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Shifting ocean conditions influence temporal variation in the fecundity of California Current rockfishes (*Sebastes* spp.)

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Abstract

Successful reproduction is critical to the growth and persistence of marine fish populations, yet how changes in the environment influence reproduction remains largely unknown. We explored how shifting ocean conditions influenced larval production in four species of long-lived, live-bearing rockfish (*Sebastes* spp.) in the California Current. Brood fecundity, body size, and environmental information were analyzed from the mid-1980s through 2020. Interannual variation in brood fecundity was greater than 50% in the single-brooding yellowtail rockfish (*S. flavidus*) and widow rockfish (*S. entomelas*). Brood fecundity varied less in chilipepper (*S. goodei*) and bocaccio (*S. paucispinis*), two species capable of multiple broods per year. In these two species, interannual fecundity variability is more likely to depend on the number of broods produced than on brood size alone. In all four species, brood fecundity was positively correlated with maternal length and body condition. Variable ocean conditions influenced the strength of maternal size effects by year. These results provide evidence for reproductive plasticity and environmental effects on fecundity, with implications for changes in population reproductive potential with climate change.

Key words: reproductive plasticity, life history, environmental variability, *Sebastes*, California Current Ecosystem

1. Introduction

Successful reproduction is essential for the growth, persistence, and resilience of marine fish populations (Lowerre-Barbieri et al. 2017). Because of this, fisheries management strategies are often based on the idea that the reproductive potential of a harvested population should not fall below a critical minimum to ensure the replenishment of individuals (Goodyear 1993). However, population models that inform the management of marine fish often assume that a population's reproductive potential is invariant to changes in the environment, even though ocean conditions vary substantially, and this variability is increasing with climate change (Cai et al. 2021). One issue hindering the study of environmental effects on reproduction in marine fish is the difficulty in collecting fecundity information, which has led to a lack of long-term datasets (Lambert 2008). Furthermore, the mechanisms underlying reproductive variability in marine fish are complex, and learning about these mechanisms requires detailed information about variable ocean conditions, bioenergetics, and reproductive success (Pankhurst and Munday 2011; Fig. 1). Laboratory studies of temperate marine fish show that fecundity and spawning frequency respond to differences in water temperature and food availability under controlled conditions (Lambert and Dutil 2000; Yoneda et al. 2014; Beyer et al. 2021). Yet only a small number of studies on wild marine populations have evaluated large-scale shifts in ocean conditions with changes in maternal energy reserves, fecundity, and recruitment (e.g., Somarakis et al. 2019; Flores et al. 2021; Friedland 2021; González-Carrión and Saborido-Rey 2022). These types of studies are important to advance the scientific understanding of how reproductive plasticity and shifting ocean conditions interact to influence temporal variation in a population's reproductive potential (Pankhurst and Munday 2011).

The rockfishes (*Sebastes* spp.) are a diverse group of ecologically and economically important marine fish. More than 100 species exist worldwide, with a hotspot of diversity in the California Current Ecosystem (CCE), a large marine ecosystem in the northeastern Pacific Ocean (Love et al. 2002). The life history traits of CCE rockfishes evolved to cope with life in a dynamic, coastal upwelling environment where both ecosystem productivity and the conditions necessary for larval survival

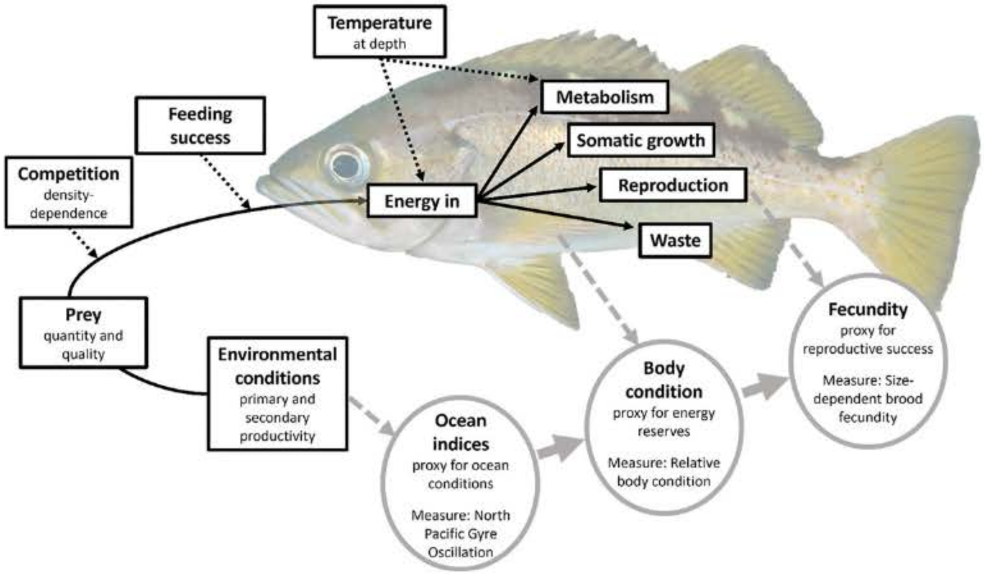

Fig. 1. Conceptual diagram of how the environment influences maternal energy reserves and reproduction. Physical ocean environmental conditions affect primary and secondary biological productivity and the availability of prey. Potential energy gained by feeding (solid black line) is mediated by competition and foraging success (black, short-dashed arrows). Assimilated energy is allocated to body maintenance, growth, and reproduction. Physiological processes are influenced by temperature-dependent consumption and metabolic rates. We use imperfect observations of these processes (long-dashed gray arrows pointing to gray circles) to understand reproductive plasticity in response to a change in maternal energy reserves and environmental conditions (solid gray arrows).

and successful recruitment are highly variable (Hickey 1979; Hickey and Banas 2008; Checkley and Barth 2009; Thorson et al. 2013; Field et al. 2021). Rockfish life history traits include longevity, high fecundity, and a live-bearing reproductive strategy (Love et al. 2002). Female rockfish invest considerable amounts of energy into reproduction to produce one (or sometimes multiple) broods of tens of thousands to millions of larvae per year over a long lifespan (Love et al. 2002). Maternal size has a well-recognized and important influence on rockfish reproduction (Dick et al. 2017), and variable ocean conditions are known to influence post-parturition larval survival (White et al. 2019). Yet much less attention has focused on other important maternal reproductive dynamics, particularly how changes in environmental conditions influence egg production and temporal variability in the reproductive potential of these populations.

Large-scale, interannual shifts in ocean conditions in the CCE are caused by changes in circulation patterns and temperature due to fluctuations in the El Niño Southern Oscillation and the Pacific Decadal Oscillation (Hickey 1979; Checkley and Barth 2009). Warm water and low productivity climate events, which occur during years of strong El Niño conditions and marine heatwaves, reduce rockfish body condition and gonad size (Lenarz et al. 1995; VenTresca et al. 1995). However, the influence of these shifting conditions on changes in a population's reproductive potential has yet to be quantified. Warm water, low productivity climate events vary in magnitude in the CCE but are increasing in frequency and intensity with climate change (Oliver et al. 2018; Cai et al. 2021).

To better understand the effects of shifting ocean conditions on rockfish reproductive output, we studied temporal variability in the fecundity of shelf-dwelling rockfishes off the coast of central California, USA. We combined historical and contemporary fish collections to develop a time series of brood fecundity (BF), maternal length, and body condition information for four species. Rockfish collections occurred over four decades during many, but not all, years, from the mid-1980s to 2020. Collections spanned a wide range of variable ocean conditions, including anomalously low ecosystem productivity in 2005–06, strong El Niño conditions in 1987–88, 1991–92, and 2015–16, and the more recent influence of marine heatwaves in 2014–16 and 2019 (Barth et al. 2007; Oliver et al. 2018; Cai et al. 2021). We studied yellowtail rockfish (*S. flavidus*), widow rockfish (*S. entomelas*), chilipepper (*S. goodei*), and bocaccio (*S. paucispinis*), all of which are abundant in shelf waters and represent the two patterns of reproduction in the genus. Female yellowtail rockfish and widow rockfish produce a single brood of larvae per year, which is the more common reproductive pattern within the genus *Sebastes*. By contrast, chilipepper, and bocaccio are capable of multiple broods per year, with one, two, or three broods possible (Ralston and MacFarlane 2010; Lefebvre et al. 2018). Thus, BF is equivalent to annual fecundity in the two single brooding species but is not equivalent to annual fecundity in the multiple brooding species if more than one brood is produced per year.

We first quantified interannual variation in reproductive potential by assessing differences in the relationship between maternal length and BF by year. Second, we explored the influence of maternal energy reserves and shifting ocean conditions to better understand reproductive plasticity. We hypothesize that rockfish exhibit reproductive plasticity given (1) the evolutionary history of CCE rockfishes in a dynamic, coastal upwelling ecosystem, (2) the high degree of recruitment variability characteristic of the genus, and (3) previous studies finding reduced growth and smaller gonads in years of warmer temperature and poor ecosystem productivity (Lenarz et al. 1995; VenTresca et al. 1995). Our results improve the scientific understanding of reproductive plasticity in these populations and will improve predictions of how directional shifts in ocean environmental conditions with climate change will influence changes in population reproductive potential.

2. Methods

2.1. Data

Historical and contemporary collections of rockfish came from Cordell Bank in the central California region of the CCE. Cordell Bank is a highly productive seamount located approximately 40 km off the coast and spans an area of 120 km^2 (Young et al. 2010). It is part of the Cordell Bank National Marine Sanctuary and has been closed to recreational and commercial groundfish fishing since 2002. Fish collections were focused on four rockfish species with different life histories. The single brooding yellowtail rockfish and widow rockfish live up to 64 and 60 years, mature around 7 and 5 years, and are most abundant at depths of 90–180 m and 140–210 m, respectively (Love et al. 2002). The multiple-brooding capable chilipepper and bocaccio are comparatively shorter-lived up to 35 and 45 years, mature earlier around 3 and 4 years, and are abundant at comparatively deeper depths over a broader range of 75–325 m and 50–250 m, respectively (Love et al. 2002). All four species are semi-pelagic but are typically associated with rocky outcroppings. We assumed the collections were sampling the same populations through time due to the geographic isolation and deep waters surrounding Cordell Bank, which likely limit adult movement in these species (Freiwald 2012).

For contemporary collections, females were sampled by hook-and-line during the late fall and winter from 2009 to 2020. We relied on local fishing knowledge to target the selected species from a chartered commercial passenger fishing vessel and a small commercial boat. Yellowtail rockfish and widow rockfish were collected from near the top of the bank at depths of 46–154 m, and chilipepper and bocaccio off the northern slope at depths of 131–244 m. Yellowtail rockfish and chilipepper were primarily targeted, whereas widow rockfish and bocaccio were sampled incidentally when encountered. This resulted in lower sample sizes in contemporary collections for the latter two species. Some data from contemporary collections were published in Beyer et al. (2015), Lefebvre et al. (2018), and Beyer (2022), which describe fecundity and reproductive patterns in chilipepper, yellowtail rockfish, and other species. Additional species and years from those projects were added to this analysis. Fish captured in the months of January, February, and March were pooled with the previous calendar year (November and December) to combine samples into a single reproductive season that occurs over the late fall and winter (e.g., females caught in January 2020 were attributed to the 2019 reproductive season).[1] After capture, fish were euthanized and placed in individual plastic bags to prevent the loss of larvae. Fish were covered with crushed ice in coolers to ensure the freshness of tissue samples, which were processed within 24–48 h of capture. We measured fork length (nearest mm), total wet weight (nearest 0.1 g), liver weight (nearest 0.01 g), and ovary weight (nearest 0.01 g). We then collected two weighed subsamples (0.5–1.0 g) of the ovaries for later fecundity analysis. Fecundity subsamples were preserved in a 10% neutral buffered formalin solution.

Protocols for fish collections were approved by the University of California Santa Cruz and Institutional Animal Care and Use Committee (Alons1808), and we followed the Guide for the Care and Use of Laboratory Animals (8th edition, National Academies Press). Fish were collected under the NOAA collecting permit No. NOAA-SRP-22-(2009 to 2020) and a scientific collecting permit issued to the NOAA Southwest Fisheries Science Center by the California Department of Fish and Wildlife (No. SC-13886).

2.1.1. Fecundity

For each female, we estimated BF using either a weight-based gravimetric counting method or an autodiametric imaging method (Beyer et al. 2015; González-Carrión and Saborido-Rey 2022; Mapes et al. 2023). The gravimetric method involves manually counting subsampled oocytes or larvae under a dissecting microscope. The autodiametric method uses images of oocytes and automated measurement software (ImageJ version 1.50i) to relate the mean oocyte diameter of a subsample to an oocyte density (oocytes per gram of gonad weight) by a species-specific calibration curve (Mapes et al. 2023). In both methods, the oocyte density for each subsample is then multiplied by the total gonad weight to estimate BF. BF was estimated for females with late-stage, unfertilized oocytes or fertilized embryos. For the unfertilized stage, we only used samples where oocytes were in late vitellogenesis and were fully recruited to the brood (Mapes et al. 2023). For the fertilized stage, we only used samples where the ovaries were fully intact and had not lost embryos during the collection process (Beyer et al. 2015). The gravimetric or autodiametric method of BF estimation used depended on developmental stage (i.e., no calibration curves were available for the fertilized stage), date of collection (i.e., more recent samples processed by the autodiametric method), and species (i.e., an autodiametric calibration curve was not available for bocaccio).

BF was modeled as a power function of body length (L, fork length, mm), which is standard in rockfishes (Dick et

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[1] It should be noted that our reproductive season is offset one year earlier than recruitment cohorts in fishery stock assessments, which assume a birthdate of all fish on January 1st. For example, our 2019 reproductive season corresponds with the 2020 cohort of age-0 fish in a typical rockfish stock assessment.

al. 2017):

$$\text{BF} = cL^b \tag{1}$$

The scalar (c) and exponent (b) parameters were estimated from the linear, natural log transformed, least squares regression of BF and length fit to the data:

$$\log(\text{BF}) = a + b * \log(L) \tag{2}$$

where $a = \log(c)$. For simplicity, we refer to b as the slope of the length–fecundity relationship because we work with the linear form of the relationship in eq. 2 to develop more complex models that explore the influence of maternal energy reserves and the environment on variation in BF. The b parameter measures the strength of maternal length effects on BF. A hyper-allometric maternal length effect on BF is shown by b greater than the exponent of the exponential, species-specific, length–weight relationship ($W = \text{c}L^{\text{d}}$), where d is commonly close to 3.0. Hyper-allometry in the maternal size-fecundity relationship is common in marine fishes and occurs in most rockfishes (Dick et al. 2017; Barneche et al. 2018). The a parameter captures proportional shifts in BF.

2.1.2. Body condition

Relative body condition served as a proxy for maternal energy reserves. Relative body condition (K_n) is a ratio of observed body weight to the expected body weight for a given length in the sampled population (Wuenschel et al. 2019):

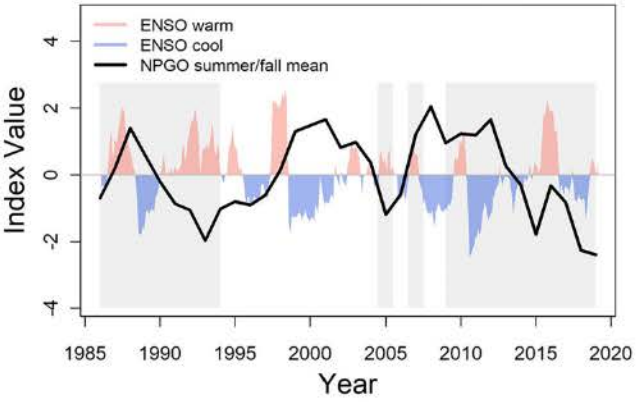
$$K_n = \frac{W_{\text{i}}}{cL_i^{\,d}} \tag{3}$$

where W_i is the somatic weight (wet weight without the gonad, g) and L_i is the body length of the i th fish of each species. Parameters of the species-specific length–weight relationship used to calculate K_n are shown in Table SA1.

2.1.3. Index of environmental variability

The North Pacific Gyre Oscillation (NPGO, http://www.o3d.org/npgo/) served as a proxy for variable ocean conditions in the CCE (Fig. 2). The NPGO is an index of relative sea surface height and large-scale circulation patterns in the Northeastern Pacific Ocean. It is correlated with salinity, nutrients, and chlorophyll levels and broadly describes conditions promoting primary and secondary biological productivity in the system (Di Lorenzo et al. 2008; Checkley and Barth 2009). Positive NPGO values are correlated with stronger equatorward flow and more subarctic source waters in the CCE, which generally indicates cooler and more productive ecosystem conditions. Negative values tend to reflect warmer, more subtropical source waters and less productive conditions. We used the combined August, September, and October mean (summer/fall NPGO) to reflect variable environmental conditions when females were developing oocytes and corresponding to an annual peak in energy reserves (Guillemot et al. 1985; Wyllie-Echeverria 1987).

Fig. 2. Environmental variability in the California Current Ecosystem over years with fecundity information (gray shading). We used the annual mean summer and fall ocean conditions, as described by the North Pacific Gyre Oscillation (NPGO, black line), as an environmental predictor of interannual variability in the length–fecundity relationship. This plot shows the NPGO conditions compared with variations in warm (pink) and cool (blue) regimes in the California Current, as indicated by the monthly means of the multivariate El Niño Southern Oscillation (ENSO). Positive values of the NPGO broadly correlate with higher ocean primary productivity in the California Current.



2.1.4. Historical datasets

To extend the fecundity time series, we added additional datasets collected prior to 2009. Historical studies targeted the same species at Cordell Bank and used similar hook-and-line methods. Some of the yellowtail rockfish fecundity information from 1986 to 1991 was published in a study of spatiotemporal variation between populations off central California and Washington State (Eldridge and Jarvis 1995). We recovered the raw data and additional unpublished information on all four species from the original datasheets from that study. Data from a third study were available from Stafford et al. (2014), which collected yellowtail rockfish, chilipepper, and widow rockfish at Cordell Bank in 2005 (with some additional collections in 2006 and 2007) to describe maternal effects on larval quality, fecundity, and the timing of parturition.

All historical studies measured fish length, wet weight, and gonad size, which allowed us to calculate K_n (eq. 3). Historical studies used gravimetric methods to estimate fecundity at the same stages of development as contemporary studies. Eldridge and Jarvis (1995) preserved a small portion of the ovary and counted three weighed subsamples of oocytes or embryos from the preserved portion. The conversion factor of preserved ovary weight to wet weight was recorded on the original datasheets and used to calculate the BF of the fresh-weighed ovary. Eldridge and Jarvis (1995) measured standard length, which was converted to fork length by using a length-type conversion (Echeverria and Lenarz 1984) and a statistical correction to standardize lengths.[2]

2.2. Statistical models

Bayesian hierarchical linear models were fitted to estimate interannual variation in the intercept and slope parameters of the length–fecundity relationship for each species, while accounting for any differences in BF due to estimation at the unfertilized or fertilized developmental stage. We later added additional predictors of maternal body condition and environmental conditions to better understand the drivers of reproductive plasticity. Models were fitted using the brms package in R (Bürkner 2017), which uses RStan for the underlying computations (Stan Development Team 2020). Parameters were estimated using four separate chains from a Markov chain Monte Carlo algorithm, each with 5000 iterations obtained after a burn-in of 2000 samples for a total of 20 000 post-warm-up draws of the posterior distribution for each model. The four species were modeled independently, and years with only a single data point were excluded from the analysis.

2.2.1. Base model

Model 1, referred to as the "base model", used maternal length and developmental stage as the sole predictors of BF. These two predictors were included in the base model because maternal length effects on rockfish BF are well established (Dick et al. 2017), and including developmental stage accounted for any bias introduced by estimating fecundity at pre- or post-fertilization in these live-bearing species. The equation for the base model was:

$$y_{ij} = \alpha_0 + a_j + \beta_0 x_{ij} + b_j x_{ij} + \lambda v_{ij} + \varepsilon_{ij} \tag{4}$$

where y_{ij} is the (centered and scaled) natural log transformed response variable of BF for an individual fish i in year j, x_{ij} is the (also centered and scaled) natural log transformed length of the i th fish in year j, α_0 and β_0 are the fixed effects for the intercept and slope, respectively, a_j and b_j are random effects (offsets) for the intercept and the slope in year j, respectively, v_{ij} is the developmental stage (unfertilized or fertilized) of the ith fish in year j with the associated fixed-effect coefficient, λ, and ε_{ij} represents the measurement error. We modeled the species-specific pairs of random effects (i.e., (a_1, b_1), (a_2, b_2),...) using a bivariate normal distribution with zero mean, marginal standard deviations ϕ and ψ, and correlation coefficient ρ. Similarly, the observational errors were assumed to be normally distributed with zero mean and standard deviation σ.

We specified prior distributions for the fixed effects, the standard deviation parameters ϕ, ψ, and σ, and the correlation ρ, following Gelman (2006). A standard normal distribution was used for the fixed effects, α_0, β_0, and λ. A sensitivity analysis using more diffuse priors with standard deviations of 10 and 100 found no qualitative differences in the parameter estimates. A half-student t distribution with 3 degrees of freedom and a scale parameter of 2.5 was used for the priors on ϕ, ψ, and σ (Gelman 2006; Bürkner 2017). We found no qualitative differences in a sensitivity analysis of the effect of these priors when adjusting the scaling parameter of the half student t distribution an order of magnitude less and greater from 2.5 to 0.25 and 25, respectively. Finally, the prior on the correlation parameter, ρ, was such that it implied a uniform prior on all correlation matrices (Lewandowski et al. 2009; Bürkner 2017).

Because of the hierarchical structure, in years where the data are sparse, the estimates of the parameters of the length–fecundity relationship shrink more strongly toward the population-level mean. In years with more data, the estimates more closely resemble the output of a fixed-effect ANCOVA-type model. A similar approach was taken for a meta-analysis of rockfish species and sub-genera-specific length–fecundity relationships (without consideration of year effects or the possibility of multiple broods) in developing the length–fecundity parameters to inform rockfish stock assessment models (Dick et al. 2017).

2.2.2. Adding predictors

We considered additional models to better understand plasticity in BF. Model 2 included maternal length and developmental stage, and added maternal body condition (K_n) as a direct predictor of BF:

$$y_{ij} = \alpha_0 + a_j + \beta_0 x_{ij} + b_j x_{ij} + \lambda v_{ij} + \delta z_{ij} + \varepsilon_{ij} \tag{5}$$

where z_{ij} is the (centered and scaled) value of K_n for fish i in year j and δ is the associated fixed-effect coefficient.

Model 3 included maternal length and developmental stage, and added the summer/fall NPGO conditions as an environmental predictor of interannual variation in BF (i.e., a predictor of the random effect of year). This was implemented using an interaction between environmental conditions (NPGO) and maternal length:

$$y_{ij} = \alpha_0 + a_j + \alpha_1 w_j + \beta_0 x_{ij} + b_j x_{ij} + \beta_1 w_j x_{ij} + \lambda v_{ij} + \varepsilon_{ij} \tag{6}$$

where α_1 and β_1 are fixed effects that capture the impact of the (centered and scaled) NPGO index (w_j) on BF. This model can be interpreted as allowing the environmental factor to affect the mean of the distribution of the random effects of both the intercepts and the slopes through a linear relationship (Qian et al. 2010). This was important for exploring changes in maternal length effects by year.

Last, we combined all predictors (maternal length, developmental stage, body condition, and environmental conditions) into a "full model" for each species, with the equation:

$$\begin{aligned} y_{ij} = \alpha_0 + \alpha_1 w_j + a_j + \beta_0 x_{ij} + b_j x_{ij} \\ + \beta_1 w_j x_{ij} + \lambda v_{ij} + \delta z_{ij} + \varepsilon_{ij} \end{aligned} \tag{7}$$

Similar to α_0, β_0, and λ, the additional fixed effects of α_1, β_1, and δ were assigned standard normal priors.

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[2] See Supplementary materials A

To compare models, we calculated the expected log pointwise predictive density (elpd) of new data using a leave-one-out (LOO) cross-validation approach (Vehtari et al. 2017). The LOO approach evaluated model fit and predictive power by sequentially removing, re-fitting, and predicting the response for the *i*th data point. This provided a quantitative assessment of model fit with respect to model complexity. We present elpd_{LOO} scores as offsets relative to the best fit model of greatest predictive power (Vehtari et al. 2017). We also used the Bayesian equivalent of the coefficient of determination (Bayes R^2) to assess differences in the amount of variance explained by each model (Gelman et al. 2019).

To visualize the results of the full model, we plotted the expected BF for females at different lengths and with differences in body condition in relation to the environmental index (conditional plots). All plots are at the unfertilized stage of development. In these plots, we show the posterior median and 95% credible intervals for the expected BF. The lengths of reference were as follows: (1) the mean length of females in the study (L_{mean}), (2) the length where 50% of females in the population are mature (L_{50}, small, approximate first-time spawners), and (3) the asymptotic length (L_{inf}, large, near maximum size females) from von Bertalanffy growth curves. The values for the reference lengths at L_{50} and L_{inf} were obtained from the most recent fishery stock assessments for each species.[3]

3. Results

3.1. Collection summary

Contemporary and historical fecundity data at Cordell Bank in central California spanned four decades from the mid-1980s to the late 2010s (reproductive seasons: 1986–1994, 2005–2007, and 2009–2019; Table 1). The complete time series had 21 years of BF and body condition information for yellowtail rockfish ($n = 775$), 11 years for widow rockfish ($n = 148$), 13 years for chilipepper ($n = 581$), and 8 years for bocaccio ($n = 130$). Years with only a single data point were excluded from the analysis. Years included in the time series spanned a range of ocean conditions in the CCE (Fig. 2).

3.2. Base model

3.2.1. Population-level, species-specific maternal length effects on brood fecundity

The influence of maternal length on BF differed by species and by the reproductive pattern at the population level (Fig. 3; population-level slope estimates, “All”). The population-level maternal length effect on BF was strongest in the single brooding yellowtail rockfish, with a slope of the length–fecundity relationship of 4.86 (95% CI 4.29–5.45) compared to the length–weight slope of 2.75 (95% CI 2.86–2.81). The influence of maternal length was also strong in the single brooding widow rockfish, with a population-level slope of 3.92 (95% CI 2.55–4.87) compared to the length–weight slope of 2.97 (95% CI 2.82–3.11), but with greater uncertainty. The overall strong influence of maternal length on BF in the single brooding species contrasted with relatively weaker population-level maternal length effects on BF in the multiple brooding species. In chilipepper, the population-level slope was 3.65 (95% CI 3.01–4.18) compared to the length–weight slope of 2.96 (95% CI 2.91–3.01). In bocaccio, the population-level slope was 3.29 (95% CI 2.57–3.79) compared to the length–weight slope of 2.65 (95% CI 2.56–2.74).

3.2.2. Interannual variation in the maternal length effect

For all four species, the strength of the maternal length effect varied by year (Fig. 3; slopes by year). The maternal length effect in yellowtail rockfish ranged from 3.19 (95% CI 1.80–4.47) in 2019 to 6.40 (95% CI 5.40–7.42) in 1988. This meant that in some years, large and small females had very similar relative fecundity (i.e., a slope close to the slope of the length–weight relationship, near 3.0). On the other hand, in years where the maternal size effect was very strong, larger females had much greater relative fecundity compared to small females (i.e., a slope near 6.0). The maternal length effect in widow rockfish ranged from 3.11 (95% CI −0.57–4.90) in 2017 to 4.61 (3.59–5.78) in 1987. In chilipepper, the maternal length effect ranged from 2.80 (1.98–3.68) in 2016 to 4.41 (3.16–5.90) in 2010, and in bocaccio, from 3.10 (95% CI 1.85–3.85) in 2015 to 3.46 (3.12–3.81) in 1987. The much smaller sample size available for widow rockfish and bocaccio and the fewer years sampled compared to yellowtail rockfish and chilipepper led to greater uncertainty in the parameter estimates by year for those species.

3.2.3. Interannual variation in brood fecundity

Interannual variability in BF (in absolute terms and by % variation) was greatest in the two single brooding species compared to the two multiple brooding species (Table 2). To illustrate BF variability for females of different sizes, we calculated the difference in expected BF between the year of highest and lowest fecundity at the three reference lengths for each species (Table 2). BF varied the most by year in yellowtail rockfish, where a large female at L_{inf} was expected to produce 2.06 million larvae in 2017 compared to only 0.86 million larvae in 2019. This was a 58% difference in BF of nearly 1.20 million fewer larvae produced by a single, large female relative to the high year in the 21-year time-series. Similarly, the expected BF of small and mean-sized female yellowtail rockfish varied by 50% fewer larvae from the highest to the lowest years (Table 2). Widow rockfish also exhibited high interannual variability in BF. BF declined by more than 55% relative to high years in the 11-year time series across the size range of mature females (Table 2). Interannual variability in BF was considerably less in the two multiple brooding species, with a decline in BF in poor years ranging from 30% to 51% in chilipepper and from 18% to 24% in bocaccio relative to the high fecundity years in the 13- and 8-year time series, respectively (Table 2).

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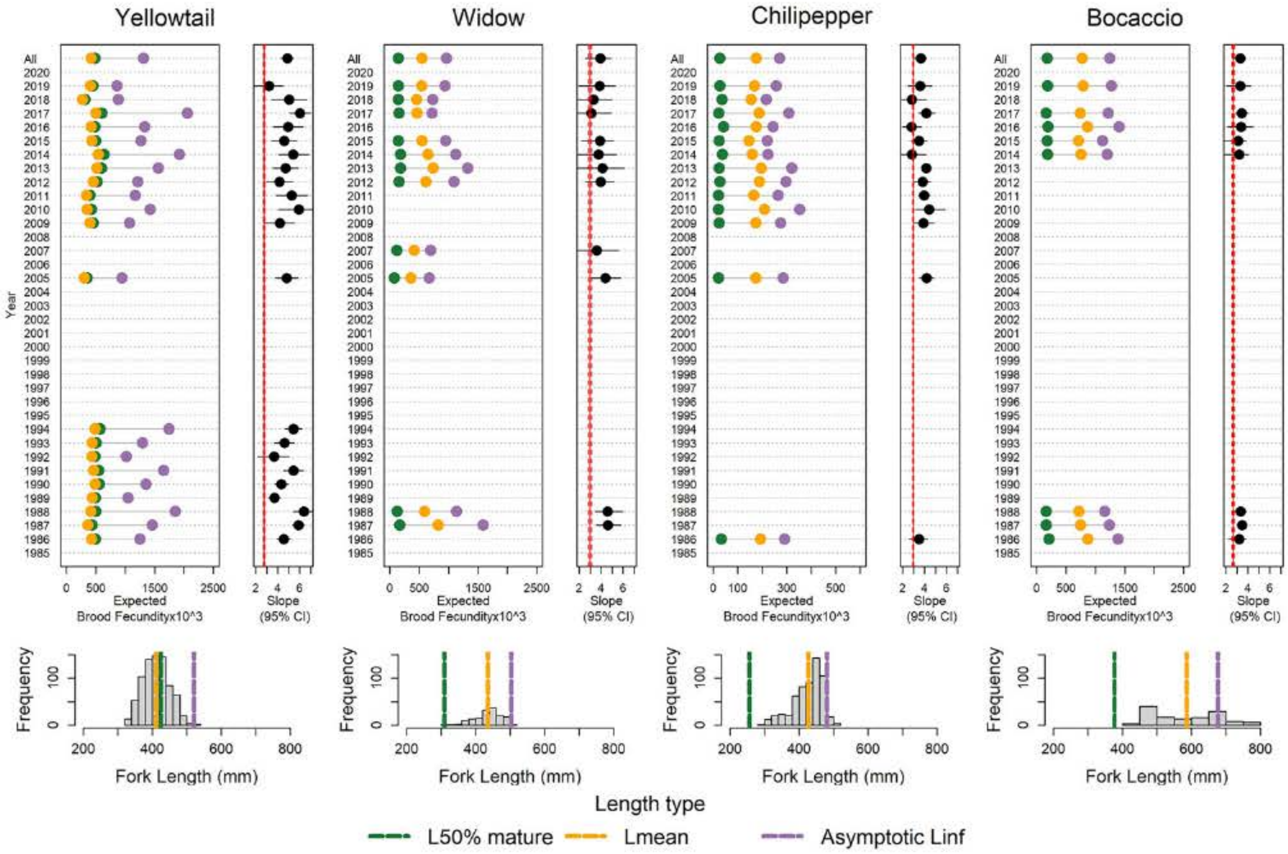
[3] See Supplementary materials B.

Table 1. Summary of fecundity samples collected at Cordell Bank in central California.

	Yellowtail			Widow			Chilipepper			Bocaccio			
Year	*n*	Mean length (mm)	Length range (mm)	*n*	Mean length(mm)	Length range (mm)	*n*	Mean length(mm)	Length range (mm)	*n*	Mean length (mm)	Length range (mm)	Reference
1986	61	437	331–531				28	428	336–495	29	654	566–790	Eldridge and Jarvis (1995)
1987	64	405	331–531	49	456	376–500				45	557	433–771	
1988	28	425	360–502	21	435	376–505				21	538	475–746	
1989	83	412	348–514										
1990	83	410	325–485										
1991	43	429	360–497										
1992	18	431	371–485										
1993	24	403	337–497										
1994	52	395	337–502										
2005	50	426	335–505	21	445	359–489	130	415	370–505				Stafford et al. (2014)
2006	1	450											
2007				4	444	419–454	1	460					
2009	21	412	373–480				31	429	350–475				Beyer et al. (2015); Lefebvre et al. (2018); Beyer (2022); current study
2010	9	404	380–443	1	400		24	432	350–469	1	779		
2011	30	409	363–463				31	403	290–470				
2012	32	407	361–476	16	414	345–462	62	447	305–480	1	589		
2013	35	416	351–480	4	412	376–439	102	416	306–506				
2014	21	418	355–481	15	435	415–470	18	463	450–500	2	682	658–705	
2015	24	411	353–456	2	386	308–464	21	424	302–487	6	682	560–755	
2016	8	401	332–450	1	454		48	417	335–482	3	682	637–745	
2017	51	396	350–462	6	406	370–425	51	445	372–505	19	527	465–694	
2018	13	403	360–450	6	391	365–430	12	458	432–487				
2019	25	394	341–461	4	395	332–443	23	448	394–505	5	551	541–571	
Total	776			150			582			132			

Note: Sample size (*n*), mean fork length (mm) of females, and range of female lengths (mm) are shown for each reproductive season (year). The time series included published and unpublished datasets and collections from this study. Note that years with only a single fecundity sample were omitted from the statistical analyses.

Fig. 3. Quantification of interannual variation in brood fecundity (BF, results of the base model). Dot charts show the expected BF at the reference lengths (colored left plots) and the strength of the maternal length effect (slope of the length–fecundity relationship, right plots) by year for the four rockfish species. The slopes are compared with the slope of the length–weight relationship (vertical, red-solid line, 95% CI red-dashed lines), where a greater length–fecundity slope indicates the disproportionate production of larvae by large compared to small females (more eggs per gram of female biomass). Length–frequency histograms (bottom) show the range of female lengths in the study compared to the reference lengths (vertical, colored, dashed lines). Reference lengths were the mean length of females in the study (L_{mean}, orange), the length where 50% of females in the population are mature (L_{50}, green), and asymptotic length (L_{inf}, purple) estimated from the von Bertalanffy growth function in the most recent stock assessment. Note the smaller range in the *x*-axis of expected BF for chilipepper, which reflects a comparatively smaller BF in that species.



3.3. Body condition and NPGO as predictors of brood fecundity variability

For all four species, we found that BF increased in females with better body condition (i.e., a higher K_n). Adding K_n to the BF models significantly increased predictive power, as shown by the large difference in $\Delta\mathrm{elpd}_{\mathrm{LOO}}$with respect to the base model of length and stage alone (comparison of models 1 and 2 relative to the model of best fit; Table 3). In all four species, the effect size of K_n in the full model was positive and did not include zero in the 95% credible interval of the posterior distribution.[4] These results show that maternal body condition is a significant and strong predictor of BF, in addition to the already significant and strong predictor of maternal length.

For all four species, adding the NPGO index to the base model, without body condition, did not result in any significant gain in predictive power (comparison of models 1 and 3 relative to the model of best fit; Table 3). Adding the NPGO to the full model for yellowtail rockfish, widow rockfish, and chilipepper led to essentially identical $\mathrm{elpd}_{\mathrm{LOO}}$values compared to a model with maternal length and body condition, but a higher Bayes R^2 for widow rockfish and chilipepper (comparison of models 2 and 4 relative to the model of best fit). In bocaccio, adding the NPGO to the full model resulted in worse predictive power and no increase in Bayes R^2.

Although adding the NPGO to the models did not improve predictive power, the effect of NPGO conditions on the intercept and slope parameters of the length–fecundity relationship in the full models was generally positive across species.[5] The posterior probability of a positive NPGO effect on the slope parameter of the length–fecundity relationship was 0.82 in yellowtail rockfish, 0.88 in widow rockfish, 0.85 in chilipepper, and 0.63 in bocaccio (Fig. 4). The posterior prob-

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[4] See full model results in Supplementary materials C.

[5] See full model results in Supplementary materials C.

Table 2. The greatest variation in expected brood fecundity relative to the highest fecundity year in the time series for each species at each reference length.

				Highest		Lowest		Difference	
Species	Size class	Length type	Fork length (mm)	Expected brood fecundity	Year	Expected brood fecundity	Year	Number of larvae	%
Yellowtail rockfish	Large	L_{inf}	521	2 061 804	2017	863 419	2019	1 198 385	58%
	Small	L_{50}	425	639 642	2014	317 636	2018	322 006	50%
	Mean	L_{mean}	412	540 670	2014	271 545	2018	269 125	50%
Widow rockfish	Large	L_{inf}	503	1 589 884	1987	673 663	2005	916 221	58%
	Mean	L_{mean}	436	822 934	1987	359 630	2005	463 304	56%
	Small	L_{50}	310	182 438	2014	80 440	2005	101 998	56%
Chilipepper	Large	L_{inf}	481	353 806	2010	216 653	2018	137 153	39%
	Mean	L_{mean}	427	209 269	2010	146 114	2015	63 155	30%
	Small	L_{50}	257	42 260	2016	20 936	2005	21 324	51%
Bocaccio	Large	L_{inf}	677	1 405 306	2016	1 120 877	2015	284 429	20%
	Mean	L_{mean}	586	875 455	1986	716 231	2015	159 224	18%
	Small	L_{50}	377	213 576	1986	163 451	1987	50 125	24%

Note: Large females are defined as females at the asymptotic length (L_{inf}) for the species. Small females are defined as females at the length at which 50% of females in the population are mature (L_{50}). Length at mean size (L_{mean}) is the mean length of females in the study. Reference lengths are ordered from largest to smallest size.

Table 3. Comparisons of the fecundity models used to quantify interannual variation in brood fecundity and to explore variables related to reproductive plasticity.

Species	Model	n	Years	Explanatory variables	Bayes R^2	$\Delta\text{elpd}_{\text{LOO}}$	ΔSE
Yellowtail rockfish	1. base	775	21	log length + stage	0.761	−76.4	13.00
	2. base + body condition	775	21	log length + stage + K_n	0.804	−0.1	0.8
	3. base + environment	775	21	log length + stage + NPGO	0.761	−76.3	13.0
	4. base + body condition + environment	775	21	log length + stage + K_n + NPGO	0.804	0	0
Widow rockfish	1. base	148	11	log length + stage	0.764	−10.0	6.0
	2. base + body condition	148	11	log length + stage + K_n	0.794	0	0
	3. base + environment	148	11	log length + stage + NPGO	0.767	−10.0	6.1
	4. base + body condition + environment	148	11	log length + stage + K_n + NPGO	0.796	−0.3	0.8
Chilipepper	1. base	581	13	log length + stage	0.720	−29.7	9.6
	2. base + body condition	581	13	log length + stage + K_n	0.747	−0.1	1.2
	3. base + environment	581	13	log length + stage + NPGO	0.721	−30.1	9.6
	4. base + body condition + environment	581	13	log length + stage + K_n + NPGO	0.748	0	0
Bocaccio	1. base	130	8	log length + stage	0.854	−14.0	5.0
	2. base + body condition	130	8	log length + stage + K_n	0.882	0	0
	3. base + environment	130	8	log length + stage + NPGO	0.855	−15.2	5.0
	4. base + body condition + environment	130	8	log length + stage + K_n + NPGO	0.882	−1.0	0.8

Note: The base model (model 1) included maternal length and developmental stage (unfertilized or fertilized) as the explanatory variables and year as a random effect. Separately, the potential explanatory variables of body condition (K_n, model 2) and environmental conditions (NPGO, model 3) were considered. Last, all predictors were modeled together in the full model (model 4). Models were compared by leave-one-out (LOO) cross-validation (Vehtari et al. 2017). Predictive accuracy was summarized as the expected log pointwise predictive density (elpd_{LOO}) and presented as the offset of the best fit model that scored a zero ($\Delta\text{elpd}_{\text{LOO}}$) with the standard error of the Monte Carlo simulation (ΔSE). The Bayesian coefficient of determination (Bayes R^2) was a measure of variance explained by the model.

ability of a positive NPGO effect on the intercept parameter was 0.61 in yellowtail rockfish, 0.82 in widow rockfish, and 0.98 in chilipepper. In bocaccio, there was a 0.79 probability of a negative effect of the NPGO on the intercept parameter.[6]

The parameters of the length–fecundity relationship are used to calculate the expected BF for females of different sizes. The resulting combined influence of the NPGO on BF varied by species and by female size (Fig. 5). The influence of the NPGO on BF was most evident in large, female yellowtail rockfish and large, female chilipepper (Fig. 5). The NPGO had a more proportional effect on BF across all sizes of female widow rockfish. There was no significant influence of NPGO conditions on BF in bocaccio (Fig. 5).

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[6] See full model results in Supplementary materials C.

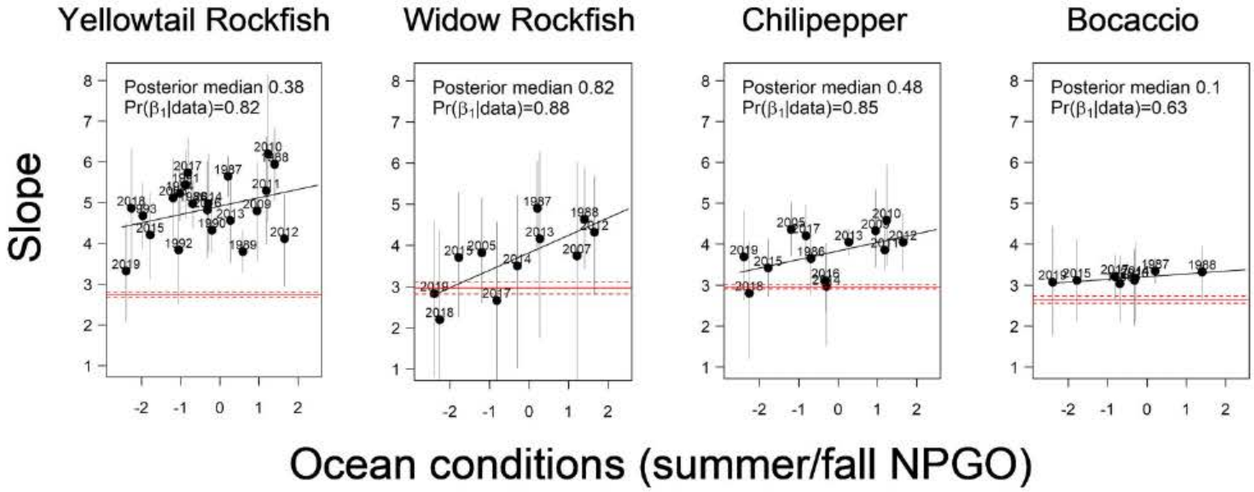

Fig. 4. Variable ocean conditions (summer/fall NPGO) influenced the year-specific estimate of the slope parameter of the length–fecundity relationship (slope, year-specific estimate with a 95% credible interval from the full model). This meant that the difference in the relative fecundity (eggs per gram of female biomass) in large compared to small females was stronger when ocean conditions were more favorable (i.e., a slope of the length–fecundity relationship greater than the slope of the length–weight relationship, red horizontal line with 95% confidence intervals, red dashed lines).

All models included the developmental stage to account for potential differences in BF estimated at the unfertilized or fertilized stage. The influence of developmental stage on BF was mixed among the four species. Fertilized broods had lower BF compared to unfertilized broods in widow rockfish, but no significant difference by stage was found in the other three species (i.e., the 95% CI of the posterior distribution included zero).[7]

4. Discussion

4.1. Quantifying temporal variation in fecundity

We document interannual variability in the BF of four Pacific rockfish species in central California by analyzing differences in the length–BF relationship through time. BF varied more by year in the two single brooding species than in the two species capable of multiple broods. The greatest absolute variation by year occurred in yellowtail rockfish, where the expected BF of a large female was reduced by more than 50% and by nearly 1.20 million fewer larvae in the lowest year relative to the highest. This high interannual variation was due, in part, to interannual differences in the strength of the maternal length effect on BF, which depended on ocean environmental conditions. Yellowtail rockfish had the longest time series and the most data available. However, similar high interannual variability in BF of greater than 55% also occurred in widow rockfish, despite the shorter time series and fewer samples, but with greater uncertainty in the resulting estimates.

The high interannual variability in BF for the two single brooding species in this study contrasted with comparably less variability in the two species capable of multiple brooding, chilipepper and bocaccio. Even though interannual variability in BF was less in the two multiple brooding species, it is likely that greater variability in annual fecundity exists for these species if the number of broods produced by individual females each year depends on environmental conditions. Environmentally driven variability in the number of annual broods was found in a laboratory study of the similar but smaller-sized rosy rockfish (*S. rosaceus*), where females had higher annual fecundity due to more broods of larger size when fed higher food rations (Beyer et al. 2021). Multiple brooding also occurs more often in large females compared to small females (Ralston and MacFarlane 2010; Lefebvre et al. 2018). This highlights an additional influence of maternal size on reproductive variability.

Our comparison among species demonstrates the challenges and importance of understanding the reproductive pattern to accurately evaluate variability in a population's reproductive potential over time. Multiple brooding was observed for chilipepper and bocaccio in many of the recent samples collected for this study, but previous studies have demonstrated the challenges associated with robustly quantifying the frequency of multiple brooding (Lefebvre et al. 2018). Multiple brooding was not reported for any rockfish in central California in a study from 1977 to 1982, except for a single, female boccaccio (Wyllie-Echeverria 1987). This was despite early recognition of the potential for multiple broods from conspecifics in the southern California region, where multiple brooding is more common (Moser 1967; MacGregor 1970). Similarly, multiple brooding was not detected in samples collected in central California from 2005 to 2008 (Stafford et al. 2014). In the contemporary dataset, multiple brooding in these two species at Cordell Bank has become more common since 2013 (Beyer et al. 2015; Lefebvre et al. 2018). The BF of additional broods is similar to the

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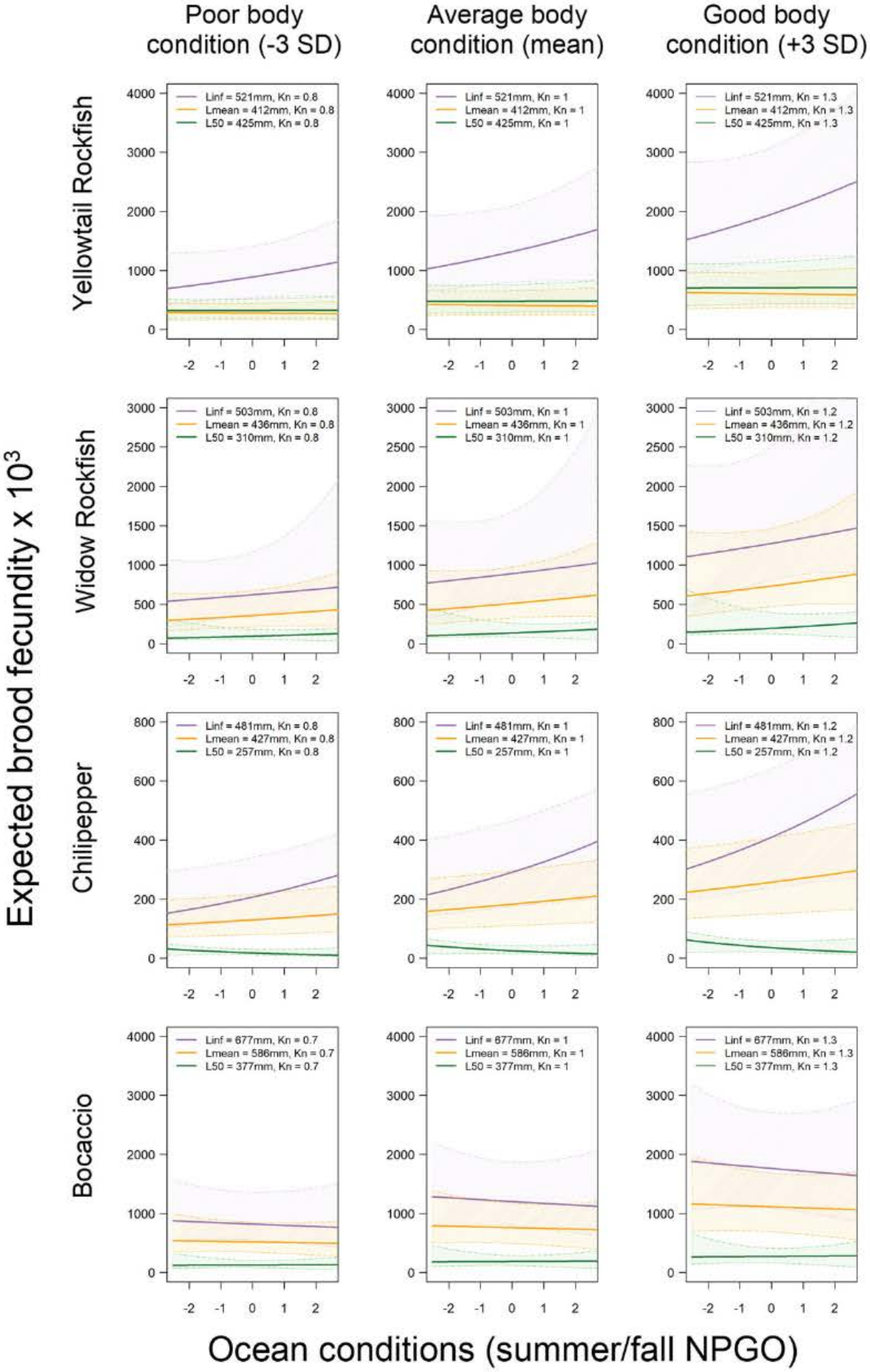
[7] See full model results in Supplementary materials C.

Fig. 5. Conditional plots of the full models showing the strong influence of maternal length and body condition on brood fecundity (BF, expected median, *y*-axis). By column, expected BF is shown for females in poor (left), average (center), and good (right) body conditions (K_n). Differences in body condition were defined as K_n at the mean and ±3 standard deviations for the mean-centered and scaled data. The results also show that the influence of ocean conditions (summer/fall NPGO, *x*-axis) on BF was strongest in large females (L_{inf}, purple lines) compared to small (L_{50}, green lines) or mean-sized (L_{mean}, orange lines) females in some species. Results are shown for unfertilized broods. Shading is the 95% credible interval for the expected BF at each reference length. Corresponding unscaled K_n and reference lengths are listed for each species.



first, which means that annual fecundity is nearly doubled (or tripled) by producing two (or three) broods a year for chilipepper and bocaccio (Beyer et al. 2015). Up to five broods were possible in captive rosy rockfish under controlled temperature and feeding conditions (Beyer et al. 2021). Future investigations should improve the documentation for how to identify multiple brooding, given the challenges in detection, as well as more deeply explore the ecological and demographic factors that are associated with spatiotemporal variation in the occurrence of multiple brooding. This knowledge is important to better quantify how multiple brooding contributes to variability in the reproductive potential of a population.

Sampling the size range of mature females in this study was important to accurately assess interannual variability in population reproductive potential. We successfully sampled the size range of mature widow rockfish, chilipepper, and boccaccio. However, most samples of yellowtail rockfish from central California fell short of the coast-wide species estimate of asymptotic size (L_{inf}) at 521 mm. This is consistent with trends in rockfish body size along the US west coast, where individuals of some species grow to larger sizes in the north compared to our study location in central California (Gertseva et al. 2017). The unavoidable lack of data on the largest-sized yellowtail rockfish females in the coast-wide population introduced greater uncertainty at the largest female sizes in the year of the highest fecundity estimate. The highest fecundity year occurred in 2017, where the expected BF of a L_{inf} female was 2.06 million larvae. This estimate was outside the range of observed BF in our study but was not out of reason for the species. For perspective, a yellowtail rockfish collected off Washington State in 1988, without associated length information, produced 1.99 million larvae (Eldridge and Jarvis 1995). In comparison, the largest brood observed in our time series was 1.36 million larvae by a 457 mm female, which was considerably shorter than L_{inf} for this species. Variability in the BF of the largest yellowtail rockfish in years of favorable ocean conditions should continue to be investigated, given that our results for the highest fecundity year (2017) fell outside of the observed BF in this species in central California. Despite greater uncertainty in the BF of the largest yellowtail rockfish in the most productive year, the BF of smaller and mean-sized female yellowtail rockfish in this study still varied by 50% from the highest to the lowest year. These expected brood sizes were all within the range of observations. In the other three species, the expected BF in large L_{inf} females was also within the size range of BF observations in our study.

4.2. Reproductive plasticity

In all four species, females with better body conditions produced larger-sized broods. This finding supported our hypothesis that variability in maternal energy reserves influences BF. The mechanism for this is likely that interannual variability in physical and biological ocean conditions influences the total energy reserves a female acquires and can then allocate to reproduction and other life history traits, such as growth and energy storage for survival. Flexibility in this allocation strategy is likely an adaptation to aid survival during periods of poor conditions and to enable future reproductive opportunities in years when favorable conditions return, especially in long-lived species (Stearns 1992). Longevity itself is an adaptation to cope with life in a strongly fluctuating environment where the survival of offspring is highly variable and uncertain (Stearns 1992).

At the extreme, mature female rockfish can forego reproduction entirely when conditions are very poor, called skipped spawning. Skipped spawning is not common in the shelf species studied here but can occur in other species to the north and in the deepwater slope species (Head et al. 2020; Conrath and Hulson 2021). Abortive maturation, a somewhat similar life history strategy for foregoing reproduction under poor environmental conditions in first-time spawners, occurs in chilipepper and the deepwater blackgill rockfish (*S. melanostomus*) in California waters (Lefebvre and Field 2015; Lefebvre et al. 2018). Abortive maturation generally occurs at the early stages of oocyte development, prior to the late vitellogenic and fertilized stages in which fecundity is measured. This is relevant because our fecundity estimates only included females that would have reproduced in the year of collection. Further investigation into the environmental and energetic effects on fecundity regulation, abortive maturation, and skipped spawning (fecundity regulation at the extreme of no viable eggs) is needed to more completely understand differences in interannual variability between young, first-time spawners and older, mature females.

On the other hand, strong reproductive plasticity also means that females can quickly "take advantage" of intermittent, favorable environmental conditions to greatly increase egg production. This was most evident in yellowtail rockfish and chilipepper, where favorable ocean conditions had the most influence on the BF of large females. Large females presumably have a greater capacity for storing energy as lipids in fat tissues compared to smaller females and require less energy allocated to growth since they are already near a maximum size. A greater proportion of excess energy reserves can therefore be allocated to reproduction. The differences in energetics and relative reproductive output between large and small females are important to consider in understanding the influence of shifting environmental conditions on changes in the reproductive potential of a population, particularly with respect to shifts in population structure to smaller and younger individuals due to exploitation (Berkeley et al. 2004).

Interestingly, some large-scale environmental conditions appear to affect multiple species similarly, whereas other conditions do not. The late transition to upwelling conditions in the spring of 2005 in the CCE had broad negative ecological consequences across trophic levels, including record low abundance levels of juvenile rockfish and other groundfish species (Barth et al. 2007; Ralston et al. 2015). We found generally poor larval production for the three rockfish species observed in 2005 (bocaccio were not sampled in 2005). BF in widow rockfish and small chilipepper was lowest in 2005. Yellowtail rockfish BF was also low in 2005, suggesting that 2005 was a generally poor year for reproduction in shelf rockfishes. Other years of low reproductive output in the time series included 2015, 2018, and 2019, two of which were the years of the poorest ocean conditions (lowest NPGO) in the time series. There was less consistency among species for the years of highest reproductive output, although this was potentially due, in part, to differences in sampling effort across years. Even though some environmental signals are likely to appear across multiple species and trophic levels, it is also expected that the effects of the environment will differ among species in consideration of habitat, feeding ecology, density dependence, and species-specific bioenergetics (Fig. 1).

Other environmental variables not considered here may also influence energy reserves and reproductive output. For example, the oxygen metabolic demand of pregnant females late in gestation is 80% higher than the baseline metabolic rate in yellowtail rockfish (Hopkins et al. 1995). This elevated demand has the potential to influence reproduction because warmer, subtropical waters typically contain less oxygen, and oxygen levels at depth can vary considerably by year, with the potential to influence the survival and reproductive success of females gestating embryos (Schroeder et al. 2019). Density-dependence will also affect per-capita food availability through competition for food resources and, thus, maternal energy reserves. Future investigations should continue to explore the complex roles of physical, biological, and demographic factors on reproductive success, especially where it is possible to measure localized conditions directly affecting feeding success and the bioenergetics of individuals. These conditions may not have been fully captured by the NPGO index in our study. Regardless, reproductive effort in these four species clearly varies by year and is influenced by maternal bioenergetics and shifting ocean conditions.

4.3. Implications for conservation and management

It is important to know that reproductive traits are plastic in response to changes in environmental conditions to better assess how the reproductive potential of a population, a key component of reproductive success and population persistence, will be influenced by future environmental change. This knowledge is critical to improving predictions of population dynamics and reproductive resilience as ocean conditions and the pattern of environmental variability in large marine ecosystems shift with climate change (Lowerre-Barbieri et al. 2017; McClure et al. 2023). Furthermore, fisheries management reference points and harvest rates are predicated on sustaining specific levels of spawning potential (Goodyear 1993). These estimates of spawning potential historically have not considered the influence of environmental shifts on reproductive effort due to a lack of information. In age- and size-structured stock assessments of west coast rockfishes, maternal length effects on BF are already accounted for in the estimate of spawning potential; however, the possibility for multiple brooding and phenotypic plasticity in reproductive output is currently not. Not accounting for these effects could result in misleading estimates of spawning potential with shifting ocean conditions for these and other marine fish populations. Furthermore, future studies could explore the potential for using forecasts of environmental conditions, such as shifts from El Niño to La Niña conditions, to improve short-term population projections for management.

5. Conclusion

Any changes in the reproductive potential of marine fish populations will be important to recognize for achieving sustainable management goals, as ocean conditions are increasingly influenced by climate change in large marine ecosystems. Our study leverages BF and body size information collected over four decades to provide new insight into how reproductive plasticity and fluctuating environmental conditions interact to influence temporal variation in reproductive output. Even so, it remains largely unknown how novel environmental conditions associated with climate change will influence population reproductive potential and the reproductive success of marine fishes. Therefore, continued investigation is needed to better understand the complex mechanisms, dynamics, and trade-offs influencing reproductive plasticity to improve knowledge of whether phenotypic plasticity in reproductive traits will help or hinder population persistence as ocean conditions change.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2023-0253.

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