



A meta-analysis of fecundity in rockfishes (genus *Sebastes*)



E.J. Dick^{a,*}, Sabrina Beyer^{a,b}, Marc Mangel^{c,d}, Stephen Ralston^a

^a Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 Shaffer Road, Santa Cruz, CA 95060, USA

^b University of California, Santa Cruz, Cooperative Institute for Marine Ecosystems and Climate, Award Number NA150AR4320071, 1156 High Street, Santa Cruz, CA 95064, USA

^c University of California, Santa Cruz, Center for Stock Assessment Research and Department of Applied Mathematics and Statistics, 1156 High Street, Santa Cruz, CA 95064, USA

^d University of Bergen, Department of Biology, Theoretical Ecology Group, Bergen 9020, Norway

ARTICLE INFO

Article history:

Received 23 August 2016

Received in revised form

10 November 2016

Accepted 12 November 2016

Handled by Prof. George A. Rose

Keywords:

Fecundity

Sebastes

Meta-analysis

Hierarchical models

ABSTRACT

Estimates of fecundity at size are a key component of age-structured population dynamics models such as those used for stock assessment purposes. Fecundity-length relationships for many exploited fish stocks are often poorly understood due to small sample sizes and high levels of intrinsic variability among individuals. Several species in the genus *Sebastes* match this description, and are important components of commercial and recreational fisheries off the U.S. West Coast. We used a hierarchical Bayesian modeling framework for simultaneous estimation of parameters in the fecundity-length relationships for 29 species of rockfish while accounting for variability within and among subgenera. Hierarchical models that account for subgeneric phylogenetic structure and variability among species outperformed models that treat all species in the genus as exchangeable or ignored variation among species within a subgenus, based on a predictive information criterion. Our results confirm that weight-specific fecundity increases with size in nearly all *Sebastes* species, and that the assumption of proportionality between mature female biomass and total egg production is inappropriate for most *Sebastes* stock assessments. Benefits of the hierarchical framework include prediction of fecundity-length parameters at the genus, subgenus, and species level, as well as predictive distributions for unobserved *Sebastes* species.

Published by Elsevier B.V.

1. Introduction

Successful management of fisheries requires an understanding of factors that influence each stock's reproductive potential. One such factor, the relationship between fecundity and size or age, is a common component of stock assessments, population dynamics models that form the scientific basis for management of harvested fish stocks. A common simplifying assumption in stock assessments is that spawning output (total egg production) is proportional to spawning biomass, i.e., the weight of mature females in the population. However, when this direct proportionality does not hold, the demographic effects of fishing, e.g. truncation of age and size structure, can result in disproportionate reductions in spawning output relative to reductions in spawning biomass (Trippel et al., 1997; Murawski et al., 1999; Dick 2009; Brooks 2013; Cooper et al., 2013; Spencer and Dorn, 2013). In addition, He et al. (2015) showed that

the magnitude of bias introduced by incorrectly assuming proportionality between spawning biomass and egg production is greater than the bias introduced when erroneously assuming a disproportionate relationship. These population-level effects are driven by age- or size-dependent reproductive traits, such as increases in relative fecundity (eggs produced per unit body weight) and/or larval survival rates with female size or age (Berkeley et al., 2004; Sogard et al., 2008; Stafford et al., 2014; Beyer et al., 2015; Le Bris et al., 2015).

Given the potential implications for fisheries management, it is important to accurately characterize fecundity-size relationships in stock assessments. Perhaps the most common functional form used to describe the relationship between fecundity and fish size is

$$F = aL^b \quad (1)$$

where F is fecundity (number of eggs or larvae for *Sebastes* spp.) and L is fish length (Bagenal, 1967). Weight as a function of length, is often expressed similarly,

* Corresponding author.

E-mail address: edward.dick@noaa.gov (E.J. Dick).

$$W = cL^d \quad (2)$$

where W is the measured weight of each individual. When the exponents of these two functions are equal for a given species ($b = d$), then spawning output (the number of eggs produced) is proportional to the mass of females in the population. When the fecundity-length exponent exceeds the weight-length exponent ($b > d$), then relative fecundity also increases with size, and larger females have a disproportionate contribution to spawning output.

Although the coefficient, a , in Eq. (1) affects the magnitude of spawning output estimates (consider, for example, a change in measurement units from thousands of eggs to millions of eggs), it has little effect on the population dynamics other than to scale the measure of spawning output. On the other hand, the exponent, b , or more precisely the difference $b - d$, determines whether and how quickly relative fecundity changes with size. A greater difference produces a greater departure from the assumption of egg production proportional to spawning biomass. Since we are concerned with providing advice for stock assessment, the fecundity-length exponent parameter, b , is the focus of inference in our analyses.

Rockfishes of the genus *Sebastes* are an important target of both commercial and recreational fisheries off the West Coast of North America. They are a relatively long-lived, slow-growing, viviparous group of fishes with a center of species diversity in the Northeast Pacific. Rockfishes have a roughly cubic weight-length relationship ($d = 3.0$), and fertilization is internal with a 1–2 month gestation period (Love et al., 2002). Early studies of rockfish fecundity focused on targets of large-scale commercial fisheries such as *S. alutus* in Oregon (Westrheim, 1958) and several species important to early California fisheries that were examined by Phillips (1964). A number of studies have described fecundity-length relationships for this relatively speciose genus, and identified reproductive traits such as increases in relative fecundity with size. Haldorson and Love (1991) reviewed 27 sources of maturity and fecundity information for 45 rockfishes. Using published fecundity-length relationships, they found that relative fecundity increased from size at sexual maturity to maximum length for 18 of 19 species with available data. Haldorson and Love (1991) also compiled point estimates for the fecundity-length exponent, reporting a range of 2.80–5.51 and an average of 4.10 across the genus.

Although fecundity data have been collected for many additional rockfish species in more current studies, as recently as 2007 the majority of rockfish stock assessments conducted off the U.S. West Coast used the assumption that total egg production was proportional to spawning biomass (Dick, 2009). A number of assessments of *Sebastes* species off the U.S. West Coast have incorporated results from Dick (2009), who used Bayesian hierarchical (multi-level) models to estimate fecundity-weight relationships for 40 species based on data from 22 studies.

In this study, we extend the modeling framework proposed by Dick (2009) to examine variability in the fecundity-length relationship among closely related *Sebastes* species (subgenera) using Hierarchical Linear Models (HLMs). Specifically, we allow estimates of parameters in the fecundity-length relationship to share information at the subgenus level, as well as the genus level, adding a third level to the hierarchical model. The models proposed by Dick (2009) were 2-level hierarchical models, in which all species in the genus were considered exchangeable. Our 3-level extension allows for prediction of fecundity-length relationships at the subgenus level (for observed subgenera) as well as for species in unobserved subgenera. The Bayesian framework also provides distributions of any function of the model parameters (e.g. back-transformations such as exponentiation of log-scale regression coefficients), and characterizes uncertainty without appeals to asymptotic properties that are unlikely to hold in data-limited situations.

Our results are based on the convention of treating measured fecundity as an estimate of total annual fecundity. Given that *Sebastes* species are viviparous, we examine the available data for differences introduced by measurement of fecundity at successive stages of gonad development (pre-fertilized eggs through eyed larvae). Atresia of eggs is one mechanism that may introduce differences in fecundity estimates among stages. Kusakari (1991) noted a decline in fecundity of captive *S. schlegeli* with successive egg and embryo stages. Similar declines were noted for *S. melanops* (Bobko and Berkeley, 2004), *S. paucispinis* (Ralston and MacFarlane, 2010), and *S. goodei* (southern California samples) and *S. melanostomus*, although the latter may have been due to higher incidences of premature extrusion during capture in later stages for this deep-water species (Beyer et al., 2015). A decline in fecundity with developmental stage was also observed for Atlantic species *S. norvegicus* (Raitt and Hall, 1967) and *S. mentella* (Saborido-Rey et al., 2015). The studies examining stage effects usually focused on multiplicative changes (e.g. differences in the coefficient, a). Since stock assessments are most sensitive to changes in the exponent term, we focus our attention on differences in this parameter that may result from collecting data at successive gonad development stages.

Our meta-analysis spans several independent studies conducted by different researchers, with specimens collected at different times and places and from different stages of egg and larval development. This introduces the possibility of confounding effects related to methodological differences among studies. Until recently, few studies considered spatial and temporal effects (with notable exceptions Eldridge and Jarvis, 1995 and Beyer et al., 2015). In the absence of adequate spatial and temporal coverage for most species, we examine variability among studies to determine whether fecundity-length exponents are consistent within a species.

2. Materials and methods

2.1. Data sources and preliminary analyses

We compiled fecundity estimates (number of eggs or larvae per female) for 4162 rockfish from 29 studies representing 44 *Sebastes* species in 9 subgenera and 2 clades, as defined by Hyde and Vetter (2007). Data on length (mm), age (years), total weight (g), gonad weight (g), and stage of development (unfertilized eggs, fertilized eggs, or larvae) were recorded for each specimen, when available, along with the location and date of collection.

We classified species into subgenera following the consensus tree with maximum posterior probability from Hyde and Vetter (2007). We excluded data from subgenera with fewer than three species in order to account for variability at the level of subgenus as well as among species within each subgenus (see model description for details). Fecundity observations with missing length data were also omitted from the analysis. The final data set used for comparison of alternative model structures contained 3565 rockfish from 25 studies representing 29 *Sebastes* species in 6 subgenera (Tables 1 and 2).

Length data were the most commonly available direct measurement of fish size among studies. We standardized fish lengths to total length (mm) for consistency among studies. Conversion between length types is very precise for *Sebastes* (correlations are typically greater than 0.99; Echeverria and Lenarz, 1984), and therefore predicted total length as a covariate is unlikely to affect model results. Direct measurements of weight (total, somatic, or gonad) were not available for all studies and, although somatic weight is often used to predict fecundity, these estimates can be difficult to include in stock assessments because the biomass of harvested fish is tracked in units of total weight. For these reasons,

Table 1

Rockfish fecundity data sources, collection areas, and collection time periods. CA = California, OR = Oregon, WA = Washington, USA.

Source Number	Source	Collection Area	Collection Period
1	Benet et al. (2009)	CA	2002–2004
2	Beyer et al. (2015)	CA	2009–2013
3	Beyer et al. (unpublished data)	CA	2010–2015
4	Cooper (2003)	WA	2001–2002
5	DeLacy et al. (1964)	WA	1959–1960
6	Corlett (1964)	Greenland (Atlantic sp.)	1961–1962
7	Eldridge et al. (1991)	CA	1985–1990
8	Gunderson (1976)	WA	1973
9	Ito (1977)	WA	1977
10	Love and Westphal (1981)	CA	1972–1977
11	Love et al. (1990)	CA	1980–1987
12	Love and Johnson (1998)	CA	1977–1996
13	MacGregor (1970)	CA	1961
14	Nichol and Pikitch (1994)	OR	1986–1987
15	Phillips (1964)	CA	1957–1961
16	Ralston et al. (2003)	CA	1991
17	Ralston and MacFarlane (2010)	CA	2003
18	Richards and Emmett (1988)	British Columbia	1986
19	Romero (1988)	CA	1982–1983
20	Schmidt (2014)	CA	2010–2012
21	Snytko and Borets (1973)	OR and Vancouver	1967
22	Sogard et al. (2008)	CA	2003–2006
23	Stafford et al. (2014)	CA	2005–2008
24	Wallace et al. (2008)	WA	1989–1992
25	Westrheim (1958)	OR	1951–1952

Table 2

Sebastes species included in the meta-analysis with subgeneric assignments, total number of samples by species (N), contributing data sources (see Table 1), and sample size per source (n).

<i>Sebastes</i> species	Subgenus	Total Sample Size (N)	Source Numbers (Table 1) and sample size (n)
<i>alutus</i>	<i>Sebastes</i>	91	8 (78), 25 (13)
<i>atrovirens</i>	<i>Pteropodus</i>	86	13 (2), 19 (67), 22 (17)
<i>auriculatus</i>	<i>Pteropodus</i>	52	3 (17), 5 (35)
<i>carnatus</i>	<i>Pteropodus</i>	17	3 (1), 13 (4), 22 (12)
<i>caurinus</i>	<i>Pteropodus</i>	134	3 (3), 4 (54), 5 (33), 9 (23), 18 (21)
<i>chlorostictus</i>	<i>Sebastomus</i>	70	1 (47), 3 (7), 11 (16)
<i>constellatus</i>	<i>Sebastomus</i>	32	3 (6), 11 (21), 13 (5)
<i>crameri</i>	<i>Sebastes</i>	60	14 (43), 15 (12), 21 (5)
<i>dalli</i>	<i>Pteropodus</i>	23	11 (23)
<i>ensifer</i>	<i>Sebastomus</i>	4	3 (2), 11 (2)
<i>entomelas</i>	<i>Sebastosomus</i>	125	3 (16), 11 (27), 15 (20), 21 (2), 23 (60)
<i>flavidus</i>	<i>Sebastosomus</i>	456	2 (158), 3 (30), 7 (126), 11 (34), 15 (15), 21 (2), 22 (19), 23 (72)
<i>goodei</i>	<i>Sebastodes</i>	853	2 (363), 3 (259), 11 (39), 15 (23), 23 (169)
<i>helvomagulatus</i>	<i>Sebastomus</i>	4	21 (4)
<i>hopkinsi</i>	<i>Acutomentum</i>	79	3 (40), 11 (39)
<i>jordani</i>	<i>Sebastodes</i>	546	3 (7), 15 (10), 16 (529)
<i>maliger</i>	<i>Pteropodus</i>	253	18 (253)
<i>melanops</i>	<i>Sebastosomus</i>	38	24 (38)
<i>mystinus</i>	<i>Sebastosomus</i>	211	3 (35), 20 (159), 22 (17)
<i>nebulosus</i>	<i>Pteropodus</i>	4	3 (4)
<i>norvegicus</i>	<i>Sebastes</i>	20	6 (20)
<i>ovalis</i>	<i>Acutomentum</i>	50	2 (35), 3 (8), 11 (2), 13 (5)
<i>paucispinis</i>	<i>Sebastodes</i>	145	3 (14), 11 (52), 13 (13), 15 (24), 17 (38), 21 (4)
<i>rastrelliger</i>	<i>Pteropodus</i>	8	11 (8)
<i>rosaceus</i>	<i>Sebastomus</i>	52	3 (22), 11 (23), 13 (7)
<i>rosenblatti</i>	<i>Sebastomus</i>	26	11 (26)
<i>rufus</i>	<i>Acutomentum</i>	29	3 (2), 11 (27)
<i>serranoides</i>	<i>Sebastosomus</i>	94	3 (3), 10 (83), 13 (1), 22 (7)
<i>simulator</i>	<i>Sebastomus</i>	3	3 (3)

we chose length, rather than weight, as the size covariate in our analyses.

As noted above, estimates of fecundity can vary with the stage of gonad development for some *Sebastes* species (Raitt and Hall, 1967; Kusakari, 1991; Bobko and Berkeley, 2004). Methods for classifying stages of eggs and embryos differ among studies, so reported stages were reclassified into three general categories: unfertilized eggs, fertilized eggs, and eyed larvae. Details of the reclassification for each study are described by Dick (2009). To examine the effect of development stage on fecundity at length, we identified studies

with fecundity estimates for multiple stages and fit linear models for log-fecundity as a function of log-length, stage (coded as a categorical variable), and the interaction between log-length and stage. We fit separate linear models for each species within each study to minimize the effect of methodological differences among studies. Tests of significance were based on $\alpha = 0.05$.

The available fecundity data are compiled from multiple, independent research programs so that differences in fecundity at length among species may be confounded with methodological differences among studies (e.g. sampling location, collection date,

sample preparation, gonad development stage). To examine the effect of study on fecundity at length, we identified species with fecundity estimates from multiple studies and fit linear models for log-fecundity as a function of log-length, study (categorical variable), and the interaction between log-length and study.

As described by Dick (2009), fecundity and length data from three sources (Love and Westphal, 1981; Romero 1988; Love et al., 1990) were no longer available in numeric format so we digitized published scatterplots (see Appendix A in Dick (2009) for details of the digitization process, including methods used to verify accuracy of the recovered data). Based on comparisons of fitted parameter values and a test comparing digitized data to original values, Dick (2009) found that the digitization process introduced negligible error into the analysis.

Fecundity relationships in stock assessments typically describe the number of eggs or larvae produced by an average female, as a function of size or age, during a single time step of the model (e.g. one year). Using the terminology for female reproductive strategies in Murua and Saborido-Rey (2003), species in the genus *Sebastes* are effectively treated as *determinate*, *total spawners* in stock assessments. *Determinate*, meaning the standing stock of yolked oocytes is not replaced during the spawning season, and *total spawners*, meaning all larvae are released in a single event (after accounting for atretic losses). In practice, estimates of fecundity in rockfish stock assessments are treated as if they represent total annual fecundity. However, some *Sebastes* species exhibit evidence of *batch spawning*, in which multiple broods are released over the course of a single spawning season (Moser, 1967; MacGregor, 1970; Love et al., 1990; Beyer et al., 2015). This phenomenon has been observed in *S. constellatus*, *S. chlorostictus*, *S. ensifer*, *S. eos*, *S. goodei*, *S. hopkinsi*, *S. levis*, *S. ovalis*, *S. paucispinis*, *S. rosaceus*, *S. rosenblatti*, and *S. rufus* (Moser 1967; MacGregor, 1970; Love et al., 2002). The potential for bias in fecundity estimates due to multiple brooding is discussed below, but is beyond the scope of this analysis.

2.2. Models, diagnostics, and information criterion

HLMs represent a compromise between two traditional models commonly considered when evaluating differences among groups: models that consider each group (e.g. species) as independent, or ‘no pooling’ models, and those that combine data across groups, or ‘complete pooling’ (Gelman et al., 2004). The hierarchical models in our study can be thought of as a generalization of the Analysis of Covariance (ANCOVA) model. HLMs use information from closely-related species (i.e. within subgenera) to inform species with little (or no) data. They eliminate the need to choose between a high-bias/low-variance estimator that ignores differences among species and a low-bias/high-variance estimator that treats each species separately (Jackman, 2009). This property of the HLM is sometimes referred to as ‘partial pooling’ or ‘borrowing strength’ (Gelman et al., 2004). In a hierarchical model, ‘partial-pooling’ estimates are allowed to vary by species, but are drawn toward the ‘complete pooling’ estimate to an extent determined by the amount of variability in the data and the distance between the independent estimate and the pooled mean. Species with more information retain estimates that are similar to those obtained from the ‘no pooling’ model. In addition to providing estimates for data-limited species that ‘borrow strength’ from other species, hierarchical models provide a natural framework for predicting observations from unobserved species.

We estimated the parameters a and b in Eq. (1) using the log-linearized model

$$\log(F) = \log(a) + b\log(L) + \varepsilon \quad (3)$$

$$\varepsilon \sim N(0, \sigma) \quad (4)$$

Estimates of the slope, b , in the linearized model [3] are identical to the exponent in Eq. (1), and, therefore, we use the terms ‘slope’ and ‘exponent’ interchangeably. We obtained maximum likelihood estimates of parameters $\log(a)$ and b for each species by separate

Table 3

Alternative models for rockfish fecundity at length. In all cases, the dependent variable (y) is the natural logarithm of fecundity (eggs or larvae), and the independent variable (x) is the natural logarithm of total length (mm). Subscripts index: i = fish, j = species, k = subgenus. Normal distributions are parameterized in terms of their mean (μ) and standard deviation (σ). Priors on all standard deviation parameters (σ , ϕ , ψ , γ , ν) are uniform distributions with an upper bound (c), chosen for each parameter such that truncation of the posterior distributions is negligible. $\Delta_{\text{ModelX}} = \text{WAIC}_{\text{ModelX}} - \min(\text{WAIC}_{\text{ModelX}})$.

Model Number	Model Description	WAIC (Δ)
Model 1a ("ANCOVA")	(T1) $y_{ij} = a_j + b_j x_{ij} + \varepsilon_{ij}$ (T2) $\varepsilon_{ij} \sim N(0, \sigma)$ (T3) $a_j \sim N(0, 10^2)$ (T4) $b_j \sim N(0, 10^2)$ (T5) $\sigma \sim \text{Unif}(0, c)$	3551 (109)
Model 1b Model 2a ("2-Level HLM")	Model 1a with subgenus-level residual variance parameters ($\varepsilon_{ijk} \sim N(0, \sigma_k)$) (T6) $y_{ij} = a_j + b_j x_{ij} + \varepsilon_{ij}$ (T7) $\varepsilon_{ij} \sim N(0, \sigma)$ (T8) $a_j \sim N(\alpha, \phi)$ (T9) $b_j \sim N(\beta, \psi)$ (T10) $\alpha \sim N(0, 10^2)$ (T11) $\beta \sim N(0, 10^2)$ (T12) $\sigma, \phi, \psi \sim \text{Unif}(0, c)$	3456 (14) 3588 (146)
Model 2b Model 2c Model 3a ("3-Level HLM")	Model 2a with species pooled within subgenera ($y_{ijk} = a_k + b_k x_{ijk} + \varepsilon_{ijk}$) and ($\varepsilon_{ik} \sim N(0, \sigma_k)$) Model 2a with subgenus-level residual variance parameters ($\varepsilon_{ijk} \sim N(0, \sigma_k)$) (T13) $y_{ijk} = a_{jk} + b_{jk} x_{ijk} + \varepsilon_{ijk}$ (T14) $\varepsilon_{ijk} \sim N(0, \sigma_k)$ (T15) $a_{jk} \sim N(\alpha_k, \phi_k)$ (T16) $b_{jk} \sim N(\beta_k, \psi_k)$ (T17) $\alpha_k \sim N(A, \gamma)$ (T18) $\beta_k \sim N(B, \nu)$ (T19) $A \sim \text{Unif}(-25, -3)$ (T20) $B \sim \text{Unif}(1, 7)$ (T21) $\sigma_k, \phi_k, \psi_k, \gamma, \nu \sim \text{Unif}(0, c)$	4419 (977) 3497 (55) 3443 (1)
Model 3b Model 3c Model 3d	Model 3a with common slopes within subgenera ($y_{ijk} = a_{jk} + b_k x_{ijk} + \varepsilon_{ijk}$) Model 3a with common intercepts within subgenera ($y_{ijk} = a_k + b_{jk} x_{ijk} + \varepsilon_{ijk}$) Model 3a with a shared residual variance parameter ($\varepsilon_{ijk} \sim N(0, \sigma)$)	3446 (4) 3442 (0) 3536 (94)

calls to the “lm” function in R (R Core Team, 2016). These parameter estimates are similar to those obtained from a Bayesian ANCOVA model, which we refer to as ‘Model 1a’ (Table 3), in which intercepts and slopes are allowed to vary by species and have independent prior distributions for each parameter. The ANCOVA model differs from the individual regression models in that all species in the ANCOVA share a single residual error term (σ).

We explore several hierarchical model structures for the fecundity-length data (Table 3). Model 1b relaxes the assumption of constant variance in the ANOVA (Model 1a) by estimating an independent residual standard deviation parameter for each subgenus (Table 3). We did not test models in which the residual standard deviation varied by species due to small sample sizes for some species (Table 2).

Model 2a is similar to the approach implemented by Dick (2009), although in that study fecundity was modeled as a function of fish weight. Model 2a is sometimes referred to as a “varying intercepts and slopes” model (Gelman and Hill, 2007), and differs from Model 1a in the specification of the prior for the intercept and slope parameters. In Model 1a, the intercepts and slopes for each species are independent of parameters for other species (Table 3, Eqs. (T3) and (T4)), whereas in Model 2a the slope for each species is a draw from a common distribution of slopes, and likewise for the intercepts (Table 3, Eqs. (T8) and (T9)). Parameters for the distributions of slopes and intercepts are given diffuse priors (Table 3, Eqs. (T10)–(T12)), and are estimated from the data. In a data-limited setting, the focus of inference in Model 2a is the mean of the random effect distributions (Table 3, Eqs. (T8) and (T9)). These quantities can be used to predict fecundity for an unobserved *Sebastes* species under the assumption that all species within the genus *Sebastes* are exchangeable (Dick, 2009).

Models 2b and 2c are similar to Model 2a in that they have a 2-level hierarchical structure (Table 3). Unlike Model 2a, Model 2b ignores species-level effects, estimating one slope, intercept, and standard deviation parameter for each subgenus and allowing for partial pooling of information at the genus level. Model 2c then returns to the assumption that all species are exchangeable, similar to Model 2a, but only relaxes the assumption of constant variance (Table 3).

Model 3a considers the possibility that the j species within subgenus k are exchangeable, with intercept and slope distributions for each subgenus (Table 3, Eqs. (T15) and (T16)). At the next level of the hierarchy, Model 3a also assumes that subgenera within the genus *Sebastes* are exchangeable (Table 3, Eqs. (T17) and (T18)). In this way, the 3-level hierarchical linear model extends the focus of inference in Model 2a to include a slope and intercept at the level of subgenus, as well as at the genus level.

Models 3b and 3c in Table 3 are simplifications of Model 3a, with Model 3b estimating a single slope (b_k) and Model 3c a single intercept (a_k) for species within each subgenus. These models

still allow for species-level variability in the fecundity-length relationship, but constrain the effects to either the slope or intercept parameters within each subgenus. All three models (3a–c) estimate a separate residual standard deviation (σ_k) for each subgenus (e.g. Table 3, Eq. (T14)). Model 3d also simplifies Model 3a, but only in the assumption of a common residual standard deviation among all subgenera (i.e. σ instead of σ_k).

We specified uniform prior distributions for all standard deviation parameters ($\sigma_k, \phi_k, \psi_k, \gamma, \nu$), which ensures a proper posterior distribution for subgenera having at least 3 species-level effects (Gelman, 2006). We chose bounds on all uniform prior distributions based on preliminary model runs to ensure that truncation of the marginal posterior distributions was negligible. Each model was fit to the same data set (Table 2) to allow for direct comparison of model structures.

We generated posterior simulations for Bayesian models using JAGS (Just Another Gibbs Sampler, version 4.0.0), called from the R environment (version 3.2.2) using the package “rjags” (version 4–4). Each model run consisted of two Markov Chain Monte Carlo (MCMC) chains run for a 100,000 sample “burn-in” period, followed by 1 million samples thinned every 100 iterations (producing 10,000 draws from each chain). Convergence diagnostics of the MCMC simulations for each model were generated using the package “ggmcmc” (version 0.7.2) in R, including density plots, trace plots, running means, autocorrelation plots, potential scale reduction factors, and Geweke diagnostics. Simulated draws from posterior predictive distributions were generated using the “rnorm” function in R, integrating across uncertainty in the mean and standard deviation parameters (e.g. generating random normal draws across the set of posterior draws for both the mean and standard deviation parameters).

To compare models, we used the Watanabe-Akaike Information Criterion (WAIC), a predictive information criterion for Bayesian models (Watanabe 2010; Gelman et al., 2014). As with other information criteria, models with lower WAIC scores are preferred. We calculated WAIC for each model using the R package ‘loo’ (version 0.1.4), and also reported differences (Δ) between the WAIC for each model and the smallest WAIC value in the set of candidate models.

To help inform stock assessments with limited fecundity data, we summarize posterior predictive distributions for unobserved species in each of the six observed subgenera. Specifically, predictive distributions of subgenus-level means were simulated for the intercept and slope parameters (Table 3, Model 3a; α_k and β_k , respectively). Likewise, we simulated posterior predictive distributions of the intercept and slope for the genus *Sebastes* to inform assessments of species in subgenera that were not included in this analysis. For comparison, the genus-level predictive distributions were generated using both the 2-level (Table 3, Eqs. (T10) and (T11)) and 3-level (Table 3, Eqs. (T19) and (T20)) hierarchical model structures.

Table 4

Tests for effect of gonad development stage (1 = unfertilized eggs, 2 = fertilized eggs, 3 = eyed larvae) on fecundity, by species and source. Tests for the additive effect of log(length) were significant for all species ($p < 0.05$, results omitted). See Table 1 for Source numbers. Data with sample sizes in parentheses were omitted from the analysis of stage effects.

<i>Sebastes</i> species	Source Number	Stage Sample Size			Additive Stage Effect			Stage:Length Interaction		
		1	2	3	df1,df2	F	p	df1,df2	F	p
<i>caurinus</i>	4	26	10	18	2,48	0.093	0.911	2,48	0.723	0.491
<i>entomelas</i>	23	(2)	33	25	1,54	3.135	0.083	1,54	0.004	0.951
<i>flavidus</i>	2	78	52	28	2,152	3.183	0.044	2,152	0.356	0.701
	7	100	26	–	1,122	6.142	0.015	1,122	1.440	0.232
	23	(2)	29	41	1,66	3.101	0.083	1,66	0.026	0.873
<i>goodei</i>	2	67	175	121	2,357	11.64	<0.01	2,357	8.828	<0.01
	3	100	81	78	2,253	1.567	0.211	2,253	7.839	<0.01
	23	(2)	85	82	1,163	14.21	<0.01	1,163	0.027	0.870
<i>paucispinis</i>	17	28	8	(2)	1,32	19.38	<0.01	1,32	5.56	0.025

Table 5

Effect of data source on fecundity at length, by species. Results for the additive effect of log(length) were significant for all species ($p < 0.05$, results omitted). Sources with sample sizes less than 10 for a given species were omitted from this analysis. See Table 1 for Source numbers.

Sebastes species	Source Numbers (sample sizes)	Additive Source Effect			Source: Length Interaction		
		df1,df2	F	p	df1,df2	F	p
<i>alutus</i>	8 (78), 25 (13)	1,87	25.10	<0.01	1,87	0.850	0.359
<i>atrovirens</i>	19 (67), 22 (17)	1,80	9.35	<0.01	1,80	1.389	0.242
<i>auriculatus</i>	3 (17), 5 (35)	1,48	0.755	0.389	1,48	0.277	0.601
<i>caurinus</i>	4 (54), 5 (33), 9 (23), 18 (21)	3,123	28.39	<0.01	3,123	8.255	<0.01
<i>chlorostictus</i>	1 (47), 11 (16)	1,59	1.673	0.201	1,59	0.099	0.754
<i>crameri</i>	14 (43), 15 (12)	1,51	1.905	0.174	1,51	0.069	0.794
<i>entomelas</i>	3 (16), 11 (27), 15 (20), 23 (60)	3,115	15.87	<0.01	3,115	1.092	0.356
<i>flavidus</i>	2 (158), 3 (30), 7 (126), 11 (34), 15 (15), 22 (19), 23 (72)	6,440	40.11	<0.01	6,440	1.189	0.311
<i>goodei</i>	2 (363), 3 (259), 11 (39), 15 (23), 23 (169)	4,843	11.61	<0.01	4,843	4.509	<0.01
<i>hopkinsi</i>	3 (40), 11 (39)	1,75	0.076	0.784	1,75	4.385	0.040
<i>jordani</i>	15 (10), 16 (529)	1,535	6.537	0.011	1,535	0.081	0.776
<i>mystinus</i>	3 (35), 20 (159), 22 (17)	2,205	16.80	<0.01	2,205	0.769	0.465
<i>paucispinis</i>	3 (14), 11 (52), 13 (13), 15 (24), 17 (38)	4,119	7.466	<0.01	4,119	1.836	0.126
<i>rosaceus</i>	3 (22), 11 (23)	1,41	0.667	0.419	1,41	2.023	0.163

3. Results

3.1. Effects of gonad development stage on fecundity at length

We tested the effect of gonad development stage on fecundity at length for five species, some of which had data from multiple studies: *S. caurinus* (Cooper, 2003), *S. entomelas* (Stafford et al., 2014), *S. flavidus* (Beyer et al., 2015; Eldridge et al., 1991; Stafford et al., 2014), *S. goodei* (Beyer et al., 2015; Beyer, unpublished data; Stafford et al., 2014), and *S. paucispinis* (Ralston and MacFarlane, 2010). Across studies, stage-specific sample sizes were highest for *S. goodei*, followed by *S. flavidus*, *S. entomelas*, *S. caurinus*, and *S. paucispinis* (Table 4). All multiple regression analyses showed a significant effect of log-length ($p < 0.001$) on log-fecundity.

Available data for *S. caurinus* (Cooper, 2003) included fecundity estimates from all three development stages (coded as follows: stage 1 = unfertilized eggs, stage 2 = fertilized eggs, and stage 3 = eyed larvae). The multiple regression analysis predicting log-fecundity found no significant additive effect of stage or the interaction of log-length and stage (Table 4). Stafford et al. (2014) also collected fecundity and length data for *S. entomelas* from stages 1–3, but stage 1 samples were excluded from the regression analysis due to small sample size ($n = 2$). Neither the additive effect of gonad development stage nor the interaction between stage and length were significant for *S. entomelas* (Table 4).

Significant effects of development stage on fecundity were detected for both *S. flavidus* and *S. goodei*, but differed between the two species in terms of which parameters were affected, and was not consistent among data sources. Tests for an additive stage effect for *S. flavidus* indicated significant differences in two of the three data sources that reported stage-specific fecundity information (Beyer et al., 2015 and Eldridge et al., 1991; Table 4). However, the effect sizes for Beyer et al. (2015) were positive in both stages 2 and 3 suggesting higher fecundity than in stage 1 (see Supplemental Material S1). The interaction between stage and length was not significant for any of the three sources, suggesting that the exponent parameter in Eq. (1) does not vary by gonad development stage for *S. flavidus*.

Stage-specific sample sizes were largest for *S. goodei* (Table 4). Tests for significance of additive stage effects and the interaction between stage and length were both significant based on *S. goodei* data from Beyer et al. (2015), as well as for *S. paucispinis* data from Ralston and MacFarlane (2010). For these species and data sources, estimates of the slope (exponent) parameter increased in later stages of gonad development. A significant interaction term

was also detected using unpublished data from Beyer et al. (Table 4), but in this study the direction of the effect was reversed relative to Beyer et al. (2015), with a decreasing exponent in later stages (see Supplemental Material S1). Lastly, *S. goodei* data from Stafford et al. (2014) suggested that differences in fecundity between stages are best described by variability in the additive stage effect, but not the interaction term (Table 4).

3.2. Effects of study (data source) on fecundity at length

Data from multiple sources were available for 14 species, with sample sizes ranging from 10 (the selected minimum sample size) to 529 per combination of species and source (Table 5). Additive (log-scale) differences among studies were more consistently found to be significant at the 0.05 level than differences in the slope (exponent) parameter (Table 5). Specifically, tests for differences among sources in the (log-scale) intercept parameter were significant for 9 of 14 species. Tests for differences in slopes (the interaction term) were significant for 3 species (*S. caurinus*, *S. goodei*, and *S. hopkinsi*). Among the species with the largest sample sizes (*S. goodei*, *S. jordani*, *S. flavidus*, *S. mystinus*, and *S. paucispinis*), the additive log-scale source effect was significant for all species, and the interaction term was significant for one (*S. goodei*) (Table 5).

Tests for differences in the fecundity-length exponent due to gonad development stage and data source were most often insignificant (Tables 4 and 5). We view this result as inconclusive, because few studies were designed to test for this effect, often resulting in small sample sizes. Data for the majority of species were drawn from 1 to 2 studies (Table 2) and a single gonad development stage, preventing inclusion of these categories in the hierarchical model structure. For these reasons, we pooled data for each species across studies and development stages in the final analysis.

3.3. Model comparison, evaluation, and diagnostics

Based on WAIC (Models 3a–c; Table 3), models that accounted for variability at both the species and subgenus level had the best predictive accuracy. Small differences in WAIC (Δ) between these three models ($\Delta \leq 4$; Table 3) suggest the data could not discriminate between a model with species-specific parameters (Model 3a), and models that shared either a common slope (Model 3b) or intercept (Model 3c) among species in each subgenus. The importance of retaining some form of species-level variability is emphasized by the relatively poor fit of Model 2b, which allows for difference among subgenera, but not among species in each subgenus.

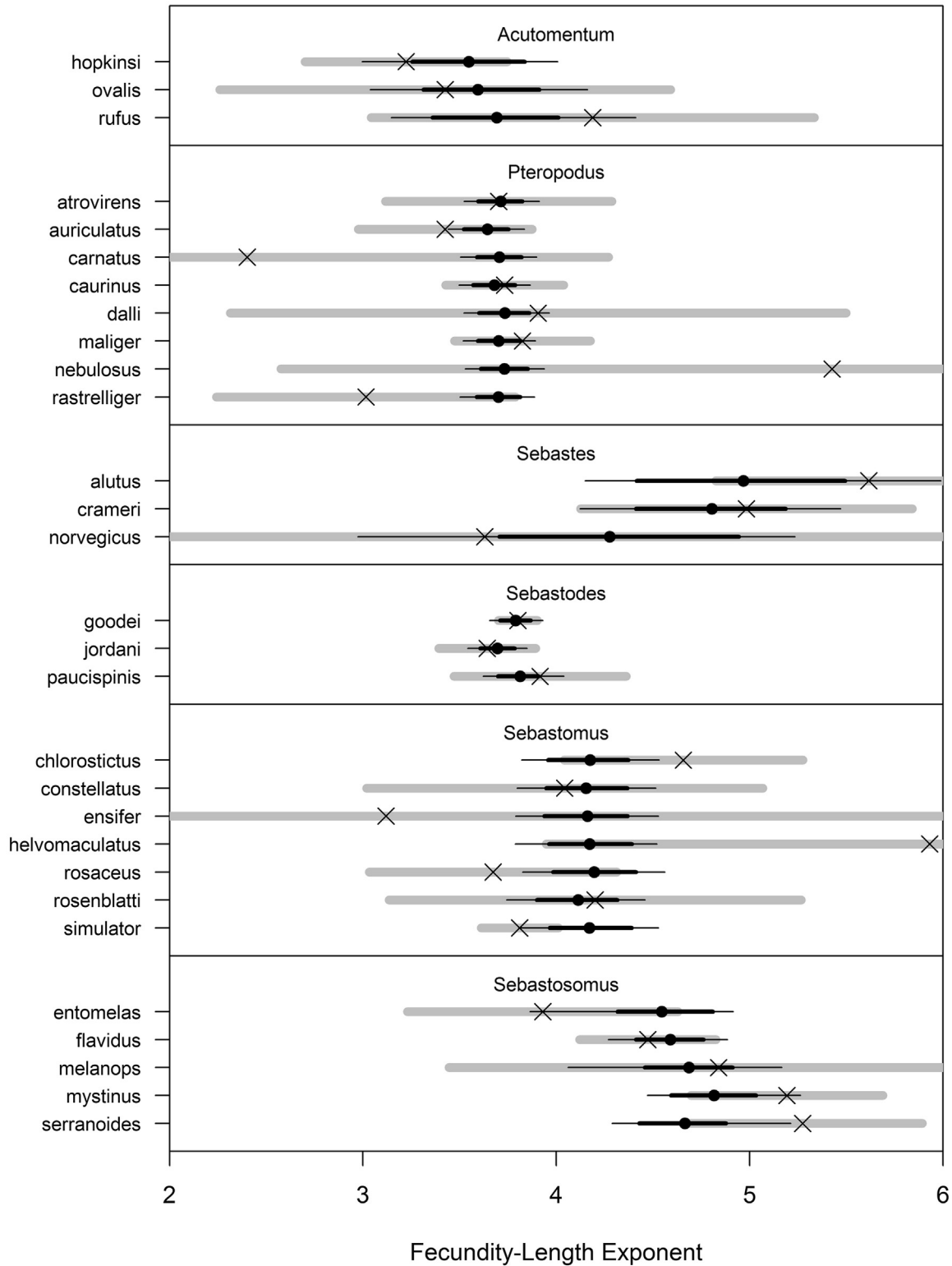


Fig. 1. Highest posterior density intervals (thin line = 95%, thick line = 75%) for the exponent of the fecundity-length relationship, by subgenus and species (Model 3a). Solid circles are posterior medians. Maximum likelihood estimates (x) based on independent, species-specific regressions are shown for comparison with 95% confidence intervals (gray lines). Confidence intervals of MLEs are truncated below 2 and above 6 due to differences in scale.

Models that assume a constant residual standard deviation (models 1a, 2a, and 3d) had reduced predictive accuracy (higher WAIC) than similarly structured models in which the standard deviation was allowed to vary among the *k* subgenera (models 1b, 2c, and 3a, respectively). However, among the set of models with

non-homogeneous residual standard deviations, those with hierarchical structure at both the species and subgenus level performed the best (Table 3; models 3a–c).

To illustrate differences between a traditional, 1-level analysis and a model with hierarchical structure, in Fig. 1 we show

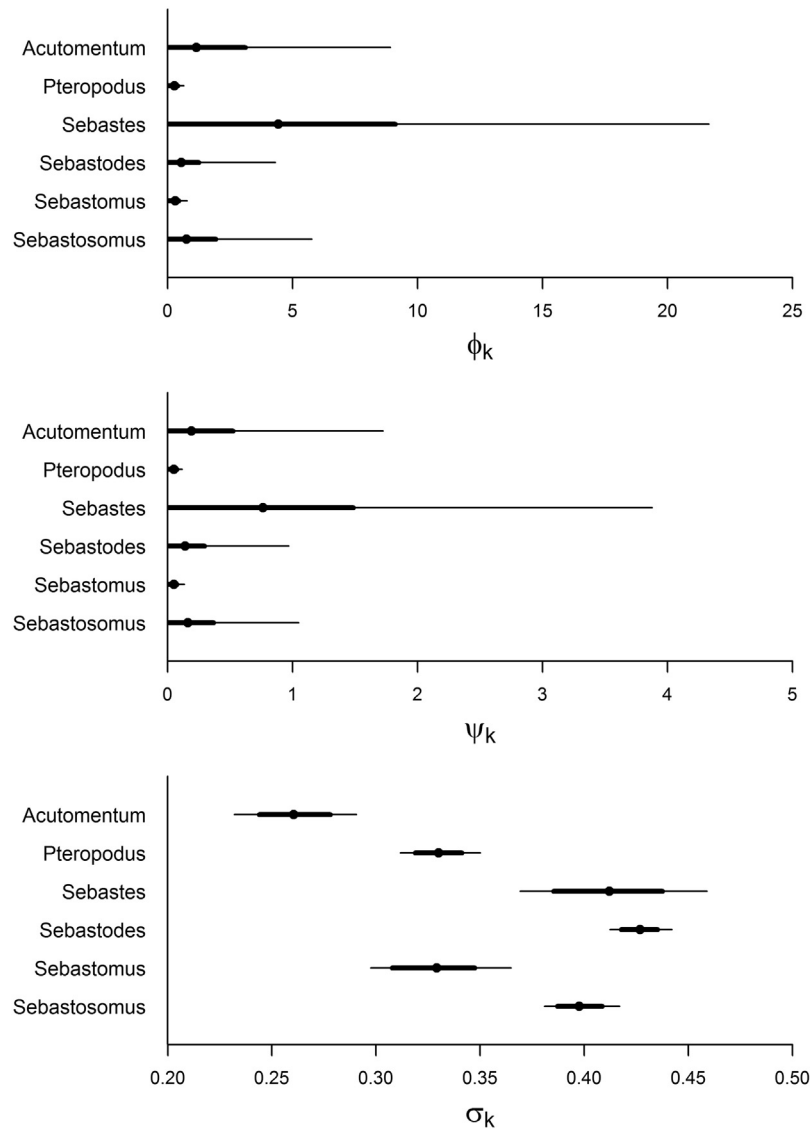


Fig. 2. Highest posterior density intervals (thin line = 95%, thick line = 75%) and posterior medians (circles) for standard deviation parameters in the 3-level hierarchical model (Model 3a).

maximum likelihood estimates (MLEs) of the fecundity-length exponents (slope parameters in the linear model) plotted relative to posterior distributions from Model 3a. MLEs from the separate regressions are unbiased, but imprecise relative to estimates from the HLM (Fig. 1). The hierarchical model estimates benefit from ‘partial pooling’ of information, whereby the posterior distributions are ‘shrunk’ from the MLE toward the mean, β_k , of the hyperprior in subgenus (i.e. Eq. (T16) in Table 3). The degree of shrinkage is determined by both the distance between the species-level mean and the mean of the hyperprior, as well as the relative precision of the two quantities (Gelman et al., 2004).

The amount of shrinkage in species-level slope parameters varied by subgenus in Model 3a (Fig. 1). Slopes for the *Pteropodus* and *Sebastomus* groups showed relatively little variability among species, whereas the subgenera *Sebastosomus* and *Sebastes* had greater species-level differences. Posterior distributions of the intercept parameters (not shown) are a ‘mirror image’ of the slope distributions in Fig. 1. This is expected due to negative correlations between slope and intercept parameters when covariates have a mean far from zero. Distributions of the 2nd level hierarchical standard deviation parameters (ϕ_k and ψ_k for intercepts

and slopes, respectively) describe species-level variability among subgenera (Fig. 2, top and middle panels). The magnitude of variability among subgenera is qualitatively similar for both intercepts and slopes. Residual standard deviations vary considerably among subgenera (Fig. 2, bottom panel), consistent with the reduced predictive accuracy (higher WAIC) for models that assumed constant variance among subgenera.

Although WAIC scores indicate that predictive accuracy increases after accounting for variability among species and subgenera (Table 3), the amount of variability in slopes among subgenera exceeds that within any single subgenus (Fig. 1). Posterior medians for species-level slope parameters from Model 3a (Table 3, Eq. (T16)) were lowest for subgenera *Acutomentum* and *Pteropodus*, and highest for the *Sebastes* and *Sebastosomus* groups (Table 6, Fig. 1). *S. alutus*, *S. crameri*, and *S. mystinus* had the three highest median slope estimates, whereas *S. hopkinsi*, *S. ovalis*, and *S. rufus* had the lowest median slope.

There is considerable variation among posterior distributions of the subgenus-level slopes (β_k), which represent the exponents of an ‘unobserved’ species in each of the six observed subgenera (Table 6). All six of the observed subgenera have 95% Highest

Table 6

Medians and 95% highest density intervals for posterior distributions of regression coefficients in the 3-level hierarchical linear model (Model 3 in Table 3). Posterior distributions for unobserved species in observed subgenera correspond to parameters α_k and β_k for the intercept and slope, respectively.

Subgenus	Species	a	exp(a)	b
<i>Acutomentum</i>	(unobserved)	-9.838 (-14.09, -6.43)	5.340 e-05 (5.96 e-13, 7.28 e-04)	3.673 (3.09, 4.42)
	<i>hopkinsi</i>	-9.004 (-11.59, -6.18)	1.229 e-04 (3.19 e-07, 1.47 e-03)	3.548 (3.00, 4.01)
	<i>ovalis</i>	-9.638 (-13.00, -6.34)	6.523 e-05 (2.09 e-09, 9.67 e-04)	3.595 (3.04, 4.16)
	<i>rufus</i>	-9.983 (-14.45, -6.73)	4.620 e-05 (6.67 e-10, 5.79 e-04)	3.692 (3.15, 4.41)
<i>Pteropodus</i>	(unobserved)	-9.432 (-10.51, -8.38)	8.009 e-05 (1.84 e-05, 2.00 e-04)	3.702 (3.51, 3.89)
	<i>atrovirens</i>	-9.356 (-10.48, -8.30)	8.646 e-05 (1.91 e-05, 2.18 e-04)	3.713 (3.52, 3.91)
	<i>auriculatus</i>	-9.719 (-10.90, -8.57)	6.012 e-05 (9.94 e-06, 1.61 e-04)	3.643 (3.44, 3.84)
	<i>carinatus</i>	-9.379 (-10.51, -8.30)	8.449 e-05 (1.84 e-05, 2.15 e-04)	3.706 (3.50, 3.90)
	<i>caurinus</i>	-9.561 (-10.68, -8.52)	7.040 e-05 (1.43 e-05, 1.74 e-04)	3.679 (3.50, 3.86)
	<i>dalli</i>	-9.231 (-10.33, -8.18)	9.798 e-05 (2.02 e-05, 2.37 e-04)	3.734 (3.52, 3.96)
	<i>maliger</i>	-9.458 (-10.56, -8.37)	7.809 e-05 (1.65 e-05, 1.98 e-04)	3.702 (3.52, 3.89)
	<i>nebulosus</i>	-9.264 (-10.41, -8.12)	9.479 e-05 (1.78 e-05, 2.51 e-04)	3.732 (3.53, 3.94)
	<i>rastrelliger</i>	-9.415 (-10.52, -8.26)	8.152 e-05 (1.60 e-05, 2.15 e-04)	3.701 (3.50, 3.89)
<i>Sebastes</i>	(unobserved)	-14.937 (-20.57, -8.12)	3.256 e-07 (4.09 e-23, 9.20 e-05)	4.423 (3.38, 5.38)
	<i>alutus</i>	-18.510 (-24.66, -13.58)	9.142 e-09 (6.22 e-14, 4.78 e-07)	4.967 (4.15, 5.99)
	<i>crameri</i>	-16.833 (-20.81, -12.74)	4.891 e-08 (5.84 e-12, 1.26 e-06)	4.804 (4.12, 5.47)
	<i>norvegicus</i>	-15.534 (-21.33, -7.15)	1.793 e-07 (1.24 e-12, 2.76 e-04)	4.276 (2.97, 5.23)
<i>Sebastodes</i>	(unobserved)	-11.065 (-13.12, -9.24)	1.566 e-05 (5.82 e-13, 5.05 e-05)	3.778 (3.41, 4.21)
	<i>goodei</i>	-11.023 (-11.88, -10.22)	1.632 e-05 (5.48 e-06, 3.29 e-05)	3.790 (3.66, 3.93)
	<i>jordani</i>	-11.062 (-11.89, -10.20)	1.569 e-05 (5.75 e-06, 3.36 e-05)	3.695 (3.54, 3.85)
	<i>paucispinis</i>	-11.028 (-12.47, -9.83)	1.624 e-05 (8.06 e-07, 4.16 e-05)	3.813 (3.62, 4.04)
<i>Sebastomus</i>	(unobserved)	-11.989 (-13.95, -9.95)	6.211 e-06 (1.50 e-07, 3.38 e-05)	4.162 (3.80, 4.52)
	<i>chlorostictus</i>	-12.016 (-14.07, -9.99)	6.048 e-06 (1.23 e-07, 3.45 e-05)	4.174 (3.82, 4.53)
	<i>constellatus</i>	-12.033 (-14.10, -10.00)	5.944 e-06 (1.45 e-07, 3.33 e-05)	4.154 (3.80, 4.51)
	<i>ensifer</i>	-12.012 (-13.97, -9.98)	6.070 e-06 (8.82 e-08, 3.34 e-05)	4.161 (3.79, 4.53)
	<i>helvomaculatus</i>	-11.960 (-13.99, -9.93)	6.397 e-06 (8.55 e-08, 3.51 e-05)	4.172 (3.79, 4.52)
	<i>rosaceus</i>	-11.713 (-13.65, -9.74)	8.190 e-06 (2.86 e-07, 4.32 e-05)	4.195 (3.83, 4.56)
	<i>rosenblatti</i>	-12.296 (-14.46, -10.11)	4.570 e-06 (5.03 e-08, 2.82 e-05)	4.113 (3.74, 4.46)
	<i>simulator</i>	-11.932 (-13.95, -9.88)	6.579 e-06 (1.02 e-07, 3.72 e-05)	4.171 (3.81, 4.53)
<i>Sebastosomus</i>	(unobserved)	-15.127 (-17.54, -11.39)	2.693 e-07 (2.40 e-11, 7.03 e-06)	4.624 (3.89, 5.01)
	<i>entomelas</i>	-14.966 (-17.21, -10.79)	3.165 e-07 (2.62 e-09, 1.38 e-05)	4.545 (3.86, 4.91)
	<i>flavidus</i>	-15.062 (-16.86, -13.10)	2.875 e-07 (1.34 e-08, 1.61 e-06)	4.590 (4.27, 4.88)
	<i>melanops</i>	-15.052 (-18.06, -11.40)	2.903 e-07 (1.25 e-11, 5.09 e-06)	4.685 (4.06, 5.17)
	<i>mystinus</i>	-15.561 (-18.15, -13.62)	1.746 e-07 (4.36 e-10, 8.11 e-07)	4.816 (4.47, 5.26)
<i>serranoides</i>	-15.861 (-19.15, -13.61)	1.293 e-07 (2.18 e-11, 6.57 e-07)	4.665 (4.29, 5.21)	
Genus		A	exp(A)	B
<i>Sebastes</i>	(unobserved)	-11.938 (-16.25, -8.30)	6.538 e-06 (1.63 e-11, 1.03 e-04)	4.043 (3.43, 4.71)

Posterior Density (HPD) intervals greater than 3, providing strong evidence that relative fecundity increases with size. The *Acutomentum* group has the lowest median slope (3.67), followed by *Pteropodus* (3.70) and *Sebastodes* (3.78). The *Sebastosomus* group has the highest posterior median slope (4.62), as well as a lower bound of the 95% HPD interval almost identical to the upper bound of the interval for the *Pteropodus* group. The posterior slope distribution for the *Sebastes* subgenus has the next highest median (4.42) but is relatively imprecise compared to the other subgenera, with a 95% HPD interval of 3.38 to 5.38 (Table 6). The genus-level slope posterior median was 4.0, with a 95% HPD interval of 3.4–4.7 (B, Table 6).

In data-limited situations (i.e. when estimating fecundity for an unobserved species), posterior predictive slope distributions are less precise than the posterior distributions in Table 6 because they integrate over uncertainty in the group-level mean and standard deviation. This additional uncertainty is reflected in the posterior predictive distributions of the fecundity-length exponent for the six subgenera, again based on Model 3a (β_k , Fig. 3). Similarly, the variance of the genus-level posterior predictive slope distribution is higher for the 3-level hierarchical model (Model 3a), relative to the 2-level HLM (Model 2a), because the 3-level model accounts for variability among subgenera rather than assuming all *Sebastes* species are exchangeable (Fig. 4). Given Model 3a, there is a 93% posterior probability that the fecundity-length exponent is greater than 3 for an unobserved rockfish species (Fig. 4).

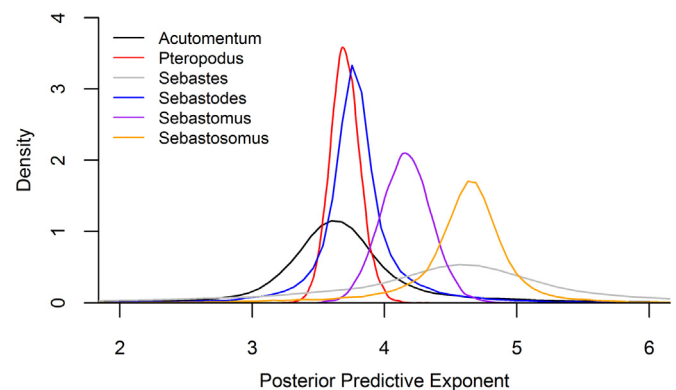


Fig. 3. Posterior predictive distributions of the subgenus-level exponent in the 3-level hierarchical model for fecundity at length (Model 3a).

Predicted median fecundity at length varies considerably by subgenus (Fig. 5). However, groups with larger exponents are not necessarily the most fecund at a given length. For example, a 400 mm rockfish in the *Sebastes* subgenus has a predicted median fecundity of approximately 100,000 eggs, whereas a fish of the same length in the *Sebastosomus* group is predicted to have nearly 300,000 eggs. These two subgenera have the highest median slope values in our analysis, but differ greatly in absolute fecundity at length. In contrast, the estimated exponent for the *Pteropodus* group

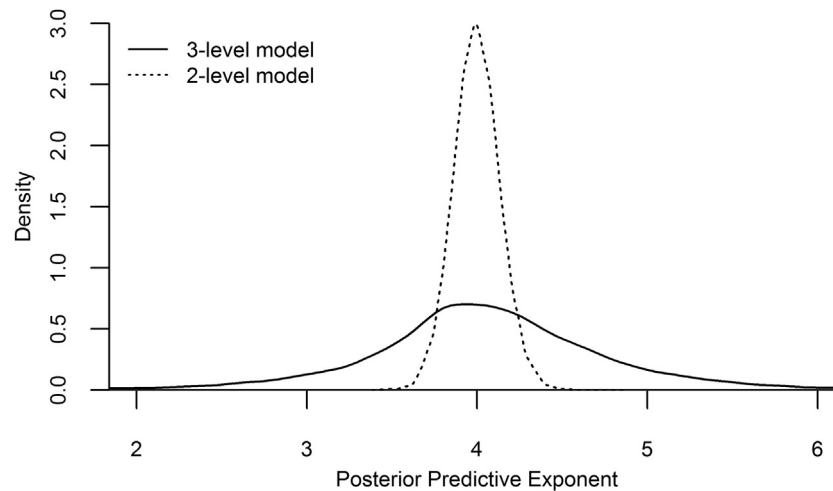


Fig. 4. Posterior predictive distributions of the fecundity exponent for *Sebastes* spp. from an unobserved subgenus (Models 2a and 3a in Table 3).

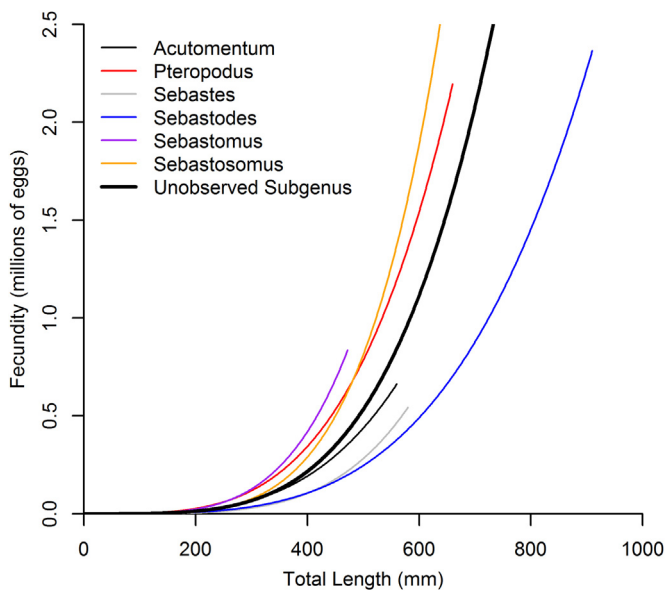


Fig. 5. Predicted fecundity at length (Model 3a) by *Sebastes* subgenus (thin lines) and for an unobserved subgenus (thick, black line). Maximum lengths set equal to the maximum reported length among observed species in each subgenus.

is relatively small, but a 400 mm fish has a predicted median fecundity of 350,000 eggs.

Visual analysis of MCMC output using density plots, trace plots, running means, and autocorrelation plots suggested that parameters converged to similar target distributions with adequate mixing. Potential scale reduction factors for all models and parameters were very close to 1, i.e. variances between and within chains were similar, a result also consistent with convergence. Geweke diagnostics (z-scores) were consistent with equal means in the first 10% and last 50% of each chain.

4. Discussion

Our research describes a framework for characterizing and predicting fecundity at length for species in the genus *Sebastes*. We find that accounting for differences among subgenera, as well as among species, improves model predictive ability. Our results also suggest that relative fecundity (eggs per gram body weight) increases with size in most *Sebastes* species. Therefore, *Sebastes* assessments

in which spawning output is assumed proportional to spawning biomass are likely to produce biased estimates of quantities important to fisheries managers (Dick 2009; Spencer and Dorn, 2013; He et al., 2015). As noted earlier, absolute fecundity has little effect on stock assessment models used for management (other than to scale the result), whereas the exponent parameter determines the rate at which relative fecundity increases with size.

Based on the data available for this study, the effect of gonad development stage on the fecundity-length exponent is not consistent among species. Effects of development stage have been noted by previous authors (e.g. Eldridge et al., 1991; Kusakari, 1991; Bobko and Berkeley, 2004; Ralston and MacFarlane, 2010), but analyses have mainly focused on the multiplicative coefficient in the fecundity-length relationship, rather than the exponent (which has a greater effect on population dynamics). Bobko and Berkeley (2004) modeled absolute fecundity of black rockfish (*S. melanops*) as a linear function of age and detected a difference in slope between pre-fertilized and fertilized eggs. However, they found no difference in slope between development stages based on a linear model of relative fecundity versus age. Sample sizes by stage for *S. caurinus* and *S. entomelas* in our analysis were small, and may limit our ability to detect differences in the exponent among studies (Table 4). However, sample sizes for *S. flavidus* were reasonably large (26–100 per stage) and no effects on the exponent were detected. Sample sizes by stage were also large for *S. goodei* (ranging from 67 to 175), nevertheless only 2 of the 3 studies (Beyer et al., 2015 and Beyer et al., unpublished data) detected a significant change in the exponent among stages (Table 4) and the differences were not consistent between the two studies. No exponent stage effect was detected for *S. goodei* using data collected by Stafford et al. (2014), despite relatively large samples for stages 2 and 3 (Table 4).

Further research is needed to determine which stage of gonad development best represents size-dependent weight-specific fecundity in *Sebastes*. Later stages (e.g. eyed larvae) are more susceptible to premature extrusion during collection, particularly for species caught at deeper depths, which may produce fecundity estimates that are biased low (Beyer et al., 2015). Alternatively, early stages (pre-fertilization) may never be fertilized or may undergo atresia in later stages. Standardization of development stages used in fecundity studies could reduce variability in fecundity caused by differences among stages, but would require additional sampling effort to ensure adequate sample sizes.

The studies included in this meta-analysis span several decades and sampling locations (Table 1). Sources also differ in terms of sampling methodology and sample preparation, although efforts

were made to standardize definitions of gonad development stage. Due to confounding of these effects, we are unable to identify the exact nature of differences among studies, but we found no significant effect of data source on the fecundity-length exponent in 11 of 14 species (Table 5). However, some species had small sample sizes per source. Results for species having at least 30 samples in two or more sources were inconsistent, with no significant interaction term among studies of *S. flavidus*, *S. mystinus*, and *S. paucispinis*, but significant interaction among studies of *S. caurinus*, *S. goodei* and *S. hopkinsi* (Table 5). We did not incorporate data source into the hierarchical model structure (although it is possible, in principle) because several species were observed by only a single study.

Beyer et al. (2015) examined spatiotemporal patterns in fecundity for *S. goodei* and *S. flavidus* over 4 years at 5 sites off California. They found that egg production per unit weight varied spatially for both species, but did not vary among years. They note that oceanic conditions were relatively stable over the sampling period, and it is possible that inter-annual variability is greater over longer time periods spanning a wider range of environmental conditions. Monitoring of fecundity at larger spatial and temporal scales within the entire size range of a species is needed to better understand the influence of spatial and temporal variation in fecundity on our results.

In our analyses, we do not account for size- or age-dependent ‘maternal effects,’ e.g. larval phenotypes that vary according to the mothers’ phenotype. Measures of larval quality such as energy reserves (lipid stores) are known to increase with maternal size and age (Berkeley et al., 2004; Sogard et al., 2008). If larval survival rates increase with the size and/or age of the mother, then the effective fecundity of females (the proportion of surviving offspring) also increases. Increases in relative fecundity with size, as seen in our results, are therefore only one mechanism for increased reproductive potential in older, larger females. A comprehensive treatment of reproductive potential in *Sebastes* stock assessments would also account for size-dependent effects such as the frequency of multiple broods and larval survival rates.

The dependent variable in our models is equivalent to “brood fecundity” as defined by Beyer et al. (2015). Brood fecundity is equivalent to annual egg production for species that release a single brood per year. However, some *Sebastes* species are known to produce multiple broods within a spawning season. Use of a single, fixed, fecundity-length relationship in an assessment is adequate if brood fecundity is proportional to total annual fecundity and egg production at size does not vary spatially or temporally. However, among the species that exhibit multiple brooding, there is increasing evidence that the frequency of multiple brooders in the population varies by year, area, and maternal size. Slight decreases in brood fecundity between primary and secondary broods have been detected in Chilipepper rockfish, *S. goodei*, but were not observed in Speckled rockfish, *S. ovalis* (Beyer et al., 2015). This suggests that, for some species, the timing of sampling within the spawning season could affect estimates of brood fecundity. The proportion of females producing multiple broods also increases with size in some species (Love et al., 1990; Ralston and MacFarlane 2010; Beyer et al., 2015), which could produce a multiplicative increase in annual fecundity that increases with size. Size-dependent changes in the frequency of multiple brooding would interact with changes in the demographic structure of the spawning population, amplifying the effects of size-dependent relative fecundity. Further research is needed on the occurrence of multiple broods in rockfishes, including its frequency among species, size/age classes, years, and locations.

Hierarchical models with subgenus and species effects provide a systematic approach to characterizing the fecundity-size relationship in *Sebastes* stock assessments. Posterior distributions for the parameters a_{jk} and b_{jk} can be used directly in stock assessments for

species that are included in our analysis (after back-transformation of the intercept). Assessments of species that are not included in the hierarchical analysis, but that are part of an observed subgenus, can use posterior predictive distributions for the appropriate subgenus (α_k and β_k). Perhaps most importantly, assessors of species in unobserved subgenera can use posterior predictive distributions for the genus *Sebastes* (A and B). Although most age-structured modeling frameworks represent fecundity parameters as fixed point estimates, it is possible to integrate uncertainty in the fecundity-length relationship into assessments using bivariate distributions from the HLM. However, the benefits or drawbacks to this approach are unknown and beyond the scope of this paper.

Our genus-level results are consistent with those of Haldorson and Love (1991), who calculated an average fecundity-length exponent of 4.10 using published point estimates. Dick (2009) modeled fecundity as a power function of weight in a 2-level hierarchical model and concluded that the posterior predictive distribution for the exponent of the fecundity-weight relationship had a mean of 1.3, which is consistent with a fecundity-length exponent of 4 (our result) given a cubic weight-length relationship. Our analysis builds upon these previous studies by identifying patterns in the fecundity-length relationship among subgenera, providing predictive distributions for unobserved species, and quantifying uncertainty in parameters at the species, subgenus, and genus level.

We omitted some species with available data from the analysis due to an insufficient number of taxa in the subgenus (<3 species), or because the phylogenetic tree of Hyde and Vetter (2007) did not categorize a species into a subgenus (e.g. *S. melanostomus* or *S. levis*). When data are available for a species that was omitted from this analysis, it is possible to use posterior distributions from the 3-level HLM as prior distributions in a Bayesian linear model for the omitted species. Due to correlations between the slope and intercept parameters, a bivariate prior would best summarize the information gained from our analysis.

A non-hierarchical analysis of the fecundity-length data (e.g. ANCOVA) finds significant differences among species in both the intercept and slope parameters (results not shown). However, while estimates from this type of analysis are unbiased, there is a cost associated with decreased precision (Fig. 1). Three models in the candidate set (Models 3a–c) performed similarly in terms of predictive accuracy, according to WAIC (Table 3). We note that all three models retain some form of species-level structure (with varying intercepts, slopes, or both) in addition to the subgenus-level effects, but the data are unable to strongly discriminate among the alternative structures.

We recommend the use of results from Model 3a in *Sebastes* stock assessments (Table 6, Figs. 1 and 2), since this model retains differences among species in both the slope and intercept parameters, reducing the potential for bias while sharing information among species within a subgenus. At the genus level, posterior means of the exponent from the 2- and 3-level hierarchical models are similar (Fig. 4), but the predictive variance is underestimated by the 2-level model due to the lack of structure at the subgenus level. Further research is needed to better understand variation in fecundity at the subgenus level, which may be linked to differences among subgenera in life history trade-offs associated with maternal effects or frequency of multiple broods (Lack 1947; Sogard et al., 2008).

Distributions for the fecundity-length exponent vary among species, but to different degrees depending on the subgenus (Fig. 1). Hierarchical standard deviation parameters (ϕ_k and ψ_k) for each subgenus reflect this variability (Fig. 2), with smaller species-level differences in the *Pteropodus* and *Sebastes* groups, and larger variances in the *Sebastes*, *Acutomentum* and *Sebastesomus* groups. The *Sebastes* subgenus has most variability among species, but this may be driven by the inclusion of an Atlantic species (*S. norvegicus*).

Additional data from other Atlantic species would help determine if this difference is unique to *S. norvegicus*, or a characteristic (e.g. environmental response) common to Atlantic *Sebastes*. Differences in species-level variability among subgenera are also reflected in the precision of subgenus-level predictive distributions (Fig. 3).

Due to the opportunistic nature of this meta-analysis, some questions remain unanswered and will require future research. Targeted data collection would allow for expansion of the current models to include other *Sebastes* subgenera. Given their importance to fisheries off the U.S. West Coast, we consider *S. levis*, *S. miniatus* (and *S. crocotulus*), *S. pinniger*, and *S. ruberrimus* to be high priorities for data collection in that region. Although the Northeast Pacific is the most speciose region (Love et al., 2002) for *Sebastes*, subgenera missing from this analysis include the *Eosebastes*, *Sebastichthys*, *Rosicola*, and *Sebastopyr*, as well as 9 species categorized under “clades A and B” (following Fig. 3 in Hyde and Vetter, 2007). Our data are heavily weighted toward *Sebastes* in the Northeast Pacific. This region is the center of *Sebastes* diversity (Love et al., 2002), but species from the Northwestern Pacific, Atlantic (other than *S. norvegicus*), Southeastern Pacific, and Gulf of California are not represented. Recent studies of Atlantic *Sebastes* species report fecundity-length relationships that are consistent with the general findings of our analysis (i.e. fecundity-length exponents >3). Saborido-Rey et al. (2015) report fecundity-length relationships for *S. mentella* and *S. norvegicus* in the Irminger Sea and Icelandic waters, with exponents of 3.64 and 4.61, respectively. Both estimates were significantly different from 3, consistent with an increase in relative fecundity with size. Drevetnyak and Kluev (2005) reported a fecundity-length relationship for *S. viviparus* in the Norwegian and Barents seas, with an exponent of 3.86 based on 38 females (also significantly different from 3).

Future meta-analyses of rockfish fecundity could benefit from standardization of sampling methodology, as well as greater spatial and temporal coverage. Standardized sampling would remove confounding effects (e.g. gonad development stage) among studies. Expanded spatial and temporal coverage could improve our understanding of the relationship between changes in fecundity and fluctuations in recruitment, both among years and across each species' range. Fine scale sampling also presents opportunities to link changes in fecundity to environmental factors (e.g. food availability) that influence the physical condition of the spawning stock.

Acknowledgements

We sincerely thank Dr. Raquel Prado (Department of Applied Mathematics and Statistics, University of California, Santa Cruz) who provided valuable advice on the implementation of hierarchical models while serving on the dissertation committee of Dr. Dick. The analyses in this paper would not have been possible without the generous assistance of several researchers who provided fecundity data. Specifically, we thank David Benet (University of California, Santa Cruz/NMFS), Daniel Cooper (NMFS), Don Gunderson (University of Washington), Dan Ito (NMFS), Neosha Kashef (University of California, Santa Cruz/NMFS), Lisa Lacko (Department of Fisheries and Oceans, Canada), Milton Love (University of California, Santa Barbara), Bruce MacFarlane (NMFS), Dan Nichols (NMFS), Laura Richards (Department of Fisheries and Oceans, Canada), Katherine Schmidt (California State University/NMFS), Susan Sogard (NMFS), David Stafford (University of California, Santa Cruz/NMFS), Rick Stanley (Department of Fisheries and Oceans, Canada), Farron Wallace (Washington Department of Fish and Wildlife), and Lynn Yamanaka (Department of Fisheries and Oceans, Canada). We would also like to thank Susan Sogard and two anonymous reviewers for helpful comments on the draft manuscript. SB was partially supported by NOAA Cooperative

Institute Award NA150AR4320071. MM was partially supported by NSF grant DEB 15-55729.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2016.11.009>.

References

- Bagenal, T., 1967. A short review of fish fecundity. In: Gerking, S.D. (Ed.), *The Biological Basis of Freshwater Fish Production*. John Wiley & Sons, Inc., New York, pp. 89–111.
- Benet, D., E. Dick and D. Pearson, 2009. Life history aspects of greenspotted rockfish (*Sebastes chlorostictus*) from central California. NOAA Technical Memorandum, NOAA-TM-NMFS-SWFSC-446. 43 p.
- Berkeley, S., Chapman, C., Sogard, S., 2004. Maternal age as a determinant of larval growth and survival in a marine fish (*Sebastes melanops*). *Ecology* 85, 1258–1264.
- Beyer, S., Sogard, S., Harvey, C., Field, J., 2015. Variability in rockfish (*Sebastes* spp.) fecundity: species contrasts maternal size effects, and spatial differences. *Environ. Biol. Fishes* 98, 81–100.
- Bobko, S.J., Berkeley, S.A., 2004. Maturity, ovarian cycle, fecundity, and age-specific parturition of black rockfish (*Sebastes melanops*). *Fish. Bull.* 102, 418–429.
- Brooks, E., 2013. Effects of variable reproductive potential on reference points for fisheries management. *Fish. Res.* 138, 152–158.
- Cooper, W., Barbieri, L., Murphey, M., Lowerre-Barbieri, S., 2013. Assessing stock reproductive potential in species with indeterminate fecundity: effects of age truncation and size-dependent reproductive timing. *Fish. Res.* 138, 31–41.
- Cooper, D., 2003. Possible Differences in Copper Rockfish (*Sebastes Caurinus*) Fecundity and Parturition with Maternal Size and Age. Masters Thesis. University of Washington.
- Corlett, J., 1964. Fecundity of redfish from east Greenland. *Annal. Biol. Copenh.* 19, 78.
- DeLacy, A.C., Hitz, C.R., Dryfoos, R.L., 1964. Maturation, gestation, and birth of rockfish (*Sebastes*) from Washington and adjacent waters. *Wash. Dep. Fish. Res. Pap.* 2, 51–67.
- Dick, E., 2009. Modeling the Reproductive Potential of Rockfishes (*Sebastes* Spp.) Ph.D. Dissertation. University of California Santa Cruz, Santa Cruz, CA.
- Drevetnyak, K., Kluev, A., 2005. On fecundity of *Sebastes* viviparus from the north east arctic. In: Report Submitted to the 2005 ICES Annual Science Conference, September 20–24, Aberdeen, U. K, 11 p.
- Echeverria, T., Lenarz, W., 1984. Conversions between total, fork and standard lengths in 35 species of *Sebastes* from California. *Fish. Bull.* 82, 249–251.
- Eldridge, M.B., Jarvis, B.M., 1995. Temporal and spatial variation in fecundity of yellowtail rockfish. *Trans. Am. Fish. Soc.* 124, 16–25.
- Eldridge, M.B., Whipple, J.A., Bowers, M.J., Jarvis, B.M., Gold, J., 1991. Reproductive performance of yellowtail rockfish, *Sebastes flavidus*. *Environ. Biol. Fishes* 30, 91–102.
- Gelman, A., Hill, J., 2007. *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, 625 p.
- Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. *Bayesian Data Analysis*, 2nd ed. Chapman and Hall/CRC, 668 p.
- Gelman, A., Hwang, J., Vehtari, A., 2014. Understanding predictive information criteria for Bayesian models. *Stat. Comput.* 24, 997–1016.
- Gelman, A., 2006. Prior distributions for variance parameters in hierarchical models. *Bayesian Anal.* 3, 515–533.
- Gunderson, D.R., 1976. Population Biology of Pacific Ocean Perch (*Sebastes Alutus*) Stocks in the Washington–Queen Charlotte Sound Region, and Their Response to Fishing Ph.D. dissertation. University of Washington, 140 p.
- Haldorson, L., Love, M., 1991. Maturity and fecundity in the rockfish, *Sebastes* spp., a review. *Mar. Fish. Rev.* 53 (2), 25–31.
- He, X., Field, J., Beyer, S., Sogard, S., 2015. Effects of size-dependent relative fecundity specifications in fishery stock assessments. *Fish. Res.* 165, 54–62.
- Hyde, J., Vetter, R., 2007. The origin, evolution, and diversification of rockfishes of the genus *Sebastes* (Cuvier). *Mol. Phylogenet. Evol.* 44, 790–811.
- Ito, D. H., 1977. Fecundity of the copper rockfish, *Sebastes caurinus* (Richardson) from Puget Sound, Washington. Paper submitted to Professor Bruce Miller as part of project for Fisheries 499, a class at the University of Washington, Seattle. This report does not constitute a published work. Used by permission.
- Jackman, S., 2009. Hierarchical statistical models. In: *Bayesian Analysis for the Social Sciences*. John Wiley & Sons, Ltd., Chichester UK, <http://dx.doi.org/10.1002/9780470686621.ch7>.
- Kusakari, M., 1991. Mariculture of kurosoi, *Sebastes schlegelii*. *Environ. Biol. Fishes* 30, 245–251.
- Lack, D., 1947. The significance of clutch-size. *Ibis* 89, 302–352.
- Le Bris, A., Pershing, A., Hernandez, C., Mills, K., Sherwood, G., 2015. Modelling the effects of variation in reproductive traits on fish population resilience. *ICES J. Mar. Sci.*, <http://dx.doi.org/10.1093/icesjms/fsv154>.
- Love, M., Johnson, K., 1998. Aspects of the life histories of grass rockfish, *Sebastes rastrelliger*, and brown rockfish, *S. auriculatus*, from southern California. *Fish. Bull.* 87, 100–109.

- Love, M., Westphal, W., 1981. Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, off central California. *Fish. Bull.* 79, 533–545.
- Love, M., P. Morris, M. McCrae, and R. Collins, 1990. Life history aspects of 19 rockfish species (Scorpaenidae: *Sebastes*) from the Southern California Bight. NOAA Technical Report NMFS 87: 38 p.
- Love, M., Yoklavich, M., Thorsteinson, L., 2002. *The Rockfishes of the Northeast Pacific*. University of California Press.
- MacGregor, J. S., 1970. Fecundity, multiple spawning, and description of the gonads in *Sebastes*. United States Fish and Wildlife Service Special Scientific Report, Fisheries No. 596. 12 pp.
- Moser, G., 1967. Reproduction and development of *Sebastes paucispinis* and comparison with other rockfishes off Southern California. *Copeia* 1967 (4), 773–797.
- Murawski, S., Rago, P., Trippel, E., 1999. Impacts of Demographic Variation in Spawning Success on Reference Points for Fishery Management. NOAA Tech. Memo., pp. 77–85, NMFS-F/SPO-40.
- Murua, H., Saborido-Rey, F., 2003. Female reproductive strategies of marine fish species of the North Atlantic. *J. Northwest Atlantic Fish. Sci.* 33, 23–31.
- Nichol, D.G., Pikitch, E.K., 1994. Reproduction of darkblotched rockfish off the Oregon coast. *Trans. Am. Fish. Soc.* 123, 469–481.
- Phillips, J.B., 1964. Life history studies on ten species of rockfish (genus *Sebastes*). California Department of Fish and Game. *Fish Bull.* 126, 158.
- R Core Team, 2016. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna Austria URL <https://www.R-project.org/>.
- Raitt, D., Hall, W., 1967. On the fecundity of the redfish, *Sebastes marinus* (L.). *J. du Conseil Int. pour l'Exploration de la Mer* 31 (2), 237–245.
- Ralston, S., MacFarlane, B., 2010. Population estimation of bocaccio (*Sebastes paucispinis*) based on larval production. *Can. J. Fish. Aquat. Sci.* 67, 1005–1020.
- Ralston, S., Bence, J., Eldridge, M., Lenarz, W., 2003. An approach to estimating rockfish biomass based on larval production, with applications to *Sebastes jordani*. *Fish. Bull.* 101, 129–146.
- Richards, L.J., Emmett, B., 1988. Methods Used for Fecundity Estimation of Rockfish and Lingcod Ovaries. Canadian Data Report of Fisheries and Aquatic Sciences No. 707, 44 p.
- Romero, M., 1988. Life History of the Kelp Rockfish, *Sebastes Atrovirens* (Scorpaenidae). Masters Thesis. San Francisco State University, 49 p.
- Saborido-Rey, F., Dominguez-Petit, R., Garabana, D., Sigurdsson, B., 2015. Fecundity of *Sebastes mentella* and *Sebastes norvegicus* in the Irminger Sea and Icelandic waters. *Ciencias Marinas* 41 (2), 107–124.
- Schmidt, K., 2014. Life History Changes in Female Blue Rockfish, *Sebastes Myxistinus*, Before and After Overfishing, in Central California. Masters Thesis. California State University, Monterey Bay, 108 p.
- Snytko, V., Borets, L., 1973. Some Data on the Fecundity of Ocean Perch in the Vancouver–Oregon Region (translated from Russian). Fisheries Research Board of Canada Translation Series No. 2502, 5 p.
- Sogard, S., Berkeley, S., Fisher, R., 2008. Maternal effects in rockfishes *Sebastes* spp.: a comparison among species. *Mar. Ecol. Prog. Ser.* 360, 227–236.
- Spencer, P., Dorn, M., 2013. Incorporation of weight-specific relative fecundity and maternal effects in larval survival into stock assessments. *Fish. Res.* 138, 159–167.
- Stafford, D., Sogard, S., Berkeley, S., 2014. Maternal influence on timing of parturition, fecundity, and larval quality in three shelf rockfishes (*Sebastes* spp.). *Aquat. Biol.* 21, 11–24.
- Trippel, E., Kjesbu, O., Solemdal, P., 1997. Effects of adult age and size structure on reproductive output in marine fishes. In: *Early Life History and Recruitment in Fish Populations*. Chapman and Hall, pp. 31–62, 596 p.
- Wallace F., Cheng Y. W., Tsou T., 2008. Status of the black rockfish resource north of Cape Falcon, Oregon to the U.S.–Canadian border in 2006. Status of the Pacific Coast groundfish fishery through 2007, Stock assessment and fishery evaluation Stock Assessments and Rebuilding Analyses. 2008. Portland, Oregon, PFMC.
- Watanabe, S., 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *J. Mach. Learn. Res.* 11, 3571–3594.
- Westrheim, S.J., 1958. On the Biology of the Pacific Ocean Perch, *Sebastes Alutus* (Gilbert). Masters Thesis. University of Washington, 106 p.