Hierarchical analysis of taxonomic variation in intraspecific competition across fish species

Andrew P. Foss-Grant,[1,5] Elise F. Zipkin,[2] James T. Thorson,[3] Olaf P. Jensen,[4] and William F. Fagan[1]

[1]*University of Maryland Department of Biology, College Park, Maryland 20742 USA*
[2]*Michigan State University Department of Integrative Biology, Michigan State University Ecology, Evolutionary Biology and Behavior Program, East Lansing, Michigan 48864 USA*
[3]*Fisheries Resources Assessment and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Seattle, Washington 98112 USA*
[4]*Rutgers University Department of Marine and Coastal Sciences, New Brunswick, New Jersey 08901 USA*

Abstract. The nature and intensity of intraspecific competition can vary greatly among taxa, yet similarities in these interactions can lead to similar population dynamics among related organisms. Variation along the spectrum of intraspecific competition, with contest and scramble competition as endpoints, leads to vastly different responses to population density. Here we investigated the diversity of intraspecific competition among fish species, predicting that functional forms of density-dependent reproduction would be conserved in related taxa. Using a hierarchical model that links stock–recruitment parameters among populations, species, and orders, we found that the strength of overcompensation, and therefore the type of intraspecific competition, is tightly clustered within taxonomic groupings, as species within an order share similar degrees of compensation. Specifically, species within the orders Salmoniformes and Pleuronectiformes exhibited density dependence indicative of scramble competition (overcompensation) while the orders Clupeiformes, Gadiformes, Perciformes, and Scorpaeniformes exhibited dynamics consistent with contest competition (compensation). Maximum potential recruitment also varied among orders, but with less clustering across species. We also tested whether stock–recruitment parameters correlated with maximum body length among species, but found no strong relationship. Our results suggest that much of the variation in the form of density-dependent reproduction among fish species may be predicted taxonomically due to evolved life history traits and reproductive behaviors.

Key words: density-dependence; hierarchical model; intraspecific competition; stock–recruitment; recruitment compensation; Shepherd stock-recruitment model; stock assessment; meta-analysis.

INTRODUCTION

Intraspecific competition for resources, including food, territory, and mates, can play a large role in the survival and reproduction of individuals and thus influence population dynamics. The strength of intraspecific competition for these resources is often a limiting factor in overall population size (Pomerantz et al. 1980, Boström-Einarsson et al. 2013, Ward et al. 2013). Ecologists traditionally view intraspecific competition in terms of a dichotomy or gradient of contest vs. scramble competition (Bellows 1981, Parker 2000). Just as resources are rarely split evenly among individuals (e.g., scramble competition), it is equally uncommon to observe cases where superior competitors can wholly exclude inferior individuals (e.g., contest competition; Bellows 1981). This spectrum of intraspecific competition produces a wide range of functional forms that have been

used to describe density-dependent reproduction (Bellows 1981). Under contest competition, density-dependence is compensatory, such that the reproductive output of a population is greatest when the population size becomes large enough to reach the maximum number of reproductive winners that limited resources will allow. This generally occurs by reaching a maximum number of mates (Simmons and Ridsdill-Smith 2011), mating sites (Warner 1987), or territories (Marden and Waage 1990). Once the maximum number of winners is reached, additional reproductive competitors will neither increase nor decrease reproductive output, as resources are only split among the best competitors. Scramble competition, however, leads to overcompensatory density dependence wherein production of offspring actually declines at high densities (Zipkin et al. 2009). Limited resources are split evenly reducing the reproductive success of all individuals. This reproductive scramble competition can happen as a result of adult resource consumption, juvenile resource consumption, nest destruction, or cannibalism (Bellows 1981). Given this variety of possible outcomes, natural populations undergoing density-dependent reproduction tend to exhibit recruitment

relationships somewhere along the contest–scramble gradient (which we term the "strength of overcompensation").

Recent studies have examined the influence of evolution on aspects of population dynamics (Coulson et al. 2011, Schoener 2011, Fagan et al. 2013), suggesting that closely related species may share certain population-level dynamics due to similarities in life history traits. Such relationships are a key part of the "ecogenetic loop" that links life history traits, demography, and evolution (Kokko and Lopez-Sepulcre 2007, Coulson et al. 2010). These linkages raise the question of whether the strength of overcompensation, which is rooted in life history strategy and related behaviors, may be similar across closely related species. If phenotypic variation exists in how individual reproductive output changes in response to population density, it follows that the strength of overcompensation is itself a trait under selection and suggests that there may be similarities in density dependence among related taxa.

Body size is a key trait connecting life history characteristics to population dynamics. Research suggests that there is a link between the maximum reproductive output of a population and the maximum body size of individuals within the population for a large variety of taxa including unicellular organisms, insects, fish, and mammals (Fenchel 1974, Blueweiss et al. 1978, Honěk 1993, Savage et al. 2004). The fecundity of an individual and population-level maximum reproductive rate have both been shown to increase with body size both within and among related species (Honěk 1993). In fisheries, maximum reproductive rate is much higher for a population when large, old females are present (Venturelli et al. 2010). Species that reach a large maximum body size are likely to be relatively more fecund and have a greater maximum reproductive rate (Goodwin et al. 2006).

Fish populations are an excellent system for studying variations in the relationship between reproductive competition and density dependence because fish species exhibit a wide variety of dynamics and life history strategies (Rose et al. 2001). At a mechanistic level, the relationship between population density and reproductive success varies among fish species and populations because of resource limitations, habitat constraints, and potentially intrinsic, species-specific traits. For example, anadromous salmonids, which reproduce in spatially constrained rivers and creeks, are known to have poor reproductive output at high densities because spawning sites, or redds, of some individuals are destroyed by other spawners (Van Den Berghe and Gross 1989). As this behavior has the potential to reduce the fitness of all spawners roughly equally, it can be seen as a form of reproductive scramble competition. On the other end of the spectrum, older, larger females of the black rockfish, *Sebastes melanops*, lay eggs that are competitively superior to those of their younger counterparts (Berkeley et al. 2004), endowing their offspring with a survival advantage typically observed in contest competition.

Stock–recruitment relationships, or the relationships between the maximum annual number or biomass of spawners (i.e., the stock) and the annual number or biomass of offspring that reach a threshold age (i.e., recruits), vary greatly among fish species and taxa (Myers et al. 1999). These relationships provide an ideal system to test ecological theory, as fisheries data sets are large scale with high amounts of replication, allowing broad-scale investigations of ecosystem-level questions (Jensen et al. 2012). However, estimating the functional relationships between spawners and their recruits presents many challenges and complications. For example, decades of time series data that span a wide range of abundances are generally required to estimate individual stock–recruitment relationships accurately (Walters 1985, Myers 1997). Moreover, such time series data typically include substantial measurement error, which can lead to bias in parameter estimates (Walters and Ludwig 1981, Sethi et al. 2005, Pitchford et al. 2007). In addition, a wide variety of biotic and abiotic factors naturally leads to variation in the stock-recruit relationship. For example, changes in environmental conditions can introduce variability to the number of recruits produced from a population, with habitat changes and phenological shifts affecting recruitment success (Rijnsdorp et al. 2009).

Because of this variability in stock–recruitment data, hierarchical models (Berliner 1996, Gelman and Hill 2007) offer a valuable improvement on traditional Stock–recruitment methods that estimate parameters one population at a time (Dorn 2002, Forrest et al. 2010). Hierarchical models provide a structure in which data can be grouped to observe stock–recruitment parameters at multiple levels, such as taxonomic order. Similarly, Bayesian techniques have become popular in recent decades as researchers have looked for ways to integrate data from multiple sources into one analysis (Liermann and Hilborn 1997, Stewart et al. 2013). Bayesian approaches facilitate estimation of hierarchical stock–recruitment curves by easily allowing for shared parameter estimation (Forrest et al. 2010). By integrating information from multiple sources, hierarchical models analyzed using Bayesian methods greatly improve the accuracy of stock–recruitment models by reducing the effect of noise around the stock–recruitment relationship (Maunder and Punt 2013).

We developed a hierarchical model to investigate variation in stock–recruitment parameters, and thus types of intraspecific competition, among different taxonomic groupings of commercially harvested fish. Our multi-species model accommodates a wide range of stock-recruit functional forms in a single estimation framework using data from a large stock–recruitment database (Myers et al. 1995). We used this model to examine variation in maximum recruitment per unit spawning biomass and degree of compensation at both the species and order levels. We also used maximum body length as a covariate to investigate the effect of body size on maximum recruits per spawner. We expected that the parameters governing the functional forms of stock–recruitment relationships of

species would be clustered by taxonomic order, with orders that have highly spatially constrained spawning grounds or nurseries displaying the highest levels of overcompensation. We further expected that maximum recruitment per unit spawning biomass would be greatest in highly fecund species and orders and that maximum body length would be positively correlated with the maximum recruitment per unit spawning biomass among species of the same order.

METHODS

The data set

We analyzed the Myers Stock–Recruit database, which was compiled and standardized from assessments of exploited marine fisheries worldwide (Myers et al. 1995). The database includes 281 reproductively isolated subpopulations from 62 species in eight orders with time series ranging from 6 to 73 yr (mean = 25 yr) and consists primarily of marine and anadromous species with a small number of freshwater species. For each population in this database, annual stock and recruitment data were estimated using commercial catch-at-age data and/or research survey estimates. The data were standardized into spawning-stock biomass (SSB) for the stocks and thousands of metric tons or millions of fish for the recruits of marine fish and river-spawning salmonids, respectively (Myers et al. 1995). We then standardized the recruitment data further by dividing recruits by maximum annual spawning biomass per recruit (using values of natural mortality, maturity, and body mass at age compiled by R. A. Myers and C. Minto [*personal communication*]). This ensures that we regress a measure of spawning success (in units of mass) against a measure of spawning potential (in units of mass), such that the productivity of each population (e.g., slope at the origin) is a dimensionless quantity, comparable among stocks, that complies with the exchangeability assumption of hierarchical models (Gelman et al. 2004). A deterministic equilibrium of spawners and recruits is achieved at a ratio of 1 (i.e., the 1:1 line is replacement rate), such that the slope of the stock–recruit relationship at the origin must be >1 for the population to be reproductively viable (Myers et al. 1995). All data come from assessments that used standard, species-specific procedures for aging of individuals and follow stock boundary conventions set by the Northwest Atlantic Fisheries Organization (NAFO) and the International Council for the Exploration of the Sea (Myers et al. 1995). We used this data set instead of its successor, the RAM Legacy Stock Assessment Database (Ricard et al. 2012), because many stock and recruitment values from the latter data set were projected from population models that assume an underlying stock–recruitment relationships and parameters for each population, which can bias the results of meta-analyses (Ricard et al. 2012, Dickey-Collas et al. 2015). In contrast, the Myers Stock–Recruit database contains recruitment estimates from sequential population analysis methods or direct survey

estimates, which do not assume any a priori stock–recruit relationship. Maximum body length values were taken for each species from the FishBase database (*available online*)[6]. After standardizing recruitment using natural mortality, maturity, and body size information, maximum body length values within each order were then rescaled to have a within-order mean of zero and a standard deviation of one. This rescaling was used for all subsequent analysis of the relationship between standardized maximum body length and SR parameters, and is done (1) to ensure that estimated parameters within a taxonomic order represent values given the average body length in that order and (2) to ease mixing of Bayesian sampling.

We excluded populations with under 10 years of data because temporal autocorrelation rendered the effective sample size too small (Worm and Myers 2003, Thorson et al. 2014). We also excluded orders with fewer than five species (i.e., Lophiformes and Alopiformes). Members of the orders Osmeriformes and Esociformes (Ayu and Pike, respectively) were grouped with the Salmoniformes because those species all belong to the superorder Protacanthopterygii. These steps left us with six orders (Clupeiformes, Gadiformes, Perciformes, Pleuronectiformes, Salmoniformes, Scorpaeniformes), all of which were well represented with 9–110 populations in 5–14 species. To avoid overparameterizing our models, we aggregated species within orders ($n = 6$) rather than within families ($n = 18$). The final 256 populations, representing 54 species in 6 orders, appear in Appendix S1.

The stock–recruitment relationships

The Beverton-Holt (1957) and Ricker (1954) stock–recruitment models are commonly used spawner–recruit models for fish populations undergoing density-dependent reproduction (Goodyear 1993, Myers 2001). The Beverton-Holt model describes a system where the number of recruits reaches a maximum at high spawner densities, beyond which additional spawners do not affect overall recruitment. This population behavior is one outcome of contest competition, where the ability to survive and reproduce varies among individuals (Brännström and Sumpter 2005). The Beverton-Holt model can also be derived from foraging arena theory and associated assumptions about risk-sensitive foraging behavior (Walters and Korman 1999). Under the Beverton-Holt model, the worst competitors decline in fitness at high densities as resources are disproportionately consumed by the best competitors. Such compensatory recruitment can be expressed as

$$R_{t+1} = \alpha S_t / (1 + \beta S_t), \qquad (1)$$

where S_t is the stock value at time t and R_{t+1} is the recruits produced at the following time step, $t + 1$. The

[6] www.fishbase.org

parameters α and β, constrained to be non-negative, govern the shape of the stock–recruitment relationship. The parameter α represents the maximum reproductive output of an individual in the absence of density-related effects, or per-capita recruitment at very low spawner abundance. Thus the slope of the stock–recruitment curve is α at the origin. The parameter β determines the rate at which the number of recruits decreases as spawner density increases, and, in effect, determines the carrying capacity for a specified α parameter.

The Ricker (1954) model is a stock–recruitment relationship where the number of recruits reaches a maximum at an intermediate spawner density beyond which recruitment falls as spawner abundance increases. This overcompensatory behavior is generally a result of scramble competition, where reproductive success depends on competition with neighbors and access to resources is equal among individuals (Brännström and Sumpter 2005). This decline in recruits with increased spawner abundance is due to interference by neighbors, which results in lower juvenile survival at high densities. The Ricker model is written as

$$R_{t+1} = \alpha S_t e^{-\beta S_t}, \qquad (2)$$

where the non-negative α is directly comparable to the estimate from the Beverton-Holt model, while β is not directly comparable to the Beverton-Holt model.

An alternative to the Ricker and Beverton-Holt models is the Shepherd (1982) stock–recruitment model. Through the addition of a third parameter, the Shepherd model accommodates stock–recruitment relationships that range from compensatory (as observed in the Beverton-Holt model) to overcompensatory (as observed in the Ricker model), as well as other asymptotic and non-asymptotic forms of density dependence (Shepherd 1982). As such, the Shepherd model allows for a wide range of functional forms, spanning from contest to scramble competition, as well as density-independent dynamics (Fig. 1). The three-parameter Shepherd model is

$$R_{t+1} = \alpha S_t / (1 + (\beta S_t)^\delta), \qquad (3)$$

where the α and β parameters again define the maximum number of recruits per spawner and the carrying capacity, respectively. The additional non-negative parameter δ represents the degree of compensation, or the extent to which per capita reproduction declines at high densities. When δ = 1. the Shepherd model reduces to the Beverton-Holt model and, when δ > 1, the model represents increased overcompensation similar to the Ricker model. When δ < 1, the recruitment curve grows indefinitely at a declining rate, becoming increasingly density independent as δ approaches zero. At δ = 0, the relationship is exactly linear. The Shepherd model is therefore particularly useful as a general framework for analyses that span multiple taxa of fish because it does not make
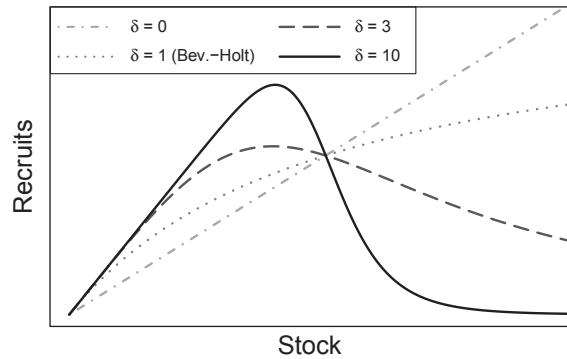

Fig. 1. Examples of the Shepherd model for fixed α and β parameters (α = 2.5, β = 0.01), where δ, which regulates the degree of compensation, is varied from 0 to 10. Curve shapes range from linear (δ = 0), to compensatory (0 > δ ≥ 1), to overcompensatory (δ > 1). At δ = 1, the Shepherd model is equivalent to the Beverton-Holt model.

a priori assumptions about the structure of intraspecific competition.

The hierarchical model

We constructed a hierarchical community model to link stock–recruitment parameters among species and compare parameter estimates across taxonomic groupings and maximum body lengths. We designed our model to test two hypotheses: (1) taxonomic orders in which fish experience substantial spatial constraints on their reproductive output, particularly the Salmoniformes and Pleuronectiformes, have higher levels of overcompensation (e.g., higher values of δ) compared to other orders (Clupeiformes, Gadiformes, Perciformes, and Scorpaeniformes) in the data set and (2) maximum recruitment per unit spawning biomass (α) correlates with the species-level maximum body length in all orders of fish. Our hierarchical model assumes that, for both α and δ, parameter estimates are related taxonomically. That is, populations of the same species should be similar dynamically, as should species belonging to the same order. We assume that there is no hierarchical relationship in the parameter β among populations, as carrying capacity can fluctuate greatly for a variety of abiotic reasons, and we would thus expect β to be similar neither among populations within species nor among species within orders (Myers et al. 2001, MacKenzie et al. 2003). At the most basic level, the Shepherd model is fit to data from each population:

$$R_{ijk,t+1} = \alpha_{ijk} S_{ijk,t} / (1 + (\beta_i S_{ijk,t})^{\delta_{ijk}}), \qquad (4)$$

where $S_{ijk,t}$ and $R_{ijk,t+1}$ are the stock and standardized recruit values at time t and $t + 1$, respectively, for population i of species j within order k, and α_{ijk}, β_i, and δ_{ijk} are the Shepherd parameters for each population i. β_i does not have species- (j) and order-level (k) indices, as it is not modeled hierarchically.

We assume that the population-level δ and α parameters each come from species-specific distributions. The

logarithm of the parameter δ_{ijk} is assumed to be drawn from a normal distribution

$$\log(\delta_{ijk}) \sim \mathrm{N}(\log(\mu_{\delta_{jk}}), \sigma_{\delta_j}), \qquad (5)$$

where $\log(\mu_{\delta_{jk}})$ is the log-mean value of δ across all populations that belong to species j of order k, and σ_{δ_j} is the standard deviation among populations of species j. We model δ on the log scale so that it remains positive. The species-level parameter, $\mu_{\delta_{jk}}$, is governed by an additional, order-level parameter such that it is also a random variable that comes from a common, normal, order-level distribution

$$\log(\mu_{\delta_{jk}}) \sim \mathrm{N}(\log(\mu_{\delta_k}), \sigma_{\delta_k}), \qquad (6)$$

where $\log(\mu_{\delta_k})$ represents the mean of $\log(\mu_{\delta_{jk}})$ (e.g., the mean δ value across all species in order k) and σ_{δ_k} is the standard deviation among all species within order k.

We similarly specified α at the stock level

$$\log(\alpha_{ijk}) \sim \mathrm{N}(\log(\mu_{\alpha_{jk}}), \sigma_{\alpha_j}, \qquad (7)$$

where $\log(\mu_{\alpha_{jk}})$ is the mean α for species j in order k and σ_{α_j} is the standard deviation of α for populations in species j. At the species level, we allow maximum body length to serve as a covariate on $\mu_{\alpha_{jk}}$ by assuming that

$$\log\left(\mu_{\alpha_{jk}}\right) = C1_{jk} + L_{\max_j} C2_{jk}, \qquad (8)$$

where $L_{\max_j}$ is the standardized maximum body length covariate for species j in order k, and $C1_{jk}$ and $C2_{jk}$ are the species-level intercept and slope terms that specify the relationship between maximum body length and α. These parameters are linked at the order level as follows:

$$C1_{jk} \sim \mathrm{N}(\log(\mu_{C1_k}), \sigma_{C1_k}), \qquad (9)$$

$$C2_{jk} \sim \mathrm{N}(\log(\mu_{C2_k}), \sigma_{C2_k}), \qquad (10)$$

where μ_{C1_k}, σ_{C1_k}, μ_{C2_k}, and σ_{C2_k} are the order-level log-mean and standard deviation for the intercept and slope parameters, respectively. Recruit values were standardized using lifetime spawning biomass per recruit in the absence of fishing ($\mathrm{SPR}_{F=0}$) to ensure that α was comparable among populations (Myers et al. 1999). This gives spawner and recruit values the same units such that α is a dimensionless summary of the strength of lifetime compensation (i.e., maximum lifetime spawning biomass per spawning biomass) and that any differences between parameter values among taxa are meaningful.

We modeled each population by additionally assuming that the recruit data could contain process and/or sampling error that is not adequately captured with the recruitment function (Myers 2001). To account for this potential error, we assumed that each of the recruit data points is drawn from a normal distribution centered on the "true" recruitment value

$$\tilde{R}_{i,t+1} \sim \mathrm{N}\left(R_{i,t+1}, R_{i,t+1}\sigma_{R_i}\right).$$

Here, $\tilde{R}_{i,t+1}$ is the recruit data point for year $t+1$ for population i, $R_{i,t+1}$ is the expected recruitment value for population i, and σ_{R_i} is the population-specific standard deviation around the mean recruitment value.

We analyzed our model with a Bayesian approach using Markov chain Monte Carlo (MCMC) to obtain samples from the posterior distributions of all model parameters. MCMC allowed us to easily estimate model parameters and directly present the probability that a parameter has a certain value. We specified vague prior probabilities for all parameters in our model to represent a lack of knowledge on the order-level means, the variations among stocks, species, and orders, and the carrying capacity within stocks

$$\mu_{\delta_k} \sim \mathrm{N}(3,10) \quad \mu_{\delta_k} \geq 0,$$

$$\beta_i \sim \mathrm{N}(0.01,0.1) \quad \beta_i \geq 0,$$

$$\mu_{C1_k} \sim \mathrm{N}(3,10) \quad \mu_{C1_k} \geq 0,$$

$$\mu_{C2_k} \sim \mathrm{N}(0,10),$$

$$\sigma_{\delta_j}, \sigma_{\delta_k}, \sigma_{\alpha_j}, \sigma_{C1_k}, \sigma_{C2_k} \sim U(0,100).$$

The first parameter in each normal distribution is the mean and the second is the standard deviation. The first and second parameters in the uniform distribution represent the limits of that distribution. These prior distributions cover a range much larger than the expected possible parameter values, such that each prior is relatively flat over the expected parameter ranges. Normal distributions were chosen over uniform distributions for mean parameter values because of improved model convergence. We analyzed our model using the programs R and JAGS (Plummer 2003) to estimate posterior parameter distributions. We ran 100,000 MCMC iterations and thinned the chains by keeping only every 20th iteration after a burn-in of 40,000. We analyzed model convergence using the Gelman-Rubin statistic $\hat{R}$ (Appendix S2). Further tests of fit and validation of our model are found in Appendix S3, and figures showing posteriors produced without fitted data are found in Appendix S4 for comparison. We tested hypothesized differences in stock–recruitment behavior among orders by comparing posterior distributions of parameters among species and order groups.

Results

Order-level results

Parameter estimates from order-level stock–recruitment curves suggest a wide range of dynamics across orders

ranging from scramble competition to varying degrees of contest competition (Fig. 2). Posterior distributions of δ for Clupeiformes, Gadiformes, Perciformes, and Scorpaeniformes exhibited low degrees of density-dependence, as credible intervals (CIs) ranged primarily between δ = 0 (density-independent) and δ = 1 (Beverton-Holt-form compensation) (Fig. 2). Curves with these values of δ have a declining slope, but never fully reach a saturated recruitment value (although an equilibrium population size still exists at the intersection of the recruitment curve and the 1:1 replacement line). The orders Pleuronectiformes and Salmoniformes, however, had 50% credible intervals completely above the δ = 1 line. These results correspond to an overcompensatory stock–recruitment relationship (similar to the Ricker model), suggesting that populations within these two orders generally display overcompensation. These two orders reach maximum total recruitment at stock values that vary by species and then show a decline in recruitment at populations beyond this size.

The parameter α was highest in the Clupeiformes, Gadiformes, and Perciformes, all with median parameter values of α > 4 (Fig. 3), suggesting high maximum lifetime spawners per spawner for species in these orders. The orders Pleuronectiformes, Salmoniformes, and Scorpaeniformes had comparatively lower median α parameter values (median α < 3 for all orders).

There was no strong relationship between α and maximum body length (mean order-level covariate, μ_{C2_k}) for any of the orders (Fig. 4). The 50% credible interval for Gadiformes and Pleuronectiformes both overlap zero, suggesting no relationship between α and L_{max} whereas Perciformes and Scorpaeniformes have positive order-level slopes and the Clupeiformes and Salmoniformes have negative order-level slopes. When the order-level structure was removed from our model (e.g., all species were grouped together), no relationship was found between α and maximum body length. When similarly tested, δ also showed no relationship with maximum body length (Appendix S5).

Species-level results

We found that, within a given order, species generally exhibit clustered values of δ and more variation in α. All
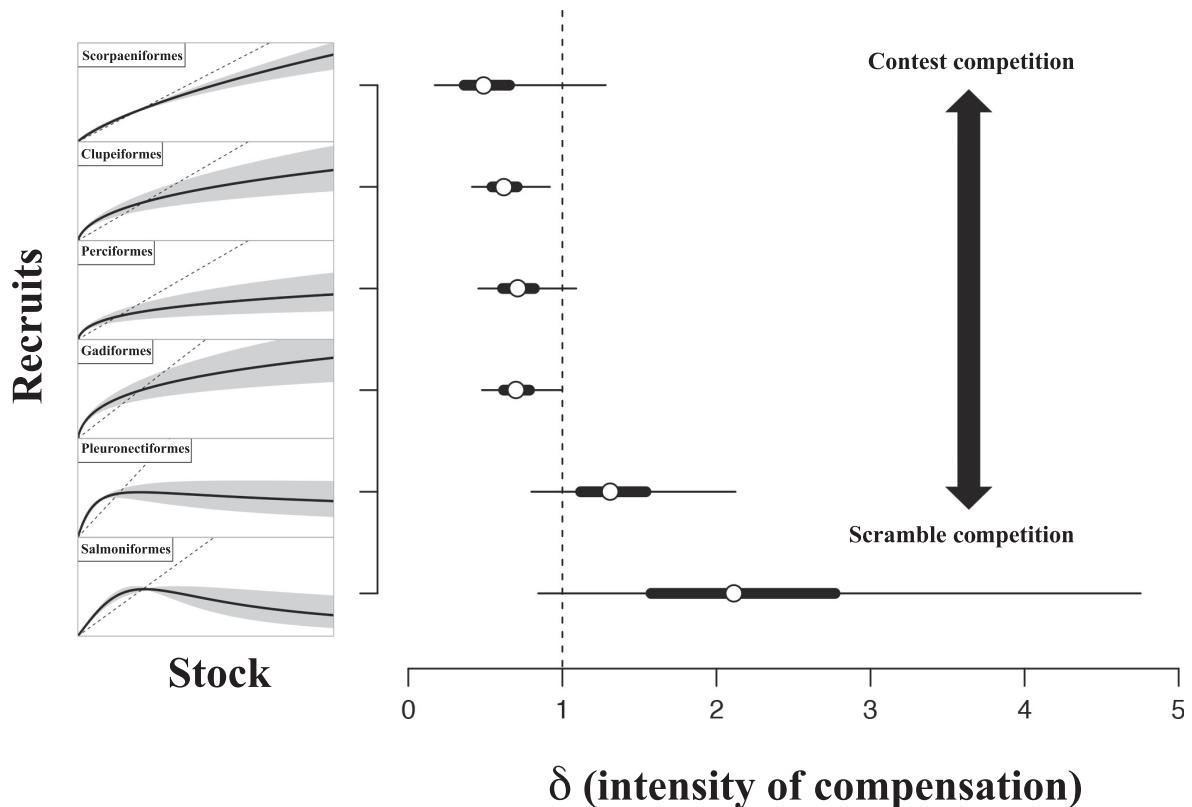

FIG. 2. Order-level stock recruitment curves showing intraspecific competition ranging from contest/compensatory competition (top) to scramble/overcompensatory competition (bottom). On the left, median order-level stock–recruitment relationships (black lines) are shown with 50% credible intervals (gray shading), as estimated using the Shepherd model. Dotted lines indicate the 1:1 line of stock and recruits. Axes vary in size between orders to facilitate comparisons among functional forms rather than carrying capacity. Values of β for each were determined by averaging median β values across all populations of a species and all species of an order. Stock and Recruit units are not given, as population sizes vary greatly within orders. On the right, the 95% (thin lines) and 50% (thick lines) credible intervals for order level δ (intensity of compensation) values are shown. Median values are represented by open circles. The dashed line at δ = 1 indicates where the Shepherd model is equivalent to the Beverton-Holt Model.
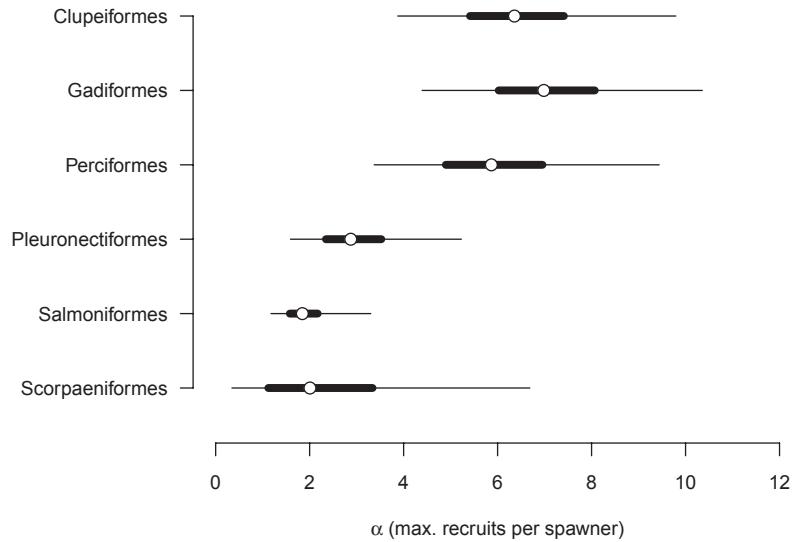
FIG. 3. The 95% (thin lines) and 50% (thick lines) credible intervals for order-level α (per capita recruitment at low densities) values. Median values are represented by open circles.
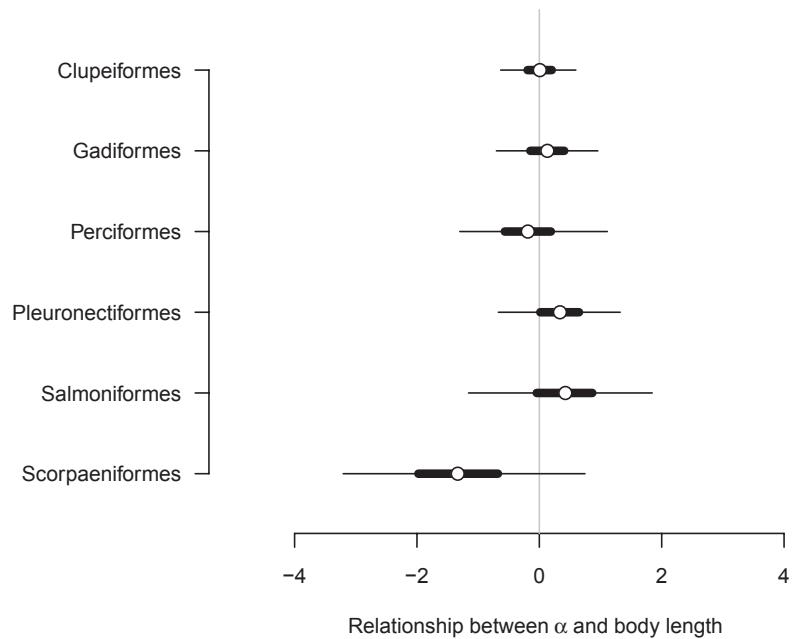

FIG. 4. Order-level effects of maximum body length on the parameter α. A value of 0 indicates no relationship while a positive (negative) value indicates a positive (negative) relationship between maximum body length and maximum per-capita recruitment. Open circles represent median values and the lines indicate the 50% (thick lines) and 95% (thin lines) credible intervals.

species within the orders Pleuronectiformes and Salmoniformes had median δ values in the range of over-compensation (δ > 1). Species of all other orders lie within the range between a linear and a compensatory stock–recruitment relationship (0 < δ < 1). The α parameter has a much greater amount of variation among species, especially within the Clupeiformes, Gadiformes, and Perciformes orders (Fig. 5). Exploratory

analysis showed that the sample mean of delta among species was similar in a model lacking grouping by order with some shrinkage of the variance (results not shown).

DISCUSSION

Our analyses document striking divergence in the strength of overcompensation and intraspecific
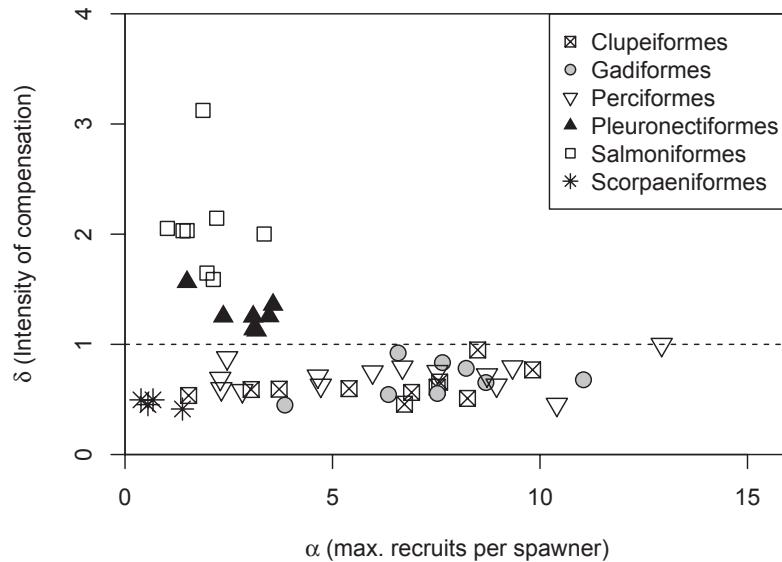
Fig. 5.   Median α plotted against median δ for all 54 fish species included in our model. Species are grouped into symbols based on taxonomic order. The dashed line at δ = 1 indicates pure contest competition. Values above the line indicate scramble competition. Values below the line indicate weak intraspecific competition.

competition among orders and species. We found that the degree of intraspecific competition (δ parameter) for the Salmoniformes (here defined as salmonids and relatives, including other members of the superorder Protacanthopterygii) and Pleuronectiformes (flatfishes) lies primarily in the overcompensatory range (Fig. 2), suggesting that for these taxa, high stock levels can depress recruitment. This result agrees with the common use of the Ricker model and observations of overcompensation in salmonids (Walters 1975, Krkošek et al. 2008), and with observed spawner–recruit relationships found in some studies of flatfish (Iles 1994, Rijnsdorp and Van Leeuwen 1996, Van der Veer et al. 2000, Wilderbuer et al. 2002, 2013, Archambault et al. 2014).

The results for both of these orders accord with our prediction that fish with spatially constrained reproduction are severely suppressed by intraspecific competition at high abundances. For stream-dwelling salmonids, such scramble competition may come about via several mechanisms. One example involves limitation on suitable spawning habitat (Armstrong et al. 2003) and redd superimposition (destruction of existing nests by subsequent spawners), which can cause strong overcompensation through the loss of a large percentage of eggs laid (Van Den Berghe and Gross 1989, Fukushima et al. 1998). Moreover, immediately following emergence, juvenile salmonids at high densities also experience high mortality as severe competition and less efficient foraging behavior lead to greater mortality through starvation than when fry densities are low (Nislow et al. 2011). Flatfish similarly experience density dependence due to spatially constrained nursery habitats. Eggs and larvae for many flatfishes drift in a pelagic phase before becoming demersal juveniles and

concentrating in nurseries (Rijnsdorp et al. 1995). Density-dependent processes come into effect and the concentration of individuals relative to nursery carrying capacities may limit successful recruitment (Beverton 1995, Rijnsdorp et al. 1995). The spatial constraint of nurseries with limited seabed habitat promotes competition, and strong density dependence is observed in populations with high juvenile concentrations in these habitats (Archambault et al. 2014).

The four other orders included in our model (Clupeiformes, Gadiformes, Perciformes, and Scorpaeniformes) exhibit competition between density-independent (δ = 0) and compensatory (δ = 1) dynamics (Fig. 2). For density dependence in the range 0 < δ < 1, recruitment can increase indefinitely with increasing spawning output. We note that this does not suggest an indefinitely growing population, as there is an equilibrium abundance (e.g., carry capacity) whenever δ > 0, which is identified as the point where the stock–recruit curve crosses the 1:1 replacement line. Beyond this point, increasing spawner abundance will continue to increase recruitment, but at a net loss. The functional form of these orders differ from those found in studies that investigate stock–recruitment dynamics across taxa, such as in Scorpaeniformes (Dorn 2002, Forrest et al. 2010), as few studies have used models that allow for variation in the degree of compensation. It is clear from their low values of δ that these orders have similar forms of intraspecific competition that are distinctly on the contest side of the contest–scramble gradient. Overall, our δ parameter results suggest that even though the degree of compensation varies widely across taxa, much of that variation among fish species may be predicted taxonomically as a function of evolved life history traits and reproductive behaviors.

Our results demonstrated that the α parameter of the Shepherd model differs greatly among fish orders (Fig. 3). Because α is a standardized reproductive output of individuals at low population levels without density-dependent effects (i.e., maximum lifetime spawners per spawner), we expected that orders with greater fecundity and higher per-capita spawning biomass would have greater α values (Andersen et al. 2008). Many of the species of the orders Clupeiformes, Gadiformes, and Perciformes do indeed have high fecundity, while the Salmoniformes are generally much less fecund (Mertz and Myers 1996). The fecundity values for the orders Pleuronectiformes and Scorpaeniformes are much less consistent, but fish belonging to those orders do generally have higher fecundities than members of the Salmoniformes. As fecundity is only one part of the recruitment process, other factors that affect survival of juveniles, such as predation or habitat quality, could greatly affect reproductive output at low densities (Karatayev et al. 2015). Large, late-maturing fish have been associated with relatively higher fecundities, small eggs, and few reproductive bouts per season (Winemiller and Rose 1992). Specifically, Scorpaeniformes tend to have small eggs and low maximum replacement rates (Winemiller and Rose 1992, Myers et al. 1999), which would indicate a low α parameter value. Our results suggest that there are distinct differences in α among fish orders, which appear to follow similar differences in fecundity and life history.

Contrary to expectation, we did not find a consistent effect of maximum body length on the maximum lifetime replacement rate (α parameter; Fig. 4). The allometric dependence varied from positive to negative by order, but no strong pattern emerged. When we analyzed all taxa together, we found no effect of maximum body length on α. This appears to indicate that, at these broad levels, body size does not show a strong effect on maximum lifetime compensation, contrary to previous hypotheses (Andersen et al. 2008).

We found strong clustering by order when looking at the species-level α and δ Shepherd model parameters (Fig. 5). This is especially true for the δ parameter. Median parameter estimates suggest that all species of the Pleuronectiformes and Salmoniformes orders exhibit overcompensatory dynamics, whereas none of the species of any of the four other taxonomic orders show a similar response. This implies that the type and degree of intraspecific competition is maintained through taxonomic groupings, mediated perhaps through similarities in life history and behavior. The lack of similar clustering in the α parameter within taxonomic orders indicates a much higher variation in maximum recruitment per unit spawning biomass between taxa, as the orders Clupeiformes, Gadiformes, and Perciformes especially high variation in α among species.

A key strength of the hierarchical modeling approach is that it can leverage population-level variation in reproductive rate and the strength of compensation (whether that variation manifests from reaction norms or from genotypic variation) to yield species-level and order-level insights relevant for management. Often, recruitment models are selected based on convention, model selection techniques, or by prior usage in related species. These decisions are based on biological considerations at some level, but in cases where data are poor or limited, it can be difficult to determine which model is most appropriate for a particular species. There is no standard approach for choosing a stock–recruitment model for a particular fish species, whether large amounts of data exist or not. Our modeling approach provides insight into the most appropriate density dependent models for a number of species.

We found that the type and degree of intra-specific competition are tightly clustered within orders indicating strong similarities in the form of intra-specific competition among related species. In contrast, maximum lifetime replacement rate shows a greater spread across species. Overall, these results indicate that evolutionary history leaves a clear signal in the population dynamics of fish through tight, within-taxa clustering of reproductive density-dependence, likely mediated by taxonomic similarities in life history and behavior. Ultimately these findings may provide a pathway for leveraging information across species to further explore the ecology, evolutionary trajectories, and management of fish species.

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