.59 (43.43, 50.61)	3.31; 106	7; 2.51×10^{-6}
Less intense	194	0 (fixed)	0.22 (0.20, 0.23)	48.91 (47.59, 50.87)	2.22; 192	4; 1.98×10^{-6}

Note: Statistical results include sample size (n), model parameter estimates (t_0 = age in years of fish at average length of 0 cm, k = growth rate coefficient, L_∞ = asymptotic average fork length), and 95% CI. Model fit statistics include residual SE and df. Model convergence is described as the number of iterations to convergence and achieved tolerance.

(e.g., intensity, duration, rate of onset, and spatial extent). In 2014, ecosystem dynamics shifted from several years of high ocean productivity to lower productivity with strong positive temperature anomalies associated with the Pacific Decadal Oscillation and the formation of a large MHW. The MHW that occurred from 2014 to 2016 ("the blob") created novel and extreme conditions in the CCLME that challenged past assumptions regarding relationships between regional climate patterns and ecosystem dynamics (Asch, 2015; Auth et al., 2018; Litzow et al., 2020; Schroeder et al., 2019). Following "the blob," an El Niño event in 2015–2016 prolonged the warm water period in the northeast Pacific Ocean. In 2018, another MHW began to form, but then ultimately dissipated, only to be followed by large-scale MHWs occupying the northeast Pacific Ocean every year from 2019 to 2023 (Harvey et al., 2023). Our work would have benefited from also estimating maturity and growth in a period of time that did not have MHWs, but those conditions did not occur in the northeast Pacific Ocean during the last decade and future conditions may or may not return to the climatic average of the past.

In our study, we found that Black Rockfish were larger and older on average when they reached functional maturity compared to biological maturity. Fishes with complex reproductive strategies can have large differences in L_{50} (or A_{50}) estimates depending on the criteria used to classify maturity (Head et al., 2016, 2020; Pacicco et al., 2023; Reed et al., 2023), and these differences can alter estimates of population productivity (Head et al., 2020), but it was not until recently that the functional maturity definition was considered in fish stock assessment models and management decisions (Cope et al., 2016, 2023). Our estimate of L_{50} for functional maturity is comparable to that estimated by Bobko and Berkeley (2004), which also accounted for immature cycling/abortive maturation. Their study used maturity samples collected off the coast of Oregon, USA, from 1995 to 1998, which was also a relatively warm period (Harvey et al., 2023). We found an ~3.8 year difference in biological and functional maturity-at-age, indicating a multi-year delay in maturation due to abortive maturation which may be further postponed during poor environmental conditions. Few other studies report abortive maturation to occur over several years (Junquera et al., 2003; Lefebvre & Field, 2015; Parkerk & Grimes, 2010).

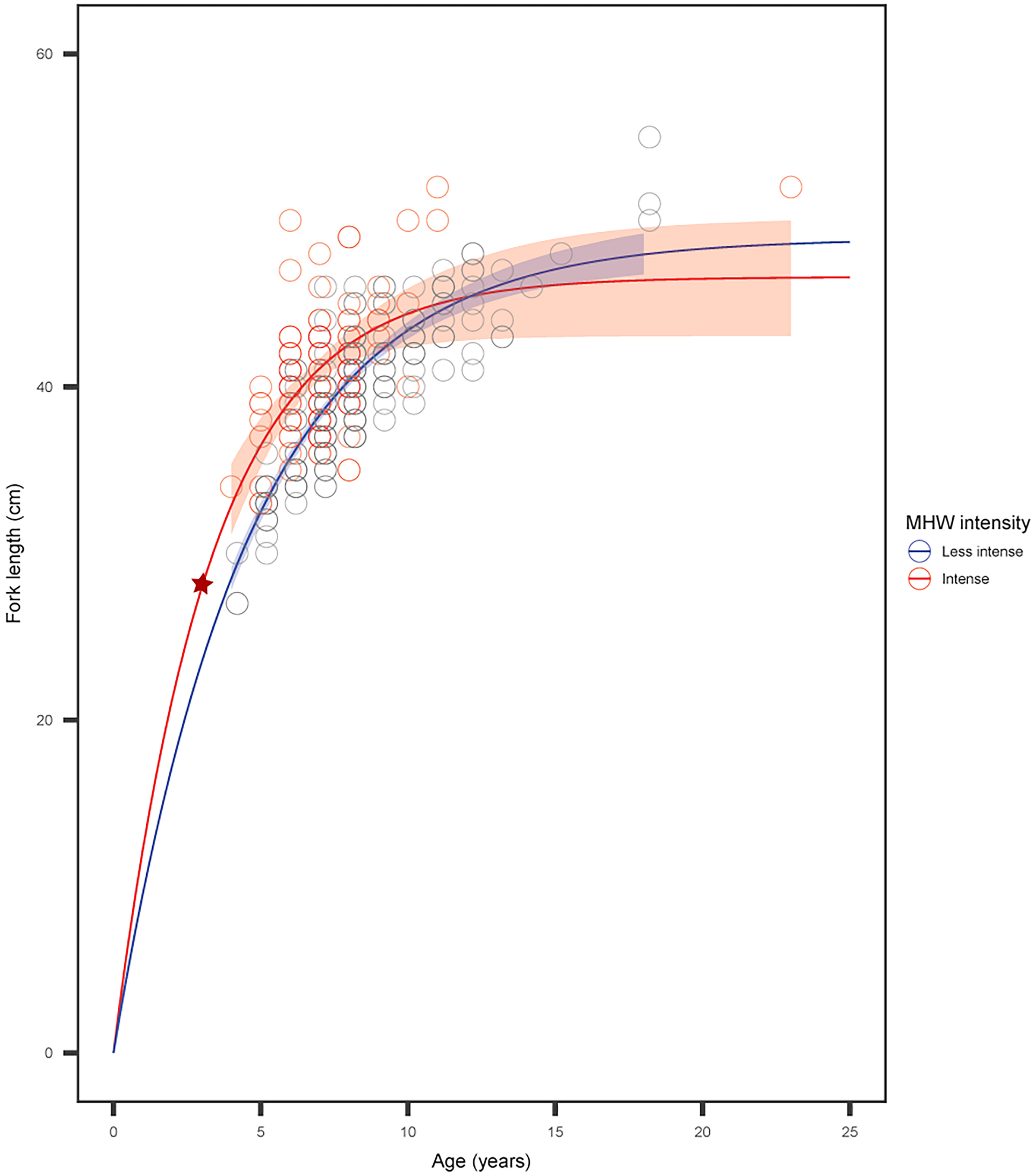

FIGURE 6 Female Black Rockfish length-at-age during intense marine heatwaves (MHWs) and less intense MHWs. Predicted von Bertalanffy growth functions (and 95% CIs) during intense MHWs (shown in red and designated with a star) and less intense MHWs (shown in blue). Length-at-age data points are denoted by the circles.

Both biological and functional maturity estimates varied temporally and with environmental conditions. Maturation was postponed during intense MHW conditions and resulted in a shift in both biological and functional maturity schedules. This indicates that individuals were allocating energy reserves away from reproduction to meet other physiological needs, like maintenance, growth, or behavior, to the extent that smaller females abstained altogether from investing energy into reproductive development and thus did not display the physiological indicators that would be present if they had "tried and failed" to spawn. Another recent study on a species of rockfish found increased rates of abortive maturation and skipped spawning during the 2014–2016 MHW but did not have a large enough sample size to explicitly explore environmental drivers of variation (Head et al., 2020). We found evidence that Black Rockfish reached functional maturity at older ages on average during intense MHWs. Our limited number of age samples may have hindered our understanding of the magnitude of this shift. Understanding the impacts of environmental conditions on maturation should be a focus of future work, because shifts in maturity-at-length or -age due to environmental conditions that are not accounted for in the stock assessment process could underestimate or overestimate population productivity relative to management decision thresholds (Head et al., 2020; Pacicco et al., 2023; Reed et al., 2023).

Peak female Black Rockfish reproductive development occurred from September through April, with the phenology of oocyte development and parturition consistent with the developmental cycle described in other studies (Bobko & Berkeley, 2004; Martin-Mills, 2007), but there were some differences in the proportion of females in each developmental stage during intense versus less intense MHWs. During intense MHWs, we found a higher proportion of females in a more advanced developmental stage in September, but then in the following months, a smaller proportion progressed toward spawning capability during intense MHWs compared to the proportion during less intense MHWs. The overall proportion of females that successfully released larvae (post-parturition) was lower by a third during intense MHWs (0.26) than during less intense MHWs (0.40). Even though overall development toward spawning capacity was depressed during intense MHW conditions, we found no obvious shift in the phenology of the reproductive development cycle. Our study would have benefited from expanded sampling in each month of peak reproductive development to pinpoint any phenological differences.

Our study documents the presence of parasites in the ovaries of Black Rockfish, which to our knowledge has not been previously documented (Love and Moser, 1984). Parasites occurred in 9% of ovarian tissue samples, with a higher prevalence during intense MHW conditions than during less intense MHWs (11.2% and 8.1%, respectively). We histologically identified parasitic flatworms (class: Digenea) and observed evidence of encysted, degenerate parasites likely being broken down within the ovaries. Our maturity analysis was restricted to the months of September through April, but given the prevalence of degenerate parasites, known cycles of ocean productivity (i.e., upwelling; Pauly & Christensen, 1995), and host feeding patterns (Kjesbu & Witthames, 2007; Love et al., 2002), we suspect that parasitic infections or at least encounter rates may be higher during peak upwelling and cycle seasonally with reproductive development (Bakenhaster et al., 2014; Clarke et al., 2006). Some of the parasites that we recorded were large enough that they displaced a substantial volume of the ovaries, with potential consequences for fecundity (Bakenhaster et al., 2014). We also documented cases of parasites in samples with mass atresia and/or granulosa inflammation, which usually signals an immune system response (Blazer, 2002; Kumar & Joy, 2015). While sampling, we also macroscopically identified and recorded the presence of parasitic copepods (genus: *Sarcotaces*) in the body cavities of Black Rockfish, but we did not document their presence consistently (and did not include those data in our analysis). These copepods are known to parasitize other rockfish species in the northeast Pacific Ocean and form a physical blockage that can interrupt oocyte development and fertilization (Conrath, 2019; Meyers et al., 2019). The transmission and prevalence of parasites may increase with elevated temperatures associated with climate change, especially in northern temperate regions where these dynamics are driven by seasonality (Lõhmus & Björklund, 2015). Pulse warming events, such as MHWs, that occur on the same physiological timescale as hosts and parasites, may amplify the effects of temperature on host–parasite interactions (Claar & Wood, 2020).

Reproductive success, survival, and growth are intrinsically linked through physiological trade-offs (Mangel et al., 2007). We observed an elevated growth rate coefficient for Black Rockfish during the 2014–2016 MHW relative to the growth rate coefficient during less intense MHWs, and both were higher overall than what is typically expected for slower-growing fishes, like rockfishes (Love et al., 2002) and for this species (Cope et al., 2016, 2023). Under climate change scenarios, growth rates for long-lived fishes are expected to increase (Rountrey et al., 2014), but with potential costs for reproduction, maximum body size, and lifespan longevity (Atkinson, 1994; Kindsvater et al., 2024; Kingsolver & Huey, 2008; Mangel et al., 2007). The growth rate coefficient that we observed during intense MHW conditions approached the threshold value for rockfishes (0.35 year^{-1}) below which reproductive effort is assumed to drop to zero due to the cost of faster somatic growth (Mangel et al., 2007). Similarly, the growth rate coefficient observed for Black Rockfish by Bobko and Berkeley (2004) in the late 1990s was also high (0.33 year^{-1}). Their study used samples collected during the second-most intense El Niño event in the last 70 years, with water temperature anomalies only slightly less than those measured during the El Niño event in 2015–2016 (Huang et al., 2017; NOAA Climate Prediction Center, 2023).

During the 2014–2016 MHW, the base of the food web changed, with a shift in the zooplankton community from more lipid-rich northern species of copepods to more southern species, which are typically lower quality prey (Ashlock et al., 2021; Brodeur et al., 2019; Peterson et al., 2017). While adult Black Rockfish likely do not feed directly on copepods, they may have encountered lower quality prey during the 2014–2016 MHW. When combined with increased metabolism and growth, this may have resulted in fish having poorer body condition (Rogers et al., 2021; Rosemond, 2024), potentially leading to the decrease in reproductive effort that we observed during intense MHW conditions. A recent field-based study on larval Black Rockfish during a similar time period and location as our study found that growth and development increased with warm water anomalies associated with "the blob," but that did not translate to increased survival; in fact, settlement rates had a dome-shaped relationship with temperature and were lower during 2014 and 2015 (Fennie et al., 2023), which highlights that increased growth may come at a cost for other aspects of fish life history.

In this study, we explored the impacts of novel ecological conditions and elevated ocean temperatures associated with MHWs on the reproductive development, maturity, and growth of Black Rockfish. Theoretical frameworks, like the metabolic theory of ecology and the temperature-size rule, are used to contextualize the impacts of ocean warming due to climate change on fish life histories (Daufresne et al., 2009; Oke et al., 2022; van Rijn et al., 2017; Wootton et al., 2022). Using these theoretical frameworks, we would expect an increase in juvenile growth rates, earlier maturation, and smaller adult body sizes with higher ocean temperatures (Atkinson, 1994; Brown et al., 2004; Kingsolver & Huey, 2008). Recent studies found patterns of growth, maturation, or adult body size that matched these predictions (Fennie et al., 2023; Kindsvater et al., 2024; Oke et al., 2022; Wootton et al., 2022). Our study focuses on a species with a complex reproductive strategy and the ability to postpone participation in a reproductive event through abortive maturation or skipped spawning as part of their life history strategy (Bobko & Berkeley, 2004; Conrath, 2017; Frey et al., 2015; Hannah & Parker, 2007; Head et al., 2020; Martin-Mills, 2007; McDermott, 1994; Rideout et al., 2000), likely as an evolutionary response to maximize reproductive success in a variable environment (Bobko & Berkeley, 2004; Mangel et al., 2007; Thorson et al., 2023). The elevated growth rate coefficient and larger size-at-age for younger females that we observed during intense MHWs match theoretical predictions, but the delay in maturation during intense MHWs contradicts theoretical predictions and the findings of other studies (Conrath & Hulson, 2021; Kingsolver & Huey, 2008; Kuparinen et al., 2011; Neuheimer & Grønkjær, 2012; Wootton et al., 2022). These differences may be due to a plastic response in reproductive strategy or because extreme climatic events, such as MHWs, induce changes over short periods of time that may differ from what is expected under gradual warming (Claar & Wood, 2020; Jentsch et al., 2009). Additionally, it is possible that the environmental conditions experienced during early life history influenced how individuals responded during each spawning season to environmental stress (Jonsson & Jonsson, 2014).

The impacts of human-driven climate change are evident across the globe (IPCC, 2023). Even the most optimistic carbon emission models predict increased ocean warming (Meinshausen et al., 2022) and that anomalous events, like MHWs, will occur with greater intensity and frequency in the future (Frölicher et al., 2018; IPCC, 2019; Oliver et al., 2019). The impact of MHWs may not be of the same consequence or magnitude for every fish population (Fredston et al., 2023), but some populations have experienced substantial declines (Barbeaux et al., 2021; Laurel & Rogers, 2020; PFMC, 2019a, 2019b; Rogers et al., 2021). An understanding of how anomalous environmental conditions interact with fish life histories may help predict population vulnerability, which will be critical for future fisheries management under climate change, especially for species with complex reproductive strategies for which our current theoretical frameworks may not be adequate. This research highlights the importance of investigating the realized impacts of novel climate events on the expression of fish life history traits and emphasizes that we should be alert to the persistence of biological and ecological relationships that challenge our theoretical frameworks for predicting individual- and population-level responses to climate change.

AUTHOR CONTRIBUTIONS

Funding: R. Claire Rosemond. *Study design*: R. Claire Rosemond, Melissa A. Head, and Scott A. Heppell. *Data collection or sources*: R. Claire Rosemond, Melissa A. Head, and Scott A. Heppell. *Histological analysis*: R. Claire Rosemond and Melissa A. Head. *Statistical analysis*: R. Claire Rosemond and Melissa A. Head. *Interpretation*: R. Claire Rosemond, Melissa A. Head, and Scott A. Heppell. R. Claire Rosemond wrote the manuscript. All authors contributed to manuscript revisions and approved the final submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Rosemond et al., 2024) are available in Zenodo at https://doi.org/10.5281/zenodo.14279278.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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