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CAUSES AND CONSEQUENCES OF PHENOTYPIC PLASTICITY IN REPRODUCTIVE TRAITS FOR ROCKFISHES (*SEBASTES* SPP.) OF THE CALIFORNIA CURRENT ECOSYSTEM

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

In

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Sabrina G. Beyer

December 2022

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Abstract

CAUSES AND CONSEQUENCES OF PHENOTYPIC PLASTICITY IN

REPRODUCTIVE TRAITS FOR ROCKFISHES (*SEBASTES* SPP.) OF THE

CALIFORNIA CURRENT ECOSYSTEM

by

Sabrina G. Beyer

Phenotypic plasticity in life history traits is common for marine fish as part of

a life history strategy evolved to cope with spatiotemporal variation in ocean

environmental conditions. Knowing how and why phenotypic plasticity in life history

traits occurs improves predictions of growth, reproductive potential, and population

dynamics as ocean conditions change through time or vary through space. Here, I use

the live-bearing rockfishes (*Sebastes* spp.) of the California Current Ecosystem to

explore environmental and energetic causes of reproductive plasticity and

consequences for spatiotemporal variation in reproductive potential. Within the

genus, intra- and inter-specific variation in the frequency of reproduction exists. Most

rockfish produce a single larval brood annually once mature. However, a subset of

species (and individuals of those species) reproduce with greater frequency in the

southern region of the California Current Ecosystem, where ocean conditions most

differ. Temporally, warm climate events negatively impact fish body condition and

gonad size. I hypothesize that spatiotemporal variation in the ocean environmental

conditions of the California Current influences variation in maternal energy reserves

and the reproductive output of fish, with respect to maternal size. To test this, I use empirical study and theory. In Chapter 1, I find larger body size and greater food resources for the rosy rockfish (*Sebastes rosaceus*), a species capable of multiple broods, increases the frequency of reproduction and thus annual fecundity in optimal, stable laboratory feeding conditions. In Chapter 2, I use a 20+ year time series of rockfish from central California to find strong inter-annual variation in size-dependent fecundity relationships, and a greater capacity of large females to increase offspring production during years of favorable ocean conditions compared to small, mature females. In Chapter 3, I develop a state-dependent model to better understand the energy dynamics of reproduction and the evolutionary causes of spatial variation in reproductive traits. I find latitudinal variation in the life history traits of rockfish is adaptive to maximize expected lifetime egg production in different biogeographic regions of the California Current. These regions from north to south differ in seasonality, ocean productivity, and temperature. Strong seasonality in the north favors a single brood reproductive strategy to cope with food scarcity in the late winter that causes an annual period of net energetic losses. Multiple brooding is favored for environments with weaker seasonality as an opportunity to increase annual reproductive output after females obtain an asymptotic size, stop growing, and reallocate energy from growth to reproduction. However, the maximum female size is expected to differ by region and to depend on the mean amount of food in the environment. Therefore, due to weaker seasonality, poorer ocean productivity, and warmer temperatures in the southern region of the California Current, females are

expected to be smaller, have small-sized broods, and be less productive compared to females in the north. This is despite the expectation for increased multiple brooding. My dissertation improves the knowledge of how and why spatiotemporal variation in the frequency of reproduction occurs among rockfishes of the California Current Ecosystem. Importantly, phenotypic plasticity in life history traits influences spatiotemporal variation in growth and reproductive output and should be accounted for when considering how future changes in ocean environmental conditions will influence fisheries productivity and population dynamics for these economically important species.

Acknowledgements

I am grateful to the coauthors on the published chapter and chapters in preparation for journal submission. The co-authors listed in this publication directed and supervised the research which forms the basis for the dissertation. The text of this dissertation includes reprints of the following previously published material:

Chapter 1: Beyer SG, Alonzo SH, Sogard SM. 2021 Zero, one or more broods: reproductive plasticity in response to temperature, food, and body size in the live-bearing rosy rockfish *Sebastes rosaceus*. Marine Ecology Progress Series 669:151-173. https://doi.org/10.3354/meps13718

Introduction

Successful reproduction is critical to the stability, persistence, and growth of wild fish populations. Considering how the environment influences reproduction is therefore important for the sustainable management of marine fish as ocean environmental conditions shift with global climate change. However, the life history parameters used to assess the health and status of fish populations are often treated as static through time and invariable in response to environmental change, even though phenotypic plasticity of reproductive traits may exist. A growing body of evidence suggests that fluctuating ocean conditions and a history of exploitation often drive variation in growth, the timing of maturation, reproductive output, and recruitment for marine species (Jørgensen et al. 2007, Narimatsu et al. 2010, Palkovacs et al. 2012, Tu et al. 2018, Somarakis et al. 2019, Tanner et al. 2019, Flores et al. 2021). Therefore, understanding the causes and consequences of phenotypic plasticity in reproductive traits in response to spatiotemporal variation in ocean environmental conditions will improve assessments of population reproductive potential and predictions of population dynamics.

Phenotypic plasticity in life history traits can occur at different scales. Through time, phenotypic plasticity in reproductive traits allows individuals to adaptively modify energy allocated to reproduction in response to fluctuating environmental conditions (Piersma & Drent 2003, Baker et al. 2015). Variation in reproductive traits may include a change in offspring number, size, timing, and/or the frequency of reproduction. Temporal variation influences the reproductive potential of a population

by shifting the numbers of females contributing to reproduction each year and total reproductive output. Thus, population reproductive potential may vary strongly year to year if reproductive output is correlated with variation in ocean environmental conditions. Additionally, phenotypic plasticity may cause intra-specific trait variation among individuals that are spatially distributed across habitats that have different environmental conditions, such as differences in temperature and seasonality in the ocean by latitude (Conover 1992, Varpe 2017). Phenotypic plasticity, which causes spatial variation in traits, allows organisms to cope and adapt to different environmental conditions that vary through space within the distributional range.

Theoretical studies suggest that phenotypic plasticity in life history traits leads to a host of population-level advantages. This may include increased population growth, decreased risk of extinction, and quicker adaptation to new environments (Forsman 2015). However, empirical evidence is often lacking (Forsman 2015) and competing theory suggests that trait plasticity can negatively affect populations and increase the extinction risk when an environmental cue and plastic trait become uncoupled (Visser et al. 1998, 2021, Reed et al. 2010, Murren et al. 2015). This is especially true when environmental conditions shift to conditions favoring a different life history strategy (Botero et al. 2015). For example, historically fluctuating yet predictable, environments are likely to favor the evolution of phenotypic plasticity (Botero et al. 2015). But if the pattern of environmental conditions changes to become less predictable, phenotypic plasticity in traits may no longer be well suited to cope with the new conditions. Populations in these "transition zones" may be especially

vulnerable to reproductive failure and extinction (Botero et al. 2015). Thus, as ocean environments become more variable and less predictable with climate change, phenotypic plasticity in reproductive traits may be critically important to buffer populations against the possible negative effects of environmental change. Alternatively, phenotypic plasticity could have negative consequences, itself, if mismatches in the environment and the plastic trait occur. Such as if an environment becomes too extreme or less predictable (Moreno & Møller 2011, Botero et al. 2015, Sergio et al. 2018). Therefore, it is important to understand the cause and consequences of phenotypic plasticity in reproductive traits to better predict what effect shifting ocean conditions will have on population reproductive potential with climate change and with respect to sustainable fisheries management to maintain productive fisheries.

Environmental changes in ocean conditions are already occurring for large-scale marine ecosystems such as the California Current Ecosystem (CCE), which supports numerous economically important commercial and recreational fisheries (Cai et al. 2014). How fisheries productivity in this ecosystem will respond to shifting ocean environmental conditions is currently not well understood (Perry et al. 2010). A marine heatwave in the Northeast Pacific Ocean, which occurred from 2014 to 2016, induced large-scale alterations in ocean temperatures, primary productivity, and northern range expansions for southern species in the CCE (Di Lorenzo & Mantua 2016, Peterson et al. 2017, Sanford et al. 2019). The effects of this anomalous, multi-year event on fish reproduction are largely unknown, but an increase in warm water climate events is predicted for the Northeast Pacific Ocean that influence conditions in the CCE

(Sydeman et al. 2013, Joh & Di Lorenzo 2017). Other climate events impacting the CCE, such as warm water El Niño conditions, decrease fish body condition and gonad size (Lenarz et al. 1995, VenTresca et al. 1995). The combination of anomalous climate events and increasing ocean temperatures influence physical ocean conditions, primary biological productivity, and fish bioenergetics. Changes in these conditions are likely to influence reproductive output if reproductive traits are plastic in response to a fluctuating environment. Therefore, understanding the effects of fluctuating ocean environmental conditions on spatiotemporal variation in reproductive traits provides insight into how population reproductive productivity may change as the ocean becomes warmer, and climate events more extreme and less predictable.

Life history theory posits that traits are not only shaped by the environment, but also by energetic trade-offs that influence maturity schedules, the frequency of reproduction, fecundity, and life expectancy (Lack 1954, Roff 1992, Stearns 1992). Finite energy resources are allocated between reproduction and other life history traits, such as growth, survival, and future reproductive opportunities (Roff 1992, Stearns 1992). I argue that research aimed at predicting and understanding how these trade-offs interact with the environment to shape the evolution of plastic traits is needed because it will provide novel insights on the role and importance of phenotypic plasticity to population dynamics. This is especially true as the patterns of environmental variation change with global climate change. These insights are critical to predicting population dynamics for different environmental conditions and for developing sustainable natural

resource management strategies to ensure adequate levels of reproduction for species that are more (or less) vulnerable to climate change.

For my dissertation, I explored different scales of phenotypic plasticity in reproductive traits within and among individuals of closely related marine fish species that had different reproductive strategies. I used the economically important, live-bearing rockfishes (*Sebastes* spp.) of the CCE in the Northeast Pacific Ocean as a model system. Reproductive traits vary within and among rockfish species and differ most by latitude in the CCE. Most rockfish produce a single brood of larvae annually once mature (i.e., a single brood reproductive strategy), but at least 15 species (and individuals of those species) reproduce with greater frequency in the south (i.e., a multiple brooding reproductive strategy) (Love et al. 2002, Lefebvre et al. 2018). Furthermore, maternal body condition and smaller gonads occur for some species during years of warm water El Niño conditions (Lenarz et al. 1995, VenTresca et al. 1995). This is likely to reduce the reproductive output of individuals but has not been quantified. Not accounting for large spatiotemporal variation in reproductive traits hampers efforts to accurately assess the reproductive potential for these moderate- to long-lived rockfishes, where individuals are distributed across a range of ocean environmental conditions that vary by region from north to south and by year in the CCE.

I used empirical methods (Chapters 1 & 2) and mathematical theory (Chapter 3) to explore the causes and consequences of phenotypic plasticity in the reproductive traits of rockfish. I first conducted a laboratory study to test the effects of temperature

and food availability on reproductive output and the possibility for multiple broods by Rosy rockfish, *Sebastes rosaceus* (Chapter 1). Next, I continued the empirical work with a study of 20+ years of fecundity data for four rockfish species from central California to better understand how larval brood sizes varied through time and in relation to fluctuating ocean conditions (Chapter 2). Last, I applied knowledge gained from the laboratory and field to develop a state-dependent life history model to better understand spatial variation in the frequency of reproduction. I used this model to better understand how spatial variation in life history traits is adaptive, and how the reproductive potential of geographically distinct sub-populations is expected to vary by region, given mean differences in ocean environmental conditions that occur from north to south in the CCE (Chapter 3). My research advances the understanding of how and why phenotypic plasticity in reproductive traits occurs. Importantly, I show how phenotypic plasticity in life history traits influences spatiotemporal variation in the growth and reproductive potential of individuals and should be accounted for when predicting how changing environmental conditions with global climate change will influence population dynamics and fisheries productivity.

Chapter 1: Zero, one or more broods: Reproductive plasticity in response to temperature, food, and body size in the live-bearing Rosy Rockfish (*Sebastes rosaceus*)

Abstract

Patterns of reproduction, such as size-fecundity relationships used in models to assess fish populations, are generally treated as static through time and invariant to environmental change. However, growing evidence suggests that changes in ocean conditions, such as warming water temperatures and reduced primary productivity, affect life history traits including reproduction. Under controlled experimental conditions, we documented reproductive plasticity in the live-bearing Rosy Rockfish, *Sebastes rosaceus,* in response to different temperature and feeding regimes with maternal size as a covariate. Females produced zero to five larval broods annually. Larger females had disproportionately higher fecundity in comparison with smaller females by producing larger-sized broods and a greater number of annual broods. Warmer water temperature decreased the time interval between brood releases, likely reflecting faster egg and larval development. However, warmer temperature did not increase the total number of broods, potentially reflecting a tradeoff with increased metabolic demand. Well-fed females had better body condition and higher annual fecundity compared to poorly-fed females, primarily due to a greater number of broods. Conversely, females with poor body condition at the start of the reproductive season did not reproduce, providing possible evidence of delayed maturation at smaller sizes

or skipped spawning at larger sizes. Reproductive plasticity (in terms of whether and how many broods are produced per year) in response to the environment likely contributes to high inter-annual variation in population larval production. Understanding the causes and consequences of reproductive plasticity is critical to developing sustainable management strategies and predicting population response to changing climate conditions.

Key words: reproductive plasticity, maternal size, body condition, food availability, temperature, *Sebastes,* climate change, fisheries management

1. Introduction

Successful reproduction is critical to the stability and growth of wild fish populations and is therefore a vital component of natural resource management (Roff 1992, Stearns 1992, Hilborn et al. 1995, Lambert 2008, Clutton-Brock & Sheldon 2010, Kindsvater et al. 2016, Lowerre-Barbieri et al. 2017). Climate change is likely to affect the reproductive success of marine fishes through changes to the biological and physical environments, affecting resource availability, temperature, and bioenergetics (Hilborn et al. 1995, Harvey et al. 2011, Pankhurst & Munday 2011, Lowerre-Barbieri et al. 2017). However, size-dependent fecundity relationships currently used in population models to assess the health and status of fish populations are often treated as static through time and unaffected by environmental change (Lambert 2008) even as a growing body of evidence suggests that changes in the ocean environment, such as

temperature and food availability, drive variability in life history traits (Narimatsu et al. 2010, Tillotson & Quinn 2018). Classic life history theory states that tradeoffs exist under limiting resources, leading to predictable shifts in energy allocation affecting growth, maturity, and reproductive effort (Stearns 1992). Phenotypic plasticity in life history traits may evolve, allowing populations to rapidly respond to environmental change (Pigliucci 2001, Piersma & Drent 2003, Botero et al. 2015), yet the extent of reproductive plasticity exhibited by individuals, and the subsequent effects on population-level productivity are largely unknown. Understanding the causes and consequences of reproductive plasticity, including change in size-dependent fecundity relationships, where females of the same size produce more or less eggs depending on prevailing environmental conditions, will allow resource managers to better assess and predict annual reproductive output of marine fishes.

To study phenotypic plasticity in reproductive effort, an understanding of how fecundity increases with maternal size must be well established. Fecundity generally increases in a hyper-allometric relationship with maternal size in marine fishes (Barneche et al. 2018). This is important to fisheries management because removals of old, large females from a population disproportionately reduce reproductive output (Scott et al. 1999, Berkeley, Hixon, et al. 2004, O'Farrell & Botsford 2006, He et al. 2015, Barnett et al. 2017). Once the size-dependent fecundity relationship is established, then environmental variables may be explored to explain additional variability in reproductive output. Therefore, maternal size is a requisite covariate in any study of reproductive plasticity in marine fishes.

The speciose genus *Sebastes* (rockfishes) is well suited for the study of reproductive plasticity in response to variable environments. The effect of maternal size on fecundity is well documented across these species (Dick et al. 2017), providing a clear baseline for assessing whether and how this relationship changes with the environment. All rockfishes are live bearers with internal fertilization, releasing larvae that have completed embryogenesis and are ready to begin exogenous feeding (Love et al. 2002). During a relatively short mating season, females copulate with one to several males and store sperm in the ovaries (Sogard, Gilbert-Horvath, et al. 2008). Fertilization may occur months after mating, and gestation time is variable depending on species and temperature (Moser 1967, Love et al. 2002). For example, mean gestation of Yellowtail Rockfish, *S. flavidus*, embryos was 29.2 days for females held in the laboratory at 11.9 °C (Eldridge et al. 2002). In comparison, mean gestation was 48 days in *S. schlegeli* held at 9.8 °C (Yamada & Kusakari 1991). Both species-specific genetics and the environment, such as temperature, are likely to influence the length of the gestation period with shorter gestation possible at lower latitudes and warmer temperatures (Moser 1967).

Individual females exhibit a range of phenotypic plasticity within and across species, with two distinct reproductive strategies in the genus. In the majority of *Sebastes*, mature females are limited to the production of a single larval brood annually (i.e., a single brood strategy). However, females of at least 15 species are capable of releasing one or more additional broods per year (i.e., a multiple brooding strategy) (Moser 1967, Love et al. 2002, Lefebvre et al. 2018). Though rockfishes were

historically considered determinate spawners, the recruitment of oocytes for secondary broods throughout the reproductive season recategorizes multiple brooding rockfishes as indeterminate spawners (Murua & Saborido-Rey 2003, Murua et al. 2003, Lefebvre et al. 2018). Thus, potential annual fecundity in multiple brooding rockfishes, which is the total number of advanced, vitellogenic oocytes produced per female per year (Murua et al. 2003), cannot be determined by counting oocytes at the start of the reproductive season because not all oocytes for all broods have been recruited yet. Instead, annual realized fecundity, which is the total number of larvae released per female in a year, is a function of the total number of broods and brood fecundity over the entire reproductive season (Murua et al. 2003). This concept is well established for indeterminate, batch spawning marine fishes that release eggs (Fitzhugh et al. 2012) but is less well-defined for the live-bearing, multiple brooding rockfishes (Lefebvre et al. 2018).

The number of larvae in a second brood is often comparable to the first brood (MacGregor 1970, Beyer et al. 2015, Lefebvre et al. 2018), meaning the production of a second brood can nearly double reproductive output. In addition, multiple broods per year increases the number of times at which larvae are released into the ocean environment, increasing the likelihood some larvae will encounter favorable environmental conditions that increase their survival (Cushing 1975). Larger females may also produce more broods annually in comparison with smaller females, representing an additional effect of maternal size on reproductive output and

exponentially increasing the fecundity of larger, multiple brooding females (Love et al. 1990, Ralston & MacFarlane 2010, Beyer et al. 2015, Lefebvre et al. 2018).

In contrast to multiple brooding, at least some rockfishes have the ability to forego reproduction in any given year but spawn again in subsequent years (Head et al. 2016, Conrath 2017). This behavior is called skipped spawning and also occurs in other marine fishes (Rideout et al. 2005, Rideout & Tomkiewicz 2011, Skjæraasen et al. 2012, 2015). Skip spawning means reproductive failure in the current year but may result in an increase in allocation of energetic reserves to growth, survival, and future reproductive opportunities (Stearns 1992). A variation on skipped spawning that also occurs in rockfishes is delayed or abortive maturation during the first spawning attempt, where oocytes either take longer than one year to develop, or oocytes are recruited but later aborted and resorbed through a mass atresia event (Nichol & Pikitch 1994, Lefebvre & Field 2015, Lefebvre et al. 2018). The occurrence of delayed or abortive maturation in a first time spawner is considered an adolescent or developing phase, where a female may be physiologically mature but has yet to contribute to population larval production and is thus considered functionally immature (Brown-Peterson et al. 2011, Lowerre-Barbieri et al. 2011). Both skipped spawning and delayed or abortive maturation affect population larval production in terms of which females contribute each year. The diversity of reproductive strategies and behaviors observed in the *Sebastes* genus, ranging from less plastic (i.e., 0 or 1 annual broods) to more plastic (i.e., 0, 1 or more annual broods), provides an excellent study system for understanding how individual reproductive output is affected by environmental variability and how

reproductive success may respond to climate change in a widespread, diverse, and economically important species complex.

At least 56 rockfish species are found in the California Current Ecosystem along the West Coast of the United States (Love et al. 2002). The California Current is characterized by high spatiotemporal variability in environmental conditions (Checkley & Barth 2009), with a major geographic break near Point Conception (N 34.449, W 120.471). To the north, seasonal cycles in temperature and biological productivity are the result of strong upwelling events in coastal waters during the spring and early summer that circulate cold, nutrient rich waters from depth into the photic zone, driving primary and secondary productivity (Parrish et al. 1981, Checkley & Barth 2009). To the south, ocean temperatures are warmer and upwelling in coastal areas is less seasonal and more muted throughout the year (Parrish et al. 1981, Legaard & Thomas 2006, Checkley & Barth 2009). For example, a comparison of regional temperature gradients showed a 2 to 3 °C difference between central California and the southern California Bight, with mean temperature of coastal waters at 10 m depth (all months combined) between 12 to 13 °C in the central region and 14 to 15 °C in the south (Lynn 1967). On a temporal scale, warming trends are documented for the California Current (Di Lorenzo et al. 2005) and the frequency of climate warming events such as El Niño and marine heatwaves has increased in recent history (Checkley & Barth 2009, Cai et al. 2014, Di Lorenzo & Mantua 2016). Ocean warming events in the California Current are correlated with decreased primary productivity through disruptions to ocean

circulation, nutrient availability, and shifts in prey quantity or quality affecting energy transfer to upper trophic levels (Legaard & Thomas 2006, Piatt et al. 2020).

In rockfishes, the strong 1982-83 and 1992-93 El Niño ocean warming events reduced female body condition and gonadosomatic indices in Blue rockfish, *S. mystinus* (VenTresca et al. 1995). The more recent 2014-15 marine heatwave and 2015-16 El Niño had large ecosystem effects on biological communities at multiple trophic levels, such as a shift in the composition of copepod communities, the northern range expansion of sub-tropical species, declines in the abundance of forage fishes, and disruptions to the reproductive success of marine mammals and seabirds (Leising et al. 2015, McClathchie et al. 2016, Peterson et al. 2017, Sanford et al. 2019, Piatt et al. 2020). The abundance of pelagic, young-of-the-year rockfishes in 2015-16 varied spatially in the California Current, with high abundance in the central region but lower than average abundance to the north and south (McClathchie et al. 2016). Spatially, reproductive patterns of adult rockfishes differ between the north and south regions of the California Current and reproductive success is likely correlated with environmental conditions affecting female body condition (MacGregor 1970, Love et al. 2002, Beyer et al. 2015, Lefebvre et al. 2018).

Elevated water temperatures increase metabolic demands in ectotherms, affecting female body condition (Johnston & Dunn 1987), and may shorten the gestation period of rockfish embryos (Moser 1967). Warmer water temperatures and reduced seasonality, as occur in the southern range of the California Current, may contribute to the faster production of broods during a spawning season if females

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have adequate energy reserves. The effect of warming water temperatures on metabolic rates, coupled with shifts in primary and secondary productivity affecting the quality and quantity of food supply, likely both affect female energetic reserves and reproductive decisions. Thus, seasonal, annual, and inter-annual changes in temperature and food abundance are expected to drive spatiotemporal patterns in the reproductive output and reproductive plasticity in rockfishes, for which multiple brooding is most commonly observed in the south, less often in the central region, and has yet to be documented farther north (Wyllie-Echeverria 1987, Love et al. 1990, 2002).

In rockfishes, we hypothesize that both water temperature and food availability affect female body condition and energy allocation to reproductive effort, including the production of multiple broods. We expect that females in poor body condition will reduce their annual fecundity by producing fewer broods and/or producing broods of fewer larvae. We also expect that warmer temperatures will decrease gestation time, potentially affecting the likelihood of a female producing multiple broods. We tested our hypotheses under controlled, experimental conditions, manipulating both water temperature and food availability to show how the environment affects female body condition and reproductive plasticity in a multiple brooding rockfish species. Our study aimed to provide a better understanding of the spatiotemporal dynamics in the reproductive ecology of rockfishes in the California Current and to improve knowledge of how reproduction is likely to be affected by climate change.

2. Materials and Methods

2.1 Study species

Rosy Rockfish, *Sebastes rosaceus*, were used as a model to study multiple brooding in rockfishes. Rosy Rockfish are a tractable species for laboratory study due to their relatively small size. Individuals are distributed throughout the California Current from the Strait of Juan de Fuca, Washington to central Baja California, Mexico (Love et al. 2002), with a center of biomass in the central and south regions of the California Current (Holder & Field 2019). Rosy Rockfish are associated with rocky reef habitats at depths of 40 to 150 meters (Love et al. 2002). They are generalists, feeding on small invertebrates and small fishes associated with the benthos and in the water column (Love et al. 2002). Historically, Rosy Rockfish were commercially important to markets in central California (San Francisco) and are commonly encountered in the California recreational hook-and-line fishery, although typically not targeted due to a small size (Love et al. 1990, 2002, Mason 1998). There has been no formal assessment of population abundance or stock status, but Rosy Rockfish was among the top six most abundant species in a 2012-14 fishery independent hook-and-line survey in central California (Marks et al. 2015).

Life history information is relatively limited for Rosy Rockfish in comparison to other rockfishes. A maximum size of 36 cm is often cited but was questioned as a likely mis-identification with the larger, similar appearing Rosethorn Rockfish, *S. helvomaculatus* (Chen 1971). For comparison, a maximum length of 31 cm fork

length (FL) was observed in central California (Echeverria & Lenarz 1984) and 27 cm FL in southern California (Love et al. 1990). Length-at-maturity is also variable, suggesting spatiotemporal differences in the maturation schedule and/or differences in the identification of immature and mature fish based on method of either macroscopic or histological examination of the ovaries. In California, 50% of females collected from 1977 to 1982 were mature at 18.6 cm FL (Wyllie-Echeverria 1987). More recently in central California, 50% of females collected from 2012 to 2014 were mature at 16.6 cm FL (Fields 2016). A smaller size at maturity was found in females collected from southern California between 1980 to 1987, with 50% mature at 14.7 cm FL (Love et al. 1990). Wyllie-Echeverria (1987) used both macroscopic and histological methods to identify immature and mature fish, Fields (2016) used macroscopic methods, and Love et al. (1990) used temporally-restricted macroscopic methods, where maturity status was determined only during the active reproductive season to avoid mis-identification of immature, developing, and resting mature females. Note, total lengths were converted to fork lengths to compare across studies (Echeverria & Lenarz 1984).

Gravid females have been observed from December through September in the central and southern regions of the California Current, suggesting nearly year-round reproduction (Love et al. 2002). Male Rosy Rockfish gonadosomatic indices peak in the month of October, then decline through November and December to low levels over the rest of the year, indicating a fall mating season (Love et al. 1990). Age determination through the identification of growth increments in otoliths is difficult

for this species and has not been validated, but it is thought that females mature around 6 years of age, with a maximum age of 35 years (Wyllie-Echeverria 1987, Fields 2016). Because of imprecision and difficulty in ageing Rosy Rockfish, age determination was not attempted in this study.

2.2 Collections

Laboratory collections- A total of 46 female Rosy Rockfish were collected at 73 meters depth by hook-and-line methods near Monterey, California at the start of the mating season in October through December of 2015 and 2016 with the help of the Monterey Bay Aquarium (MBA) collecting staff. Rockfishes have a physoclistous swim bladder and are susceptible to injury from barotrauma during capture from depth. To alleviate barotrauma symptoms, fish were re-pressurized to 70 PSI in a two-chamber, flow-through seawater hyperbaric chamber immediately following capture (J. Welsh, MBA). Because of space limitations in the hyperbaric chamber, a limit of 10 to 15 Rosy Rockfish could be collected per sampling trip depending on cumulative fish size. Fish in the chamber were monitored for changes in neutral buoyancy and the pressure was reduced incrementally each day. After five days, fish were acclimated to ambient surface pressure, allowing release into standard, unpressurized seawater tanks. Following acclimation, fish were transported to the flow-through seawater facility at the NOAA National Marine Fisheries Service (NOAA NMFS) in Santa Cruz, California.

Wild collections- Laboratory fish were compared to a dataset of wild fish to better understand how the resulting body condition and fecundity in the laboratory compared with fish in the wild. Wild Rosy Rockfish were opportunistically collected by similar hook-and-line methods from rocky reefs at depths of 27 to 73 m in central California from 2012 to 2014 as part of a Rockfish Conservation Area monitoring project and ongoing reproductive studies by researchers at NOAA NMFS (Marks et al. 2015). A subset of 17 females with a mean size of 20.6 cm FL (range 16.7 cm to 23.7 cm) had available brood fecundity data to compare with laboratory females. Fecundity of wild females was determined by the gravimetric method of counting weighed subsamples of eggs or larvae from the ovaries, following methods described in Beyer et al. (2015).

The comparison of body condition of laboratory fish to that of wild fish was restricted to the month of August in 2014, a year of moderate ocean conditions prior to an end of year warming event (Leising et al. 2015). The fish were collected at the end of the reproductive season, when all females were most likely to be in the resting reproductive stage. Wild fish samples came from a single location at the Farallon Islands, approximately 74 nm northwest of the location in Monterey Bay where laboratory fish were collected. A total of 83 wild females, with a mean size of 20.6 cm FL (range 13.8 cm to 25.8 cm), were used for comparison of body condition.

2.3 Laboratory set-up

The laboratory set-up and experimental design followed established protocols for reproductive studies of single brooding rockfish species in captivity (Fisher et al. 2007, Tsang et al. 2007, Sogard, Berkeley, et al. 2008, Sogard, Gilbert-Horvath, et al. 2008, Kashef et al. 2014). To provide females the opportunity to mate, males and females were housed in outdoor group tanks in their respective treatments from October through December during the mating season. The group tank set-up and methods followed those described for the successful mating of Kelp rockfish, *S. atrovirens*, in captivity (Sogard, Gilbert-Horvath, et al. 2008). The group tanks measured approximately 2.29 m in diameter by 1.52 m height, with 4,165 liters of flow-through seawater. Water flow was set to 250 ml/sec. The group tanks were covered with a tarp, which lowered the light levels in the tank to more closely mimic reduced natural light at depth but still allowed for some light to pass, ensuring exposure to a natural photoperiod. Even though females were expected to mate in the laboratory, some females may have already mated, acquired, and stored sperm prior to capture, which has been documented in captive rockfish studies (Tsang et al. 2007, Sogard, Gilbert-Horvath, et al. 2008).

Females were assigned a combined temperature and feeding regime in a size-stratified, semi-randomized design, ensuring that the size range and mean size of females across treatments was similar. For example, the four largest females from one collection date were randomly assigned to each of the four combination treatments, followed by randomly assigning the next four largest females until all were assigned. This method ensured that the largest females, considered the most likely to produce

multiple broods, were evenly distributed across treatments and that a range of sizes

occurred in each treatment (Beyer et al. 2015, Lefebvre et al. 2018). Males were

distributed in the same fashion to ensure a size range of males in each treatment.

Following the mating season, females were isolated from males and moved to

smaller indoor tanks of dimensions 0.91 m diameter by 1.52 m depth, with

approximately 1,040 liters of flow-through seawater. The set-up of smaller indoor

tanks closely followed methods described for fecundity and larval collection for other

rockfishes in the laboratory (Fisher et al. 2007, Sogard, Berkeley, et al. 2008, Kashef

et al. 2014). Successful fertilization, gestation and parturition of larvae by females

isolated from males is common in rockfish rearing studies because of the ability of

females to store sperm for extended periods (Fisher et al. 2007, Tsang et al. 2007,

Sogard, Berkeley, et al. 2008, Sogard, Gilbert-Horvath, et al. 2008, Kashef et al.

2014). The smaller-sized tanks allowed for individual tracking of female reproductive

status through the reproductive season and the collection of larvae at parturition,

which was not possible in large group tanks. A 200 μm mesh filter was attached to the

outflow pipe of each tank to prevent the escape of free-swimming larvae following a

parturition. Natural photoperiod cycles were maintained in the indoor aquarium.

Flows were set to 25 ml/sec and life support systems, including seawater flow, water

temperature, and compressed air supply, were checked daily. Tanks were cleaned

twice a week by siphoning detrital material and rinsing the mesh outflow filters to

prevent clogging of debris and overflow of the tank when larvae were released

(Sogard, Berkeley, et al. 2008). The experiment was conducted from October to the

following September during the 2015-16 and 2016-17 reproductive seasons, referred

to as the 2016 and 2017 reproductive seasons.

2.4 Experimental design

Our experimental design examined the interactive effects of water temperature

and food availability on reproductive effort. Two temperature levels were tested,

ambient (warmer treatment) and chilled (cooler treatment) to mimic natural

temperature differences between central and southern California, and future

temperature increase in central California. Flow-through seawater from intake pipes

located in 9 meters of water off the coastal NOAA NMFS facility was filtered and

delivered directly to ambient treatment tanks. Water for chilled tanks passed through

a chiller to lower temperatures by 2 to 3 °C relative to ambient temperatures. Water

temperatures thus fluctuated throughout the year to mimic natural cycles while

maintaining a 2 to 3 °C difference between warm and cool treatments. Resulting

temperatures cycled annually from 12 to 15 °C in the warmer treatment and from 9 to

13 °C in the cooler treatment. Temperatures in the cool treatment reflected a range in

the annual temperature cycle typically encountered at 75 m depth in Monterey Bay,

central California, where Rosy Rockfish were collected (Pennington & Chavez 2000).

Temperatures in the warm treatment reflected warmer temperatures encountered by

Rosy Rockfish in southern California (Lynn 1967) and general warming trends

predicted for central California (Di Lorenzo et al. 2005).

Food availability was manipulated using the following three feeding regimes: fish fed twice per week (high ration), once every two weeks (medium ration), and once per month (low ration). Feeding regimes were designed to mimic natural variability in body condition in the wild and were initially based on feeding regimes of captive rockfish in previous studies (Fisher et al. 2007, Sogard, Berkeley, et al. 2008, Sogard, Gilbert-Horvath, et al. 2008, Kashef et al. 2014). In 2016, all fish were fed either a high or medium ration. We found body condition of these females at the end of the reproductive season was similar to, or higher than, fish collected from the wild during a similar time period. Thus, in 2017, the feeding levels were altered to a high and a low feeding regime to reflect the greater range in body condition occurring in wild fish. During scheduled feeding days, all fish were fed to satiation with a high protein and lipid diet of Market Squid, *Doryteuthis opalescens*, and Northern Anchovy, *Engraulis mordax*. The selection of diet was based on successful captive rearing studies of closely related rockfishes (Fisher et al. 2007, Sogard, Berkeley, et al. 2008, Sogard, Gilbert-Horvath, et al. 2008, Kashef et al. 2014) and expert opinion from the Monterey Bay Aquarium animal husbandry unit experienced with Rosy Rockfish specifically (J. Welsh, MBA). Sample sizes and starting measurements for females and males in all treatment combinations in each year are listed in Table 1. Protocols for this study were approved by the University of California Santa Cruz Institutional Animal Care and Use Committee (IACUC) in a permit issued to the NOAA NMFS Fisheries Ecology Division, Santa Cruz, California.

2.5 Measurement of size and body condition

When first brought into the laboratory, fish were measured for fork length (nearest mm) and total wet weight (nearest 0.1 g), and internally tagged with a passive integrated transponder (PIT) tag in the muscle just below the dorsal spine on the left side of the body. A small fin clip from the upper (females) or lower (males) caudal fin was collected for genetic archive and to visually distinguish males from females in the group mating tanks. All fish in the study were measured in October of both years providing starting measurements prior to the mating season. Ending measurements were made in August of both years, when the majority of females had stopped reproducing. Body condition provided an index of energy reserves and was approximated by calculating the Fulton's K condition index (K):

$$K = \frac{W}{L^3} 100 \qquad (1)$$

where W is total wet weight (g) and L is fork length (cm).

We compared the body condition of laboratory females at the end of each reproductive season to wild females. These comparisons allowed us to evaluate how well the three ration treatments mimicked variability in feeding success and body condition in the wild during a year of moderate ocean productivity.

2.6 Reproductive response variables

Reproductive plasticity in response to food and temperature was measured as the following four response variables: 1) brood count, 2) brood interval, 3) brood fecundity, and 4) annual fecundity. Brood count was the total number of broods released per female in a reproductive season. The brood interval was measured as the number of days between parturition events. Brood fecundity was estimated by collecting and counting larvae from each brood release. Annual fecundity was the sum of all larvae in all broods over one reproductive season. During the study gestating females were identified by a combination of detailed daily notetaking on the visual appearance of individual females, including swelling of the abdomen when eggs were thought to be hydrated, and scanning of the internal PIT tag to confirm individual identification before and after parturition.

All parturition events in the laboratory occurred overnight, with the release of the entire brood. Mesh filters on outflow pipes retained larvae within the tank until collection the following morning. Following a parturition, adult females were carefully netted, rinsed with seawater, and removed from the tank. Larvae were free-swimming in the tank and gently collected in a two-step process of netting and siphoning seawater through a 200 μm bucket sieve. Once collected, larvae were preserved in 95% ethanol in 250 ml plastic jars.

Brood fecundity was estimated using the volumetric subsampling method (Bagenal 1957, Murua et al. 2003). Ethanol in the preserved sample was first drained through a 200 μm sieve and larvae were gently rinsed with deionized (DI) water into a 1000 ml graduated glass beaker. The beaker was then filled to 500 ml with DI water.

Next, the sample was slowly stirred in a figure-eight motion to evenly disperse larvae and four 10 ml subsamples were collected with a graduated, large aperture pipette, transferred to a 250 ml glass beaker to confirm volume, and lastly pipetted into petri dishes for counting under a dissection microscope. The count of larvae for each 10 ml subsample was multiplied by the total volume of the whole sample to estimate brood fecundity (*BF*):

$$BF = \frac{subsample\ count}{subsample\ volume} * total\ volume \tag{2}$$

Brood fecundity was the mean estimate of the four subsamples. The resulting coefficient of variation (CV) in counts from the four subsamples averaged 9.7%, with a range from 3.8% to 25.4%. Brood fecundity was calculated for broods where live larvae were released into the tanks.

Unexpectedly, a portion of the broods released in the laboratory were not of larvae, but of mature, hydrated, unfertilized eggs, or a mix of both live larvae and unfertilized eggs (Fig. 1.1). If present, hydrated, unfertilized eggs were buoyant and clearly visible at the surface of the tank following a brood release. We assumed that such events were an indication of sperm limitation and that sperm limitation was presumably a laboratory effect of females being isolated from males, which has occasionally been observed in other studies (Tsang et al. 2007). We did not consider the release of hydrated, unfertilized eggs to be evidence of skipped spawning, which is defined as mass atresia and resorption of oocytes (Rideout & Tomkiewicz 2011),

but rather a reproductive attempt by the female, which would have resulted in a brood of live larvae if sperm were present. Unfertilized eggs could not be collected and counted for fecundity due to the delicate nature and rupturing of the chorion during the collection process. Because we could not collect and count unfertilized eggs, brood releases of 100% unfertilized eggs were excluded from all fecundity analyses. However, unfertilized broods were still recorded in the brood count and assumed to represent a reproductive attempt.

In contrast, an estimate of brood fecundity for brood releases with a mix of live larvae and unfertilized eggs was possible. A brood release of both live larvae and unfertilized eggs was considered partial sperm limitation (i.e., a fraction of the brood was larvae and the other fraction mature, hydrated, unfertilized eggs, example Fig. 1.1). For broods with partial sperm limitation, a simple visual estimate of the proportion of unfertilized eggs observed in the tank was incorporated into the brood fecundity estimate to account for the additional reproductive effort that would have occurred without sperm limitation. This was done by estimating the percentage of unfertilized eggs compared to live larvae in the tank and including that percentage in the calculation of brood fecundity. Sperm limitation was minimal in such broods in the fecundity analysis, with an average of only 6% of the brood estimated to be unfertilized.

To calculate annual fecundity (AF), we summed the total number of larvae from all broods in a reproductive season for each female (Murua et al. 2003):

$$AF = \sum_{i=1}^{n} BF_i \tag{3}$$

where BF is brood fecundity of the ith brood of n annual broods per female. Females that had any broods comprised entirely of unfertilized eggs were excluded from the fecundity analyses due to the inability to count unfertilized eggs, as noted above.

2.7 Dissections

Fish were dissected at the end of the two-year study on October 4, 2017 to assess the final reproductive state following the end of the reproductive season. Fish were euthanized by an overdose of tricaine methanesulfonate (MS-222) in a buffered seawater solution (Neiffer & Stamper 2009) and placed in a cooler of crushed ice for 24 hours to maintain freshness of tissues without freezing. Dissections followed the next day. Fish were weighed (nearest 0.1 g) and measured (fork length, nearest mm). The ovaries and liver were excised and weighed (nearest 0.01 g) to calculate the gonadosomatic and hepatosomatic indices, proportional gonad and liver weights, respectively.

Macroscopic classification of ovarian development followed the general description for rockfishes (Shaw et al. 2012) and more specific description of multiple brooding in the related Chilipepper, *S. goodei* (see Table 2 in Lefebvre et al. 2018). The "pre-vitellogenic" and "resting" stages described in Lefebvre et al. (2018) were combined, as these stages represent a continuum from resting to early development of oocytes for the next season, more accurately distinguished by

histological methods not used in this study. Ovaries of Rosy Rockfish were macroscopically classified as: 1) "immature", appearing thin and translucent, 2) "resting or transitional", appearing thicker and less translucent or progressing to early oocyte development, or 3) "vitellogenic", containing larger, macroscopically visible vitellogenic oocytes in development for the next reproductive season. Other ovarian stages, including fertilized embryos, eyed-larvae, and recently spent females, were not observed at the time of dissections. It should be noted that macroscopic differentiation of immature and mature females outside of the reproductive season is not as accurate as when identified during the reproductive season due to the similar appearance of immature and resting mature ovaries (Love et al. 1990, Lefebvre et al. 2018).

2.8 Statistical analysis

Body condition - We used a linear regression model to assess how female body condition, measured by the Fulton's K condition index (K), was affected by feeding treatment and in comparison with wild fish (*lm* function in R version 3.6.1; R Core Team 2019). The categorical groupings included the three feeding regimes (high, medium, and low) and a wild fish (wild) group. The general expression for the linear model was:

$$K_i = b_0 + b_{Xi} + \varepsilon_i \qquad \qquad \varepsilon_i \sim \text{Normal}(0, \sigma^2) \qquad (4)$$

where b_0 is the intercept, X_i is an integer representing different levels of the categorical variable for the ith fish, b_{Xi} the associated coefficient, and errors (ε_i) normally distributed. A post-hoc, pairwise comparison identified significant differences across the feeding categories (Tukey Multiple Comparisons of Means Test, *aov* function in R). A similar linear regression model was used to test for differences in female body condition, prior to the reproductive season, between females that reproduced in the laboratory (reproductively active) and those that did not (reproductively inactive).

Reproductive response - We used generalized linear mixed effects models to test for environmental and maternal size effects on the four reproductive response variables of: 1) brood count, 2) brood interval, 3) brood fecundity, and 4) annual fecundity. Generalized linear mixed models are useful for behavioral studies with multiple observations of an individual because they model the combined effects of independent explanatory variables (i.e., fixed effects) while also accounting for within-individual variability (i.e., a random effect; Zuur et al. 2009). We modeled female identity as a random effect where individual females were observed in either year 1, year 2, or in both years of the study depending on when they were collected, how often they reproduced, and whether they successfully fertilized all broods within a year.

Generalized linear mixed effects models were estimated using the *lme4* package in R (Bates et al. 2015). Count data in the number of annual broods was modeled as a Poisson distribution using a canonical logarithmic link function

(GLMM, *glmer* function in R). Data for the brood interval, measured in days, and

fecundity, measured by number of larvae, were modeled as Gaussian distributions

using the canonical identity link function (LMM, *lmer* function in R), as these were

large counts for which a normal approximation seemed valid after transformation. In

particular, the response variables of brood interval, brood fecundity and annual

fecundity were natural log transformed. The general expression for the generalized

linear mixed effects model was:

$$G(\mathrm{E}(Y_{ij})) = \alpha_i + \beta_1 X_{1ij} + \ldots + \beta_n X_{nij} \tag{5}$$

where G is the appropriate link function, as discussed above. The response variable Y_{ij}

is the reproductive response for the ith fish in the jth observation, which is a function

of the fixed effects ($X_{1 \to n}$), with corresponding coefficients ($\beta_{1 \to n}$), and with the

random effect of female identity modeled as a unique intercept for each female (α_i).

The fixed effects considered in each model were maternal length, water

temperature, feeding regime, experimental year (2016 or 2017), and the interaction of

temperature and food ration. Brood number was also considered in the models of

brood interval and brood fecundity. Maternal length was treated as a continuous

covariate and natural log transformed. All other fixed effects (water temperature,

feeding regime, experimental year, and brood number) were treated as categorical

variables. This approach followed standardized methods to model fecundity as a

natural-log transformed power function of maternal size (Dick et al. 2017, Barneche

et al. 2018), allowing for the comparison of fecundity parameters and the strength of maternal size effects to other species. The general model of fecundity (FEC) is specified as (Dick et al. 2017):

$$FEC = a\,L^{\,b} \tag{6}$$

where L is maternal length (mm), and the parameters a and b are the coefficients of the natural log-transformed linear regression of fecundity and length, incorporated into the mixed effects models described above:

$$\log(FEC) = \log(a) + b\log(L) \tag{7}$$

We used post-hoc, pairwise comparisons (Multiple Comparisons of Means: Tukey Contrasts) to identify specific differences across categorical groupings within a fixed effect using the *glht* function (package *multcomp*) in R (Hothorn et al. 2008). The model assumptions of normality, linearity and homoscedasticity were assessed visually with Q-Q plots and by plotting the model residuals against the fitted values (Zuur et al. 2009). We used the Shapiro-Wilk statistic to test for normality (Zuur et al. 2009) and the Levene's test for homoskedasticity (Glaser 2006). Coefficients and 95% confidence intervals are presented for the final models.

To select the most appropriate model, we first estimated a full model including all fixed effects and compared it with an intercept-only model to test for

overall model significance (Zuur et al. 2009). If the full model was significantly different from the intercept-only model, model selection was initiated. We used backward, stepwise model selection based on a series of F tests to determine the order of testing for fixed effects (Zuur et al. 2009). Significance of the fixed effect was assessed by a Likelihood Ratio Test (LRT) using the *anova* function in R, by sequentially removing the variable of interest and comparing with the previous model, which included the effect (Zuur et al. 2009). Non-significant effects were sequentially removed and significant effects retained in the final model (Zuur et al. 2009). All final models included the random effect of female identity.

2.9 Sample sizes

The sample size for each of the reproductive response variables, including the number of unique females contributing and how often they were observed for each analysis, was as follows. The experiment included 35 females observed in both years (2016 and 2017). Three females died at the end of the 2016 reproductive season, and 8 females were added to the study in 2017. This resulted in a total of 81 observations of annual brood count from the 46 unique females over the two years. Of these 46 females, 35 were observed twice (year 1 and year 2) and 11 were observed in only a single year (year 1 or year 2). There were 43 observations of brood intervals from 15 unique females that had successfully fertilized broods and reproduced at least twice in a year. Of these 15 females, 5 were observed in both years and 10 were observed in only a single year. There were 46 observations of brood fecundity from 17 unique

females successfully fertilizing all annual broods in either year 1, year 2, or both years. This resulted in 21 observations of annual fecundity. Of these 17 unique females, 4 females were observed twice, meaning they fertilized all broods in both year 1 and year 2, and 13 females were observed once, meaning they fertilized all broods in only a single year (year 1 or year 2).

3. Results

3.1 Female body condition

Food availability affected female body condition in each of the three feeding regimes compared to body condition of wild fish (linear model, $F_{3,157} = 11.6$, $p < 0.001$, Fig. 1.2). Females in the high ration treatment were, on average, in better condition than wild females in a year of moderate ocean conditions (post-hoc Tukey, $p < 0.001$). The body condition of females fed medium rations was not significantly different than wild females (post-hoc Tukey, $p = 0.494$). Females held on low rations had significantly lower body condition than high ration females (post-hoc Tukey, $p < 0.001$) and marginally lower condition than wild females in a year of moderate ocean conditions (post-hoc Tukey, $p = 0.048$). Considering the variability within each treatment and within the wild group, the three feeding regimes resulted in a range of female body condition similar to that likely experienced by fish across years of good and poor feeding conditions in the wild. Wild fish were collected in a single year, 2014, from a single location at the Farallon Islands in central California, so the

natural variability reported here is likely a conservative estimate and expected to be greater across years of above or below average ocean conditions.

3.2 Number of annual broods

Rosy Rockfish released between zero and five broods annually. At least some females in all treatments reproduced and maternal length was positively correlated with the number of annual broods (Table 1.2, Fig. 1.3). Temperature and feeding regime were not statistically significant predictors of variation in the number of broods per year (Table 1.2); however, no female in the low ration feeding regime produced more than three broods (Fig. 1.3). Among the reproductively active females (i.e., females that released broods), the mean number of annual broods was 1.6 in the low, 2.7 in the medium, and 3 in the high feeding regime, suggesting a trend of increasing brood numbers with increasing rations. There was no evidence of an effect of experimental year on the number of annual broods per female (Table 1.2).

In each treatment combination, some females were not reproductively active, meaning they never released a brood. The number of females not reproducing in the warm treatment at high, medium, and low ration was 7 of 19 (37%), 3 of 10 (30%), and 3 of 9 (33%), respectively. The number of females not reproducing in the cool treatment at high, medium, and low ration was 6 of 20 (30%), 4 of 10 (40%), and 6 of 13 (46%), respectively. The lack of reproduction in some females was potentially due to unknown laboratory effects, but it is possible that the larger sized females may have been exhibiting skip spawning behavior (i.e., having spawned in the past, but

foregoing reproduction in the current year), and smaller females may have been either

fully immature or exhibiting delayed maturation (i.e., delaying or aborting a first-time

spawning event). Non-reproductively active females were in poorer body condition at

the start of the season compared to females that reproduced (linear model, $F_{1,79} =$

7.281, $p = 0.009$, Fig. 1.4).

3.3 Interval between broods

The brood interval was significantly shorter in the warmer water treatment

(Table 1.2, Fig. 1.5), with a mean of 55 days compared to 74 days in the cooler

treatment. We did not find evidence that food ration or maternal length affected how

quickly broods were released (Table 1.2). The interval between broods decreased

over time for multiple brooders (Table 1.2), but this quicker release could also be

explained by warmer water temperatures later in the reproductive season. There was

no evidence of an effect of experimental year on brood interval.

Only intervals between fertilized broods were considered in the interval

analysis, but a secondary comparison of the interval between fertilized broods and the

interval between non-fertilized broods showed that fertilization did not significantly

affect the amount of time between brood releases (linear model, $F_{1,80} = 0.588$, $p =$

0.446). This meant that females not fertilizing broods did not release broods more

quickly than females fertilizing broods. Females releasing unfertilized broods

appeared to internally retain hydrated eggs for a similar amount of time as gestation

of embryos. Hydrated eggs were roughly twice the size of developing, vitellogenic

oocytes and females were noticeably more rotund following maturation and hydration

of eggs. Both females that fertilized and did not fertilize broods appeared visually

"pregnant" with swollen abdomens in the weeks prior to a parturition.

3.4 Brood Fecundity

Of the 133 broods released in the laboratory, 68, or roughly half, were

fertilized. Of the 68 fertilized broods, we analyzed fecundity of 46 broods from 21

females that had fertilized all broods over the entire year, allowing a calculation of

annual fecundity (high ration, n = 5 females, medium ration, n = 7 females, low

ration, n = 9 females). Brood fecundity varied widely from 3,990 to 75,340 larvae,

depending on brood number, female size, and food rations (Table 1.2, Fig. 1.6ab). For

multiple brooders, fecundity tended to decline in late season broods (Table 1.2, Fig.

1.6a). In a few cases, second broods were more fecund than the first, potentially a

function of females adjusting to laboratory conditions and feeding regimes. Food

ration was marginally significant ($p = 0.052$, Table 1.2) and retained in the final

model, with a trend of females in the low ration treatment producing smaller broods

than females in high ration treatment (post-hoc Tukey, $p = 0.063$, Fig. 1.6b). Larger

females produced disproportionately larger-sized broods compared with small

females, with a length-fecundity exponent of b = 4.225, greater than the length-

weight exponent of b = 3.340 (Table 1.3). There was no supporting evidence of an

effect of temperature or experimental year on brood fecundity.

Brood fecundity in the laboratory was marginally lower than brood fecundity of wild fish, with respect to maternal size (multiple regression, $F_{2,60} = 12.23$, $p < 0.001$, lab-wild post-hoc Tukey, $p = 0.048$) when combining all laboratory broods. Brood fecundity did not statistically differ if the analysis was restricted to first broods released in the laboratory compared to wild broods (multiple regression, $F_{2,35} = 13.52$, $p < 0.001$, lab-wild post-hoc Tukey, $p = 0.117$, Fig. 1.6c). Restricting the analysis to first laboratory broods in comparison to wild broods removed the influence of lower fecundity in later broods. Brood number in wild fish was unknown.

3.5 Annual Fecundity

Annual fecundity ranged from 9,400 to 244,877 larvae and was significantly affected by maternal length and food ration (Table 1.2, Fig. 1.7). Larger females produced disproportionately more offspring annually compared with smaller females, with a length- annual fecundity exponent of b = 6.105 (Table 1.3). Females fed low rations produced significantly fewer larvae annually compared with females fed high rations, with an average of 63% fewer larvae in poorly-fed females (post-hoc Tukey, $p = 0.044$). Annual fecundity in the medium ration treatment was highly variable and not significantly different from the low (post-hoc Tukey, $p = 0.393$), or high (post-hoc Tukey, $p = 0.365$) ration groups. Even though broods were released more quickly at warmer temperatures, a greater number of broods were not released, and there was no supporting evidence of a temperature or experimental year effect on annual fecundity (Table 1.2). The higher annual fecundity in well-fed females was primarily

a function of a greater number of broods, but larger individual brood-sizes also contributed to higher fecundity.

3.6 Dissections

Dissections at the end of the study following the reproductive season in year two were possible for 39 of the 46 unique females, excepting 3 fish that died after 2016 and 4 that were removed from the study shortly before dissections in 2017. Of the 39 dissected at the end of the study, 33 were in a resting or transitional state, or in the early- to late- stages of vitellogenesis for the next reproductive season (Table 1.4). Six females were classified as immature; however, macroscopic identification distinguishing immature and the mature resting stage in rockfish outside of the reproductive season is difficult (Lefebvre & Field 2015). Females classified as immature were the smallest in the study in comparison to resting and vitellogenic females (ANOVA, $F_{2,36} = 14.59$, $p < 0.001$, Table 1.4). Females initiating vitellogenesis of oocytes for the next season had larger proportional gonads, measured by the gonadosomatic index (ANOVA, $F_{2,36} = 12.3$, $p < 0.001$, Table 1.4) and were in better body condition than immature females, measured by Fulton's K condition index (ANOVA, $F_{2,36} = 6.797$, $p = 0.003$, Table 1.4). There was no difference in the hepatosomatic index across females in different stages of development (ANOVA, $F_{2,36} = 0.348$, $p = 0.709$, Table 1.4).

The classification of immature and mature females provided additional information for the interpretation of females that did not reproduce in the study. Six

of the non-reproductively active females were among the smallest fish in the study and were macroscopically classified as immature, suggesting a possible adolescent phase with delayed or abortive maturation since most exceeded the reported 100% length at maturity of 175 mm FL for females in central California (Fields 2016, Fig. 1.8). The other seven non-reproductively active females that were larger in size and macroscopically classified as mature were possible examples of skipped spawning (Fig. 1.8). The dissections did not find evidence of internal trauma, such as scar tissue due to the collection process, or other abnormalities that would have prevented reproduction, although it should be noted that the dissections were conducted one‑ to two‑ years post capture and any injuries could have healed entirely if they had occurred.

3.7 Model Validation

A visual and statistical evaluation of model assumptions found departures from normality for all four mixed effects models describing brood count, brood interval, brood fecundity, and annual fecundity (Shapiro-Wilk test of normality, $p = 0.001$, $p = 0.024$, $p < 0.001$ and $p = 0.010$, respectively). Visual assessment of the Q-Q plots suggested only minor departures from normality at the tails, and linear mixed effects models are robust to violations of normality, which is why they are often useful for ecological datasets (Sokal & Rohlf 1995, Zar 1999, Zuur et al. 2009, Schielzeth et al. 2020).

We used the Levene's test for homoscedasticity and found evidence of heterogeneity in the variance for the models of brood count ($p = 0.028$) and annual fecundity ($p = 0.013$) but not in the models of brood interval ($p = 0.286$) and brood fecundity ($p = 0.356$). While small deviations from homogeneity are not likely to affect model significance, large amounts of heterogeneity will (Zuur et al. 2009, Schielzeth et al. 2020). There were no clear patterns in the residuals for the model of annual fecundity, suggesting that heterogeneity was minor and not likely to affect interpretation of the results (Zuur et al. 2009, Schielzeth et al. 2020).

Patterns in the residuals of the brood count model were evident. Further data transformation of the explanatory variable, length, was attempted but did not resolve the pattern (Zuur et al. 2009). Large departures from homogeneity in the variance can result in a higher chance of a Type I error (Zuur et al. 2009). However, we feel the results and interpretation of the brood count model are robust since length, the only significant explanatory variable, was well supported ($p = 0.001$, Table 1.2), and all other possible explanatory variables were highly non-significant (Table 1.2). It is possible, however, that a non-linear relationship between maternal length and brood count, such as an S-shaped, asymptotic curve, would better describe the relationship between maternal size and the number of broods.

4. Discussion

4.1 Annual brood production

To our knowledge, this was the first study to track individual reproductive effort in a multiple brooding rockfish over an entire reproductive season in the laboratory, providing valuable basic biological information on the frequency of how often broods are released and the total number of annual broods. Documenting reproductive effort over an entire year enabled estimates of annual fecundity for this species. Rosy Rockfish females released between zero and five broods per year, depending on maternal size. For comparison, up to three broods per year were reported in other multiple brooding rockfishes, such as Chilipepper, *Sebastes goodei*, and Bocaccio, *S. paucispinis* (Ralston & MacFarlane 2010, Lefebvre et al. 2018), but it was unknown if rockfish were capable of greater than three. The maximum of five broods in Rosy Rockfish observed in the laboratory may represent an upper physiological limit in a best-case scenario of nearly unlimited and stable food supply, and we are unsure if this would occur in the wild. Previous studies documenting multiple broods from wild collections were limited to a snapshot in time of reproductive effort. The timing of collections during the reproductive season is important for observing multiple broods in wild collections. Because of the lengthy brood interval, it is generally not possible to tell how many broods a female will produce at the beginning of the reproductive season. At the end of the reproductive season, it is generally not possible to tell how many broods a female had released because previous broods in the ovary, evident as residual eyed-larvae or post-ovulatory follicles, degrade and are resorbed over time. Therefore, outside of the

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laboratory, multiple brooding females can be identified over only a relatively short period annually and may not reflect the entire reproductive effort over the year.

Rosy Rockfish have one of the longest parturition seasons within the genus, with nearly year-round reproduction in the central and southern regions of the California Current (Love et al. 1990, 2002). The protracted reproductive season may allow this rockfish species to produce a greater number of annual broods in comparison to other multiple-brooding rockfish that have shorter periods of larval release. In many rockfish species, larvae are released over a shorter two or three month period annually, especially at more northern latitudes (Wyllie-Echeverria 1987, Love et al. 1990, 2002). The total number of annual broods possible is likely species specific.

4.2 Temperature effects on reproductive timing

Warmer water temperatures shortened the time interval between parturition events. We did not measure embryo development directly, but a shorter brood interval suggests that eggs and larvae develop more quickly at warmer water temperatures. Warmer water temperatures likely increase metabolic rates in adults, embryos, and offspring. For example, warmer water temperature was shown to increase the rate of yolk depletion of embryos in the related Rosethorn Rockfish, *S. helvomaculatus* (formerly *S. rhodochloris*) (Moser 1967). Warmer temperature is also associated with an increased rate of oogenesis and degradation of postovulatory follicles (Kjesbu et al. 2010, Kurita et al. 2011). Therefore, warmer water temperature is likely to affect

the timing of reproductive events at multiple stages, including oogenesis, gestation, spawning recovery, and the timing of when larvae are released in the wild.

Broods were released more quickly at warmer water temperatures but females in the warmer water did not release an overall greater number of annual broods compared with females in the cooler water treatment, although there was a non-significant trend in that direction. The quicker release of broods at warm temperatures is likely balanced by increased metabolic demands, which affect female body condition and reproduction. More work is required to understand how spatial patterns and increasing global ocean temperatures will affect the bioenergetics and reproduction in this and other economically and ecologically important marine fishes worldwide. For example, Somarakis et al. (2019) found similar temperature effects driving reproductive plasticity in small pelagic clupeoids. In those species, warmer water temperatures increased the rate of egg development and the frequency of spawning events in adults but came at a cost of higher metabolism and increased mortality rates of larvae (Somarakis et al. 2019). Qualitatively, adult female Rosy Rockfish in the warmer treatments were more physically active (i.e., observed swimming more often rather than sedentary) and were more aggressive feeders (i.e., fed more quickly) compared with females in the cool treatment. These qualitative observations suggested higher metabolic rates and increased energetic demands, but specific rates were not measured and should be the focus of future work.

4.3 Maternal size effects on fecundity

Both brood and annual fecundity increased in a hyper-allometric relationship with maternal length in Rosy Rockfish, meaning that spawning biomass will not reliably predict larval output in this species. Larger females produced disproportionately more young per gram of female body mass compared with smaller females. The disproportionate increase is shown by comparison of the allometric length-body weight relationship, where weight increases with length approximately volumetrically to a power of b = 3, but fecundity increases at a power greater than b = 3 (see equation 6, Table 1.3). The production of multiple broods increased the strength of the maternal size effect on fecundity from a power of b = 4.335 when only considering brood fecundity, to a power of b = 6.105 for annual fecundity (Table 1.3). The more rapid increase in annual fecundity with maternal size reflected both larger-sized broods and a greater number of annual broods by larger females in comparison with smaller females.

Our results suggest that the strength of the effect of maternal size on fecundity has been underestimated in multiple brooding rockfishes. A Bayesian hierarchical meta-analysis of fecundity-length relationships within *Sebastes*, which considered only single broods due to a lack of available data on multiple brooding, found many of the multiple brooding species to have smaller maternal size effects on fecundity in comparison with single brooding species (Dick et al. 2017). Dick et al. (2017) reported Rosy Rockfish fecundity to increase with maternal length at a power of b = 4.195, similar to our brood fecundity estimate and a genus-wide estimate for *Sebastes*

at a power of b = 4.043 (Table 1.3). When incorporating the biology of multiple

broods, Rosy Rockfish fecundity increased with maternal length at a power of b =

6.105, well above what has been reported for rockfishes. Multiple brooding is yet

another example of the effect of maternal size on reproductive effort and reinforces

the importance of age-structure and the disproportionate contribution of older, larger

females to larval production. Updating the size-dependent fecundity relationships for

multiple brooding rockfish species will increase the accuracy in calculations of larval

output used to assess the health and status of the fishery.

4.4 Environmental effects on fecundity

The large variation in annual reproductive output relative to feeding regime,

with 63% fewer larvae produced by poorly-fed females in comparison with well-fed

females, is an example of phenotypic flexibility in reproductive effort in response to

prevailing environmental conditions. The results suggest that, at the population level,

larval output is influenced by environmental conditions affecting female body

condition. In years of favorable ocean conditions, females are able to rapidly ramp up

reproductive effort. The increase in annual fecundity in well-fed females was mainly

due to the production of additional broods, though brood fecundity also increased

with higher food availability. In years of poor ocean conditions, females are likely to

be in poorer body condition, produce fewer larvae, and may exhibit skip spawning

behavior or delayed maturation, further reducing population larval output.

In addition to interannual variability, reproductive patterns differ geographically from north to south in the California Current. Across species, rockfishes are more likely to skip spawn at higher latitudes and produce multiple broods at lower latitudes (Moser 1967, MacGregor 1970, Love et al. 2002, Beyer et al. 2015, Head et al. 2016, Conrath 2017, Lefebvre et al. 2018, Holder & Field 2019). Historically, multiple brooding was considered a uniquely southern occurrence in females south of Point Conception in southern California (Moser 1967, MacGregor 1970, Wyllie-Echeverria 1987). However, recent studies have documented multiple brooding in central California, assumed to be related to interannual variability in ocean conditions favoring the production of multiple broods (Wyllie-Echeverria 1987, Beyer et al. 2015, Lefebvre et al. 2018). In waters off central California, spring and summer upwelling drive an annual pulse of high primary productivity, matched by a corresponding annual peak in female body condition prior to the fall mating and winter reproductive season (Guillemot et al. 1985, Wyllie-Echeverria 1987, Beyer et al. 2015). In the south, temperatures are warmer and upwelling is weaker but more persistent throughout the year (Parrish et al. 1981, Checkley & Barth 2009). Latitudinal differences in the seasonal patterns of food availability and temperature likely influence the accumulation of energetic reserves and reproductive patterns. Similar to multiple brooding in rockfishes, multiple batch spawning in broadcast spawners is more common at lower latitudes (McBride et al. 2015), suggesting commonality in patterns of spawning frequency across a diverse group of marine fishes. Ultimately, reproductive frequency within a year likely reflects the interplay of

physiological capabilities and evolutionary adaptation to seasonality in the environment and seasonality of larval survival probability.

4.5 Non-reproducing females

While many females in our study reproduced multiple times, some never released broods (29 of 81 observations). We attempted to collect only mature females based on previous studies reporting length at maturity (Fields 2016), but at the smallest sizes it is likely that females were either immature or in an adolescent phase. At the larger sizes it was possible that females were exhibiting skipped spawning behavior. However, we cannot exclude the possibility that failure of some females to reproduce was due to unknown laboratory effects.

We were unable to differentiate among the different reasons why females in the study did not reproduce. Dissections at the end of the study, well beyond the end of the spawning season, were inconclusive. By then, any evidence of past internal trauma from the collecting process, or evidence of recent spawning, including post-ovulatory follicles and residual eyed-larvae, or mass atresia of aborted broods were not evident by macroscopic methods. However, skipped spawning and delayed maturation occur in other rockfish species, are important to population dynamics, and should be further investigated in this species (Lefebvre & Field 2015, Head et al. 2016, 2020, Conrath 2017). Detailed histological studies during the reproductive season can differentiate between immature, adolescent, and resting mature females. Further investigations involving monthly sampling of wild fish, with histological

examination of the ovaries, are warranted to provide better information on the occurrence of delayed maturation and skipped spawning (Lefebvre & Field 2015) since these behaviors have not previously been reported for Rosy Rockfish in the wild.

Overall, non-reproducing females in our study were in poorer body condition entering the reproductive season compared with females that reproduced. Foregoing reproduction in iteroparous species due to low energy reserves is a life history adaptation to conserve, or divert, energy to growth, survival, and/or future reproduction (Stearns 1992). The act of reproducing is energetically demanding, especially in live bearing species because of the increased respiratory demand to provide oxygen to embryos during gestation (Moser 1967, Wourms 1991). The ovaries of a female rockfish weigh up to one-third of the total body weight and the gestation of fertilized embryos through the eyed-larvae stage and parturition lasts on the order of weeks to months depending on the species and water temperature (Love et al. 1990, 2002). With long-lived, iteroparous fish, such as many rockfishes (Mangel et al. 2007), the ability to divert energy to growth or over-winter survival during years of poor conditions and to invest resources into reproduction during favorable years is likely an adaptation to the highly variable environmental conditions of the California Current and low natural mortality rates of adults (Guillemot et al. 1985, Botero et al. 2015).

Nonetheless, it was previously unknown if females were capable of reproducing multiple times in the laboratory and the number of females successfully

reproducing following capture from depth and re-pressurization in a hyperbaric

chamber is remarkable. The reproductive success of captive females suggests that

capture and careful, rapid release at depth of regulated species in the fishery, such as

with commercially available descending devices (Bellquist et al. 2019), may allow for

full recovery and normal reproduction.

4.6 Sperm limitation

Sperm limitation was differentiated from skipped spawning or delayed

maturation by females that released broods of eggs at a mature, hydrated, unfertilized

stage, as opposed to females that never released broods. Tsang et al. (2007) similarly

reported sperm limitation in captive Grass rockfish, *S. rastrelliger*, isolated from

males, which released broods of mature, hydrated eggs with a degraded appearance.

The presence of hydrated, unfertilized eggs is not often observed in rockfish collected

from the wild (Beyer *et al.* unpublished data). Oocyte maturation, hydration,

ovulation, and fertilization are thought to occur rapidly and near simultaneously when

sperm are present in the ovary (Moser 1967, Shaw et al. 2012). Release of

unfertilized, hydrated eggs in the wild is likely rare or absent, as females in the wild

can mate freely and acquire additional sperm for secondary broods throughout the

reproductive season. The females in this study did not appear able to resorb eggs at

the hydrated stage.

Sperm storage is not well understood in rockfish. In general, sperm is thought

to be stored within the interstitial tissues of the ovary but no specialized internal

storage structures are evident (Shaw et al. 2012). In *S. schlegeli*, a cultivated rockfish of Japan, sperm are released from the male in batches of spermatophores (Feng et al. 2014). Sperm are observed floating within the ovarian fluid shortly after copulation, with eventual migration and long-term storage within the epithelium of the ovigerous tissue (Mori et al. 2003). Mechanisms of sperm storage may differ across the genus and potentially between single- and multiple-brooding rockfish species.

The acquisition of sperm through mating generally occurs in the months prior to vitellogenesis or during early vitellogenesis (Love et al. 1990). In rockfishes, male gonadosomatic indices peak in the months prior to a peak in female gonadosomatic indices, suggesting mating occurs well before fertilization (Guillemot et al. 1985, Wyllie-Echeverria 1987, Love et al. 1990). Prior to our study, it was unknown if females were able to reserve sperm and maintain viability while fertilizing multiple broods, or if re-mating was required between broods. Females in our study were isolated from males following the mating season and were able to reserve sperm for multiple broods without re-mating, suggesting a mechanism for maintaining viability and storage of sperm across broods and over many months. At least one female stored sperm and successfully fertilized five broods over the course of 10 months in isolation from males. Alternatively, evidence of sperm limitation suggests that females may need to mate multiple times in the wild to acquire enough sperm to fully fertilize multiple broods, or mate over a longer period during the reproductive season.

It was unknown if females mated with the captive males in the laboratory or if females had previously acquired sperm in the wild, as is common in captive

rockfishes (Tsang et al. 2007, Sogard, Gilbert-Horvath, et al. 2008). If females did not

mate in the laboratory, then sperm storage was longer than the reported 10 months.

However, males in the laboratory were observed actively courting females in the

group mating tanks, similar to courtship behavior described for wild *S. inermis*, a

small, benthic rockfish of Japan (Shinomiya & Ezaki 1991). In all four treatments, a

single male would display dominant, aggressive behavior toward other males,

including biting and chasing. Aggressive behavior of territorial males during the

mating season was also described in wild *S. inermis* (Shinomiya & Ezaki 1991). The

aggressive behavior in the laboratory resulted in the death of some males, often over a

single night, where fins and scales were entirely missing the following morning,

reducing the number of males in each treatment. Dominant males courted females by

circling and fin display similar to *S. inermis* (Shinomiya & Ezaki 1991), and also

displayed a change in head coloration from pale to bright red banding across the

mandibles and operculum (Beyer, personal observation). While courtship behavior

was observed in the laboratory, the act of copulation, which likely occurs at dusk or

night (Helvey 1982, Shinomiya & Ezaki 1991), was not observed during routine, day-

time observations. A better physiological understanding of mating behavior, mate

choice, sperm storage, and evidence for post-copulatory, cryptic female choice in

sperm selection (Eberhard 1996) would help to explain potential sperm limitation and

mating requirements of multiple brooding females in the wild and provide a broader

context for sexual selection in this diverse and species-rich group of fishes.

4.7 Implications for fisheries management

Understanding how size-dependent fecundity relationships change due to reproductive plasticity in response to the environment will improve estimates of population larval production, help to scale estimates of spawning stock biomass from ichthyoplankton surveys (Ralston & MacFarlane 2010), and inform predictions of how climate change will affect reproductive success and fishery productivity (Hare et al. 2016). The increased plasticity of the multiple brooding strategy likely allows females to take advantage of intermittent, favorable conditions, unlike closely related single-brooding species. Conversely, reduced fecundity and occurrences of delayed maturation or skipped spawning reduce population-level larval production in years of poor conditions. The reduced numbers of females contributing to larval production may be particularly important for management of exploited species during prolonged, multi-year periods of poor environmental conditions as can occur in the California Current. Over such years larval production will be less than expected based on maturity ogives and length-fecundity relationships derived from fish collected in moderate to good years.

Understanding how the environment affects larval production may help to improve stock-recruitment relationships of marine fishes. Weak correlations in stock-recruitment relationships result in reduced predictive power of future recruitment events important for decision-making in fisheries management (Myers et al. 1995). Incorporating age- and/or size- structure of females, coupled with age- and/or size-specific fecundity, has resulted in a more accurate calculation of total egg production

of mature females (Marteinsdottir & Thorarinsson 1998). Updating size-fecundity relationships in population models for stock assessment has shown how exploitation and the removal of large females disproportionately reduces larval output and is important for determining stock status (He et al. 2015). However, reproductive plasticity in response to environmental conditions is often not modeled due to a lack of data and mechanistic understanding. Efforts to estimate female energetics, such as through measurement of proportional liver weights, were successful in better estimating stock-recruitment relationships in Atlantic Cod, *Gadus morhua,* and represent a relatively straightforward method of measuring energy reserves that fluctuate with the environment (Marshall et al. 1999). Variability in the reproductive potential of small pelagic clupeoids, related to energetics, was correlated with recruitment patterns in some cases, showing a direct connection between interannual variability in body condition, fecundity, and recruitment (Somarakis et al. 2019). Clearly, bioenergetics affected reproductive plasticity in Rosy Rockfish and likely affects reproductive output in closely related rockfishes and other marine fishes with similar reproductive strategies.

It is still unknown exactly how wild populations will respond to environmental change but the prolonged parturition season and frequent occurrence of multiple brooding in the southern region of the California Current suggests that females are encountering an adequate food supply throughout the reproductive season to maintain high enough energy reserves for multiple broods, and that warmer temperatures enable broods to be released more quickly. Fewer annual broods farther

north may reflect greater seasonality in food availability and colder temperatures increasing the time interval between brood releases. In addition, the increased plasticity of multiple broods allows for the release of larvae over a longer period annually and is possibly an adaptation within the genus to geographic differences in larval survival from north to south in the California Current. Temporally, it is likely that the number of annual broods, and thus annual fecundity, will be less in years of reduced food resources, such as during El Nino, or other climate warming events, which should be considered for management and the focus of future investigation. These patterns are not unique to rockfishes and may also explain spatiotemporal variability in reproductive effort in other species that spawn over a wide latitudinal range and encounter interannual variability in environmental conditions, such as the Northeast Arctic stock of Atlantic Cod (Opdal & Jørgensen 2015).

Increased efforts to understand the causes and consequences of reproductive plasticity and the important role of maternal size in determining fecundity and total egg production of populations have the potential to improve predictions of strong and weak recruitment events. The capacity for such large variability in fecundity, including the possibility of skipped spawning of mature females and delayed maturation in adolescents, may contribute to the large recruitment variability observed in most rockfishes, where strong year classes supporting fisheries may be followed by up to a decade of poor recruitment, adversely affecting fisheries. Previous work has focused on the important role of the environment encountered by post-extrusion larvae and juveniles in structuring strong and weak year classes

(Cushing 1975), but high interannual and spatial variability in the environment experienced by females preparing for and during reproduction is also likely an important, but often overlooked, contributing factor. Even though females in better body condition produced more larvae, it remains unclear if females base current reproductive effort solely on stored energetic reserves, or if females are able to use an environmental cue, which may be related to energetic reserves, to either increase reproductive effort in years when larvae may have a higher chance of survival, or to divert energy to other life history traits, such as survival and growth, during poor years.

5. Conclusion

In conclusion, we demonstrated that annual reproductive output across individuals is not static and varies both with maternal size and environmental conditions. Female body condition and energetic reserves were important determinates of annual fecundity. Increased reproductive plasticity, through the production of multiple broods, likely provides a fitness advantage in long-lived, iteroparous species residing in highly dynamic environments, such as the rockfishes of the California Current Ecosystem. The phenotypic flexibility of the multiple brooding strategy allows females to rapidly take advantage of productive ocean conditions in a way that single brooding species are unable, and likely contributes to large fluctuations in population-level larval output depending on prevailing oceanographic conditions. Understanding the reproductive ecology and how fisheries

productivity will respond to changing climate conditions should be a high priority for the sustainable management of marine fish stocks.

Acknowledgements

Tables

Table 1.1 Starting measurements and sample size of females and males in two temperature treatments (Warm, Cool) and three feeding regimes (Low, Medium, High) over two reproductive seasons (2016, 2017). Note that 2017 experiments included 35 females also used in 2016 experiments, along with 8 new females collected prior to the setup of mating groups in 2017. In total, there were 46 unique females in the study, resulting in 81 observations of female reproductive effort across two years. Female identity was treated as a random effect to account for multiple observations.

Treatment (Year)	Females n	Females Mean +/- SD (Range)	Males n	Males Mean +/- SD (Range)
High Ration (2016)				
Cool	10	201 +/- 17 (174 - 232)	2	203 +/- 10 (196 - 221)
Warm	8	199 +/- 13 (190 - 228)	5	202 +/- 16 (184 - 221)
High Ration (2017)				
Cool	10	208 +/- 17 (190 - 240)	5	200 +/- 15 (190 - 227)
Warm	11	199 +/- 13 (179 - 225)	5	218 +/- 13 (195 - 226)
Medium Ration (2016)				
Cool	10	198 +/- 14 (178 - 219)	3	196 +/-16 (181 - 213)
Warm	10	195 +/- 16 (175 - 237)	3	205 +/- 4 (203 - 210)
Low Ration (2017)				
Cool	13	198 +/- 16 (176 - 225)	6	201 +/- 9 (189 - 213)
Warm	9	195 +/- 16 (180 - 235)	5	210 +/- 7 (203 - 218)

Table 1.2 Results of the linear mixed effects analyses showing maternal size and environmental effects on reproductive output. The table lists all fixed effects considered in the starting models. Non-significant fixed effects were removed sequentially in order from top to bottom through backward, stepwise model selection. log () indicates a natural logarithm data transformation. Significance determined by a Likelihood Ratio Test. Fixed effects retained in the final models are in bold. Coefficients of the final models are presented in Supplementary Materials 1.

Response	Fixed Effect	χ^2	df	*P* value
Annual Broods Per Female (n = 81, units = brood count)				
	Ration x Temperature	2.339	2	0.311
	Temperature	0.276	1	0.600
	Food Ration	3.028	2	0.220
	Year	1.829	1	0.176
	Log (Length)	**10.208**	**1**	**0.001**
Interval Between Broods [a] (n = 43, units = log (days))				
	Ration x Temperature	0.785	2	0.675
	Food Ration	1.686	2	0.430
	Year	2.798	1	0.094
	Brood Number	**11.653**	**3**	**0.009**
	Temperature	**5.134**	**1**	**0.024**
	Log (Length)	0.719	1	0.396
Brood Fecundity [b] (n = 46, units = log (number of larvae))				
	Ration x Temperature	0.175	2	0.916
	Year	2.076	1	0.150
	Temperature	0.197	1	0.657
	Food Ration [c]	**5.898**	**2**	**0.053**
	Brood Number	**12.213**	**4**	**0.016**
	Log (Length)	**5.750**	**1**	**0.017**
Annual Fecundity [b] (n = 21, units = log (number of larvae))				
	Ration x Temperature	5.159	2	0.076
	Temperature	0.059	1	0.808
	Year	1.607	1	0.205
	Food Ration	**6.445**	**2**	**0.040**
	Log (Length)	**4.121**	**1**	**0.042**

[a] Fertilized broods
[b] Females fertilizing all broods
[c] Marginal significance, retained in final model

Table 1.3 Comparison of the allometric length-weight relationship with the hyper-allometric length-fecundity relationship for brood and annual fecundity (this study) and in comparison with length-fecundity parameters reported in Dick *et al.* (2017). The strength of the maternal size effect on fecundity is indicated by exponent b (see equations 6, 7). Note different statistical approaches between studies where this study reported mean parameter estimates with 95% confidence intervals from linear mixed effects models and Dick *et al.* (2017) used a Bayesian hierarchical approach and reported parameter estimates as median values with 95% credible intervals of the posterior distribution.

Study	Comparison	log (a) (95% CI)	b (95% CI)
Captive Rosy Rockfish (this study)			
	Length – Total Weight	-12.610 (-12.41, -9.81)	3.340 (2.81, 3.87)
	Length - Brood Fecundity	-12.179 (-28.97, 1.51)	4.225 (1.63, 7.40)
	Length - Annual Fecundity	-21.698 (-52.39, 9.19)	6.105 (0.26, 11.92)
Bayesian hierarchical meta-analysis of Sebastes (Dick *et al.* 2017)			
	Rosy Rockfish Length – Fecundity [a]	-11.713 (-13.65, -9.74)	4.195 (3.83,4.56)
	All Sebastes Length – Fecundity [a]	-11.938 (-16.25, -8.30)	4.043 (3.43,4.71)

[a] Does not account for multiple broods

Table 1.4 Summary of dissections conducted October 4, 2017 at the termination of the experiment following the end of the second-year reproductive season. All fish were weighed and measured, and ovarian stage identified macroscopically (see **Methods**). The gonadosomatic index (*GSI*), Fulton's K condition index (*K*), and hepatosomatic index (*HSI*) were calculated with somatic weight. Sample sizes and means (+/- the standard deviation) are summarized by stage. An asterisk (*) indicates statistical difference across groups (ANOVA) and lower-case letters show specific groupings (post-hoc Tukey). Note, fertilized embryos, and spent stages were not observed at the time of dissection during the presumed resting and mating season.

Ovarian Stage	n	Length *	GSI *	K *	HSI
Immature	6	178 [a] (+/- 3)	0.23 [a] (+/- 0.05)	1.74 [a] (+/- 0.09)	2.37 (+/- 0.75)
Resting or transitional	20	201 [b] (+/- 14)	0.44 [a] (+/- 0.16)	1.90 [ab] (+/- 0.16)	2.33 (+/- 0.84)
Vitellogenic	13	215 [c] (+/- 16)	2.54 [b] (+/- 2.21)	1.99 [b] (+/- 0.12)	2.11 (+/- 0.77)

Figures

Figure 1.1 Image of a one-day old Rosy Rockfish larva (center) and a mature, hydrated, unfertilized egg (upper left) released in the same brood as an example of partial sperm limitation. The hydrated, unfertilized egg contained a large, consolidated oil globule and degrading cellular material. Below the larva is a free-floating oil globule, remnants of an egg burst during the collection process. Scale bar drawn for size.
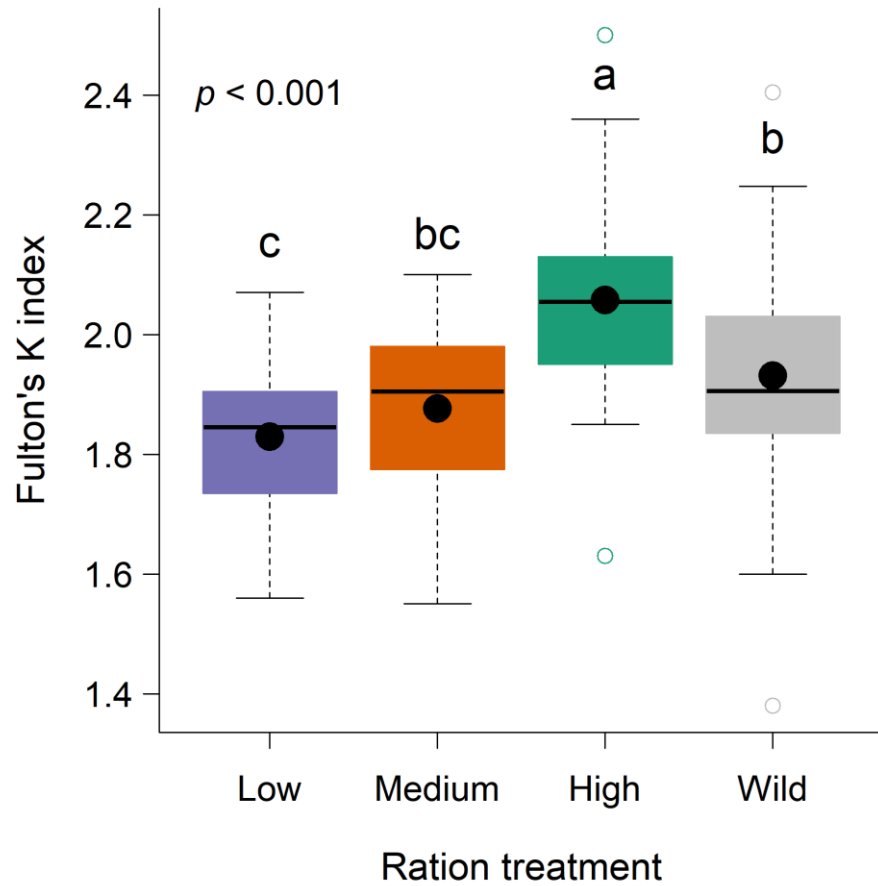
Figure 1.2 The three feeding regimes (Low, Medium, and High) successfully manipulated female body condition, measured by the Fulton's K condition index, in relation to natural variation observed in wild fish during a year of moderate ocean conditions (Wild). Body condition measurements were made in the month of August, near the end of the reproductive season. Boxplots show median values (horizontal black bar), 25th and 75th quantiles, and the range of body condition values within each category. Open circles are outlying values. Solid, black circles are the mean. Different lower-case letters indicate statistically significant differences across groups determined by a post-hoc, pairwise comparison (see statistical analysis).
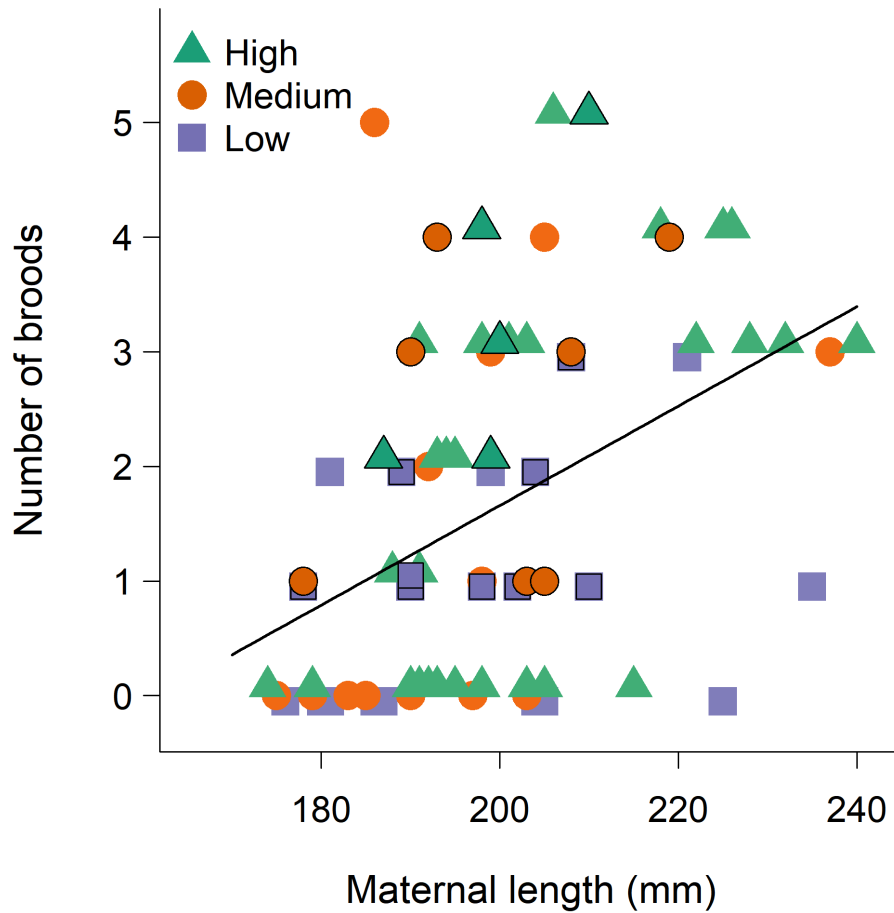
Figure 1.3 Maternal size had a positive effect on the number of annual broods per female. Data shown for all observations (n = 81) in each of the feeding regimes: Low (purple squares), Medium (orange circles), and High (green triangles). Outlined symbols are females that fertilized all broods in a year and were included in the fecundity analyses (n = 21). Symbols without an outline are either females that released at least one fully unfertilized brood (sperm limitation) and therefore could not be used in the fecundity analyses, or non-reproductively active females (shown by zero broods). Regression line is for all treatments combined (see Table 1.2).
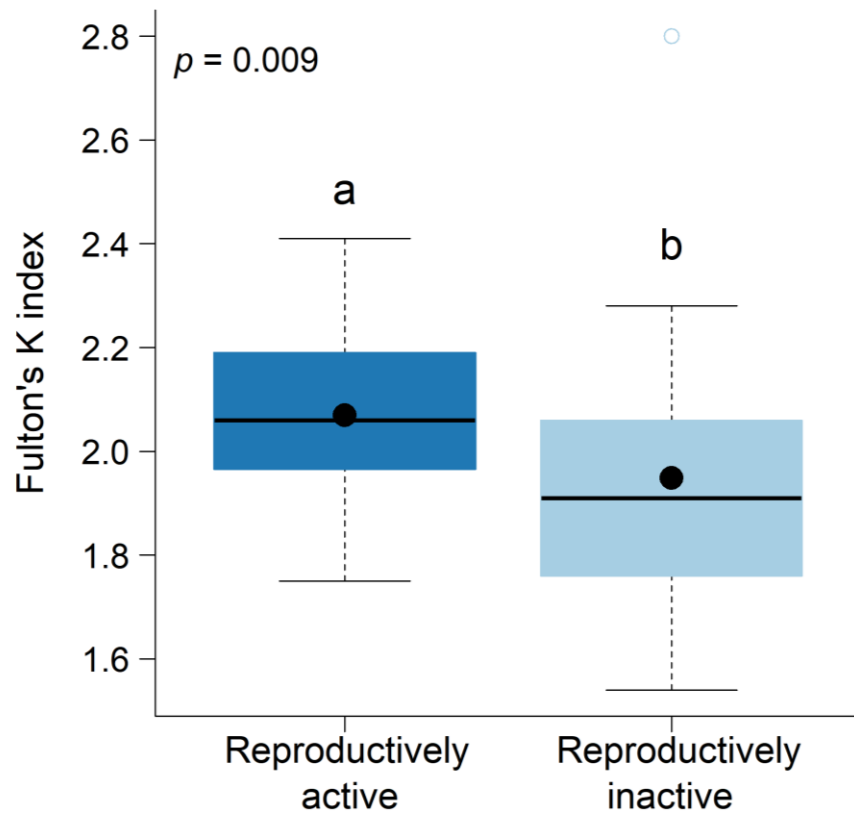
Figure 1.4 Females that released broods (reproductively active) were in better body condition at the start of the reproductive season in comparison with females that did not reproduce (reproductively inactive). Boxplots show median values (horizontal black bar), 25th and 75th quantiles, and the range of body condition values within each category. Open circles are outlying values. Solid, black circles are the mean. Different lower-case letters indicate statistically significant difference between groups.
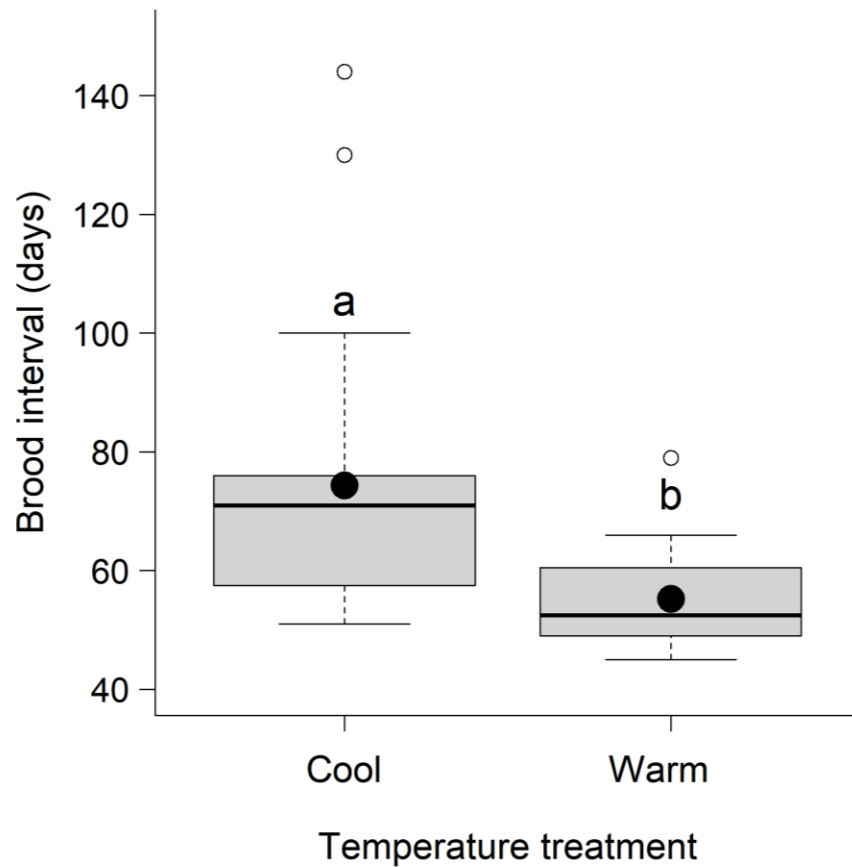
Figure 1.5 Females in the warmer water treatment released broods more quickly compared with females in the cooler water treatment. Boxplots show median values (horizontal black bar), 25th and 75th quantiles, and the range of body condition values within each category. Open circles are outlying values. Solid, black circles are the mean. Different lower-case letters indicate statistically significant difference between groups (Table 1.2).
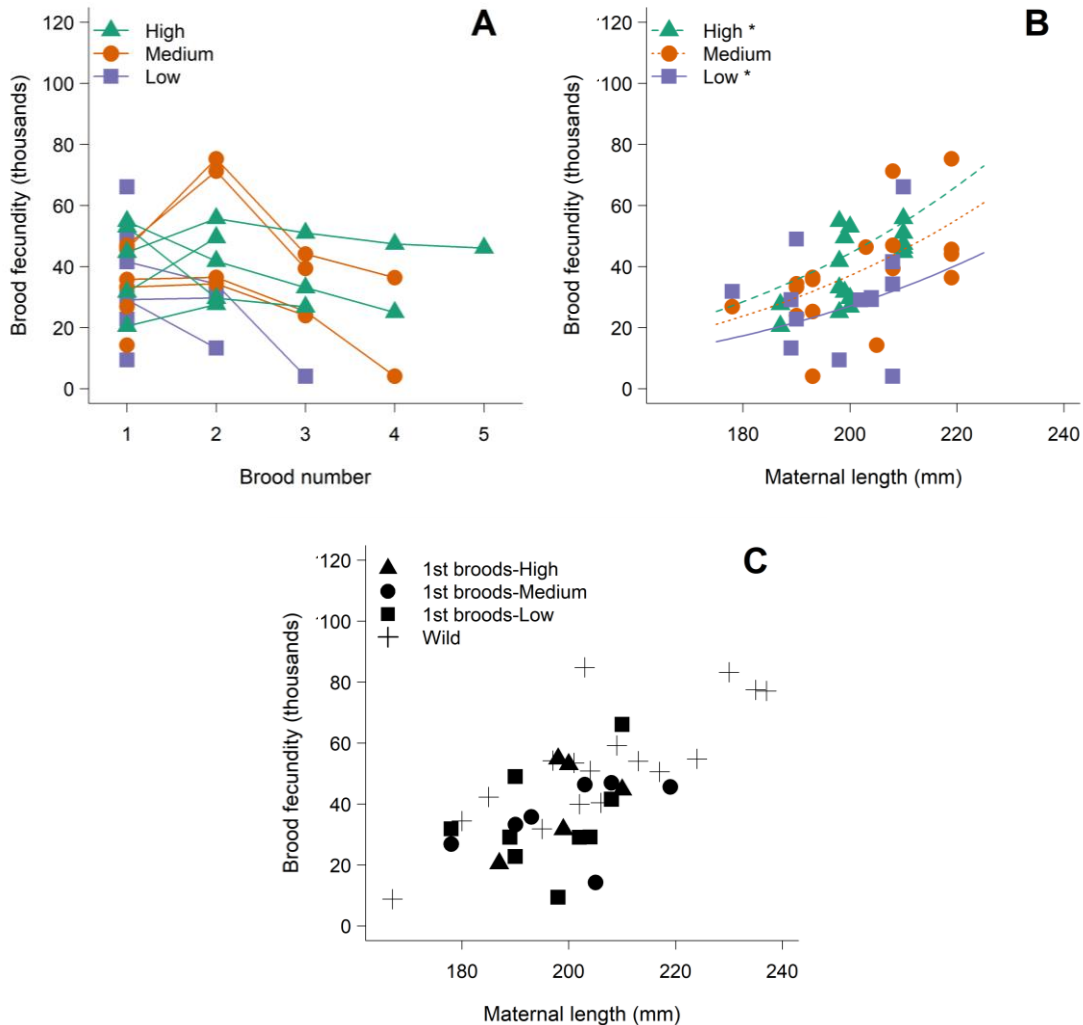
Figure 1.6 Brood fecundity tended to decline in later broods (A). Solid lines are individual females (n = 21) and symbols are broods (n = 46) in the Low (purple squares), Medium (orange circles), or High (green triangles) ration treatment. Note, some females in the fecundity analysis only released a single brood. Brood fecundity increased with maternal length and was marginally higher in the high vs low food ration (B, post-hoc Tukey, $p = 0.063$). Colored symbols inline vertically at a specific length are multiple broods by an individual female, shown in panel A. Plotted curves are predicted brood fecundity at length for each of the feeding treatments (coefficients in Table S1). A comparison of first laboratory broods, all treatments combined (n = 21), to wild broods (n = 17) found that brood fecundity in the laboratory did not significantly differ from wild broods (C, post-hoc Tukey, $p = 0.117$).
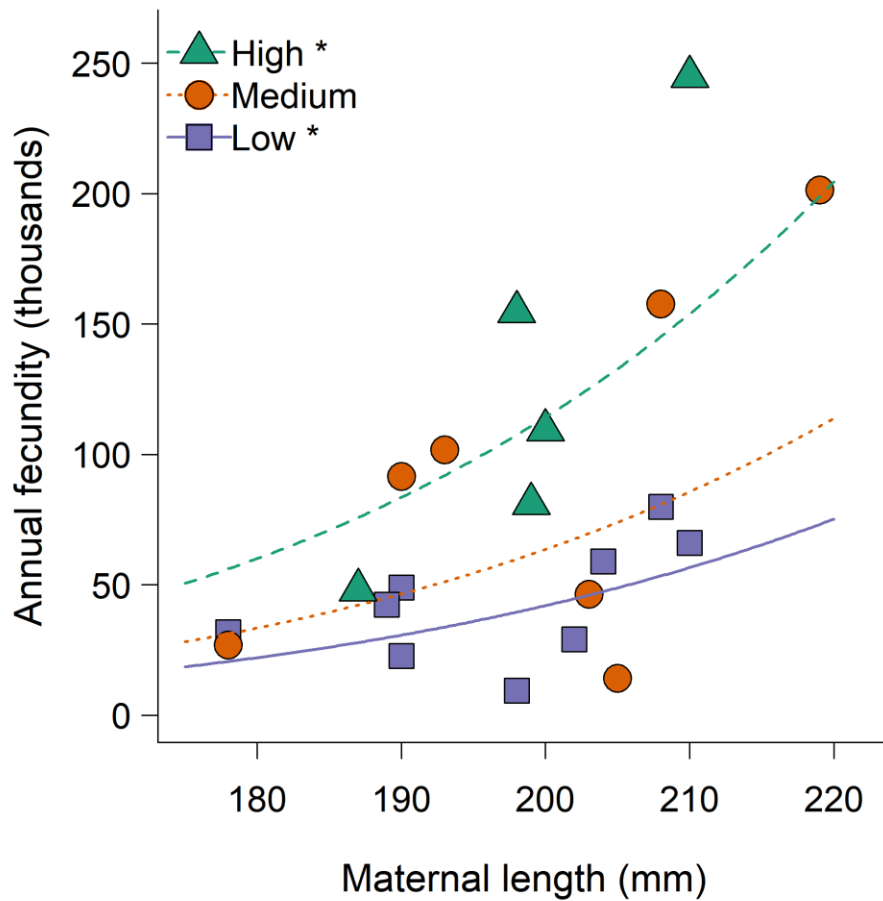
Figure 1.7 Larger females produced disproportionately more offspring in comparison with smaller females as a function of a greater number of annual broods and higher brood fecundity (Table 2, 3). Females fed high rations produced significantly more offspring annually than females fed low rations (Table 2, post-hoc Tukey, $p = 0.044$). Colored symbols are annual fecundity estimates for individual females fertilizing all broods (n = 21) and are grouped by Low (purple squares), Medium (orange circles), or High (green triangles) ration treatment. Plotted curves are predicted annual fecundity for each feeding treatment (coefficients in Supplementary S1).
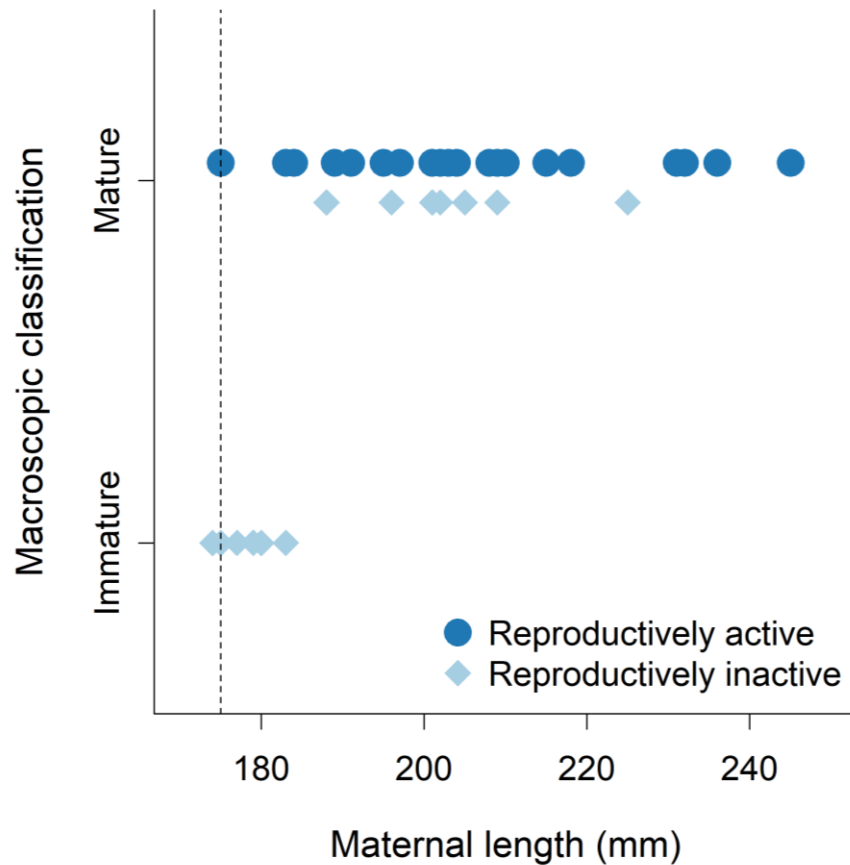
Figure 1.8 Maturity status of females that released broods in the laboratory (reproductively active, dark blue circles) and those that did not release broods (reproductively inactive, light blue diamonds) by size. Maturity status (immature vs. mature) was determined by macroscopic examination of ovaries at the end of the study and outside of the reproductive season. Reproductively inactive females at the smallest sizes were possibly physiologically immature, or more likely in an adolescent phase exhibiting delayed or abortive maturation of a first reproductive attempt. Larger mature females may have been skip spawning. Neither skipped spawning, nor delayed or abortive maturation, could be distinguished from possible laboratory effects that may have contributed to the failure to reproduce. Length at 100% maturity was most recently reported at 175 mm FL for females in central California (Fields 2016, vertical dashed line) and most females were above that size.

Chapter 2: Reproductive plasticity of long-lived, live-bearing rockfishes (*Sebastes* spp.) as part of a life history strategy to cope with inter-annual environmental variability of the California Current Ecosystem

Abstract

Phenotypic plasticity in life history traits, such as reproductive effort, can evolve to cope with life in fluctuating environments. For many marine fishes, how changing ocean environmental conditions influence reproductive traits and the consequences for shifts in population reproductive potential are not well understood. Here, we use the rockfishes (*Sebastes* spp.) of the California Current Ecosystem as a case study to better understand reproductive plasticity in response to fluctuating environmental conditions. Rockfishes of the California Current are adapted to cope with strong seasonal, inter-annual, and decadal shifts in ocean environmental conditions. The reproductive strategies of rockfishes include live-birth of small larvae, high fecundity, variation in the frequency of reproduction, and the ability to reproduce many times over an expected lifespan. These strategies provide insight into how marine fishes living in highly dynamic ocean ecosystems are expected to deal with current and future environmental change with respect to reproduction. Here, we use a time series of rockfish fecundity data, collected over four decades from the 1980s to 2019 in central California, to explore how the brood sizes of rockfish fluctuated through time given the maternal attributes of body length and energy reserves and in response to strong inter-annual variation in ocean conditions. We

found substantial temporal variation of expected brood size, especially for rockfishes that produce only a single brood annually. The expected brood size for a large, single-brooding Yellowtail rockfish (*S. flavidus*) could vary annually by over 1.5 million larvae. Similar strong inter-annual variation of up to 665,000 larvae per brood occurred for large, single-brooding Widow rockfish (*S. entomelas*). Lesser inter-annual variation occurred for deeper-water Chilipepper (*S. goodei*) and Bocaccio (*S. paucispinis*), two species capable of multiple broods a reproductive season. For large females of these species, expected inter-annual variation of over 147,000 and 276,000 larvae per brood was possible, respectively. However, annual fecundity variation is likely as strong, or stronger, for multiple brooding rockfish species when considering environmental influences on both brood size and the possibility of multiple broods when conditions allow. In addition to the strong influence of maternal length, greater maternal energy reserves were positively correlated with larger brood sizes. Beyond maternal length and body condition, inter-annual variation in brood size was weakly correlated with fluctuations in the summer and fall feeding conditions in the California Current, described by the North Pacific Ocean Gyre Oscillation. Our study found that offspring production is highly plastic in rockfishes and is part of a life history strategy to conserve energy during periods of poor environmental conditions and to greatly increase reproductive output to take advantage of intermittent, favorable conditions that are characteristic of the California Current Ecosystem. Importantly, strong reproductive plasticity of individuals will influence the

reproductive potential of populations and will consequently influence population productivity when environmental conditions shift.

1.0 Introduction

Theory predicts that phenotypic plasticity in life history traits is one strategy that can evolve to cope with life in highly variable environments (Roff 1992, Stearns 1992, Pigliucci 2001, Botero et al. 2015). However, there is often a lack of empirical study as to the causes and consequences of phenotypic plasticity of life history traits in response to a change in the environment, even though plasticity is predicted and is important to predicting population dynamics. A better understanding of how and why reproductive traits vary over the lifetime of an individual, including temporal shifts in reproductive output, in response to changes in the environment improves knowledge of population reproductive potential, population dynamics, and of which life history strategies are more or less suited to deal with current and increasing environmental variability with climate change (Canale & Henry 2010, Reed et al. 2010, Sydeman et al. 2013, Hendry 2017). For marine fishes, phenotypic plasticity in life history traits is likely common for species living in coastal and environmentally variable ocean ecosystems (Crozier & Hutchings 2014). These conditions are characteristic of Eastern Boundary Upwelling Ecosystems (EBUEs), which have high biological productivity and support a diversity of global marine fisheries (Chavez & Messié 2009). In EBUEs, the phenotypic flexibility of life history traits of individuals is likely adaptive to deal with large spatial and temporal variation in ocean conditions. In turn, high variation in environmental conditions have shaped a diversity of life and reproductive strategies to cope with strong seasonal, inter-annual, and decadal fluctuations in favorable and unfavorable conditions encountered over a lifetime

(Roff 1992, Pigliucci 2001, Piersma & Drent 2003, Reed et al. 2010, Botero et al. 2015). Phenotypic plasticity in reproductive traits in response to fluctuating ocean environmental conditions has consequences for when and by how much individuals contribute to reproduction each year. For example, reproductive plasticity in response to a change in the environment can cause shifts the timing and frequency of reproduction and the quantity and quality of offspring (Husby et al. 2014, Stahlschmidt & Adamo 2015, Froy et al. 2019, Skjæraasen et al. 2020). How changes in the reproductive traits of individuals through time influences population dynamics of marine fishes is largely unknown. Furthermore, phenotypic plasticity in reproductive traits is often unaccounted for in the study of fish population dynamics due to a lack of empirical data, where population models often assume (out of necessity) that reproductive traits are static through time, even though the environment is likely to vary (Lambert 2008, Lorenzen 2016).

In marine fishes, a lack of empirical study of phenotypic plasticity in reproductive traits, especially in highly variable ecosystems such as the EBUEs, hampers efforts to assess population reproductive potential (Lambert 2008, Lowerre-Barbieri et al. 2011, 2017). A lack of empirical study demonstrating the extent of plasticity in reproductive traits in response to temporal shifts in ocean conditions persists even though life history theory predicts that phenotypic flexibility is adaptive (and can be expected) as part of a life history strategy to cope with fluctuating and future environmental change (Piersma & Drent 2003, Botero et al. 2015). A lack of information is generally because the collection of reproductive data in wild fish

populations is difficult, time-consuming, and must cover broad spatial and temporal scales to adequately inform knowledge of how reproductive plasticity influences population dynamics (Lambert 2008). For example, reproductive plasticity is often not accounted for in the study of recruitment dynamics (Friedland et al. 2015, Friedland 2021), even though we know that the composition of females and individual attributes, such as maternal body size and age influence offspring quality and quantity (Hixon et al. 2014, Barneche et al. 2018, Marshall, Barneche, et al. 2021).

The mechanisms for how the ocean environment influences the reproductive output of individuals and subsequently affects population reproductive potential and recruitment to populations in marine fishes are complex. These processes can be non-linear and recruitment is often highly stochastic in marine fish populations (Pankhurst and Munday 2011). Physical shifts in ocean conditions, such as warming temperatures or changes in the timing and intensity of upwelling subsequently affect the amount of primary and secondary productivity in the system (Fig 2.1). A change in ocean primary productivity then influences energy dynamics through the food web, which affects the quantity and quality of prey to higher trophic-level predators (Di Lorenzo et al. 2008, Checkley and Barth 2009, Thompson et al. 2012). The feeding success of individuals also depends on other complex factors, such as density-dependent processes and foraging dynamics (Gotelli 2008). Furthermore, temperature has a strong influence on fish bioenergetics by moderating consumption and metabolic rates (Kitchell et al. 1977, Hewett and Johnson 1992). Together,

temperature and the environmental conditions that influence the feeding success of individuals affect maternal energy reserves and are likely to influence reproductive output (Fig. 2.1). How energy is then used for body maintenance and allocated to life history traits, such as growth and reproduction, is reflected in the evolutionary history of the life history strategy in response to historical patterns of environmental variability, demographics, and social dynamics (Roff 1992, Stearns 1992). In an empirical study, we have imperfect observations of these processes (Fig. 2.1), which contributes to uncertainty in understanding the mechanisms linking the physical ocean environment to biological processes that subsequently affect maternal energy reserves, reproductive success, and recruitment dynamics.

Even though difficulties exist in understanding how the environment influences reproduction in wild populations, laboratory studies of marine fish show how the reproductive traits of individuals, such as fecundity and spawning frequency, are responsive to changes in both temperature and feeding success under controlled conditions (e.g., Lambert and Dutil 2000, Donelson et al. 2010, Yoneda et al. 2014, Beyer et al. 2021). However, for wild populations there exist only a very small number of data rich studies on marine populations that investigated the full link between fluctuating environmental conditions, maternal energy reserves, reproductive output, and recruitment (Friedland et al. 2015, Somarakis et al. 2019, Flores et al. 2021, Friedland 2021). These types of empirical studies, which document inter-annual variation in the reproductive traits of individuals within a population and correlate this variation to changes in the environment advance our understanding of

how reproductive plasticity influences population reproductive potential and how organisms with different reproductive strategies are predicted to cope with future environmental change (Canale & Henry 2010). Clearly, more work is needed to understand the complex mechanisms for how the environment influences reproduction and population dynamics in marine fish (Pankhurst & Munday 2011).

In this study we contribute to the empirical understanding of reproductive plasticity as part of a life history strategy for a group of temperate, live-bearing marine fishes. The rockfishes (*Sebastes* spp.) of the California Current Ecosystem (CCE) are adapted to life in a highly variable coastal ocean upwelling system. Rockfishes are ecologically and economically important, but processes influencing variation in the reproductive output of individuals and subsequent effects on population reproductive potential are largely unknown. Furthermore, large recruitment variability and uncertainty in recruitment impedes efforts to forecast fisheries productivity, especially as the physical and biological characteristics of the ecosystem are impacted by climate change. The majority of rockfish species (65+ species) reside in the southern region of CCE (Love et al. 2002, Hyde & Vetter 2007). The CCE is a highly productive EBUE in the Northeast Pacific Ocean and is characterized by strong spatiotemporal variability in ocean environmental conditions (Hickey 1979, Hickey & Banas 2008, Checkley & Barth 2009). Subsequently, the life history strategies of rockfishes in the CCE are adapted to historically fluctuating environmental conditions. Variation in ocean conditions include latitudinal variation in the seasonality of upwelling and primary productivity, inter-annual shifts from

warm El Niño to cooler La Niña conditions, multi-year temperature and ocean productivity shifts in the Pacific Decadal Oscillation, and the impacts of marine heatwaves in the North Pacific (Mysak 1986, Checkley & Barth 2009, Di Lorenzo & Mantua 2016, Oliver et al. 2018). These climate events influence strong inter-annual variability in water temperature and primary productivity, and subsequently affects fish metabolism and foraging conditions. Temporal variation in these physical and biological ocean conditions are likely to influence maternal energy reserves and reproductive effort.

The reproductive strategy of rockfishes includes both inter- and intra-specific variation in reproductive traits within the genus (MacGregor 1970, Haldorson & Love 1991, VenTresca et al. 1995). Even though all are live-bearers and most are moderate- to long-lived, life histories differ tremendously (Love et al. 2002). The variation in life history strategies within the genus provides an opportunity to explore how reproductive plasticity is correlated with inter-annual variability in ocean conditions for species that have different reproductive strategies. For rockfishes, general patterns of size-dependent fecundity are already well established (Dick et al. 2017). But other mechanisms for maternal effects, such as the influence of the environment on variation in energy reserves and reproductive effort are not. This allows for advances in the knowledge of how phenotypic plasticity in reproductive traits plays a role in the life history strategies of these species adapted to cope with temporal environmental variability and to understand potential differences in the

response of small, first time spawners and large, near maximum-size females to environmental variation.

Inter- and intra-specific variation in the frequency of reproduction complicates assessments of population reproductive potential. Most rockfish produce a single, highly fecund brood of small larvae annually, where potential annual fecundity of the individual equals the size of the brood (Murua & Saborido-Rey 2003). In these species, inter-annual variation in ocean conditions, such as warm El Niño events, reduce rockfish body condition and gonad sizes (Lenarz et al. 1995, VenTresca et al. 1995). Smaller gonads implies a reduction in the annual reproductive output of individuals but has not been quantified. Another reproductive strategy in the genus for at least 15 species, is to produce multiple broods over an annual reproductive season (i.e., a multiple brooding strategy) (Moser 1967, MacGregor 1970, Lefebvre et al. 2018). Females with this reproductive strategy are capable of increasing their annual fecundity by producing multiple broods, but only under certain (and difficult to quantify) conditions and will otherwise produce only a single brood (MacGregor 1970, Love et al. 2002, Beyer et al. 2015, 2021). How multiple brooding is influenced by the environment and contributes to population dynamics is largely unknown. Furthermore, it is generally unknown the number of broods a female will produce at the start of the season, but up to three per reproductive season are possible for some species (Ralston & MacFarlane 2010, Lefebvre et al. 2018). Because annual fecundity for multiple brooders is a function of both brood size and the number of broods, there

is large uncertainty in the estimate of annual fecundity at both the individual and the population level.

Like single brooding species, the annual fecundity of individuals of the multiple brooding species is likely to depend on fluctuating ocean environmental conditions but the mechanisms may differ. It is possible that the environment has a greater influence on the number of broods produced a year, rather than greater inter-annual differences in brood size (Lefebvre et al. 2018, Beyer et al. 2021). Maternal size also influences the number of annual broods, where multiple brooding is more common in large females (Lefebvre et al. 2018). Furthermore, multiple brooding is more common in the southern region of the CCE and occurs occasionally among individuals in the central region (Lefebvre et al. 2018, Holder & Field 2019). This spatial pattern suggests that environmental variation from north to south in the CCE influences conditions favorable for multiple broods. In summary, strong temporal variation of ocean conditions in the CCE is likely to influence inter-annual variability in the reproductive output of both single- and multiple- brooding rockfishes. However, the extent of inter-annual brood size variability and how the environment influences annual reproductive output for species with either a single- or multiple-brooding reproductive strategy is largely unknown.

Here, we use a time series of brood sizes for four species of rockfish in the central region of the CCE to better understand temporal variation in reproductive output. We studied two species that produce only a single annual brood and two that are capable of multiple broods a year, although multiple brooding was historically not

common in the central region (Wyllie-Echeverria 1987). To clarify, we observed

brood size (also referred to as brood fecundity), which was equivalent to annual

fecundity in the single brood species but did not equal annual fecundity for multiple

brooding species if more than one brood was produced. Fish were collected over four

decades from the 1980s to 2020 to develop a time series of brood size information.

Data for this study is based on a single location to exclude spatial fecundity variation

(Beyer et al. 2015). More recent observations suggest that multiple brooding is

occurring with greater frequency in the central region since 2013 (Beyer et al. 2015,

Lefebvre et al. 2018). But because we did not have good measures of multiple

brooding in the central region through the entire time series, we instead focused on

variation in brood size as a first step to understanding reproductive plasticity for

species with different reproductive strategies. The time series spanned varying ocean

conditions, including years of warmer El Niño and cooler La Niña conditions, poor

ecosystem productivity due to a late spring transition to upwelling in 2005, and

marine heatwaves in the North Pacific influencing conditions in the CCE from 2014

through 2016 (Barth et al. 2007, Di Lorenzo & Mantua 2016, Oliver et al. 2018,

Timmermann et al. 2018). The varying ocean conditions during the time series

provided the opportunity to correlate fluctuations in environmental conditions to

fecundity variation to better understand reproductive plasticity.

Our study had two main objectives. First, we documented the extent of inter-

annual variation in brood size to ask how the relationship of maternal length and the

size of larval broods differed through time for each species. Our second objective was

to better understand reproductive plasticity in terms of how the environment influences variation in reproductive output. To do so, we correlated variation in brood size and inter-annual variation in size-dependent fecundity relationships with maternal body condition and the influence of summer and fall feeding conditions during early egg development. We discuss our results with a comparison of small and large females, where the energy dynamics are hypothesized to differ between females that are still growing and those that have reached a near maximum size. Finally, we explored whether maternal age influenced variation in brood size, beyond the explanatory variables of maternal length, body condition, and ocean environmental conditions. We did this because maternal age can influence the quality of larvae in some *Sebastes* species (Berkeley, Chapman, et al. 2004) and because of the possibility for trade-offs between fecundity and larval quality (Stearns 1992).

We hypothesize that rockfish exhibit reproductive plasticity in response to variable ocean environmental conditions given 1) the evolutionary history of rockfishes in a highly variable coastal upwelling ecosystem, 2) the large recruitment variability characteristic of the genus, 3) spatiotemporal variation in the frequency of reproduction, and 4) previous studies finding reduced growth and smaller gonads in years of warmer water temperature and poorer ocean productivity (VenTresca et al. 1995, Beyer et al. 2015, Lefebvre et al. 2018). We used a Bayesian statistical modeling approach to describe variation in fecundity-length relationships and to correlate variation in reproductive effort to environmental conditions. Our results contribute to the understanding of reproductive plasticity in four species of marine

fishes with complex reproductive strategies that are adapted to cope with high environmental variability. In doing so, we also establish a flexible statistical framework for studying the causes and consequences of reproductive plasticity and inter-annual variation of reproductive traits.

2.0 Methods

We developed a Bayesian hierarchical statistical model to better understand how maternal length, energy reserves, and environmental variability influence inter-annual variation in the brood sizes of rockfishes of the California Current Ecosystem (CCE). We first developed a "base model" to describe how the fecundity-length relationship varied by year in the time series for each of the four study species. Next, we added the explanatory variables of body condition to show how maternal energy reserves influenced brood size and an index of inter-annual variation in ocean productivity to ask how environmental conditions influenced variation in brood size, beyond the influence of maternal length and body condition. To provide additional background for our statistical analyses, we first describe large-scale temporal variation in the environmental conditions of the CCE that occurred during the time series (Study Ecosystem). Then we describe the specific study site in the central region of the CCE (Study Location) and differences in the life history and reproductive strategies of the four rockfish species studied (Study Species). Next, we describe fish collections and fecundity data used in the times series, starting with contemporary collections part of the current study (Contemporary Collections) and

historical datasets added to the time series (Historical Datasets). Last, we describe the Bayesian statistical models used to answer our questions of how the environment and changes in maternal energy reserves influenced inter-annual variation in the reproductive output of rockfishes with different reproductive strategies.

2.1 Study Ecosystem

The CCE is a highly productive nearshore ecosystem along the U.S. West Coast, described as an Eastern Boundary Upwelling Ecosystem (EBUE) (Chavez & Messié 2009). The CCE has three geographically and biologically distinct regions by latitude (north, central, and south) and has strong temporal and spatial variability in ocean environmental conditions (Checkley & Barth 2009). This includes variation in ocean temperature and primary productivity that influences prey for rockfishes. Here, we focused on the central region where a seasonal spring and summer peak in primary productivity is driven by atmospheric winds interacting with the geography of the coastline to upwell cold, nutrient rich waters into the coastal photic zone. This provides the physical conditions to promote biological primary productivity and the upward flow of energy through the food web (Checkley & Barth 2009, Thompson et al. 2012). Downwelling and lower biological primary productivity occur in the winter (Checkley & Barth 2009). This seasonal variability in physical and biological conditions, is itself, highly variable at inter-annual and decadal scales and is influenced by basin-wide climate events, such as El Niño, La Niña, marine heatwaves, and shifting temperature regimes described by the Pacific Decadal

Oscillation (Di Lorenzo et al. 2005, 2008, King et al. 2011, Di Lorenzo & Mantua 2016). These climate events result in strong inter-annual variability in temperature and overall biological primary ocean productivity in the CCE likely to influence reproductive variability in marine fishes.

Future climate models for the CCE predict an increase in the frequency of moderate-to-strong, low productivity, ocean warming events, such as El Niño, and marine heatwaves, which already occur (Di Lorenzo et al. 2005, Cai et al. 2014, Di Lorenzo & Mantua 2016). Climate shifts in the CCE result in increased ocean temperatures in normally cool regions, shifts in upwelling, the poleward dispersal of tropical species influencing the composition of biological communities, and altered primary productivity (Leising et al. 2015, Jacox et al. 2016). The effects of increased temperatures and reduced productivity on reproduction and the resulting effects on population productivity for species living in highly variable environments is mostly unknown (Mueter et al. 2011, Szuwalski & Hollowed 2016, Sharma et al. 2021). An understanding of how organisms cope with current levels of high environmental variability is likely to provide insight into how these organisms will respond to future increased environmental variability in comparison to those living in more stable environments, at least in the near-term with climate change.

2.2 Study Location

To minimize known spatial effects on fecundity (Beyer et al. 2015) and to focus on temporal variation, we examined fecundity data from at a single location in

the central region of the CCE. All fish in this study were collected at Cordell Bank, a seamount located approximately 25 km off the coast of central California (Fig. 2.2). Cordell Bank was selected because of 1) the availability of a unique time series of historical fecundity data that has been collected in this region intermittently since 1986, 2) ongoing contemporary collections, and 3) due to its importance as a highly productive geographic feature supporting a diversity of marine life and historical fisheries. Cordell Bank is part of the Cordell Bank National Marine Sanctuary and has been closed to recreational and commercial groundfish fishing since 2002.

2.3 Study Species

We focused on four species: Yellowtail Rockfish (*Sebastes flavidus*), Widow Rockfish (*S. entomelas*), Chilipepper (*S. goodei*), and Bocaccio (*S. paucispinis*). All occur throughout the shelf waters of the CCE and are abundant at Cordell Bank. Yellowtail and Widow Rockfish live up to 64 and 60 years, maturing around 7 and 5 years, and are most abundant at depths of 90m to 180m and 140m to 210m, respectively (Love et al. 2002). 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 of 75m to 325m and 50m to 250m, respectively (Love et al. 2002). Yellowtail and Widow rockfish are obligate single brooding species (i.e., a single brooding strategy); whereas, Chilipepper and Bocaccio have the ability to produce additional broods annually (i.e. a mulitple brooding strategy, Moser 1967, MacGregor 1970). Multiple brooding is less common in the central region for these

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species, and in some years females produce only a single brood (Lefebvre et al. 2018).

To measure inter-annual variation in reproductive output, we measured the brood size (brood fecundity) of individuals. This was the number of larvae released in a single parturition event. Annual fecundity, the number of larvae released in a reproductive season, is equivalent to brood fecundity in the single-brooding Yellowtail and Widow rockfishes but is the product of brood size and the total number of annual broods in the multiple brooding Chilipepper and Bocaccio. We could not assess annual fecundity variation in Chilipepper and Bocaccio because we could not quantify fecundity of broods other than those currently present in the ovaries of collected fish and could not determine the total number of broods produced per year. We instead focus on temporal variation in brood size for all four species. Implications of annual fecundity variation for life history strategies for these species are noted in the discussion.

2.4 Contemporary Collections

Females were collected by hook-and-line during the winter reproductive season from 2009 to 2020 to extend a historical time series of fecundity data at Cordell Bank. We relied on local fishing knowledge to target specific species from a chartered commercial passenger fishing vessel (CPFV), The New Sea Angler, captained by R. Powers, and a small commercial fishing vessel, The Palo, captained by J. Churchman. Both captains had extensive experience fishing for groundfish at

Cordell Bank prior to fishery closures, which was important for targeting these species. Yellowtail rockfish and Chilipepper were the primary species targeted. Female Widow rockfish and Bocaccio were sampled incidentally when encountered with the targeted species. Some fecundity data from contemporary collections were published in Beyer et al. (2015), which described spatial differences in the fecundity of Yellowtail rockfish and Chilipepper between the central and south CCE, and Lefebvre et al. (2018), which described spatial differences in the patterns of multiple brooding in Chilipepper. Fish captured in the months of January, February and March were pooled with the previous calendar year (November and December) to combine months into a single reproductive season (e.g., females caught in January 2020 were attributed to the 2019 reproductive season). This allowed us to assess inter-annual fecundity variation by reproductive season, which starts in late fall and extends through winter. However, it should be noted that our reproductive season is offset one year earlier than recruitment cohorts in stock assessments, which assume a birthdate of all fish on January 1st. Protocols for fish collections were approved by the University of California Santa Cruz Institutional Animal Care and Use Committee (IACUC).

After capture, fish were euthanized and females with evidence of eggs or larvae were placed in individual plastic bags to prevent loss and were packed in coolers with crushed ice to ensure freshness of tissue samples. Fish were processed within 24 to 48 hours of capture, with measurement of length (fork length, nearest mm), total wet weight (nearest 0.1 g), liver weight, and ovary weight (nearest 0.01 g).

Two weighed subsamples of the ovaries in the range of 0.5 – 1.0 g were collected and preserved in a 10% neutral buffered formalin solution for later fecundity analysis. Sagittal otoliths were dissected, cleaned, and stored dry in 2 ml plastic scintillation vials for later age analysis by the break-and-burn method (Beamish & Chilton 1982).

2.5 Brood Fecundity

To measure inter-annual variation in brood size, we collected data on female fecundity. To estimate the size of the brood (brood fecundity), we used either a weight-based gravimetric counting method or an autodiametric imaging method more recently adapted for five rockfish species (Mapes *et al.* in review). Fecundity estimates by the two methods are closely correlated and interchangeable (Mapes *et al.* in review). The gravimetric method consisted of manually counting the number of oocytes, fertilized embryos, or eyed larvae in the two weighed subsamples of the ovary under a dissecting microscope. The number of oocytes or embryos per gram was multiplied by the total wet weight of the ovary and averaged to estimate fecundity (Beyer et al. 2015). The autodiametric method used images of oocytes and automated measurement software to relate a mean oocyte diameter of a subsample to an oocyte density by a calibration curve. The oocyte density (oocytes $*$ gram^{-1}) for each sample was multiplied by the gonad weight to estimate fecundity. The method of fecundity estimation depended on developmental stage (i.e., no calibration curves were available for fertilized stages), date of collection (i.e., more recent samples

processed by the recently developed and more efficient autodiametric method), and

species (i.e., autodiametric calibration curves are currently only available for

Yellowtail rockfish, Widow rockfish, and Chilipepper).

Brood fecundity (Φ) was modeled as a power function of body length (fork

length, L) (Dick et al. 2017):

$$\Phi = cL^b \tag{1}$$

where the scalar (c) and exponent parameter (b) were estimated from the linear,

natural log transformed least squares regression of brood fecundity and length fit to

the data:

$$\log (\Phi) = a + b \log (L) \tag{2}$$

where $a = \log(c)$ and the parameter b indicates the strength of the effect of maternal

length on brood size. For simplicity, we refer to b as the slope of the fecundity-length

relationship because we work with the linear form of the relationship in (2) to develop

more complex models exploring fecundity variation, beyond the strong influence of

length alone. The biological significance of the slope parameter is that fish weight

generally increases in an allometric relationship with length and with a slope close to

$b = 3$. However, fecundity tends to increase at a faster rate, described by a hyper-allometric relationship with length. A hyper-allometric relationship with a slope of $b > 3$ is a case where fecundity increases disproportionately with maternal length (i.e., larger females produce disproportionately more eggs per gram of spawning biomass compared to small females). A hyper-allometric relationship of reproductive output and maternal size is common in marine fishes (Barneche et al. 2018) and occurs for most rockfishes (Dick et al. 2017). The slope parameter is important because it describes the strength of the maternal-length effect on fecundity.

2.6 Maternal Body Condition

To ask how maternal energy reserves influenced brood size, we used maternal body condition as a proxy for maternal energy reserves to correlate with length-dependent brood size. The body condition index is a scaled ratio of weight and length and is commonly referred to as the "Fulton's K" condition factor (K) (Ricker 1975, Nash et al. 2006). We modified K to use somatic weight instead of total wet weight to exclude the influence of the gonad. Our equation for K was:

$$K = \frac{W}{L^3} \, 100 \tag{3}$$

where *W* is somatic weight (wet weight without the gonad, g) and *L* is fork length (mm). This equation (3) was multiplied by a scaling factor of 100 to bring the value of *K* near 1. The body condition factor describes the cubic relationship of weight to length and is considered a measure of relative "fatness" with respect to length (Ricker 1975).

2.7 Index of Environmental Variability

To explore the effect of environmental conditions on inter-annual brood size variability, we used the North Pacific Gyre Oscillation (NPGO, http://www.o3d.org/npgo/), which is an index correlated with ocean biological productivity (Di Lorenzo et al. 2008). Specifically, the NPGO is an index of relative sea surface height and large-scale circulation patterns in the Northeast Pacific Ocean (Di Lorenzo et al. 2008). Large-scale ocean transport patterns are correlated to inter-annual and inter-decadal changes in environmental conditions in the CCE (Chelton et al. 1982, Parrish et al. 2000, Checkley and Barth 2009). The NPGO index is also correlated with salinity, nutrients, and chlorophyll levels, which broadly describe conditions promoting primary and secondary productivity in the CCE (Di Lorenzo et al. 2008). Positive values of the NPGO index correlate with stronger equatorward flow and more subarctic source waters in the California Current, which indicate generally cooler and more productive ocean conditions. Negative values tend to reflect warmer, more subtropical source waters and less productive conditions (Sydeman et al. 2013, Peterson et al. 2014).

We used the mean of the monthly NPGO index over the months of August, September, and October (Fig. 2.3) to reflect ocean conditions during the time of year when females were developing oocytes for the winter brood (Wyllie-Echeverria 1987). We chose this period with the hypothesis that feeding conditions during the summer and fall would be most influential for fecundity regulation, prior to when broods are fertilized. In other marine fishes, up- or down- regulation of fecundity, which determines the brood size mostly occurs during early oocyte development (Murua & Saborido-Rey 2003, Skjæraasen et al. 2009, McBride et al. 2015, Serrat et al. 2019). Also, the fat stores of rockfishes in the central and northern regions of the CCE increase through the spring and summer and peak in the fall. Fat stores then decline through winter when fish reproduce and when food sources are more scare (Guillemot et al. 1985, Hobson & Chess 1988, Larson 1991, MacFarlane et al. 1993, Norton & MacFarlane 1995, VenTresca et al. 1995). We assumed that ocean conditions in the late summer and fall reflected feeding conditions that would influence the amount of energy a fish acquired to use to reproduce in the winter.

2.8 Historical Datasets

To develop the time series to explore inter-annual variation in brood size, we combined the contemporary study with additional datasets of brood size for the four species collected at Cordell Bank since 1986. All historical studies targeted rockfishes for reproductive and life history information and used similar hook-and-line methods

(including collecting fish from the same CPFV, operated by the same captain),

providing a unique dataset of the same populations sampled through time. While the

Yellowtail rockfish data between 1985 and 1991 were published (Eldridge and Jarvis

1995), the raw data, and additional unpublished data on all four species that were

collected and processed during that research effort were recovered from original

datasheets for inclusion in this study (Eldridge and Jarvis unpublished). Additional

data were available from Stafford et al. (2014) for Yellowtail rockfish, Chilipepper,

and Widow rockfish collected at Cordell Bank in 2005 (with some collections in 2006

and 2007) to describe maternal effects on larval quality, fecundity, and the timing of

parturition.

All studies measured fish length, wet weight, and gonad size, allowing

calculation of the body condition factor, *K* (eq. 3) as a proxy for maternal energy

reserves at the time of capture. Historical studies used a similar gravimetric method to

estimate brood fecundity. One difference in fecundity determination was that instead

of subsampling oocytes or embryos of fresh ovaries, Eldridge and Jarvis (1995) and

Eldridge and Jarvis (unpublished) preserved a small portion of the ovary and counted

triplicate weighed subsamples from the preserved portion of the ovary. A conversion

factor of preserved weight to wet weight was used to estimate fecundity and was

recorded on the original datasheets. Another difference was that Eldridge and Jarvis

(1995) and Eldridge and Jarvis (unpublished) measured standard length. Standard

length was converted to fork length for this study using a length conversion published

by Echeverria and Lenarz (1984) and a statistical conversion to standardize lengths

(*Supplementary Materials S2.1*). It was important to standardize the length

measurement among all studies because of the strong influence of maternal length on

brood size.

2.9 Statistical Models

2.9.1 Base model

We fit Bayesian hierarchical linear models to our time series data to estimate

the intercept and the slope (strength of the maternal length) parameters of the brood

fecundity-length relationship by year from equation (2). We also used these models to

predict brood fecundity, given information on maternal body condition and

environmental conditions each year. The first model, which we refer to as the

fecundity "base model", used maternal length as the sole predictor to estimate the

intercept and slope parameters from equation (2). The equation for the base model

was:

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

where y_{ij} is the (centered and scaled) natural log transformed response variable of

brood fecundity for an individual fish i in year j, x_{jj} is the (also centered and scaled)

natural log transformed fork length of the i th fish in year j, α_0 and β_0 are the fixed

effect 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. The variable ε_{ij} represents the measurement error. We model the pairs of random effects (i.e., (a_1, b_1), (a_2, b_2), …) hierarchically as independent draws from a bivariate normal distribution with zero mean, marginal standard deviations ϕ and ψ, and correlation coefficient ρ. Similarly, the observational errors were treated as draws from a normal distribution with zero mean and standard deviation σ.

We set prior distributions (priors) for the fixed effects, the standard deviation parameters ϕ, ψ and σ, and the correlation ρ. Priors were intentionally selected to "weakly" inform the model (Gelman 2006). We used a standard normal distribution as a "generic" prior for the fixed effects, α_0 and β_0, for mean-centered and standard deviation-scaled data (Gelman, 2006). A sensitivity analysis using more diffuse priors on the fixed effects of a normal distribution (standard deviation 10 and 100) found no qualitative differences in the parameter estimates. We used a half-student t distribution with 3 degrees of freedom and a scale parameter of 2.5, for the priors on the marginal standard deviations of the random effects, ϕ and ψ, and the standard deviation of the measurement error σ (Bürkner 2017). The half-student t distribution is recommended as a "weakly" informative but proper prior that restricts the variance to positive values (Gelman 2006). 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). Parameters were estimated by MCMC using 4 chains, each with 7000 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 of the four species (i.e., models of each species were independent).

The practical effect of hierarchical modeling of the fecundity-length relationship is that in years where the data are sparse the parameters of the fecundity-length relationship will "shrink" toward the population-level mean. In years where the data are robust, the fecundity-length parameters will more closely resemble the output of a fixed-effect ANCOVA-type model, where the parameters are assumed independent by year. Hierarchical models have the added benefit of allowing us to make predictions for unobserved years due to the assumption that the year parameters (random effect) are derived from a common, population-level distribution of fecundity-length parameters and this distribution can be estimated (Hobbs & Hooten 2015). A similar approach was taken for a meta-analysis of species and sub-genera specific fecundity-length relationships (without consideration of year effects or the possibility of multiple broods) in developing the fecundity-length parameters to inform stock assessment models for the *Sebastes* genus, even for sparsely informed species (Dick et al. 2017).

We fit the fecundity base model for each species independently using the Bayesian framework with the brms package in R (Bürkner 2017). The brms package is a front-end wrapper using RStan for the underlying computations (Stan Development Team 2019, 2020). One key benefit of the brms package is that it uses

the same syntax as the lmer4 package in R to fit linear mixed effects models with maximum likelihood, which is familiar to many ecologists (Bates et al. 2015). However, the Bayesian probability framework provides greater flexibility in parameter estimation with *Markov Chain Monte Carlo* (MCMC) and is recommended when encountering problems of singular fits arising from difficulties in estimating the variance-covariance matrices via maximum likelihood that can occur with low sample size, which was the case for Widow rockfish and Bocaccio (Gelman & Hill 2006, McElreath 2015).

2.9.2 Adding predictors

Following the development of the base model to quantify how variable the length-fecundity relationship was by year for each species, we considered additional models that included maternal body condition and an index of ocean environmental conditions (summer/fall NPGO) thought to influence fecundity variability to test if these additional variables would improve model fit. First, we considered a model in which maternal body condition (K) was used as a direct predictor of the brood fecundity of individuals. We did this to test if energy reserves were correlated with fecundity. The model was:

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

where z_{ij} is the (centered and scaled) value of Fulton's K for fish i in year j and δ is the associated fixed-effect coefficient. We also considered a different model that used the annual summer and fall mean of the NPGO index as an environmental predictor of inter-annual brood size variability (i.e., a predictor on the random effect of year). This was implemented using an interaction between the environmental condition and length (Qian et al. 2010) :

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

where α_1 and β_1 are fixed effects that capture the impact of the (centered and scaled) NPGO index (w_j) on fecundity. An interesting feature of this model is that it can be reinterpreted 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).

Last, we combined all three predictors of maternal length, maternal body condition, and the environment into a "full model", defined by the equation:

$$y_{ij} = \alpha_0 + \alpha_1 w_j + a_j + \beta_0 + \delta z_{ij} + \beta_1 w_j \, x_{ij} + b_j x_{ij} + \varepsilon_{ij}. \tag{7}$$

The parameters for equation (7) are the same as those described above in equations (4, 5, and 6). Similar to α_0 and β_0, the additional fixed effects of α_1, β_1, and δ were assigned standard normal priors. We compared different models to understand

the influence of each of the added predictors of maternal body condition and environmental conditions and to determine which model had the best predictive ability.

To compare model fit and predictive ability, we calculated the expected log pointwise predictive density (elpd) of new data using a leave-one-out (LOO) cross-validation approach (loo package in R, Vehtari et al., 2017). The LOO approach evaluated model fit by sequentially removing, re-fitting, and predicting the response for the i th data point. The LOO approach identified influential data points and model sensitivities, which provided a quantitative assessment of model fit with respect to model complexity. Models with additional variables that did not improve predictive power were penalized for increased complexity. We present elpd$_{LOO}$ scores as offsets relative to the "best fit" model of greatest predictive power (Vehtari et al. 2017). We also present 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 our results for the full models, we plotted expected fecundity-length relationships for fish with different body condition and in relation to the environmental index. We show the posterior median and 95% credible intervals for expected brood fecundity by year at three reference lengths: the mean fish length of all fish for each species in the study (L_{mean}), the length where 50% of females in the population are mature (L_{50}, small, approximate first-time spawners), and at the asymptotic length (L_{inf}, large, near maximum size females). The values for the

reference lengths at L_{50} and L_{inf} came from the most recent stock assessments with documentation in *Supplementary Materials 2.2*. L_{inf} in the stock assessments were calculated from the von Bertalanffy growth function (von Bertalanffy 1938, Beverton & Holt 1957).

Last, we explored the potential for maternal age effects on brood fecundity because age can vary substantially among fish of a similar size and because maternal age is known to influence larval quality in some rockfishes above and beyond the effects of maternal size alone. Because age is closely correlated with length, we did not directly add age as a predictor in the model. Also, age data did not exist for all samples, which would have resulted in different samples sizes if models were run independently with either length or age as a predictor. Instead, we plotted the residuals of the full model by maternal age to look for any pattern in the remaining unexplained variance that could be attributed to maternal age.

3.0 Results

We first present the results of the fecundity base model to answer our question about how the length-fecundity relationship varied by year among the four rockfish species and to quantify inter-annual variation in brood size. First, we report differences in the strength of the maternal length effect (i.e., the slope parameter of the fecundity-length relationship) among the four species and how the strength the maternal length effect on brood size varied by year in consideration of the single- and multiple- brooding reproductive strategies. Second, we further explored the influence

of maternal length on variation in the expected brood size by year at different reference lengths of small, large, and mean-sized reproducing females. After presenting the results of the base model, we show how the additional predictors of maternal body condition and ocean environmental conditions influence inter-annual brood size variability to better understand phenotypic plasticity of reproductive traits in response to fluctuating environmental conditions. Last, we considered the influence of maternal age, beyond the effect of maternal length, body condition, and the environment, as another potential predictor of fecundity variability since maternal age is known to influence larval quality in some species (Berkeley, Chapman, et al. 2004) and could trade-off with fecundity (Stearns 1992).

3.1 Collection Summary

Compiled 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, 2009 – 2019, Table 2.1). The time series included 21 years of fecundity data for Yellowtail Rockfish (n = 778), 11 years for Widow Rockfish (n = 153), 13 years for Chilipepper (n =587), and 8 years for Bocaccio (n = 135). Years with only a single fecundity data point were excluded from the analysis but are shown in Table 2.1, along with the mean and range in lengths of reproductive females sampled each year.

3.2 Base model

3.2.1 Maternal length effects

To understand how the fecundity-length relationship varied by year, we analyzed the results of the base model, which included length as the sole predictor. First, we compared the overall strength of the effect of maternal length on brood fecundity (i.e., the population-level effect with all years combined in the base model) by species and in relation to the reproductive strategy to emphasize the general differences in that relationship among single- and multiple- brooding species. The single brooding Yellowtail Rockfish and Widow Rockfish had overall stronger population-level maternal size effects on fecundity than the multiple brooding species, with population-level slopes of 4.96 and 4.17, respectively. This contrasted the weaker, general maternal length effects on brood size of the multiple brooding capable Chilipepper and Bocaccio, with population-level slopes of 3.68 and 3.21, respectively. For context, a meta-analysis of rockfishes found an average genus-wide effect of maternal length on brood size of 4.043 (Dick et al. 2017). A slope greater than the slope of the species-specific, natural log transformed, weight and length relationship, which was generally around 3.0, indicated the disproportionate relative egg production of large compared to small females. This meant that the single brooding Yellowtail rockfish and Widow rockfish had stronger maternal size effects on brood size compared to Chilipepper and Bocaccio, the two species capable of multiple broods.

3.2.2 Temporal variation in the effect of maternal length

Beyond the general differences among species and between the two reproductive strategies, how the strength of the maternal length effect varied by year also differed between the single- and multiple- brooding species. This difference was important because it influenced how variable expected brood size was by year. Inter-annual variability in the strength of the maternal length effect (i.e., the slope by year) varied the most in the single brooding Yellowtail Rockfish, ranging from 3.03 in 2019 to 6.72 in 2017 (Fig. 2.4, slopes by year). The biological significance of variability in the maternal size effect is that in some years large and small females produced relatively equal numbers of offspring, in terms of relative fecundity (i.e., a slope near 3.0). In other years, the effect of maternal size was very strong, where larger females had much greater relative fecundity (i.e., a slope near 6.0). The slope of 6.72 in 2017 (indicating a very strong effect of maternal length on brood size) was not an artifact of the model. In fact, fitting a simple linear regression model to only the 2017 Yellowtail rockfish data (n = 53) produced a more extreme estimate of the slope at 7.12. The year had a large number of samples, but not many samples from the largest-sized females. This is an example of how the Bayesian approach leveraged information about the fecundity-length relationships of all years in the time series to estimate an effect size in 2017 closer to the population-level mean for Yellowtail rockfish ($b = 4.96$), and less than predicted from an independent, ANCOVA model fit only to 2017 data.

In the single brooding Widow Rockfish, inter-annual variability in the strength of the maternal size effect on fecundity was somewhat less than for Yellowtail, ranging from 3.84 in 2018 to 4.53 in 2005. The much smaller sample size available for Widow rockfish and fewer years (compared to Yellowtail rockfish) lead to greater uncertainty in the estimates of the intercept and slope parameters (Fig. 2.4). In comparison to the single brooding species, the multiple brooding capable Chilipepper and Bocaccio had less yearly variation in the strength of the maternal size effect (Fig. 2.4). Inter-annual variability in the slope parameters ranged from 2.81 (2016) to 4.49 (2010) for Chilipepper and from 2.88 (2015) to 3.46 (2016) for Bocaccio. Like Widow rockfish, Boccaccio had fewer samples and fewer years sampled.

3.2.3 Temporal variation in expected brood size

Because maternal length has such a strong influence on brood size and that the strength of this effect was highly variable by year, inter-annual fecundity variability, in absolute terms, was generally the greatest among the largest females for all species (Fig. 2.4). To further illustrate this variability, we calculated the difference in expected brood fecundity between the year of lowest and highest fecundity for each species at all three reference lengths (L_{inf}, L_{mean}, and L_{50}, Table 2.2).

For the single brooding Yellowtail Rockfish, the greatest variation in brood size from the lowest to highest fecundity year in the time series was the expectation

of a large female at L_{inf} to produce approximately 0.77 million larvae in 2018 compared to nearly 2.35 million larvae in 2017 (Table 2.2). This represented an increase in brood size of 203% and over 1.5 million more larvae in the brood of a large female from the lowest to highest fecundity year in the 21-year time series. A small Yellowtail rockfish at L_{50} was expected to produce 291,879 larvae in 2018 (lowest year for small females) and 620,596 larvae in 2014 (highest year for small females), a difference of 328,717 more larvae per brood from the low to high fecundity year for small mature females at L_{50}. The mean size of Yellowtail rockfish females in our study was slightly less than L_{50} for the population. The greatest inter-annual variation in expected brood size for mean-sized females was 262,539 more larvae per brood from the lowest (2018) to highest (2014) year for females at L_{mean}.

For the single brooding Widow Rockfish, a large female at L_{inf} was expected to produce 534,899 larvae in the lowest fecundity year (2005) and nearly 1.2 million larvae in the highest year (1987). This was an expected 124% increase of 665,063 more larvae in the brood of a large female from a poor to good fecundity year in the 11-year time series (Table 2.2). A small Widow Rockfish at L_{50} was expected to produce 59,704 larvae in 2005 (lowest year for small females) and 165,969 larvae in 2014 (highest year for small females), a difference of 106,265 more larvae per brood from a poor to a good year for small mature females. The length of mean-sized Widow rockfish females in our study was intermediate to L_{inf} and L_{50} and had an intermediate difference in brood fecundity of 372,178 larvae between the same highest to lowest year for small females (2014 and 2005, respectively).

Inter-annual variation in brood size was less for the multiple brooding species compared to the single brooding species. For the multiple brooding capable Chilipepper, a large female at L_{inf} was expected to produce 232,207 larvae in 2018 and 379,791 in 2010, an increase of 64% and 147,584 more larvae per brood from the lowest to highest fecundity year in the 13-year time series (Table 2.2). A small, mature Chilipepper at L_{50} was expected to produce only 22,303 larvae in 2005 and 44,454 in 2016, a difference of 22,151 more larvae per brood. The length of mean-sized Chilipepper in our study was closer to L_{inf}, with an expected difference of 67,000 more larvae per brood between 2015 to 2010, which was the lowest to highest year for mean-sized female Chilipepper.

The multiple brooding capable Bocaccio had the smallest relative variation from lowest to highest year in comparison to the other species. A large Bocaccio at L_{inf} was expected to produce 1.2 million larvae per brood in 2015 and over 1.4 million in 2016, a 23% increase of 276,536 more larvae from the lowest to highest fecundity year for large females in the 8-year time series (Table 2.2). A small Bocaccio at L_{50} was expected to produce 186,059 larvae in 2017 and 223,249 larvae in 2015, a difference of 37,190 more larvae per brood from a poor to a good year for small mature females. The length of mean-sized Bocaccio females in our study was intermediate to L_{inf} and L_{50}, with an expected difference in brood size of 103,734 more larvae per brood between 2015 to 2016, the lowest and highest fecundity year for mean-sized females.

It is important to emphasize that Widow rockfish and Bocaccio had fewer years in the time series (11 and 8 years, respectively) and much smaller samples sizes compared to Yellowtail rockfish and Chilipepper. The differences in sample size and sampling effort limited the assessment of inter-annual brood size variability for those species and may underestimate inter-annual variability in comparison with the other species. However, general trends emerged. In summary, inter-annual variation in brood size was greatest in the single brooding species compared to the multiple brooding species, and the extent of brood fecundity variation depended on the size of the female.

3.3 Reproductive plasticity in response to changes in body condition and ocean productivity

To better understand phenotypic plasticity of reproductive traits and the mechanisms underlying the inter-annual fecundity variability documented above, we added to the base model the potential explanatory variables of maternal body condition (as a potential predictor of individual fecundity) and environmental conditions in the summer and fall during oogenesis (as a potential predictor on inter-annual variability of the parameters of the fecundity-length relationship). To tease apart the correlation (and predictive power) of each variable, we first ran the models, which all included length and each of the additional predictors separately. Then we fit

a full model that included all three predictors of length, body condition, and the environment.

As hypothesized, we found strong evidence for all four species that females in better body condition, indicated by a higher K and standardized by maternal length, produced more larvae than females with poor body condition. Adding K to the model significantly increased predictive power, shown by the large difference in Δ elpd$_{Loo}$ in comparison to the base model of length alone (Table 2.3). Except for Chilipepper, a model with maternal length and body condition had the greatest predictive power of all models considered for each species. The full model for Chilipepper, which included the environmental variable of the NPGO, performed slightly better than a model of length and body condition alone. In all cases, the effect coefficient of K was positive and did not include zero in the 95% credible interval of the posterior distribution (see full model results in *Supplementary Materials 2.3*). This meant that maternal body condition was a significant predictor of brood size, in addition to the already strong and significant influence of maternal length.

Adding the environmental index (summer and fall NPGO mean) to the base model (without body condition) did not result in any significant gain in predictive power for any of the species (comparison of models 1 and 3, Table 2.3). However, adding the NPGO to the full model of maternal length, body condition, and the environmental index led to a small improvement in elpd$_{Loo}$ for Chilipepper, over the model with maternal length and body condition alone (comparison of models 2 and 4). Adding the NPGO to the full model led to essentially identical elpd$_{Loo}$ values in

the case of Yellowtail and Widow rockfish, and slightly worse values of elpd$_{Loo}$ for

Bocaccio (Table 3). The values of the Bayes R^2 were identical between models 2 and

4 for Yellowtail rockfish and Bocaccio, and very slightly improved for Chilipepper

and Widow rockfish (Table 2.3). The comparison of predictive power among the

models indicated that there was some evidence, albeit weak, of environmental effects

on inter-annual fecundity variability. This was beyond any influence of the

environment on maternal length and body condition and meant that some information

in the NPGO index improved predictions of brood fecundity variability beyond what

was already captured in the information about body condition and length.

Furthermore, the effect size of the NPGO in the full models on the intercept

(scaling factor) and slope (strength of the maternal size effect) parameters were

generally weakly positive, except for a weakly negative effect on the intercept of the

fecundity-length relationship by year for the Bocaccio full model (*Supplementary*

Materials 2.3). The weak, but positive correlation of more productive ocean

conditions with increasing strength in the effect of maternal size on brood fecundity

(slope parameter) showed that the largest females were more capable of "taking

advantage" of years with productive ocean conditions compared to smaller females

through increased reproductive effort (Fig. 2.5). In other words, the disproportionate

larval contribution by the larger females in comparison to small females increased in

years of more productive ocean conditions. On the other hand, the strength of the

maternal size effect on brood fecundity was less in years with poor ocean productivity

(Fig. 2.5). So brood sizes declined, no matter the maternal size, but also the larger

females were producing relatively similar amounts of larvae per gram of female biomass in years with poorer ocean conditions compared to smaller females (i.e., a fecundity-length slope closer to 3.0).

To understand the specific contributions and complex interactions of each of the explanatory variables in the full model (model 4), we plotted the conditional influence of the summer and fall NPGO mean on the expected brood size for females of difference size (i.e., reference lengths of small, large, and mean sized females) and for females with different body condition (Fig 2.6.). Similar to the full model results, which showed the weak influence of the NPGO on both the intercept and slope parameters of the fecundity-length relationship (*Supplementary Materials 2.3*), these conditional plots of expected brood size again showed a stronger influence of ocean environmental conditions on larger compared to smaller females. However, there was also greater uncertainty in the strength of the environmental effect for the largest sized females (posterior median value and 95% credible interval shown), which reflected lower sample sizes of near maximum sized fish. In these plots, we show the strong influence of maternal body condition on brood size, especially for large females, in relation to environmental conditions for females with poor, average, and good body condition (i.e., females at the mean K of samples and $\pm$ 3 standard deviations of the mean to represent good or poor body condition). In summary, the full models provided strong support for the important influence of both maternal length and body condition on expected brood size for all four study species. This was evidence for a mechanistic link between maternal energy reserves and the allocation

of energy to reproduction. Our results also showed weak, but positive support for the influence of environmental conditions in the summer and fall feeding season on expected brood size, especially among the largest sized females of each species. The influence of the summer and fall NPGO ocean conditions was in addition to the strong influence the environmental already had on energy reserves and captured by the information on maternal body condition. In other words, there was some explanatory power of the environmental index of the NPGO that was not fully captured by our measure of body condition and length at the time of capture.

Last, we explored the potential influence of maternal age on unexplained variance in the full models by plotting the model residuals and age (Fig. 2.7). We found little support for an effect of maternal age, with the slope of a fitted linear regression of model residuals and maternal age near zero for all four species. For Widow rockfish and Bocaccio, there was a slight, non-significant, negative trend with age. This largely uncertain trend provided very weak support for a trade-off in brood size and potentially larval quality (not measured in this study) with maternal age, but such weak and inconclusive evidence may not be biologically relevant and should be investigated further. We report these results as a check of the model in case we were missing any important influence of maternal age. The age range was fairly well-sampled for Chilipepper and Bocaccio but were mostly younger than maximum age for Yellowtail and Widow rockfish. A future study of trade-offs between offspring quantity and quality is warranted but was outside of the scope of this study.

4.0 Discussion

The aim of our study was to better understand the extent to which inter-annual variation in brood size is explained by maternal length, energy reserves, and the environment in four live-bearing species of rockfish of the highly dynamic California Current Ecosystem and in comparison with the two different reproductive strategies in the genus. Our first objective was to quantify inter-annual brood size variability. We found inter-annual fecundity variability was greatest in the two species with a single brooding reproductive strategy and somewhat less in the two species capable of multiple annual broods. Our second objective was to better understand phenotypic plasticity of reproductive traits in response to changes in the environment. We found maternal energy reserves strongly influenced brood size and that environmental conditions, beyond the influence on body condition, also influenced inter-annual variability in brood size, but to a weaker extent.

4.1 Temporal variation in brood size and the important influence of maternal length

Single brooding species had higher inter-annual variation in the size of larval broods compared to species capable of multiple broods. We observed increases in expected brood size of up to 203% and over 1.5 million more larvae for a large single-brooding Yellowtail rockfish from the lowest to highest year in the time series. In part, this high inter-annual variation was related to strong variation in maternal length effects on fecundity in this species. The strong influence of maternal size, with

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the slope of the fecundity-length relationship estimated up to 6.72 in 2017, was much greater than the average effect size of 4.043 for maternal length estimated for the genus (Dick et al. 2017). The benefit of the Bayesian hierarchical approach used here, is that although the estimate for 2017 was very high, it was tempered and informed by the large amount of data from multiple years in the Yellowtail rockfish model and further supported by many samples that year (n = 53).

An unavoidable short-coming of the Yellowtail rockfish model was that most of our samples from central California fell short of the coast-wide species estimate of L_{inf} = 531 mm for Yellowtail rockfish. A lack of the largest sized females in our time series introduced greater uncertainty in the expected brood size estimates of females near the asymptotic size of Yellowtail rockfish and should be interpreted with caution. For context, we compared observed fecundity of females in our study to larger females encountered north of the study site. The greatest brood size observed in a Yellowtail Rockfish in our time series was 1.36 million larvae from a 457 mm FL female collected in 1992. The largest Yellowtail rockfish females sampled during the time series were 531 mm during the 1986 and 1987 reproductive seasons, but neither produced the largest broods. Even though our time series included mostly smaller female Yellowtail rockfish, the high expected fecundity for a female at L_{inf} of 521 mm in 2017 of nearly 2.38 million larvae is not entirely out of reason for the species. For example, a Yellowtail rockfish collected to the north off Washington State in 1988 had a brood of 1.99 million larvae, but maternal size was not reported for that fish (Eldridge & Jarvis 1995). Fecundity of female Yellowtail rockfish at the largest

sizes should be investigated further, especially given that Yellowtail rockfish and Widow rockfish, as with many other species in this genus, often have greater asymptotic lengths in more northern waters compared to individuals at our study site in central California (Gertseva et al. 2017, Stephens & Taylor 2018). Even with the high uncertainty for the largest Yellowtail rockfish females, fecundity of mean-sized females in our study (the data most supporting the model) still varied by up to 104% from a low to high year, providing strong evidence for high variation in brood size by year. The expected brood sizes of large females for the other three species were all within the size range of observations in our study. Increases in brood size of up to 124% were also observed from lowest to highest years for large females of the single brooding Widow Rockfish, which provided additional support that inter-annual brood fecundity variability (equivalent to annual fecundity in these species) is very high among single brooding rockfish species.

Chilipepper and Bocaccio, the two species capable of multiple broods, had relatively less inter-annual variability in brood size compared to the single brooding Yellowtail rockfish and Widow rockfish. The difference in variation between single and multiple brooding species was interesting because it suggested a different response to environmental variability. Single brooding species had greater variation in brood size in years of poor or good ocean conditions, reflecting strong variation in annual offspring production because the single brood was equal to annual fecundity for those species. However, for species with a multiple brooding reproductive strategy, annual fecundity is a function of the number of broods per year and brood

size. We found that brood size varied less year to year for the multiple brooding species, but it was likely that even greater annual fecundity variability existed for Chilipepper and Bocaccio through the production of additional broods in "good" years rather than regulation of brood fecundity alone. Unfortunately, we did not have data on the number of broods produced by individuals over the entire time-series. Single broods (instead of multiple broods) were historically typical of Bocaccio and Chilipepper in central California (Wyllie-Echeverria 1987) even though conspecifics produced multiple broods to the south (MacGregor 1970, Love et al. 2002, Beyer et al. 2015). Also, multiple brooding has become more common in these species at Cordell Bank, especially among large females, since 2013 (Beyer et al. 2015, Lefebvre et al. 2018).

The number of broods produced each season by individuals of species capable of multiple broods is likely related to environmental conditions and may vary greatly over time. Up to three broods a reproductive season are possible in wild Chilipepper and Bocaccio (Ralston & MacFarlane 2010, Lefebvre et al. 2018) and up to five broods are possible for the multiple brooding Rosy rockfish (*Sebastes rosaceus*) under optimal feeding conditions in the laboratory (Beyer et al. 2021). The size of secondary broods are similar to primary broods, meaning that annual fecundity is nearly doubled (or tripled) by producing two (or three) broods a year (Beyer et al. 2015, 2021). Thus, it is likely that species with a multiple brooding reproductive strategy have nearly as great, or even greater inter-annual variability of annual fecundity because of the possibility for multiple broods when conditions allow.

It was interesting that even though weaker population-level maternal length effects on brood fecundity are noted for Chilipepper and Bocaccio (Dick et al. 2017), and were also found in this study, multiple broods are more common in larger compared to smaller females (Beyer et al. 2015, Lefebvre et al. 2018). The effect of a larger maternal size on annual- rather than brood- fecundity is likely to be much stronger if secondary broods are more common in larger females. This is an important consideration for any species with an indeterminate fecundity strategy, where the number of broods or clutches possible at the start of the reproductive season is unknown and is possibly dependent on maternal size and energy reserves. A maternal size effect on multiple brooding influences the annual fecundity-length relationships (Fitzhugh et al. 2012, McBride et al. 2015, Marshall, Barneche, et al. 2021). The quantification of multiple broods, and therefore annual fecundity, remains confounded by spatial and temporal variability in the frequency of which females produce multiple broods (Lefebvre et al. 2018). In a laboratory study of Rosy rockfish, the ability to account for known contributions of multiple broods over a reproductive season resulted in a much stronger maternal size effect on annual fecundity than previously observed for brood fecundity for that species (Beyer et al. 2021). The potential significance of size- and energy- dependent multiple brooding to estimates of temporal variability of annual fecundity remain critically important to quantifying the reproductive potential of populations and represents an important area of focus for future investigation. In summary, although we were not entirely able to capture the full extent of variation in the annual fecundity of the multiple brooding

species, we showed how brood size varied in relation to maternal length, body condition, and the environment as a first step in understanding how total offspring production (brood size and the number of broods per season) varies temporally.

4.2 A weak influence of maternal age

Even though maternal age influences larval quality in some rockfishes (Berkeley, Chapman, et al. 2004, Sogard, Berkeley, et al. 2008), we did not find evidence for maternal age effects on fecundity in our study. We found no significant effect of maternal age on the unexplained variance of the full fecundity models for all four species. However, we also did not find significant declines in fecundity with age, suggesting that large females are capable of maintaining fecundity while also provisioning offspring with greater energy reserves, or that the species in our study did not exhibit strong maternal age effects on larval quality (Stafford et al. 2014). Maternal age effects on larval quality are evident in the more nearshore, Black rockfish, *Sebastes melanops* (Berkeley, Chapman, et al. 2004). The study of both length and age effects is complicated because of the tight correlation between these variables. However, age could have important, independent effects on reproduction, especially if spawning experience contributes to the timing of reproduction (Stafford et al. 2014), reproductive success (Berkeley, Chapman, et al. 2004), or which females contribute to egg production (Conrath & Hulson 2021). This result also suggests that there is no evidence of senescence in fecundity in the rockfishes evaluated in this

study and ages observed. This is consistent with past research on rockfishes and other marine fishes, where senescence is not widely observed in marine fishes that are iteroparous and have long-life spans (Sauer et al. 2021).

4.3 Reproductive plasticity in response to variable ocean conditions

Females in better body condition produced larger size broods compared to females with poor body condition for all four species. This finding supported our hypothesis that females with greater energy reserves increase investment in the number of offspring and that variation in brood size is part of a life history strategy to cope with high variability in environmental conditions experienced over a lifetime. Energy reserves of rockfishes of the central CCE cycle annually in response to strong seasonality in primary production and fluctuations in the food supply. Fat reserves are accumulated through the spring and summer and peak in the fall when oocytes are developing and prior to winter fertilization and gestation of larvae (Guillemot et al. 1985). We used the Fulton's K index of body condition (K), measured at the time of capture, as a proxy for energy reserves. The measure of K did not include the weight of the gonad, so it was a measure of somatic "fatness" in relation to a cubic measure of length. Since females were captured in the fall and winter and were already developing and gestating embryos, our measure of K is a relative measure of body condition at the time of reproduction. While this is not a direct measure of energy invested in reproduction, it was easily approximated for samples through the entire

time series and was strongly correlated with variation in brood size. The inclusion of a measure of body condition, even at the time of capture during reproduction, significantly improved model fit and predictive estimates of brood fecundity beyond length alone. Because of this, the collection of body condition data (length and weight) is recommended for future study of reproductive plasticity of marine fishes. Our results for wild populations for four *Sebastes* species further emphasized the importance of energy reserves to egg production and inter-annual fecundity variability and corroborated a laboratory study that directly tested the effects of body condition on brood size and annual fecundity of Rosy rockfish finding that females fed higher rations had much higher annual fecundity compared to females fed low rations (Beyer et al. 2021). The strong influence of energy reserves on brood sizes of rockfishes is likely related to a capital breeding strategy, where females store energy reserves when conditions for feeding and energy accumulation are favorable in the spring and summer and reproduce later in the year when feeding conditions are less favorable, but prior to the return of favorable conditions for offspring in the spring (McBride et al. 2015, Varpe 2017). This means that in years with below average feeding conditions, females will not acquire as much energy to allocate to reproduction and will reduce reproductive output. But also means that females are able to take advantage of intermittent favorable conditions to greatly increase energetic investment in reproduction.

Additional environmental effects on inter-annual variation in brood size, beyond the influence on maternal body condition, were less clear in our study. The

models that included an index of ocean conditions in the late summer and early fall during early oocyte development generally did not significantly increase predictive power beyond the uncertainty generated by Monte Carlo simulation error (i.e., +/- SE of the elpd$_{LOO}$). The exception was Chilipepper, where the full model that included the NPGO had the greatest predictive power. In the other species, adding the NPGO index to either the base model of length or to a model including length and body condition did not greatly change the model fit or predictive power. However, the environmental effect appeared to differ substantially by fish size, with large fish far more responsive than small fish to favorable environmental conditions. Fecundity variability was greatest among large females. Larger females presumably have a greater capacity for storing energy as lipids in the fat storage tissues of the liver, muscle, and mesenteric fat surrounding the visceral organs compared to smaller females and then using that stored fat to increase reproductive output (MacFarlane et al. 1993, Norton & MacFarlane 1995). Because of this, large females may be more responsive to changes in the environment, which affect food supply and metabolism, and were not fully captured by a measure of body condition at the time of capture. The capacity for fat storage likely interacts with other life history traits, such as growth. Rockfish have indeterminate growth that slows but continues after maturation. Smaller rockfishes are still growing fairly rapidly at the size where 50% are mature and therefore are expected to allocate energy differently between growth and reproduction compared to large females that are near the asymptotic size. Furthermore, ontogenetic shifts in diet will contribute to a change in the

bioenergetics, where larger females can feed on higher trophic level prey items with potentially greater energetic components (i.e., krill vs fish) and fluctuations in the prey of small and large females may differ through time. These effects, in combination with the far greater total fecundity capacity of large females, suggest that large females are capable of dramatic increases in population level productivity during favorable conditions as part of a life history strategy to cope with high inter-annual variability in ocean conditions.

We used the summer and fall NPGO mean as a proxy for ocean primary productivity and feeding conditions, but the dynamics of energy flow to upper-level predators is complex and likely not captured fully by a large-scale ocean productivity index. Recent studies increasingly recognize that the complex nature of California Current circulation patterns poses challenges with respect to the practical utility of basin-scale climate indicators to relate meaningfully to indicators of biological productivity (Crawford et al. 2018). This is likely a reason for why our models of NPGO and length did not provide much of an increase in explanatory power over the models with length alone. Because of this, measures of body condition may better reflect important variation in the environmental and biological conditions experienced by individuals and at local spatial scales (including density dependent factors that affect per-capita feeding success), rather than broad-scaled, basin-wide ocean condition indices. Future investigations should continue to explore the role of the environment on bioenergetics and reproductive plasticity, especially where it is possible to measure localized measures of environmental variability and other factors

affecting the feeding success and energy reserves of individuals. Even so, the weak positive trends for large fish observed in our study provide initial support for the importance of pre-spawning environmental conditions to inter-annual variability in size-dependent fecundity and should be investigated further. Other periods of the year, such as winter conditions when rockfishes gestate larvae and release broods, could also be explored.

Interestingly, some ocean conditions seemed to affect multiple species similarly, whereas other conditions did not. For example, the late spring transition to upwelling in the central region of the CCE in 2005 had broad negative ecological consequences across trophic levels, including record low abundance levels of juvenile rockfish and other groundfish (Barth et al. 2007, Ralston et al. 2015). Those conditions resulted in generally poor egg production for the three species we observed in 2005 (Bocaccio were not sampled in 2005). Brood fecundity for all sizes of Widow rockfish and for small Chilipepper was lowest in 2005 in the time series and 2005 was also poor for Yellowtail rockfish. Other years of low fecundity in the time series included 2015 and 2018, which were also the years with the lowest values of the NPGO in our time series (indicating poor ocean productivity). Conversely, there was less consistency among species for the years of highest fecundity, although this was likely due, in part, to differences in sampling effort. Even though some environmental signals are likely to appear across multiple species and trophic-levels, it is also expected that the effect of the environment will differ among species in consideration of habitat, feeding ecology, and bioenergetics due to the complexities of how energy

flows through the food web, differences in diets, and the interactive effects of temperature on metabolic rates. For example, adult Yellowtail and Widow rockfish feed at a lower trophic level on small pelagic prey, such as krill, gelatinous zooplankton and juvenile fishes (Lee & Sampson 2009, Chiu et al. 2021). Individuals of these two species could be expected to more closely track changes in primary ocean productivity. Adult Chilipepper and Bocaccio feed at a higher trophic level, including a mix of small fishes, krill and squids, and large Bocaccio feed on progressively larger fishes such as other rockfishes, hake and sablefish (Love et al. 2002). Their responses are likely offset from environmental ocean conditions and more dependent on higher trophic-level predator and prey dynamics and the influence of temperatures at deeper depth.

Other environmental variables not considered here may also influence energy reserves and reproductive output. For example, oxygen metabolic demand of pregnant females during the final stage of gestation is over 80% the baseline metabolic rate for Yellowtail rockfish (Hopkins et al. 1995). This has the potential to influence reproduction because cooler subarctic source waters typically contain more oxygen than subtropical waters, such that oxygen levels at depth can vary considerably from year to year in the CCE (Meinvielle & Johnson 2013, Schroeder et al. 2019). Reduced oxygen saturation could influence survival and the reproductive success of females gestating embryos. Density dependence will also affect the per-capita food availability and competition for food resources, affecting consumption rates and energy reserves. These complex interactions between temperature, oxygen, other

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habitat variables, and demographic and social factors are clearly plausible drivers of the observed patterns of variable reproductive output observed in this analysis and important to future studies exploring mechanisms of changes in population productivity. Regardless, it is clear that reproductive effort varies strongly by year in these species.

4.4 Implications for conservation and management

Knowing that reproductive traits are plastic in response to a change in environmental conditions is important for assessing population reproductive potential, a key component of reproductive success and population persistence, and for predicting population dynamics with climate change, at least in the near term (Lowerre-Barbieri et al. 2017). Furthermore, fisheries management reference points and harvest rates are based on sustaining specific levels of spawning potential (Goodyear 1993, Methot Jr. & Wetzel 2013). These estimates of spawning potential historically have not considered the influence of the environment on reproduction due to a lack of data and knowledge. While maternal size effects on fecundity are accounted for in the estimate of spawning potential for West Coast rockfish, the possibility for multiple brooding and phenotypic plasticity in reproductive effort as ocean conditions change is currently not. Not accounting for these effects could result in misleading estimates of spawning potential as the ocean environment changes.

In our case study of rockfishes of the CCE, females are adapted to current patterns of high environmental variability through the evolution of long lifespans and reproductive traits of late maturation, iteroparity, and high fecundity. Here, we add reproductive plasticity as part of that life strategy to cope with strong environmental variability. The plasticity of brood size in response to changes in the ocean environment is likely even stronger when considering the contributions of multiple broods to variation in annual offspring production. An important consideration for management is that reproductive plasticity in response to a change in environmental conditions comes with the possibility of prolonged recruitment failure and population declines if poor conditions for both reproduction and larval survival persist for many years. Conversely, this behavior is assumed adaptive to take advantage of intermittent, favorable conditions and to reserve energy to survive unfavorable conditions to reproduce again when favorable conditions return (Winemiller & Rose 1992, Canale & Henry 2010). In turn, females can "take advantage" of favorable conditions by greatly increasing reproductive output.

Anthropogenic climate change is already influencing environmental conditions experienced by rockfishes in the CCE by an increased frequency of warm water, low productivity climate events (Cai et al. 2014, Di Lorenzo & Mantua 2016). As a result, there may be an overall decline in female energy reserves and the reproductive potential of *Sebastes* populations if warm, low productivity conditions persist. However, the longevity of rockfishes provides an important storage effect (Warner & Chesson 1985), in which individuals can outlive poor environmental conditions and

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take advantage of favorable conditions when they occur. Episodic recruitment success of strong year classes will likely continue in part due to the increased reproductive potential under favorable conditions (Tolimieri & Levin 2005, Bakun et al. 2015). For rockfishes of the CCE, management has led to population recoveries from historic lows in the 1990s and early 2000s, but even conservative levels of fishing mortality will greatly reduce the mean number of years a female reproduces over a lifetime relative to an unfished population and also the size and age composition of spawning females, an important consideration for management (Hixon et al. 2014). The longevity of *Sebastes* spp. in general is presumed essential for maintaining populations over extended periods of poor environmental conditions. Considering the combined anthropogenic stressors of climate change and exploitation, it remains largely unknown how the longer-term directional effects of global change on temperature, oxygen levels, primary and secondary productivity, and the intensity and persistence of such events will affect reproduction, particularly under the assumption of continued fisheries impacts on population size and age structure that reduce the numbers of old, large females in the population (Barnett et al. 2017). It should be expected that these cumulative effects are likely to lead to changes in population reproductive productivity.

5.0 Conclusion

In conclusion, our study provided new insight into the reproductive ecology of rockfishes living in the CCE. The reproductive strategies of moderate- to long- lived rockfishes includes high inter-annual variation in offspring production of individuals in response to prevailing ocean conditions. Beyond the influence of maternal length on offspring production, maternal body condition strongly influenced brood sizes. We also found some evidence that the ocean environment and feeding conditions of females during early egg development influenced offspring production, especially for large females. Large females had much greater absolute inter-annual variability, and brood size was more strongly influenced by variation in the summer and fall NPGO conditions compared to small females. Our study also highlighted differences in the strength of inter-annual brood size variability between species with different reproductive strategies. For species capable of multiple broods, inter-annual fecundity variability may be more influenced by environmental influence on the number of annual broods rather than variation in brood size. More work is needed to understand the full extent of inter-annual fecundity variation in these species. Overall, rockfishes are a case study for species well adapted to cope with strong seasonal, inter-annual, and decadal environmental variability. We find phenotypic plasticity of reproductive effort is part of this life history strategy to cope with extended periods of unfavorable conditions, while allowing females to rapidly increase reproductive output when intermittent favorable conditions arise, especially for large females. Importantly, shifts in the reproductive potential of the population are important to account for in

order to achieve and to maintain sustainable fisheries as the ocean environment is increasingly influenced by the effects of global climate change.

Acknowledgements

Tables

Table 2.1 The number of fecundity samples collected at Cordell Bank in central California listed by species and reproductive season (Year). Mean fork length (mm) and range of length in parentheses. References are published and unpublished datasets used to develop the time series. Note, years with only a single fecundity sample were omitted from the statistical analyses.

| Year | Sample size (Mean fork length (mm): range) | | | | Reference |
	Yellowtail Rockfish	Widow Rockfish	Chilipepper	Bocaccio	
1986	61 (437: 331- 531)		34 (422: 336- 495)	32 (652: 542- 790)	Eldridge and Jarvis (1995); Eldridge and Jarvis (unpublished)
1987	64 (405: 331- 531)	51 (455: 376- 500)		47 (562: 433- 771)	
1988	28 (425: 360- 502)	24 (434: 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: 3 70- 505)		
2006	1 (450)				Stafford *et al.* (2014)
2007		4 (444: 419- 454)	1 (460)		

Year					
2009	21 (412: 373- 480)		31 (429: 350- 475)		Beyer *et al.* (2015); Lefebvre *et al.* (2019); current study
2010	9 (404: 380- 443)	1 (400)	24 (432: 350- 469)	1 (779)	
2011	30 (409: 363- 463)		31 (403: 90- 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	22 (416: 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	53 (394: 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	779	155	588	137	

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Table 2.2 The greatest variation in expected brood fecundity between the year of lowest and highest fecundity in the time series for each species among large, small, and mean-sized reproducing females. Large females were defined as females at the asymptotic length (L_{inf}) for the species from von Bertalanffy growth functions. Small females were defined as the length in which 50% of females in the population are mature (L_{50}). Length at mean size (L_{mean}) was the mean length of females in the study. Reference lengths are ordered from largest to smallest.

Species	Length type	Fork length (mm)	Lowest Expected brood fecundity (Year)	Highest Expected brood fecundity (Year)	Difference Number of larvae
Yellowtail Rockfish	L_{inf}	521	774,020 (2018)	2,345,686 (2017)	1,571,666
	L_{50}	425	291,879 (2018)	620,596 (2014)	328,717
	L_{mean}	412	251,533 (2018)	514,072 (2014)	262,539
Widow Rockfish	L_{inf}	503	534,899 (2005)	1,199,962 (1987)	665,063
	L_{mean}	436	279,920 (2005)	652,098 (2014)	372,178
	L_{50}	310	59,704 (2005)	165,969 (2014)	106,265
Chilipepper	L_{inf}	481	232,207 (2018)	379,791 (2010)	147,584
	L_{mean}	427	155,550 (2015)	222,550 (2010)	67,000
	L_{50}	257	22,303 (2005)	44,454 (2016)	22,151
Bocaccio	L_{inf}	677	1,203,874 (2015)	1,480,410 (2016)	276,536
	L_{mean}	586	794,583 (2015)	898,317 (2016)	103,734
	L_{50}	377	186,059 (2017)	223,249 (2015)	37,190

Table 2.3 Comparison of fecundity models. The base model (model 1) was used to quantify inter-annual variability and included only log length as the explanatory variable. Separately, the potential predictor variables of body condition (K, model 2) and environmental conditions (summer/fall mean of the NPGO, model 3) were considered to explore factors associated with reproductive plasticity. Last, all predictors were modeled together in the full model (model 4). We used the leave-one-out (LOO) cross-validation approach to compare models (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 scored a zero ($\Delta elpd_{LOO}$) with standard error of the Monte Carlo simulation (SE). Best fit model in bold. The Bayesian coefficient of determination (Bayes R^2) measured the variance explained by the model.

Species	Model	n	Yrs	Bayes R^2	Δ $elpd_{LOO}$	SE
Yellowtail Rockfish	1. log length	778	21	0.755	-75.3	12.9
	2. log length + K	**778**	**21**	**0.799**	**0**	**0**
	3. log length + NPGO	778	21	0.756	-74.5	12.9
	4. log length + K + NPGO	778	21	0.799	0	0.7*
Widow Rockfish	1. log length	153	11	0.758	-7.2	5.5
	2. log length + K	**153**	**11**	**0.781**	**0**	**0**
	3. log length + NPGO	153	11	0.759	-8.2	5.9
	4. log length + K + NPGO	153	11	0.783	-0.8	0.9*
Chilipepper	1. log length	587	13	0.717	-33.0	9.8
	2. log length + K	587	13	0.747	-0.1	1.1*
	3. log length + NPGO	587	13	0.718	-33.2	9.9
	4. log length + K + NPGO	**587**	**13**	**0.748**	**0**	**0**
Bocaccio	1. log length	135	8	0.824	-12.3	4.5
	2. log length + K	**135**	**8**	**0.854**	**0**	**0**
	3. log length + NPGO	135	8	0.825	-13.5	4.3
	4. log length + K + NPGO	135	8	0.854	-1.0	0.8

*No statistical difference from the best fit model

Figures
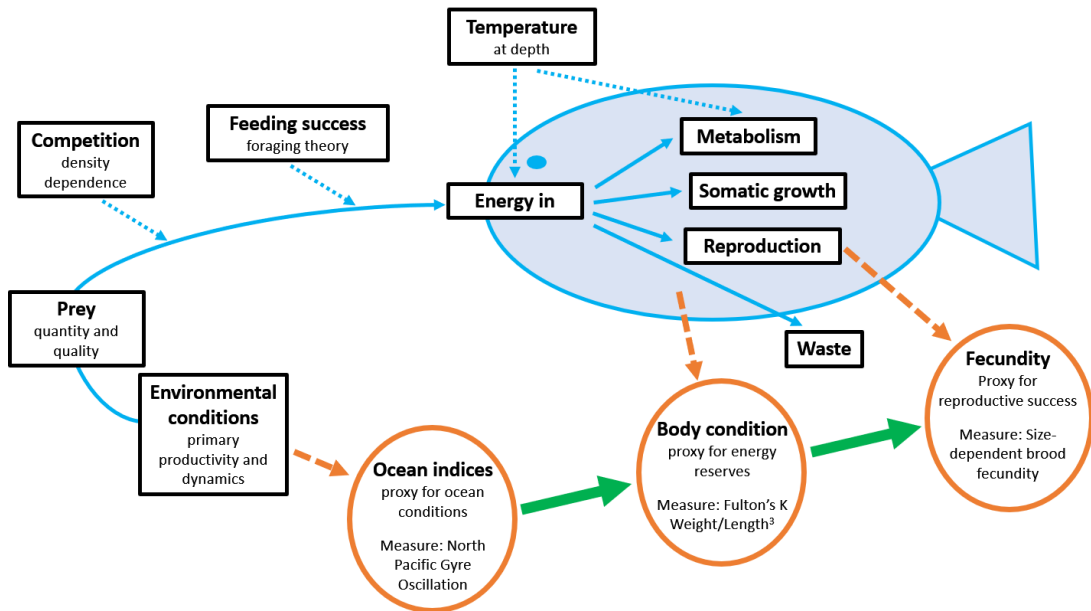
Figure 2.1 Conceptual diagram of how the environment influences maternal energy reserves and reproduction. Physical conditions in the ocean affect primary and secondary productivity and the availability of prey. Potential energy gained by feeding (solid blue line) is mediated by density dependent factors and foraging success (blue, short-dashed arrows). Temperature influences physiological processes, which include consumption and metabolic rates. Assimilated energy is then allocated to fat stores, growth, and reproduction. We use imperfect observations of these processes (long-dashed arrows pointing to orange circles) to understand variation in brood size in response to changes in ocean environmental conditions and maternal energy reserves (green arrows).
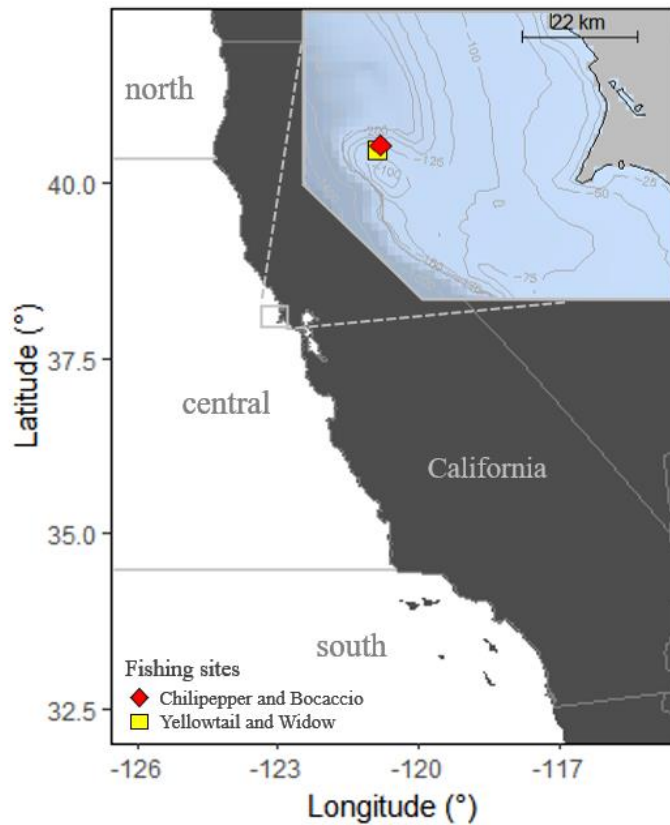
Figure 2.2 Map of the study area and fishing locations. Rockfish were sampled by hook-and-line at Cordell Bank, a seamount located approximately 25km off the coast of Central California to focus on temporal variation in reproduction. Inset shows Cordell Bank in the central region of the California Current Ecosystem. Symbols are fishing sites for Yellowtail and Widow Rockfish (yellow square) collected at shallower depth and Chilipepper and Bocaccio (red diamond) collected at deeper depth.
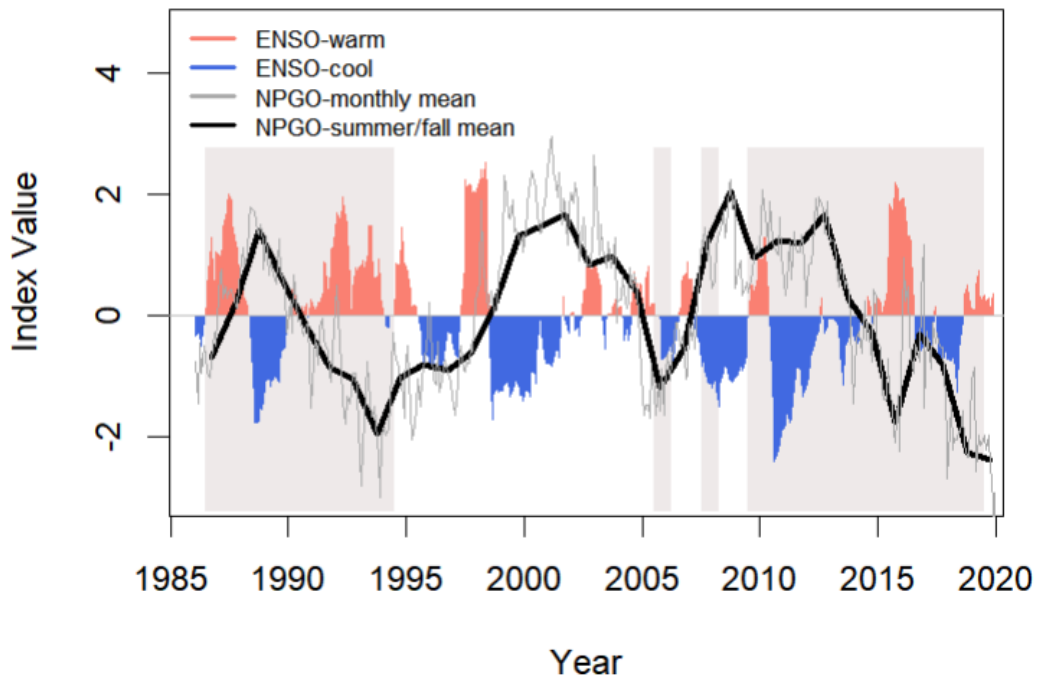
Figure 2.3 Temporal variation in environmental conditions of the California Current Ecosystem from 1985 to 2020. The years with fecundity data are highlighted to show contrasting environmental conditions in the time series (cream-colored bars). We used the mean summer and fall ocean conditions, described by the North Pacific Gyre Oscillation (NPGO, black line) as an environmental predictor of fecundity. Here, we compare the summer/fall NPGO conditions to monthly values of the NPGO (light gray line) and to the warm and cool regimes in the California Current shown by monthly means of the multivariate El Niño Southern Oscillation index, ENSO (pink is warmer El Niño conditions and blue is cooler La Niña conditions). Positive values of the NPGO broadly correlate with increased ocean primary productivity and better conditions for rockfish.
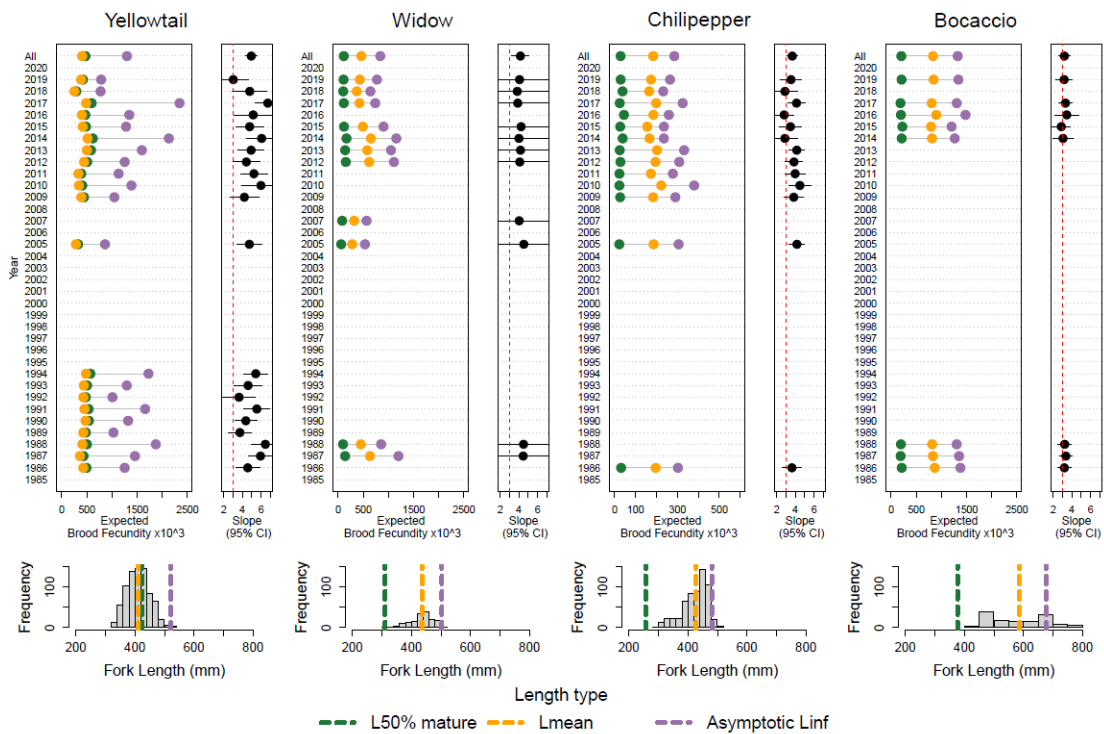
Figure 2.4 Quantification of inter-annual variation in brood sizes, especially for large females (results of the base model, model 1). Dot charts show expected brood fecundity at the lengths of reference (colored left plots) and the strength of the maternal length effect (i.e., the slope of the fecundity-length relationship) by year for the four rockfish species (right plots). A slope greater than $b = 3$ (vertical, red-dashed line) generally indicates the disproportionate production of larvae by large compared to small females (i.e., more eggs per gram of spawning biomass). Length-frequency histograms (bottom) show the range of female lengths in the study compared to the population-level reference lengths (vertical, colored, dashed lines). Length types were the mean length of females in the study (L_{mean}, orange), the length where 50% of females were mature (L_{50}, green), and asymptotic length (L_{inf}, purple) estimated from the von Bertalanffy growth function. Note the smaller range in x axis of expected brood fecundity for Chilipepper, which reflects comparatively smaller brood sizes in that species

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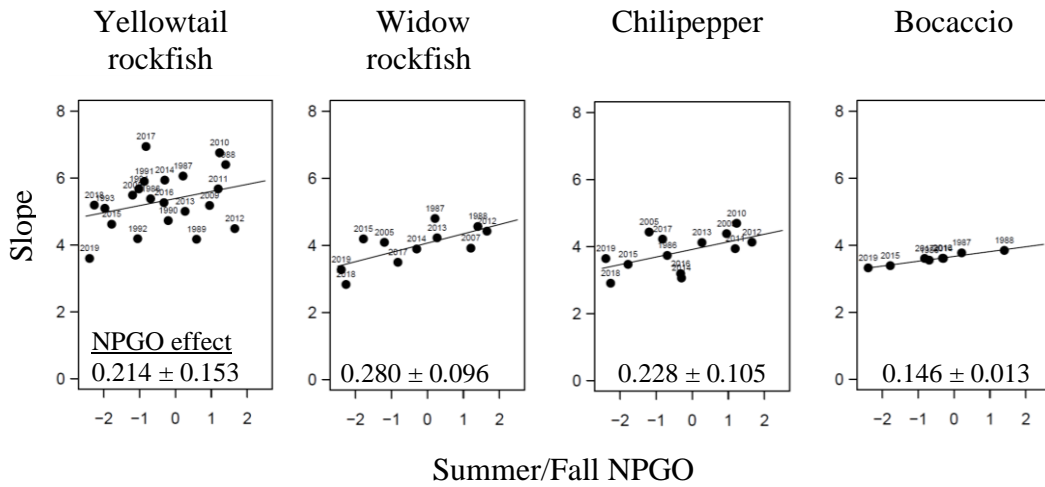
Figure 2.5 When considering the full model (model 4), which included maternal length, body condition (*K*), and the environment (NPGO) as predictors of brood fecundity, the effect of maternal length on brood size (slope of the fecundity-length relationship; Slope) varied by year and increased with more favorable summer and fall feeding conditions in the California Current (Summer/Fall NPGO). The weak, but positive correlation of slopes and ocean productivity meant that the difference in the relative offspring production of large compared to small females (i.e., more eggs per gram of female biomass) was much stronger when ocean conditions were more favorable (i.e., a slope much greater than 3.0). The maternal length effect was less when ocean conditions were poor (i.e., a slope closer to 3.0). Effect size (±SE) for the NPGO shown (i.e., the slope of slopes). Greater values of the NPGO correlate with increased ocean primary productivity and better conditions for rockfish.

Figure 2.6 The full model (model 4) included the effects of maternal length, body condition, and environmental conditions on brood size. The conditional influence of the environment (Summer/Fall NPGO) on expected brood size was strongest for large females (L_{inf}, purple lines) compared to small (L_{50}, green lines) or mean-sized females (L_{mean}, orange lines). This was both in terms of the influence of the NPGO on expected brood fecundity (each graph), and the influence of maternal energy reserves (difference by row). Expected brood size is shown for females with poor body condition (bottom row), average body condition (middle row), and good body condition (top row). Differences in body condition were defined as K at the mean and ± 3 standard deviations for the mean-centered and scaled data. Shading is the 95% credible interval for the expected brood size at each reference length. Corresponding unscaled K and the reference lengths are shown for each species.

Figure 2.6
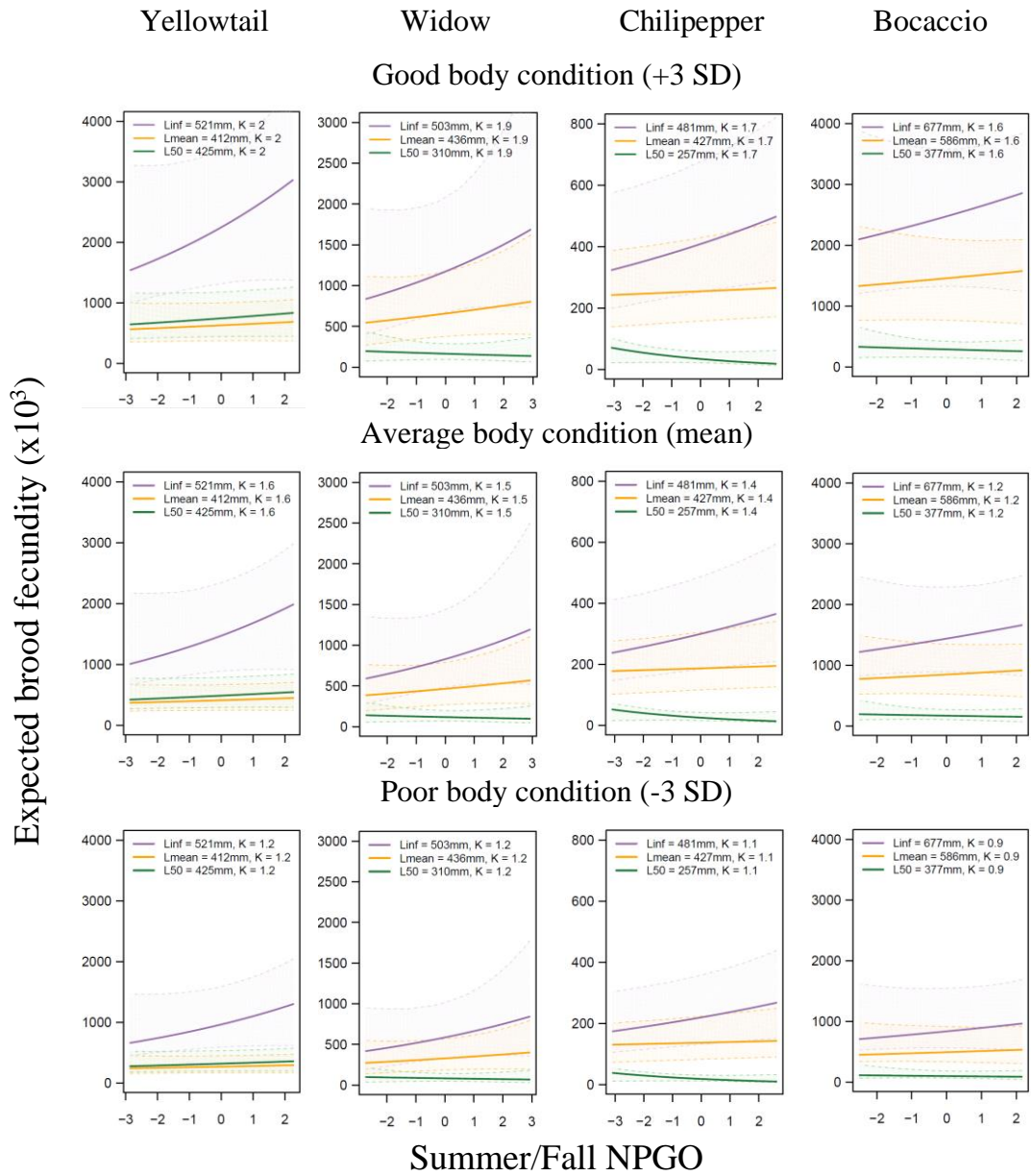
Figure 2.7 We did not find a correlation of maternal age with the unexplained, residual error of the full fecundity model (model 4). We checked for an influence of maternal age because maternal age is known to influence larval quality in some species of rockfish and larval quality could trade-off with fecundity. Note, ages were not available for all females. Model residuals are shown for the subset of females with age data: Yellowtail (777 of 778), Widow (98 of 153), Chilipepper (571 of 587) Bocaccio (99 of 135).

Chapter 3: Spatial variation of reproductive traits adaptive to cope with latitudinal differences in ocean productivity, seasonality, and temperature for rockfishes (*Sebastes* spp.) of the California Current Ecosystem

Abstract

Inter- and intra-specific spatial variation in life history traits is expected for species broadly distributed by latitude to cope with different environmental conditions. Understanding how and why spatial variation of life history traits occurs improves our ability to predict population dynamics and to better understand phenotypic plasticity in reproductive traits. Here, we use rockfishes (*Sebastes* spp.) of the California Current Ecosystem as a case study to understand the causes and consequences of latitudinal variation of reproductive traits. Reproduction of the live-bearing rockfishes occurs once annually at higher latitudes (i.e., a single brood strategy) but increases in frequency for a subset of species (and individuals of those species) at lower latitudes (i.e., a more plastic multiple brooding strategy). Why multiple brooding occurs in the south is generally unknown but is likely related to poorer ocean productivity, weaker seasonality, and warmer temperatures in the southern region. Not knowing why spatial variation occurs hampers efforts to accurately assess population reproductive potential and to understand how population productivity may shift in response to regional conditions and climate change. To address this, we developed a state-dependent life history model using stochastic

dynamic programing and bioenergetics to better understand the influence of temperature, seasonality, and food on adaptive reproductive strategies for Rosy rockfish (*Sebastes rosaceus*) of the California Current. We find that energy dynamics, which are influenced by the environment, greatly affect adaptive reproductive strategies. Strong seasonality of the environment, which influences when food is available throughout the year, favored a reproductive strategy where females reproduced only once annually to ensure enough energetic reserves to survive an annual period of food scarcity in the late winter causing net energetic losses. Moderate and weak seasonality in the food supply favored a multiple brooding strategy of smaller-sized broods. But multiple broods per year were only expected once females had reached a maximum size for their environment. This was due to a reallocation of energy from growth to additional annual reproductive output in the form of secondary broods. The amount of mean food in the environment strongly influenced growth, maximum female size, and thus, reproductive output. Females in high food environments were expected to grow large, produce larger-sized broods, and therefore had much greater expected lifetime fecundity. Females in poor food resource environments were expected to stop growing earlier in life and ceased growth at a smaller expected maximum size. Differences in temperature, which reflected different temperatures between the southern and central region of the California Current, slightly influenced growth. This was because temperature influenced monthly consumption and metabolic rates. Because of this, females in the warmer, southern temperature regime were favored to produce more broods outside

of a winter peak reproductive season compared to females in the cooler, central temperature regime. Our model of adaptive life history strategies for different environmental conditions of the California Current suggested that multiple brooding and a longer reproductive season of rockfish in the south is likely adaptive to maximize reproductive output in a region with weaker seasonality, warmer temperature, and lower food resources compared to the north. But females in in the south are expected to be smaller, have smaller-sized broods, and thus be less productive overall, even with an expected greater frequency of reproduction. Conversely, larger females capable of much larger-sized broods, a single annual brood strategy, and a shorter winter reproductive season are expected for females in the north. This is because of better food resources resulting in larger fish size, but also the need to store energy to survive an annual period of net energetic losses due to strong seasonality in the north. Our models offer a bio-energetic and state-dependent hypothesis for why the frequency of reproduction, reproductive output, and growth patterns vary by latitude for rockfishes of the California Current Ecosystem. These models can be used to better predict spatiotemporal variation in the life history traits of rockfish and other marine fishes, and the consequences for population dynamics in terms of expected shifts in population reproductive potential as environmental conditions change.

1.0 Introduction

Spatial variation in life history traits is expected for species that have a broad distribution by latitude to cope with different environmental conditions, such as latitudinal variation in temperature and seasonality in food availability (Conover 1992, Schultz & Conover 1997, Varpe 2017). Spatial variation in life history traits may be caused by phenotypic plasticity as part of a life history strategy to deal with different selective pressures imposed by spatial variation in environmental conditions and to maximize overall reproductive output (Crozier & Hutchings 2014, Merilä & Hendry 2014, Hendry 2016). Marine fishes commonly have broad geographic distributions by latitude, but often little is known about how and why life history traits vary spatially in response to different environmental conditions. For example, Eastern Boundary Upwelling Ecosystems (EBUEs) are some of the world's most productive ocean ecosystems that support a diversity of marine life and fisheries (Chavez & Messié 2009, Bakun et al. 2015). Each spans a range of latitudes. Because of this, fish in these ecosystems must cope with ocean conditions that vary through space in temperature, ocean biological productivity, and seasonality. Variation in physical and biological conditions influences fish bioenergetics and also when food is available throughout the year. Seasonality in primary productivity (influencing prey availability) and temperature can vary strongly by latitude. This variation influences how females acquire energy and allocate stored energy to growth and reproduction (Conover 1992, Ganias et al. 2015, McBride et al. 2015). Strong seasonality and cooler temperatures, which generally occur at higher latitudes, are often correlated

with a capital breeding strategy where females acquire energy when feeding conditions are good, store energy, and then use stored energy later to reproduce (McBride et al. 2015). A capital breeding strategy is associated with a determinate fecundity strategy and a lesser frequency of reproduction. Weaker seasonality and warmer temperatures, which generally occur at lower latitudes, are often correlated with an income breeding strategy (McBride et al. 2015). An income breeding strategy is where females take advantage of the current feeding conditions and more quickly convert net energy gains into eggs. This is often associated with an indeterminate fecundity strategy and a greater frequency of reproduction. Although these trends in reproductive strategy occur broadly across marine fishes and can vary by latitude (Ganias 2013, Ganias et al. 2015, McBride et al. 2015), less is known about intra-specific variation for species where individuals are broadly distributed by latitude and in environments that favor different reproductive strategies (Schultz & Conover 1997, Ganias 2013, Wuenschel et al. 2013). Understanding the causes and consequences for why intra-specific variation in life history traits occurs spatially helps us to better understand how organisms with broad distributions by latitude cope with a variety of environmental conditions (Williams et al. 2017). Furthermore, it is important to accurately account for spatial variation in life history traits that result in differences in reproductive potential across the distribution. These differences affect our understanding of population dynamics. Therefore, knowing how and why reproductive traits vary by latitude improves our knowledge of population dynamics, and predictions for how species with broad distributions that exhibit phenotypic

plasticity of life history traits may cope with life in different environmental conditions and future environmental change.

In temperate ocean upwelling ecosystems, the environmental conditions that differ by latitude and are most likely to influence variation in life history traits are temperature, mean food, and seasonality in the food supply (Parrish et al. 1981, Kwiecien et al. 2022). Ocean temperatures differ by latitude and are an important abiotic driver of biological and physiological processes. This is especially true for ectotherm marine fishes, where bioenergetics are strongly influenced by water temperature (Johnston & Dunn 1987, Gillooly et al. 2001, Harvey 2009). Furthermore, ocean and global temperatures are increasing and can negatively impact physiology and reproduction (Deutsch et al. 2015, Alix et al. 2020). However, within physiological tolerance limits the influence of temperature can be offset by food resources to overcome the increased energetic demands of warmer environments. The high biological productivity and upwelling conditions of EBUEs may play a role in offsetting the negative effects of globally rising temperatures. High biological productivity in these systems is due, in part, to the timing and strength of seasonal upwelling events and other physical factors that promote the conditions favorable for photosynthesis by primary producers (Hickey 1979). Annual and seasonal variation in these conditions subsequently influence the energy dynamics of the food web from the bottom up (Thompson et al. 2012). Stronger seasonality at higher latitudes in temperate ocean upwelling ecosystems can result in a greater amplitude in the seasonal maxima and minima of primary productivity compared to regions with

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weaker seasonality (Parrish et al. 1981, Checkley & Barth 2009, Kwiecien et al. 2022). The environmental variables of temperature, seasonality in primary production, and mean differences in ocean productivity all influence the bioenergetics of higher trophic-level marine fishes by influencing feeding rates and energy dynamics (Thompson et al. 2012). Therefore, variation of these environmental variables by latitude is likely to create different selective pressures, which favor different reproductive strategies and cause spatial variation in reproductive traits when phenotypic plasticity exists (Stearns 1992).

We use rockfishes (*Sebastes* spp.) of the California Current Ecosystem (CCE) as a case study to better understand the influence of the environment on spatial variation in reproductive traits. The CCE is a highly productive EBUE that supports a diversity of fish and fisheries (Hickey 1979, Chavez & Messié 2009, Checkley & Barth 2009). The *Sebastes* genus is composed of over 100 species worldwide, with a "hotspot" of diversity in the southern region of the CCE (Love et al. 2002, Hyde & Vetter 2007). Species of the CCE span a broad latitudinal range along the U.S. West Coast in the Northeastern Pacific Ocean. Rockfishes exhibit a diversity of inter- and intra-specific variation in life history and reproductive strategies (Love et al. 2002). By latitude, the CCE is divided into three bio-geographically distinct regions (Checkley & Barth 2009, Bakun et al. 2015). We focus on a major bio-physical break between the central and southern regions at Point Conception, California, U.S.A. (latitude: N 34.4481). This is where life histories and reproductive strategies vary the most from north to south (Parrish et al. 1981, Checkley & Barth 2009). Specifically,

the higher latitude central and northern regions are cooler, more productive, and have greater seasonality in upwelling processes that influence when food is available throughout the year compared to warmer temperatures, poorer ocean primary productivity, and weaker seasonality at lower latitude in the southern region (Parrish et al. 1981, Hickey & Banas 2008, Checkley & Barth 2009). These regionally different environmental conditions are likely to influence spatial variation in the frequency of reproduction for rockfishes.

In general, rockfishes are live-bearers and moderate- to long- lived (Love et al. 2002, Mangel et al. 2007). Two reproductive strategies exist within the genus. The first is a single brood strategy to reproduce only once per year. The second is a multiple brooding strategy, where females may reproduce with greater frequency by producing one or more broods annually. To the north, individuals of most rockfish species appear genetically limited to a single, annual larval brood. In some cases females will skip spawning if conditions are unfavorable caused by low energy reserves (Rideout & Tomkiewicz 2011, Head et al. 2016, Conrath 2017). In the central region there is a mix of single- and multiple- brooding species and females of species capable of multiple broods will intermittently produce either single- or multiple- broods depending on environmental conditions (Wyllie-Echeverria 1987, Beyer et al. 2015, Lefebvre et al. 2018). Species with more southern distributions are more likely to be capable of multiple broods and multiple brooding is most common among individuals of those species residing in the south (Moser 1967, MacGregor 1970, Holder & Field 2019). The regional differences in seasonality in primary production by latitude are likely to

play a role in the observed spatial variation in reproductive traits for rockfishes related to a capital or income breeding strategy (McBride et al. 2015).

Although the phenomena of multiple brooding for rockfishes in the south has been known for some time (MacGregor 1970), why it occurs remains largely unknown. Previous hypotheses (Love et al. 1990, 2002) suggested that multiple brooding is likely related to the different environmental conditions of the south (see *Supplementary Materials 3.1*). Thus, it is plausible that weaker seasonality, but warmer temperatures, and less ocean biological productivity in the south may favor multiple broods and restrict the production of broods farther north. In summary, inter- and intra-specific variation of rockfish reproductive traits vary spatially by latitude in the CCE with a greater frequency of reproduction (i.e., multiple brooding) more common at lower latitudes and more limited reproduction (i.e., single broods) and the potential for skipped spawning at higher latitudes. The consequences of multiple brooding and intra-specific variation in the frequency of reproduction are largely unknown, but the challenges associated with quantifying the impact on total population reproductive potential complicate stock assessment and management efforts for these broadly distributed and economically important species.

The ultimate cause of phenotypic plasticity causing variation in reproductive traits, along with the evolution of a long lifespan, is likely a life history strategy for rockfishes to cope with the regional, seasonal, inter-annual, and decadal environmental variability of the CCE (Checkley & Barth 2009). The proximate cause of variation in reproductive traits, including spatial variation, is likely related to maternal energy

reserves and bioenergetics. When energy reserves are low, mature females may fail to reproduce (Conrath 2017, Conrath & Hulson 2021). But when energy reserves are sufficient, the capability to produce multiple broods, in some species, increases annual fecundity where secondary broods are nearly as large as single broods (Beyer et al. 2015, 2021, Lefebvre et al. 2018). Thus, reproductive plasticity and a long reproductive lifespan provide many opportunities to reproduce over a lifetime. These traits are likely important components of a life strategy to cope with highly variable offspring survival and high recruitment variability of rockfishes in the CCE (Thorson et al. 2013, Field et al. 2021). Reproductive plasticity (i.e., single- or multiple- brooding and skipped spawning) affects population reproductive potential by shifting the total number of eggs produced by mature females annually and influencing regional differences in productivity that depend on environmental conditions. The considerable spatiotemporal variability in the frequency of reproduction for rockfishes from zero, one, or more broods a year results in large uncertainty in population-level spawning output estimates. More accurate estimates of spawning potential and understanding the role of reproductive plasticity in contributing to variable egg production is important to understanding the ecology of the species, predictions of population dynamics, and understanding how reproductive potential is influenced by the environment.

Here, we develop a state-dependent life history theory (SDLHT) model to provide insight into the causes and consequences of reproductive plasticity of rockfishes and to establish the framework for studying spatial variation in life history traits correlated with variation in environmental conditions by latitude (Mangel & Clark

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1988, Houston & McNamara 1992, McNamara & Houston 1996, Clark & Mangel 2000, Mangel 2015). SDLHT allows us to determine what set of environmental conditions favor different reproductive strategies, including single- or multiple-brooding and skipped spawning (Jørgensen & Fiksen 2006, Jørgensen et al. 2006). By developing SDLHT we can directly test the idea that the frequency of reproduction is related to maternal energy reserves and the strength of seasonal variation in temperature and the food supply. Because SDLHT uses energy as the currency to allocate among life history traits, we integrate a bioenergetics approach to ask how the environment influences net energy gains and losses each month and how trade-offs in the allocation of energy among life history traits influences variation in the frequency of reproduction for different sets of environmental conditions. To focus on the influence of the environment on maternal energy reserves and reproduction, we make no assumptions about larval survival. However, we return to the influence of this assumption in the discussion.

Our study objective was to better understand how different ocean conditions, which vary by latitude in the CCE, influence maternal energy reserves and spatial variation in the timing and frequency of rockfish reproduction. We hypothesize that variation in the reproductive strategy (i.e., single- or multiple- brooding) will depend on female bioenergetics and state dynamics to maximize egg production in regions that differ in mean environmental conditions. We predict that temperature, ocean productivity (i.e., the mean level of food in the environment influencing the per-capita feeding success), and the strength of seasonality in when food is available will

influence the timing and frequency of reproduction. More specifically, we predict strong seasonality, such as occurs in the central and northern regions of the CCE will favor a shorter spawning season and fewer or single broods because energy must also be allocated to overwinter survival during an annual period of food scarcity (Larson 1991). We predict that weak seasonality and warmer temperatures, such as is present in the southern region, will lengthen the spawning season and increase reproductive frequency, but only if food availability is adequate through the year. We model the Rosy rockfish (*Sebastes rosaceus*), a species with a broad latitudinal distribution in the CCE, where multiple brooding is more common among individuals in the south (Love et al. 2002). As a check of our models to accurately reflect the reproductive patterns of wild fish, we compared model predictions to field and laboratory observations of Rosy rockfish (Beyer et al. 2021, Beyer *et al.* unpublished). Because we do not generally observe skipped spawning in this species (at least in the central and southern regions), we predict that most females will reproduce at least once annually when mature.

2.0 Methods

2.1 Study ecosystem and rockfish reproduction

To justify the environmental conditions modeled, we first elaborate on latitudinal variation in ocean conditions that occur in the California Current Ecosystem (CCE) and are most likely to influence spatial variation of rockfish reproductive traits. The causes of multiple brooding in southern rockfishes, including by Rosy rockfish is

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not well understood but likely related to latitudinal variation of environmental conditions from north to south. Greater seasonality in primary productivity in the central and northern regions is driven by a peak in ocean upwelling in the spring and early summer months. Upwelling brings cold, nutrient rich waters from depth into the photic zone of coastal waters (Parrish et al. 1981, Checkley & Barth 2009). This results in a spring and summer peak of primary and secondary productivity that influences food web dynamics and prey to higher trophic levels (Thompson et al. 2012). Downwelling and less primary productivity occur during the fall and winter. Accordingly, the energy reserves of rockfishes in these regions increase over the summer feeding season and peak in the early fall (Guillemot et al. 1985, Wyllie-Echeverria 1987, Larson 1991, Beyer et al. 2015). Energy reserves then decline through winter as energy is allocated to reproduction (for many shelf rockfishes) and when food resources become more scarce. At the lower latitudes of the southern region, upwelling is weaker but more persistent through the year (Parrish et al. 1981). In turn, seasonal variation of upwelling patterns influence overall ocean primary productivity and prey availability to higher trophic level predators (Thompson et al. 2012). Weaker seasonality in upwelling and primary productivity, and warmer temperatures in the southern region is contrasted by stronger seasonality in upwelling and primary productivity, and cooler temperatures in the central and northern regions.

2.2 General modeling approach:

We developed a state-dependent life history (SDLHT) model using stochastic dynamic programming (SDP) to solve for the reproductive strategy that maximized an individual's expected lifetime reproductive success for different sets of environmental conditions that vary by latitude in the CCE. We modeled the state variables of female length (L) and energy reserves (E) to determine how energy should be allocated between growth and reproduction in monthly time steps over the lifespan of an individual. This allowed us to compare adaptive reproductive strategies arising from different combinations of environmental conditions possible for the CCE. Monthly energy gains and losses were modeled based on rockfish bioenergetics (Harvey 2005, 2009, Harvey et al. 2011) and the effect of temperature on feeding rates and metabolism (Kitchell et al. 1977, Hewett & Johnson 1992). We then used SDP to solve for the optimal allocation of stored energy to growth and reproduction that maximized expected reproductive success, given the environment. We base the structure of our model on a SDP model describing the growth and reproductive dynamics of Atlantic cod, *Gadus morhua* (Jørgensen & Fiksen 2006), but with important modifications for rockfish (*Supplementary Materials 3.2*). Growth and reproductive traits (such as the age and size at maturation, the timing and frequency of reproduction, and fecundity) were emergent properties of our model. This allowed us to compare adaptive reproductive strategies for different sets of environmental conditions to better understand spatial variation in the frequency of reproduction in the wild and the consequences of this variation to regional differences in reproductive potential.

2.3 Bioenergetics overview and equations

We used equations from bioenergetic theory (Kitchell et al. 1977, Hewett & Johnson 1992) to model energy gains and losses at each time step (t) given a female's current length, l (in centimeters, cm) and current energy stores, e (in kilojoules, kJ) at the start of each month (Fig. 1, Figure adapted from Kindsvater et al. 2022). This was done to model incoming energy from food and metabolic rates that varied with fish size and depended on environmental conditions. We followed three rockfish bioenergetic models (Harvey 2005, 2009, Harvey et al. 2011) and calculated monthly energy gains and losses based on fish size and environmental conditions with the following equations.

2.3.1 Somatic Weight

At the start of each month, we first calculated a baseline somatic weight (w_{soma}) for the female, given the current l. It was important to first calculate somatic weight because the size of the fish (length and weight) influenced other physiological processes such as feeding and metabolic rates and energy storage capacity. We defined somatic weight as the skeletal mass, visceral organs, and a minimum muscle mass needed to survive, given l (Jørgensen & Fiksen 2006). Somatic weight did not include the gonad weight, or the weight of current levels of excess e stored in fat tissues. We calculated w_{soma} based on a minimum body condition factor (Fulton's K, K_{min}) observed for wild fish (Jørgensen & Fiksen 2006). We assumed that we did not observe fish in the wild with a body condition factor lower than K_{min} because they

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died from starvation. We also assumed we did not observe fish in the wild with a condition factor greater than the maximum body condition ($K_{\max}$) because there is a physical limit to body weight and the weight of stored energy. By defining $K_{\min}$ and $K_{\max}$, we set a biologically relevant constraint on minimum and maximum energy reserves. This constraint was size-dependent and reflected natural variation of body condition for wild fish. We followed Jørgensen and Fiksen (2006) to standardize $K_{\min}$ and $K_{\max}$ at a specific length (L_{std}) and to use a correction parameter (ε) to adjust for a difference in the rate of increase of fish weight with fish length above the cubic increase assumed by the equation for Fulton's K condition factor (i.e., weight $\approx$ length^3). The correction parameter, ε, is species-specific and found by plotting the length-weight relationship for a species. The w_{soma} was then calculated by rearranging the equation for Fulton's K body condition factor ($K = 100$ weight/ length^3), then accounting for the correction $L_{\text{std}}{}^\varepsilon$ and solving for the minimum structural weight at $K_{\min}$ for a given l (Jørgensen & Fiksen 2006):

$$w_{\text{soma}}(l) = \frac{K_{\min} \cdot l^{3+\varepsilon}}{100 \cdot L_{\text{std}}{}^\varepsilon} \tag{1}$$

2.3.2 Total Weight

After calculating $w_{\text{soma}}(l)$, we converted the known kilojoules of e a female had at the start of the month into grams of fat storage tissues. We did this to add the weight of energy storage tissues to the somatic weight to calculate a total weight for

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the fish (w_{total}). To do this, we used an energy density conversion factor for energy storage tissues (ρ_{stores}, units: g/kJ). Therefore, the total weight, w_{total} for a female of a given l and e at the start of a month was the weight of the fat storage tissues added to the structural weight of the fish:

$$w_{total}(l, e) = w_{soma}(l) + \frac{e}{\rho_{stores}} \tag{2}$$

2.3.3 Constraint on maximum energy reserves

Similar to the limit on the minimum structural weight and energy reserves needed to survive given l, we calculated the maximum energy reserves possible ($e_{max}(l)$) based on the difference in K_{max} and K_{min} for wild fish at L_{std} (Jørgensen & Fiksen 2006). The difference approximated the maximum extra weight of fat storage tissues, above a minimum w_{soma}, and was assumed to be a physiological limit to e. The maximum possible weight in grams was converted to a maximum cap on energy (in kilojoules) and was based on the energy density of fat storage tissues (Jørgensen & Fiksen 2006):

$$e_{max}(l) = (K_{max} - K_{min}) \frac{\rho_{stores} \cdot l^{3+\varepsilon}}{100 \cdot L_{std}^{\varepsilon}} \tag{3}$$

2.3.4 Energy Gains

Following the calculation of total weight, $w_{\text{total}}(l,e)$, and the constraints on minimum and maximum e, we modeled a weight-dependent consumption rate to determine the energy gained each month by feeding (Kitchell et al. 1977, Hewett & Johnson 1992, Harvey 2005). The consumption rate (C), which was in units of grams of prey, per gram of female biomass, per day ($\text{g·g}^{-1}\text{·day}^{-1}$) was:

$$C = a_c \cdot w_{\text{total}}(l, e)^{b_c} \cdot f_c(T_{\text{ambient}}) \cdot P_c \tag{4a}$$

where a_c and b_c are coefficients of the weight-based, allometric consumption function, $f_c(T_{\text{ambient}})$ is a concave-shaped, temperature-dependence function to adjust C to ambient temperature, T_{ambient}, and P_c is the proportion of maximum C at a given size that is used to adjust growth in bioenergetics models to match realized growth curves for the species modeled (Kitchell et al. 1977, Hewett & Johnson 1992, Harvey 2009, Harvey et al. 2011). The feeding rate ($\text{g·g}^{-1}\text{·day}^{-1}$) was then converted to total kilojoules of energy gained per month (C_{kJ}) as the product of C, the energy density of prey (ρ_{prey}), w_{total}, and an assumed 30 days per month:

$$C_{\text{kJ}} = C \cdot \rho_{\text{prey}} \cdot w_{\text{total}}(l, e) \cdot 30 \tag{4b}$$

2.3.5 Energy Losses

We used a similar bioenergetics approach to calculate catabolic losses each month to account for energetic losses to respiration and the digestion of prey (Kitchell et al. 1977, Hewett & Johnson 1992, Harvey 2005, 2009, Harvey et al. 2011). The respiration rate (R), which was measured in the units of grams of oxygen (gO_2), per gram of female biomass, per day ($gO2 \cdot g^{-1} \cdot day^{-1}$) was converted to units of energy using the oxycalorific conversion, ω (Kitchell et al. 1977, Harvey 2005, 2009, Harvey et al. 2011). The equation to calculate energetic losses to R was:

$$R = a_R \cdot w_{\text{total}}(l, e)^{b_R} \cdot f_R(T_{\text{ambient}}) \cdot P_R \cdot \omega \qquad (5a)$$

where a_R and b_R are coefficients of the weight-based, allometric respiration function, $f_R(T_{\text{ambient}})$ is a concave-shaped, temperature-dependence function to adjust R to T_{ambient} (given oxygen consumption at optimal and maximal temperatures), and P_R is a proportional modification of the respiration rate to allow for adjustments based on the activity level of the fish (Kitchell et al. 1977, Hewett & Johnson 1992, Harvey 2005, 2009). We use P_R to model an increase in the respiration rate during the month that females gestate embryos (Hopkins et al. 1995) The metabolic loss to respiration ($kJ \cdot g^{-1} \cdot day^{-1}$) was then converted to total kilojoules of energy lost each month (R_{kJ}):

$$R_{kJ} = R \cdot w_{\text{total}}(l, e) \cdot 30 \qquad (5b)$$

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Other energetic losses to digestion included the non-digestible components of prey (egestion, F), waste lost as urine (excretion, U), and the metabolic costs of digestion (specific dynamic action, D; Kitchell et al. 1977, Hewett & Johnson 1992). These losses were modeled proportional to C:

$$F = a_F \cdot C \tag{6a}$$

$$U = a_u \cdot (C - F) \tag{7a}$$

$$D = a_{SDA} \cdot (C - F) \tag{8a}$$

where a_F, a_u, and a_{SDA} are scaling coefficients of ingested energy (C) or assimilated energy ($C - F$) (Kitchell et al. 1977, Harvey 2005). Energy loss rates associated with digestion ($g \cdot g^{-1} \cdot day^{-1}$) were also converted to total kilojoules of energy lost each month to digest prey:

$$F_{kJ} = F \cdot \rho_{prey} \cdot w_{total}(l, e) \cdot 30 \tag{6b}$$

$$U_{kJ} = U \cdot \rho_{prey} \cdot w_{total}(l, e) \cdot 30 \tag{7b}$$

$$D_{kJ} = D \cdot \rho_{prey} \cdot w_{total}(l, e) \cdot 30 \tag{8b}$$

Therefore, the total catabolic losses each month ($e_{\text{total\_losses}}$) was the sum of energetic losses to R and the total energetic costs of digestion (Kitchell et al. 1977, Hewett & Johnson 1992):

$$e_{\text{total\_losses}} = R_{\text{kJ}} + F_{\text{kJ}} + U_{\text{kJ}} + D_{\text{kJ}} \qquad (9)$$

2.3.6 Constraint on gonad size

A biologically relevant constraint on the maximum weight of the gonad (w_{GonadMax}) was determined based on the hyper-allometric scaling of reproductive output and maternal weight common for marine fishes (Barneche et al. 2018). The biological meaning of a hyper-allometric fecundity and maternal weight relationship (i.e., when $b_{\text{fecundity}} > 1$) is a disproportionate increase in the reproductive output (in terms of eggs per gram of spawning biomass) for larger females compared to smaller females (Dick et al. 2017, Barneche et al. 2018, Marshall, et al. 2021). This relationship is considered important to the life history strategy of rockfishes (Hixon et al. 2014). We used the fecundity-length relationship to develop an equation for a limit on the maximum gonad size, given the size of the fish and allowing for a hyper-allometric increase of gonad size with maternal weight. Details are provided in *Supplementary Materials 3.3*. The equation we developed to constrain the maximum gonad size, w_{GonadMax}, was:

$$w_{\text{GonadMax}}(w_{\text{total}}(l, e)) = a_{\text{gonad}} \cdot w_{\text{total}}(l, e)^{b_{\text{gonad}}} \qquad (10a)$$

where the intercept, a_{gonad} and exponent, b_{gonad} coefficients come from a natural-log transformed regression of an expected gonad weight and maternal size, which is species-specific and further described in *Supplementary Materials 3.3*. The constraint on the maximum weight of the gonad was converted to energy units to limit on the amount of energy that could be allocated to the gonad (e_{GonadMax}), given $w_{\text{total}}(l, e)$. This was the product of the maximum gonad weight and the energy density of ovarian tissue at early embryogenesis (ρ_{ovary} ; kJ·g^1):

$$e_{\text{GonadMax}}(w_{\text{total}}(l, e)) = w_{\text{GonadMax}}(w_{\text{total}}(l, e)) \cdot \rho_{\text{ovary}} \qquad (10b)$$

2.3.7 Energy to allocate to growth, reproduction, or energy stores

The net gain in energy (e_{net}) each month was the total energy consumed less catabolic losses:

$$e_{\text{net}} = C_{\text{kJ}} - e_{\text{total\_losses}} \qquad (11)$$

Net incoming energy was added to existing energy stores, which could then be allocated to growth or reproduction or could remain as stored energy for future use (Fig. 1). Energy reserves available to allocate (e_{allocate}) was the sum of current e at

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the start of the month, any net gains (or losses) from feeding (e_{net}) and discounted by the efficiency of converting molecules of assimilated energy from prey to lipids in fat storage tissues (δ_{store}). We retained a minimum reserve of stored energy ($E_{reserve}$) to avoid an initial starvation threshold if the fish decided to allocate the maximum amount of energy reserves to growth or reproduction.

$$e_{allocate} = e + (e_{net} \cdot \delta_{store}) - E_{reserve}$$

$$e_{allocate} \leq e_{max}(l) \quad (12)$$

Stored energy available to allocate to growth or reproduction was limited by the maximum storage capacity ($e_{max}(l)$, equation 3). Energy above the maximum could not be physically stored and was lost. The fish was allowed to use energy reserves to pay any net energy deficits if the fish did not consume enough prey to meet metabolic costs each month. The fish was assumed to starve and die if the combined energy gains from feeding and current e did not cover metabolic costs greater than $E_{reserve}$ (Fig. 3.1).

2.4 State dynamics and overview of the SDP Model:

After determining energy gains and losses each month and in order to understand how energy reserves should be allocated to growth and reproduction, we used SDP to find the optimal strategy for the allocation of stored energy that maximized expected lifetime reproductive success, given the environmental

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conditions (Mangel & Clark 1988, Clark & Mangel 2000, Mangel 2015). We determined maximum expected lifetime reproductive success by choosing the optimal allocation strategies for fat storage (*u*), growth (1-*u*), and reproduction (*r*). (Fig. 1). The maximization of *u* and *r* was calculated for all combinations of *l* and *e* over the lifespan of an individual. All possible options for how stored energy could be allocated to *u* and *r* at each time step are listed in Table 3.1. Because of computing limitations, we modeled a course set of proportional energy allocation options within the range of all to no energy allocated to growth, reproduction, or storage.

The allocation of energy to growth (an increase in length and somatic structures) or to reproduction (the production of gonadal tissues and offspring) was irreversible (Jørgensen & Fiksen 2006). That is, a fish was not allowed to shrink in length and eggs were not allowed to be resorbed if the reproductive effort failed. The allocation of energy to storage as lipids in fat storage tissues such as in the muscle, liver, or as mesenteric fat, was reversible. This meant that the "fatness" of a fish could increase or decrease as a fish accumulated and used energy through time (Jørgensen & Fiksen 2006). Stored energy could be used in the future, including for over-winter survival during periods of food scarcity and for future reproductive opportunities. In each time step, we specify the state-dynamics (how the size and energy dynamics of a fish change through time) by the set of equations below.

2.4.1 Growth

The amount of energy allocated to growth (e_{grow}) was a function of the proportion of stored energy allocated (1-u) and the amount of energy available ($e_{allocate}$) determined from bioenergetics (equation 12). Therefore, energy allocated to grow larger was:

$$e_{grow}(l, e, u) = (1 - u) \cdot e_{allocate} \tag{13}$$

An increase in length then depended on the current length (l), the growth allocation decision (u), and energy reserves (e) that influenced the amount of energy available to grow. An increase in growth also depended on K_{min} (assuming a necessary minimum structural weight to survive) and the efficiency of converting energy stored in fat tissues to the growth of structural tissues (δ_{grow}). Together, this resulted in an increase in length to l', following Jørgensen & Fiksen (2006):

$$l'(l,e,u) = \left[l^{3+\varepsilon} + \frac{e_{grow}(l,e,u) \cdot \delta_{grow} \cdot 100 \cdot L_{std}{}^{\varepsilon}}{K_{min} \cdot \rho_{structure}} \right]^{1/(3+e)}$$

$$l'(l,e,u) - l \leq \Delta l_{max} \tag{14a}$$

where an increase in length each month could not exceed a maximum growth rate (Δl_{max}), derived from a species-specific von Bertalanffy growth function (von Bertalanffy 1938) and scaled to a maximum growth increment possible in one month.

There was no increase in length if no energy was allocated to growth (i.e., $l'(l,e,u,r) = l$).

2.4.2 Energy Storage

Energy that remained stored in fat tissues (e_{storage}) following the allocation to growth (Fig. 1), was a function of that allocation decision and the amount of energy available to allocate:

$$e_{\text{storage}}(l, e, u) = u \cdot e_{\text{allocate}} \tag{15}$$

If the fish then decided to use stored energy to reproduce (Fig. 3.1), the amount of energy available to invest in gonads ($e_{\text{gonad}}(l, e, u, r)$) was the product of $e_{\text{storage}}(l, e, u)$ and the efficiency of converting stored energy in fat tissues to the synthesis of gonadal tissue (δ_{gonad}):

$$e_{\text{gonad}}(l, e, u, r) = \delta_{\text{gonad}} \cdot e_{\text{storage}}(l, e, u)$$

$$e_{\text{gonad}}(l, e, u, r) \le e_{\text{GonadMax}}(w_{\text{total}}(l, e)) \tag{16}$$

where the size of the gonad was constrained by a limit on the maximum energy allowed for the gonad at a given maternal $w_{\text{total}}(l, e)$ (equation 10b). If reproducing,

fish used all stored energy to reproduce up to $e_{\text{GonadMax}}(w_{\text{total}}(l,e))$. Any energy reserves above this maximum ($e_{\text{extra}}(l,e,u,r)$) were not lost and remained as stored energy for future use (Fig. 1).

Remaining stored energy, $e'(l,e,u,r)$, was then the sum of E_{reserve} (reserved to avoid initial starvation if allocating all energy reserves to growth or reproduction) and any $e_{\text{extra}}(l,e,u,r)$ remaining after the allocation of energy reserves to u and r:

$$
e'(l,e,u,r) = \begin{cases} E_{reserve} + e_{storage}\,(l,e,u) & \text{if not reproducing} \\ E_{reserve} & \text{if reproducing and } e_{gonad}(l,e,u,r) \leq e_{gonadMax}(w_{total}(l,e)) \\ E_{reserve} + e_{extra}(l,e,u,r) & \text{if reproducing and } e_{gonad}(l,e,u,r) > e_{gonadMax}(w_{total}(l,e)) \end{cases}
$$

(17)

2.4.3 Brood fecundity

Brood fecundity, $\Psi(l,e,u,r)$, was the number of offspring (larvae) produced per reproductive bout. A single brood of larvae was possible each month. We used $\Psi(l,e,u,r)$ as a measure of current fitness gains. To calculate brood fecundity, we converted kilojoules of $e_{\text{gonad}}(l,e,u,r)$ to a gonad weight ($w_{\text{gonad}}(l,e,u,r)$) by using the energy density of ovarian tissues at the onset of embryogenesis (ρ_{ovary}):

$$
w_{\text{gonad}}(l,e,u,r) = \frac{e_{gonad}(l,e,u,r)}{\rho_{ovary}}
$$

(18)

Brood fecundity was then the quotient of $w_{gonad}(l, e, u, r)$ and the mean

weight of an embryo at fertilization in grams (W_{embryo}):

$$\Psi(l, e, u, r) = \frac{w_{gonad}(l,e,u,r)}{W_{embryo}} \qquad (19)$$

If not reproducing, or if there was not enough energy to reproduce, then $\Psi(l, e, u, r) =$

0.

2.4.4 Survival

Beyond the risk of starvation, survival had two components: 1) a baseline

monthly risk of mortality, and 2) an increase in the monthly mortality risk when

females reproduced to reflect an increased susceptibility to predation and death

(Jørgensen & Holt 2013). We modeled the monthly survival probability (S) as a

function of a constant monthly mortality rate (M_{month}) through time. This was simply

the annual mortality rate divided by 12 months in a year. The probability of survival

each month was:

$$S = \beta_{rep} \cdot e^{-M_{month}} \qquad (21)$$

where β_{rep} is a scalar of survival set to 1 if not reproducing and $\beta_{rep} < 1$ when the female reproduces to reflect the added risk of mortality while gestating embryos. In summary, we assumed a baseline stochastic monthly risk of mortality, such as from predation. Any additional mortality factors, such as the risk of starvation, could differ by the environment and were based on energy dynamics. This could include starvation if a minimum amount of energy reserves (E_{crit}) was not maintained each month (Fig. 3.1).

2.5 Expected lifetime reproductive success

We use a fitness function, $V(l, e, t)$, to find the optimal energy allocation strategy for growth (u) and reproduction (r) in each time step. The fitness function was defined as the maximum expected reproductive success between time t and time $T = 12 \cdot A_{max}$, given that $L(t) = l$ and $E(t) = e$, where the maximum is taken over each of the energy allocation options characterized by u and r (Table 1), and the expectation over the stochastic process of survival (Mangel & Clark 1988, Clark & Mangel 2000). The end condition is:

$$V(l, e, T) = 0 \qquad (22)$$

An end condition of zero reflected death or senescence at the maximum possible life span, at which point there was no possibility of future fitness. Knowing the terminal

condition, the SDP algorithm then iterated backward from T to time $t = 1$ to solve for the energy allocation strategy u and r that maximized V at every monthly time step and for all combinations of l and e (Mangel & Clark 1988, Clark & Mangel 2000). The full dynamic programming equation was:

$$V(l, e, t) = \max_{u,r} \left[\Psi(l, e, u, r) + S \cdot V[l'(l, e, u), e'(l, e, u, r), t + 1] \right] \qquad (23)$$

Equation 23 generates the optimal allocation strategies u*(l,e,t) and r*(l,e,t) for every state variable combination and time. We developed SDP models for different environmental conditions of the CCE that vary by region and with latitude, described next. For each set of environmental conditions, we calculated u*(l,e,t) and r*(l,e,t) for 18,729,300 combinations of all states and time. This included 300 states of length in a range from 0.1 cm to 30.0 cm by 0.1 cm increments, 149 states of energy in a range from 0 kJ to 2960 kJ by 20 kJ increments, and for 419 monthly time steps, where fitness was known at $t = 420$. The optimal allocation strategies u*(l,e,t) and r*(l,e,t) were saved in decision matrices and represented the adaptive life strategy that would maximize expected lifetime fecundity for each environment and given any possible (or impossible) state of length and energy reserves. To be clear, we assumed that an individual exhibited perfect plasticity in response to their internal state and influenced by their environment (by following the optimal energy allocation strategies, given their environment). We also assumed that expected lifetime egg production (fecundity) was a direct proxy for reproductive success and fitness.

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We developed models for different environmental scenarios that spanned a range of conditions that vary by region in the CCE. We did this to learn how the environmental variables of temperature, ocean productivity, and seasonality in feeding success affect spatial variation in growth and reproductive traits of rockfish. The biology and bioenergetics remained the same for each scenario (i.e., we assumed no local adaptation to different environmental conditions, such as temperature). Seasonality of feeding success was explicitly modeled with a seasonality feeding function, described below. However, natural cycles in ocean temperatures throughout the year also influenced seasonality in the energetics by modifying consumption and respiration rates each month. To model seasonality in feeding success, we modified monthly feeding rates based on the annual cycle of food availability in the environment, which was assumed to influence an average monthly per-capita feeding success. To include the effect of seasonality in water temperature, we modeled seasonal variation in temperature at depth throughout a year, which reflected natural temperature cycles in the central and southern regions of the CCE, at depths where rockfish were collected, and between regions where reproductive patterns most differed.

Within each temperature regime, we modeled three levels of mean food in the environment to reflect regional differences in ocean productivity, and three levels in the strength (amplitude) of seasonality of when food was available throughout the

year. We did this by modifying the monthly feeding rate, C with the feeding seasonality function ($\phi(t)$, eq. 25). We used a sinusoidal function to reflect an annual cycle in primary productivity that was assumed to influence feeding rates over a one year period (Pirotta et al. 2020). The equation for the feeding seasonality function was:

$$\phi(t) = \phi_{mean} \cdot [1 + \lambda \cdot \sin(2\pi t/12)] \tag{25}$$

where ϕ_{mean} is the mean level of food in the environment and λ is the relative amplitude of seasonal fluctuations in the food supply. We modeled a high, medium, and low level of mean food in the environment. Mean food was set at 80%, 70%, and 60% of maximum C from bioenergetic equations to model good, average, and poor feeding conditions. We modeled strong, moderate, and weak seasonality in the food supply, where λ was 1.0, 0.5, and 0.1, respectively. These parameters reflected regional differences in the amplitude of seasonality in the CCE by latitude, where weak seasonality occurs in the south and progressively stronger seasonality occurs at higher latitudes of the central and northern regions. The combination of ϕ_{mean} and λ of the feeding seasonality function, $\phi(t)$, modified C each month. In practice, the feeding modification function replaced P in the bioenergetics equation (4a). The parameter P is used in bioenergetics modeling to tune feeding rates to fit realized species-specific growth curves, but growth was an emergent property of our models and feeding rates

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were determined by the monthly feeding conditions and temperature. We assumed a complete cycle over twelve months in a one-year period.

2.7 Visualizing adaptive life strategies for different environmental conditions

We used a forward, numerical projection to simulate growth, energy reserves, and the frequency of reproduction for an individual over their maximum expected lifespan for individuals living in different environmental scenarios (Mangel & Clark 1988, Clark & Mangel 2000). In other words, in the forward individual simulation we modeled a "lucky" individual that lived to the maximum age. The forward simulation of an individual, which started at the age and size of recruitment and ended at the maximum expected age allowed us to "observe" optimal behavioral patterns of a fish over an expected lifespan and to compare adaptive growth and reproductive strategies across different environmental conditions. We assumed no mortality in the individual forward simulation. However, because most fish do not live to the maximum age, we used a forward simulation of a cohort in different environments to "observe" the probability of survival to a specific age (i.e., the "realized" survival of how many individuals survived to each age). We assumed the same stochastic risk of monthly mortality for the forward cohort simulation as assumed for the backward iteration used to solve for the adaptive life history strategy. The stochastic monthly risk of mortality was the same for each set of environmental conditions. Any differences in

"realized" survival between models was due to the different environmental conditions and was an emergent property of the model.

2.8 Overview of the model parameters

We specify parameters to model the biology of the Rosy rockfish (Table 3.2). Rosy rockfish is a relatively small species within the *Sebastes* genus with a moderate lifespan up to 35 years (Fields 2016). We chose to model Rosy rockfish because 1) they are capable of multiple broods, 2) are abundant throughout the CCE, and 3) the frequency of reproduction and length of the spawning season differ between the north, central, and southern regions (*Supplementary Materials 3.4, Fig. S3.4.1*). Similar to other rockfishes, multiple brooding of Rosy rockfish is more common among individuals in the south (Love et al. 2002). Furthermore, we had information about how temperature and food availability influenced reproduction for Rosy rockfish in the laboratory (Beyer et al. 2021). Also, we could compare models to field collections (Marks et al. 2015, Fields 2016, Beyer *et al.* unpublished).

Beyond spatial differences in the frequency of reproduction, Rosy rockfish growth is highly variable through time and space. Fish grow up to 27.4 cm FL (28 cm TL) in southern California (Love et al. 1990) and up to 31.6 cm FL in central California (Echeverria & Lenarz 1984). The size at maturation also varies, with 50% mature at 14.7 cm FL in southern California collected from 1980 to 1987 (Love et al. 1990), and 50% of females mature at 16.6 cm FL in central California collected from 2012 to 2014 (Fields 2016). A larger size of 18.6 cm FL at 50% maturity was reported for Rosy

rockfish collected throughout California from 1977 to 1982 (Wyllie-Echeverria 1987). These differences suggest spatial and temporal variation in life history traits for this species. We used maximum growth rate information to inform the maximum monthly growth rate in the model. We used size at 50% maturity to compare with predicted maturation from the models, where the age of maturation in the wild is around 6 years of age (Fields 2016). The diet of Rosy rockfish is not well-studied, but adults are associated with rocky reefs and are likely opportunistic generalists. Rosy rockfish feed near the benthos on invertebrates, such as krill, shrimp, amphipods, salps, small octopus, and crabs, and on small fishes, such as young-of-the-year rockfishes (Love et al. 2002). When information was available, we based parameters on the biology of Rosy rockfish. When unknown, we borrowed information from other rockfish species or other marine fishes.

2.8.1 Energy gain and loss parameters for Rosy rockfish

We used the energy gain and loss parameters previously developed for rockfish bioenergetics modeling (Harvey 2005, 2009, Harvey et al. 2011) and further described in *Supplementary Materials 3.5*. These parameters were based on laboratory studies of feeding and respiration rates for different rockfish species. We altered some of the parameters, such as prey density, to better reflect the ecology and diet of Rosy rockfish. Rosy rockfish are benthic, relatively inactive, and non-migratory (MacFarlane et al. 1993, Love et al. 2002). Therefore, we assumed fish spent most of their time at or near the baseline metabolic rate. We did not account for

possible activity modifiers, such as increased swimming exertion while capturing prey, courtship and mating behavior, or aggression to defend territories. We assumed these activities occurred quickly and did not substantially change the baseline monthly respiration rate (Harvey 2005, 2009, Harvey et al. 2011).

An important exception is that we modeled an increased respiration rate in the month when females gestated embryos and reproduced (P_R, equation 5a). The increase in respiration was based on higher respiration rates of late-stage gestating Yellowtail rockfish (*S. flavidus*) compared to the respiration rates of spent females (Hopkins et al. 1995). Respiration rates of gestating females remained fairly similar to non-gestating females through most of gestation, but increased up to 82% above the resting respiration rate for spent females in the final days when larvae had hatched and prior to parturition (Hopkins et al. 1995). The greater respiration rate late in the gestation period was averaged over a one-month period to determine the total extra energy lost in the month due to respiration costs when a female gestated embryos and reproduced. Specifically, we used a weighted average (approximate integral) over the month of gestation for the increased respiration rate of females gestating embryos (based on Fig. 2 in Hopkins et al. 1995). We estimated the increased monthly rate to be an additional 30% of the monthly resting respiration rate.

2.8.2 Constraints on the growth of Rosy rockfish

Growth was an emergent property of the SDP model but growth was constrained by a maximum increase in length each month. We based this constraint on the maximum rate of change from the von Bertalanffy growth function for Rosy rockfish, assuming an $L_{inf} = 25.6$ cm, $k = 0.241$, and $t_0 = 0$ (Fields 2016; *Supplementary Materials 3.4* Fig. S3.4.2). The resulting maximum increase in length was 5.48 cm·year^{-1} and equal to an increase of 0.46 cm·month^{-1}. Because individual fish vary, we set the growth potential slightly higher at a less constraining $\Delta l_{max} = 0.5$ cm per month. We constrained minimum and maximum limits on the total weight of a fish by setting $K_{max} = 2.4$ and $K_{min} = 1.3$ to reflect a range of body condition for wild fish at a standard length of $L_{std} = 20$ cm, a size where we had many samples (*Supplementary Materials 3.4*, Fig. S3.4.3 and S3.4.4). We used the difference in the rate of increase of fish weight with length greater than a cubic increase of 3 to set the adjustment parameter ε at 0.35. This was based on a length-weight relationship exponent of 3.35 for female Rosy rockfish (*Supplementary Materials 3.4*, Fig S3.4.5).

2.8.3 Energy densities of rockfish tissues

Knowing the energy density of different tissue types was important to convert between kilojoules of energy to grams of energy of different tissue types, such as prey, fat storage tissues, structural tissues, and gonadal tissue. We could not find appropriate information on the energy density of specific body tissues types for rockfish so we assumed a similar energy density of fat storage and somatic tissues as

for Atlantic cod, *Gadus morhua* (Jørgensen & Fiksen 2006). The energy density assumed for fat storage tissues was 8.7 kJ·g^{-1} and for somatic tissues was 4.0 kJ·g^{-1}. We justified this based on our understanding of other aspects of rockfish bioenergetics. For example, the rockfish bioenergetics models assumed a whole-body energy density (somatic tissues, fat tissues, and gonadal tissues combined) of 6.07 kJ·g^{-1} from Perez (1994), but that study did not distinguish among tissue types. The energy density of 6.07 kJ·g^{-1} for a whole rockfish was roughly a weighted average of the fat and soma tissues of Atlantic cod (Jørgensen & Fiksen 2006) and seemed a reasonable approximation.

We did not have good information on the energy density of an individual rockfish embryo so to calculate brood fecundity we first converted energy allocated to the gonad to a gonad weight by multiplying by the energy density of rockfish ovarian tissue at the onset of embryogenesis and then divided by the weight of an early developing embryo (for which we had information). We set the energy density of rockfish ovarian tissue to ρ_{ovary} = 8.627 kJ·g^{1}, which was measured from gonads at the onset of embryogenesis for *S. flavidus* and *S. jordani* (Norton & MacFarlane 1999 in Harvey 2005). We estimated the weight of an individual embryo by taking weighed subsamples of ovaries from Rosy rockfish that had early developing embryos and divided by the count of the weighed subsample (n = 39, Beyer *et al.* unpublished). The mean weight for a Rosy rockfish embryo was 0.0003 g. The embryo weight of a Rosy rockfish was equivalent to a mean embryo weight derived for several other rockfish species (Love et al. 1990, Harvey 2005, Harvey et al. 2011).

2.8.4 Conversion efficiency parameters

Some energy is lost in the physical conversion of energy molecules to the synthesis of different body tissue types. We modeled the conversion efficiency at three different stages: 1) from prey intake to storage as lipids in fat storage tissues, 2) during the mobilization of fat stores to the synthesis of somatic tissues, and 3) during the mobilization of fat stores to the synthesis of gonadal tissue. We had high uncertainty in the three energy conversion parameters. We followed the assumptions for energy conversion dynamics of the Atlantic cod SDP model (Jørgensen & Fiksen 2006) and combined this with knowledge of rockfish bioenergetics (Harvey 2009, Harvey et al. 2011), lipid dynamics of rockfish (Norton & MacFarlane 1995), and tuning the model to roughly fit expected and average growth and reproductive patterns for Rosy rockfish in the absence of seasonality, at a mean stable temperature of 11.5 C, and a mean level of food at 70% of maximum *C*. Jørgensen & Fiksen (2006) modeled energy dynamics slightly differently by modeling the allocation of net incoming energy instead of stored energy. For those processes, they assumed an efficiency of 0.4 to convert energy molecules of ingested prey to lipids in fat storage tissues and for the conversion of stored energy to gonadal development (equaling a 0.16 efficiency of converting energy from ingested prey to gonads). They assumed a lower 0.08 efficiency to convert ingested energy to the direct growth of skeletal and somatic mass. Because we had already accounted for most of the energetic losses associated with digesting prey (equations 6, 7, and 8), we set the efficiency of

converting molecules of assimilated energy from prey to lipids in fat storage tissues at $\delta_{store} = 0.825$. We set the conversion efficiency of stored energy to growth of structural tissues at $\delta_{grow} = 0.15$, which approximated average growth conditions for Rosy rockfish (*Supplementary Materials 3.6*).

We had better information on the total energetic costs to convert stored energy to the development of gonads and the energetic costs to oxygenate developing embryos. A study on the annual cycle of fat stores of female Yellowtail Rockfish tracked the accumulation of lipids in energy storage tissues and how stored energy was then used for gonad development (Norton & MacFarlane 1995). That study found a conversion efficiency of stored energy as lipids in fat storage tissues to gonad development of 30% (Norton & MacFarlane 1995). The remaining 70% of stored energy was lost to metabolic costs associated with female reproduction (Norton & MacFarlane 1995). We accounted for the greater energetic costs associated with female reproduction and the development of gonads in two ways. First, we increased the respiration rate for females gestating embryos (described in section *2.8.1 Energy gain and loss parameters for rockfishes*). Second, we accounted for additional losses by applying a conversion efficiency of 0.6 (δ_{gonad}) for the conversion of stored energy in the form of lipids that were mobilized to the synthesis of gonad tissue. This was based on the already accounted for respiration losses during reproduction in the respiration function and a sensitivity of the model to provide females enough energy to reproduce more than once annually in the absence of seasonality, at a stable temperature of 11.5 C, and at a mean level of food at 70% of maximum *C*

(*Supplementary Materials 3.6*). Although we model energetics slightly differently than for Atlantic cod (resulting in different conversion efficiency values), the resulting total percentage of energetic losses for each conversion step was similar (*Supplementary Materials 3.6*).

2.8.5 Rockfish survival

We estimated the expected total annual mortality rate of 0.2 based on catch curves of Rosy rockfish for collections from central and southern California (Fields 2016). A mortality rate estimate of 0.2 is also a common starting point in fisheries management (Jørgensen & Holt 2013). To be clear, this rate reflected total mortality currently experienced by fish and the assumption that some fraction of total mortality was a result of fishing. The annual mortality rate was divided over 12 months of a year to calculate a monthly survival probability of 0.98. We assumed a reduced probability of survival of 0.79 during the month of reproduction. An increased risk of mortality while reproducing is a common assumption of SDLHT models (Mangel & Clark 1988, Clark & Mangel 2000) and is based on the idea that activities associated with reproduction, such as courtship and mating expose females to a greater predation risk (Jørgensen & Holt 2013). Furthermore, additional mortality risk associated with reproduction is an important determinate of age at maturation in SDP models (Jørgensen & Holt 2013). The survival rates we used approximated maturation rates for Rosy rockfish in the wild at around 6 years of age. As noted, pregnant rockfish also have higher respiration rates to provide oxygen to developing embryos (Hopkins

et al. 1995). This extra energetic demand can increase the risk of maternal mortality, especially in low-oxygen conditions that has been found in the laboratory (Stafford and Kashef unpublished). The increased risk of mortality due to reproduction is highly uncertain in our model. As noted, assuming an increase in the risk of mortality with reproduction influences the timing of maturation (Jørgensen & Holt 2013). Without other information, we assumed a 20% reduction in the probability of surviving during the month of reproduction. This assumption produced an age at maturation similar to that observed for Rosy rockfish of approximately 6 years of age at baseline conditions.

2.8.6 Parameters to model environmental conditions in the CCE

We modeled two temperature regimes. These regimes reflected the natural differences in the annual cycle of temperatures between the central and southern regions, where reproductive patterns differed the most (Fig 3.2). The "cooler" temperature regime was the monthly mean temperatures at 50 m depth in central California along a survey line from the coast (Monterey Bay) to 150 km offshore (Zaba et al. 2018). The cooler regime cycled annually from 10 °C to 12 °C. The "warmer" temperature regime was the monthly mean temperatures at 50 m depth in southern California along a survey line from the coast (Dana Point) to 200 km offshore (Zaba et al. 2018). The "warmer" regime cycled annually from 11 °C to 13 °C (Fig. 3.2). The mean difference in temperature between the two regimes was 1.2 °C. All temperatures were well within normal temperatures experienced by Rosy

rockfish and within physiological tolerance limits. The temperature regimes modeled

spanned the depths for Rosy rockfish collections in central and southern California.

However, Rosy rockfish can also be distributed at deeper depths, not considered here.

For each temperature regime, we modeled a mean level of food in the

environment to reflect mean differences in feeding rates. We set mean food at 60%

(low), 70% (medium), and 80% (high) of maximum C (Fig. 3.3). We did not have

good information about differences in the quantity and quality of Rosy rockfish prey

between regions. Because of this, we approximated variation of feeding rates based

on proportional scaling adjustments from a bioenergetics model for Chilipepper, *S.*

goodei (Harvey et al. 2011). The scaling adjustment, *P* ranged from 0.57 to 0.986 of

maximum C to produce growth patterns similar to expected growth for Chilipepper in

different environmental conditions (Harvey et al. 2011). A medium level of food,

$\phi_{mean} = 0.7$, was assumed to reflect average environmental productivity and feeding

success; we assumed good feeding conditions for $\phi_{mean} = 0.8$ and poor feeding

conditions for $\phi_{mean} = 0.6$. This was a necessary simplification of spatiotemporal prey

dynamics and rockfish feeding success to compare general differences when overall

environmental productivity and feeding success of the focal species differs between

regions.

For each temperature regime and mean level of food, we modeled strong,

moderate, or weak seasonality in the availability of food (i.e., variability in per-capita

feeding success through the year, Fig. 3.3). To do this we varied the amplitude, λ, of

seasonality (equation 25) by setting λ to 1.0, 0.5, or 0.1 to reflect strong, moderate, or

weak fluctuations in the food supply, and thus feeding success, over a one-year period. We chose values for moderate and strong seasonality for environments with average feeding conditions (medium food) that would produce annual fluctuations in C and energy reserves that roughly matched a range in the amplitude of annual cycles of fat reserves of rockfish in the north and central regions of the CCE. These were the two regions with strong seasonality and where we had data on seasonal fat cycles (Guillemot et al. 1985). We could not find good information on the seasonal variation of fat reserves for rockfishes in the south, but upwelling patterns are more muted and less seasonal in the south (Parrish et al. 1981, Checkley & Barth 2009). We assumed weaker seasonality of the environment resulted in weaker seasonality in the food supply and feeding success there. In all scenarios, we modeled food resources to peak in the month of September and to be lowest in March. This was similar to the timing and peak of annual fat reserve cycles, which we assumed reflected the annual cycle of feeding conditions and thus per-capita feeding success (Guillemot et al. 1985, Larson 1991, MacFarlane et al. 1993, Norton & MacFarlane 1995). The different combinations of environmental variables resulted in 18 different SDP models. The biology remained the same for each model, but the environment differed. The factorial experimental design of our model set-up for different environmental scenarios allowed us to explore the conditional effect of each environmental variable and possible interactions among environmental variables that influence reproduction. The models encompassed the range of environmental conditions that occur in the

CCE. Especially between the central and southern regions, where reproductive patterns most differ.

In order to focus on spatial variation in reproductive traits, we modeled environmental conditions that were stable through the lifespan of an individual (i.e., the annual cycle in temperature, mean food, and feeding seasonality did not change year to year), but the models reflected differences in mean conditions that vary regionally and by latitude in the CCE. These types of models are fully capable of capturing stochastic, temporal variation of the environment (such as good or poor food resources year to year), but that was not the focus of this study and was not considered here. Mortality, however, was a stochastic process in our models, which was based on a probability of surviving each month.

2.8.8 Initialization of the forward simulation

Once we obtained the decision matrices of optimal energy allocation strategies for all environmental scenarios by backwards iteration, we used a numerical, forward projection of an individual over the lifespan (without mortality) to visualize adaptive life strategies for different environmental scenarios (Mangel & Clark 1988, Clark & Mangel 2000). We introduced a juvenile to the simulation at a starting length of 11 cm and with a size-specific maximum of 75 kilojoules of e. This corresponded to a 2.3-year-old fish. The starting conditions approximated the minimum size and age of Rosy rockfish collected from rocky reefs in central and southern California (Beyer *et al.* unpublished). This also suggested a known size and age of juveniles recruiting to

the same habitat as adults. We did not model pelagic or pre-recruit dynamics. All other biological parameters remained the same in the forward simulation as for the solving of the decision matrix by backward iteration (Fig. 3.1).

To demonstrate the influence of a baseline monthly risk of mortality and different realized survival rates for each environment, we used a numerical, forward projection of a cohort of 100,000 individuals through time. All individuals followed the adaptive life strategy for their environment but were subject to a stochastic risk of mortality each month. The risk of mortality increased during the month of reproduction and reflected the same dynamics used in the backward solving of the decision matrix (Fig. 3.1).The cohort simulations allowed us to "observe" a realized survival probability to each age (i.e., the numbers of individuals of the cohort that survived to each age). Both the individual and the cohort forward simulations were important to understanding the results, in terms of expected growth and reproductive patterns with age over the lifespan and how many individuals were likely to survive to each age.

2.8.9 Confronting the model with data

We visually compared models to the growth and reproduction of Rosy rockfish collected in central and southern California and in the laboratory. We briefly describe the collection datasets and provide additional details in *Supplementary Materials 3.4*. A two-year laboratory study of Rosy rockfish from the central region

(Monterey Bay) found reproductive plasticity in response to water temperature, food ration, and maternal length (Beyer et al. 2021). Up to five broods a year were possible in the laboratory. The broods were released every 2 to 3 months over the reproductive season. This interval provided justification to model energy reserves and reproduction on monthly time steps (*Supplementary Materials 3.4,* S3.4.6). We compared size-dependent multiple brooding in the laboratory to model predictions for the optimal number of annual broods. In addition to laboratory information, Rosy rockfish field collections occurred from 2009 to 2019 in both the central and southern regions of the CCE (Marks et al. 2015, Fields 2016, Beyer *et al.* unpublished). Females produced multiple broods and had a longer reproductive season in the south compared to fewer broods and a shorter reproductive season in the central region, where reproduction was limited to the winter months (*Supplemental materials 3.4*, Fig. S3.4.1).

3.0 Results

3.1 Ocean environmental productivity

The mean amount of food in the environment, which was a proxy for ocean environmental productivity and thus the average per-capita feeding success of an individual over a lifetime, was a strong determinant of growth (Fig 3.4). The mean amount of food also influenced the maturation schedule and expected lifetime egg production (Table 3.3). Females in high food environments were expected to mature later in life (by 2 to 5 years), at a larger size (by 5.3 to 8.4 cm), and to obtain a larger

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maximum size (by 8.8 to 10.1 cm). Because of this, females in high food environments had much greater expected lifetime fecundity (by millions of larvae) compared to females in low food environments (Table 3.3). Expected survival was slightly greater (following maturation) in high food environments and lowest in environments with poor food resources (Fig 3.4). If multiple brooding occurred, females in low food environments tended to produce more broods earlier in their life compared to females in environments with medium or high food resources (Fig 5). However, the broods by females in low food environments were generally smaller in size because fish were smaller and maternal body size was a strong determinate of brood fecundity (Figs. 3.6 & 3.7).

The much greater expected lifetime fecundity in high food environments (Fig 3.6) resulted from a larger maternal size (related to the greater growth potential in high food environments) and thus larger brood-sizes (Fig 3.7). Greater expected lifetime fecundity in high food environments occurred even though females matured later in life. This was because the delay in maturation and longer period of growth contributed to a larger maternal size and much larger-sized broods. Females in high food environments generally had greater monthly energy reserves in the weakly seasonal environments compared to medium and low food, but higher peaks in energy reserves in environments with moderate or strong seasonality (Fig. 3.8). In general, energy reserves were lowest in late spring and early summer, which was the period following winter reproduction and a period of reduced food resources in all environments. Energy reserves accumulated through the summer and fall and stored

energy peaked in the winter months just prior to when most fish used that energy to reproduce. Energy reserves declined after reproduction occurred and in response to poor feeding conditions in the late winter and early spring. Differences of mean food in the environment did not have much effect on the timing or length of the spawning season (Fig 3.9).

3.2 Seasonality in the food supply

Changes in the amplitude of seasonality, which reflected differences in the strength of seasonality in the food supply and thus the monthly per-capita feeding success through the year had the greatest influence on the number of annual broods and the timing of the reproductive season. Seasonality influenced the annual cycle of how energy was acquired, stored, and then allocated to reproduction (Fig. 3.8). However, differences in the amplitude of seasonality did not have a strong influence on growth or survival (Fig 3.4). In strongly seasonal environments, females produced only a single annual brood as an adaptive reproductive strategy (Fig. 3.5). Multiple brooding in strongly seasonal environments was only expected at the very end of the lifespan, where females depleted energy stores prior to expected end of life. Multiple brooding was more common as an adaptive strategy in weak or moderately seasonal environments, but also depended on the mean level of food in the environment (Fig. 3.5). For each environment where multiple brooding was possible, the relatively larger and older females produced more than one brood (Figs. 3.5, 3.6). In years

where females produced multiple broods, the broods tended to be smaller than if only a single brood was produced for a given maternal length (Fig. 3.7).

The strong influence of seasonality on reproductive patterns was the result of fluctuating feeding rates through the year causing fluctuations in energy reserves and including a period of food scarcity (Fig, 3.8). This annual period of food scarcity resulted in net energetic losses in strongly seasonal environments, but not in environments with weak or moderate seasonality (*Supplementary Materials 3.7, Fig. S3.7.1*). The annual period of net energetic losses that resulted from strong seasonality favored a single brood strategy throughout the lifespan. Females in strongly seasonal environments had to survive severe food scarcity and net energetic losses in the late winter and early spring after reproducing and then re-build energy reserves over the summer and late fall when food resources became more available. In environments with moderate or weak seasonality and regardless of mean food in the environment, females did not have the same energetic demands to survive the early spring period of food scarcity after reproducing (*Supplementary Materials 3.7*). As an optimal strategy, females in these environments were favored to produce multiple annual broods once they had stopped growing, obtained the maximum size for their environment, and could then reallocate energy from growth to the production of additional broods within the year.

Strong seasonality that favored a single brood strategy shortened the reproductive season and greatly influenced the timing of reproduction (Fig. 3.9). In environments with strong seasonality, females generally produced broods over a

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winter reproductive season. Reproduction was restricted to the months of December, January, and/or February. In moderate and weakly seasonal environments, the production of broods still peaked in the winter months of January and February, but broods were also possible at other times of the year. The possibility for broods outside of the winter peak lengthened the reproductive season.

3.3 Contemporary temperature regimes

The difference between the cooler and warmer temperature regimes did not strongly influence spatial variation of growth or reproduction. However, because temperature influenced consumption and respiration rates, there was a slight effect on energy gains each month, which then slightly influenced growth patterns and reproduction. In some cases, females in warmer temperatures grew to slightly larger sizes than in the cooler regime (Table 3.3). The slight differences in growth and energy dynamics resulted in the possibility for more broods outside of the peak winter reproductive season in the warmer compared to cooler regimes. For environments with weak seasonality, slightly higher expected lifetime fecundity occurred in the warmer regime compared to the cooler regime across all levels of mean food, likely because of the difference in growth (Table 3.3).

The influence of temperature was moderated by the mean level of food and seasonality in the food supply. In high food environments, slightly less multiple brooding was expected in the warmer regime over a lifetime (Fig. 3.5). In medium

and low food environments, more multiple brooding was expected in the warmer regime compared to the cooler regime (Fig. 3.9). For example, alternating between 1 and 3 broods each year was favored in warmer compared to cooler temperatures in environments with weak seasonality and poor food resources (Fig. 3.5).

Temperature did not have much effect on brood size, other than influencing the single- or multiple- brooding pattern. Females producing multiple broods had smaller brood sizes, but sometimes a slightly larger maximum size in warmer compared to cooler environments (Fig. 3.7). In weakly seasonal environments, there were generally greater energy reserves throughout the year in the warmer compared to cooler regime, which could have been due to the slight shift in the timing of when temperatures fluctuated throughout the year affecting the energy dynamics (Fig. 3.8). This slight shift likely influenced and favored the production of broods outside of the peak winter reproductive season in the warmer regime. It is important to note that both temperature regimes were modeled as contemporary temperature regimes that are experienced by fish in the central and southern regions. All temperatures were well within physiological tolerance limits for this species and temperature differences between the cooler and warmer regimes was not large.

3.4 Maternal age and length

Growth generally slowed after maturation, but fish continued to grow slowly to a maximum size over the expected lifespan (Fig. 3.4). If multiple brooding was

expected, more broods were produced by the older and relatively larger females in environments with high or medium amounts of food (Fig. 3.5). In low food environments, multiple brooding started at younger ages, but likely because females reached a smaller maximum size earlier in life and had slightly reduced survival (Fig. 3.5). In all scenarios, multiple broods were common at the maximum age (age 35) in anticipation of senescence or death and no future fitness opportunity (Fig. 3.5). Since most females generally did not survive to the maximum age (Fig. 3.4), we removed growth and reproductive patterns of age 35 females in figures 3.6 through 3.9 to show the more general expected life strategy patterns and to exclude the increased brooding and subsequent effects on energy reserves in the expected last year of life.

In addition to age, maternal length influenced the number of annual broods. If multiple brooding was expected, it generally occurred in the relatively larger females compared to smaller females and after females had reached the maximum size for their environment (Fig. 3.6). However, females in environments with strong seasonality produced only a single brood each year, regardless of size. No matter the environment, maternal length had a strong influence on brood size. Larger females were capable of larger-sized broods. Because of this, females achieved the greatest expected lifetime fecundity in high food environments, where they grew large and were expected to produce many more offspring over a lifetime (Fig. 3.7).

Although we show adaptive growth and reproductive strategies of an individual surviving to the maximum age in each environment, the forward simulation of a cohort of 100,000 individuals found only 50% of females were

expected to survive to age 6 or 7, and only 10% between the ages of 10 and 12. The expectation for a female to live beyond 20 years in any of the models was rare. However, seven of the 18 models had at least one individual surviving to age 33 and three models had at least one fish surviving to the maximum age of 35. Mortality in the forward, cohort simulation was a stochastic process (i.e., a random draw each month to see if the individual survived given the probability of surviving). Therefore, differences in realized survival rates among environments, beyond the constant baseline stochastic risk of mortality (i.e., from predation), were due to energy dynamics influencing the risk of starvation and/or reproductive decisions resulting in a greater risk of mortality when reproducing. In general, expected survival was slightly less in low food environments compared to environments with medium or high food resources (Fig. 3.4).

3.7 Comparison to Rosy rockfish

Average growth and reproductive patterns of captive and wild Rosy rockfish most closely matched females in the medium or high food environments (Fig. 3.10). We compared wild fish to model outcomes to see if the models could replicate reproductive patterns in the wild (i.e., a check of the models). A medium level of food (mean at 70% of C_{max}) produced growth patterns like the growth of Rosy rockfish in the central and southern regions of the CCE (Fig. 3.10). We did not have growth information for Rosy rockfish farther north, but rockfish are expected to grow faster

and to a larger asymptotic size the north (Gertseva et al. 2017). Furthermore, the fat

cycles of five rockfish species in the central and northern regions of the CCE had fat

volume ratios for the annual maxima to minima with a range from 1.67 to 3.61 across

different species (Guillemot et al. 1985). These ratios of peak to minimal energy

stores a year most closely matched modeled cycles of energy reserves for females in

environments where the mean feeding success was 70% of maximum consumption

rates (i.e., the medium food scenarios). High food resources (mean feeding rate at

80% of C_{max}) produced larger fish like the greater growth for Rosy rockfish observed

in the 1980s (Fig. 3.10). Low food (mean feeding rate at 60% of C_{max}) produced

smaller fish than reported growth curves for this species.

This qualitative comparison suggested that a feeding rate around 70% of the

maximum feeding rate was appropriate to model average growth conditions for Rosy

rockfish. The high and low food scenarios were more likely bounds on environmental

conditions to produce larger and smaller fish but were important to consider because

of the strong influence of environmental productivity on feeding success and growth.

Also, Rosy rockfish growth patterns vary greatly by region and through time based on

observations (Fig. 3.10). These differences likely reflect regional differences in

environmental conditions, modeled here, but also reflect temporal variation of

environmental conditions, not modeled. Because of this, it was expected that models

of adaptive life strategies for environments that don't change year to year may not

completely re-create spatial and expected lifetime patterns of growth and

reproduction for these moderately long-live fish but were still representative of general patterns in the spatial variation of traits in the wild.

The medium and low food environments produced expected patterns of maturity and multiple brooding most like laboratory observations of Rosy rockfish (Fig. 3.10), even if the patterns did not match entirely. Captive Rosy rockfish, reared in similar "warmer" and "cooler" temperature regimes, but under stable high, medium, and low food rations produced more broods (with a mean of three, and up to five possible) compared to expected brooding patterns from our models of one to up to three broods per year (Fig. 3.10, Beyer et al. 2021). Captive fish were collected from central California as adults and had experienced variable and unknown environmental conditions in the wild prior to reproducing in captivity. Again, inter-annual variability in environmental conditions and the stable laboratory feeding conditions (i.e., no seasonality in feeding conditions) likely influenced reproductive patterns that contributed to differences between model outcomes and observations of captive and wild fish.

Even though we did not account for temporal environmental stochasticity of good and poor years, we approximated the growth patterns of Rosy rockfish reasonably well and recovered the general reproductive patterns, such as an increased frequency of reproduction and longer reproductive season in the south where seasonality is weaker, ocean biological productivity is less, and temperatures are warmer. The comparison of models to field and laboratory observations suggested that we were able to capture many of the biological dynamics of this species, given

the parameters we chose. Importantly, female rockfish store sperm and likely do not need to re-mate between broods. This capability allows more flexibility for when broods are produced throughout a year. One female in the laboratory stored sperm up to 10 months in the absence of males and fertilized five broods with the stored sperm over a single reproductive season (Beyer et al. 2021). This suggests that after mating occurs in the fall that females can fertilize broods and reproduce independent of requiring additional sperm from males.

Brood sizes of modeled females were generally at the maximum allowed, given $l, e,$ and w_{total} of the female in the month of reproduction (Fig. 3.10). Emergent brood size in our models was near the upper range of size-dependent brood fecundity for wild Rosy rockfish in central and southern California. The similar brood sizes of wild females and our models was expected because we modeled a constraint on gonad size and thus brood fecundity was based on data from wild fish (Fig. 3.10). The notable exception was for smaller than maximum-sized broods when females in the model reproduced more than once per year. This was somewhat different from patterns in the wild, where sizes of single and multiple broods for a given maternal size are generally similar (i.e., brood fecundity of primary vs secondary broods for wild fish, Fig. 3.10). In general, the variability of brood size for a given maternal length was much more variable for wild fish. This was expected given strong inter-annual variability in the environment for wild fish that would, in theory, influence brood size. However, this suggested that we did not fully capture brood size dynamics in our model.

4.0 Discussion

4.1 Larger fish and greater egg production expected in higher productivity
environments

Ocean productivity had the most effect on expected growth patterns by
influencing the expected average lifetime per-capita feeding success of an individual.
Females in high food environments were expected to grow to a much larger size and
therefore produced larger sized broods. Larger brood sizes resulted in much greater
expected lifetime egg production compared to females in medium or low food
environments. The striking differences in expected lifetime fecundity across the three
levels of mean food emphasize the importance of prey resources and per-capita
feeding success over the lifespan of an individual as a strong determinate of adaptive
growth patterns. In turn, larger maternal size enabled females to produce millions
more offspring over an expected lifetime in high food environments. Thus,
populations where the per-capita food resources are routinely high are expected to
produce larger females with greater reproductive potential (regardless of differences
in seasonality) and given the biology of rockfish and environments considered. A
expectation of larger-sized fish in more productive ocean regions is supported by field
observations of groundfish (rockfish and other bottom-dwelling species) growing to a
larger asymptotic size in more productive coastal regions of the Northeast Pacific

Ocean and smaller fish in less productive regions, such as in the southern CCE (Gertseva et al. 2017, Kapur et al. 2020).

Furthermore, reproductive plasticity (in terms of how females respond to mean differences in food or fluctuations in the amount of food resources through time) is shown to strongly influence body condition and reproductive output of marine fishes in the field and in the laboratory (Lambert & Dutil 2000, Skjæraasen et al. 2009, 2015, 2020, Donelson et al. 2010, Mion et al. 2018, Rodgveller 2019, Beyer et al. 2021). In those studies, female fish increased reproductive output with increasing energetic resources and reduced offspring production or skipped spawning entirely when food resources were low. Therefore, differences in ocean environmental productivity (specifically the average per-capita feeding success) will strongly influence adaptive growth patterns and expected lifetime egg production for fish with life histories like Rosy rockfish, and how reproductive effort varies through time. This is important because a change in ocean productivity (in time and/or space) is expected to strongly influence fish size and population reproductive potential based on our models. This is important to account for in the development of best-practice conservation and fisheries management strategies to ensure a sustainable level of reproduction in the population.

4.2 Seasonality strongly influences the timing and frequency of reproduction

Strong seasonality in the food supply favored a single brooding reproductive strategy and shorter spawning season. Females in strongly seasonal environments had to cope with maintaining enough energy reserves to survive an annual period of extreme food scarcity shortly after reproducing (i.e., feeding rates close to zero and a period of net energetic losses). Females in these environments were then able to capitalize on high food availability and subsequent feeding success and energy gains in the late summer and fall to produce a single, large brood over the winter. For females in environments with moderate or weak seasonality, energy reserves also dropped after reproducing in the winter and prior to a period of poor feeding conditions, but females in these environments did not have to deal with extreme food scarcity (i.e., feeding rates were never at zero and fish generally did not experience a period of net energy loss). Because females in moderate and weakly seasonal environments did not have as great of a seasonal peak in food resources, it was sometimes more efficient to produce two or more smaller broods (generally over the winter, but sometimes later in the year) as a strategy to maximize annual and expected lifetime fecundity. However, multiple brooding was expected after females had reached a maximum size given their environment as a way to reallocate energy from growth to reproduction. Although expected lifetime egg production varied greatly with mean food, differences in seasonality within each of those different feeding environments did not have a strong influence. In general, the single brooding strategy in strongly seasonal environments and multiple brooding strategies (among the larger and older females) in moderate or weakly seasonal environments produced

similar estimates of expected lifetime fecundity for a given mean amount of food. Therefore, these were two different strategies that both achieved roughly the same expected lifetime fecundity for a given amount of mean food, but were adaptive to cope with a seasonal period of poor food resources (which could be extreme in highly seasonal environments) and to take advantage of energy gained during good feeding periods in a way that would produce the most eggs possible.

For all levels of seasonality considered, reproduction was expected to occur during the winter months of December, January, and/or February. This was especially true for females in strongly seasonal environments, where reproduction never occurred outside of the winter. Females in those environments capitalized on high food resources and good body condition in the fall to store energy and to reproduce in the winter but needed to maintain enough energy reserves to survive food scarcity in the early spring after reproducing. Females in moderate or weakly seasonal environments also reproduced mostly in the winter, but some broods were expected outside of the winter peak, when the energy dynamics allowed it. If multiple brooding occurred, most secondary broods were released quickly following the first brood in the winter but some of the second (or third) broods were possible later in the season. This was when defining the reproductive season as starting in October (the month of mating) and extending through September of the following year.

Our models highlight the importance of maternal energy reserves and energetic trade-offs to explain both inter- and intra-specific spatial variation of the frequency of reproduction as adaptive for rockfishes to maximize reproductive

output. Single brooding and skipped spawning is more common among shelf species at higher latitudes, likely to cope with food scarcity in the winter, and multiple brooding is more common among species (and individuals of those species) at lower latitudes as a way to capitalize on energy dynamics to produce the most larvae a year possible (even if broods are smaller when producing multiple). Multiple brooding earlier in life in poor food environments was likely due to females reaching a smaller maximum size earlier in life compared to females in environments with medium and high food resources and then reallocating energy from growth to the production of second or third broods. Alternatively, it is possible that multiple brooding occurring earlier in life in poor food environments is in response to the slightly lower expected survival in those environments, which would shift reproduction earlier in life (Stearns 1992). This is shown by the earlier age of maturation of females in poor food environments compared to females with better food resources but should be explored further.

As expected for these parameters, we did not find much skipped spawning. Skipped spawning is defined as when a mature female that has reproduced in the past does not reproduce in the current year (i.e., a year of 0 broods after maturation). If it occurred, skipped spawning in our models happened early in life (close to the year after maturation) or much later in life (close to the maximum female size) for the environmental conditions considered (Fig. 3.5 & 3.6). Given what we know about the reproductive biology of Rosy rockfish and other shelf rockfish species, we did not expect much skipped spawning because it is more prevalent in species and individuals

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at higher latitudes or in the deeper-water, slope species (Lefebvre & Field 2015, Conrath 2017, Lefebvre et al. 2018, Holder & Field 2019). Also, we did not model temporal variation in environmental conditions, which are likely to influence poor years where skipped spawning may be adaptive as a strategy to conserve energy and survive poor conditions to reproduce later in more favorable conditions. For example, a previous model structured and parameterized for north Atlantic cod (*Gadus morhua*) did predict skipped spawning, which was consistent with empirical observations for that species and included temporal environmental dynamics (Jørgensen et al. 2006). An important difference in life histories is that Atlantic cod make energetically costly migrations to spawning grounds and rockfishes do not. So more prevalent skipped spawning by Atlantic cod is expected given those energy dynamics and energetic demands. The comparison to the Atlantic cod SDP model strengthens our confidence in these types of models to accurately reflect energy dynamics and reproductive patterns of diverse marine fishes living in different environmental conditions and with different life histories. Because of this, it is likely that modeling a rockfish species with lower natural mortality, slower growth, and in colder temperatures (such as the slope rockfishes) would result in less or no multiple brooding as an adaptive strategy, and more skipped spawning based on the energy dynamics, habitats, and life histories of those species. Thus, state-dependent modeling provides a powerful approach to understanding how and why the environment influences variation in life history traits for species broadly distributed across different environmental conditions, such as by latitude.

4.3 Other possible effects of temperature

The two temperature regimes that had a mean difference of 1.2 °C did not have much effect on the adaptive life strategies of Rosy rockfish but did slightly influence growth and an expectation for more broods outside of the winter peak reproductive season. It was important to consider that we modeled contemporary temperature regimes and at relatively shallow depths for shelf species, which were well within the physiological tolerance limits for rockfish. Temperature is expected to have a much greater influence at physiological tolerance limits (Alix et al. 2020) and perhaps a greater influence on growth if the temperature regimes had a greater mean difference between them. In our models, temperature influenced energy reserves by modifying size- and temperature- dependent consumption and respiration rates each month. This ultimately determined the amount of energy gained or lost and contributed to seasonality in the model because temperatures cycled annually. The temperature-dependence functions for consumption and respiration rates were assumed to be the same across all environments that we considered. This excluded the possibility for local temperature adaptation of physiological processes. Local adaptation to temperature could influence metabolic rates and therefore has the potential to alter our results. However, spatially-explicit temperature performance curves for these processes are lacking for rockfishes (and most marine fishes). Additionally, there is an expectation that wide dispersal of larvae may inhibit local adaptation. More work on temperature performance curves and the possibility for

local adaptation by latitude, or across environmental gradients, would improve predictions for how temperature is likely to influence life histories, especially if individuals and spatially distinct populations are thermally adapted.

Temperature can impact life histories in other ways beyond the influence on energy gains and losses. One possibility is that higher temperatures with global warming may increase mortality rates. For example, warmer ocean waters have reduced oxygen saturation, which affects both respiration and metabolic rates of fishes (Gillooly et al. 2001). Warmer temperatures can also increase physiological stress and parasite loads, which affect the immune system response (Alfonso et al. 2021). Extreme high temperatures cause death. Any factor that affects survival rates and reduces the expected lifespan would strongly influence the adaptive life strategies shown here. This is partly due to the reduced opportunities for reproduction over the lifespan if adult mortality rates increase (Stearns 1992). Therefore, the impacts of increasing ocean temperature, changing upwelling dynamics, and shifting oxygen saturation regimes with climate change on marine fishes are important to consider for how species and populations will cope with environmental change (Bakun et al. 2015, Pozo Buil et al. 2021). These conditions could be incorporated into our models if more information about temperature-dependence for these processes becomes available.

4.5 Maternal-offspring conflict in the timing of reproduction?

Given our model assumptions, it was interesting that the timing and frequency of reproduction was largely driven by the strength of seasonality in the food supply and subsequent influence on maternal energy reserves. Seasonality in the food supply and subsequent feeding success strongly influenced the annual cycle of maternal energy reserves and therefore the timing and frequency of when broods were produced. These annual fluctuations are often correlated with a capital breeding strategy where females acquire and store energetic resources during good feeding conditions and prior to reproducing when food resources are scarce (McBride et al. 2015). We did not include any assumptions about larval survival in our models, which could also influence maternal fitness and the timing of reproduction. Instead, we used expected lifetime fecundity as our measure of fitness and made no assumptions about different survival rates of larvae born at different times of the year or of different sizes or quality.

A strong and seasonally driven larval survival rate is expected to influence the evolutionary timing of the spawning season to release broods when larvae have the greatest chance to survive (Cushing 1975, Conover 1992). However, here we show how the annual cycle of maternal energy reserves strongly influenced the timing of reproduction to occur over the winter. Females fed and stored energy through the summer and fall to build up energy reserves and then allocated stored energy to the development of gonads to reproduce in the winter (when total maternal energy stored in both somatic tissues and in the gonads was greatest). This strategy, driven solely by maternal energetics, maximized the number of offspring produced over a lifetime. A

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mis-match in the optimal reproductive timing for the mother and optimal timing of release for larvae to survive can lead to maternal and offspring conflict in reproductive timing. It is therefore likely that rockfishes evolved the live-birth and larval provisioning strategy to overcome conflict in the timing for larval release in the CCE (Love et al. 2002). Live birth and larval provisioning means that larvae born at suboptimal times of the year can feed right away (if food is available), but also have some stored energetic reserves to lengthen the window to starvation and increase their chances of encountering food (Berkeley, Chapman, et al. 2004). In the wild, many shelf rockfishes in central California release broods in the winter from December through February or March (Wyllie-Echeverria 1987). This is prior to upwelling conditions in the spring and summer that increase primary productivity and, in theory, increase food for rockfish larvae. It is interesting that rockfish species that reproduce over the winter provision larvae with larger oil globules (a lipid energy source used to avoid initial starvation) than spring spawners (Fisher et al. 2007, Sogard, Berkeley, et al. 2008). Of the winter-reproducing shelf species, those capable of multiple broods produce broods in the winter in the central region during the winter peak, but continue to develop and release broods through the spring and summer in the south (Love et al. 2002). The production of broods generally ceases in the fall when mating occurs for most species (Love et al. 2002).

Because multiple brooding is energetically costly but occurs in the south, we assume at least some larval survival is possible at different times of the year, outside of the winter peak reproductive season, and this contributed to the evolution of a

multiple brooding strategy in the south. It is also possible that conditions in the south provide a greater opportunity for larval survival throughout the year and favors a longer reproductive season, not considered here. These hypotheses and assumptions should be tested in the future to better understand the full eco-evolutionary dynamics driving the timing and frequency of reproduction for rockfishes, but clearly maternal energy dynamics play a considerable role.

4.6 Future work

Although our models successfully re-create the general spatial reproductive patterns for rockfishes of the CCE, they did not fully account for temporal environmental variability and the possibility for environmental conditions to change year to year. Ocean conditions of the CCE are highly variable by year and can include substantial inter-annual changes in temperature and ocean productivity (Legaard & Thomas 2006). Climate events, such as years of warmer El Niño and cooler La Niña conditions, marine heatwaves, and inter-decadal variation in temperature and ocean productivity strongly influence inter-annual and inter-decadal variability in ocean environmental conditions (Hickey 1979, Checkley & Barth 2009). Although we focused on spatial patterns and seasonal fluctuations to model mean environmental differences among regions of the CCE, inter-annual variation in environmental conditions is likely to add another layer of complexity. Incorporating stochastic variability in environmental conditions, such as temperature and productivity, has

been found to closely approximated real world dynamics with state dependent modeling approaches due decisions that are moderated by uncertainty in the environment (Jørgensen & Fiksen 2006, Jørgensen et al. 2006, Mangel 2015). The next step is to explicitly test how inter-annual variation and stochasticity of annual feeding success through time influences adaptive life strategies for these long-lived species with respect to the spatial variation among mean conditions found here. The benefit of first modeling spatial, mean environmental variation, where environments vary within a year but not year to year, was that we were able to tease apart how each of the environmental variables considered influenced adaptive reproductive strategies likely to cause spatial variation in life history traits. By doing so, we were able to show the important effects of maternal energy reserves and seasonality of those reserves on adaptive growth and reproductive patterns. The addition of inter-annual environmental variation to include fluctuating years of poor and good food resources, and uncertainty in the availability of food each year, is likely to influence adaptive life strategies and expected lifetime fitness for long-lived rockfishes. This is likely to favor the possibility of skipped spawning in years of poor food resources and greater brood size variability, not fully captured in our model. A long lifespan, itself, is considered adaptive to cope with strong stochastic temporal variation of environmental conditions (Stearns 1992). Incorporating temporal environmental stochasticity is an important next step to fully comprehend the life history strategies of rockfishes and the influence on the reproductive potential of these populations through time. Importantly, climate models predict an increase in ocean warming

events, such as more frequent El Niño and marine heatwaves impacting the CCE, along with changes to upwelling patterns, primary productivity, oxygen concentration and a broad range of other environmental factors (Cai et al. 2014, Bakun et al. 2015, Di Lorenzo & Mantua 2016, Pozo Buil et al. 2021). We know from our models that lower ocean productivity is likely to strongly influence growth, maternal energy reserves, and reproduction and is therefore important to consider how sustained temporal changes in the environment will influence reproductive potential and population dynamics. Combining bioenergetics, state-dependent life history theory, and climate change forecasts for how ocean productivity, temperature, and other environmental conditions influence adaptive life strategies is an important next step.

5.0 Conclusion

We show how spatial variation and phenotypic plasticity in life history traits is expected as an adaptive life history strategy for marine fishes when individuals of a species are distributed across habitats that have differences in mean environmental conditions. This is especially true for non-migratory fish species of coastal upwelling regions that span a broad range of latitudes. Individuals of these species must cope with regional differences in temperature, seasonality, and ocean primary productivity. Developing this theory allowed us to better understand why rockfishes of the southern region of the California Current commonly produce multiple larval broods annually when their counterparts and species with more northern distributions produce only a single brood per year. We show a greater frequency of reproduction in the south is

likely adaptive to maximize offspring production in a region with poorer ocean productivity, warmer temperatures, and weaker seasonality compared to the north. However, total reproductive productivity is expected to be less overall due to the expectation for smaller-sized fish in regions with lower ocean productivity. Single broods and a shorter winter reproductive season are expected to the north as an adaptive life history strategy to cope with strong seasonality in the food supply that may cause poor feeding conditions and net energetic losses in the late winter and early spring. But strong seasonality and greater ocean productivity in the north also allows females to take advantage of the seasonal peak and greater food resources in the north to grow large, produce large-sized broods, and to have higher expected reproductive output overall, compared to smaller females in the south.

Accounting for spatial variation in growth and reproductive traits is important for assessing the reproductive potential of a population and for predicting population dynamics in different environmental conditions. We find expected lifetime reproductive output is much lower for individuals in low productivity environments, even with the possibility for a greater frequency of reproduction. Therefore, any shifts in ocean productivity (spatially or temporally) are expected to greatly alter population reproductive potential for species that exhibit phenotypic plasticity in life history traits. Furthermore, changes to the timing and intensity of seasonal upwelling patterns and ocean temperature will influence the timing and frequency of reproduction in these species. This is likely to alter the reproductive success of individuals and populations. Especially for populations in highly productive ocean upwelling

ecosystems, such as the California Current, where seasonality in primary productivity varies strongly by latitude. Knowing that spatial variation in life history traits is adaptive and can be expected, especially for species distributed across a broad range of latitudes, will improve estimates of regional differences in population reproductive potential. This work advances the knowledge of how these species are expected to cope with future changes in ocean temperature, upwelling dynamics, and primary productivity, important to consider when developing sustainable management and conservation strategies.

Acknowledgements

Tables

Table 3.1. Options for the allocation of energy each month to energy stores in fat tissues (*u*) or the mobilization of stored energy to growth (1-*u*). After an allocation of energy reserves to growth, the fish has the option to use the remaining energy stores to reproduce (*r*, yes or no). We use Stochastic Dynamic Programming to solve for the combination of *u**(*l,e,t*) and *r**(*l,e,t*) that maximizes the fitness value (*V*) for every combination of maternal state: length (*l*), energy (*e*), and time (*t*).

| Option | Proportion of stored energy allocated to: | | Use stored energy to: |
	Remain as stored energy (*u*)	Growth (1-*u*)	Reproduce (*r*)
1	1.00	0.00	Yes
	1.00	0.00	No
2	0.75	0.25	Yes
	0.75	0.25	No
3	0.50	0.50	Yes
	0.50	0.50	No
4	0.25	0.75	Yes
	0.25	0.75	No
5	0.00	1.00	Yes
	0.00	1.00	No

Table 3.2. Description of the model parameters. We include the values used, units (where applicable), and references. Parameters are listed by category.

Category	Parameter	Value	Units	Description	Reference
Growth					
	K_{min}	1.3	g·cm^{-3}	Minimum body condition at L_{std}	Fish collections
	K_{max}	2.4	g·cm^{-3}	Maximum body condition at L_{std}	Fish collections
	L_{std}	20	cm	Length at which K_{min} and K_{max} are specified	Model input
	Δl_{max}	0.5	cm	Maximum increase in length each month	Fields (2016)
	ε	0.35		Difference in the exponent of the length-weight relationship above an allometric increase of 3	Fish collections
Energy Density					
	$\rho_{structure}$	4.000	kJ·g^{-1}	Energy density of structural tissues	Jørgensen & Fiksen (2006)
	ρ_{stores}	8.700	kJ·g^{-1}	Energy density of fat storage tissues	Jørgensen & Fiksen (2006)
	ρ_{ovary}	8.627	kJ·g^{-1}	Energy density of ovarian tissue at onset of embryogenesis	Norton & MacFarlane (1999), Harvey *et al.* (2011)
	ρ_{prey}	4.000	kJ·g^{-1}	Energy density of prey	Perez (1994), Harvey *et al.* (2011)
Bioenergetics					
	a_C	0.1330		Scalar of the allometric consumption function	Harvey *et al.* (2011)
	b_C	-0.3479		Body mass scaling exponent for consumption	Harvey *et al.* (2011)
	Q_C	2.80		Q10 for consumption	Harvey *et al.* (2011)
	$T_{optimum\_C}$	17.825	°C	Optimal temperature for consumption	Harvey *et al.* (2011)
	$T_{maximum\_C}$	23	°C	Maximum temperature for consumption	Harvey *et al.* (2011)
	P_c	$\phi(t)$		Proportional scaling factor of C (Bioenergetics: P adjusts C to match realized growth patterns; SDP: P adjusts C by seasonal feeding function, $\phi(t)$)	Model input
	a_R	0.0100		Scalar of the allometric respiration function	Harvey *et al.* (2011)
	b_R	-0.2485		Body mass scaling exponent for respiration	Harvey *et al.* (2011)
	Q_R	2.5		Q10 for respiration	Harvey *et al.* (2011)
	$T_{optimum\_R}$	23	°C	Optimal temperature for respiration	Harvey *et al.* (2011)
	$T_{maximum\_R}$	28	°C	Maximum temperature for respiration	Harvey *et al.* (2011)
	P_R	No reproduction: 1.0 Reproduce: 1.3		Activity multiplier for respiration	Harvey *et al.* (2011), Hopkins *et al.* (1995)
	ω	13.560	kJ·gO2^{-1}	Oxycalorific conversion	Harvey *et al.* (2011)
	a_{SDA}	0.163		Proportion of assimilated energy lost to digestion	Harvey *et al.* (2011)

a_F	0.104		Proportion of consumed energy lost to egestion	Harvey *et al.* (2011)
a_U	0.068		Proportion of assimilated energy lost to excretion	Harvey *et al.* (2011)
Conversion Efficiency				
δ_{store}	0.825		Efficiency of storing ingested energy	model input
δ_{grow}	0.15		Efficiency of converting stored energy to growth of somatic body mass	model input
δ_{gonad}	0.60		Efficiency of converting stored energy to growth of gonad tissue	model input
SDP parameters				
A_{max}	35	years	Maximum age	Fields (2016)
t	0-420	months	Time-step	Model input
E_{crit}	20	kJ	Critical minimum of energy stores to survive	Model input
L_{max}	30	cm	Maximum length	Fields (2016)
a_{gonad}	0.026		Scalar of the hyper-allometric maximum gonad weight function	Fish collections
b_{gonad}	1.22		Exponent of the hyper-allometric maximum gonad weight function	Fish collections
W_{embryo}	0.0003	g	Weight of an embryo at onset of embryogenesis	Fish collections
$V_{[l,e,T]}$	0		Terminal fitness for the last month at A_{max}	Model input
Survival				
M_{annual}	0.20		Annual mortality	Fields (2016)
M_{month}	0.0167		Monthly mortality	Calculated
S	0.983		Baseline probability of surviving each month	Calculated
β_{rep}	Not reproducing: 1.0 Reproducing: 0.8		Scalar of survival (lower when reproducing)	Model input
Environmental conditions				
ϕ_{mean}	High: 0.8 Medium: 0.7 Low: 0.6		Mean food in the environment (scalar of C_{max})	Model input
λ	Strong: 1.0 Moderate: 0.5 Weak: 0.1		Amplitude of seasonality in the food supply	Model input
$T_{ambient}$	Cooler: 10.9 (10-12) warmer: 12.1 (11-13)	°C	Temperature regime: annual mean (range)	Zaba *et al.* (2018)

Table 3.3 Model outcomes for the 18 different environmental scenarios. Expected length and age at maturity, the expected maximum length, and expected lifetime fecundity for each set of environmental conditions.

| Temperature regime	Mean Food	Seasonality	Age at maturity (years)	Length at maturity (cm)	Max length (cm)	Lifetime fecundity (larvae)
Central "cooler"	High	Strong	10	21.4	27.7	4,239,330
		Moderate	10	21.3	27.7	4,142,592
		Weak	9	21.5	27.8	4,280,042
	Medium	Strong	9	18.5	23.7	2,380,112
		Moderate	8	17.6	23.4	2,298,242
		Weak	7	16.2	24	2,307,477
	Low	Strong	6	15.3	18.9	1,136,888
		Moderate	8	16	18.3	1,369,233
		Weak	5	13.2	18.7	1,349,955
Southern "warmer"	High	Strong	10	21.6	28.1	4,300,652
		Moderate	11	23.2	27.5	4,581,175
		Weak	9	21.3	29	5,079,659
	Medium	Strong	8	18.6	23.5	2,283,529
		Moderate	8	17.7	23.5	2,519,271
		Weak	7	17.7	24.9	2,778,941
	Low	Strong	7	15.4	18.5	1,050,232
		Moderate	6	14.8	17.8	1,322,038
		Weak	5	13.9	18.9	1,386,048

Figures

Figure 3.1 Flow chart showing how energy is gained, lost, and allocated between *u* **(growth)** and *r* **(reproduction)**. Energy dynamics are modeled in a **one-month time step (*t*)** and depend on the **length (*l*)** and **energy reserves (*e*)** of the female at the start of the month. We use fecundity as a proxy for fitness. The **expected fitness value (*V*)** is the sum of **current fitness gains (Ψ(*l, e, u, r*))**, given the decision of whether to reproduce, and **expected future fitness gains *V*[*l'*(*l, e, u*), *e'*(*l, e, u, r*), *t*+1]**, given the state dynamics and discounted by the probability of **survival to the next time step (*S*)**. To solve for the optimal life strategy, *V* is maximized over all energy allocation options, *u* and *r* (Table 1) for all possible (and impossible) combinations state. We model 300 states of *l* (0.1 to 30.0 cm by 0.1 cm units) and 149 states of *e* (0 to 5980 kJ by 20 kJ units). The SDP algorithm solves for the optimal decisions for *u**(*l,e,t*) and *r**(*l,e,t*) starting from the last month of life (month 420), where expected future fitness gains are zero, and backward through time to month 1. Optimal *u**(*l,e,t*) and *r**(*l,e,t*) decisions are saved in a decision matrix. We use a forward, numerical projection of an individual from the age and size at recruitment to maximum age to visualize adaptive growth and reproduction strategies for different environments. We use a forward, cohort simulation to show the realized probability of surviving to each age. Diagram adapted from (Kindsvater et al. 2022).
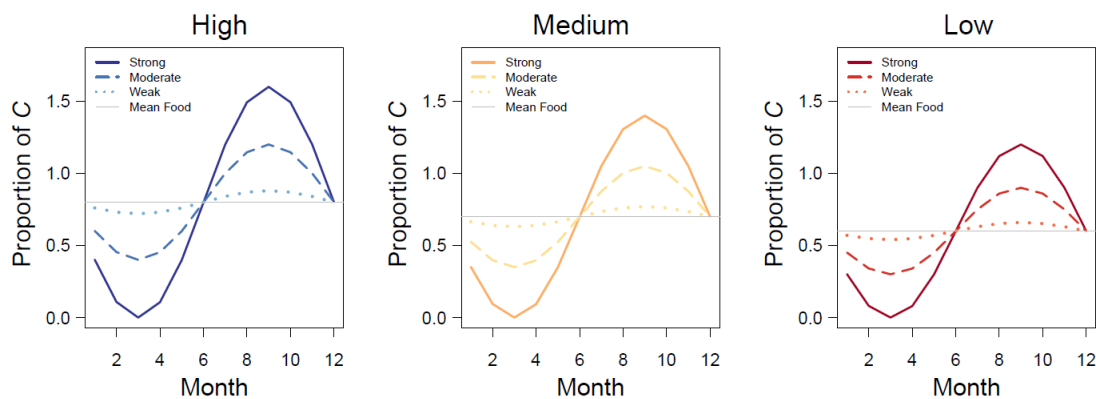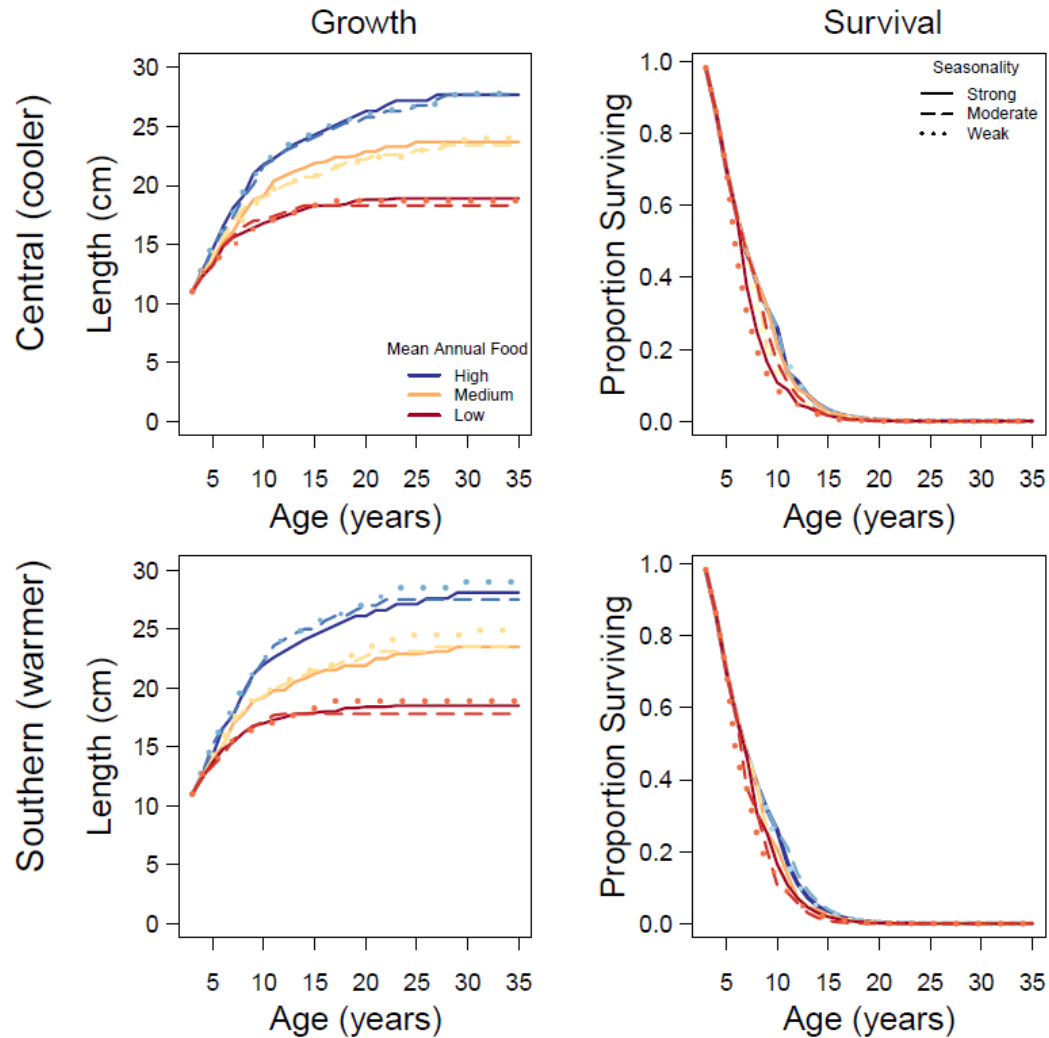
Figure 3.1
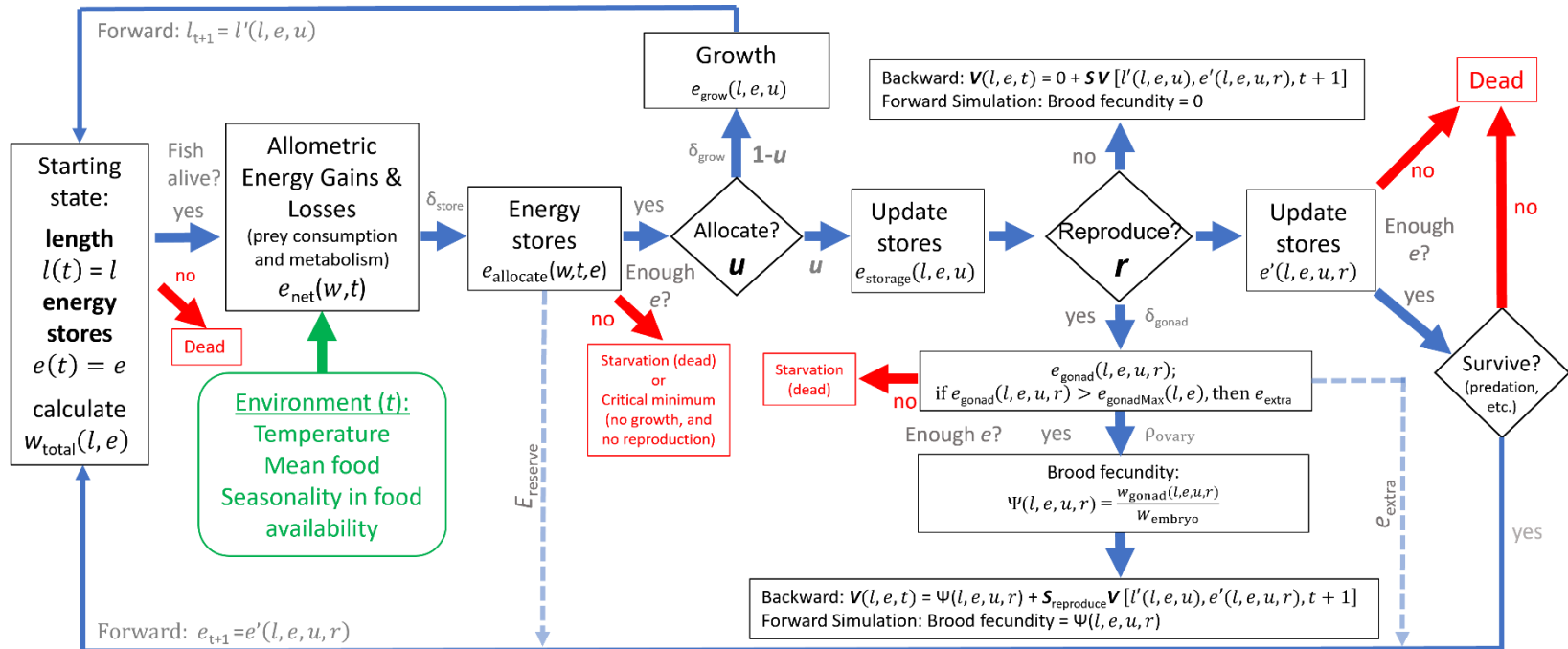
$V(l, e, t)$ is the expected fitness value, which is the current gain in fitness, $\Psi(l, e, u, r)$, and the expected future fitness gain, $V[l'(l, e, u), e'(l, e, u, r), t + 1]$, given the state dynamics and discounted by the probability of survival, S
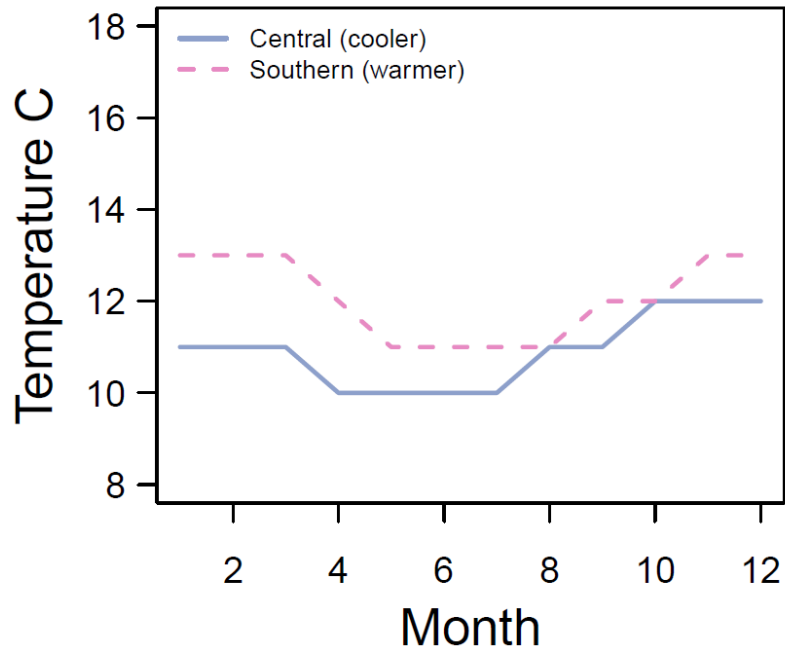
Figure 3.2 We modeled two temperature regimes that were based on the annual cycle of mean monthly temperature in the cooler, central region (**blue, solid line**) and warmer, southern region (**pink, dashed line**) of the California Current Ecosystem, where reproductive patterns of Rosy rockfish most differ. We modeled monthly mean temperatures at 50 m depth (Zaba et al. 2018), which was the approximate depth where most Rosy rockfish were collected.

Figure 3.3 For each temperature regime, we modeled three levels of mean food in the environment and three differences in the strength of seasonality in when food is available through the year. This totaled 18 different environmental scenarios. We modeled mean food (ϕ_{mean}) as high (**left, blues**), medium (**middle, orange and yellows**), or low (**right, reds**) based on feeding rates at 80%, 70%, and 60% of a maximum consumption rate (C). For each level of mean food, we modeled different amplitudes (λ) of a sinusoidal seasonal feeding function, which determined the strength of seasonality in the food supply. We modeled environments with strong (**solid lines**), moderate (**long-dash lines**), or weak (**dotted lines**) seasonality at 1.0, 0.5, and 0.1 λ, respectively. The combination of ϕ_{mean} and λ influenced the feeding rate each month by modifying C ($\phi(t)$, equation 25).

Figure 3.4 The mean level of food in the environment strongly influenced expected growth patterns (**left panels, different colors**). Mean food also influenced realized survival rates (**right panels, different colors**). Emergent adaptive growth patterns and survival are shown for females in different temperature regimes of cooler (**upper panels**) and warmer (**lower panels**) temperatures, with high (**blue colors**), medium (**orange/yellow colors**), or low (**red colors**) level of mean food in the environment, and given strong (**solid lines**), moderate (**long dashed lines**), or weak (**dotted lines**) seasonality in the food supply. Emergent growth patterns are from a forward simulation of an individual that follows the adaptive life strategy for the given environment from the age and size at recruitment to the maximum age. The probability of survival was from a forward cohort simulation of 100,000 individuals through time. Differences from a baseline risk of mortality, which was the same for all environments, are due to different energy dynamics and reproductive decisions.
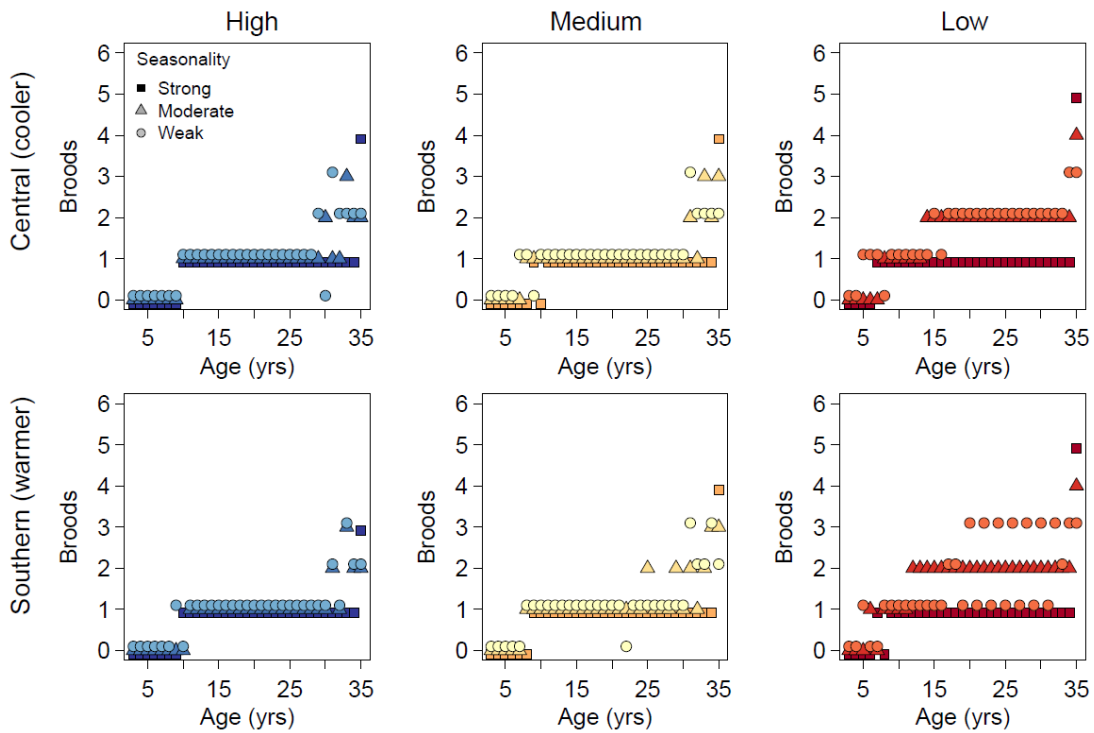
Figure 3.5 Strong seasonality favored single broods as an adaptive reproductive strategy (**squares**), whereas multiple broods were favored in environments with moderate or weak seasonality (**triangles and circles**). Multiple brooding was most common in low food environments, especially in the warmer, southern temperature regime (**lower right panel**). Graphs show the annual number of broods expected over the lifespan, which was influenced by age (years), mean food in the environment (**high, medium, low food: blues, orange/yellows, reds**), seasonality (**strong, moderate, weak: squares, triangles, circles**), and temperature (**cooler: upper panels; warmer: lower panels**). The high number of broods at (or near) the maximum age reflected a terminal investment in reproduction near senescence or death.
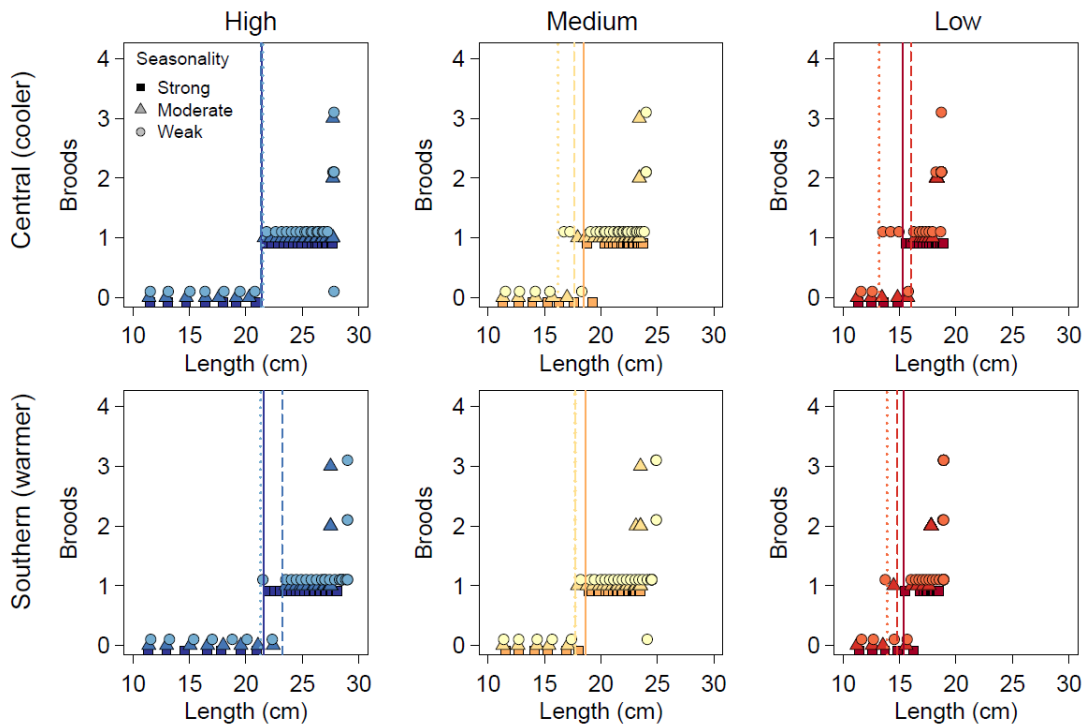
Figure 3.6 Multiple brooding was favored for the relatively largest females in each environment, but only in environments with moderate or weak seasonality (**triangles and circles**). Single broods were favored in strongly seasonal environments (**squares**), no matter maternal size. Mean food and sometimes the strength of seasonality influenced the length at maturation, shown by vertical lines (**blues-high food, orange/yellows-medium food, reds-low food; solid line-strong seasonality, long-dashed line-moderate seasonality, short-dashed line-weak seasonality**). Plots exclude broods at the maximum age of 35 to exclude boundary effects. Symbols and panels as described in Figure 5.
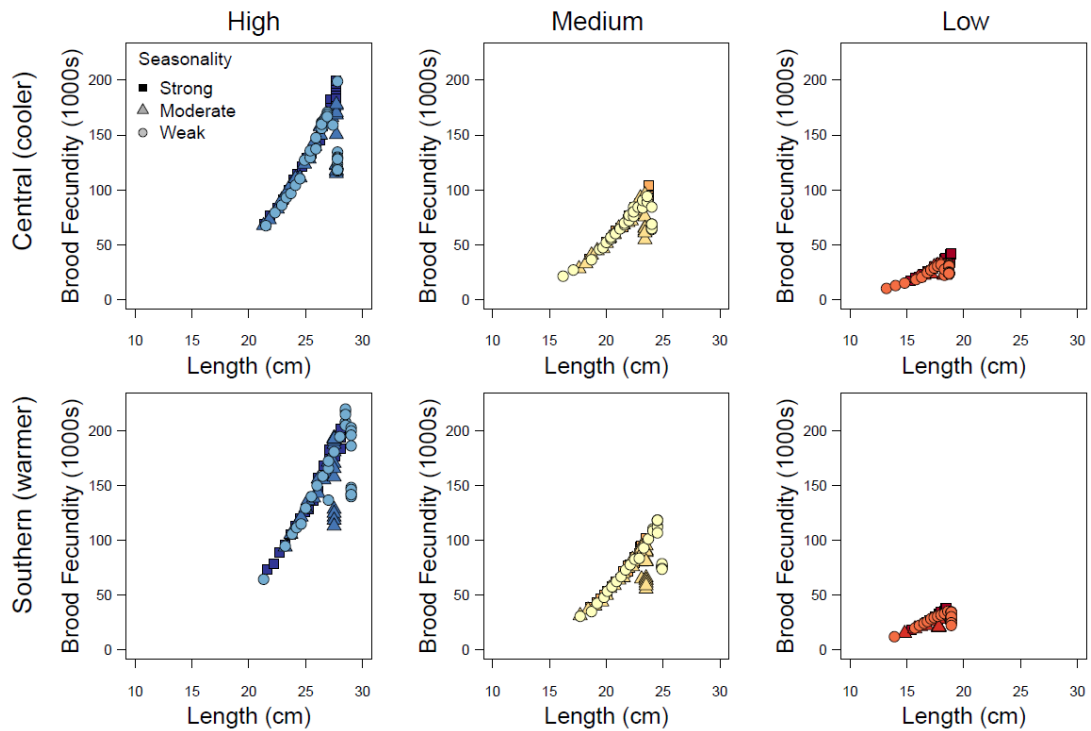
Figure 3.7 Brood size (brood fecundity) greatly increased with maternal length. Females generally produced the largest brood possible, given their current length and energy reserves when only producing a single brood. If producing multiple broods, broods were somewhat smaller for a given length. The large-sized broods of larger females greatly influenced a higher expected lifetime fecundity for females in environments with high food resources. Plots exclude broods at the maximum age of 35 to exclude boundary effects. Symbols and panels as described in Figure 3.5.
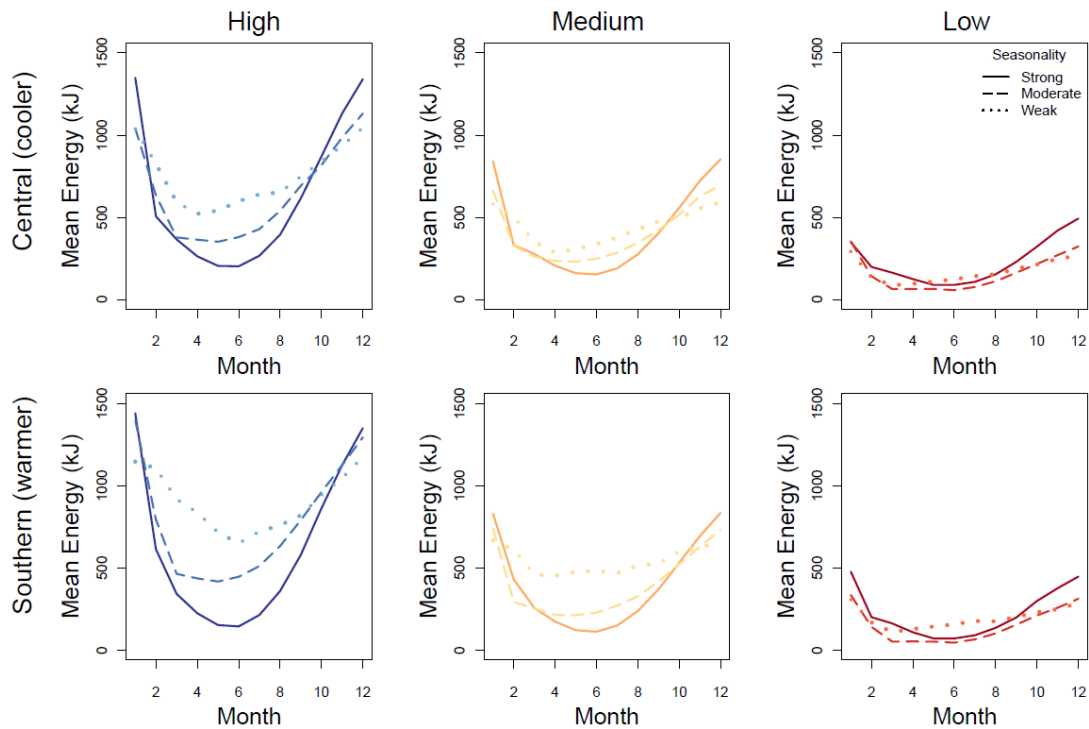
**Figure 3.8** Total energy reserves cycled annually depending on the environment. Total energy reserves were less for females in low food environments. In medium and high food environments, energy reserves fluctuated more when seasonality was stronger. Graphs show monthly variation in mean energy reserves (kilojoules) at the start of each month averaged over the lifespan of an individual. This was before allocating energy to growth and reproduction. The annual cycle of energy reserves reflected environmental patterns in the strength of seasonality modeled as strong (**solid lines**), moderate (**long-dashed**), or weak (**dotted**) seasonality. Mean food also influenced overall energy reserves for environments with high (**blues**), medium (**orange/yellows**), or low (**reds**) food resources. Temperature slightly influenced energy reserves between cooler (**upper**) and warmer (**lower**) environments. Plots exclude energy dynamics at the maximum age of 35 to exclude boundary effects.
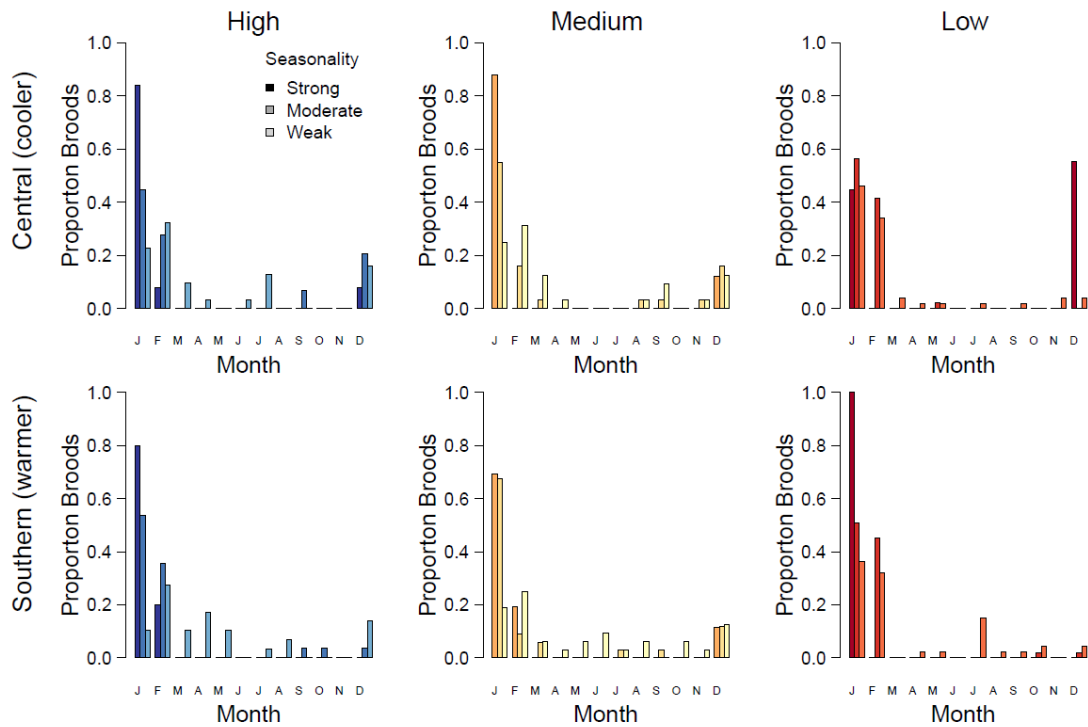
Figure 3.9 Stronger seasonality (**dark bars**) restricted reproduction to winter in the months of December, January, and February. A winter peak also occurred in environments with moderate and weak seasonality (**medium and lighter bars**), but broods could be produced outside of winter. Broods outside of the winter peak were generally the second (or third) of the season. If multiple brooding was expected, slightly more broods were expected outside of the winter peak season in warmer (**lower**) compared to cooler (**upper**) environments. Plots exclude the maximum age of 35 to exclude boundary effects.

Figure 3.10 Models (**colored lines and symbols**) were compared to Rosy rockfish collected in the central and southern regions of the California Current Ecosystem (**grey circles**, Fields 2016, Beyer et al. 2021, Beyer *et al.* unpublished data). **Left panels** show expected lifetime growth for females in high (**blue**), medium (**orange**), and low (**red**) food environments. Rosy rockfish von Bertalanffy growth curves of wild fish are shown as **grey, solid and dashed lines** (Chen 1971, Fields 2016). **Grey circles** are observations of females with age data for collections from 2009 to 2014 in the central and southern regions (Fields 2016). **Center panels** show annual broods of females in the medium (**orange/yellow colors**) and low (**red colors**) food environments, which most closely matched reproductive patterns of captive Rosy rockfish (**grey circles**, Beyer et al. 2021). **Right panels** show modeled brood sizes (**colored symbols**) compared to brood sizes of primary (first) and secondary (2nd +) broods for Rosy rockfish collected in central and southern California from 2009 to 2019 (Beyer *et al.* unpublished data). Note, the Rosy rockfish field and lab data do not differ between upper and lower panels.

Figure 3.10
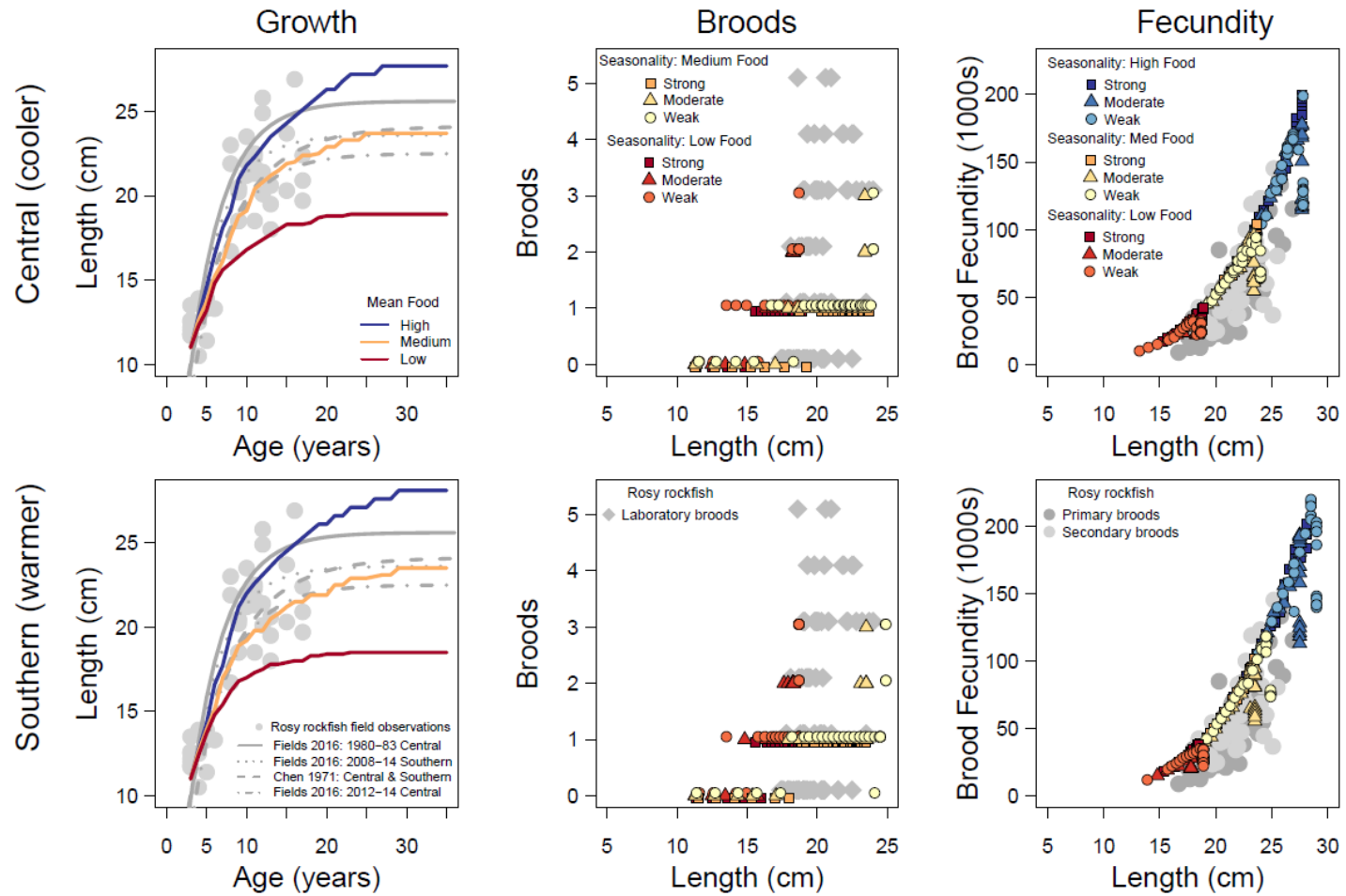
Conclusion

My dissertation research explored the causes and consequences of phenotypic plasticity in the reproductive traits of rockfishes of the California Current Ecosystem (CCE). Through empirical study in Chapters 1 and 2, I showed how reproductive traits, such as brood size and the frequency of reproduction are plastic and are influenced by fluctuating ocean environmental conditions. My laboratory study in Chapter 1 was important to demonstrate phenotypic plasticity in reproductive traits in response to different water temperature and feeding conditions and with respect to maternal body size. I found rosy rockfish (*Sebastes rosaceus*) collected from central California were capable of up to five larval broods a year under optimal and stable laboratory feeding conditions. Also, that multiple brooding increased annual fecundity, especially for large females with good food resources. The different environmental treatments of temperature and food availability in the laboratory strongly influenced maternal body condition and reproductive output. Reproductive variability included the possibility for skipped spawning when the body condition of females was very poor. The results of this study show how reproductive effort varies greatly depending on prevailing environmental conditions. Interestingly, I found that females could store sperm and fertilize up to five broods over a period of at least 10 months in the absence of males. This finding was important because it suggests that females of multiple brooding species do not need to re-mate in the wild between broods if enough sperm is acquired during the mating season, allowing for more flexibility in the timing of female reproduction.

In Chapter 2, I quantified inter-annual, size-dependent reproductive plasticity in the wild by collecting and analyzing a 20+ year time series of brood sizes for four shelf rockfish species of central California. This work contributed to knowledge about the importance of big, old, fat, fecund, female fish (BOFFFFs) (Hixon et al. 2014) and demonstrated high inter-annual variation in reproductive effort, especially for large females. I found that large females "take advantage" of years with favorable ocean conditions more so than smaller, younger spawners to greatly increase reproductive effort (by hundreds-of-thousands to millions more larvae per brood of an individual in a year with favorable conditions). Greater ocean productivity, described by the summer and fall mean conditions of the North Pacific Gyre Oscillation, was weakly but positively correlated with stronger maternal size effects for all four species. This meant that under favorable conditions the largest females disproportionately increased reproductive output compared to small females. This could be because small females were still growing and were more limited by energetic storage capabilities. These findings suggest that old, large females may be important to influencing strong year classes when ocean conditions are favorable for reproduction because they already produce disproportionately more offspring compared to small females (Dick et al. 2017) and can greatly increase reproductive output during favorable conditions.

In Chapter 3, I applied information gained from the laboratory and the field to develop a state-dependent life history model using Stochastic Dynamic Programming (SDP) and fish bioenergetics. I used the SDP model to explain spatial variation in the frequency of reproduction of rockfishes distributed from north to south in the California

Current Ecosystem (CCE). I found that spatial variation in the CCE was adaptive for rockfishes to cope with different environmental conditions that vary by latitude. Through this model, I mathematically showed how a single brooding strategy by females to the north is adaptive to cope with strong seasonality, which results in an annual period of food scarcity that causes net energetic losses. I show that multiple brooding is a strategy to increase and maximize fecundity in environments with weaker seasonality once females cease growth and reallocate energetic resources from growth to increased reproductive effort. However, the expected maximum size of a female will differ depending on the mean amount of food in the environment. Because of this, females in poor food environments are expected to be small, have small-sized broods, and therefore have much less expected lifetime fecundity compared to females in high food environments. My models suggest that multiple brooding is more prevalent in the southern region of the CCE because of weaker seasonality, warmer temperatures, and poorer ocean productivity there compared to regions to the north. However, if ocean productivity is less in the south, females are expected to cease growth earlier in life and thus will be smaller, produce small-sized broods, and be less productive overall even with a greater prevalence of multiple brooding. This hypothesis should be further explored.

Importantly, my dissertation research demonstrates environmental, energetic, and adaptive causes of phenotypic plasticity in reproductive traits and the expected consequences for both individual and population reproductive potential as environmental conditions vary through space and time. I conclude that reproductive

plasticity is adaptive and is also part of a life history strategy for moderate- to long-lived rockfishes to cope with contemporary seasonal, inter-annual, and spatial variation in ocean conditions that occur in the CCE. Phenotypic plasticity of reproductive traits is likely to buffer these populations against the negative impacts of climate change in the near term, as long as physical environmental conditions are within physiological tolerance limits. Phenotypic plasticity in reproductive traits allows females (especially large females) to "take advantage" of intermittent, favorable conditions and to survive extended periods of poor ocean conditions in the CCE (i.e., a storage effect) (Warner & Chesson 1985). However, longer-term shifts to warmer and less productive ocean waters are expected to produce smaller and less productive females over time. Therefore, it is important to consider how the environment, in addition to other anthropogenic stressors, such as exploitation, will influence growth, reproduction, and population dynamics of marine fishes, especially with climate change.

My dissertation inspires new questions and future directions of research. Clearly, bioenergetics strongly influence life history strategies for marine fish, including the evolution of phenotypic plasticity in life history traits. This has important implications for population reproductive potential as ocean environments change. Future work on fish bioenergetics in relation to growth and reproductive strategies is warranted, especially for how temperature affects metabolic and consumption rates. Globally, ocean temperatures are increasing and can influence seasonality, ocean productivity, and fish bioenergetics. A better understanding of temperature-dependence functions, including species-specific relationships (rather than a "general" relationship

for rockfish) and any evidence for local temperature adaptation will improve state-dependent model predictions for how temperature influences growth and reproductive strategies. Furthermore, combining better informed temperature-dependence functions with global ocean climate forecasting (Pozo Buil et al. 2021) will improve predictions about how growth and reproductive potential are expected to change as the ocean warms and primary productivity of large-sclae ecosystems changes. I argue that considering both annual cycles of temperature and changes in ocean primary productivity will be of key importance to understanding the vulnerability of marine fish to climate change and expected differences in growth and reproduction.

Another area of future research is the study of how reproduction affects survival. Theory posits that an increase in the risk of mortality due to reproduction is an important component driving state-dependent life history strategies (Jørgensen & Holt 2013). However, empirical evidence of this is lacking and therefore estimates of increased mortality with reproduction are highly uncertain. Empirical research will improve natural mortality estimates, which strongly influence selective pressures for life history strategies, and are also critically important to predicting population dynamics. Reproductive success, growth, and mortality influence population dynamics and knowing how these components of life histories change through time and space in relation to the environment is critical to understanding the vulnerability of populations to climate change and to inform sustainable management strategies.

Last, I recommend incorporating temporal stochastic environmental variability into the state-dependent model I developed in chapter 3 to fully understand the life

history strategy of rockfishes to cope with high spatiotemporal variation in environmental conditions in the CCE. Strong variation and high uncertainty in oceanographic conditions year to year is likely to influence the bioenergetics, probabilities of risk (in the food supply and survival), and thus will influence the adaptive life history strategy. For rockfishes, a long lifespan, itself, is adaptive to cope with years of unfavorable ocean conditions to reserve and invest energy into future reproduction when intermittent, good conditions arise. If the amount of food through time is uncertain, animals must mitigate their risk with strategies to ensure enough energy is stored to avoid starvation and that they reproduce before death (Mangel & Clark 1988, Clark & Mangel 2000, Jørgensen et al. 2006, Mangel 2015). Therefore, skipped spawning of rockfishes caused by poor energetic reserves may be predicted as a response to fluctuating ocean conditions of good and poor years through time rather than average spatial differences in seasonality, ocean productivity, and temperature modeled here. Incorporating temporal stochastic variation in fluctuating ocean conditions will also improve predictions for which reproductive and life history strategies (i.e., single- or multiple- brooding) are better suited to deal with increased temporal variability, temperature, and more extreme, less predictable climate events predicted for the CCE.

In conclusion, I show how phenotypic plasticity in life history traits is adaptive for marine fish, such as rockfishes, to cope with strong spatiotemporal variation in ocean environmental conditions. Phenotypic plasticity in life history traits maximizes egg production for individuals living in different environmental conditions. In the near

term, this strategy is likely to buffer populations against the negative impacts of climate change for these moderate- to long- lived species as long as individuals continue to survive periods of poor conditions and are able to take advantage of favorable conditions, when they arise. However, how these species will respond to future changes in ocean environmental conditions remains largely unknown, especially if prolonged unfavorable conditions persist or alterations to the expected lifespan occur, such as through the effects of exploitation (Barnett et al. 2017). My dissertation is an important step forward in linking variation in life history traits, especially reproduction, to bioenergetics and spatiotemporal variation in environmental conditions. This work will improve predictions for how populations will respond to future environmental change.

List of supplemental files

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