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Hierarchical analysis of taxonomic variation in intraspecific competition across fish species

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26 **Abstract**

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

45 **Keywords:** Intraspecific competition, Stock-recruitment, Density-dependence, Hierarchical
46 model

47

48 **Introduction**

49 Intraspecific competition for resources, including food, territory, and mates, can play a
50 large role in the survival and reproduction of individuals and thus influence population
51 dynamics. The strength of intraspecific competition for these resources is often a limiting factor
52 in overall population size (Pomerantz et al. 1980, Boström-Einarsson et al. 2013, Ward et al.
53 2013). Ecologists traditionally view intraspecific competition in terms of a dichotomy or
54 gradient of contest versus scramble competition (Bellows 1981, Parker 2000). Just as resources
55 are rarely split evenly among individuals (e.g., scramble competition), it is equally uncommon to
56 observe cases where superior competitors can wholly exclude inferior individuals (e.g., contest
57 competition; Bellows 1981). This spectrum of intraspecific competition produces a wide range
58 of functional forms that have been used to describe density-dependent reproduction (Bellows
59 1981). Under contest competition, density-dependence is compensatory, such that the
60 reproductive output of a population is greatest when the population size becomes large enough to
61 reach the maximum number of reproductive winners that limited resources will allow. This
62 generally occurs by reaching a maximum number of mates (Simmons and Ridsdill-Smith 2011),
63 mating sites (Warner 1987), or territories (Marden and Waage 1990). Once the maximum
64 number of winners is reached, additional reproductive competitors will neither increase nor
65 decrease reproductive output, as resources are only split among the best competitors. Scramble
66 competition, however, leads to overcompensatory density-dependence wherein production of
67 offspring actually declines at high densities (Zipkin et al. 2009). Limited resources are split
68 evenly reducing the reproductive success of all individuals. This reproductive scramble
69 competition can happen as a result of adult resource consumption, juvenile resource
70 consumption, nest destruction, or cannibalism (Bellows 1981). Given this variety of possible
71 outcomes, natural populations undergoing density-dependent reproduction tend to exhibit
72 recruitment relationships somewhere along the contest – scramble gradient (which we term the
73 “strength of overcompensation”).

74 Recent studies have examined the influence of evolution on aspects of population
75 dynamics (Coulson et al. 2011, Schoener 2011, Fagan et al. 2013), suggesting that closely related
76 species may share certain population-level dynamics due to similarities in life history traits.
77 Such relationships are a key part of the ‘ecogenetic loop’ that links life history traits,
78 demography, and evolution (Kokko and Lopez-Sepulcre 2007, Coulson et al. 2010). These
79 linkages raise the question of whether the strength of overcompensation, which is rooted in life

80 history strategy and related behaviors, may be similar across closely related species. If
81 phenotypic variation exists in how individual reproductive output changes in response to
82 population density, it follows that the strength of overcompensation is itself a trait under
83 selection and suggests that there may be similarities in density-dependence among related taxa.

84 Body size is a key trait connecting life history characteristics to population dynamics.
85 Research suggests that there is a link between the maximum reproductive output of a population
86 and the maximum body size of individuals within the population for a large variety of taxa
87 including unicellular organisms, insects, fish, and mammals (Fenchel 1974, Blueweiss et al.
88 1978, Honěk 1993, Savage et al. 2004). The fecundity of an individual and population-level
89 maximum reproductive rate have both been shown to increase with body size both within and
90 among related species (Honěk 1993). In fisheries, maximum reproductive rate is much higher
91 for a population when large, old females are present (Venturelli et al. 2010). Species that reach a
92 large maximum body size are likely to be relatively more fecund and have a greater maximum
93 reproductive rate (Goodwin et al. 2006).

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

107 Stock-recruitment relationships, or the relationships between the maximum annual
108 number or biomass of spawners (i.e., the stock) and the annual number or biomass of offspring
109 that reach a threshold age (i.e., recruits), vary greatly among fish species and taxa (Myers et al.

110 1999). These relationships provide an ideal system to test ecological theory, as fisheries datasets
111 are large-scale with high amounts of replication, allowing broad-scale investigations of
112 ecosystem-level questions (Jensen et al. 2011). However, estimating the functional relationships
113 between spawners and their recruits presents many challenges and complications. For example,
114 decades of time series data that span a wide range of abundances are generally required to
115 estimate individual stock-recruitment relationships accurately (Walters 1985, Myers 1997).
116 Moreover, such time series data typically include substantial measurement error, which can lead
117 to bias in parameter estimates (Walters and Ludwig 1981, Sethi et al. 2005, Pitchford et al.
118 2007). In addition, a wide variety of biotic and abiotic factors naturally leads to variation in the
119 stock-recruit relationship. For example, changes in environmental conditions can introduce
120 variability to the number of recruits produced from a population, with habitat changes and
121 phenological shifts affecting recruitment success (Rijnsdorp et al. 2009).

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

134 We developed a hierarchical model to investigate variation in stock-recruitment
135 parameters, and thus types of intraspecific competition, among different taxonomic groupings of
136 commercially harvested fish. Our multi-species model accommodates a wide range of stock-
137 recruit functional forms in a single estimation framework using data from a large stock
138 recruitment database (Myers et al. 1995). We used this model to examine variation in maximum
139 recruitment per unit spawning biomass and degree of compensation at both the species and order

140 levels. We also used maximum body length as a covariate to investigate the effect of body size
141 on maximum recruits per spawner. We expected that the parameters governing the functional
142 forms of stock-recruitment relationships of species would be clustered by taxonomic order, with
143 orders that have highly spatially-constrained spawning grounds or nurseries displaying the
144 highest levels of overcompensation. We further expected that maximum recruitment per unit
145 spawning biomass would be greatest in highly fecund species and orders and that maximum
146 body length would be positively correlated with the maximum recruitment per unit spawning
147 biomass among species of the same order.

148 **Methods**

149 *The Dataset*

150 We analyzed the Myers Stock-Recruit database, which was compiled and standardized
151 from assessments of exploited marine fisheries worldwide (Myers et al. 1995). The database
152 includes 281 reproductively isolated subpopulations from 62 species in 8 orders with time series
153 ranging from 6 to 73 years (mean = 25 years) and consists primarily of marine and anadromous
154 species with a small number of freshwater species. For each population in this database, annual
155 stock and recruitment data were estimated using commercial catch-at-age data and/or research
156 survey estimates. The data were standardized into spawning-stock biomass (SSB) for the stocks
157 and thousands of metric tonnes or millions of fish for the recruits of marine fish and river-
158 spawning salmonids, respectively (Myers et al. 1995). We then standardized the recruitment data
159 further by dividing recruits by maximum annual spawning biomass per recruit (using values of
160 natural mortality, maturity, and body weight at age compiled by R. A. Myers and C. Minto, pers.
161 comm. 2015). This ensures that we regress a measure of spawning success (in units mass)
162 against a measure of spawning potential (in units mass), such that the productivity of each
163 population (e.g., slope at the origin) is a dimensionless quantity, comparable among stocks, that
164 complies with the exchangeability assumption of hierarchical models (Gelman et al. 2004). A
165 deterministic equilibrium of spawners and recruits is achieved at a ratio of 1 (i.e., the 1-1 line is
166 replacement rate), such that the slope of the stock-recruit relationship at the origin must be
167 greater than 1 for the population to be reproductively viable (Myers et al. 1995). All data come
168 from assessments that used standard, species-specific procedures for aging of individuals and
169 follow stock boundary conventions set by the Northwest Atlantic Fisheries Organization

170 (NAFO) and the International Council for the Exploration of the Sea (Myers et al. 1995). We
171 used this dataset instead of its successor, the RAM Legacy Stock Assessment Database (Ricard
172 et al. 2012), because many stock and recruitment values from the latter dataset were projected
173 from population models that assume an underlying stock-recruitment relationships and
174 parameters for each population, which can bias the results of meta-analysis (Ricard et al. 2012,
175 Dickey-Collas et al. 2015). In contrast, the Myers Stock-Recruit database contains recruitment
176 estimates from sequential population analysis methods or direct survey estimates, which do not
177 assume any a priori stock-recruit relationship. Maximum body length values were taken for each
178 species from the FishBase database (fishbase.org). After standardizing recruitment using natural
179 mortality, maturity, and body size information, maximum body length values within each order
180 were then rescaled to have a within-order mean of zero and a standard deviation of one. This
181 rescaling was used for all subsequent analysis of the relationship between standardized
182 maximum body length and SR parameters, and is done to ensure (1) that estimated parameters
183 within a taxonomic order represent values given the average body length in that order, and (2) to
184 ease mixing of Bayesian sampling.

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

195 *The Stock-Recruitment Relationships*

196 The Beverton-Holt (1957) and Ricker (1954) stock-recruitment models are commonly
197 used spawner-recruit models for fish populations undergoing density-dependent reproduction
198 (Goodyear 1993, Myers 2001). The Beverton-Holt model describes a system where the number
199 of recruits reaches a maximum at high spawner densities, beyond which additional spawners do

200 not affect overall recruitment. This population behavior is one outcome of contest competition,
201 where the ability to survive and reproduce varies among individuals (Brännström and Sumpter
202 2005). The Beverton-Holt model can also be derived from foraging arena theory and associated
203 assumptions about risk-sensitive foraging behavior (Walters and Korman 1999). Under the
204 Beverton-Holt model, the worst competitors decline in fitness at high densities as resources are
205 disproportionately consumed by the best competitors. Such compensatory recruitment can be
206 expressed as:

$$207 \quad R_{t+1} = \alpha S_t / (1 + \beta S_t) \quad (1)$$

208 where S_t is the stock value at time t and R_{t+1} is the recruits produced at the following time step,
209 $t+1$. The parameters α and β , constrained to be non-negative, govern the shape of the stock-
210 recruitment relationship. The parameter α represents the maximum reproductive output of an
211 individual in the absence of density-related effects, or per-capita recruitment at very low spawner
212 abundance. Thus the slope of the stock-recruitment curve is α at the origin. The parameter β
213 determines the rate at which the number of recruits decreases as spawner density increases, and,
214 in effect, determines the carrying capacity for a specified α -parameter.

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

$$222 \quad R_{t+1} = \alpha S_t e^{-\beta S_t} \quad (2)$$

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

225 An alternative to the Ricker and Beverton-Holt models is the Shepherd (1982) stock-
226 recruitment model. Through the addition of a third parameter, the Shepherd model
227 accommodates stock-recruitment relationships that range from compensatory (as observed in the

228 Beverton-Holt model) to overcompensatory (as observed in the Ricker model), as well as other
229 asymptotic and non-asymptotic forms of density-dependence (Shepherd 1982). As such, the
230 Shepherd model allows for a wide range of functional forms, spanning from contest to scramble
231 competition, as well as density-independent dynamics (Fig. 1). The three parameter Shepherd
232 model is:

$$233 \quad R_{t+1} = \alpha S_t / (1 + (\beta S_t)^\delta) \quad (3)$$

234 where the α and β parameters again define the maximum number of recruits per spawner and the
235 carrying capacity, respectively. The additional non-negative parameter δ represents the degree
236 of compensation, or the extent to which per capita reproduction declines at high densities. When
237 $\delta=1$ the Shepherd model reduces to the Beverton-Holt model, and when $\delta>1$ the model
238 represents increased overcompensation similar to the Ricker model. When $\delta<1$ the recruitment
239 curve grows indefinitely at a declining rate, becoming increasingly density-independent as δ
240 approaches zero. At $\delta=0$, the relationship is exactly linear. The Shepherd model is therefore
241 particularly useful as a general framework for analyses that span multiple taxa of fish because it
242 does not make a priori assumptions about the structure of intraspecific competition.

243

244 *The Hierarchical Model*

245 We constructed a hierarchical community model to link stock-recruitment parameters
246 among species and compare parameter estimates across taxonomic groupings and maximum
247 body lengths. We designed our model to test two hypotheses: 1) taxonomic orders in which fish
248 experience substantial spatial constraints on their reproductive output, particularly the
249 Salmoniformes and Pleuronectiformes, have higher levels of overcompensation (e.g., higher
250 values of δ) compared to other orders (Clupeiformes, Gadiformes, Perciformes, and
251 Scorpaeniformes) in the dataset; and 2) maximum recruitment per unit spawning biomass (α)
252 correlates with the species-level maximum body length in all orders of fish. Our hierarchical
253 model assumes that, for both α and δ , parameter estimates are related taxonomically. That is,
254 populations of the same species should be similar dynamically, as should species belonging to
255 the same order. We assume that there is no hierarchical relationship in the parameter β among
256 populations, as carrying capacity can fluctuate greatly for a variety of abiotic reasons, and we

257 would thus not expect β to be similar, either among populations within species or among species
258 within orders (Myers et al. 2001, MacKenzie et al. 2003). At the most basic level, the Shepherd
259 model is fit to data from each population:

$$260 \quad R_{ijk,t+1} = \alpha_{ijk} S_{ijk,t} / (1 + (\beta_i S_{ijk,t})^{\delta_{ijk}}) \quad (4)$$

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

265 We assume that the population-level δ and α parameters each come from species-specific
266 distributions. The logarithm of the parameter δ_{ijk} is assumed to be drawn from a normal
267 distribution:

$$268 \quad \log(\delta_{ijk}) \sim N(\log(\mu_{\delta_{jk}}), \sigma_{\delta_j}) \quad (5)$$

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

$$274 \quad \log(\mu_{\delta_{jk}}) \sim N(\log(\mu_{\delta_k}), \sigma_{\delta_k}) \quad (6)$$

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

277 We similarly specified α at the stock level:

$$278 \quad \log(\alpha_{ijk}) \sim N(\log(\mu_{\alpha_{jk}}), \sigma_{\alpha_j}) \quad (7)$$

279 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
 280 populations in species j . At the species level, we allow maximum body length to serve as a
 281 covariate on $\mu_{\alpha_{jk}}$ by assuming that:

$$282 \quad \log(\mu_{\alpha_{jk}}) = C1_{jk} + L_{max_j} C2_{jk} \quad (8)$$

283 where L_{max_j} is the standardized maximum body length covariate for species j in order k , and
 284 $C1_{jk}$ and $C2_{jk}$ are the species-level intercept and slope terms that specify the relationship
 285 between maximum body length and α . These parameters are linked at the order level as follows:

$$286 \quad C1_{jk} \sim N(\log(\mu_{C1_k}), \sigma_{C1_k}) \quad (9)$$

$$287 \quad C2_{jk} \sim N(\log(\mu_{C2_k}), \sigma_{C2_k}) \quad (10)$$

288 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
 289 intercept and slope parameters, respectively. Recruit values were standardized using lifetime
 290 spawning biomass per recruit in the absence of fishing ($SPR_{F=0}$) to ensure that α was
 291 comparable among populations (Myers et al. 1999). This gives spawner and recruit values the
 292 same units such that α is a dimensionless summary of the strength of lifetime compensation (i.e.,
 293 maximum lifetime spawning biomass per spawning biomass) and that any differences between
 294 parameter values among taxa are meaningful.

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

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

299 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
 300 recruitment value for population i , and σ_{R_i} is the population-specific standard deviation around
 301 the mean recruitment value.

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

$$308 \quad \mu_{\delta_k} \sim N(3,10) \quad \mu_{\delta_k} \geq 0$$

$$309 \quad \beta_i \sim N(0.01,0.1) \quad \beta_i \geq 0$$

$$310 \quad \mu_{C1_k} \sim N(3,10) \quad \mu_{C1_k} \geq 0$$

$$311 \quad \mu_{C2_k} \sim N(0,10)$$

$$312 \quad \sigma_{\delta_j}, \sigma_{\delta_k}, \sigma_{\alpha_j}, \sigma_{C1_k}, \sigma_{C2_k} \sim U(0,100).$$

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

326 **Results**

327 Order-level Results

328 Parameter estimates from order-level stock-recruitment curves suggest a wide range of
329 dynamics across orders ranging from scramble competition to varying degrees of contest
330 competition (Fig. 2). Posterior distributions of δ for Clupeiformes, Gadiformes, Perciformes, and
331 Scorpaeniformes exhibited low degrees of density-dependence, as credible intervals (CIs) ranged
332 primarily between $\delta = 0$ (density-independent) and $\delta = 1$ (Beverton-Holt-form compensation)
333 (Fig. 2). Curves with these values of δ have a declining slope, but never fully reach a saturated
334 recruitment value (although an equilibrium population size still exists at the intersection of the
335 recruitment curve and the 1-1 replacement line). The orders Pleuronectiformes and
336 Salmoniformes, however, had 50% credible intervals completely above the $\delta = 1$ line. These
337 results correspond to an overcompensatory stock-recruitment relationship (similar to the Ricker
338 model), suggesting that populations within these two orders generally display overcompensation.
339 These two orders reach maximum total recruitment at stock values that vary by species and then
340 show a decline in recruitment at populations beyond this size.

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

346 There was no strong relationship between α and maximum body length (mean order-level
347 covariate, μ_{C2k}) for any of the orders (Fig. 4). The 50% credible interval for Gadiformes and
348 Pleuronectiformes both overlap zero, suggesting no relationship between α and L_{max} whereas
349 Perciformes and Scorpaeniformes have positive order-level slopes and the Clupeiformes and
350 Salmoniformes have negative order-level slopes. When the order-level structure was removed
351 from our model (e.g., all species were grouped together), no relationship was found between α
352 and maximum body length. When similarly tested, δ also showed no relationship with maximum
353 body length (Appendix E).

354 Species-level Results

355 We found that, within a given order, species generally exhibit clustered values of δ and
356 more variation in α . All species within the orders Pleuronectiformes and Salmoniformes had

357 median δ values in the range of overcompensation ($\delta > 1$). Species of all other orders lie within
358 the range between a linear and a compensatory stock-recruitment relationship ($0 < \delta < 1$). The α
359 parameter has a much greater amount of variation among species, especially within the
360 Clupeiformes, Gadiformes, and Perciformes orders (Fig. 5). Exploratory analysis showed that
361 the sample mean of delta among species was similar in a model lacking grouping by order with
362 some shrinkage of the variance (results not shown).

363 **Discussion**

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

374 The results for both of these orders accord with our prediction that fish with spatially
375 constrained reproduction are severely suppressed by intraspecific competition at high
376 abundances. For stream-dwelling salmonids, such scramble competition may come about via
377 several mechanisms. One example involves limitation on suitable spawning habitat (Armstrong
378 et al. 2003) and redd superimposition (destruction of existing nests by subsequent spawners),
379 which can cause strong overcompensation through the loss of a large percentage of eggs laid
380 (Van den Berghe and Gross 1989, Fukushima et al. 1998). Moreover, immediately following
381 emergence, juvenile salmonids at high densities also experience high mortality as severe
382 competition and less efficient foraging behavior lead to greater mortality through starvation than
383 when fry densities are low (Nislow et al. 2011). Flatfish similarly experience density-dependence
384 due to spatially constrained nursery habitats. Eggs and larvae for many flatfishes drift in a
385 pelagic phase before becoming demersal juveniles and concentrating in nurseries (Rijnsdorp et
386 al. 1995). Density-dependent processes come into effect and the concentration of individuals

387 relative to nursery carrying capacities may limit successful recruitment (Beverton 1995,
388 Rijnsdorp et al. 1995). The spatial constraint of nurseries with limited seabed habitat promotes
389 competition, and strong density-dependence is observed in populations with high juvenile
390 concentrations in these habitats (Archambault et al. 2014).

391 The four other orders included in our model (Clupeiformes, Gadiformes, Perciformes,
392 and Scorpaeniformes) exhibit competition between density-independent ($\delta=0$) and compensatory
393 ($\delta=1$) dynamics (Fig. 2). For density-dependence in the range $0 < \delta < 1$, recruitment can increase
394 indefinitely with increasing spawning output. We note that this does not suggest an indefinitely
395 growing population, as there is an equilibrium abundance (e.g., carry capacity) whenever $\delta > 0$,
396 which is identified as the point where the stock-recruit curve crosses the 1-1 replacement line.
397 Beyond this point, increasing spawner abundance will continue to increase recruitment, but at a
398 net loss. The functional form of these orders differ from those found in studies that investigate
399 stock-recruitment dynamics across taxa, such as in Scorpaeniformes (Dorn 2002, Forrest et al.
400 2010), as few studies have used models that allow for variation in the degree of compensation. It
401 is clear from their low values of δ that these orders have similar forms of intraspecific
402 competition that are distinctly on the contest side of the contest-scramble gradient. Overall, our
403 δ parameter results suggest that even though the degree of compensation varies widely across
404 taxa, much of that variation among fish species may be predicted taxonomically as a function of
405 evolved life history traits and reproductive behaviors.

406 Our results demonstrated that the α parameter of the Shepherd model differs greatly
407 among fish orders (Fig. 3). Because α is a standardized reproductive output of individuals at low
408 population levels without density-dependent effects (i.e., maximum lifetime spawners per
409 spawner), we expected that orders with greater fecundity and higher per-capita spawning
410 biomass would have greater α values (Andersen et al. 2008). Many of the species of the orders
411 Clupeiformes, Gadiformes, and Perciformes do indeed have high fecundity, while the
412 Salmoniformes are generally much less fecund (Mertz and Myers 1996). The fecundity values
413 for the orders Pleuronectiformes and Scorpaeniformes are much less consistent, but fish
414 belonging to those orders do generally have higher fecundities than members of the
415 Salmoniformes. As fecundity is only one part of the recruitment process, other factors that affect
416 survival of juveniles, such as predation or habitat quality, could greatly affect reproductive

417 output at low densities (Karatayev et al. 2015). Large, late-maturing fish have been associated
418 with relatively higher fecundities, small eggs, and few reproductive bouts per season (Winemiller
419 and Rose 1992). Specifically, Scorpaeniformes tend to have small eggs and low maximum
420 replacement rates (Winemiller and Rose 1992, Myers et al. 1999), which would indicate a low α
421 parameter value. Our results suggest that there are distinct differences in α , among fish orders,
422 which appear to follow similar differences in fecundity and life history.

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

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

439 A key strength of the hierarchical modeling approach is that it can leverage population-
440 level variation in reproductive rate and the strength of compensation (whether that variation
441 manifests from reaction norms or from genotypic variation) to yield species-level and order-level
442 insights relevant for management. Often, recruitment models are selected based on convention,
443 model selection techniques, or by prior usage in related species. These decisions are based on
444 biological considerations at some level, but in cases where data are poor or limited, it can be
445 difficult to determine which model is most appropriate for a particular species. There is no
446 standard approach for choosing a stock-recruitment model for a particular fish species, whether

447 large amounts of data exist or not. Our modeling approach provides insight into the most
448 appropriate density dependent models for a number of species.

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

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662 **Appendices**

663 Appendices A-E are available online in the Ecological Archives

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687 **Figure Legends**

688 **Figure 1** – Examples of the Shepherd model for fixed α and β parameters ($\alpha = 2.5$, $\beta = 0.01$),
689 where δ , which regulates the degree of compensation, is varied from 0 to 10. Curve shapes range
690 from linear ($\delta=0$), to compensatory ($0 < \delta \leq 1$), to overcompensatory ($\delta > 1$).

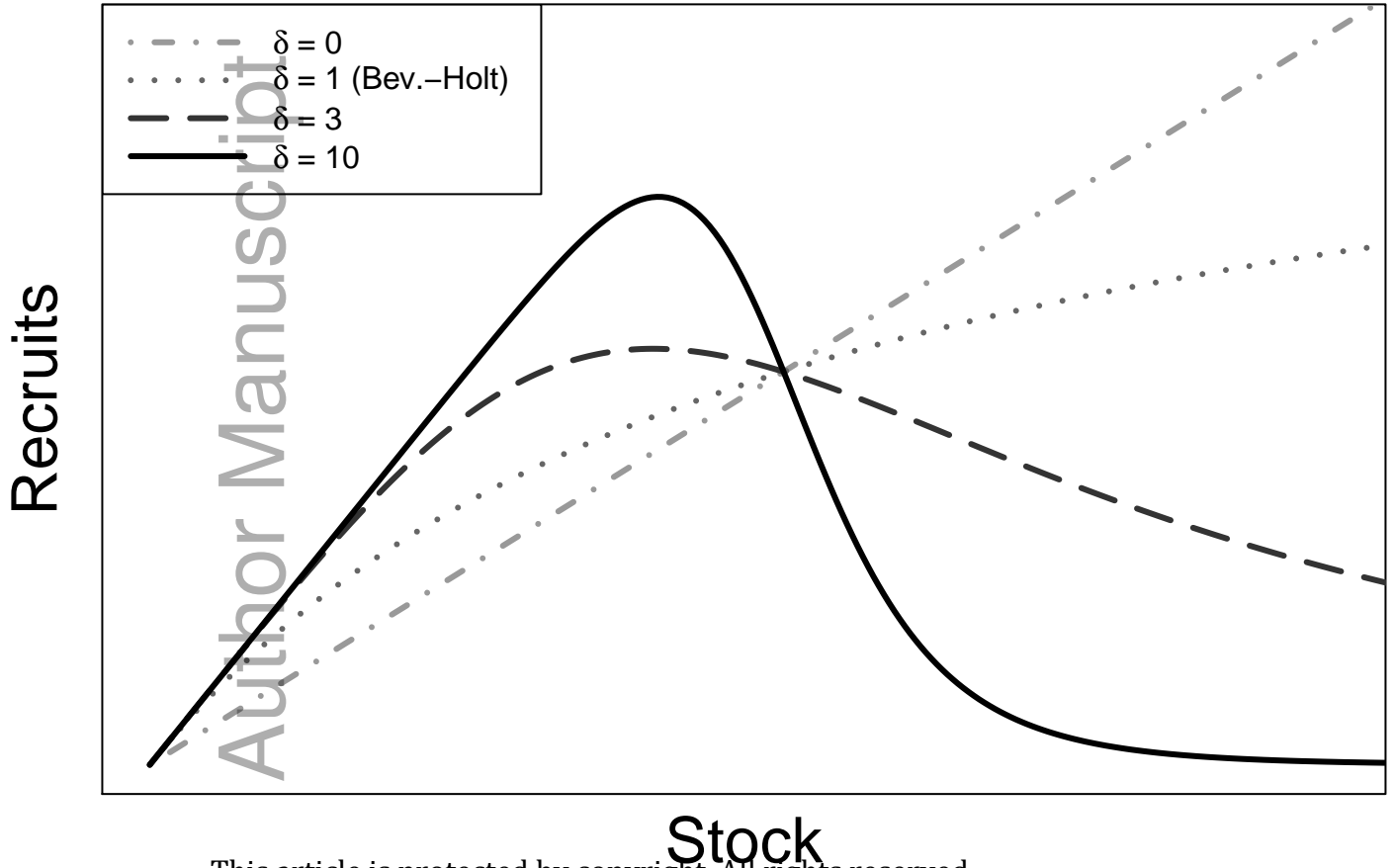
691 **Figure 2** – Order-level stock recruitment curves showing intraspecific competition ranging from
692 contest/compensatory competition (top panels) to scramble/overcompensatory competition
693 (bottom panels). On the left, median order-level stock-recruitment relationships (black lines) are
694 shown with 50% credible intervals (grey shading), as estimated using the Shepherd model.
695 Dotted lines indicate the 1:1 line of stock and recruits. Axes vary in size between orders to
696 facilitate comparisons among functional forms rather than carrying capacity. Values of β for
697 each were determined by averaging median β values across all populations of a species and all
698 species of an order. Stock and Recruit units are not given, as population sizes vary greatly

699 within orders. On the right, the 95% (thin lines) and 50% (thick lines) credible intervals for
700 order level δ (intensity of compensation) values. Median values are represented by open circles.
701 The dashed line at $\delta = 1$ indicates where the Shepherd model is equivalent to the Beverton-Holt
702 Model.

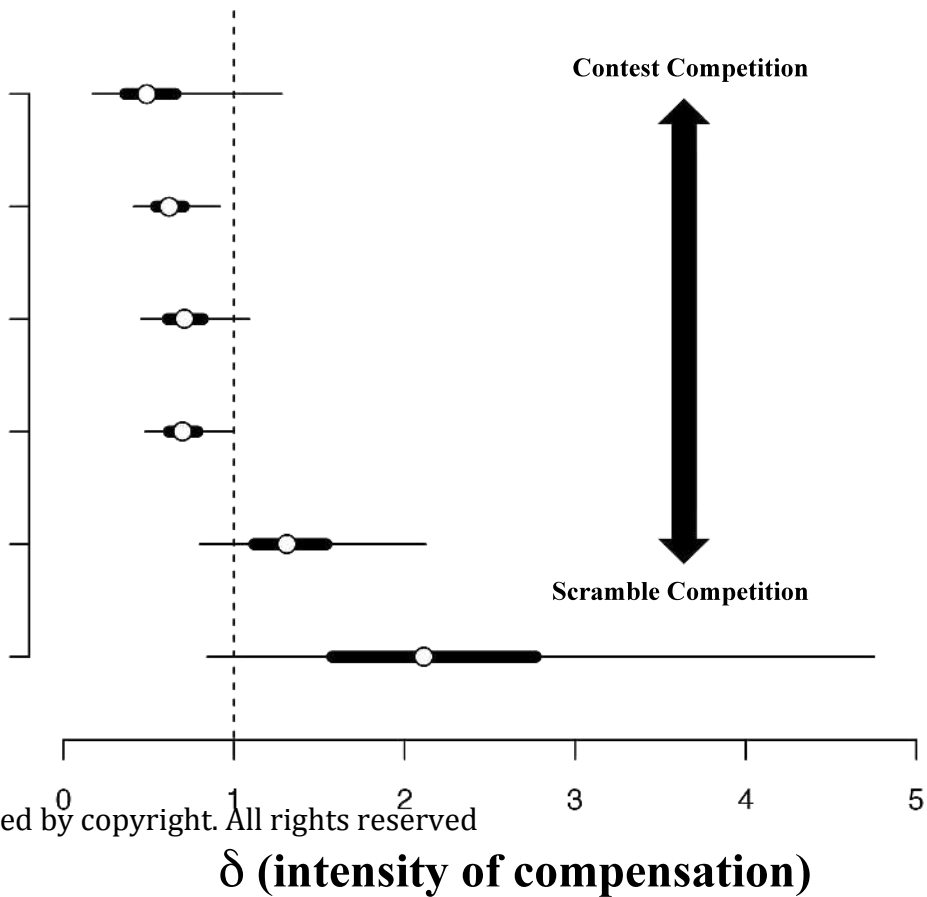
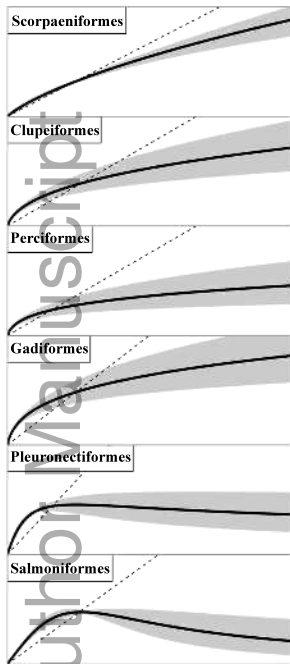
703 **Figure 3** – The 95% (thin lines) and 50% (thick lines) credible intervals for order-level α (per
704 capita recruitment at low densities) values. Median values are represented by open circles.

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

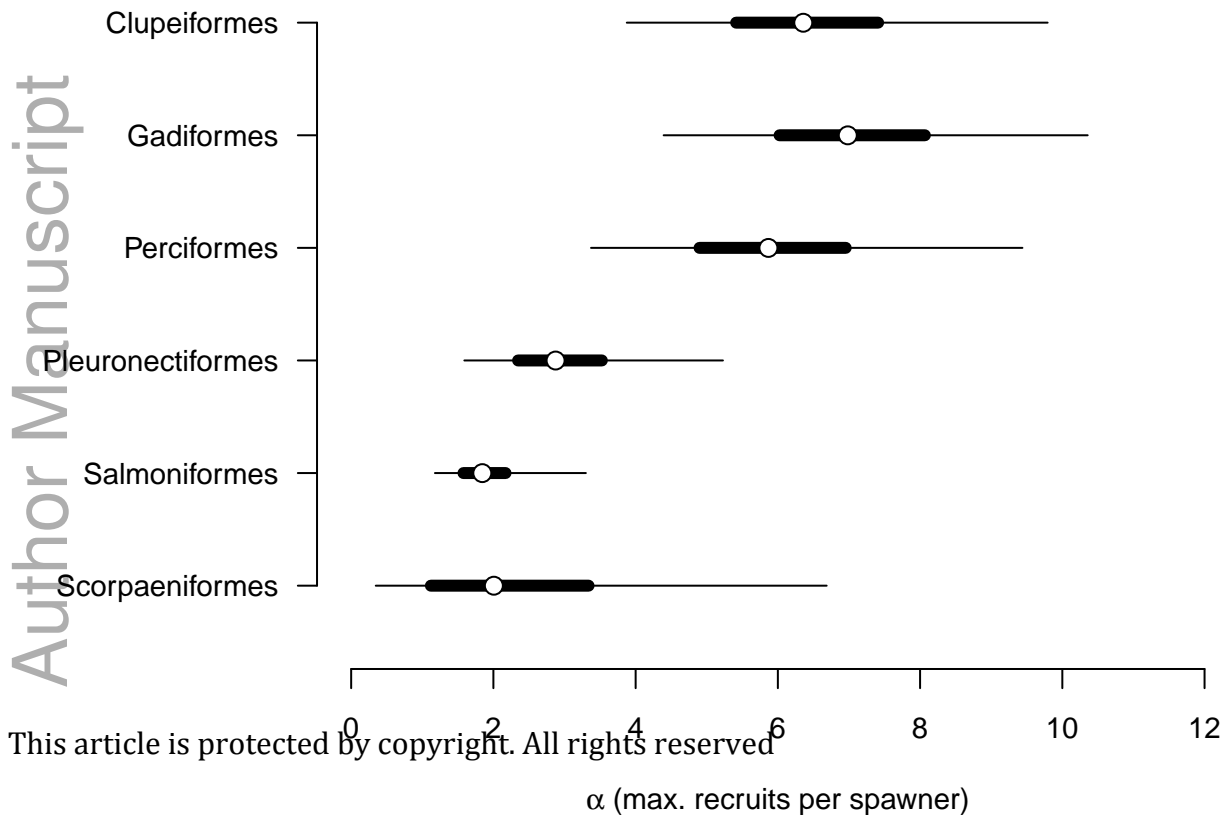
710 **Figure 5** – Median α plotted against median δ for all 54 fish species included in our model.
711 Species are grouped into symbols based on taxonomic order. The dashed line at $\delta = 1$ indicates
712 pure contest competition. Values above the line indicate scramble competition. Values below
713 the line indicate weak intraspecific competition.



Recruits



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α (max. recruits per spawner)

