THE REPRODUCTIVE BIOLOGY OF

YELLOWEYE ROCKFISH (*SEBASTES RUBERRIMUS*) IN

PRINCE WILLIAM SOUND AND THE NORTHERN GULF OF ALASKA

By

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Abstract

Over the last half century, Yelloweye Rockfish *Sebastes ruberrimus* have experienced dramatic declines along the West Coast of the United States and British Columbia. Efforts have been made throughout the species' range to rebuild and sustainably manage stocks, including the introduction of a Statewide Rockfish Initiative by the State of Alaska, which intends to develop management strategies for Yelloweye Rockfish in the Gulf of Alaska. To support this effort and address information gaps in Yelloweye Rockfish reproductive biology throughout their range, I estimated important reproductive parameters and life history information for Yelloweye Rockfish in Prince William Sound and the Northern Gulf of Alaska, Alaska, that included maturity, parturition timing, skip spawning, and fecundity relationships. I identified that ages-at-50% maturity (A_{50}) for males and females were similar (A_{50} = 15 years and A_{50} = 16, respectively), but males reached full maturity (A_{95}) earlier than females (male A_{95} = 19 years and female A_{95} = 31 years). Female Yelloweye Rockfish fork length-at-50% and 95% maturity (L_{50} and L_{95}) was greater in the Northern Gulf of Alaska (L_{50} = 46.7 cm and L_{95} = 55.8 cm) than in Prince William Sound (L_{50} = 41.1 cm and L_{95} = 50.2 cm). Similarly, male L_{50} and L_{95} was greater in the Northern Gulf of Alaska (L_{50} = 44.0 cm and L_{95} = 49.2 cm) relative to Prince William Sound (L_{50} = 40.8 cm and L_{95} = 46.0 cm), and males matured at a smaller size than females. Female L_{50} was consistent with data from southern populations, but A_{50} was younger than predicted based on a latitudinal trend, indicating that Yelloweye Rockfish in this region may experience greater than expected growth rates. Yelloweye Rockfish underwent parturition between May and August and peaked in June and July, and parturition timing was earlier for larger and older females. I documented that female Yelloweye Rockfish skip-spawned at a rate of 9.8%. Skip spawning rate was associated with fork length and peaked at sizes between 40.2

cm and 52.3 cm; the peak in stock reproductive potential is shifted toward larger females in response to skip spawning. I conducted egg and larvae counting in an image-analysis software, which was more than four times faster than manual counting and was equally accurate and precise. Yelloweye Rockfish fecundity scaled hyperallometrically with FL and relative fecundity increased with length, indicating that spawning stock biomass may not be proportional to total egg production. Combining these results, I found that ignoring the hyperallometric fecundity relationship and skip spawning could overestimate reproductive potential by as much as 66% and 45% for Prince William Sound and the Northern Gulf of Alaska, respectively. The results of this study will improve the estimates of stock-recruitment dynamics and can be readily integrated into a stock assessment that will guide the sustainable management of Yelloweye Rockfish in Prince William Sound and the Northern Gulf of Alaska.

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General Introduction

Since the origin of modern fisheries management, biologists have attempted to quantify the spawning stock necessary to sustain recruitment and harvest (Ricker 1954; Beverton and Holt 1957). Hence, management targets based on principles of sustainability were created and employed by fisheries management over the next several decades: maximum sustainable yield (MSY; Schaefer 1954), optimum sustainable yield (OSY; Roedel 1975), and other yields that are derivatives of these seminal yield concepts (e.g., Pretty Good Yield; Hilborn 2008). These fundamental concepts form the basis for target and limit/threshold reference points that define harvest levels for fisheries around the globe (Barber 1988; Quinn et al. 1990; Mace 2001), and are intended to prevent recruitment overfishing, which is when the reproductive capacity of a stock has been depleted to a level where it can no longer replenish itself (Walters and Martell 2004). Most concepts of sustainable yield require some fundamental understanding of stock-recruitment dynamics and/or a knowledge of the species' reproductive biology. Unfortunately, stock-recruitment relationships are lacking for many marine species and recruitment data are often highly variable (Goodyear 1993).

A group of marine fishes with understudied stock-recruitment relationships is rockfishes (genus *Sebastes*). Species within this genus are long-lived with numerous year classes contributing to spawning stocks (Love et al. 2002). Rockfishes experience highly variable recruitment with sporadic peaks (Parker 2000; Love et al. 2002) and exhibit maternal effects on viability of eggs and larvae that can complicate stock-recruitment relationships (Berkeley et al. 2004; Sogard et al. 2008). Further, rockfishes are late maturing (Love et al. 2002) and many species experience fishing mortality prior to, or at, maturity (Parker 2000). The life-history strategy of rockfish has complicated the application of sustainable yield concepts such as MSY

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to rockfish management and rockfish life-history traits have contributed to widespread declines in rockfish stocks (Ralston 1998; Musick 1999; Parker 2000)

For years, fisheries researchers have attempted to predict parameters of rockfish stock-recruitment relationships (Dorn 2002) and develop spawning stock biomass per recruit (SSBR) proxies of MSY for rockfishes (Clark 1993; Clark 2002; Dorn 2002), often using other groundfish and/or data-rich rockfish species as proxies. However, no consensus on a single proxy for the genus has yet to be determined. Initially, a fishing mortality (F) that reduced SSBR to 35% of unfished levels ($F_{35\%}$) was adopted as the West Coast groundfish proxy for F at MSY (F_{MSY}; Clark 1993; Mace 1994), but continued declines in rockfish revealed that this fishing intensity was too aggressive for the life history of rockfish. Dorn (2002) and Clark (2002) both showed that a more conservative proxy (e.g., $F_{50\%}$ to $F_{60\%}$) is necessary for risk-averse management of rockfish, especially for long-lived stocks with low resiliency (e.g., Yelloweye Rockfish *Sebastes ruberrimus*). Estimating these MSY proxies relies heavily on estimates of reproductive potential (RP), which requires accurate estimates of life-history parameters, including maturity and fecundity (Marshall 2009).

Spawning biomass per recruit is used to approximate F_{MSY}. Such estimates are often based on reproductive output, estimated as female spawning stock biomass (SSB) which carries many assumptions including constant relative fecundity and egg quality with age or length. These assumptions may not suit the complex facets of rockfish reproductive life history. Female SSB is defined as the total biomass of mature females in a stock and is the product of the number (*n*), proportion mature (*Q*), and mean weight (*w*) for females at age or length (*i*):

$$SSB = \sum_{i=1}^{\max.i} n_i Q_i w_i.$$

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Spawning stock biomass as a measure of reproductive output assumes that mature female biomass is proportional to total egg production (TEP; Rothschild and Fogerty 1989). Total egg production is estimated as:

$$TEP = \sum_{i=1}^{\max. i} n_i Q_i f_i,$$

where f_i is the fecundity at age or length i. While TEP provides a more realistic representation of RP than SSB (Kell et al. 2015), these metrics can fail to take into account parental condition and experience, sex ratio, spawning omission, and other factors that affect offspring viability (e.g., preferential spawn timing, lipid content; Trippel 1999; Kell et al. 2015). Trippel (1999) introduced the term stock reproductive potential (SRP) as an improvement over SSB and TEP because it attempts to incorporate maternal effects and more comprehensive reproductive biology information, including size-fecundity relationships and non-annual reproduction (i.e., skip spawning). Traditional estimates of RP and stock-recruitment models may be biased and mis-specify stock-recruitment dynamics if the metrics noted above are not included in analyses (Trippel 1999; Marshall et al. 2003); this would influence the estimates of biomass at maximum sustainable yield (B_{MSY}), F_{MSY}, and stock-assessment results. Stock reproductive potential and even TEP demands the need for further research into parent-progeny relationships and reproductive biology.

Spawning biomass of Yelloweye Rockfish stocks from California to British Columbia have declined to as low as 12% of estimated pre-fished levels (Wallace 2001; Drake et al. 2010; Yamanaka et al. 2011). For example, stocks along the West coast were declared overfished in 2002 relative to a spawning biomass of 25% of pre-fished level ($SB_{25\%}$; Gertseva and Cope 2017). These stocks have been rebuilding since 2002 with an exploitation rate restricted to no

greater than a spawning potential ratio (reproductive output of fished stock relative to an unfished stock) of 76% (Gertseva and Cope 2017). In 2008, the Committee on the Status of Endangered Wildlife in Canada listed the inside and outside British Columbia (BC) populations of Yelloweye Rockfish as stocks of special concern (COSEWIC 2008). In addition, a distinct population segment (DPS) of Yelloweye Rockfish in Puget Sound and the Georgia Basin was listed as threatened under the Endangered Species Act in 2009 (NMFS 2017). The widespread decline of Yelloweye Rockfish from California to BC has raised concerns about the unknown status of Alaskan stocks (Howard et al. 2019; S. Meyer, Alaska Department of Fish and Game, *personal communication*). A stock assessment has yet to be conducted for many populations of Yelloweye Rockfish in Alaska, including Prince William Sound and the Northern Gulf of Alaska, owing in part to a lack reproductive information for the species in this region (Howard et al. 2019). The stock assessments conducted for Yelloweye Rockfish outside of Alaska have leaned on estimates and reference points based on spawning stock and reproductive output. The overall goal of my thesis research is to provide robust estimates of Yelloweye Rockfish reproductive parameters to improve the accuracy of RP, B_{MSY}, and F_{MSY} models for the sustainable management of Yelloweye Rockfish in Alaska.

Chapter 1: Maturity, Ovarian Cycle, and Skip Spawning of Yelloweye Rockfish *Sebastes ruberrimus* in Prince William Sound and the Northern Gulf of Alaska[1]

ABSTRACT

Life-history information for Yelloweye Rockfish *Sebastes ruberrimus* is lacking in Alaska and, has limited the development of a regional stock assessment. This project investigated Yelloweye Rockfish reproductive biology at their northernmost distribution in Prince William Sound (PWS) and the Northern Gulf of Alaska (NGOA) and provided reproductive parameters that are inputs to stock assessments. We collected Yelloweye Rockfish in PWS and NGOA during 2018–2019, and individuals were assigned development stage and maturity values through histological examination. The probability of maturity was estimated as a function of fork length, sex, and sample area. Females reached age-at-50% (A_{50}) and 95% (A_{95}) maturity at 16 and 31 years, respectively; A_{50} and A_{95} were 15 and 19 years for males. Female Yelloweye Rockfish in the NGOA reached length-at-50% (L_{50}) and 95% (L_{95}) maturity at 46.7 cm and 55.8 cm, respectively, and in PWS, reached L_{50} at 41.1 cm and L_{95} at 50.2 cm. Males matured at a smaller size than females in both sample areas. Female L_{50} was consistent with data from southern populations, but A_{50} was younger than predicted based on a latitudinal trend, indicating that Yelloweye Rockfish in this region may experience faster growth. Parturition of Yelloweye Rockfish larvae occurred between May and August, with timing earlier for older and larger females. Mature females were documented to skip spawn at a rate of 9.8%, and mean skip spawning rates were greatest at intermediate lengths (40.2 to 52.3 cm). These results advance our understanding of the reproductive biology for this species, and will be useful for accurate estimation of reproductive potential while providing information for stock assessments that inform management decisions for Yelloweye Rockfish in PWS and NGOA.

INTRODUCTION

The life-history strategy of a species or group of species is indicative of environmental adaptations to maximize lifetime reproductive success (Bell 1980; Roff 1992; Wootton 1992). Winemiller and Rose (1992) classified life-history strategies into three main groupings: equilibrium, periodic, and opportunistic strategists. Later, a salmonic strategy was later added to this framework (E-P-O-S; McCann and Shuter 1997). Within the E-P-O-S framework, Pacific rockfishes (genus Sebastes) are categorized as periodic strategists owing to their protracted reproductive cycle (i.e., longevity and late maturity) and low juvenile survival. Rockfishes, like many other periodic strategists, may experience extended periods between strong recruitment classes. Delayed maturity coupled with longevity ensure eventual reproductive success over long time scales. As a result, estimates of maturity are critical to understanding a stock's reproductive capacity and response to environmental conditions by periodic strategists such as Pacific rockfishes.

Generally, rockfishes grow slowly, mature late, and exhibit low rates of natural mortality as adults (Love et al. 2002). For example, an individual Yelloweye Rockfish *Sebastes ruberrimus* from Southeast Alaska was aged to be 121 years old, placing this species amongst the longest-lived teleosts (O'Connell et al. 2002). This longevity corresponds to a low natural mortality rate for Yelloweye Rockfish and suggests that high levels of fishing mortality may not be sustainable for the species (Hoenig 1983; Leaman and Beamish 1984; Cortés 2002). Based on life history information from the California Current ecosystem and Southeast Alaska, Yelloweye Rockfish have a late maturity (7–22 years) schedule relative to most other rockfishes (Love et al. 2002; O'Connell et al. 2002). Such delayed maturation is likely a bet-hedging strategy to ensure eventual reproductive success in a highly variable ocean environment

(Goodman 1984; Philippi and Seger 1989; Hixon et al. 2014). Successful recruitment of planktonic rockfish larvae is episodic across years and survival requires ideal oceanographic conditions, including onshore Eckman transport and upwelling and downwelling regimes that align with life cycle stages (Parrish et al. 1981; Norton 1987; Love et al. 2002). Owing to these life-history characteristics, Yelloweye Rockfish are highly vulnerable to over-fishing, which emphasizes the need for a detailed stock assessment for this species throughout its range.

Yelloweye Rockfish range from northern Baja California along the West Coast of the United States and British Columbia to as far north as Prince William Sound, AK and west as the Aleutian Islands, AK (Mecklenburg et al. 2002). Outside of Alaska, many Yelloweye Rockfish stocks have undergone significant reductions in spawning biomass, with some reduced to as low as 12% of estimated pre-fished levels (Wallace 2001; Drake et al. 2010; Yamanaka et al. 2011). Further, a distinct population segment (DPS) of Yelloweye Rockfish in Puget Sound and the Georgia Basin was listed as threatened under the U.S. Endangered Species Act in 2009 (NMFS 2017), and this DPS is estimated to require 60 years to rebuild with costs exceeding US$82 million (NMFS 2017). A stock assessment has not been conducted for northern populations of Yelloweye Rockfish in the Gulf of Alaska, owing in part to a lack reproductive information for this species in this region (Howard et al. 2019).

Increasing age-at-maturity with latitude has been documented in numerous fishes (Ni and Sandeman 1994; Abookire and Macewicz 2003; Farley et al. 2014). The Northern Gulf of Alaska (NGOA) and, more specifically, Prince William Sound (PWS) in Southcentral Alaska, represent the most northern distribution of Yelloweye Rockfish (Love et al. 2002; Mecklenburg et al. 2002). Maturity estimates for this species in NGOA and PWS have yet to be developed (Haldorson and Love 1991), and it is expected that age at maturity in these areas will be older

than those elsewhere in the species' range based on latitude. This late onset of maturity could result in increased risk of harvesting immature fish (Holt 1895; Myers and Mertz 1998). In addition, subtle changes in reproductive parameters (e.g., age or length at maturity) can affect estimates of stock reproductive potential (RP), productivity (Morgan and Brattey 2005), and the uncertainty of these estimates (Marteinsdottir and Begg 2002). It is important to generate region-specific maturity estimates for Yelloweye Rockfish in Prince William Sound and the Northern Gulf of Alaska owing to the implications of maturity on estimates of RP and the trend of increasing maturity with latitude.

Yelloweye Rockfish are viviparous and primitively matrotrophic (i.e., females give birth to live young and embryos receive nutrients from the mother in addition to the yolk; Boehlert and Yoldavich 1984; Love et al. 2002), similar to other *Sebastes* species. The gestation period (fertilization to parturition of larvae) for some rockfish species is protracted and highly variable within and among populations, varies as a function of size or age, and larger females have been observed to complete parturition earlier relative to smaller females (Bobko and Berkley 2004; Sogard et al. 2008; Stafford et al. 2014). Early parturition timing in larger, older fish has been hypothesized to be a bet-hedging strategy in the form of diversified annual reproductive effort (Sogard et al. 2008). Yelloweye Rockfish courtship and copulation is thought to occur during the late fall and early winter with a later parturition date at northern latitudes (Love et al. 2002), but information on reproductive timing in PWS and NGOA is lacking.

Skip spawning is the omission of mating by a mature fish during a reproductive season (Rideout et al. 2005; Rideout and Tomkiewicz 2011). According to reproductive theory, skip spawning is the trade-off between immediate reproductive output and survival as a strategy to increase lifetime reproductive output, since fecundity increases with size and age (Bull and Shine

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1979; Jørgensen et al. 2006; Folkvord et al. 2014). This strategy has been documented in many

iteroparous fishes (Rideout et al. 2005; Secor 2007; Skjæraasen et al. 2015). Three deepwater

rockfishes (Blackspotted Rockfish *Sebastes melanostictus*; Rougheye Rockfish *S. aleutianus*;

Shortraker Rockfish *S. borealis*) were recently documented to skip spawn (Conrath 2017). Skip

spawning is not well-documented in Yelloweye Rockfish, but mature fish classified as 'resting'

throughout the gestational period have been observed (Hannah et al. 2009). These fish would

likely be classified as skip spawners but were not formally identified as such. Neglecting skip

spawning can result in overestimates of RP, which can lead to biased biological reference points

and, potentially, overfishing (Rideout et al. 2005; Secor 2007; Skjæraasen et al. 2015).

The goal of this study was to quantify the reproductive biology of Yelloweye Rockfish

in the northernmost extent of their range to provide information that fisheries managers can use

to manage this commercially and recreationally important species. Our objectives were to: (1)

estimate age- and length-at-maturity as a function of sex and sample area; (2) produce an ovary

development schedule to identify important reproductive events such as copulation and peak

parturition; (3) determine whether parturition timing is age- and/or length-specific; and (4)

investigate the presence of skip spawning and relate skip spawning rates to fish age and length.

In addition, we set our results in the context of age and length at maturity data collected from

southern populations. Overall, our results contribute to more accurate estimation of RP, aid

parameterization of stock assessments models, and inform management objectives (e.g., maintain

stock age-structure).

METHODS

Study area.—Prince William Sound is characterized by a diversity of coastal habitats that

include glacial fjords, high-relief rocky islands, and tidally influenced bays and estuaries

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(Schmidt 1977). The inner waters of PWS are separated and protected from the NGOA by a series of barrier islands, which include the expansive Montague (791 km^2) and Hinchinbrook (445 km^2) islands. With over 4,000 km of rocky coastline, potential demersal rockfish habitat is plentiful in PWS. For the purpose of this study, the inside waters of PWS were defined as all waters north of lines between the eastern tip of Hinchinbrook Island and Cordova, the eastern tip of Montague Island and the southern tip of Hinchinbrook Island, and all waters north of a line at 60°N extending from Montague Island to Cape Puget (Figure 1.1).

The NGOA, which is adjacent to PWS to the south, is bounded by lines at Gore Point in the west (148°00'25"W) and near Cape Suckling in the east (144°00'00"W), and extends south to a longitudinal line at 59°00'00"W (Figure 1.1). The NGOA is more oceanic than PWS and contains portions of the Alaska outer continental shelf, shelf break, and slope. The coastline is noticeably more rugged with unique geological formations and erosion from large oceanic swells. Swells in excess of 2 m are not uncommon in the outside waters, and access is limited to larger recreational and commercial vessels. Away from the coastline, much of the NGOA seafloor is flat and mostly comprised of soft sediment. However, there are intermittent small mounds, rocky reefs, and pinnacles that provide habitat for demersal fish species such as rockfishes and Lingcod *Ophiodon elongatus*.

Sample Collection.—Yelloweye Rockfish were collected opportunistically throughout the year during 2018 and 2019. Samples were collected using hook-and-line during surveys, primarily between Gore Point and Cape Suckling, and included the inside waters of PWS. Additional samples were collected from Alaska Department of Fish and Game (ADFG) commercial and recreational port sampling programs, commercial catch in Seward and Cordova, and recreational catches in Whittier and Valdez, Alaska. Each fish was measured for FL (cm) and weighed to the

nearest 0.05 kg with date of capture and location recorded. Whole gonads were removed and weighed to obtain a fresh gonad weight (g) and then preserved in a glyoxal solution (Glyofixx™) or 10% neutral buffered formalin. Fixed gonad weight (g) was measured in the laboratory prior to histological processing.

Aging.—Otoliths were collected from each Yelloweye Rockfish, cleaned in soapy water, and stored in an envelope. Age estimation (in years) was performed by two readers using the break-and-burn method (Chilton and Beamish 1982). The two readers worked to resolve any discrepancy and come to an agreement on the age (Failor 2016; Rumble et al. 2017). If a consensus on an age was reached, it was reported as a final resolved age and used in data analysis.

Maturity.—All Yelloweye Rockfish gonads were initially assessed for development stage based on macroscopic observations. If possible, the initial macroscopic determination of stage of development and maturity was made in the field, prior to preservation. As a result, a binary maturity value was assigned: mature (1) or immature (0). The stage of development and maturity for male testis was determined using the criteria described in Wyllie Echeverria (1987), which focuses on size, shape, and the presence of sperm in sampled testes. Female macroscopic staging and maturity were based on criteria adapted from Westrheim (1975; Table 1.1).

Histological examination was used to validate the initially assigned macroscopic stage and maturity of Yelloweye Rockfish gonads. Histological slides were prepared from preserved gonads by embedding a subsample in paraffin wax, thin-sectioning the tissue to 5–7 μm, and then staining the subsample with haematoxylin and eosin Y (West 1990; Hannah et al. 2009). Slides were viewed at 100–200x magnification with a Leica DM1000 light microscope (Leica Microsystems, Wetzlar, Germany) and photographs were captured with a mounted Leica MC170

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camera. Ovarian staging and maturity were verified or corrected based on the stage of the most advanced oocyte or embryo, as described by Conrath (2017) based on a modified key by Bowers (1992). Males maturity status was validated using histological classifications described in Wyllie Echeveria (1987). Shaw et al. (2012) was frequently used as a supplemental reference to identify key cellular features of gonadal tissue. Histological evaluation was performed on all gonads except for ovaries that contained eyed eggs or larvae. These histological examination methods were used to assign final stage of gonad development and a binary maturity value.

Binary maturity values were used as the response variable to estimate the probability of maturity as a function of age or FL, sample area (PWS or NGOA), and sex (female or male). The full model included a three-way interaction of age or FL, sample area, and sex. Zero-one indicator variables were used with PWS (x_{il}=0) and females (x_{ik}=0) as the baseline for sample area and sex, respectively. The logistic function was given as:

$$log\left(\frac{\pi_{ijkl}}{1-\pi_{ijkl}}\right) = \beta_0 + \beta_1 x_{ij} + \beta_2 x_{il} + \beta_3 x_{ik} + \beta_4 x_{ij}x_{il} + \beta_5 x_{ij}x_{ik} + \beta_6 x_{ik}x_{il} + \beta_7 x_{ij}x_{ik}x_{il}, \quad (1)$$

where π_{ijkl} is the probability that an individual i of length or age j and sex k captured from sample area l was mature. The response π_{ijkl} was assumed to follow an approximately Bernoulli distribution. The age or FL at 50% maturity (A_{50} or L_{50}) can be determined by simply setting π_{ijkl} to 0.5, and reorganizing the model parameters to one of following equations depending on sample area and sex:

$$A_{50} \text{ or } L_{50} | \text{ age or FL, PWS, Female} = -\frac{\beta_0}{\beta_1} \quad (2)$$

$$A_{50} \text{ or } L_{50} | \text{ age or FL, NGOA, Female} = -\frac{\beta_0+\beta_2}{\beta_1+\beta_4} \quad (3)$$

$$A_{50} \text{ or } L_{50} | \text{ age or FL, PWS, Male} = -\frac{\beta_0+\beta_3}{\beta_1+\beta_5} \quad (4)$$

$$A_{50} \text{ or } L_{50} | \text{ age or FL, NGOA, Male} = -\frac{\beta_0+\beta_2+\beta_3+\beta_6}{\beta_1+\beta_4+\beta_5+\beta_7} \quad (5)$$

The sum of terms in the numerator of each A_{50} or L_{50} equation is the intercept of the logistic regression of maturity and the sum of denominators is the slope. Additionally, age or FL at 95% maturity (A_{95} or L_{95}) were estimated by subtracting $log\left(\frac{0.95}{0.05}\right)$ from the numerator of each possible A_{50}/L_{50} equation. The shape of a given maturity curve can be determined by simply reporting A_{50} and A_{95} or L_{50} and L_{95} together rather than the logistic regression slope and intercept, which can be relatively abstract to interpret. For this reason, we also reported A_{95} and L_{95}.

We used Bayesian inference to estimate parameters for the maturity logistic regression. A three Markov-chain Monte Carlo (MCMC) simulation with uninformative, normally distributed priors for each parameter. Simulations were conducted in the statistical program environment R (R Core Team 2018) using the jagsUI package (Kellner 2018). All parameters were assumed to follow a normal distribution, with a mean θ and variance σ^2 (Doll and Lauer 2013). Each chain was comprised of 50,000 iterations with a 10,000 initial burn-in period for each chain. A model selection process was executed by running an MCMC for all models nested between the full model presented above and a simpler form of the model that only incorporated age or FL. The full model represented four maturity curves with different intercepts and slopes for each sex and sample area. We used a Bayesian leave-one-out cross-validation (LOO) with Pareto-smoothed importance sampling (PSIS) to assess the pointwise out-of-sample prediction accuracy for the 14 candidate models (Vehtari et al. 2016); models that did not include age or length were excluded from the model evaluation and selection process. Log-likelihood was evaluated at each of the posterior simulations for the parameter values of each model and each data point. From the resulting matrix of log-likelihoods, we estimated the PSIS-LOO expected log pointwise predictive density (elpd) and the leave-one-out information criterion (LOOIC; -2*elpd) for each

model using the 'loo' package (Vehtari et al. 2016a, 2016b). The model with the greatest elpd, or equivalently, the lowest LOOIC value was selected as the model best represented by the data (Vehtari et al. 2016). The median and 95% credible intervals (CI) of the posterior distribution were reported for all parameters including all subsets of A_{50}/L_{50} and A_{95}/L_{95} for the selected model.

Latitudinal effects on female age- and length-at-maturity.—We reviewed published papers on Yelloweye Rockfish maturity based on the bibliography in Love et al. (2002) and a literature search for additional papers. Data on sample size, mean or median estimates of A_{50} and L_{50}, methods, and location were compiled from each study. Individual study locations were classified as the median latitude of the described study area or the latitude of the sampling port. A simple linear regression analysis was conducted for female Yelloweye Rockfish maturity-at-age and -size as a function of latitude.

Ovarian Cycle.—We generated an ovary development schedule confirmed by histology for each month of the year based on the proportion of mature Yelloweye Rockfish at a given macroscopic stage of development. Samples from PWS and NGOA were combined to evaluate development timing. A calendar for male development could not be created because males were not sampled during their reproductive season; as a result, only two stages of development were documented: immature or a sexually inactive mature state (resting). The ovarian development calendar was used to identify peak parturition, which was identified as the two months with the largest decrease in the proportion of ripe females (stage 5) and largest increase in spent females (stage 6).

Age- and size-specific parturition.—We tested for relationships between parturition timing and female age or size using a logistic regression. Binary values were assigned based on status of

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parturition: post-parturition (1 = stage 6) or gravid (0 = stage 4 or 5). All immature and sexually inactive (resting) fish were excluded. Sample month was included as a covariate; however, only months of possible parturition were used. The form of the model follows:

$$log\left(\frac{\pi_{ijm}}{1-\pi_{ijm}}\right) = \beta_0 + \beta_1 x_{ij} + \beta_2 x_{im}, \tag{6}$$

where π_{ijm} was the probability that an individual i of length or age j captured during month m was in a post-parturition state. A likelihood ratio test was conducted to determine the significance of sample month in the logistic regression of the probability of a mature female being spent, using an $\alpha = 0.05$. The null hypothesis (H_0) is a reduced model without a term for capture month. If the month and FL or age term were found to be significant, we would infer that age and/or length influenced the timing of parturition. A significant positive coefficient for the month effect (β_2) indicates that size decreases over the parturition season and, therefore, larger or older females give birth earlier. Conversely, a negative coefficient indicates that smaller or younger females give birth earlier in the season.

Skip spawning.— Based on the aforementioned reproductive calendar, we examined female Yelloweye Rockfish for skip spawning based on a reproductive season defined as April through June. Ovary development has progressed enough by this time period that females will continue to develop through to parturition if they are beyond stage 4 (fertilized), and the ovaries of any skip spawners would have regressed (Rideout et al. 2005; Conrath 2017). Skip spawning identification was based on histological examination and criteria from Conrath (2017) for three different rockfish species. A mature female was classified as a skip spawner if there was clear evidence of previous reproductive activity, namely post-ovulatory follicles and/or a relatively high proportion ($\geq 15\%$) of beta- or delta-atretic cells (Shaw et al. 2012; Conrath 2017). Skip spawning rate was evaluated at the population level as the proportion of skip spawning females

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relative to the number of mature females examined from April to June. The proportion of skip spawners was modeled as function of age and FL using second order polynomial logistic regression, as shown below:

$$log \left(\frac{\pi}{1-\pi}\right) = \beta_0 + \beta_1 x + \beta_2 x^2,$$ (7)

where π is the proportion of female Yelloweye Rockfish at a given length or age, x. We used a likelihood ratio test to determine the significance of squared term for age or length in the logistic regression of skip spawning, based on $\alpha = 0.05$. All analyses were performed using the statistical program environment R, version 3.6.1 (R Core Team, 2019).

RESULTS

Maturity.— We collected 520 Yelloweye Rockfish that ranged from 25.3 to 80.0 cm in length (mean = 50.6 cm, SD = 10.5; N = 520) and 6 to 93 years in age (mean = 27 year, SD = 10.5; N = 497). There were 253 and 267 Yelloweye Rockfish collected from PWS and the NGOA, respectively (Table 1.2). In total, 147 Yelloweye Rockfish were classified as immature and 373 fish were identified as mature. The smallest mature female was 36.4 cm, while the largest immature female was 59 cm. The smallest mature male observed was 39.2 cm and the largest immature male was 47.5 cm. The oldest immature Yelloweye Rockfish were 34 and 21 years for females and males, respectively. Of the 418 females macroscopically examined for maturity, stage of development was revised for 14.6% (N = 51) and maturity was reclassified for 7.7% (N = 32) following reexamination of histological subsamples. Errors in stage and maturity classifications were most common between stages 2 and 7. For the 83 males examined macroscopically, stage of development was corrected for 28.9% (N = 24) after histological examination, which resulted in a 7.2% (N = 6) maturity reclassification.

The best model explained by the Yelloweye Rockfish maturity-at-age data included an age-sex interaction based on out of sample prediction accuracy, but did not include a term for sample area (Table 1.3). The age-sex interaction resulted in separate maturity-at-age curves for females and males with distinct slopes and intercepts (Figure 1.2). Female and male A_{50} were similar (approximately 16 and 15 years, respectively; Table 1.4). However, the substantial difference in slopes for females and males resulted in distinct curves where female probability of maturity increases gradually with age but males exhibited a steeper, knife-edge curve (Figure 1.2). The median estimate for female A_{95} was approximately 31 years and male A_{95} was 19 years (Table 1.4).

Yelloweye Rockfish maturity-at-length was best explained by sex, length, sample area, and the interaction between length and sex (Table 1.3). Therefore, the best model predicted four distinct maturity curves with different slopes and/or intercepts, depending on sample area and sex (Figure 1.3 and 1.4). Length-at-maturity for female Yelloweye Rockfish in NGOA was approximately 46.7 cm and 55.8 cm for L_{50} and L_{95}, respectively (Table 1.5). Female Yelloweye Rockfish in PWS reached 50% maturity (L_{50}) at approximately 41.1 cm and 95% maturity (L_{95}) at 50.2 cm (Table 1.5). The two female maturity curves are parallel logistic regression curves (equal regression slopes), indicating that the female Yelloweye Rockfish in PWS and NGOA matured at the same rate with respect to length. Female Yelloweye Rockfish in the NGOA matured at a larger size than females in PWS (Figure 1.3). Length-at-maturity was estimated at approximately 44.0 cm for L_{50} and 49.2 cm for L_{95} for male Yelloweye Rockfish in NGOA, and 40.8 and 46.0 cm, respectively, for males in PWS (Table 1.5). Similar to females, NGOA male Yelloweye Rockfish matured at a larger size than PWS males (Figure 1.4). Male maturity-at-

length curves were much steeper than female curves, with females maturing at a slightly larger

size relative to males from the same area.

Latitudinal effects on female age- and length-at-maturity.—We reviewed female Yelloweye

Rockfish maturity estimates from six publications that included eight estimates of A_{50} and L_{50}

(Table 1.6). The studies ranged from California to Southeast Alaska. Age-at-50% maturity ranged

from 7 to 22 years (mean = 16.4 years, SD = 4.6; N = 8) and L_{50} ranged from 38.8 to 52 cm

(mean = 44.3 cm, SD = 4.5; N = 8). Age-at-50% maturity was positively associated with latitude

($r^2 = 0.92$; F-statistic = 68.45, df = 6, $P < 0.001$) and increased by 0.86 year per degree of

latitude. Using the derived linear relationship of age-at-maturity and latitude, we predicted A_{50}

for NGOA (59.75°W) and PWS (60.5°N) to be 25.5 years (95% prediction interval: [20.8,30.3])

and 26.2 years (95% prediction interval:[21.3,31.0]), respectively. We found the relationship

between L_{50} and latitude was insignificant (F-statistic = 3.08, df = 6, $P = 0.13$). The range wide

comparison of Yelloweye Rockfish maturity studies revealed a strong trend of increasing age-at-

maturity with increasing latitude, but length-at-maturity did not increase with latitude.

Ovarian Cycle.—Mature female Yelloweye Rockfish were examined for ovarian stage of

development during all months except January owing to poor weather and minimal fisheries

participation in that month (Table 1.2). In total, 328 mature females were used to construct a

calendar of ovary development. We observed the highest proportion of stage 3 females in

February (Figure 1.5). Parturition of larvae was protracted and spanned several months with the

earliest parturition taking place in early May and the latest gravid fish (stage 5) observed in late

July. Therefore, we determined May through August as months of possible parturition (Figure

1.5). Many spent female Yelloweye Rockfish were observed between the months of June and

August (Figure 1.5). By September, most female Yelloweye Rockfish had regressed to a resting

state characterized by the reestablishment of oogonial nests and the presence of basophilic oocytes. Based on the ovarian development schedule, females remained in this state into November and December, when vitellogenesis and the reproductive cycle would begin again (Figure 1.5).

Age- and size-specific parturition.—Ovaries from 204 mature females were examined for the months of parturition (May to August). We found that capture month was a significant predictor (Likelihood ratio = 162.17, df = 1, $P < 0.001$) in the logistic relationship between female probability of post-parturition and FL. The fitted logistic model was, as follows:

$$log\left(\frac{\pi_{ijm}}{1-\pi_{ijm}}\right) = -16.98 + 0.16 * FL + 3.54 * month, \tag{8}$$

where the positive coefficient indicates that size of spent fish decreases as the parturition season progresses (Figure 1.6). Similarly, a term for sample month was determined to be significant (likelihood ratio = 157.75, df = 1, $P < 0.001$). The following relationship was derived for the relationship between female probability of post-parturition and age:

$$log\left(\frac{\pi_{ijm}}{1-\pi_{ijm}}\right) = -11.85 + 0.11 * age + 3.64 * month, \tag{9}$$

where the positive coefficient indicates that the age of spent fish decreases through the parturition period (Figure 1.6). In conclusion, larger and older Yelloweye Rockfish females released larvae earlier than smaller, younger females.

Skip spawning.—Eighteen of 184 (9.8%) mature Yelloweye Rockfish were determined to have skip spawned. Females that skip-spawned ranged from 40 to 53 cm in length (mean = 47.3 cm, SD = 4.1; N =18) and 15 to 49 years in age (mean = 23.9 year, SD = 9.4; N =18). The proportion of skip spawning females was related to FL as a second order polynomial logistic regression (Likelihood ratio = 19.99, df = 2, $P < 0.001$) :

$$log\left(\frac{\pi}{1-\pi}\right) = -57.61 + 2.44 * FL - 0.026 * FL^2. \tag{10}$$

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The proportion of skip spawners predicted as a function of FL peaked at $\pi = 0.23$ and a FL of 46.2 cm (Figure 1.7). Age was not a significant predictor of the proportion of skip spawning female Yelloweye Rockfish, based on a second order polynomial logistic regression (Likelihood ratio = 5.47, df = 2, P = 0.71) and a simple logistic regression (Likelihood ratio = 5.46, df = 1, P = 0.60). In summary, the proportion of skip spawning was greatest at intermediate lengths but constant (π = 0.098) across ages.

DISCUSSION

Knowledge of the reproductive biology of fishes is critical to calculate reproductive potential (Rothschild and Fogerty 1989; Trippel 1999), establish biological reference points for fisheries management (Gabriel and Mace 1999; Brooks et al. 2010), and determine the local exploitation and extinction risk of a species (Myers and Mertz 1998; Hutchings et al. 2002). This study provided the first detailed estimates of maturity, skip spawning rates, and parturition timing for Yelloweye Rockfish in the northernmost distribution of the species. Further, we found the first evidence that Yelloweye Rockfish parturition timing is dependent on maternal age and size, which can affect the fate of larval offspring. These results will help parameterize stock-assessment models that inform Yelloweye Rockfish fisheries management and guide future research on rockfish reproductive biology.

Maturity.—In general, male Yelloweye Rockfish matured earlier and smaller than females, a form of sexual size dimorphism. Additionally, Yelloweye Rockfish males matured faster with respect to age and size compared to females. Males and females reached similar A_{50} and L_{50} in the respective areas, but maturity schedules for the two sexes diverged between 50% and 95% maturity. This difference in maturity schedules could be explained by the difference in physiological cost of producing milt and eggs. Physiological cost of reproduction is assumed to

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be greater in females than males (Parker et al. 1972; Parker 1992; Hayward and Gillooly 2011). For rockfishes, viviparity, high fecundity, and matrotrophy can further increase female energetic cost of reproduction (Wourms 1991). The high cost of female Yelloweye Rockfish reproduction could drive maturity later, relative to males, and an interaction between high reproductive cost and varying productivity across the heterogenous environments of PWS and the NGOA could explain the gradual female maturity rate. To better understand the mechanisms driving the differences observed between male and female maturity, we suggest future studies explore the reproductive energetic investment for male and female Yelloweye Rockfish. The difference in maturity-at-age or length between males and females can be incorporated into stock assessments (Cope 2013; Methot and Wetzel 2013) and sex-specific estimates of RP (Trippel 1999).

Latitudinal effects on female age- and length-at-maturity.—Our comparison of female size-at-maturity across the range of Yelloweye Rockfish indicated no effect of latitude (Table 1.6). Ray (1960) hypothesized that ectotherms abide to Bergmann's rule for endotherms, which states that maximum size (and consequently, size-at-maturity) increases with latitude. Ray's hypothesis (1960) is based on the results from laboratory experiments that revealed fish grew and matured larger when reared at lower temperature and that this would be the same for fish in colder waters of higher latitudes. Belk and Houston (2002) explored Ray's hypothesis and found that freshwater fishes do not follow Bergmann's rule. A similar analysis has yet to be investigated for marine fishes. Our results of Yelloweye Rockfish contradict Ray's hypothesis. Conover and Present (1990) suggest that the observation of constant maximum size and size at maturity may be a result of adaptations to periodically maximize growth by fish in northern latitudes to compensate for colder temperature and shorter growing seasons. A meta-analysis of size-at-maturity for other rockfish species could be conducted to examine if constant size at maturity

across latitudinal gradients is universal among marine species, including other *Sebastes spp.* Further, the relationship between size-at-maturity and latitude could be examined using range-wide female length and maturity data and modeled with latitude as a predictor variable. If a species exhibits constant length-at-maturity, it may be possible to use a mean maturity-at-length for unassessed stocks in length-structured methods (Hordyk et al. 2015) or stock assessments (Methot and Wetzel 2013).

While we found size at maturity to be constant with latitude, age at maturity for female Yelloweye Rockfish increased with latitude, with the implication that Yelloweye Rockfish achieve a similar size-at-maturity that is reached by an age determined by growth rate. Yelloweye Rockfish in PWS and the NGOA reached maturity at a younger age than expected. Growth rate can vary with latitude as a factor of temperature, growing season, and/or productivity (Conover and Present 1990; Jobling 1996; Trip et al. 2014). Additionally, this hypothesis could be tested by a comparison of von Bertalanffy growth parameters for Yelloweye Rockfish across its range, including PWS and the NGOA. Furthermore, biochronology methods (Morrongiello et al. 2012; Matta et al. 2020; Torvinen et al. *in review*) could be used to gain a better understanding of the mechanisms for increased growth that result in younger than expected age-at-maturity for Yelloweye Rockfish in PWS and the NGOA by correlating annual growth indices with environment variables, prey abundances, and harvest history.

The methods used for studies included in the comparison of maturity varied widely. Publication years for studies used to conduct the review of size and age at maturity for Yelloweye Rockfish were from 1987 to 2009 (Table 1.5). Aging methods varied among the studies, and included: surface aging (Wyllie Echeverria 1987), break-and-burn (O'Connell 2002; Hannah et al. 2009), and burnt otolith sectioning (Kronlund and Yamanaka 2001; Yamanaka et

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al. 2011). Surface-aging otoliths tends to underestimate the age of older, slow growing fish (Chilton and Beamish 1982; Wyllie Echeverria 1987), and therefore, can underestimate age-at-maturity. Moreover, there is evidence that the use of histological examination of ovarian tissue is more accurate than macroscopic staging (Gunderson et al. 1980; West 1990; Nichol and Pikitch 1994). Only two studies (Wyllie Echeverria 1987; Hannah et al. 2009) used histological methods. With the recent discovery of skip spawning and the presence of recruit spawners (abortive mature fish) in *Sebastes*, use of histological methods is critical to ensure accurate and precise maturity estimates (Conrath 2017). Mis-specified maturity schedules based on variable methods could have biased the Yelloweye Rockfish age-at-maturity comparison in this study and could influence stock assessment results. Future maturity studies would benefit from consistent protocols of aging and the use of histology.

Ovarian Cycle.—The ovarian development timing for Yelloweye Rockfish in PWS and the NGOA is similar to the schedules reported for Yelloweye Rockfish in previous studies (Rosenthal et al. 1982; O'Connell 1987; Wyllie Echeverria 1987). Mature/unfertilized (stage 3) were the predominant stage in February and stored sperm was documented in multiple stage 3 ovaries during this time. The proportion of fertilized eggs (stage 4) increased in March and were the dominant stage by April; thus, we inferred copulation took place from January through March. Parturition occurred exclusively between May and August.

Yelloweye Rockfish in PWS and the NGOA exhibited parturition over a more contracted period relative to Southeast Alaska, where it spanned up to eight months (Rosenthal et al. 1982; O'Connell 1987). Winds that favor downwelling in the coastal portions of the NGOA persist between September and May, and downwelling ceases for a brief period between May and August (Weingartner et al. 2002). This period of weakened downwelling could explain the

parturition timing of Yelloweye Rockfish in PWS and the NGOA. Downwelling could be detrimental to recently released larvae because they are underdeveloped for settlement in demersal habitat. As ocean temperatures continue to warm or the frequency and longevity of anomalous ocean events (e.g., the Pacific blob; Kintisch 2015) increase, warmer ocean temperatures could reduce the embryonic development time of Yelloweye Rockfish in PWS and the NGOA, potentially creating a mismatch in timing between parturition and seasonally low downwelling.

Age- and size-specific parturition.—Few studies have investigated maternal effects (e.g., increasing relative fecundity, egg quality, reproductive timing with age or size) in Yelloweye Rockfish (Blain-Roth and Sutton 2019). We found that larvae of larger and older females are more likely to be released earlier. Younger and smaller females may balance energetic input into growth and initial life reproductive events; therefore, embryonic development is delayed relative to older and larger female rockfish (Love et al. 2002). In PWS and the NGOA, earlier parturition in May or June would allow for larvae to experience an extended period of growth during the summer months when productivity is high and downwelling conditions are minimal, which could increase growth and survival. Because factors that affect the fate of offspring influence estimates of stock RP (Trippel 1999), differences in survival between early and late parturition could further increase the contribution to stock RP by older and larger females and impact the stock-recruitment dynamics of Yelloweye Rockfish.

Skip spawning.—Our study represents the first research to quantify the presence of skip spawning in Yelloweye Rockfish and we found mature female Yelloweye Rockfish in PWS and the NGOA skip spawned at a lower rate (9.8%) relative to other rockfish species: Shortraker Rockfish (60.0%), Rougheye Rockfish (37.4%), and Blackspotted Rockfish (93.9%; Conrath

2017). These three species are among the slowest-growing and longest-lived *Sebastes* species owing to their occupancy of deep and less productive waters of the continental slope (Love et al. 2002). Comparatively, the observed lower skip spawning rate that we observed in Yelloweye Rockfish in PWS and the NGOA may be a result of the more productive shallow, continental shelf habitat in which the species occurs. Our results represent a two-year average rate of skip spawning for the 2018-2019. However, skip spawning rate has been documented to vary annually in marine fishes (Engelhard and Heino 2006; Rideout et al. 2006; Conrath 2017). By neglecting skip spawning, SSB (Sitar et al. 2014) or egg production per recruit can be overestimated (Rideout et al. 2005; Rideout and Rose 2006; Sitar et al. 2014). Due to the wide range of skip spawning rates observed in *Sebastes,* the interannual variability in skip spawn rate documented in marine species, and the strong influence of these rates on metrics used in fisheries management, there is need for further research into spawning omission across this generally long-lived genus.

Yelloweye Rockfish skip spawning was greatest at an intermediate size range (40.2 to 52.3 cm). Skip spawning at intermediate age and size has been observed in Atlantic Cod *Gadus morhua* (Marshall, 1998; Rideout et al. 2005), and Rougheye Rockfish appear to skip spawn within a similar size range as Yelloweye Rockfish (45 to 55 cm; Conrath 2017). Because individuals at or near L_{50} have yet to reach asymptotic growth, they must balance the energetic cost of reproduction and growth (Rideout et al. 2005; Jørgensen et al. 2006). For fish within this size range, additional growth through spawning-omission can produce benefits that include higher survival and increased fecundity with age (Jørgensen et al. 2006). Our logistic regression approach produced a proportion of skip spawning Yelloweye Rockfish at a FL that can be readily be applied to a model of RP (Trippel 1999). We hypothesize that the skip spawning

observed at intermediate sizes will shift the stock RP towards larger female Yelloweye Rockfish that skip spawn at a lower a rate, further indicating that maintaining age and size structure may be critical to maintain Yelloweye Rockfish stocks (Hixon et al. 2014).

Maturity and skip spawning are important reproductive parameters with which to estimate stock reproductive potential and reduce uncertainty around stock-recruitment dynamics. However, reproductive information such as age- and size-specific parturition timing is more complicated to apply to RP models and stock assessments because it is difficult to quantify the effect of parturition timing on recruitment. Further research is necessary to examine the effect of parturition timing on larvae viability in the form of survival. With the many maternal effects documented in rockfishes (e.g., increasing relative fecundity, greater larval quality; Berkeley et al. 2004, Chapter 2) delayed full maturity (31 years), and size-specific skip spawning, maintaining age and size-structure may be critical to the population maintenance of Yelloweye Rockfish in PWS and the NGOA. The results of this study can increase accuracy of stock-dynamics in stock assessment models and reduce bias in estimates of RP, but also guide management objectives such as maintaining population age structure.

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Table 1.1 Macroscopic (Westrheim 1975) and histological (Bowers 1992; Shaw et al. 2012; Conrath 2017) descriptions of rockfish ovaries for assessment of maturity and development stage.

	Stage of Development	Macroscopic Description	Histological Description
1	Immature	Ovaries small, translucent, and peach or yellow in color.	Oogonia with highly basophilic cytoplasm (deep purple staining) and relatively large nucleus, early and late perinucleus stages present.
2	Maturing (Immature)	Ovaries small to medium, firm, translucent or opaque, yellowish in color.	Early vitellogenic oocytes, no postovulatory follicles or other indications of previous reproduction present; abortive mature females may have signs of widespread early stage atresia.
3	Mature (Vitellogeneis)	Ovaries medium to large, translucent or opaque, yellow in color.	Large oocytes with migratory nucleus or numerous small pink-staining oil globules and clear oil droplets.
4	Fertilized	Ovaries large, may be hydrated or loose (not firm), translucent, yellow-orange in color.	Egg has ovulated, nucleus is no longer present, yolk in single uniform mass.
5	Ripe (Eyed Egg/Larvae)	Ovaries large, hydrated or loose, yellow or gray in color with black dots (presence of eye pigment from embryos or larvae).	Embyro bodies present, retinal pigment may be present, yolk reduced in more developed embryos
6	Spent	Ovaries medium to large, flaccid, gray, red, or purple in color, residual larvae may be present.	Widespread cell degeneration, residual embryos or eye pigment may be present.
7	Resting	Ovaries medium, firm, gray-red, yellow or peach in color, dark or black blotches may be present during or soon after regeneration.	Oogonial nests present, postovulatory follicles present, late stage atretic cells may be present

Table 1.2. Number of female and male Yelloweye Rockfish sampled by month and sample area.

Month	Female	Male
January	0	0
February	19	0
March	7	0
April	26	1
May	145	51
June	67	17
July	106	5
August	25	3
September	7	1
October	4	4
November	14	1
December	17	0
PWS	206	47
NGOA	231	36
Total	437	83

Table 1.3. Model summaries for Yelloweye Rockfish maturity, 2018–2019. Comparison of expected log pointwise predictive density (elpd) and leave-one-out information criteria (LOOIC) for models predicting age-at-maturity and length-at-maturity. All possible combinations of the predictor variables age or length (FL), sex, and area were considered except for models that did not include age or FL.

Model	Variables	elpd	LOOIC
Age-at-maturity	age * sex	-175.9	351.8
	age * sex + area	-176.1	352.2
	age * sex + sex * area	-177.6	353.2
	age * sex + age * area	-177.0	354.0
	age * sex * area	-177.1	354.2
	age * sex + age * area + sex * area	-177.4	354.8
	age * area + age * area	-177.4	354.8
	age	-183.5	367.0
	age + sex	-183.8	367.6
	age + area	-184.1	368.2
	age + sex + area	-184.2	368.4
	age + sex * area	-185.2	370.4
	age * area	-185.2	370.4
	age * area + sex	-185.4	370.8
Length-at-maturity	FL * sex + area	-149.6	299.2
	FL * sex + length * area	-150.6	301.3
	FL * sex * area	-150.8	301.5
	FL + area	-151.2	302.3
	FL + sex + area	-151.3	302.6
	FL* sex + sex * area	-151.4	302.8
	FL * sex + FL * area + sex * area	-151.6	303.1
	FL + sex * area	-152.1	304.2
	FL * area	-152.2	304.3
	FL * area + sex	-152.5	305
	FL * area + sex * area	-153.2	306.5
	FL * sex	-163.2	326.3
	FL	-163.8	327.7
	FL + sex	-164.1	328.3

Table 1.4. List of parameters from a multivariate logistic regression of maturity as a function of age and sex for N = 497 Yelloweye Rockfish from Prince William Sound and the Northern Gulf of Alaska. Posterior median estimates and 95% credible intervals (CI) are shown for each parameter, including age-at-50% maturity (A_{50}) and age-at-95% maturity (A_{95})

Sex	Parameter	Estimate	95% CI
Both	β_0	-3.36	(-4.38,-2.47)
Both	β_1	0.20	(0.16,0.26)
Male	β_3	-8.30	(-14.49,-3.87)
Male	β_5	0.57	(0.28,0.98)
Female	A_{50}	16	(14.8,17.8)
	A_{95}	31	(28.0,34.4)
Male	A_{50}	15	(14.0,16.2)
	A_{95}	19	(17.1,21.5)

Table 1.5. List of parameters from a multivariate logistic regression of maturity as a function of length, sex, and area (PWS = Prince William Sound, NGOA = Northern Gulf of Alaska) for N = 520 Yelloweye Rockfish. Posterior median estimates and 95% credible intervals (CI) are shown for each parameter, including fork length-at-50% maturity (L_{50}) and fork length-at-95% maturity (L_{95}).

Area	Sex	Parameter	Estimate	95% CI
Both	Both	β_0	-13.19	(-16.18,-10.61)
Both	Both	β_1	0.32	(0.26,0.39)
NGOA	Both	β_2	-1.80	(-2.54,-1.13)
Both	Male	β_3	-9.89	(-20.52,-1.79)
Both	Male	β_5	0.25	(0.05,0.50)
NGOA	Female	L_{50}	46.7	(45.2,48.0)
		L_{95}	55.8	(53.9,58.1)
	Male	L_{50}	44.0	(42.4,45.8)
		L_{95}	49.2	(46.7,52.8)
PWS	Female	L_{50}	41.1	(39.6,42.43)
		L_{95}	50.2	(48.3,52.5)
	Male	L_{50}	40.8	(39.2,42.2)
		L_{95}	46.0	(44.2,48.7)

Table 1.6. Age (A_{50}; years)- and length (L_{50}; cm)-at-50% maturity estimates for female Yelloweye Rockfish by location. Sources, aging methods (S = Surface aging, BB = Break-and Burn, BOS = Burnt Otolith Sectioning), the use of histology, and sample sizes (N) are shown for each study.

Location	N	A_{50}	L_{50}	Aging	Histology	Source
North and Central California	132	7	40	S	Yes	(Wyllie Echeverria 1987)
Oregon	158	11.6	38.8	BB	Yes	(Hannah et al. 2009)
Vancouver Island Outside (B.C.)	88 / 204	16.5 / 17.2	42.1 / 42.4	BOS	No	(Kronlund and Yamanaka 2001)
Vancouver Island Inside (B.C.)	455	17.68	--	BOS	Unknown	(Yamanaka et al. 2011)
Queen Charlotte Island (B.C.)	123 / 107	18.9 / 20.3	48.5 / 49.1	BOS	No	(Kronlund and Yamanaka 2001)
Southeast Alaska (Central outside)	51	--	52	BB	No	(Rosenthal et al. 1982)
Southeast Alaska (Outside)	892	22	41.8	BB	Unknown	(O'Connell et al. 2002)
Prince William Sound	206		41.1	BB	Yes	This study
Northern Gulf of Alaska	231	16	46.7	BB	Yes	This study
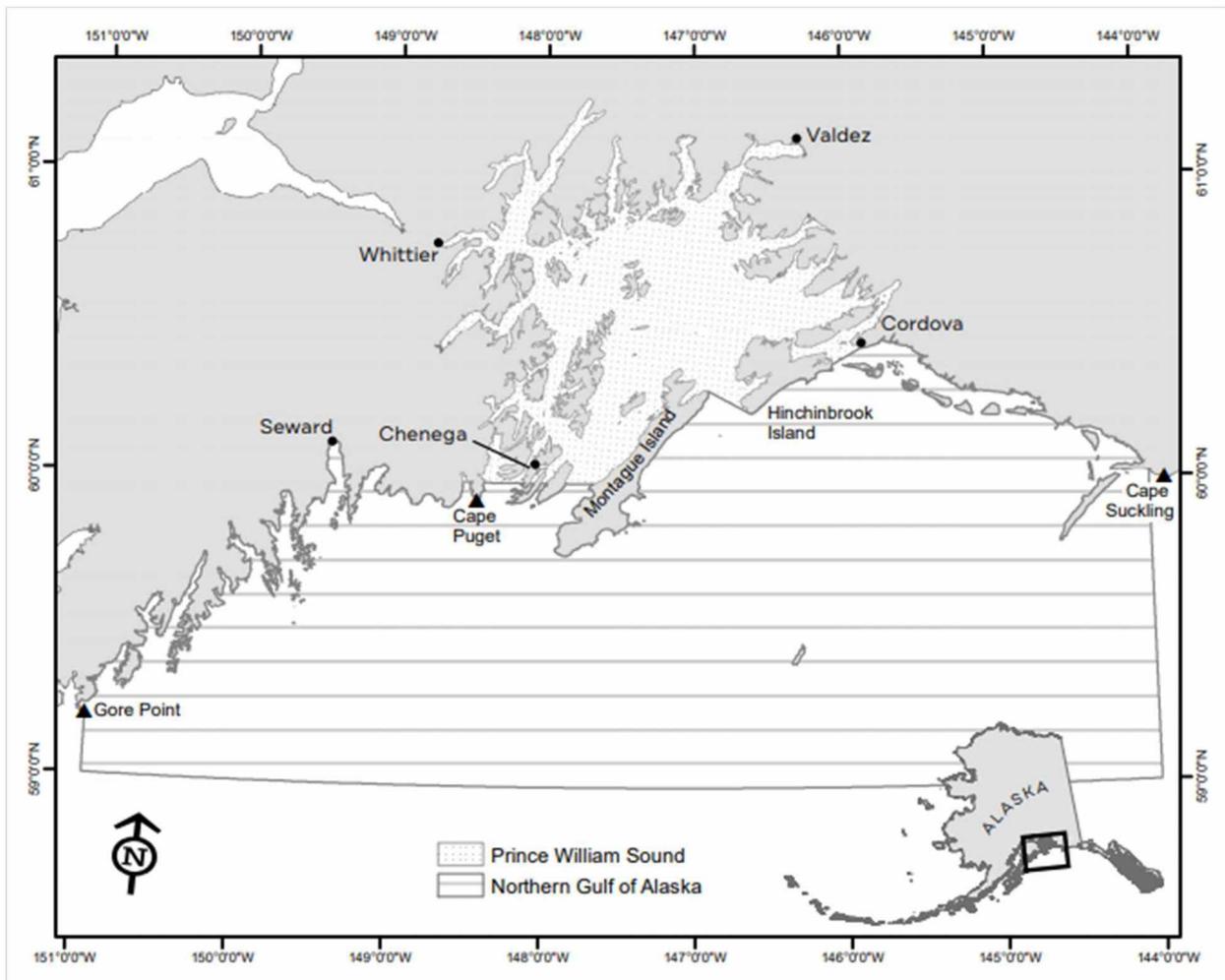
Figure 1.1. Map of the study area in Prince William Sound and the Northern Gulf of Alaska, Alaska, USA.
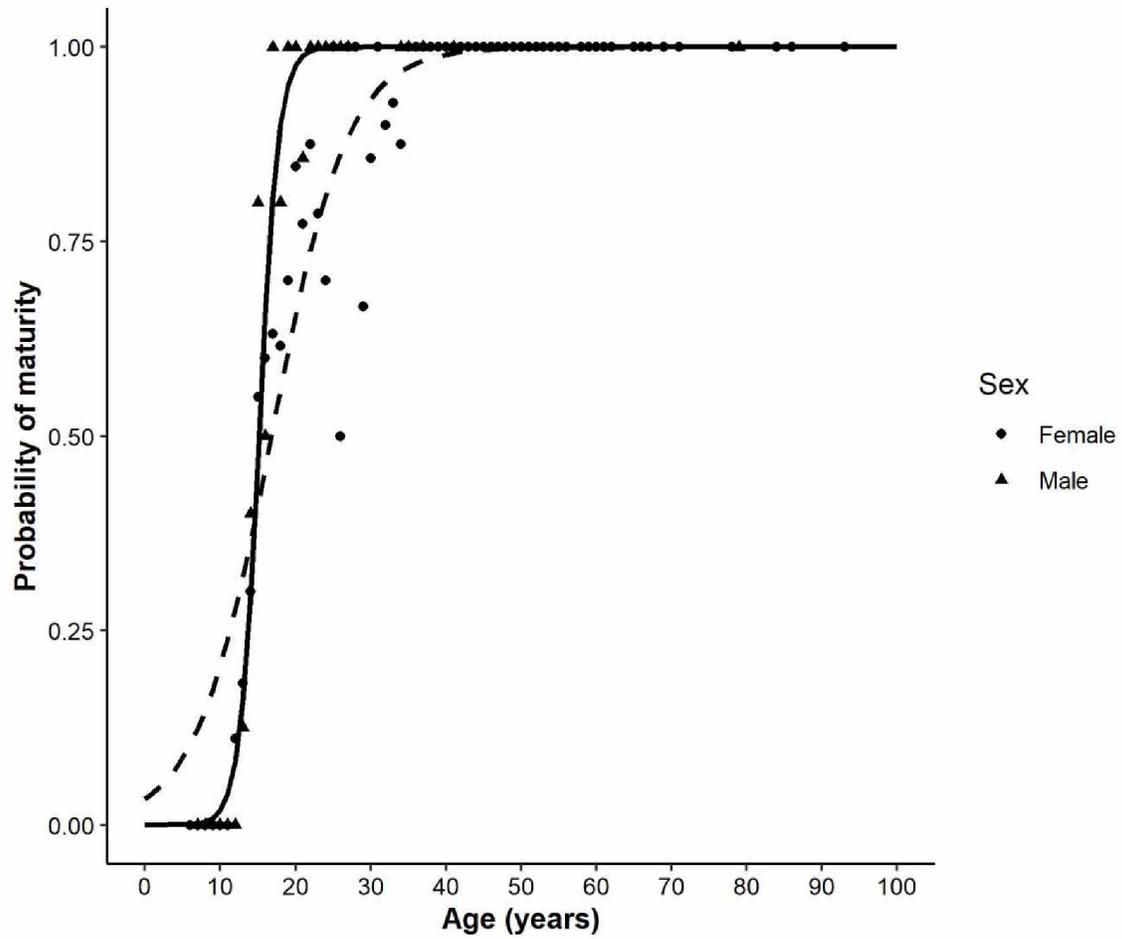
Figure 1.2. Probability of maturity (y-axis) as a function of age (x-axis; years) and sex (solid line, triangles = males, dashed line, points = females) for N = 497 Yelloweye Rockfish from Prince William Sound and the Northern Gulf of Alaska, Alaska, USA.
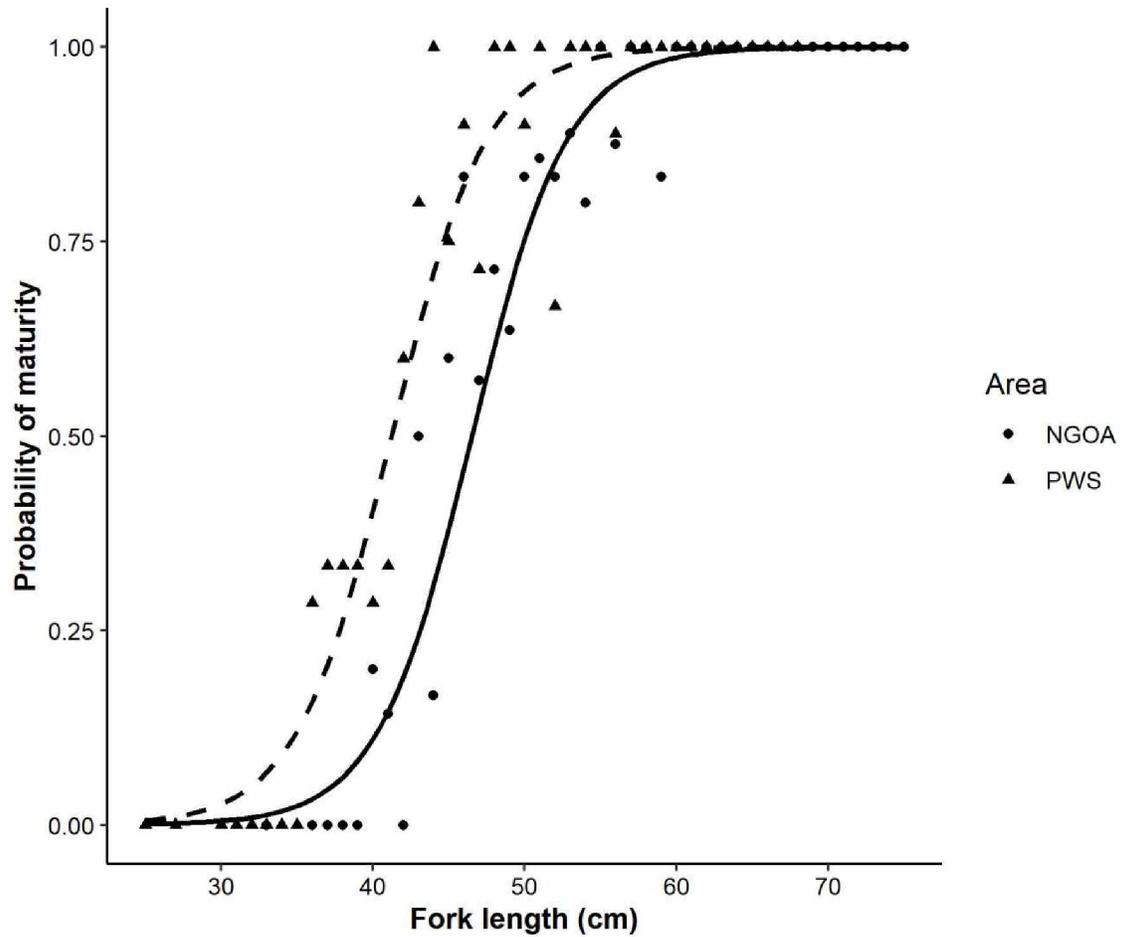
Figure 1.3. Probability of maturity (y-axis) as a function of fork length (x-axis; cm) and area (solid line, points = NGOA, dashed line, triangles = PWS) for N = 437 female Yelloweye Rockfish from Prince William Sound (PWS) and the Northern Gulf of Alaska (NGOA), Alaska, USA.
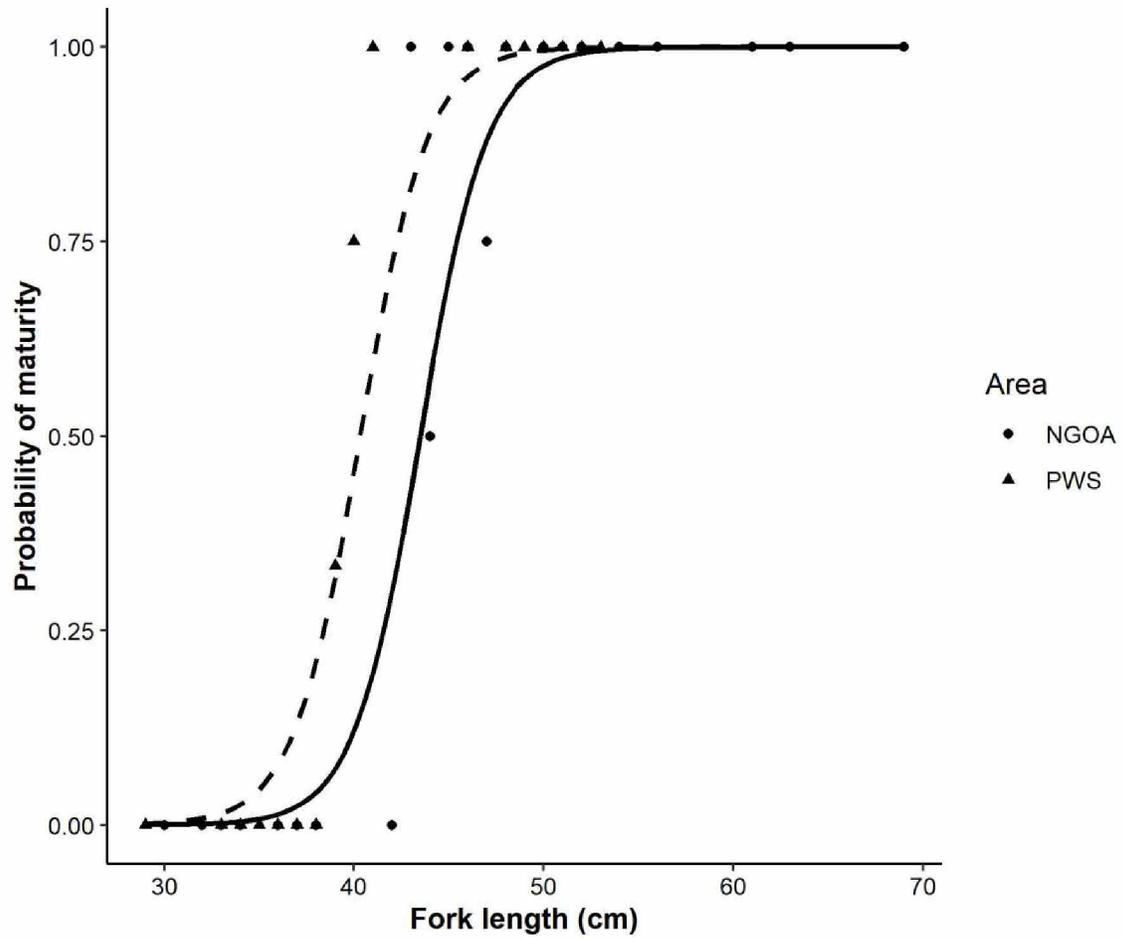
Figure 1.4. Probability of maturity (y-axis) as a function of fork length (x-axis; cm) and area (solid line, points = NGOA, dashed line, triangles = PWS) for N = 83 male Yelloweye Rockfish from Prince William Sound (PWS) and the Northern Gulf of Alaska (NGOA), Alaska, USA.
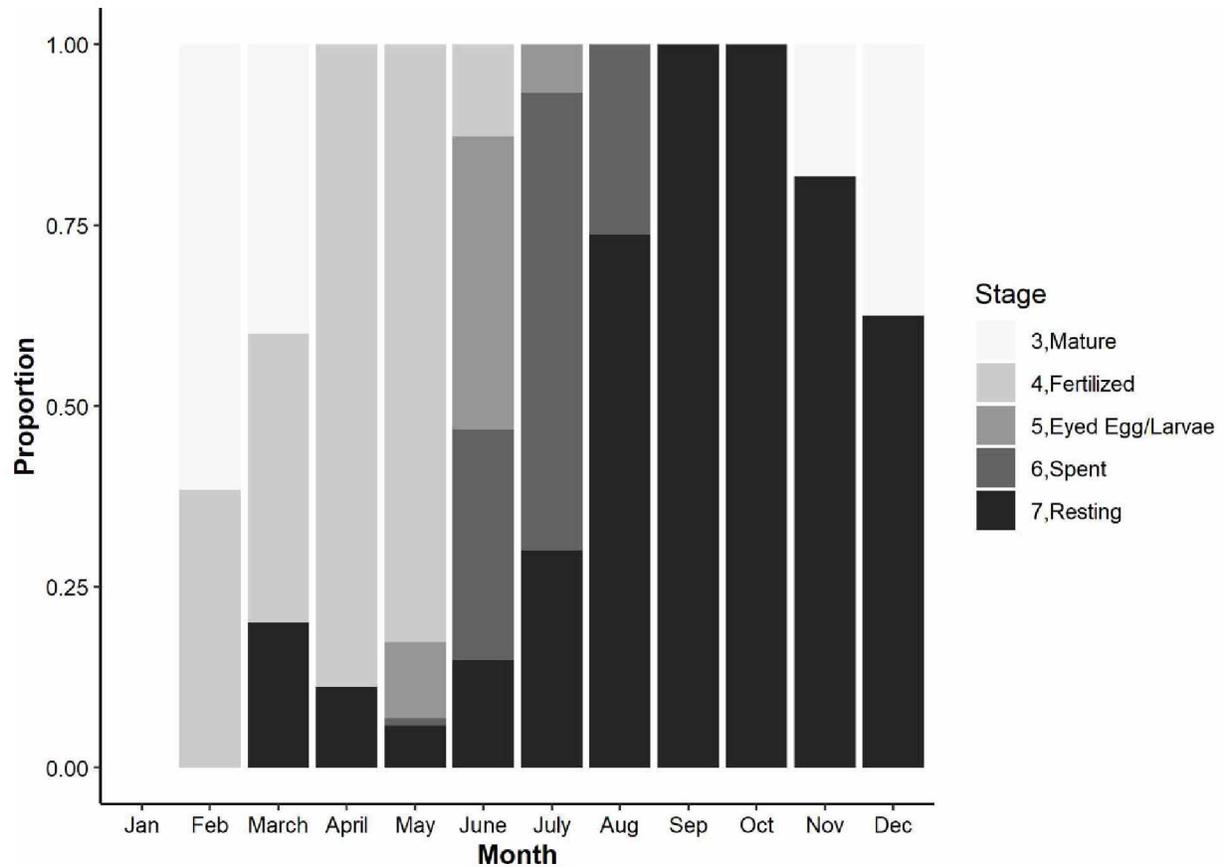
Figure 1.5. Proportion of mature female Yelloweye Rockfish (N = 328) sampled from Prince William Sound and the Northern Gulf of Alaska, Alaska for each month by reproductive stage. Only mature stages of development (stages 3 through 7) were considered in the analysis. Refer to Table 1.1 for the definition of each stage.
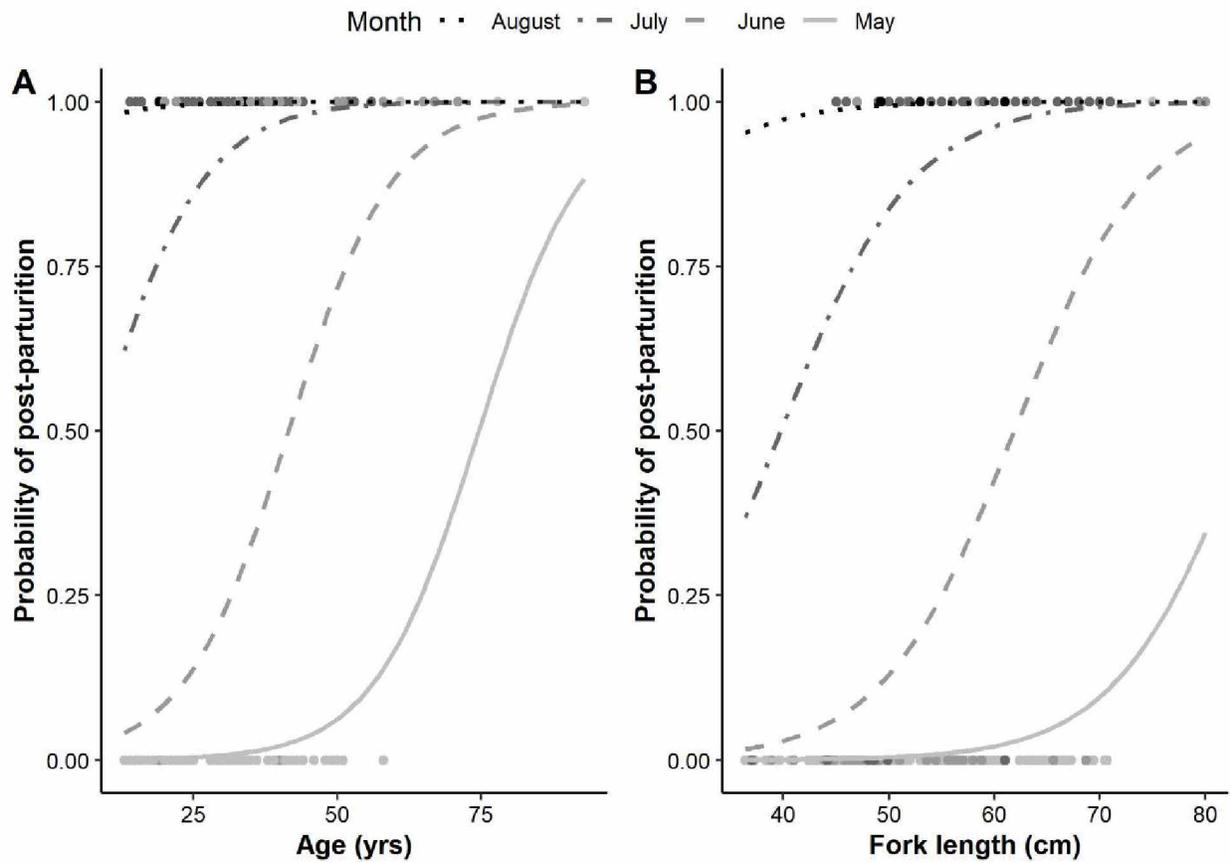
Figure 1.6. Probability of a mature Yelloweye Rockfish being in a post-parturition state (y-axis; spent) as a function of age (A; years) or length (B; cm) and month for Prince William Sound and the Northern Gulf of Alaska, showing the age-specific parturition timing of Yelloweye Rockfish.
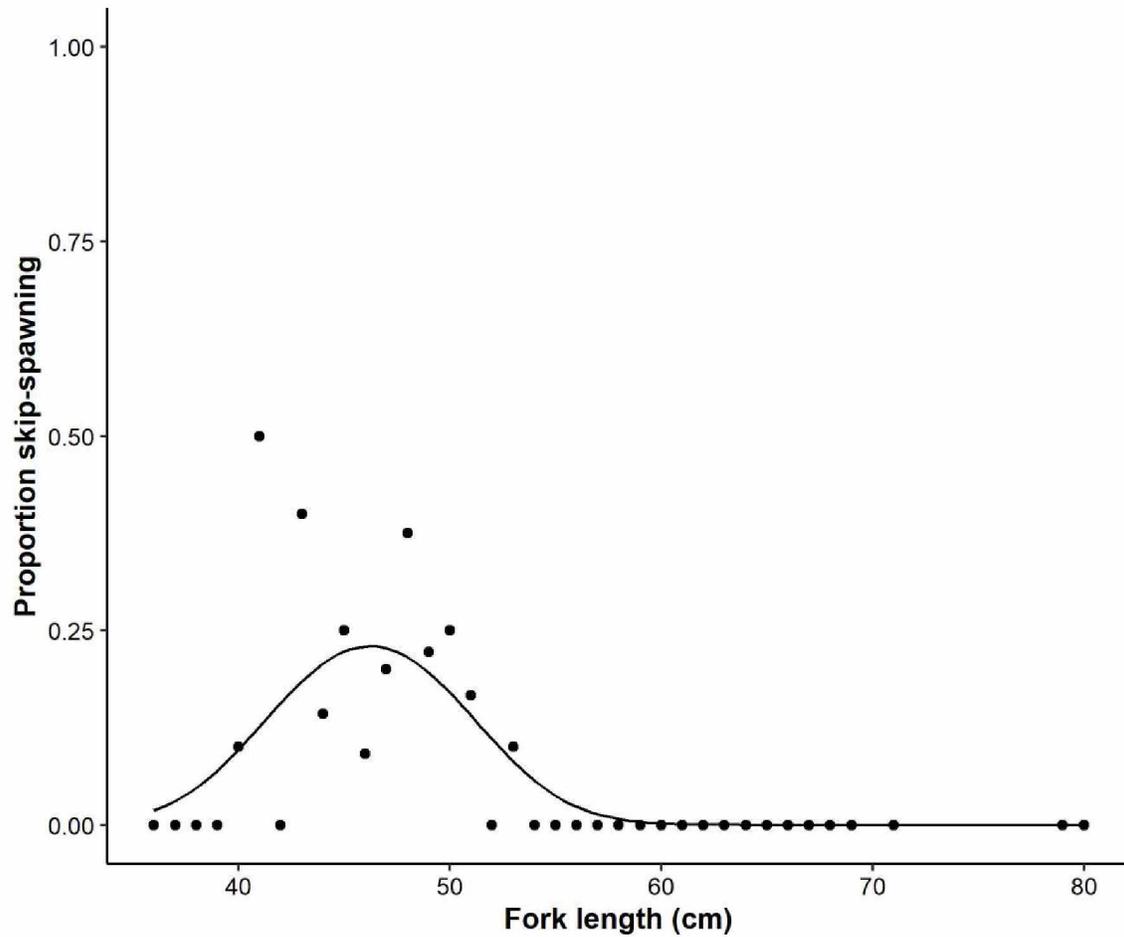
Figure 1.7. Proportion of mature females skip spawning (y-axis) as a function of fork length (x-axis; cm) for Yelloweye Rockfish in Prince William Sound and Northern Gulf of Alaska. The curve is a polynomial logistic regression fit to binary skip spawning (1 = skip spawning, 0 = actively spawning).

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Chapter 2: Fecundity of Yelloweye Rockfish *Sebastes ruberrimus* in the Northern Gulf of Alaska[2]

ABSTRACT

Spawning stock biomass (SSB) is often used as an index for reproductive potential (RP) in fisheries stock assessments, yet this method assumes that mature female biomass is proportional to total egg production (TEP). This assumption implies that the fecundity-length relationship follows a cubic function similar to the weight-length relationship and that relative fecundity is constant. This study estimated fecundity and fecundity relationships for Yelloweye Rockfish *Sebastes ruberrimus*, a commercially and recreationally important species. We collected ovaries (N = 90) from Yelloweye Rockfish in the Northern Gulf of Alaska, Alaska, including Prince William Sound, during 2018-2019 and used the gravimetric method and image-analysis software to count eggs. A subsample of ovaries (N = 30) were manually counted to evaluate the speed, accuracy, and precision of the automated counting procedure. Image-analysis software was approximately four times faster, but equally accurate and precise for fecundity estimates as manual counts. Fecundity ranged from 53,249 to 3.052×10^6 eggs (mean = 896,762 ± 699,504 SD) and relative fecundity increased by 6.7 eggs or larvae per gram of fish weight with each cm of female fork length. The use of SSB for Yelloweye Rockfish stock assessment could underestimate the contribution to egg production by larger (> 5.6 kg) females, overestimate the contribution by smaller females, and lead to biased biological reference points. This study provides critical information to more realistically model RP and improve stock assessment inputs for the development of harvest control rules for Yelloweye Rockfish.

INTRODUCTION

   Annual fecundity is the capacity of an individual female to produce offspring and, in the case of fish, is measured as the number of eggs or larvae per year (Bagenal 1978). Thus, lifetime egg production is a key descriptor of reproductive success and is fundamental to the reproductive fitness of fishes (Clutton-Brock 1988). High fecundity has been empirically linked to greater recruitment variability in marine fishes with implications for stock-recruitment dynamics that include lower interannual stability in stock size and greater uncertainty in stock-recruit relationships (Rickman et al. 2000). Spatiotemporal variation in fecundity has been documented in fish and invertebrate species and is hypothesized to result from variation in environmental conditions and resources such as food and habitat (Eldridge and Jarvis 1995; Kraus et al. 2000; Mroch et al. 2012). Additionally, there is evidence of density-dependent effects on fish fecundity (Bagenal 1973; Rijnsdorp et al. 1991; Forrester et al. 2011). Because fecundity contributes directly to larval supply and juvenile recruitment in fishes, it is important to generate stock-specific estimates of fecundity for exploited fish populations to conduct accurate stock assessments.

   Spawning stock biomass (SSB) can be used in fish stock assessment as an index of reproductive potential (RP; Trippel 1999; Kell et al. 2015). This approach assumes that the total biomass of mature females is proportional to total egg production in a population (TEP; Rothschild and Fogerty 1989; Kell et al. 2015). Relative fecundity, defined as the number of eggs or larvae produced per unit of body mass, is often assumed to be constant across mature females for a species or stock and implies that the fecundity-length relationship follows a cubic function (Bagenal 1978). However, there is evidence that this assumption may not apply for some marine fishes (Haldorson and Love 1991; Marteinsdottir and Begg, 2002; Kell et al. 2015).

For many of these species, assuming proportionality between SSB and TEP may increase uncertainty associated with stock productivity and dynamics (Kell et al. 2015). Moreover, the contribution to RP by large, older females can be underestimated if the assumption of constant relative fecundity is invalid (Hixon et al. 2013; Bernache et al. 2018). As a result, the proxy used for RP (i.e., SSB or TEP) can influence estimates of sustainable harvest levels for exploited stocks (Morgan et al. 2009). However, estimates of fecundity necessary to evaluate proportionality between SSB and TEP are insufficient for many species and stocks; therefore, SSB rather than TEP remains a widely used proxy for RP (Trippel 1999, Kell et al 2015).

Within the genus *Sebastes*, Yelloweye Rockfish *S. ruberrimus* is an extreme case with respect to many life-history characteristics. The maximum age for this species has been reported to be 121 years (O'Connell et al. 2002), and mean female age at maturity has been estimated to be 16-22 years at northern latitudes, with some immature individuals exceeding 30 years of age (Kronlund and Yamanaka 2001; O'Connell et al. 2002; Chapter 1). Yelloweye Rockfish are among the longest living (Munk 2001) and latest maturing of all demersal-shelf rockfishes (Love et al. 2002). Although this species is currently reported as the most fecund *Sebastes* species (Love et al. 2002), the number of fecundity estimates is insufficient to assess the assumption of constant relative fecundity. Data on Yelloweye Rockfish fecundity are limited to estimates from three individuals (Hart 1942; Macgregor 1970), and the reported range of fecundity (1.1 to 2.7 million eggs) represents these three samples (Love et al. 2002; Dick et al. 2009). Further, the size range of Yelloweye Rockfish (53 to 61 cm; Appendix B) upon which these fecundity estimates are based is not representative of the size range of mature female Yelloweye Rockfish (36.4 to 80.0 cm) in wild populations (Chapter 1). The lack of fecundity estimates for Yelloweye

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Rockfish in part can be attributed to the time demand associated with estimating fecundity and the difficulty of sampling a viviparous species because ovaries often experience egg loss.

Although various techniques (e.g., stereological, auto-diamteric, particle counting) have been developed to overcome the time-consuming nature of fecundity estimation (Witthames and Walker 1987; Emerson et al. 1990; Thorsen and Kjesbu 2001), these techniques may not be applicable to all life-history strategies (e.g., viviparity) and may require calibration or the purchase of expensive equipment (Murua et al. 2003). The gravimetric (Zweicker 1967) and volumetric (Simpson 1951) methods are the oldest and most widely used techniques for counting oocytes and/or embryos. However, these approaches can be time consuming to generate an accurate estimate of fecundity. Viviparous Pacific rockfishes can have multiple stages of oocyte or embryo development of different shapes and size within an individual ovary (Blain and Sutton 2016); thus, the classical methods are most appropriate for fecundity analyses of these species. By applying counting techniques within an image-analysis software, the time required to produce fecundity estimates via the gravimetric method could be reduced, therefore expediting the process for future fecundity work and assessments of SSB assumptions many marine fishes.

Given the importance of accurate estimates of RP to management, known spatiotemporal variation in fecundity, and the lack of relevant fecundity data for the species, the overall goal of this study was to conduct a robust assessment of Yelloweye Rockfish fecundity estimates. Our specific objectives were to: (1) assess the efficiency, accuracy, and precision of using image-analysis software to produce automated counts for the gravimetric method of fecundity; (2) estimate fecundity for Yelloweye Rockfish and quantify relationships of fecundity with fish length and weight; and (3) evaluate the assumption of constant relative fecundity and proportionality between SSB and TEP. The automated counting method could allow for more

frequent and spatially explicit fecundity assessments for Yelloweye Rockfish and other fishes, toward improved stock assessment accuracy and sustainable management.

METHODS

Mature female Yelloweye Rockfish were collected during 2018 and 2019 from the Northern Gulf of Alaska, Alaska, U.S.A., between Cape Suckling (60°0'57.6"N, 144°0'0.0"W) and Gore Point (60°12'21.6"N, 151°0'0.0"W), and included the adjacent Prince William Sound (Figure 2.1). This area represents the northernmost distribution for Yelloweye Rockfish (Love et al. 2002; Mecklenburg et al. 2002), and is characterized by a high-relief, rocky shoreline with numerous scattered pinnacles, rock piles, and islands that are common habitat for Pacific Rockfish, Lingcod *Ophiodon elongatus*, and other demersal fishes. A directed recreational fishery (Blain-Roth et al. 2017) and commercial fisheries that yield bycatch (Rumble et al. 2017) of Yelloweye Rockfish occur within the study area.

Yelloweye Rockfish were captured using hook-and-line at depths of 10 to 120 m. Additional samples were collected from recreational and commercial catches delivered to the ports of Cordova, Seward, Valdez, and Whittier, Alaska. Each fish was measured for fork length (FL) to the nearest 0.1 cm and weighed to the nearest 0.01 kg. Ovaries were carefully dissected from each fish and examined for maturity and stage of development based on Westrheim (1975). Notes were collected on any potential egg loss during sampling and females were assigned a qualitative rating of none/minimal, moderate, or high egg loss based on these notes. Whole ovaries were preserved in a glyoxal solution (Glyo-fixx™) or 10% neutral buffered formalin and transported to the laboratory.

Fecundity was estimated using the gravimetric method (Zweicker 1967; Murua et al. 2003) and Image-Pro Plus software (version 10.0; Media Cybernetics, Rockville, Maryland) to

conduct subsample counts. Fecundity was only estimated for whole ovaries (weighed to 0.1 g) in a reproductive state (stages 3-5; pre-fertilized/mature, fertilized, and ripe, respectively) and that had minimal egg loss during handling in the field. Both ovaries were manually manipulated to release eggs and embryos and rinsed with water through a 2-mm round mesh sieve which retained most of the connective tissue. A 0.5-mm mesh sieve was placed beneath the 2-mm sieve and captured any eggs or embryos as they passed through the larger sieve. Large ovaries (> 500 g), were processed individually to prevent overflowing sieves. The mass of eggs or embryos captured with the fine mesh sieve (weighed to the nearest 0.1 g) was mixed to homogenize the density. Approximately 0.1 g subsamples of eggs were distributed into petri dishes and weighed to the nearest 0.001 g. Subsamples were distributed on petri dishes using ethanol and a probe, and a digital image was captured against a white background with a small ruler for scale. Images were captured with a Nikon Coolpix model W300 camera (Nikon Inc., Melville, New York).

Digital images were used to enumerate the eggs and embryos in each subsample with the Count/Size application in the ImagePro Plus software. The Select and Count feature within the Smart Segmentation toolbox were used to identify target objects to be counted (e.g., eggs and embryos) and non-target objects (e.g., connective tissue, debris, and the background including the petri dish). The counting recipe was saved and used to train ImagePro Plus to automatically detect and count eggs. After an automated count was conducted, the image was scanned for any selected non-target pixels and multiple eggs or embryos that might be in contact with each other. Highlighted non-targeted items were deleted and groups of eggs or embryos were separated using the Split tool. The number of eggs or embryos within a subsample was used as the final enumeration. The recipe was applied to all other ovary subsample images at the same stage of development. This process was repeated for six to 12 subsamples from all ovaries eligible for

fecundity estimates. Additionally, a randomly selected subset of ovaries (N = 30) were manually

counted to compare to automated counts. The time to complete counts for both methods were

measured using a stopwatch.

The gravimetric method (Murua et al. 2003) with automated counting was used to

estimate absolute fecundity (Φ) as:

$$\Phi = w_o * \overline{d_o},$$

where w_o was the product of the total weight of eggs or embryos in a sample, and $\overline{d_o}$ was the

mean density of eggs or embryos across subsamples. The number of eggs for each subsample

was divided by the subsample weight to produce a density of eggs per gram. A minimum of six

subsamples were weighed and counted for each fish, based on three samples per ovary

commonly used in fecundity literature (Murua et al. 2003; Kennedy et al. 2006; Daugherty et al.

2008). Subsamples were continually collected until a coefficient of variation (CV) of 5% or less

was achieved for the mean density of eggs or embryos per gram and a sample was excluded if a

CV of 5% or less was not achieved after 12 subsamples (Kjesbu 1989; Murua et al. 2003).

Relative fecundity (Φ_{rel}) was estimated by dividing the absolute fecundity by fish weight (W),

as:

$$\Phi_{rel} = \frac{\Phi}{W}.$$

We assessed the time efficiency of using the image-analysis software relative to manual

counts by comparing the time required to count subsamples of eggs or embryos for each fish by

each method. We compared the sample CVs of both counting methods as a measure of precision

and conducted a two-sample Wilcoxon test to compare the count time and the CVs between

methods. We also compared subsample egg/embryo counts and fecundity estimates produced by

each method to assess the accuracy of the image-analysis software via a simple linear regression

of automated counts as a function of manual counts. Subsample egg/embryo counts and fecundity estimates from the two methods were compared using a t-test with an offset of one to compare the fitted regression to a 1:1 line. All statistical tests were compared at an $\alpha = 0.05$.

We estimated log Φ as a function of log fork length using linear regression. Ovary development stage was included to account for possible atresia, fecundity downregulation, and egg loss that can occur as oocytes/eggs develop. The form of the log-log regression model and power function were:

$$\log(\Phi) = \beta_0 + \beta_1 * \log(FL) + \beta_2 stage + \beta_3 * stage * log(FL) + e$$

and

$$\Phi = e^{(\beta_0 + \beta_2 * stage)} FL^{(\beta_1 + \beta_3 * stage)},$$

where β_0 was the exponent of the coefficient, β_1 was the exponent of the Φ-FL relationship, and β_2 and β_3 were the effect of ovary development stage on the coefficient and exponent of the Φ-FL relationship, respectively. We used an analysis of covariance (ANCOVA) F-Test to determine the effect of the stage term on the coefficient and exponent of the Φ-FL relationship. Similarly, we fit the absolute fecundity-weight hyperallometric relationship using a log transformation of both absolute fecundity and fish weight, while testing for an effect of ovary development stage, as follows:

$$\log(\Phi) = \beta_0 + \beta_1 * \log(W) + \beta_2 stage + \beta_3 * log(W) + e,$$

and

$$\Phi = e^{(\beta_0 + \beta_2 * stage)} * W^{(\beta_1 + \beta_3 * stage)}.$$

We used ANCOVA to test for the effect of development stage on the relationship between Φ and fish weight and the additive or interactive effect of ovary development stage was excluded if deemed statistically insignificant. We constructed 95% confidence intervals to evaluate if the

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exponent of the Φ-weight relationship was > 1, which indicated a hyperallometric relationship.

Additionally, we fit the isometric Φ-weight relationship as a simple linear model without the log-transformation and forced the model through the origin ($\beta_0 = 0$) to compare the assumption of proportionality between SSB and TEP. Lastly, we tested the significance of the relationship between relative fecundity and FL using a linear regression F-test. Simple linear and multiple linear regression analysis were conducted in statistical software R (R Core Team 2019) and all ANCOVA were tested against an $\alpha = 0.05$.

RESULTS

The time necessary to complete a subsample count of eggs or embryos using automated counting ranged from 0.2 to 5.0 minutes (mean = 1.3 minutes, SD = 0.9; N =180) and manual counts ranged from 2.0 to 30.5 minutes (mean = 5.8 minutes, SD = 3.7; N = 180). Automated counting produced faster counts for 94.4% of subsamples (173/180) and for all 30 samples. The time to complete automated egg counts with the software was significantly less than manual counts ($P < 0.001$). The within sample CV for automated counts ranged from 0.02 to 0.05 (mean = 0.04, SD = 0.01; N = 30), and CV for manual counts ranged from 0.02 to 0.05 (mean = 0.04, SD = 0.01; N = 30). We found that the mean CV across samples for automated versus manual counts did not differ ($P = 0.25$), and the mean difference between fecundity estimates produced using automated and manual counts ranged from -38,030 to 74,284 eggs (mean = 10,205 eggs, SD = 28,389; n = 30) and percent difference ranged from -2.9 to 6.7 (mean = 1.6 %; SD = 2.6; N = 30); negative differences correspond to an underestimate by ImagePro Plus. The slope of the linear regression between automated and manual subsample counts did not differ from a 1:1 line ($\beta_0 = 0.996$, $r^2 = 0.99$, $P < 0.001$; 95% CI = [0.98, 1.01]; Figure 2.2). Similarly, the slope of the linear regression between automated and manual fecundity estimates did not differ from a 1:1

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line ($\beta_0 = 0.997$, $r^2 = 0.999$, $P < 0.001$; 95% CI = [0.98, 1.01]; Figure 2.3). Overall, automated egg counts were more than 4 times more efficient than manual counts, and the automated method produced similarly precise and accurate counts and fecundity estimates relative to manual counting.

In total, 437 female Yelloweye Rockfish were collected, of which 90 were gravid females with ovaries that experienced minimal egg loss during sampling. Fork length and weight for female Yelloweye Rockfish assessed for fecundity ranged from 37.1 to 70.7 cm (mean = 55.0 cm, SD = 9.4; N = 90) and 0.84 to 7.60 kg (mean = 3.50 kg, SD = 1.74; N = 86), respectively. Absolute fecundity ranged from 56,463 to 3.052 million eggs (mean = 896,762 eggs; SD = 699,504.0; N = 90). Relative fecundity ranged from 68 to 435 eggs per g body weight (mean = 226 eggs per g body weight; SD = 87; N = 86).

Stage of development was not related to the fecundity-FL and fecundity-W relationships as additive (P = 0.36 and P= 0.08, respectively) or interactive terms (P=0.84 and P=0.67, respectively), and consequently the ovary stage terms were omitted from both models. Based on simple linear regression, the relative fecundity-FL ($r^2 = 0.51$, $P < 0.001$; Figure 2.4) and absolute fecundity-FL ($r^2 = 0.89$, $P < 0.001$; Figure 2.5) were:

$$\Phi_{rel} = -141.32 + 6.69 * FL$$

and

$$\log(\Phi) = -5.49 + 4.72 * \log(FL),$$

with the following power function derived from the log-log linear regression:

$$\Phi = 0.0041 * FL^{4.72}.$$

The exponent (b) of the fecundity-FL relationship ($b = 4.72$; 95% CI = 4.36, 5.08) was significantly different (P < 0.001) than the cubic function assumed with proportional SSB and TEP.

Absolute fecundity was positively associated with fish weight in the isometric and hyperallometric relationships. The following power relationship was derived from the log-transformation of absolute fecundity and weight ($r^2 = 0.88$, $P < 0.001$; Figure 2.6):

$$\log(\Phi) = 11.70 + 1.49 * \log(W)$$

$$\Phi = 120{,}805 * W^{1.49}.$$

The 95% CI for the exponent (b) of the power function of absolute fecundity and weight was (1.38, 1.61), indicating a hyperallometric ($b > 1$) relationship. For the purpose of comparison between the hyperallometric and isometric relationship, we conducted a simple linear regression which resulted in the following isometric model for the fecundity-weight relationship ($r^2 = 0.79$, $P < 0.001$; Figure 2.6):

$$\Phi = 280{,}753W.$$

The isometric and hyperallometric curves intercept at W = 5.6 kg. At W below this intercept, the isometric relationship overestimates egg production, while egg production is underestimated above this W.

DISCUSSION

All fecundity estimates used in this study to evaluate the assumptions associated with SSB were generated using the gravimetric method with automated counting using image-analysis software, and automated counts were faster than manual counts for fecundity estimation. The automated counts were as precise as manual counts, and importantly, we found that there was much agreement between subsample counts and fecundity estimates generated from each

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method. Manual counting requires additional technician time following egg extraction, whereas counting using image-analysis software can be conducted outside of the laboratory. This technique can result in sufficient personnel cost savings to offset the cost of an image-analysis software. Beyond the gravimetric methods used here, the automated solution could also be applied to volumetric fecundity estimation methods and to calibrate the auto-diametric curve (Thorsen and Kjesbu 2001). We successfully enumerated subsample counts and estimated fecundity for ovaries containing both eggs and larvae. Quick and precise fecundity estimates could support more studies of fecundity and larger sample sizes within these studies, which may allow for opportunities to analyze fecundity of various fish species across previously understudied spatial and temporal scales (Lambert 2008).

This research resulted in the first robust fecundity estimates for Yelloweye Rockfish and refined fecundity estimation methods that may be useful for other viviparous species. We found that Yelloweye Rockfish absolute fecundity estimates had a wide range that spanned nearly two orders of magnitude and reduced the lower fecundity estimate for the species from 1.1 million to 56,463 eggs. Lengths of several female Yelloweye Rockfish analyzed were below the 50% length-at-maturity threshold for the species in our study area (Chapter 1) and were smaller than the smallest Yelloweye Rockfish previously assessed for fecundity. The upper bound of observed Yelloweye Rockfish fecundity increased from 2.7 to 3.05 million eggs. However, our upper fecundity bound likely does not represent the maximum fecundity for the species as our largest fish (70.7 cm FL) was well below the maximum size reported for the species (96.0 cm; Love et al. 2002). Indeed, the absolute fecundity-length relationship generated in this study predicted Yelloweye Rockfish fecundity at maximum length (96.0 cm) to be 9.47 million eggs (95% prediction interval: 4.99 million, 17.97 million).

This is the first study to examine allometric fecundity relationships for Yelloweye Rockfish. We found that Yelloweye Rockfish absolute fecundity scaled hyperallometrically with fish weight ($b = 1.49$) and increased with fork length at an exponential rate ($b = 4.72$) greater than the assumed cubic rate. Further, relative fecundity increased linearly with fork length. Together, these findings provide evidence that the assumption of proportionality between SSB and TEP is invalid for Yelloweye Rockfish. Our results support a recent meta-analysis that used a hierarchical framework that drew on phylogenetic differences within and among subgenera topredict that nearly all *Sebastes* spp. exhibit a linear relationship between relative fecundity and length (Dick et al. 2017). It is a common misconception that extinction risk in marine fishes is inversely related to fecundity, but in fact, high fecundity may be a compensatory response and adaptation to patchiness in food, habitat, and recruitment, indicating that highly fecundity fishes are less resilient (Savoy 2001). This warrants future monitoring of fecundity (Savoy 2001; Lambert 2008), which may be possible with rapid fecundity estimation techniques.

Non-constant relative fecundity, the high fecundity-length exponent, and non-linear fecundity-weight relationships are all indicators that Yelloweye Rockfish reproductive effort increased with size, a unique evolutionary trait and bet-hedging strategy in response to a stochastic environment (Stearns 1992). Since reproductive strategies are an environmental adaptation of a species to regulate and/or maintain population size via fitness, the greater than predicted fecundity-length exponent may indicate that Yelloweye Rockfish have adapted to relatively high environmental variability and, therefore, prolonged periods of low larval survival and recruitment. Yelloweye Rockfish and other periodic strategists forgo years of reproductive potential via delayed maturity and must compensate for this forgone reproductive potential with an increasingly high number of offspring at larger maternal size (Winemiller and Rose 1992;

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Winemiller and Rose 1993). Larger and presumably older female Yelloweye Rockfish that have disproportionally high fecundity and have survived long periods of poor environmental conditions may be essential to long-term population maintenance (Hixon et al. 2013).

MANAGEMENT IMPLICATIONS

We provided evidence of non-constant relative fecundity and disproportionality between SSB and TEP for Yelloweye Rockfish. These results could interact with other maternal effects that have been documented in *Sebastes* such as increased egg or larvae quality (Berkeley et al. 2004; Kang and Chang 2004; Sogard et al. 2008) and parturition timing (Rodgveller et al. 2011; Beyer et al. 2015; Chapter 1) to influence stock-recruitment dynamics of Yelloweye Rockfish. In addition, age- or size-specific skip spawning could further magnify how much the isometric relationship under- or over-estimates RP (Conrath 2017; Chapter 1). These factors are incorporated into stock-reproductive potential, which more accurately represents annual variation in egg or larvae viability and, in turn, recruitment (Trippel 1999). Because larger and older females produce a disproportional quantity of eggs compared to smaller females and many maternal effects favor large and old females, age and size-truncation as a result of fishing mortality is of high concern for Yelloweye Rockfish. Incorporating the fecundity relationships established in this study will be important to accurately model in a stock-assessment framework and reduce bias in biological reference points meant to inform sustainable management.

Based on the intercept of the isometric and hyperallometric curves, we have shown that the isometric fecundity-weight relationship (analogous to the SSB assumptions) underestimates egg production for an individual large Yelloweye Rockfish (W > 5.6 kg) compared to the hyperallometric relationship and overestimates egg production for smaller Yelloweye Rockfish (W < 5.6 kg). This bias in SSB will result in biased estimates of biological reference points used

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in management such as F_{MSY} (fishing mortality at maximum sustainable yield; Clark 1991; Clark 1993) and spawning potential ratio (SPR; Kell et al. 2015). The interaction between the fecundity-weight relationships and stock demographic information (e.g., natural mortality or proportion at age or size) will indicate the scale to which SSB under- or over- estimates stock reproductive potential (Bernache et al. 2018). For example, and contrary to existing literature (e.g., Bernache et al. 2018), in exploited populations where large individuals are increasingly rare SSB may overestimate RP rather than underestimating as suggested by previous literature (Bernache et al. 2018). Overestimating RP is especially concerning as it gives estimates of stock status and productivity that may be overly optimistic, and potentially result in catch limits that are too high to support sustainable exploitation (Morgan and Brattey 2005; Rideout and Rose 2006). Incorporating the fecundity relationships established in this study into a stock assessment framework will improve biological reference points that are essential for setting sustainable harvest goals.

ACKNOWLEDGMENTS

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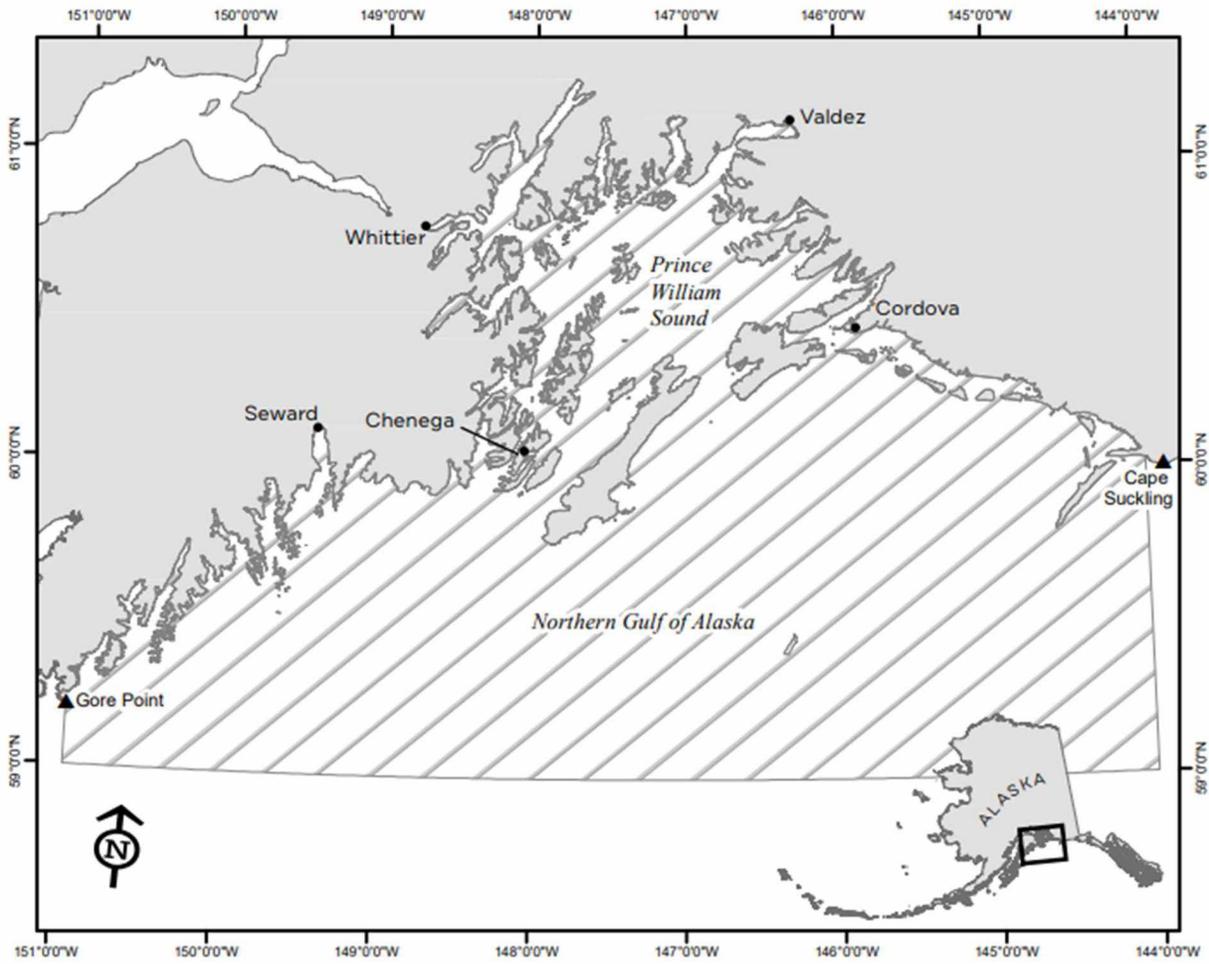
Figure 2.1. Map of the study area in the Northern Gulf of Alaska, including Prince William Sound, Alaska, USA.
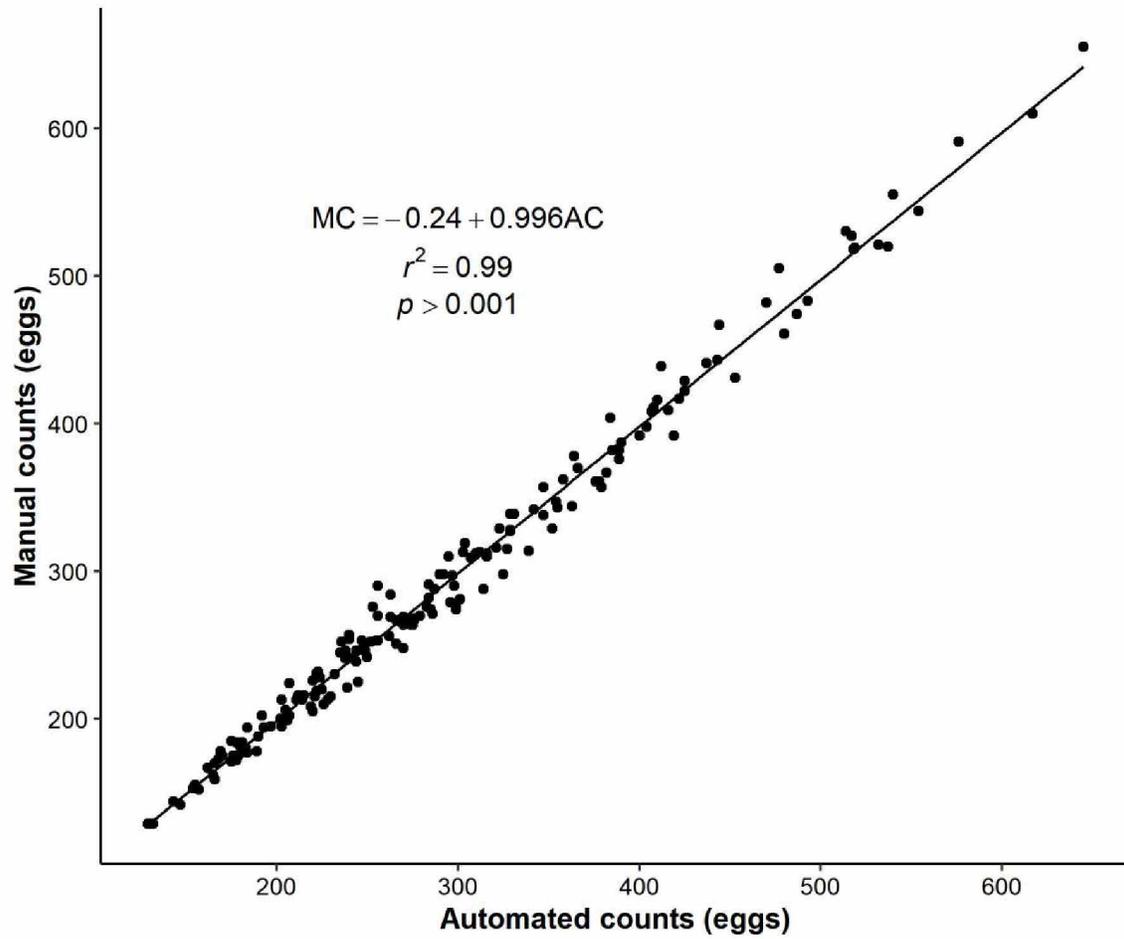
Figure 2.2 Bivariate scatter of Yelloweye Rockfish subsample counts (eggs and/or larvae) enumerated using automated counts (AC; x-axis) and manual counts (MC; y-axis), N = 180 subsamples.
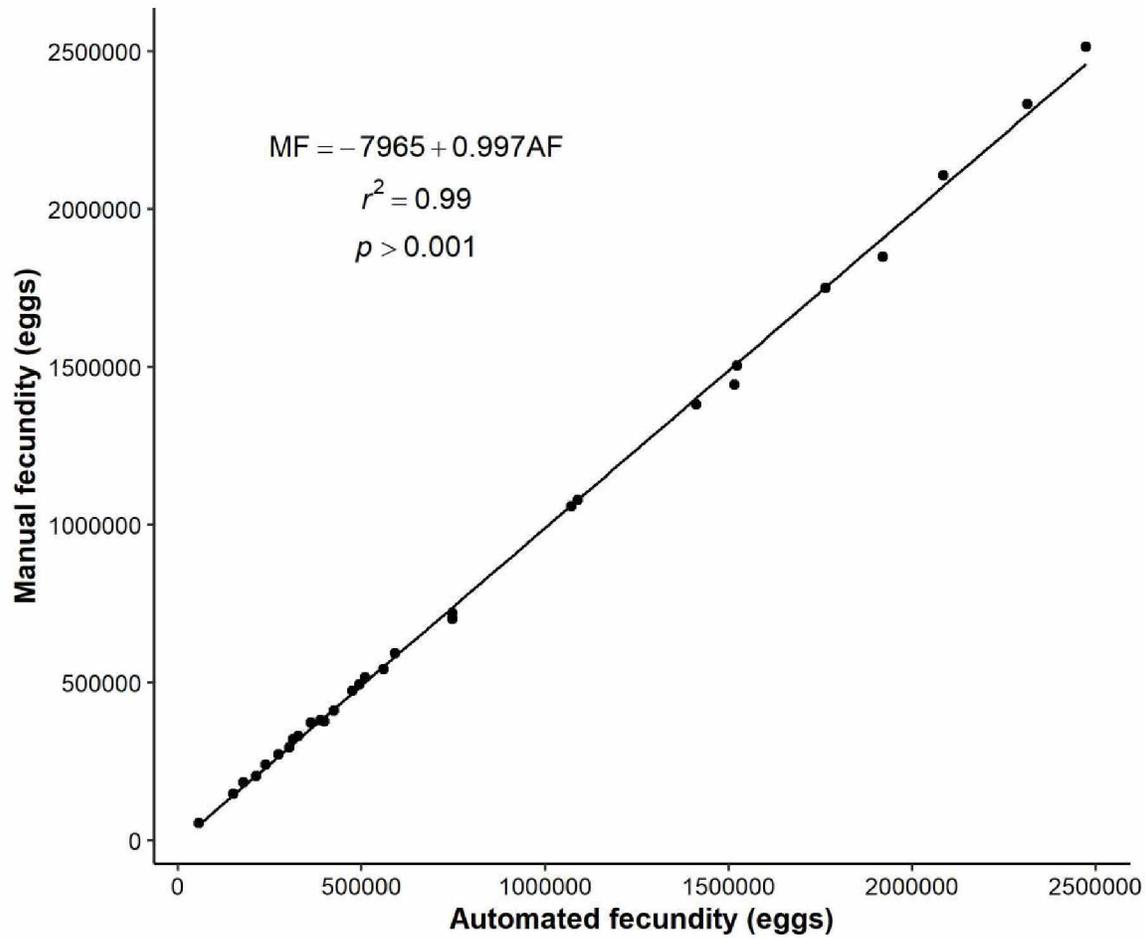
Figure 103. Bivariate scatter of Yelloweye Rockfish fecundity (eggs and/or larvae) estimated by the gravimetric method with automated counts (AF; x-axis) and manual counts (MF; y-axis), N = 30 fish.
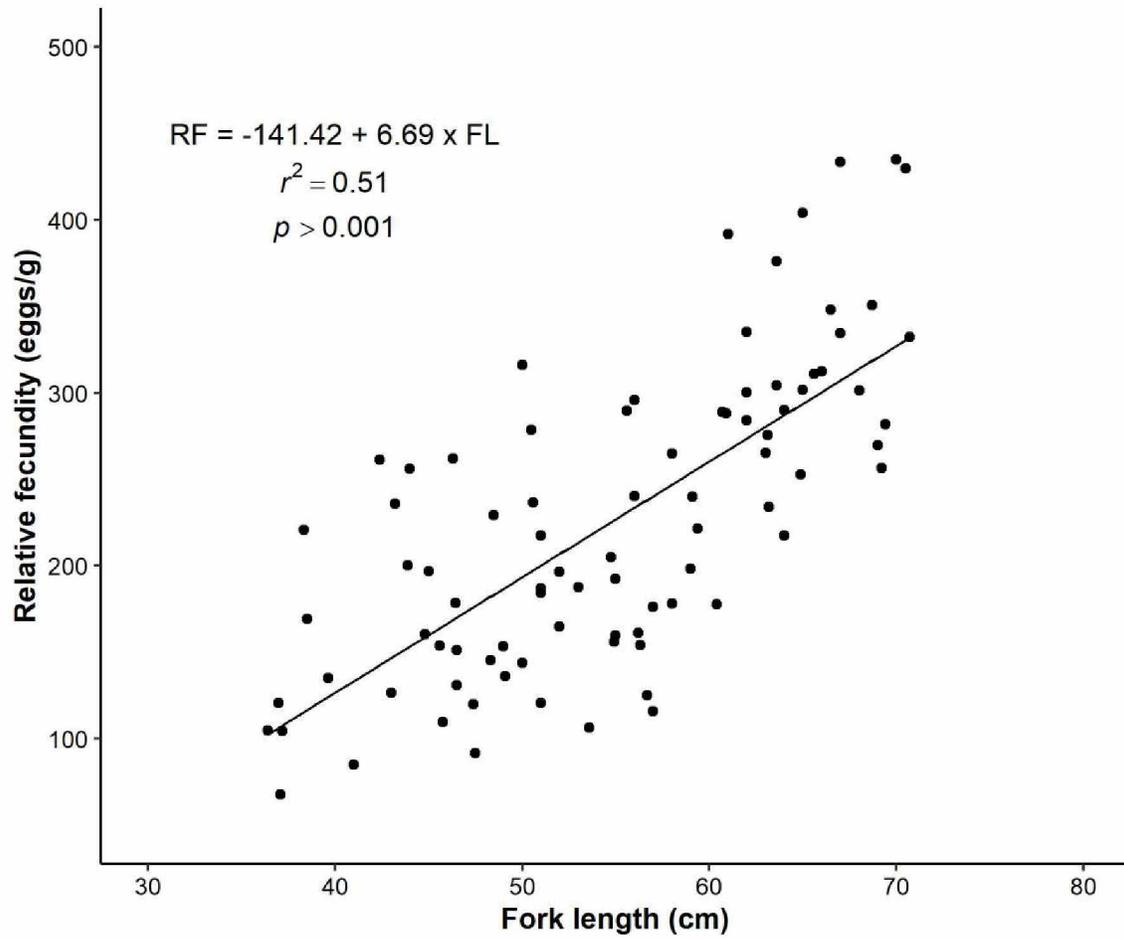
Figure 2.4. Relative fecundity (RF; number of eggs and/or larvae per g fish weight) as a function of fork length (FL; cm) for female Yelloweye Rockfish from the Northern Gulf of Alaska.
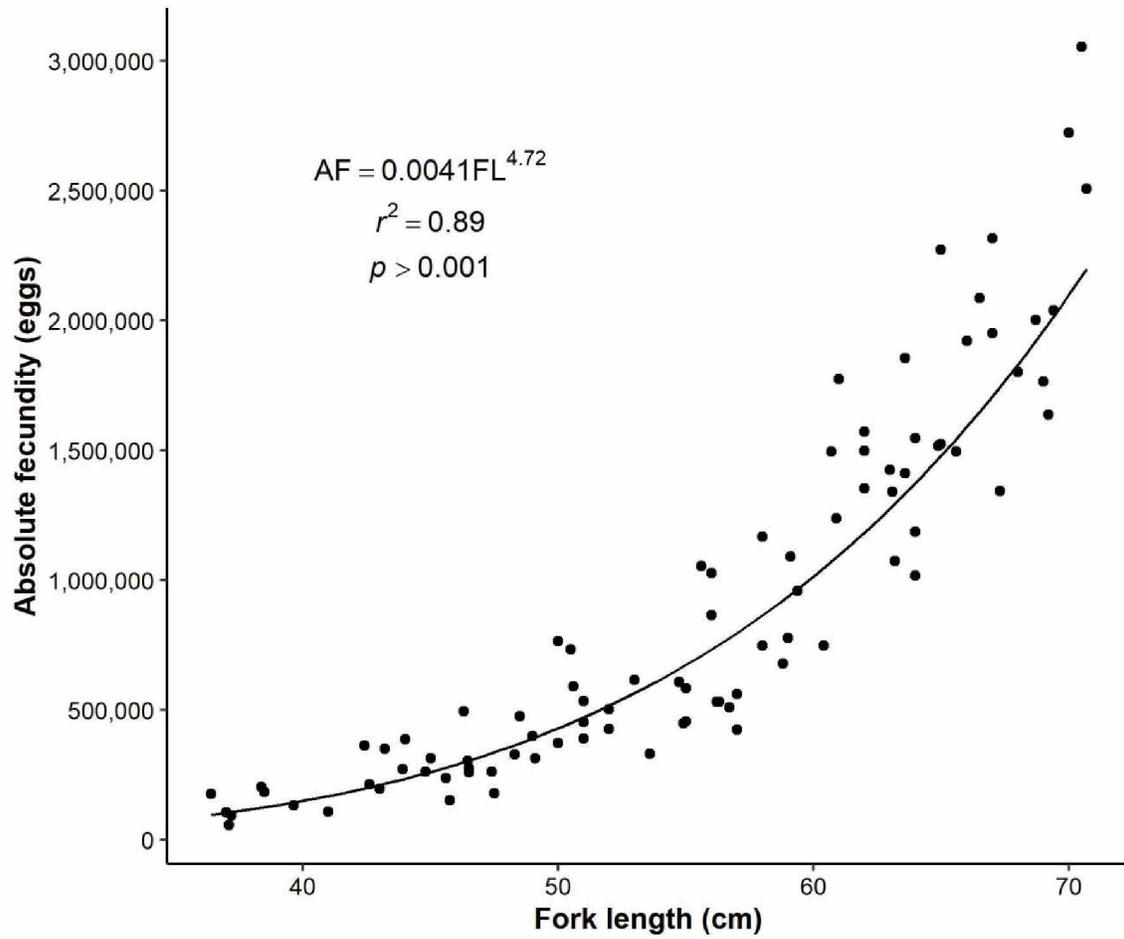
Figure 12. Absolute fecundity (AF; number of eggs and/or larvae) as a function of fork length (FL; cm) for female Yelloweye Rockfish from the Northern Gulf of Alaska.
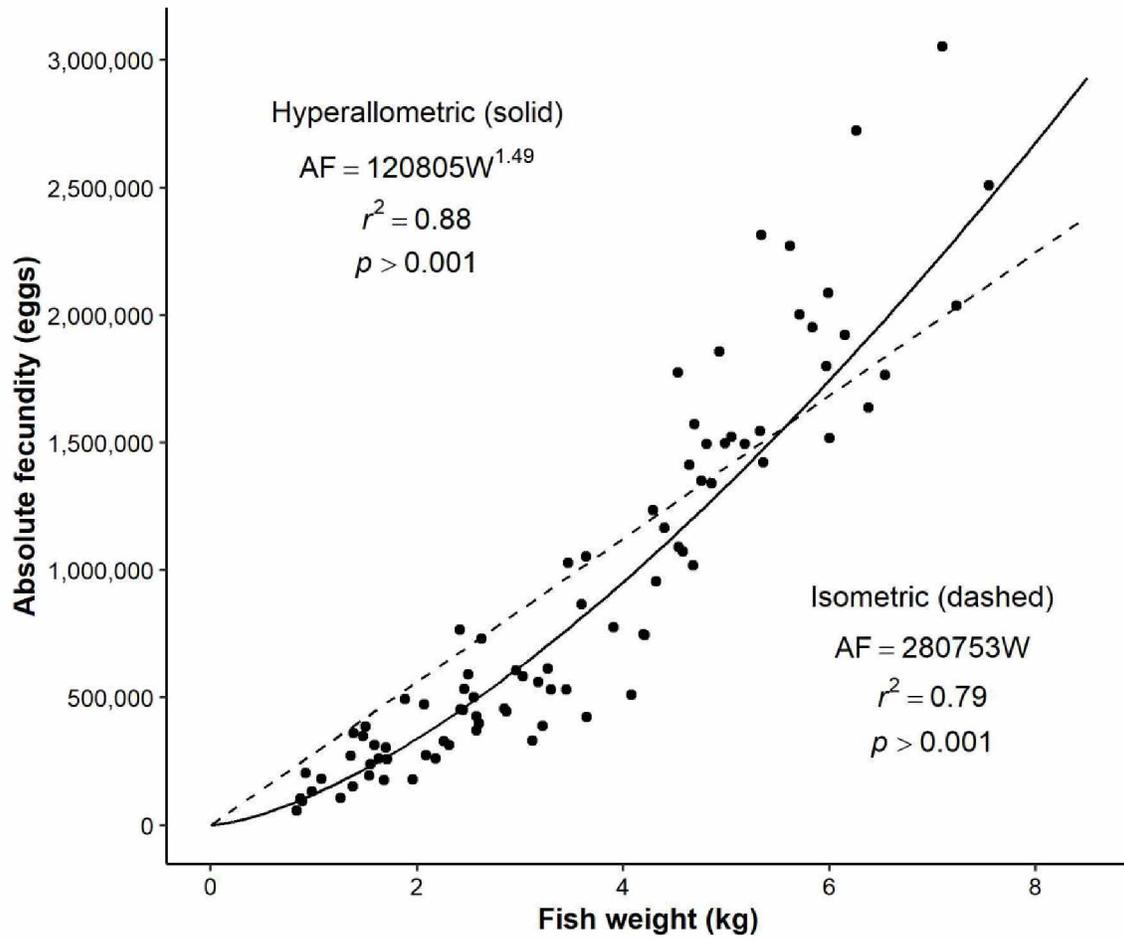
Figure 13. Absolute fecundity (AF; number of eggs and/or larvae) as an isometric (dashed line) and hyperallometric (solid line) function of weight (W; kg) for female Yelloweye Rockfish from the Northern Gulf of Alaska.

General Conclusions

In this study, I advanced knowledge about the reproductive biology of Yelloweye Rockfish at the northern extent of their range. Yelloweye Rockfish maturity was modeled as a multivariate logistic regression using a Markov Chain Monte Carlo and conclusions about maturity were made using Bayesian inferences. All maturity values were assigned using histology examination to determine stage of development. Sex and area (PWS or NGOA) were included as predictor variables in the full model of maturity-at-age and maturity-at-length, and a Bayesian model selection approach (leave-one-out information criterion) was applied to select from 14 candidate models. I compared Yelloweye Rockfish maturity in PWS and the NGOA to populations from California to British Columbia, and developed a calendar of ovarian development using stage of development from the maturity analysis. Further, I identified the timing of parturition for Yelloweye Rockfish and tested for the effect of age and length on the parturition timing. Absolute fecundity was estimated using the gravimetric method with automated counts conducted in an image-analysis software. Absolute and relative fecundity relationships with length were estimated to assess the assumption of constant relative fecundity. These results were input into an estimate of RP that is an improvement on SSB and TEP and progress towards the more comprehensive SRP proposed by Trippel (1999). The key results of these studies were:

- The age-at-maturity of Yelloweye Rockfish from PWS and NGOA varied by sex. Age-at-50% and 95% maturity (A_{50} and A_{95}) was 16 and 31 year for female Yelloweye Rockfish, respectively, and 15 and 19 years for males.

- Length-at-maturity was sex and area specific where Yelloweye Rockfish in the NGOA reached maturity at larger size than in PWS and males matured at a smaller size

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compared to females in both areas. Female length-at-50% (L_{50}) and 95% (L_{95}) maturity was 5.6 cm greater in NGOA than in PWS. Male L_{50} and L_{95} was 3.2 cm greater in NGOA than in PWS.

- Yelloweye Rockfish age-at-maturity increased with latitude and length-at-maturity was constant based on a meta-analysis of A_{50} and L_{50}. Yelloweye Rockfish A_{50} in PWS and NGOA was much less than predicted by a linear regression of A_{50} and latitude. Length-at-50% maturity in PWS and NGOA was similar to the L_{50} estimates from California through BC.

- Yelloweye Rockfish copulated in January through March and parturition occurred between May and August with a peak in June and July. Parturition timing was age- and length-specific; larger and older female released larvae earlier than smaller and younger fish.

- Skip spawning in female Yelloweye Rockfish was documented at a rate of 9.8%. Skip spawning rate was associated with length as a polynomial logistic regression that peaked at 46.2 cm.

- Conducting automated egg counting in image-analysis software was more than four times faster than manual counting and was as accurate and precise as manual counts.

- Yelloweye Rockfish fecundity was estimated to range from 53,249 to 3.052×10^6 eggs. The fecundity-length relationship power function exponent was 4.72 and relative fecundity increased with length, thus the proportionality assumption between SSB and TEP was not met.

- Reproductive potential estimated using the isometric fecundity relationship grossly overestimated RP for PWS and NGOA Yelloweye Rockfish relative to estimates that use

the hyperallometric fecundity relationship and incorporate length-specific skip spawning rate (Appendices F and G).

Yelloweye Rockfish reached maturity at a greater length in the NGOA than in PWS, which was consistent with the contrast in the von Bertalanffy growth function (VBGF) parameters estimated for these areas with Yelloweye Rockfish (Appendix D). Even though these areas are adjacent and closely connected via currents, after age 11, NGOA Yelloweye Rockfish are consistently larger-at-age than PWS Yelloweye Rockfish. This difference in maturity and size-at-age could be explained by several factors: temperature, productivity, and ecological interactions. Future research should explore the mechanisms for the differences in growth and maturity between these two areas, but also quantify growth rates and relationships with environmental variables, harvest history, and abundance of prey using biochronology.

Few studies have estimated maturity for male Yelloweye Rockfish. Wyllie Echeverria (1987) reported male Yelloweye Rockfish A_{50} and L_{50} at 5 years and 30 cm, respectively. In Southeast Alaska, A_{50} and L_{50} were reported to be 23 years and 50 cm for male Yelloweye Rockfish (O'Connell 2002). Rosenthal (1982) estimated male L_{50} to be between 52 and 60 cm for southeast Alaska Yelloweye Rockfish. Age-at-50% maturity for males in the NGOA (including PWS) was 15 years, while length-at-maturity for males in PWS and the NGOA was 40.8 cm and 44.0 cm, respectively. Males in PWS and the NGOA reached maturity smaller and younger than in the southeast Gulf of Alaska. The lack of studies on Yelloweye Rockfish male maturity did not allow for the level of meta-analysis conducted for females. Stock reproductive potential as proposed by Trippel (1999) incorporates paternal quality and experience such as size, sperm density and motility, and mating competition. Paternal effects are often ignored in estimates of rockfish RP, and if paternal quality can affect larval fitness and early life survival of

offspring then it is a factor that should certainly be considered. For this reason, I suggest continued research in estimating male maturity and reproductive biology to better understand the contribution of Yelloweye Rockfish males to RP.

Parturition timing is influential to larval survival in rockfish, and arguably more important than timing of copulation. Parturition timing can have important consequences for offspring recruitment. The parturition timing of Yelloweye Rockfish in the NGOA including PWS coincides with the most productive time of the year (Childers et al. 2005) and the cessation of downwelling (Weingartner et al. 2002). Planktonic larvae of larger and older female Yelloweye Rockfish released earlier in the summer may be benefit from exposure to a longer period of high productivity prior to the onset of autumn downwelling. In addition, offspring from older and larger females are more resistant to starvation and more adapted to a longer planktonic stage (Berkeley et al. 2004; Sogard et al. 2008; Stafford et al. 2014). Conversely, the larvae of smaller and younger females are released briefly before downwelling resumes, and therefore may experience a shorter growth period prior to demersal settlement and consequently, higher mortality rates. The difference in survival as a product of parturition timing is an input of SRP and research into this matter could greatly improve our understanding of the interaction between maternal effects and recruitment dynamics.

This study focused on multiple aspects of reproductive biology, each of which had subtle differences in sample collection and preservation needs. Fecundity, in particular, requires careful handling and the most fixative. The whole gonad needs to be preserved for fecundity estimation, which for the largest of Yelloweye Rockfish ovaries can exceed 4 L of fixative. Fixative can be diluted further for fecundity estimation, but because all tissues had the potential to be processed for histology to assess maturity, skip spawning, or development staging, I had to maintain the

concentration of the fixative. In total, nearly 300 L of fixative was used to address all objectives of this research project. From my experience, I would suggest that future studies carefully decide on the objectives of reproductive biology projects. For studies that focus specifically on maturity, skip spawning, and/or gonad development schedule, a small subsample could be collected in the field instead of collecting and fixing the entire gonad, therefore reducing the volume of fixative needed and waste material. For studies that focus on fecundity alone, the fixative can be diluted to cut back on fixative cost.

Using image-analysis software to estimate fecundity proved to be an effective alternative to manual counting eggs and larvae. Manual counting requires additional time counting eggs in petri dishes in the laboratory and eggs must be counted immediately after processing. Whereas, automated counting in an image-analysis software allows for egg or larvae counting to take place outside of laboratory after all samples have been processed. In March 2020, the outbreak of a novel coronavirus infection (COVID19) began (Wang et al. 2020) and by April 2020, access to laboratories and offices across the University of Alaska Fairbanks campus was restricted. I had captured digital images of all ovary samples at the time of the outbreak, yet counting had not been conducted. With the use of ImagePro Plus, I was able to count Yelloweye Rockfish eggs and larvae remotely. Reduced laboratory time and the order of processing and counting with automated counting was pivotal in completing the fecundity estimations and this thesis research in a timely matter with the complications from the COVID19 pandemic. This was an unforeseen and immeasurable benefit of using an image-analysis software to estimate fecundity. The added benefit of reduced laboratory time could be considered in ways to streamline fecundity studies.

Yelloweye Rockfish fecundity estimates from the NGOA broaden the range of fecundity for the species in the literature. But more importantly, I found that the assumption of constant

relative fecundity was not met. Traditional stock-recruitment models developed by Beverton and Holt (1957) and Ricker (1954), and methods of generating biological reference points (Shepard 1982) were originally developed using fecundity (Rothschild and Fogarty, 1989). Additionally, SRP is a product of fecundity-at-age or length (Trippel 1999). By applying the Yelloweye Rockfish fecundity-relationships established in this thesis, stock assessment scientists can generate RP estimates that are more realistic, which can aid in understanding stock-recruitment dynamics.

Female reproductive potential was estimated as a length-based metric and on a per-recruit basis. I applied the reproductive parameters from Chapter 1 and 2 into estimates of RP (Appendix I). The hyperallometric fecundity-weight relationship with skip spawning represents a more comprehensive understanding of Yelloweye Rockfish reproductive biology than SSB or TEP. I found that the isometric SSB proxy of RP drastically overestimated RP when compared to the hyperallometric relationship with and without skip spawning. In Chapter 2, I approximated the intercept between the isometric and hyperallometric fecundity-length relationship at $W = 5.6$ kg. Below this weight the isometric relationship overestimates fecundity and the contribution to RP for an individual fish and above this weight the isometric relationship underestimates fecundity and the contribution to RP for an individual. The asymptotic length ($L_\infty = 64.1$ cm) from the VBGF for PWS Yelloweye Rockfish corresponds to a mean $W < 5.6$ kg, therefore on average, Yelloweye Rockfish in PWS never exceed the weight where the isometric and hyperallometric relationships intercept. Yelloweye Rockfish in the NGOA reached an asymptotic length ($L_\infty = 69.5$ cm) that exceeded $W > 5.6$, but only by a few cm, hence my SSB estimate of RP was less biased in NGOA. It is the VBGF that largely determines the amount of bias associated with RP estimates and because most Yelloweye Rockfish in both areas spend all or

most of their lives at W < 5.6, RP is overestimated by the isometric relationship and SSB. Modern stock-assessment programs such as Stock Synthesis are capable of incorporating fecundity relationships as a linkage between RP and expected number age-0 fish (Methot and Wetzel 2013; J. Cope, Northwest Fisheries Science Center, personal communication). This considered, I suggest that future stock assessment efforts for Yelloweye Rockfish incorporate fecundity, skip spawning, and maternal effects on survival and viability.

The results from this thesis research can guide the management of Yelloweye Rockfish and other fishes with long reproductive lifespans. The reproductive parameter estimates reveal the bet-hedging strategy of Yelloweye Rockfish through late maturity (16 years), disproportional fecundity and lower skip spawning at larger size, and a diversified parturition timing (Hixon et al. 2014). These results highlight the management needs to maintain age and size structure, and more importantly, maintenance of diverse age structure (King and McFarlane 2003; Hixon et al. 2014). Beyond the stock assessment application and direct management action (e.g., establishing a maximum size or slot limit; Froese 2004; Vasilakopoulos et al. 2011), a great management tool for Yelloweye Rockfish is angler education to induce voluntary conservation (Cooke et al. 2013). Yelloweye Rockfish are an excellent candidate for voluntary conservation as they are charismatic with their bright coloration and old age. Outreach efforts could work to connect the public's fascination with the old age of Yelloweye Rockfish to the importance of maintaining old age structure. Much of the simple reproductive information gained in this research such estimates of full maturity (> 30 years) and maximum fecundity (> 3 million eggs) could resonate with public stakeholders to alter harvest behavior that could enhance institutional regulations.

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Appendix A. 2019 University of Alaska Fairbanks Institutional Animal Care and Use Committee approval.

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May 7, 2019

To: Jeff Falke
            Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [1206971-4] Spawning Potential Ratio (SPR) assessment and sensitivity analysis
            utilizing estimates of age at maturity and fecundity for Yelloweye Rockfish in Prince
            William Sound, AK

The IACUC has reviewed the Progress Report by Designated Member Review and the Protocol has been
approved for an additional year.

Received:	March 28, 2019
Initial Approval Date:	March 28, 2018
Effective Date:	May 7, 2019
Expiration Date:	March 28, 2020

This action is included on the May 9, 2019 IACUC Agenda.

PI responsibilities:

Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol.

Appendix B. Yelloweye Rockfish fecundity and relative fecundity estimates from two previous studies.

Source	Total length (cm)	Weight (kg)	Estimated fecundity (millions of eggs)	Relative Fecundity (egg per g of fish)
Hart (1942)	--	8.8	2.698	305
Macgregor (1970)	61.5	5.0	1.356	271
	53.0	3.2	1.096	342

Appendix C. Methods and results for estimating and comparing Yelloweye Rockfish reproductive potential with and without incorporating fecundity-relationships and skip spawning.

METHODS

Study area

For the purpose of this thesis, PWS was defined as all waters north of lines between the eastern tip of Hinchinbrook Island and Cordova, the eastern tip of Montague Island and the southern tip of Hinchinbrook Island, and all waters north of a line at 60°N extending from Montague Island to Cape Puget (Figure 1.1). The NGOA, which is adjacent to PWS to the south, is bounded by lines near Gore Point in the west (148°00'25"W) and Cape Suckling in the east (144°00'00"W), and extends south to a longitudinal line at 59°00'00"W.

Length-at-age

Yelloweye Rockfish harvested in recreational and commercial fisheries have been biologically sampled at ports in Southcentral Alaska by the Alaska Department of Fish and Game (ADFG) since 1991 (Failor 2016; Rumble et al. 2017). Staff from the ADFG Divisions of Sportfish and Commercial Fish provided sample area, age, sex, length, and weight data for Yelloweye Rockfish sampled in both port sampling programs from 1991 to 2019 (Alaska Department of Fish and Game, *unpublished data*). The data provided from these programs were combined into one dataset. Female fork length-at-age data was fit using the von Bertalanffy growth function (VBGF; Beverton and Holt 1957) and defined in the "FSA" package (Ogle et al. 2020). Growth equations were generated for PWS and the NGOA. The parameters of each VBGF were estimated using the nls() function in the R statistical environment. Reasonable starting values for the parameters were provided by using the vbStarts() function in the "FSA" package (Ogle et al. 2020). For each equation, 999 nonparametric bootstrap samples of mean

centered residuals were computed with the Boot() function from the "car" package (Ogle and

Isermann 2017).

Weight-length relationship

A total weight-fork length relationship was generated from the data provided by

ADF&G. We fit the standard allometric weight-length relationship, as follows,

$$W = cFL^d,$$

using a log-log transformation of total weight and FL and conducting a simple linear regression

to estimate c and d. A single weight-length relationship was generated for PWS and NGOA

combined.

Reproductive potential was estimated as egg or larval production through established

fecundity-weight relationships for Yelloweye Rockfish in the NGOA, including PWS (Chapter

2). An estimate of the weight-length relationship was established for the purpose of converting

RP estimated via female SSB into egg production and comparing isometric (fecundity-

relationship $b = 3$) and hyperallometric (fecundity-relationship $b > 3$; Chapter 2) relationships in

a common unit. The linear fecundity-weight relationship (isometric) assumes that relative

fecundity is constant; this is analogous to the assumptions associated with SSB. Therefore, RP

was estimated using weight-at-length and the fecundity-weight relationship rather than

estimating TEP directly using the fecundity-length relationship. This transformation is shown

algebraically as:

$$\Phi_{isometric} = 280,753 * (cFL^d)$$

and

$$\Phi_{hyperallometric} = 120,805 * (cFL^d)^{1.49},$$

where c and d are the coefficient and exponent of the weight-length relationship, respectively.
This transformation allowed for us to convert RP estimated via SSB into egg or larval
production.

Per-recruit survival-at-length

Probability of survival to FL (S_l) for an individual recruit was estimated as:

$$S_l = S_{FL-1}(\frac{FL_\infty - FL - 1}{FL_\infty})^{\frac{Z}{K}} \quad \text{for FL} < FL_\infty$$

where Z was the instantaneous rate of total mortality, FL_∞ was the asymptotic length and K was
the Brody growth coefficient of the VBGF (Hordyk et al. 2016). Natural mortality (M) was only
considered when estimating survival, therefore $Z = M$.

Per-recruit reproductive Potential

Female reproductive potential (RP) per-recruit was estimated individually for PWS and
the NGOA as:

$$RP = \sum_{l=1}^{n} S_l \, Q_l \Phi_{W|l}(1 - \sigma_l)$$

where S_l was the probability of survival to length, l, Q_l maturity at l, $\Phi_{W|l}$ was the fecundity at
weight, w, given l, and σ_l was the probability of skip spawning at l. Because RP was estimated
on per-recruit basis, S_l was adequate for quantifying demographics of the populations and
therefore, number of females-at-length was not needed. Maturity and skip spawning relationships
with fork length developed in Chapter 1 were applied to estimates of RP. Reproductive potential
was estimated using the isometric fecundity-weight relationship (RP$_{iso}$; SSB equivalent) without
skip spawning, hyperallometric relationship without skip spawning (RP$_{hyper}$; TEP equivalent) and
the hyperallometric relationship with consideration of skip spawning (RP$_\sigma$). Bias in RP was
calculated by dividing RP$_{hyper}$ and RP$_\sigma$ by RP$_{iso}$, which represented assumptions associated with

SSB. A mortality rate of 0.044 yr^{-1} was applied to RP estimates based on M used in a stock assessment of Washington, Oregon, and California Yelloweye Rockfish (Gertseva and Cope 2017).

<div align="center">Results</div>

Length-at-age

Length and age data were analyzed for 10,504 female Yelloweye Rockfish. Female Yelloweye Rockfish fork length assessed ranged from 25.6 to 78.8 cm (mean = 52.3 cm, SD = 8.2; N = 3,234) for PWS and 23.7 to 87.3 cm (mean = 57.7 cm, SD = 8.7; N = 7,228) for NGOA. Ages for ranged from 7 to 107 years (mean = 33 years, SD = 13.1; N = 3,256) and 5 to 107 years (mean = 33 years, SD = 13.1; N = 7,249) for PWS and NGOA, respectively. The estimates (95% bootstrap confidence intervals [CIs]) of the VBGF parameters for PWS Yelloweye Rockfish were L_∞ = 64.1 cm (95% CIs: 63.2, 65.1), K = 0.048 (95% CIs: 0.043, 0.052), and t_0 = -7.08 (95% CIs: -8.82, -5.52; Figure 3.1). The estimates (95% bootstrap CIs) of the VBGF parameters for NGOA Yelloweye Rockfish were L_∞ = 69.5 cm (95% CIs: 68.9, 70.1), K = 0.056 (95% CIs: 0.052, 0.059), and t_0 = -2.65 (95% CIs: -3.49, -1.87; Appendix D). In summary, Yelloweye Rockfish in the NGOA reach a greater L_∞ and grow faster than PWS Yelloweye Rockfish.

Weight-length relationship

Weight data was available for 7,335 female Yelloweye Rockfish. Total weight ranged from 0.3 to 13.2 kg (mean = 3.9 kg; SD = 1.8; N = 7,335). The following power function of the weight-length relationship was derived from the log-log linear regression (Appendix E):

$$W = 0.000015 * FL^{3.07}$$

Per-recruit reproductive potential

The isometric estimate of RP was consistently greater than estimates of RP_{hyper} and RP_σ in both study areas (Appendices F and G). The isometric estimate of RP was 49% greater than RP_{hyper} in PWS and 34% greater than RP_{hyper} in the NGOA. The isometric estimate of RP was 66% greater than RP_σ in PWS and 45% greater than RP_σ in the NGOA.

Appendix D. Fits of the von Bertalanffy growth equation of fork length (FL; y-axis; cm) and age (x-axis; years) data for female Yelloweye Rockfish in Prince William Sound, AK (light grey circles; dashed line) and the Northern Gulf of Alaska (dark grey circles; solid line).

NGOA: $FL = 69.5 \left(1 - e^{-0.056\,(age+2.652)}\right)$

PWS: $FL = 64.1 \left(1 - e^{-0.048\,(age+7.081)}\right)$
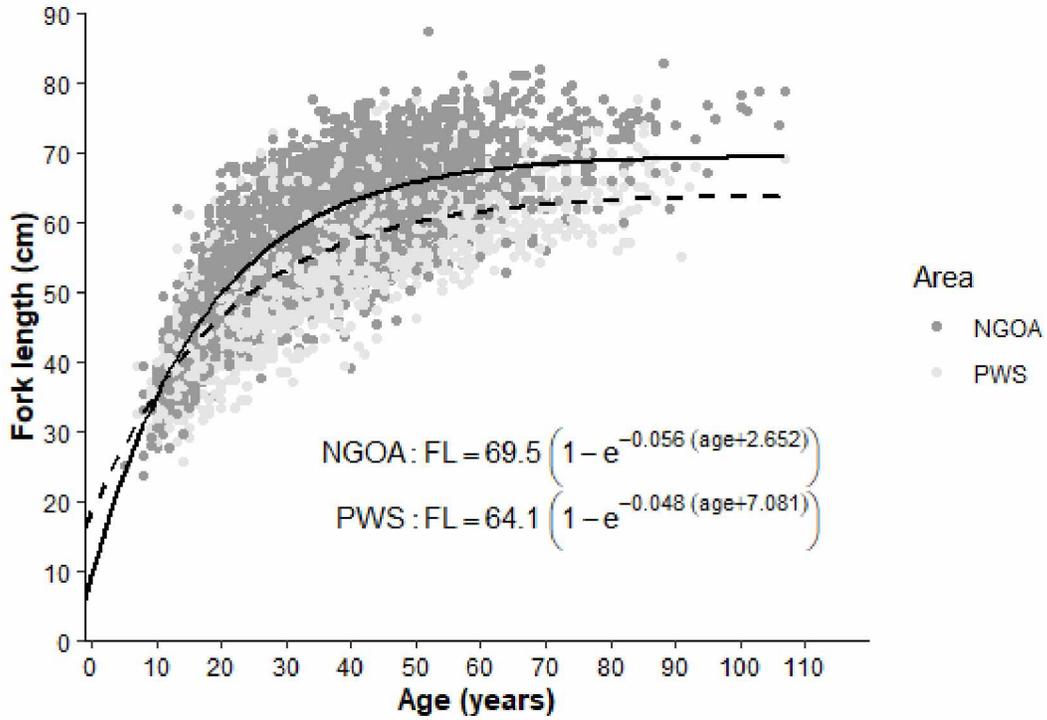
Appendix E. Fish weight (kg) as a function of fork length (cm) for female Yelloweye Rockfish from the Northern Gulf of Alaska, including Prince William Sound, AK.

$$W = 1.5\text{e-}05\,FL^{3.07}$$

$$r^2 = 0.94$$

$$p > 0.001$$
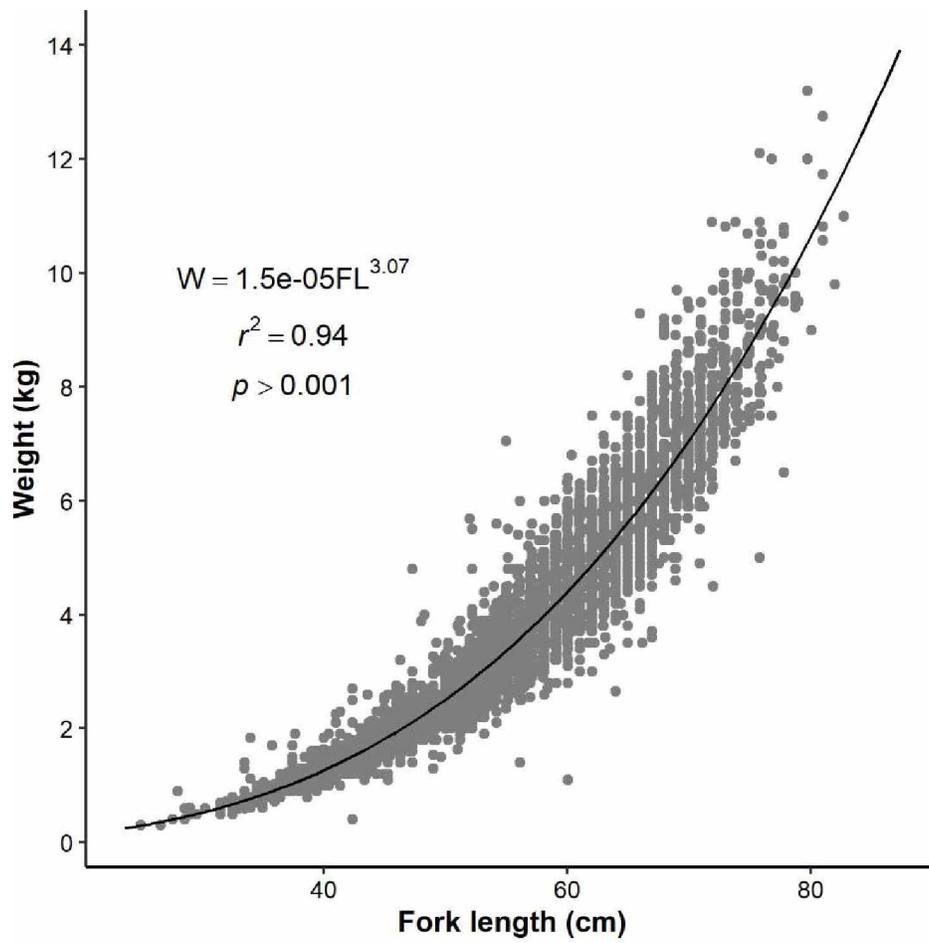
Appendix F. Length-based reproductive potential per recruit (eggs or larvae) for Yelloweye Rockfish in Prince William Sound estimated using the isometric fecundity-weight relationship without skip spawning, the hyperallometric fecundity without skip spawning, and the hyperallometric relationship with consideration of skip spawning (σ).
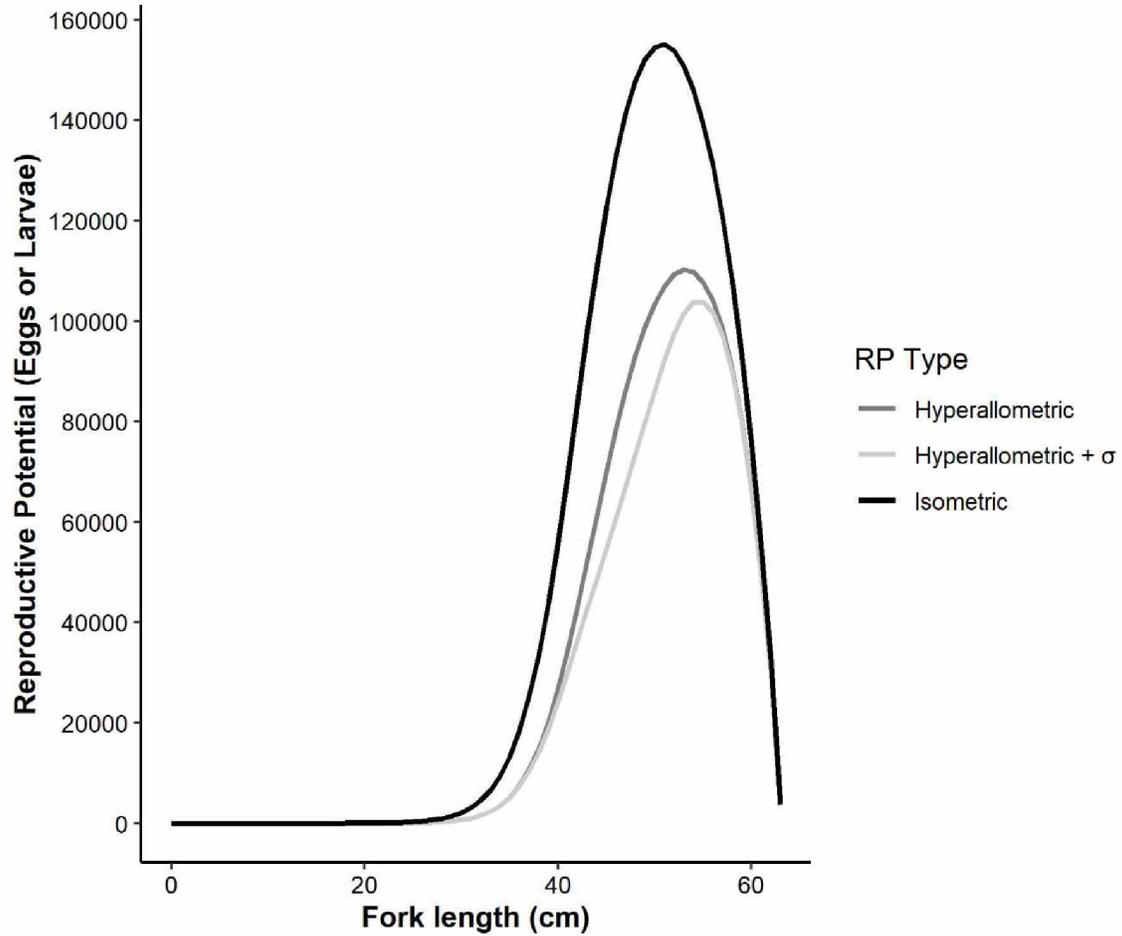
Appendix G. Length-based reproductive potential per recruit (eggs or larvae) for Yelloweye Rockfish in the Northern Gulf of Alaska estimated using the isometric fecundity-weight relationship without skip spawning, the hyperallometric fecundity without skip spawning, and the hyperallometric relationship with consideration of skip spawning (σ).