

Abstract—Fish bioenergetics models estimate relationships between energy budgets and environmental and physiological variables. This study presents a generic rockfish (*Sebastes*) bioenergetics model and estimates energy consumption by northern California blue rockfish (*S. mystinus*) under average (baseline) and El Niño conditions. Compared to males, female *S. mystinus* required more energy because they were larger and had greater reproductive costs. When El Niño conditions (warmer temperatures; lower growth, condition, and fecundity) were experienced every 3–7 years, energy consumption decreased on an individual and a per-recruit basis in relation to baseline conditions, but the decrease was minor (<4% at the individual scale, <7% at the per-recruit scale) compared to decreases in female egg production (12–19% at the individual scale, 15–23% at the per-recruit scale). When mortality in per-recruit models was increased by adding fishing, energy consumption in El Niño models grew more similar to that seen in the baseline model. However, egg production decreased significantly—an effect exacerbated by the frequency of El Niño events. Sensitivity analyses showed that energy consumption estimates were most sensitive to respiration parameters, energy density, and female fecundity, and that estimated consumption increased as parameter uncertainty increased. This model provides a means of understanding rockfish trophic ecology in the context of community structure and environmental change by synthesizing metabolic, demographic, and environmental information. Future research should focus on acquiring such information so that models like the bioenergetics model can be used to estimate the effect of climate change, community shifts, and different harvesting strategies on rockfish energy demands.

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Effects of El Niño events on energy demand and egg production of rockfish (*Scorpaenidae: Sebastes*): a bioenergetics approach

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Over 90 species of rockfish (*Sebastes* spp.) are found in kelp beds, rocky reefs, pelagic habitats, and continental shelf and slope zones of the temperate and subarctic North Pacific; these species feed on a range of organisms, from zooplankton to fish (Love et al., 2002). Although they are a key component of groundfish fisheries on the U.S. Pacific Coast, many rockfish have declined considerably in recent decades, owing to overfishing and climate-induced downturns in production (Parker et al., 2000). Conservation efforts, ranging from coast-wide fishery closures to establishment of marine reserves, have been enacted in order to rehabilitate rockfish stocks. The efficacy of such actions depends in part on the dynamics of the communities in which rockfish exist. Key among these dynamics are trophic interactions, as influenced by abiotic factors and rockfish population structure.

Although rockfish are widely distributed and important to the ecology, fisheries, and conservation efforts of the Pacific Coast, little is known about their trophic dynamics. For example, of the 65 rockfish species that live along the North American West Coast, quantitative diet data are available for only 15 species (Murie, 1995). Better information on the food habits and energetics of both juvenile and adult rockfish would facilitate a greater understanding of the role they play in their communities, and how their role is affected by external forces. This is particularly true given observations that environmental variation can have strong effects on rockfish growth and condition (Lenarz et al., 1995; Woodbury, 1999).

Fish bioenergetics models relate the energy consumption, growth, and energy allocation patterns of fishes to environmental and physiological variables such as temperature, food quality, body size, and reproductive status (Kitchell et al., 1977). These models, founded in thermodynamic laws of mass and energy balance, can successfully predict patterns of energy demands by fish (Madenjian et al., 2000). At the scale of the individual fish, bioenergetics models can estimate effects of a fish on its community (in terms of the amount of prey it consumes) and effects of the environment on the fish, such as how changes in temperature or food availability influence energy consumption and growth (Rice et al., 1983). When coupled to population models, bioenergetics models can predict prey-predator supply-demand relationships (Negus, 1995) and determine how different fishery management policies will affect prey resources in the community from which the targeted fish is extracted (Kitchell et al., 1997; Essington et al., 2002; Schindler et al., 2002). Thus, these models may facilitate a more community- or ecosystem-level approach to rockfish management.

In this study, I develop a generic *Sebastes* bioenergetics model. My first objective is to detail the parameters and the sensitivity analysis of the model, thereby offering a synthesis of what is known about *Sebastes* energetic physiology and identifying parameters for which greater information is desirable. The second goal is to present a simple application of the model: an estimation of the effects of

El Niño related environmental changes on the energy demands of blue rockfish (*S. mystinus*) under unfished and fished conditions. Two relevant characteristics of El Niño events in U.S. West Coast waters are elevated temperatures and reductions in growth rates and reproductive condition of *Sebastes* (Lenarz et al., 1995; VenTresca et al., 1995; Woodbury, 1999). The bioenergetics approach can incorporate these changes and can therefore help to characterize the role of rockfish as consumers in a dynamic environment.

Methods

Model structure

I followed the basic structure of bioenergetics models established for other fishes (e.g., Kitchell et al., 1977; Hewett and Johnson, 1992), in which energy intake (consumption) equals all energy outputs (respiration, wastes, growth, and reproduction). The basic model equation is

$$C = (R + A + S) + (F + U) + (\Delta B + G), \quad (1)$$

where C = consumption, R = respiration, A = active metabolism, S = specific dynamic action (digestive costs), F = egestion, U = excretion, ΔB = somatic growth, and G = gonad production. The respiration and active metabolism portions of Equation 1 take the form

$$R = RA \times W^{RB} \times f(T) \times ACT, \quad (2)$$

where RA and RB are constants that describe the allometric respiration function, W is wet biomass, $f(T)$ is a temperature dependence function, and ACT is an activity multiplier (Kitchell et al., 1977). The function $f(T)$ (Kitchell et al., 1977) is a hump-shaped function that requires estimates of optimal (RTO) and maximum (RTM) temperatures for respiration, and a Q_{10} (RQ).

The terms S , U , and F all scale to total consumption (Kitchell et al., 1977). One can thus think of them as a general energy loss term

$$Loss = (S + U) \times (C - F) + F. \quad (3)$$

Model parameters

Although parameters are derived from studies of many rockfish species, I developed the present model to describe energetic dynamics of *S. mystinus*, for which a considerable literature exists regarding diet and responses to climate variability (e.g., Hallacher and Roberts, 1985; Bodkin et al., 1987; Hobson and Chess, 1988; Lenarz et al., 1995; VenTresca et al., 1995).

Respiration parameter estimates came from studies of other *Sebastes* species or related scorpaenid fishes (Table 1). For RTM , I used published estimates for *S. thompsoni* and *S. schlegeli* (Ouchi, 1977; Tsuchida and Setoguma, 1997), and assumed that RTO would be 5°C

Table 1

Parameter values for the generic *Sebastes* bioenergetics model.

| Parameter | Description | Value |
|-------------|--|-----------|
| RA | Intercept of the allometric respiration function | 0.0143 |
| RB | Slope for allometric respiration function | -0.2485 |
| RQ | Slope for temperature dependence of respiration (Q_{10}) | 2 |
| ACT | Multiplier for active metabolism | 1 |
| RTO | Optimum temperature for respiration | 23°C |
| RTM | Maximum temperature for respiration | 28°C |
| SDA | Specific dynamic action coefficient | 0.163 |
| FA | Egestion coefficient | 0.104 |
| UA | Excretion coefficient | 0.068 |
| ED | Energy density (somatic tissue) of wet mass | 6,120 J/g |
| GED | Energy density (female gonadal tissue) of wet mass | 8,627 J/g |
| GA | Coefficient of the female length-fecundity relationship | 1.559 |
| GB | Exponent of the female length-fecundity relationship | 3.179 |
| GSI_{max} | Maximum male gonadosomatic index | 0.008 |

cooler. The resulting RTO was similar to upper temperatures at which juvenile *S. diploproa* experienced zero growth while feeding (Boehlert, 1981). RQ was based on low-temperature Q_{10} values in several scorpaenid respiration studies (Boehlert et al. 1991; Yang et al., 1992; Kita et al., 1996; Vetter and Lynn, 1997). RA , the oxygen consumption rate for a 1-g fish at RTO , was derived from data for nongestating *S. schlegeli* (Boehlert et al., 1991). RB , which describes the allometric scaling of respiration, was also derived from data for nongestating *S. schlegeli* spanning a range of roughly 0.7 to 1.9 kg body mass (Boehlert et al., 1991). Respiration terms were converted to energy units by an oxycaloric correction (13.56 J/mg O_2), and then to biomass by assuming that rockfish energy density (ED) = 6,120 J/g wet mass (Perez, 1994).

The ACT multiplier was assumed to equal 1. This assumption is best justified in cases where routine respiration rates were used to determine parameters for the model. Boehlert et al. (1991) stated that *S. schlegeli* in their analysis were generally inactive, which implies that rates derived from their data represent resting

metabolism. I chose to keep *ACT* at 1, however, because I could find no data describing a reasonable activity multiplier. Thus, *Sebastes* model outputs may underestimate energy consumption under conditions in which individuals are especially active.

I obtained growth (ΔB in Eq. 1) terms using von Bertalanffy length-at-age curves and data for length-to-mass conversions for *S. mystinus* as summarized by Love et al. (2002). Because female *S. mystinus* are larger at age than males, growth was modeled with sex-specific von Bertalanffy curves with the difference equation method of Gulland (1983). Digestion and waste terms *S*, *F*, and *U* were derived from previous teleost models (Hewett and Johnson, 1992).

I estimated gonad production (*G*) with gonadosomatic indexes (GSI) and size-fecundity relationships (females only), assuming that female and male *S. mystinus* mature gradually over the range of lengths observed by Wyllie-Echeverria (1987), and reproduce once annually. For males, I assumed that gonads have the same *ED* as somatic tissue; for females, I assumed that gonadal energy density (*GED*) = 8,627 J/g, which was the average of gonadal energy density at the onset of embryogenesis for *S. flavidus* and *S. jordani* (MacFarlane and Norton, 1999). Estimated maximum female GSI was based on a fecundity-length relationship:

$$\text{fecundity} = GA \times TL^{GB}, \quad (4)$$

where *GA* and *GB* were taken from a generic rockfish length-fecundity relationship (Love et al., 2002) and *TL* is total length in cm. Fecundity was converted to biomass units by assuming that each egg weighed 0.0003 g, which I derived from Love et al. (1990) by dividing the mean maximum female gonad weight by the estimated fecundity of modal mature females for several species. For mature males, I assumed a constant maximum GSI based on data for other species (Love et al., 1990). Post-spawning GSI was assumed to be 10% of the maximum for each sex, as with other rockfish (Love et al., 1990). The *G* terms were the difference between the maximum and minimum GSIs for each sex, expressed as mass (and, in females, adjusted by multiplying by *GED/ED*).

Rockfish are viviparous, and developing larvae may receive energy from both yolk and maternal sources (Love et al., 2002). During gestation in a laboratory, female *S. schlegeli* consumed 35% to 117% more oxygen than nongestating fish of similar size (Boehlert et al., 1991). To account for the possibility that blue rockfish may also be matrotrophically viviparous, I increased female respiration by 50% during the gestation period (assumed to be 45 days per year based on gestation times of other species [Boehlert et al., 1991]).

Model application: effects of El Niño on blue rockfish energy consumption

To examine the effects of El Niño on *S. mystinus* energy consumption, I created two model conditions: a baseline model and an El Niño model that estimated *S. mystinus*

Table 2

Changes in the *S. mystinus* bioenergetics model that were implemented in El Niño scenarios in relation to the baseline model.

| Variable | Change |
|---------------------------|--|
| Temperature | Increased 1.5°C in El Niño years ¹ |
| Growth (length increment) | Decreased 17.5% in El Niño years ¹ |
| Female condition factor | Decreased 10% in El Niño years; decreased 5% the year following an El Niño ² |
| Male condition factor | Decreased 7.5% in El Niño years; decreased 5% the year following an El Niño ² |
| Fecundity | Decreased 67% in El Niño years ² |

¹ Source: Lenarz et al., 1995.

² Source: VenTresca et al., 1995.

energy demands, in megajoules (MJ), required for necessary growth, reproduction, and related metabolic costs. I used MJ rather than prey biomass as the currency because quantitative, seasonal diet data for *S. mystinus* in northern California were available for average years (Hobson and Chess 1988) but not for El Niño years. During the 1982–83 El Niño, Lea et al. (1999) found that central Californian *S. mystinus* consumed large numbers of the pelagic crab *Pleuroncodes planipes*, which is typically found south of Point Conception during average years. During the same time period, *S. mystinus* ate few tunicates or scyphozoans (Lea et al., 1999), which were the predominate prey of *S. mystinus* in average years (Hobson and Chess, 1988). These findings suggest a major shift in *S. mystinus* prey composition during El Niño events.

The baseline model simulates energy consumption of northern California *S. mystinus* from age 0 to age 30, based on quarterly growth estimates from sex-specific von Bertalanffy curves (Love et al., 2002) and seasonal temperature data from Hobson and Chess (1988). Mature females released larvae in the fourth quarter of each year, and mature males released gametes in the third quarter (Wyllie-Echeverria, 1987). Energy consumption for both sexes from ages 0 to 30 was expressed at two scales: for the 30-year life span of an individual; and on a per-recruit basis (under the assumption that there was no fishing mortality and that the natural mortality rate [*M*] was 0.2, applied in quarterly time steps).

The El Niño model was similar to the baseline model, except an El Niño occurred every three to seven years. During these years there were changes in temperature, growth, condition, and fecundity (Table 2). Temperature increases in El Niño years were similar to temperature anomalies in northern California waters during major El Niño events from 1957 to 1993 (Lenarz et al., 1995). Changes in growth (in terms of length increment), con-

dition (the ratio of actual to expected weight, based on length-weight relationships), and fecundity were based on empirical measures of *S. mystinus* during El Niño years (Lenarz et al., 1995; VenTresca et al., 1995). As in the baseline model, I expressed energy consumption by both sexes at individual and per-recruit scales.

Finally, I ran simulations at the per-recruit scale in which the total mortality rate (Z) was increased by adding a fishing-induced mortality rate (F) in increments of 0.05 to M ; fishing mortality was imposed on fish greater than 20 cm, the size at which *S. mystinus* enters fisheries in California waters (Laidig et al., 2003). The range of Z examined was 0.2 (natural mortality only) to 1.0 (a heavily overfished condition). These simulations were run under baseline conditions and El Niño conditions to determine if there was any interaction between El Niño effects and Z .

Sensitivity analysis

To measure sensitivity of the *Sebastes* bioenergetics model to different parameters, I used a Monte Carlo error analysis method (Bartell et al., 1986). In this method, parameters are drawn randomly from normal distributions with means equal to parameter estimates (Table 1) and with a coefficient of variation (CV) of either 2%, 10%, or 20%. Cases where randomly drawn RTO was greater than RTM were discarded. Female and male models were run 1000 times for each of the three CVs. Individual simulations ran to age 30 at 0.25-year increments; seasonal temperatures were those used in the baseline model. Parameter influence on 30-year cumulative consumption estimates was judged according to the parameters' relative partial sums of squares (RPSS), which quantify the influence of a parameter after all other parameters have been accounted for. RPSS for all parameters were calculated with SYSTAT (version 10.2, SYSTAT Software Inc., Richmond, CA). Additionally, means and standard deviations of consumption estimates from RPSS analyses were calculated to capture the range of energy consumption possible over the lifetime of female and male *S. mystinus*.

Results

Northern California *S. mystinus* baseline energy demands

Baseline energetic demands of northern California *S. mystinus* were a function of size, sex, and the scale of calculation (i.e., individual versus per recruit). As size increased, more energy was allocated to respiration, elimination of wastes, and reproduction, and steadily less energy was allocated to growth (Fig. 1). At the individual scale, females consumed more than males at all ages. The sexes diverged markedly as fish matured (beginning at age 3 for females, age 4 for males), and continued to diverge as fish approached asymptotic sizes (Fig. 2A). The disparity was related to sex-based differences in growth rate, maximum size, GSI, and

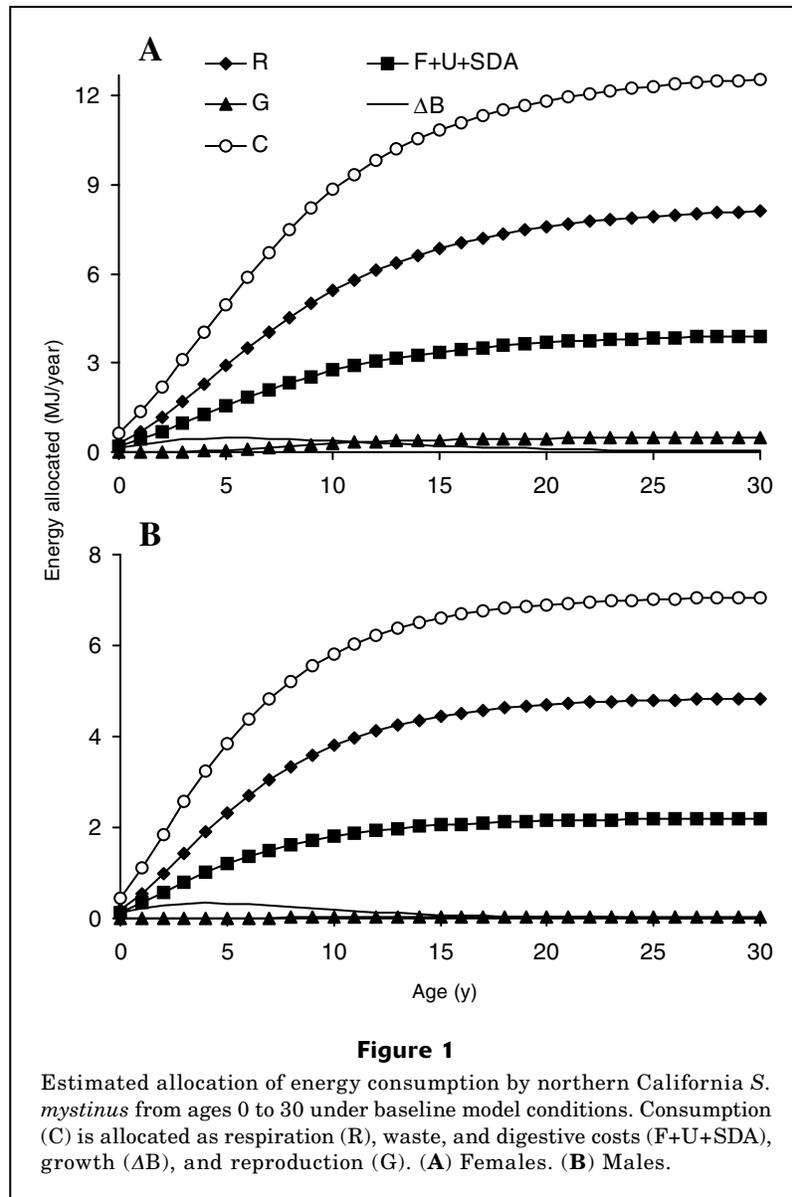
the increased respiration of gestating females. Cumulative consumption through age 30 was 285.0 MJ for individual females, and 174.6 MJ for individual males. Assuming a prey energy density of 1500 J/g (given *S. mystinus* diets [Hobson and Chess, 1988] and prey-density measurements of the same or related prey species [Paine and Vadas, 1969; Thayer et al., 1973; Foy and Norcross, 1999]), this energy density equates to a long-term average energy consumption rate of 2.7% body mass per day for females and 2.8% body mass per day for males.

Females also had greater requirements than males at the per-recruit scale, although mortality gradually lessened the contribution of older age classes (Fig. 2B), nullifying some of the disparity between the sexes at the individual scale. Cumulative female and male per-recruit energy consumption was 20.7 MJ and 14.8 MJ, respectively. Per-recruit energy consumption, the product of age-specific consumption rate and relative fish abundance, peaked at ages 4–6, indicating that those age groups have the greatest potential to affect their prey species.

Effects of El Niño on *S. mystinus* energetics

El Niño events changed *S. mystinus* energy consumption compared to that in the baseline model, but the direction and magnitude of change were dependent on sex, age, scale of calculation (individual vs. per recruit), and the number and frequency of El Niño events experienced by a given cohort. To demonstrate this change, I modeled growth of two cohorts that experienced El Niño regimes of moderate or high intensity. The first cohort ("cohort A") experienced five El Niño events by age 30, whereas the second cohort ("cohort B") experienced eight El Niño events (Figs. 3 and 4).

At the scale of individual fish, cohorts A and B experienced lower energy consumption in El Niño events, particularly among females. During El Niño years, which first occurred at age 3 for cohort A and at age 1 for cohort B, consumption by females was always lower than the baseline value (Fig. 3A). In immature females, the disparity was 7–10% lower than the baseline value and was 12–13% lower for mature females. These reductions in consumption were a function of lower growth rates, poor condition factor, and reduced fecundity during El Niño years. In contrast, consumption by males during El Niño years was 4–9% lower than the baseline value among immature individuals, but was roughly equal to the baseline value for mature individuals (Fig. 3B), in part because males did not experience drastic changes in reproductive condition during El Niño years. Both sexes experienced years when energy consumption was greater than the baseline value, particularly two years after an El Niño event when the somatic condition factor returned to normal and greater-than-average growth for that age occurred. By age 30, sizes of fish in both El Niño models were close to the asymptotic maxima and were therefore similar to baseline sizes (Table 3). Cumulative 30-year energy consumption values were



also similar in all models and in both sexes, despite the declines experienced by females.

Repeated exposure to El Niño also affected reproduction by *S. mystinus*. Both sexes experienced delays in maturation as a result of slowed growth rates during El Niño events, and the delay was related to the number of El Niño years experienced at young ages. In the baseline model, 50% maturity was reached at age 6 for both sexes. In cohort A, 50% maturity was reached at age 6 by females, but at age 7 by males. Under the more arduous conditions of cohort B, both sexes reached 50% maturity at age 7. The effect of delayed maturation in terms of energy consumption should be greatest in females because of their greater investments in reproduction, although this was not especially noticeable at the scale of cumulative consumption per individual

(Table 3). A further effect of El Niño events occurred in female egg production. The dramatic reduction in fecundity during El Niño years over the course of an individual female's life caused cumulative egg production in cohort A to be only 87.9% of the baseline level, and cohort B female egg production was only 81.3% of the baseline level (Fig. 3C).

More pronounced El Niño effects occurred at the per-recruit scale. El Niño conditions reduced per-recruit energy consumption in both sexes in contrast to baseline conditions (Fig. 4, A and B). Incorporating mortality lowered the contribution of older age groups, where individual consumption was highest (Fig. 3, A and B), thereby magnifying the El Niño effects on young fish. The negative effects on young age classes were exacerbated in females by slowed maturation and reduced

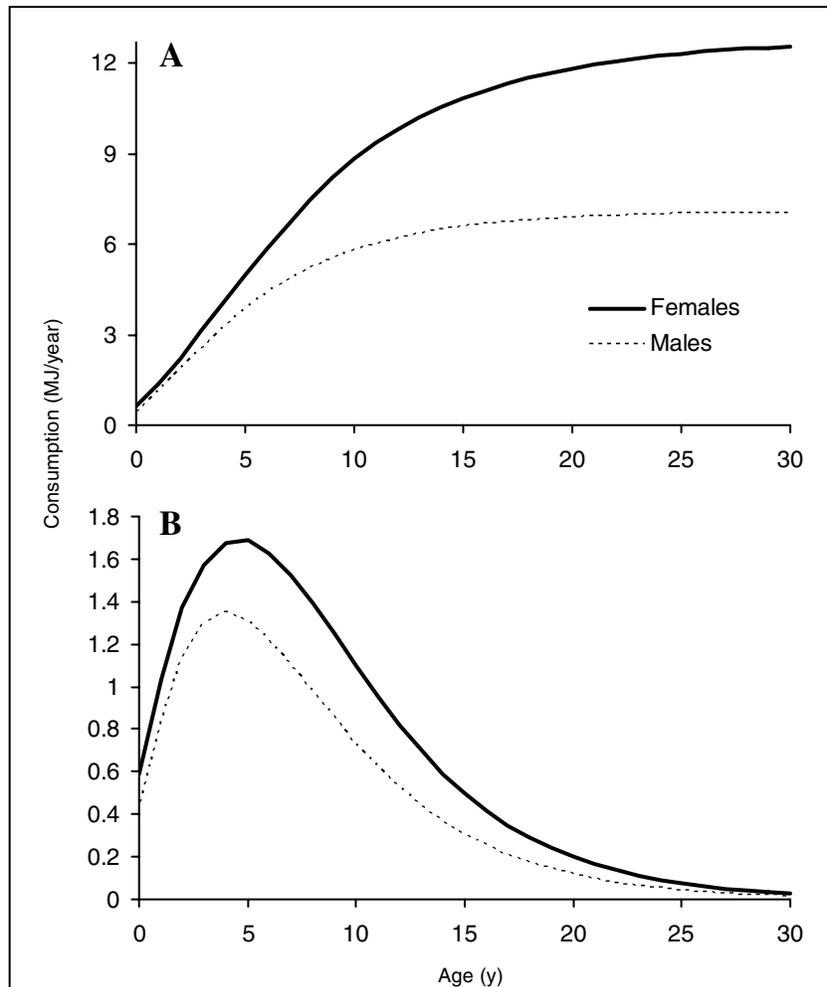


Figure 2

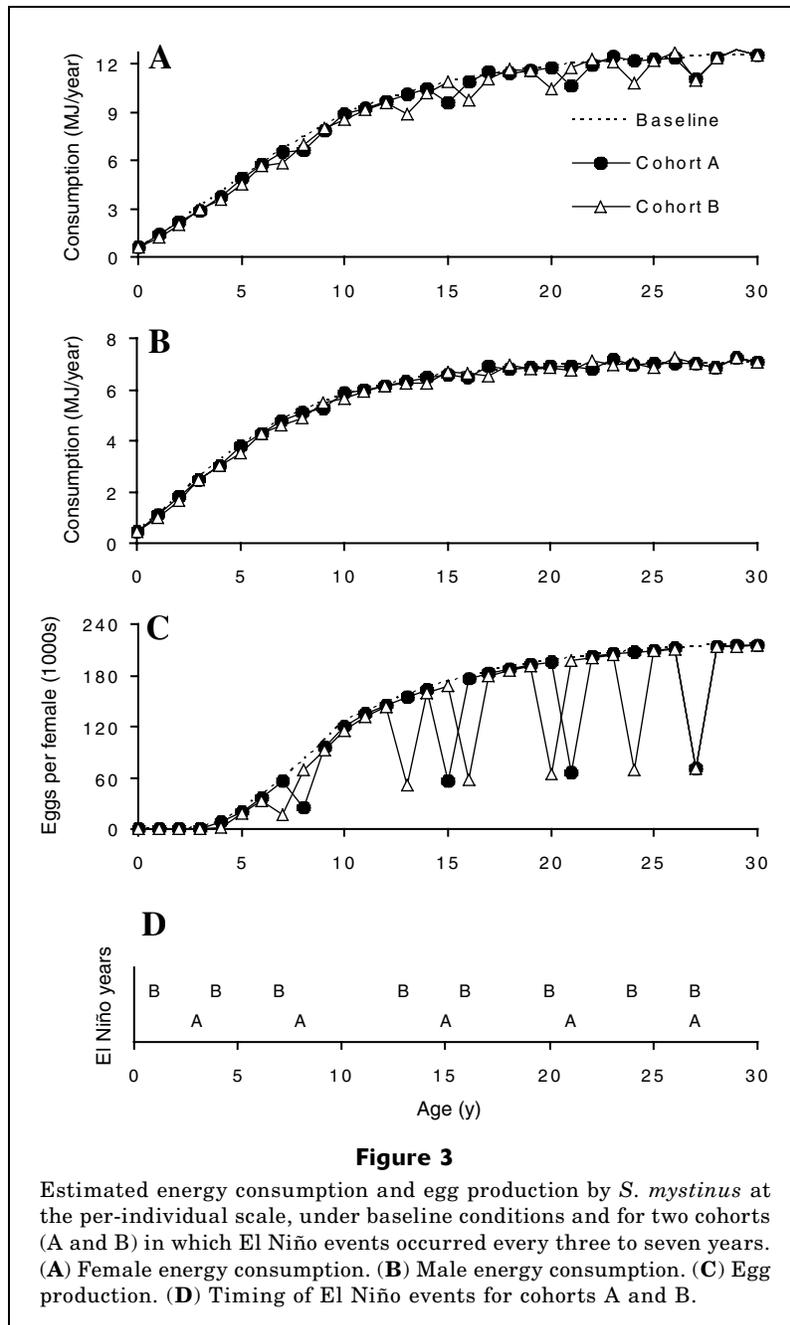
Estimated energy consumption by *S. mystinus* under baseline model conditions. (A) Females and males at the per-individual scale. (B) Females and males at the per-recruit scale, assuming a mortality rate (Z) of 0.2 (i.e., no fishing mortality).

Table 3

Final weights and cumulative energy consumptions for female and male *S. mystinus* from bioenergetics models run under baseline and El Niño conditions. All values are taken from the end of the 30th year. Cohort-A and cohort-B individuals experienced five and eight El Niño events, respectively (see Figs. 3 and 4).

| Model | Final weight (g) | | Total consumption (MJ) | |
|----------|------------------|-------|------------------------|-------|
| | Females | Males | Females | Males |
| Baseline | 1,134.3 | 617.2 | 285.0 | 174.6 |
| Cohort A | 1,129.4 | 616.5 | 278.1 | 173.3 |
| Cohort B | 1,126.8 | 616.1 | 273.6 | 172.1 |

fecundity (due to slower growth), resulting in lower per-recruit consumption to meet reproductive costs. Thirty-year cumulative per-recruit energy consumption was 20.0 MJ for cohort-A females (3.2% lower than the baseline value), and 19.4 MJ for cohort-B females (6.3% less than the baseline value). Cumulative per-recruit consumption by cohort-A males was 14.5 MJ (1.9% lower than baseline), whereas cohort-B males consumed 14.2 MJ (4.4% less than the baseline level). The reduction of cumulative egg production was also more drastic at the per-recruit scale: cohort-A females produced 15% fewer eggs than the baseline level, whereas cohort-B females produced 23% fewer eggs at the per-recruit scale (Fig. 4C). These reductions in egg production were related to smaller size, lower fecundity in El Niño years, delayed maturation, and accumulative mortality, all of which allowed fewer females to reach maturity.

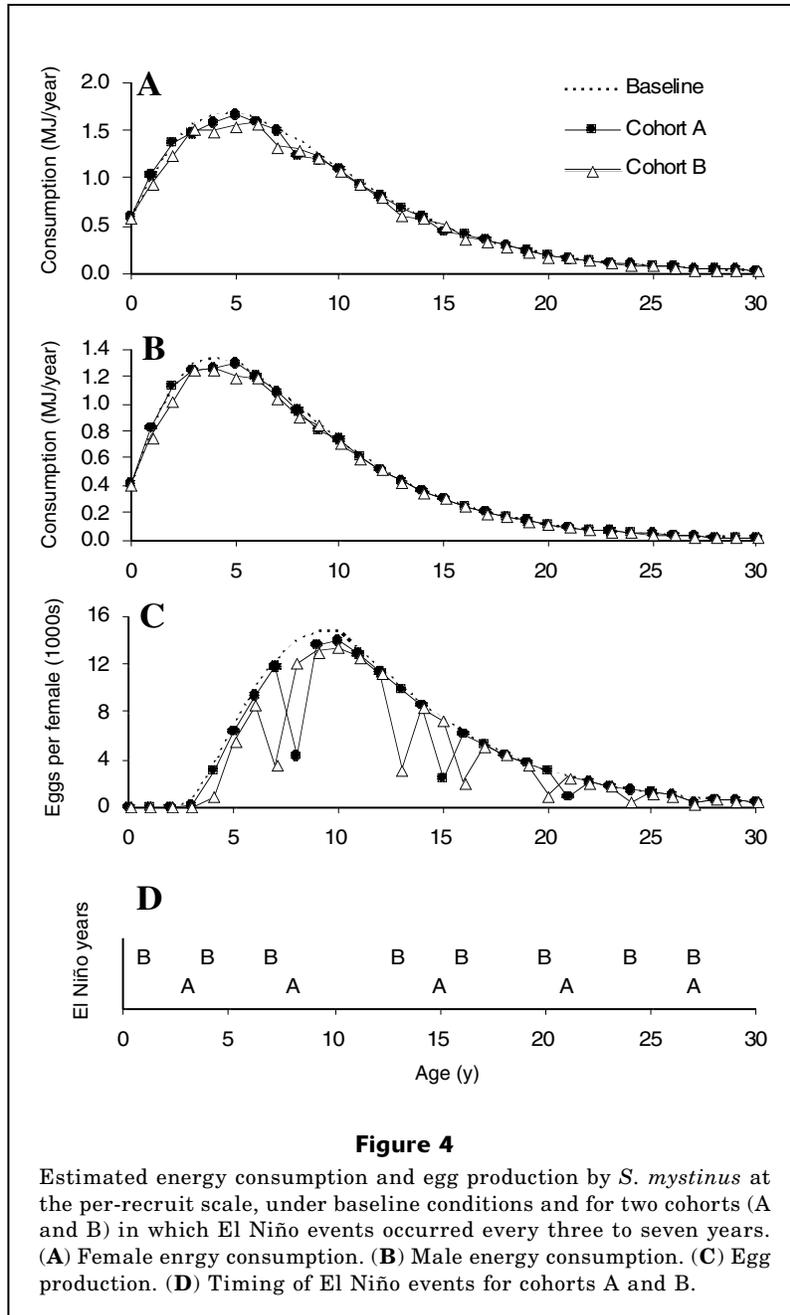


Effects of El Niño on fished cohorts

Adding fishing mortality to the total mortality rate applied in the per-recruit simulations caused changes in the total energy consumption and egg production of *S. mystinus* experiencing repeated El Niño events, in contrast to the baseline state. Under both El Niño regimes, per-recruit consumption by both sexes increased slowly as Z increased until it was nearly identical to the baseline level for cohort A (Fig. 5A) or exceeded the baseline for cohort B (Fig. 5B). The reason for this is that the slower growth experienced during El Niño years meant

that fish reached 200 mm (the size of recruitment into the fishery) later and therefore were not as rapidly subjected to fishing mortality as baseline fish. This extra period of feeding prior to reaching 200 mm was sufficient to equal or exceed the per-recruit energy consumption level in the baseline model.

In contrast, increased Z caused strong declines in egg production, and that effect was exacerbated by the frequency of El Niño years, as demonstrated by the steeper decline in cohort B (Fig. 5B). Delayed maturation caused by El Niño meant that many females were removed by fishing before they were able to reproduce;

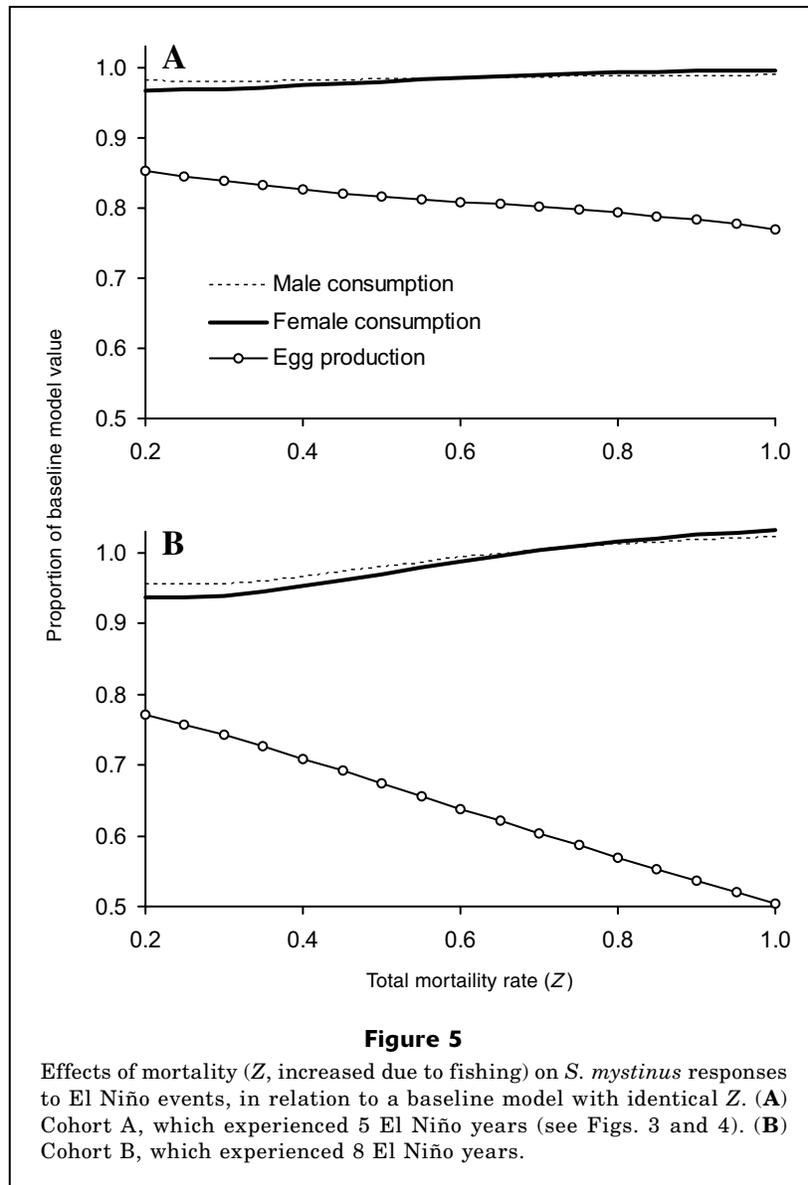


furthermore, those that escaped fishing had lower fecundities because of their smaller size and reduced egg production because of the number of El Niño years experienced.

Sensitivity analysis

Based on the RPSS analysis, sensitivity of rockfish bioenergetics models to parameter variation was a function of sex, size, and the CV of the parameter set. When $CV = 2\%$, the model was most sensitive to respiration

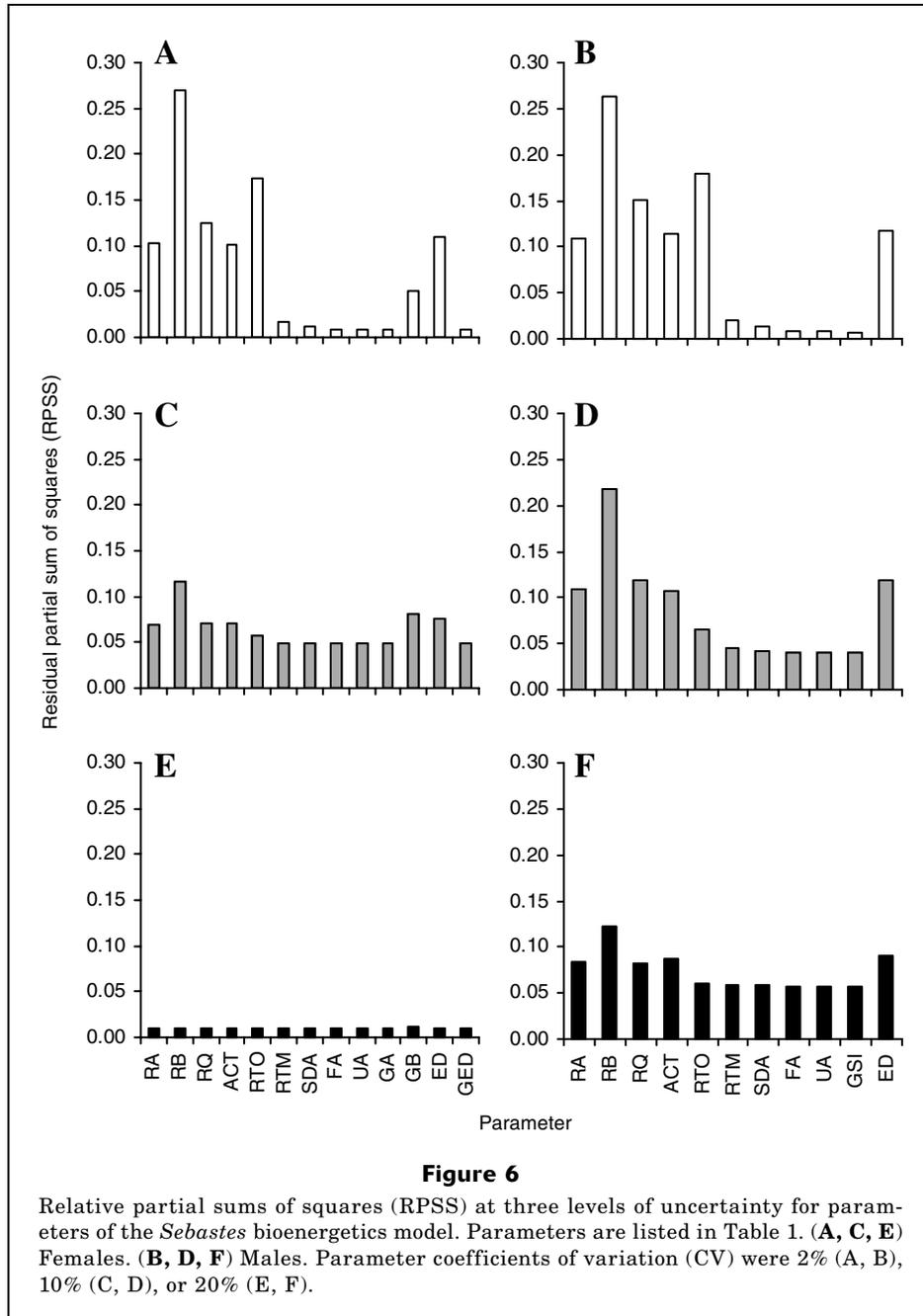
parameters in Equation 2 (particularly RB , RQ , and RTO) and to ED , although the rank order varied slightly by sex (Fig. 6, A and B). The sum of the $RPSS_{CV=2\%}$ for all parameters was >0.99 for both the male and female models. This result implies that energy consumption responded linearly to parameter variation because summed RPSS values scale from 0 to 1, with 1 implying a linear response to parameter perturbation (Bartell et al., 1986). When CV increased to 10%, the rank order of parameter sensitivity changed slightly, although respiration parameters and ED remained most important



(Fig. 6, C and D). $RPSS_{CV=10\%}$ values declined to 0.84 and 0.94 for females and males, respectively, indicating a greater degree of nonlinearity in response to parameter variation. Finally, when CV increased to 20%, there were major changes in parameter rank order and $RPSS$, especially for females (Fig. 6E). All female parameters essentially had equal weight, and $RPSS_{CV=20\%}$ dropped dramatically to 0.14, indicating a nonlinear response to parameter variation. Males experienced slight changes in parameter rank order at $CV = 20\%$ (Fig. 6F) and increasingly nonlinear behavior related to parameter variation ($RPSS_{CV=20\%} = 0.81$). Because the major difference in the models for the two sexes is the reproductive terms (i.e., Eq. 4 for females vs. the simple GSI calculation for males), the GA or GB terms (or both) appear

to be the cause of poor female model performance at high parameter uncertainty. Also, because GA and GB should only affect female energy budgets as the females mature, model sensitivity to those parameters is likely size dependent.

Energy consumption estimates generated in $RPSS$ analyses were consistently greater than estimates generated by the baseline deterministic model, which used the parameter values from Table 1. Mean consumption estimates and standard deviations increased as the parameter CV increased (Table 4). This effect was more pronounced in females than in males, especially when parameter $CV=20\%$. At that level of parameter uncertainty, male and especially female consumption estimates had very large standard deviations.



Discussion

According to the generic rockfish bioenergetics model, repeated exposure to El Niño conditions lowered the growth, maturation rate, and reproductive level of *S. mystinus*. This happened at both the individual and per-recruit scales; the latter may be most relevant when placing a cohort of fish into a community context because younger age groups have the greatest potential energy demand when mortality is accounted for. In El Niño years, increased temperatures caused respiration rates

of both sexes to increase in contrast to respiration rate in the baseline model, whereas lower growth rates and poor fecundity reduced energy demands. In the long term, these rates equated to a net decrease in energy consumption, which was more pronounced in females than in males because of the higher growth rate and reproductive investment for females. Ironically, adding mortality through fishing pressure lessened the effect of El Niño on *S. mystinus* consumption in contrast to baseline conditions, but that was because rockfish in the El Niño models took longer to reach sizes vulnerable to

Table 4

Energy consumption estimates for *S. mystinus* by a deterministic baseline model (parameters given in Table 1) and simulations run for relative partial sums of squares (RPSS) analysis. Estimates from the RPSS analysis were determined at three levels of parameter uncertainty, with parameter coefficients of variation (CV) equal to 2, 10, or 20%.

| Model | Estimated energy consumption (MJ; mean \pm SD) | |
|----------|--|-------------------|
| | Females | Males |
| Baseline | 285.0 | 174.6 |
| CV = 2% | 286.0 \pm 16.1 | 175.3 \pm 10.1 |
| CV = 10% | 314.3 \pm 102.8 | 183.9 \pm 57.6 |
| CV = 20% | 515.1 \pm 1131.4 | 209.0 \pm 131.7 |

fishing. However, the El Niño models may have overestimated per-recruit consumption because I did not add in direct El Niño related mortality; natural mortality may actually increase during El Niño years, as suggested by anecdotal mass mortality events affecting *S. mystinus* during the 1982–83 El Niño (Bodkin et al., 1987).

More dramatic than the effect of El Niño on energy consumption was the effect on egg production. Individual and per-recruit lifetime fecundity dropped (by roughly 12–19% and 15–23%, respectively) in the El Niño models—an effect that was even more drastic as fishing pressure increased. These declines were disproportionate in comparison to changes in long-term energy consumption, which declined by <4% at the individual scale and <7% at the per-recruit scale under even an arduous El Niño regime; and compared to changes in the size of age-30 individuals, which were essentially equal in the baseline and El Niño models. In other words, under a long-term climate regime with El Niño events, total energy demand of females is similar to a baseline regime, and lifetime gross conversion efficiency (growth/consumption) increases, but the conversion efficiency of consumption into reproduction is constrained considerably. That constraint is due largely to delayed maturity, poorer overall fecundity (particularly in El Niño years), and, at the per-recruit scale, the culling effect of natural and fishing mortality.

Of course, the implications from the models for *S. mystinus* must be viewed as hypotheses based on a generic *Sebastes* model. Although the ability of the bioenergetics approach to synthesize demographic, physiological, and environmental data makes it a powerful tool for characterizing dynamic linkages between fish, prey communities, and climate, use of this approach for studies of *Sebastes* will require additional empirical data. A rich body of information exists for some parameters, such as growth rate, fecundity, and depth distribution (Love et al., 1990; Love et al., 2002). However, many

relevant data are lacking, notably diet data. Because of seasonal changes in temperature and reproductive state, rockfish energetics are also seasonal. Seasonal diet changes have been observed in several (largely inshore) species (Love and Ebeling, 1978; Hallacher and Roberts, 1985; Hobson and Chess, 1988; Murie, 1995). Diets may also change with fish size (Love and Ebeling, 1978; Murie, 1995). Data that capture the trophic ontogeny of different species would allow a better depiction of how energy consumptive patterns of a population change with demographics, particularly given the disproportionate demands of younger age classes (Fig. 4). When possible, diet data should be based on weight or volume so that estimates of energy requirements can be readily converted into masses of prey consumed.

Properly incorporating environmental variability will require information not just on temperature variability, but on how rockfish growth, reproduction, and diet vary under different climate regimes. As discussed previously, El Niño and Pacific Decadal Oscillation events have been shown to affect growth, fecundity, and recruitment success of some well-studied species of rockfish. Little information is available on how these factors are affected by La Niña events, however. Furthermore, climate variability may lead to markedly different prey communities (Brodeur and Pearcy, 1992; Lea et al., 1999), resulting in diet shifts about which we currently have little information for most rockfish. Because *S. mystinus* maintained relatively high energy demand during El Niño years, despite slower growth rates and lower fecundity, the prey quality and quantity during such events is clearly important.

Ultimately, these models can be expanded to the population level to place rockfish in the context of their communities. This approach can elucidate how factors such as fishing, environmental variability, and recruitment variability influence the role of rockfish as predators on specific prey taxa, as has been done in bioenergetics models for other predators (Kitchell et al., 1997; Essington et al., 2002; Schindler et al., 2002). Because energy budgets are influenced by fish size and reproductive state, expanding to the population level will require size- or age-structured population models, such as those used in many rockfish stock assessments (e.g., Pacific Fishery Management Council, 2000). Most *Sebastes* stock assessments to date are for species that live in shelf or slope habitats, whereas the species whose food habits and basic energetic information are best known are inshore species. Therefore, a key part of producing useful bioenergetics analysis at the population level will be to prioritize populations or species assemblages for which bioenergetics models might be most useful, and to identify which type of information (population structure or basic biology and ecology) is lacking.

Finally, the generic model parameters in this study required information from several species. Interspecies parameter borrowing has been criticized (Ney, 1993), and the results from such models deserve careful appraisal. The sensitivity analysis demonstrates the importance of this issue: with increasing parameter uncertainty,

the model not only became less reliable (i.e., RPSS decreased, especially for females), but also projected higher energy consumption rates. However, the sensitivity analysis points specifically to the parameters (respiration, energy density, female fecundity) that are most influential and deserve attention in laboratory studies. Additional work is required to better characterize *ACT*, the activity multiplier, particularly for *Sebastes* species that are more pelagically oriented. In many bioenergetics models, consumption is a parameter, such that growth, not consumption, can be the model output. Although studies of energy consumption by juvenile black rockfish (*S. melanops*) have been undertaken (Boehlert and Yoklavich, 1983), more effort is needed in this area.

Conclusion

Although there are limitations to realizing the potential of bioenergetics models in the study of rockfish ecology, those limitations do not overshadow the value of using available information to produce general heuristic models to examine important questions. Such questions include how climate variability affects rockfish consumption patterns, reproduction, and predation rates on different prey taxa; how size-selective fishing may influence rockfish consumption patterns; and how rockfish energy demands compare with available prey resources in regions where population rebuilding efforts are proposed or under way. When ultimately coupled with population models, the bioenergetics approach offers a means to clarify the role that rockfish play in their communities.

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