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Modeling growth and reproduction of chilipepper rockfish under variable environmental conditions

Chris J. Harvey[a,*], John C. Field[b], Sabrina G. Beyer[b], Susan M. Sogard[b]

[a] NOAA Fisheries, Northwest Fisheries Science Center, 2725 Montlake Blvd. E, Seattle, WA 98112, United States
[b] NOAA Fisheries, Southwest Fisheries Science Center, 110 Shaffer Rd., Santa Cruz, CA 95060, United States

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ABSTRACT

Chilipepper rockfish (*Sebastes goodei*), a long-lived, highly fecund commercial species in the California Current ecosystem, contend with a variable environment on several time scales. Using a bioenergetics model, we simulated alternate strategies of energy allocation by female chilipeppers under variable conditions, and examined resulting patterns in age-dependent size and fecundity. Variable conditions consisted of single climate events (one anomalous year, one 4-year regime shift, or one 10-year regime shift) that occurred at different points over the lifespan of the fish and were either "poor" or "good" relative to baseline conditions. Poor years or regimes reduced growth and fecundity, while good years or regimes increased growth and fecundity. Fecundity losses during poor conditions could be mitigated by partially or fully reallocating energy from gonadal production into somatic growth, thereby increasing potential fecundity in future years. However, when mortality was incorporated, those energetic re-routing strategies only increased lifetime reproductive output if we assumed that old (≥age 8) females produce more viable larvae than young females, and if the event occurred prior to age 8. Young females also increased output of larvae beyond age 8 if they skipped spawning or reallocated reproductive energy during good conditions, instead investing the surplus energy into additional somatic growth and enhancing future fecundity. Our results are consistent with recent estimates of growth rate variability in the chilipepper population, and with observations of young females of other rockfish species skipping spawning during poor conditions. Models like this may help improve stock assessment parameters and biological reference points for species with environmentally driven variability in size at age.

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1. Introduction

Rockfish (*Sebastes* spp.) are a species-rich, ecologically important and commercially valuable component of the California Current ecosystem. Most species epitomize the "periodic" life history strategy among marine fishes (King and McFarlane, 2003): a long life span with slow growth, late maturity and high fecundity (Parker et al., 2000; Love et al., 2002). Females of most species may experience decades of reproductive activity, and their high reproductive potential increases the likelihood that larvae will be abundant in years with conditions that favor larval growth and survival (King and McFarlane, 2003; O'Farrell and Botsford, 2005; Sogard et al., 2008). While this general notion of "bet-hedging" – producing large numbers of larvae for many decades so that occasional years will yield strong cohorts – is broadly accepted for rockfish, many of the mechanistic details of their life histories are complex, unknown, or emerging. For example, female rockfish face a tradeoff in terms of the size and timing of maturation: an early age at maturity increases the probability of spawning prior to death, but also leads to an earlier slowing of somatic growth and thus a lower maximum fecundity (e.g., Berrigan and Charnov, 1994). Also, older females of some rockfish species may confer a survival advantage on their offspring by producing larvae with greater lipid stores and faster growth rates (Berkeley et al., 2004; Sogard et al., 2008). Reproductive-age females of some species may skip spawning in some years, potentially as a consequence of poor female condition (Hannah and Parker, 2007; Thompson and Hannah, 2010).

The basic life history patterns of rockfish are superimposed on a highly variable marine environment, and rockfish growth, condition and reproduction appear to be related to short- and long-term climate variability. For example, growth rates of yelloweye rockfish (*Sebastes ruberrimus*) throughout the northeast Pacific Ocean were correlated with large-scale, decadal shifts in production and temperature (Black et al., 2008). Annual aurora rockfish (*S. aurora*) growth was negatively correlated to average sea level, a proxy for ocean productivity (Thompson and Hannah, 2010). Growth rates of yellowtail rockfish (*S. flavidus*) and widow rockfish (*S. entomelas*) off of California showed interannual variation, including sharp

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* Corresponding author.
E-mail address: chris.harvey@noaa.gov (C.J. Harvey).

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decreases during poor conditions associated with the 1983 El Niño event (Woodbury, 1999). Similarly, somatic condition and gonadal weight of blue rockfish (*S. mystinus*) off of California were dramatically lower during El Niño years (VenTresca et al., 1995). Yellowtail rockfish fecundity showed significant interannual variability in the California Current, but only for young (<age 15) females in California waters and not for older females in California nor for females of any age off of Washington state (Eldridge and Jarvis, 1995). Hannah and Parker (2007) hypothesized that young adult female Pacific ocean perch (*S. alutus*) may skip spawning in some years as a result of low fat reserves related to poor ocean conditions. Understanding these sources of variability is critical to proper rockfish fishery management and conservation because population models and stock assessments depend on reasonable estimates of adult growth (e.g., Helser et al., 2007) and larval production (Ralston et al., 2003; Ralston and MacFarlane, 2010).

Here, we use bioenergetics modeling to assess patterns of energy allocation in chilipepper rockfish (*S. goodei*). The chilipepper is a mid-size, semi-pelagic rockfish found primarily in shelf and shelf-break waters off of California, where they have been among the most important commercial and recreational rockfish species in both historical and contemporary fisheries (Love et al., 2002). Past chilipepper stock assessments have documented periodic shifts in size at age, but it is unclear if these changes are due to variable growth or to changes in fishery selectivity (e.g., Ralston et al., 1998). Field (2008) found that allowing the von Bertalanffy growth parameter *k* to vary between set time periods coincident with major climate regime shifts resulted in significant improvement of stock assessment model fits to observed length and age frequency data. That finding, though useful, does not mechanistically tie chilipepper growth to climate, nor does it suggest specific strategies for how chilipeppers allocate energy to growth and reproduction in the face of climate variability. Mechanistic linkage of rockfish growth and reproduction to climate variability has been achieved with bioenergetics models, which are dynamic models that express fish energy budgets as functions of environmental conditions such as temperature, prey quantity and prey quality (Harvey, 2005, 2009).

Our goal in this paper is to examine how female chilipepper growth and egg production is affected by climate variability on short, moderate and long time scales (1, 4 and 10 years). Using a bioenergetics approach, we vary temperature, prey availability and prey quality at each of these time scales and examine responses in terms of growth rate, asymptotic length, condition, and lifetime egg production. We consider climate conditions that either improve (good years or regimes) or reduce (poor years or regimes) foraging success relative to a baseline model. We examine whether or not lifetime egg production can be maximized if females reallocate surplus energy away from reproduction and into somatic growth. We also ask if the timing of climate variability matters in terms of lifetime growth or reproduction. Finally, we put our findings into the context of improving chilipepper stock assessments.

2. Methods

We used a modified form of a generic *Sebastes* bioenergetics model used in previous studies (Harvey, 2005, 2009). The model follows a core thermodynamic equation:

$$C–R–S–F–U = \Delta B + G \tag{1}$$

where the rates of somatic growth (ΔB) and gonadal production (G) are functions of consumption (C) and losses due to respiration (R), specific dynamic action (S), egestion (F) and excretion (U). These symbols represent functions (Table 1) that are typically dependent upon fish weight (W, in g) and/or temperature (T, in °C). Generic model parameters for *Sebastes* are shown in Table 2. The general nature and derivation of equations and parameters are described in detail by Kitchell et al. (1977); the derivation of the rockfish parameters in particular is described by Harvey (2005, 2009). Because our primary focus was on energy allocation as it relates to population biology, all simulations are for female chilipepper rockfish only. This is reasonable because chilipeppers exhibit sexually dimorphic growth and mortality, and the larger and longer-lived females contribute more to total biomass and landings (Field, 2008).

Table 1
Equations used in bioenergetics models. Parameters are defined in Table 2.

Metabolic function	Equations
Consumption	$C = CA \quad W^{CB}Pf_C(T)$, where : $f_C(T) = V^X e^{(X\cdot(1-V))}$ $V = (CTM - T)/(CTM - CTO)$ $X = Z^2(1+(1+40/Y)^{0.5})^2/400$ $Z = \ln(CQ)(CTM - CTO)$ $Y = \ln(CQ)(CTM - CTO + 2)$
Respiration	$R = RA \quad W^{RB}f_R(T)ACT\omega$, where : $f_R(T) = RV^{RX} e^{(RX\cdot(1-RV))}$ $RV = (RTM - T)/(RTM - RTO)$ $RX = RZ^2(1+(1+40/RY)^{0.5})^2/400$ $RZ = \ln(RQ)(RTM - RTO)$ $RY = \ln(RQ)(RTM - RTO + 2)$
Specific dynamic action	$S = SDA(C - F)$
Egestion	$F = FAC$
Excretion	$U = UA(C - F)$

2.1. Baseline model

We first established a baseline model, calibrated to recreate empirical measures of age-specific fork length (FL), weight, maturation rate, and reproductive output of female chilipepper rockfish. The model began with 1.0-cm, post-flexion larvae (Love et al., 2002), which subsequently grew according to female von Bertalanffy length-at-age relationships and weight–length relationships used in the most recent chilipepper stock assessment (Field, 2008). We assumed knife-edge maturation at FL = 25.7 cm, which was the size of 50% maturity of female chilipepper in the stock assessment (Field, 2008). Mature females were assumed to gestate and release larvae entirely during the month of January. Fecundity estimates were based on data from 179 females containing fertilized eggs

Table 2
Parameters for the chilipepper rockfish bioenergetics model functions listed in Table 1. Derivation of parameters is described by Harvey (2005, 2009).

Parameter	Description (units)	Value
CA	Intercept of the allometric consumption function ($g\,g^{-1}\,d^{-1}$)	0.1330
CB	Body mass scaling exponent for consumption	−0.3479
CQ	Q_{10} for consumption	2.80
CTO	Optimal temperature for consumption (°C)	17.825
CTM	Maximum temperature for consumption (°C)	23
RA	Intercept of the allometric respiration function ($g\,O_2\,g^{-1}\,d^{-1}$)	0.0100
RB	Body mass scaling exponent for respiration	−0.2485
RQ	Q_{10} for respiration	2.50
ACT	Activity multiplier for respiration	1
ω	Constant to convert *R* from oxygen consumed to energy expended ($J\,g{-}O_2{}^{-1}$)	13,560
RTO	Optimal temperature for respiration (°C)	23
RTM	Maximum temperature for respiration (°C)	28
SDA	Proportion of assimilated energy spent on digestion	0.163
FA	Proportion of consumed energy lost to egestion	0.104
UA	Proportion of assimilated energy lost to excretion	0.068
ED	Energy density ($J\,g^{-1}$)	6371