Predicting recruitment density dependence and intrinsic growth rate for all fishes worldwide using a data-integrated life-history model

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Complete List of Authors:	Thorson, James; Alaska Fisheries Science Center, Habitat and Ecosystem Process Research Program
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Abstract:	Fisheries managers and scientists use biological models to determine sustainable fishing rates, understand environmental responses, and forecast future dynamics. These models typically require both life-history parameters (mortality, maturity, growth, and size) and stock-recruit parameters (production of juveniles). However, there has been surprisingly little research to simultaneously predict life-history and stock-recruit parameters. I therefore develop the first "data-integrated life-history model," which modifies the recent FishLife model to fit a simple model of evolutionary dynamics to field-measurements of life-history parameters as well as historical estimates of spawning output and subsequent recruitment. This evolutionary model predicts recruitment productivity ("steepness") and variability (variance and autocorrelation in recruitment deviations) as well as mortality, maturity, growth, and size, and uses these to predict intrinsic growth rate (r) for all described fishes. The model confirms previous analysis showing little correlation between recruitment productivity ("steepness") and either natural mortality or asymptotic maximum size (W_∞). However, it does reveal strong taxonomic patterns, where family Sebastidae has lower steepness (mean=0.63, SD=0.18) and Lutjanidae has elevated steepness (mean=0.77, SD=0.16) relative to the prediction for bony fishes (class Actinopterygii, mean=0.69, SD=0.22). Similarly, genus Sebastes has growth rate r (0.07) similar to several shark families (Lamniformes: 0.07; Carcharhiniformes: 0.10). Predictions are tighter for species than for higher-level organizations (e.g., families), and predictions (including multivariate confidence intervals) are available for >32,000 described fishes worldwide in R package FishLife. I conclude by outlining how multivariate predictions of life-history and stock-recruit parameters could be useful for stock-assessment, decision theory, ensemble modelling, and strategic management.

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6   James Thorson

7

8   Habitat and Ecosystem Process Research program, Alaska Fisheries Science Center, National

9   Marine Fisheries Service, NOAA, Seattle, WA, USA

10

11   Previously at: Fisheries Resource Assessment and Monitoring Division, Northwest Fisheries

12   Science Center, National Marine Fisheries Service, NOAA, Seattle, WA, USA

13

14   James.Thorson@noaa.gov

15

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19 **Outline**

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1. Abstract

Fisheries managers and scientists use biological models to determine sustainable fishing rates, understand environmental responses, and forecast future dynamics. These models typically require both life-history parameters (mortality, maturity, growth, and size) and stock-recruit parameters (production of juveniles). However, there has been surprisingly little research to simultaneously predict life-history and stock-recruit parameters. I therefore develop the first "data-integrated life-history model," which modifies the recent *FishLife* model to fit a simple model of evolutionary dynamics to field-measurements of life-history parameters as well as historical estimates of spawning output and subsequent recruitment. This evolutionary model predicts recruitment productivity ("steepness") and variability (variance and autocorrelation in recruitment deviations) as well as mortality, maturity, growth, and size, and uses these to predict intrinsic growth rate (r) for all described fishes. The model confirms previous analysis showing little correlation between recruitment productivity ("steepness") and either natural mortality or asymptotic maximum size (W_∞). However, it does reveal strong taxonomic patterns, where family Sebastidae has lower steepness (mean $= 0.63$, $SD = 0.18$) and Lutjanidae has elevated steepness (mean $= 0.77$, $SD = 0.16$) relative to the prediction for bony fishes (class Actinopterygii, mean $= 0.69$, $SD = 0.22$). Similarly, genus Sebastes has growth rate r (0.07) similar to several shark families (Lamniformes: 0.07; Carcharhiniformes: 0.10). Predictions are tighter for species than for higher-level organizations (e.g., families), and predictions (including multivariate confidence intervals) are available for >32,000 described fishes worldwide in R package *FishLife*. I conclude by outlining how multivariate predictions of life-history and stock-recruit parameters could be useful for stock-assessment, decision theory, ensemble modelling, and strategic management.

2. Introduction

Fisheries managers worldwide seek to regulate fishing industries based on biological determination of maximum sustainable yield.   Maximum sustainable yield is generally identified by fitting a population-dynamics model to data obtained from a given population. Population-dynamics models are a simplified representation of basic biological processes including natural mortality, individual growth, sexual maturation, and production of juveniles (termed "recruitment"). These processes are typically represented using a small set of population-dynamics parameters, and identifying plausible values for these parameters is a central task for theoretical and applied ecologists for the management of both poor- and well-studied species.

Unfortunately, available data are often insufficient to determine the rate of important biological processes for a given stock. Parameters representing size and growth are often unknown for low-value species, where resources have not been dedicated to collect the age and size of representative individuals. Similarly, sexual maturity requires field sampling of ovaries, and natural mortality rates are estimated from some combination of tag-capture data and by treating the history of a fishery as a depletion experiment. In the following, I refer to adult mortality, growth, and sexual maturity rates as "life-history parameters," and there is an extensive literature regarding the expected relationship among life-history parameters in fishes (Roff 1984; Winemiller 1989; Charnov and Berrigan 1990; Beverton 1992). Recent research has sought to integrate life-history and evolutionary theory to predict life-history parameters for all fishes worldwide while distributing results in a public, reproducible, and well-documented manner (e.g., Froese *et al.* 2014). For example, *FishLife* is an R package that distributes predictions of adult life-history parameters for all fishes while combining information from taxonomic relatedness and fish records worldwide, and while estimating the degree of

77   uncertainty from the quantity and quality of records for a given taxon and its relatives (Thorson

78   *et al.* 2017). Improved documentation and access to these meta-analytic results can presumably

79   improve fisheries management for species that currently have little direct biological information.

80   Despite progress in predicting adult life-history parameters for fishes, these parameters

81   are insufficient to predict population dynamics. In fact, fisheries scientists have recognized for

82   nearly 100 years that fish populations are often composed of a single or few small cohorts (Hjort

83   1926), and that fluctuations in population size are largely driven by the production of juveniles.

84   Recruitment is typically predicted as a function of spawning output, and parameters governing

85   the expected relationship between spawning output and recruitment are rarely included in

86   classical life-history theory. Instead, stock-recruit parameters have historically been predicted

87   using meta-analyses (e.g., Myers 2001) applied to a database of spawning biomass and

88   subsequent recruitment (termed "stock-recruit data") or via ecological theories of marine

89   community structure (Andersen and Beyer 2006). The stock-recruit relationship has received a

90   great deal of research attention over the past thirty years both using theoretical arguments

91   (Charnov *et al.* 1991; Neill *et al.* 1994; Iles and Beverton 1998; Mangel *et al.* 2010) and

92   empirical methods (Rose *et al.* 2001; Minto *et al.* 2008; Thorson *et al.* 2014; Foss-Grant *et al.*

93   2016; Britten *et al.* 2016) to predict variation in stock-recruit parameters. However, there have

94   been surprisingly few empirical studies that simultaneously analyze variation in stock-recruit and

95   adult life-history parameters.

96   Ecologists increasing use models combining data from multiple collection protocols

97   (termed "integrated models") to estimate ecological parameters. These integrated models are

98   useful to estimate processes that are not identifiable using one data set in isolation and are

99   common, e.g., when estimating population-dynamics for assessing stock status (Maunder and

100   Punt 2013), when estimating growth from tagging and length sampling data (Eveson *et al.* 2004),

101   or when estimating population density using encounter and count data (Zipkin *et al.* 2017).

102   However, data-integrated modelling has not to my knowledge been used in life-history analysis

103   (which typically analyzes databases of field-measurements of population rates) or stock-recruit

104   analysis (which typically analyzes stock-recruit data while assuming that population-dynamics

105   parameters are known and fixed exogenously). Combining these two analyses is sufficient to

106   describe adult fish dynamics (e.g., spawning biomass per recruit without fishing) and recruit

107   dynamics (e.g., recruits per spawning biomass) and therefore is sufficient to describe the entire

108   life-cycle under alternative scenarios regarding fishing effort and selectivity (e.g., Thorson *et al.*

109   2015b).

110   In this study, I develop the first data-integrated model for life-history analysis and

111   demonstrate this approach by combining data from life-history and stock-recruit databases. By

112   combining life-history and stock-recruit information, I am able to generate predictions of life-

113   cycle dynamics for all described fishes. I specifically modify the evolutionary model used by

114   *FishLife* to fit both adult life-history parameters as well as stock-recruit measurements for over

115   150 fish populations worldwide, and use this integrated model for population-dynamics

116   parameters to estimate the strength of recruitment compensation for all fishes. I then use these

117   predictions to generate a full life-cycle model and estimate the intrinsic growth rate *r* for all

118   fishes. This parameter is widely used in theoretical and applied studies, e.g., as one of two key

119   parameters in the surplus production models that are taught in introductory fisheries science

120   classes (Haddon 2010). In the discussion, I compare resulting estimates with previous studies to

121   evaluate plausibility of model results. Finally, I distribute predictions of recruitment density

122   dependence and intrinsic growth rate (and associated uncertainty) as a fully documented,

123 publicly available R package *FishLife* release 2.0.0, so that future users can generate multivariate

124 predictions of life-history and stock-recruit parameters for any described fish species.

3. Methods

126 I seek to predict stock-recruit parameters (the strength of recruitment compensation and the

127 variance and autocorrelation in recruitment variation) and use results to describe life-cycle

128 dynamics (i.e., intrinsic growth rate) for all fishes worldwide. To do so, I integrate two previous

129 meta-analytic models:

130 1. An evolutionary model of life-history parameters (Thorson *et al.* 2017) fitted to field-

131   measurements of size, growth, mortality, and maturity for thousands of species worldwide as

132   compiled by FishBase (Froese 1990);

133 2. A hierarchical model for stock-recruit parameters (Thorson *et al.* 2014) fitted to stock and

134   recruitment measurements from the original RAM database (Myers *et al.* 1995).

135 By fitting an evolutionary model to both data sets simultaneously, I am able to characterize

136 uncertainty arising from estimates of individual life-history parameters as well as stock-recruit

137 processes. I then distribute results using an R package *FishLife* release 2.0.0.

138   For this analysis, I draw heavily upon previous advice regarding good-practices in

139 fisheries meta-analysis (Thorson *et al.* 2015a). Specifically, I address both experimental

140 variability, e.g., errors in field-measurements of life-history parameters, and parametric

141 variability, e.g., differences in larval and adult survival rates (defined by Osenberg *et al.* 1999).

142 To account for both types of variability, I apply a hierarchical model that explicitly estimates the

143 variance of measurement vs. process errors (Thorson and Minto 2015). Hierarchical models

144 automatically implement "shrinkage," i.e., the tendency for parameter estimates for each species

145 to be shrunk towards both (1) the average of available data and (2) the prediction given other

146   model components (Gelman and Hill 2007). Shrinkage permits parameter estimates even for

147   species with no field-records. Shrinkage will also bias estimates for a given taxon towards

148   estimates for related species, but theory suggests that it will minimize expected errors even in

149   cases when some species are mis-categorized or otherwise greatly different from other taxa

150   (Efron and Morris 1977).

3.1 Evolutionary model for life-history parameters

152   I first summarize *FishLife* (Thorson *et al.* 2017), an evolutionary model for size, growth,

153   mortality, and maturity parameters for all fishes worldwide. This model adapts the coalescent

154   model for molecular evolution (Felsenstein 1973) to predict a vector $\mathbf{x}_g$ of life-history values $x_{g,j}$

155   for taxon g and parameter j (of G and J modeled taxa and parameters).

156   Life-history parameters $\mathbf{x}_g$ evolve along a phylogenetic lineage following a multivariate

157   random walk:

$$\mathbf{x}_g \sim MVN(\mathbf{x}_{p(g)}, \mathbf{\Sigma}_{l(g)}) \tag{1}$$

158   where $p(g)$ is the taxonomic "parent" of taxon g (e.g., if $\mathbf{x}_g$ is the average life-history values for

159   for genus Sebastes, then $\mathbf{x}_{p(g)}$ is the average values for family Sebastidae). $\mathbf{\Sigma}_{l(g)}$ is the

160   evolutionary covariance among life-history parameters:

$$\mathbf{\Sigma}_{l(g)} = \lambda_{l(g)}(\mathbf{L}_\Sigma \mathbf{L}_\Sigma^T + \mathbf{D}) \tag{2}$$

161   where $\mathbf{L}_\Sigma$ is a lower-diagonal matrix that approximates covariance among parameters, $\mathbf{D}$ is a

162   diagonal matrix representing additional variance for the evolution of each trait, and $l(g)$

163   represents the taxonomic level of taxon g (e.g., Class, Order, Family, Genus, or Species) such

164   that $\lambda_{l(g)}$ represents the proportion of evolutionary covariance occurring at taxonomic level $l(g)$.

165   This specification is completed by specifying the mean traits for the top of the fish taxonomy

166   (phylum Chordata) as fixed effects with expected value $\mathbf{\mu}_x$. The evolutionary covariance from

167   phylum Chordata to any fish species can be calculated as $\mathbf{\Sigma} = \sum_{l=1}^{5}\mathbf{\Sigma}_l$. This model approximates

168   many different evolutionary mechanisms, e.g., by assuming that evolution rates of life-history

169   and stock-recruit parameters are identical for all evolutionary lineages despite likely differences

170   in evolutionary mechanisms and effective population size, and future research could expand the

171   model by incorporating additional information regarding evolutionary rates and divergence times

172   within the fish taxonomic tree.

173   The association of one trait (e.g., natural mortality M) and another trait (e.g., asymptotic

174   mass W_∞) can be interpreted using major axis regression (Warton *et al.* 2006). Major axis

175   regression (MAR) involves calculating the eigen-decomposition of evolutionary covariance $\mathbf{\Sigma}$,

176   and the ratio of elements in a given eigen-vector is interpreted as the regression "slope" between

177   two variables. MAR is useful given that the slope does not require defining which variable is

178   "dependent" or "independent", and an estimated slope of β can be interpreted as "a 1% change in

179   variable X_1 is associated with a β% change in variable X_2" whenever both variables have been

180   log-transformed prior to analysis (see Thorson *et al.* 2017 for an example). By contrast,

181   conventional linear modelling (e.g., a regression of natural mortality M on growth coefficient K)

182   requires specifying a dependent and independent variable, and estimates of the slope will depend

183   upon that choice.

184   The evolutionary model in *FishLife* is completed by specifying a distribution for life-

185   history measurements $\tilde{\mathbf{y}}_i$ for study i:

$$\tilde{\mathbf{y}}_i \sim MVN(\mathbf{x}_{g(i)}, \mathbf{V}) \tag{3}$$

186   where $g(i)$ is the taxon for study i, such that $\mathbf{x}_{g(i)}$ is the expected value for each field-

187   measurement for that study, and $\mathbf{V}$ represents covariance among studies for a given taxon

188   (resulting from a combination of field-measurement errors and biological variation among stocks

189   for a given species, years for a given stock, etc). However, most studies do not measure all life-

190   history parameters simultaneously, so I use a "missing-data" model under the assumption that

191   data are missing at random:

$$\tilde{\mathbf{y}}_i = \begin{cases} \varepsilon_{i,j} & \text{if } y_{i,j} \text{ was not measured by study } i \\ y_{i,j} & \text{if } y_{i,j} \text{ was measured by study } i \end{cases} \quad (4)$$

192   where $\varepsilon_{i,j}$ is assigned a uniform prior distribution, $\varepsilon_{i,j} \sim Uniform(LB,UB)$ (where the lower

193   bound LB and upper bound UB are chosen such that further changes in their values have no

194   effect on model results).

195   This model was previously fitted to seven life history parameters and average

196   environmental temperature (which I collectively call "life-history parameters"; Table 1), where

197   all were log-transformed prior to analysis (except for average temperature $Temp$). Results from

198   Thorson et al. (2017) showed:

199   1. Well-known life-history patterns, e.g., a positive association between observed values for

200   growth coefficient (K) and natural mortality rate (M) and the close-to-isometric relationship

201   between asymptotic length (L_∞) and asymptotic mass (W_∞).

202   2. Major axes of evolution in life-history parameters, wherein the first axis is associated with

203   temperature, the second with body size, and the third represents a nonlinear relationship

204   between mortality rate and growth coefficient (M/K) and the timing of maturation (L_{mat}/L_∞

205   ).

206   3. Useful predictions of uncertainty for both well- and poorly-studied species, where predicted

207   life-history parameters for individual species are more precise (smaller predictive intervals)

208   than predictions for higher-level taxa.

209   However, that analysis could not predict population dynamics because it did not include

210   parameters governing recruitment.

211   **3.2 Hierarchical model for stock-recruit parameters**

212   I next extend the existing FishLife model to fit to estimates of spawning stock size $S_{i,t}$ and

213   subsequent recruitment $R_{i,t}$ for stock-recruit study i and spawning biomass in year t. In the

214   following, I use notation from Thorson et al. (2014), but modify this model by (1) embedding it

215   within the evolutionary model for life-history parameters, and (2) defining a hyper-distribution

216   for maximum recruits per spawning biomass for each stock. I note that the original RAM

217   database records the age-at-recruitment for each stock i, and I align data such that $\hat{R}_{i,t}$ is the

218   record of recruitment arising from spawning that occurs given spawning biomass $S_{i,t}$.

219   I specify a Beverton-Holt model for expected recruitment $\hat{R}_{i,t}$ for study i in year t:

$$\hat{R}_{i,t} = \frac{\alpha_i S_{i,t}}{1 + S_{i,t}/\beta_i} \tag{5}$$

220   where α_i is maximum recruits per spawning biomass for stock i and β_i represents the density-

221   dependent decrease in recruits per spawning biomass with increasing $S_{i,t}$. I then specify a

222   distribution for process errors around this assumed relationship:

$$\log(R_{i,t}) = \begin{cases} \log(\hat{R}_{i,t}) + \rho_i\big(\log(R_{i,t-1}) - \log(\hat{R}_{i,t-1})\big) + \delta_{i,t} & \text{if } t > 1 \\ \log(\hat{R}_{i,t}) + \delta_{i,t} & \text{if } t = 1 \end{cases} \tag{6}$$

223   where ρ_i is the first-order autocorrelation coefficient for study i and residual errors are normally

224   distributed, $\delta_{i,t} \sim N(0, \tau_i^2)$, where τ_i^2 is the conditional variance for recruitment deviations. This

225   model involves estimating four parameters for every study i: α_i, β_i, τ_i^2, and ρ_i.

226   I apply a hierarchical model that shrinks α_i, τ_i^2, and ρ_i towards expected values for a

227   given taxon. I assume that carrying capacity varies greatly among species (e.g., because

228   spawning biomass and recruits are expressed in different units among different studies, or

229   mechanisms differ among species), so I treat β_i as a fixed effect for every study i such that it is

230   not shrunk towards a common value. By contrast, I specify a hierarchical model for maximum

231   recruits per spawning biomass α_i, which varies among taxa but is shrunk towards a predicted

232   value in the following way. First, I use the observation that maximum annual spawners per

233   spawner is less variable than other measures of density dependence (Myers *et al.* 1999). I

234   therefore define maximum annual spawners per spawner in excess of replacement r_i for each

235   study i:

$$p_i = 1 + \frac{r_i}{1 - \exp\left(-M_i^*\right)} \tag{7}$$

236   where p_i is maximum lifetime spawners per spawner and $\exp\left(-M_i^*\right)$ is the annual survival

237   fraction given adult natural mortality rate M_i^*. The $p_i = 1 + ...$ in the right-hand-side of Eq. 7

238   ensures that $p_i > 1$ for all values of $\log\left(r_i\right)$, which is a necessary condition for persistence of the

239   population in the absence of fishing, such that r_i is defined as maximum annual spawners per

240   spawner *in excess of replacement*. Converting between r_i and α_i is made possible by the

241   observation that maximum annual recruits per spawning biomass (α_i) times lifetime spawning

242   biomass per recruit in the absence of fishing ($SPR_{F=0}$) must equal maximum lifetime spawners

243   per spawner (p_i) (Myers and Mertz 1998), such that $\alpha_i = p_i / SPR_{F=0}^*$ In summary, I predict r_i,

244   convert r_i to p_i (Eq. 7) and then convert p_i to α_i, where α_i and β_i are used to predict recruitment

245    $\hat{R}_{i,t}$ for the levels of spawning biomass $S_{i,t}$ that have been observed for each population. In this

246   analysis, I use values $SPR_{F=0}^*$ and M_i^* compiled by Ram Myers in the original stock-recruit

247   database.

248   Given this model, I then define the variables used in the evolutionary model as the set of

249   life-history parameters that are comparable across different fish species worldwide (see Table 1

250   for list).

$$\mathbf{x}_g \equiv \{\log(M_g), \log(A_{max,g}), \log(K_g), \log(L_{\infty,g}), \log(W_{\infty,g}), \qquad (8)$$

$$\log(A_{mat,g}), \log(L_{mat,g}), T_i, \log(\tau_g), \log(\rho_{R,g}), \log(r_g)\}$$

251 where the vector of life-history parameters $\mathbf{x}_g$ includes r_g such that maximum annual spawners

252 per spawner in excess of replacement is shrunk towards a value that is correlated both

253 taxonomically and with other life-history parameters.

254   Given predicted values for life-history parameters $\mathbf{x}_g$ for each taxon g, I calculate derived

255 quantities that are useful for other models or management purposes:

256 1. *Intrinsic growth rate*: Many theoretical and applied studies in ecology have used the intrinsic

257   growth rate (r) as an integrated measure of population resilience (Levins 1969). This growth

258   rate is also one of two parameters in the Schaeffer surplus production model, which is the

259   first model that many students learn in introductory fisheries science (Haddon 2010). I

260   calculate r as the dominant eigenvalue for a Leslie matrix representing population growth in

261   numbers and reproductive output, and it represents the instantaneous rate of population

262   growth at asymptotically low population sizes; it is identical if expressed as growth rate in

263   numbers or biomass (McAllister *et al.* 2001). The calculation requires the parameters

264   predicted by FishLife (Table 1), as well as several that are not available including: the

265   allometric scaling of asymptotic biomass and length (fixed at 3.04 based on the average from

266   Froese et al. (2014)), the extrapolated age at zero length in the von Bertalanffy growth curve

267   (fixed at -0.1), and the slope of the maturity ogive at 50% maturity (fixed at 25% of age-at-

268   maturity). I recommend future research to incorporate these parameters into FishLife,

269   although sensitivity analysis suggested that results are relatively insensitive to small changes

270   in these values.

271   2. *Steepness*: Many stock assessment models use the steepness parameterization of the

272   Beverton-Holt stock-recruit model (Mace 1994)

$$h_g = \frac{p_g}{4 + p_g} \tag{9}$$

273   where this calculation is derived e.g. by Myers and Mertz (1998) and has been re-derived

274   with small differences elsewhere (Mangel *et al.* 2010 Eq. 26).

275   3. *Standard deviation for recruitment*: the marginal (pointwise) standard deviation of

276   recruitment is calculated as:

$$\sigma_g = \sqrt{\tau_g^2/(1 - \rho_g^2)} \tag{10}$$

277   where this standard deviation (and its standard error) can be used, e.g., when fitting an age-

278   structured surplus production model in data-poor assessments (Thorson *et al.* In press).

279   I calculate these derived quantities for each taxon g, append them to the vector of estimated

280   parameters, $\tilde{\mathbf{x}}_g = (\mathbf{x}_g, \sigma_g^2, h_g, \varphi_g)$, and calculate the expectation and covariance of $\tilde{\mathbf{x}}_g$ using Monte

281   Carlo sampling.

282   **3.3 Parameter estimation**

283   I estimate parameters for this evolutionary model of life-history and stock-recruit parameters

284   given life-history measurements $y_{i,j}$ in FishBase (Froese 1990) as downloaded using *rfishbase*

285   (Boettiger *et al.* 2015) on Aug. 25, 2016, and stock-recruit data $R_{i,t}$ and $S_{i,t}$ from the Myers

286   stock-recruit database (Myers and Mertz 1998). Parameters are estimated using maximum

287   marginal likelihood as implemented using Template Model Builder (Kristensen *et al.* 2016),

288   while using the Laplace approximation (Skaug and Fournier 2006) to integrate the joint

289   likelihood of data and random effects with respect to random effects $\mathbf{x}_g$ for all taxa. Further

290   details are available in Appendix S1: Computational details. I then distribute results as a

291   publicly available R package *FishLife* version 2.0.0 (URL will be provided upon acceptance). I

292   specifically provide predicted values $\hat{\mathbf{x}}_g$ for every described fish species, as well as the predictive

293   covariance $\widehat{\text{Cov}}(\hat{\mathbf{x}}_g)$ as calculated using a generalization of the delta-method (Kass and Steffey

294   1989).

4. Results

296   I first illustrate the predictive intervals for life-history and recruitment parameters for three

297   commercially important species, *Sebastes pinniger, Thunnus albacares,* and *Salmo trutta* and the

298   taxonomic family for each species (Fig. 1). As expected, predictions for each individual species

299   are much more precise (have smaller confidence interval width) than predictions for a given

300   family, and predictions for species generally fall within the 95% confidence interval for a given

301   family.

302   I next present the relationship between parameters using major axis regression (Table 2).

303   This show that the model fitted to life-history and stock-recruit records preserves the life-history

304   relationships documented by Thorson et al. (2017), e.g., the nonlinear relationship between the

305   ratio of mortality and growth rates (M/K) and the timing of maturation (L_{mat}/L_{inf}). However,

306   FishLife also now fits stock-recruit records, and there is no evidence that the model fits these

307   data poorly (Appendix 2, Suppl. Fig. S1). By fitting to both data sets simultaneously, FishLife is

308   able to estimate the relationship between stock-recruit and life-history parameters. The 1st axis

309   (temperature) indicates that a 1°C increase in temperature is associated with a 0.01 increase in

310   steepness on average and a 1% decrease in the standard deviation of recruitment. Similarly, the

311   2nd axis (body size) indicates that a 10% increase in asymptotic body size (W_∞) is associated

312   with a 0.4% ($\frac{0.039}{0.833} = 0.04$) increase in recruitment autocorrelation (ρ_R), but has an essentially

313   negligible effect on steepness. Finally, the 3rd axis (timing of maturation) shows that a 10%

314   increase in the ratio of mortality and growth (and resulting decrease in $\frac{L_{mat}}{L_\infty}$) is associated with a

315   6% decrease in recruitment variation ($\frac{-0.076}{0.472 - 0.346} = -0.60$). In summary, steepness has a weak-

316   to-nonexistent relationship with body size and timing of maturity, and recruitment

317   autocorrelation (ρ_R) has a positive association with age-at-maturity (A_{mat}) via axes representing

318   increased body size and the timing of maturation.

319   I next visualize the predictive relationships between steepness (h) or intrinsic growth rate

320   (r) and both natural mortality and asymptotic mass (Fig. 2). This shows that steepness has a

321   weakly positive relationship with natural mortality (Fig. 2, 1st column), and a weakly negative

322   relationship with asymptotic mass (Fig. 2, 2nd column), resulting from the net effect of

323   temperature, body size, and timing of maturation patterns. Although steepness does not have a

324   strong association with either mortality or body size, there does appear to be some taxonomic

325   clustering in both natural mortality and steepness values. For example, Sebastidae generally has

326   lower values for natural mortality and steepness while Scombridae has elevated values of natural

327   mortality and steepness. By contrast, intrinsic growth rate has a strong positive relationship with

328   natural mortality (Fig. 2, 3rd column) and a strong negative relationship with asymptotic body

329   size (Fig. 2, 4th column). Again, there is strong taxonomic clustering along this axis of variation,

330   where Sebastidae has relatively low natural mortality and intrinsic growth rate, and is somewhat

331   of an outlier in having a asymptotic body size in the middle range of predicted values. Finally,

332   there is also some taxonomic signal in recruitment variance and autocorrelation (Appendix 2,

333   Suppl. Fig. S2), where Sebastidae has somewhat higher recruitment variation than other taxa.

334   Exploring these taxonomic patterns for steepness in detail (Fig. 3, left column), I confirm

335   that the mean of the predictive distribution for Sebastidae is 0.63 while the mean for Lutjanidae

336   is 0.77, and Salmonidae (0.74) and Scombridae (0.69) are intermediate. By contrast, intrinsic

337   growth rate for Sebastidae is on the low-end (0.11) and genus Sebastes is particularly low (0.07);

338   these values are near those for several Chondrythian families (Carcharhiniformes: 0.10;

339   Lamniformes: 0.07). Meanwhile, Scombridae has a relatively high intrinsic growth rate among

340   the fish families explored here (0.45) and Lutjanidae (0.40) and Salmonidae (0.36) are

341   intermediate.

5. Discussion

343   In this study, I have developed the first integrated life-history model for population-

344   dynamics parameters in fishes, which simultaneously fits to public life-history and stock-recruit

345   databases. The analysis specifically builds upon a simple model for evolution along

346   phylogenetic lineages to reconcile both data sets, and results can be used to predict parameters

347   for species that otherwise have no known information (Thorson *et al.* 2017). Unlike past life-

348   history studies, this model estimates the uncertainty for each parameter (including the correlation

349   between parameters) in a logical way, e.g., where species with many life-history records are

350   more precise than those with few or no records, where species are shrunk towards related species

351   that are well-studied, and where uncertainty is greater for poorly studied species that have few

352   well-studied relatives than those with many well-studied relatives.

353   This analysis shows that the strength of recruitment compensation ("steepness") is not

354   strongly correlated with the major axes of life-history variation in fishes (temperature, body size,

355   or timing of maturation), but does cluster taxonomically (e.g., with lower steepness for family

356   Sebastidae and higher for Scombridae). By contrast, intrinsic growth rate has strong correlations

357   with body size, as expected given the dependence of intrinsic growth rate upon natural mortality

358   rates. By using a simple evolutionary model, I am able to predict a unique value for life-history

359   parameters for every species in either data set, as well as all higher-level taxonomic groups of

360 those species. This contrasts with previous attempts to estimate steepness and intrinsic growth

361 rate, which have typically estimated a single, average value for these quantities for all species

362 (e.g., Jensen *et al.* 2012) or within a given taxonomic grouping (Shertzer and Conn 2012).

363 I evaluate results by comparing predictions of steepness for higher-level taxa (e.g., for a

364 given genus, family, or order) with those from previous studies to look for differences with

365 previously-published studies (see Table 3). For example, the mode of the predictive distribution

366 of steepness for bony fishes (Actinopterygii) is 0.69 in this study, compared with the predictive

367 mean of 0.75 for all data sets analyzed by Shertzer and Conn (2012). The current analysis did

368 not observe the strong, positive association between steepness and asymptotic size that is

369 predicted from size-structured community theory (Andersen and Beyer 2015). Instead, results

370 were consistent with Shertzer and Conn (2012), who found no strong life-history predictor for

371 steepness. Exploring this in more detail, FishLife predictions of the slope-at-the-origin of the

372 stock-recruit relationship (α) shows a strong negative correlation with asymptotic biomass

373 (Appendix S2 and Suppl. Fig. S3) as previously shown by Hall et al. (2006 Fig. 1). However,

374 this negative relationship is counter-balanced by a strong positive correlation with unfished

375 spawning biomass per recruit ($SPR_{F=0}^{*}$), as previously shown by Goodwin et al. (2006), such

376 that *FishLife* identifies little correlation of body size with either maximum lifetime spawners per

377 spawner ($p = \alpha \times SPR_{F=0}^{*}$) or steepness ($h = \frac{p}{4+p}$).

378 The predictive mode for steepness of genus *Sebastes* (Pacific rockfishes) is 0.54 in this

379 study, compared with 0.58-0.78 obtained from six biannual iterations of a regional meta-analysis

380 for these species on the US West Coast (Thorson *et al.* In press). Steepness predictions from that

381 biannual regional meta-analysis rose sharply between 2007-2011, likely reflecting improved

382 environmental conditions for West Coast rockfishes in the mid-2000s. Predictions in this paper,

383   by contrast, are based on data from the Myers and Mertz (1998) database, prior to these years of

384   good recruitment. Different steepness predictions from these two meta-analyses emphasizes that

385   meta-analytic results are reflective of stock-recruitment parameters during an historical period

386   that might differ from current environmental conditions. Finally, the current analysis shows that

387   family Sebastidae has higher recruitment variance and autocorrelation that Salmonidae

388   (Supporting Information S1), and this is consistent with results from Thorson et al. (2014) for

389   orders Scorpaeniformes and Salmoniformes. The low value for steepness for genus *Sebastes*,

390   combined with unusually low mortality for their body size, causes Sebastes species to have an

391   intrinsic growth rate (0.07) that is similar to several shark families (Lamniformes: 0.07;

392   Carcharhiniformes: 0.10). Large differences in productivity among different fish genera suggest

393   the importance of predicting life-history parameters using taxonomic information in addition to

394   life-history theory.

395   I note that any meta-analysis is confronted with a trade-off between using aggregated

396   data (e.g., output from an assessment model) for many stocks, or using lower-level data (e.g.,

397   output from an index standardization model) for a small number of stocks (Thorson *et al.* 2015a).

398   In this study, I have fitted to the largest data sets available for both life-history parameters

399   (FishBase) and stock-recruit estimates (the RAM database), and results are therefore sensitive to

400   the biases that arise from using model output as "data" (Dickey-Collas *et al.* 2014; Brooks and

401   Deroba 2015). Although it is possible to conduct a meta-analysis for steepness using lower-level

402   data, this has been done previously for only a small number of species (Thorson *et al.* In press).

403   I therefore recommend ongoing research to use lower-level data (e.g., individual records of size

404   and age to estimate growth parameters) within future data-integrated life-history models to

405   eliminate the potential bias arising from analyzing model output as data in a meta-analysis.

406   I believe that multivariate predictions for multiple population-dynamics parameters will

407   be useful for stock-assessment, decision theory, ensemble modelling, and strategic decision-

408   making, and discuss each of these briefly:

409   1. *Stock assessment*: These multivariate predictions can be used to define a joint prior

410   distribution (or penalty) for parameters used in a Bayesian (or maximum likelihood) stock

411   assessment model. For example, a recent data-poor assessment model using length-

412   composition data to estimate stock status requires values for maturity, mortality, size,

413   steepness, and recruitment variability (Rudd and Thorson 2017), and a joint prior for all of

414   these parameters can be generated using the results. Using a joint prior distribution prevents

415   assessments from estimating a combination of life-history parameters that are highly unlikely

416   (Brandon *et al.* 2007), e.g., by estimating high mortality M in combination with large

417   maximum body size W_∞. The concern with biologically implausible life-history values has

418   motivated development of data-poor assessment models that employ life-history invariants to

419   restrict parameter inputs to plausible values (Hordyk *et al.* 2015; Kokkalis *et al.* 2017).

420   Similarly, using multivariate predictions as a joint prior distribution would restrict parameter

421   estimates to plausible life-history strategies for any assessment model that can use

422   multivariate prior distributions.

423   2. *Decision theory*: Similarly, a multivariate distribution for life-history parameters can guide

424   the design of simulation experiments that are widely used to evaluate likely performance for

425   ecological models or management procedures (Sainsbury *et al.* 2000). In particular, analysts

426   could use predictions to generate plausible population-dynamics parameters for different life-

427   history types, e.g., by using the predictive distribution for all parameters for genus *Sebastes*

428   to evaluate harvest strategies given simulated dynamics for Pacific rockfishes (Punt 2008).

429   This would allow researchers to link management decision-theory to the likely population-

430   dynamics for all species worldwide.

431   3. *Ensemble modelling*: Stock assessment will generally be more robust if management advice

432   is based on an ensemble of alternative life-history assumptions (Stewart and Martell 2015).

433   Results from a model ensemble can be presented using a decision-table (Hilborn *et al.* 1993)

434   or via ensemble-weighting of model results (Anderson *et al.* 2017), but either presentation

435   requires some objective method for determining the weight of different unknown "states of

436   nature". I therefore recommend that stock assessments increasingly present results using an

437   ensemble of life-history values, where model weights can be obtained from the multivariate

438   distribution for these parameters.

439   4. *Strategic decisions*: Finally, strategic decision-making in ocean management is increasingly

440   informed by models that include dynamics for multiple species and physical drivers (Fulton

441   *et al.* 2011). For example, ecosystem models have been used to forecast likely impacts of

442   ocean acidification, temperature changes, or invasive species on fisheries potential (Cheung

443   *et al.* 2008; Morello *et al.* 2014; Marshall *et al.* 2017). However, these models often require

444   values for population-dynamics parameters for several to hundreds of species

445   simultaneously, and there is increased interest in characterizing uncertainty in ecosystem

446   model predictions given uncertainty about population-dynamics parameters (Link *et al.* 2012;

447   Collie *et al.* 2016). One source of uncertainty is fixing biological parameters (and their

448   associated standard errors), and this uncertainty could be dealt with uniformly across

449   different species or taxonomic groups using results from this analysis.

450   For these reasons and more, I encourage continued research regarding data-integrated life-history

451   modelling. These models lie at the intersection of evolutionary, life-history, and stock-recruit

452 theory, and can translate insights from these theories into tools for applied ecologists and

453 fisheries managers. For this purpose, I distribute the predictions of life-history and stock-recruit

454 parameters (and associated confidence intervals) within R package *FishLife* version 2.0.0 and

455 interested users can read the vignette[1] to learn more.

6. Acknowledgements

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[1] The vignette can be accessed using the following commands within an R terminal:
```R
install.packages("devtools")
devtools::install_packages("james-thorson/FishLife")
vignette(topic="tutorial", package="FishLife")
```

References

Andersen, K.H. and Beyer, J.E. (2006) Asymptotic size determines species abundance in the marine size spectrum. *The American Naturalist* **168**, 54–61.

Andersen, K.H. and Beyer, J.E. (2015) Size structure, not metabolic scaling rules, determines fisheries reference points. *Fish and Fisheries* **16**, 1–22.

Anderson, S.C., Cooper, A.B., Jensen, O.P., et al. (2017) Improving estimates of population status and trend with superensemble models. *Fish and Fisheries*.

Beverton, R.J.H. (1992) Patterns of reproductive strategy parameters in some marine teleost fishes. *Journal of Fish Biology* **41**, 137–160.

Boettiger, C., Chamberlain, S., Lang, D.T. and Wainwright, P. (2015) *rfishbase: R Interface to "FishBase."*

Brandon, J.R., Breiwick, J.M., Punt, A.E. and Wade, P.R. (2007) Constructing a coherent joint prior while respecting biological realism: application to marine mammal stock assessments. *ICES Journal of Marine Science: Journal du Conseil* **64**, 1085–1100.

Britten, G.L., Dowd, M. and Worm, B. (2016) Changing recruitment capacity in global fish stocks. *Proceedings of the National Academy of Sciences* **113**, 134–139.

Brooks, E.N. and Deroba, J.J. (2015) When "data" are not data: the pitfalls of post hoc analyses that use stock assessment model output. *Canadian Journal of Fisheries and Aquatic Sciences* **72**, 634–641.

Charnov, E.L. and Berrigan, D. (1990) Dimensionless numbers and life history evolution: age of maturity versus the adult lifespan. *Evolutionary Ecology* **4**, 273–275.

Charnov, E.L., Berrigan, D. and Bevertron, R.J.H. (1991) Dimensionless numbers and the assembly rules for life histories [and discussion]. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **332**, 41–48.

Cheung, W.W.L., Lam, V.W.Y. and Pauly, D. (2008) Modelling present and climate-shifted distribution of marine fishes and invertebrates.

Collie, J.S., Botsford, L.W., Hastings, A., et al. (2016) Ecosystem models for fisheries management: finding the sweet spot. *Fish and Fisheries* **17**, 101–125.

Dickey-Collas, M., Payne, M.R., Trenkel, V.M. and Nash, R.D.M. (2014) Hazard warning: model misuse ahead. *ICES Journal of Marine Science* **71**, 2300–2306.

Efron, B. and Morris, C.N. (1977) *Stein's paradox in statistics*. WH Freeman.

Eveson, J.P., Laslett, G.M. and Polacheck, T. (2004) An integrated model for growth incorporating tag recapture, length frequency, and direct aging data. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 292–306.

Felsenstein, J. (1973) Maximum-likelihood estimation of evolutionary trees from continuous characters. *American Journal of Human Genetics* **25**, 471.

Forrest, R.E., McAllister, M.K., Dorn, M.W., Martell, S.J.D. and Stanley, R.D. (2010) Hierarchical Bayesian estimation of recruitment parameters and reference points for Pacific rockfishes (*Sebastes* spp.) under alternative assumptions about the stock-recruit function. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 1611–1634.

Foss-Grant, A.P., Zipkin, E.F., Thorson, J.T., Jensen, O.P. and Fagan, W.F. (2016) Hierarchical analysis of taxonomic variation in intraspecific competition across fish species. *Ecology* **97**, 1724–1734.

Froese, R. (1990) FishBase: An information system to support fisheries and aquaculture research. *ICLARM Fishbyte* **8**, 21–24.

Froese, R., Thorson, J.T. and Reyes, R.B. (2014) A Bayesian approach for estimating length-weight relationships in fishes. *Journal of Applied Ichthyology* **30**, 78–85.

Fulton, E.A., Link, J.S., Kaplan, I.C., et al. (2011) Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries*.

512 Gelman, A. and Hill, J. (2007) *Data analysis using regression and multilevel/hierarchical models*.
513   Cambridge University Press, Cambridge, UK.
514 Goodwin, N.B., Grant, A., Perry, A.L., Dulvy, N.K. and Reynolds, J.D. (2006) Life history correlates of
515   density-dependent recruitment in marine fishes. *Canadian Journal of Fisheries and Aquatic*
516   *Sciences* **63**, 494–509.
517 Haddon, M. (2010) *Modelling and Quantitative Methods in Fisheries, Second Edition*. CRC Press.
518 Hall, S.J., Collie, J.S., Duplisea, D.E., Jennings, S., Bravington, M. and Link, J. (2006) A length-based
519   multispecies model for evaluating community responses to fishing. *Canadian Journal of Fisheries*
520   *and Aquatic Sciences* **63**, 1344–1359.
521 Hilborn, R., Pikitch, E.K. and Francis, R.C. (1993) Current Trends in Including Risk and Uncertainty in Stock
522   Assessment and Harvest Decisions. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 874–
523   880.
524 Hjort, J. (1926) Fluctuations in the year classes of important food fishes. *ICES Journal of Marine Science*
525   **1**, 5.
526 Hordyk, A., Ono, K., Sainsbury, K., Loneragan, N. and Prince, J. (2015) Some explorations of the life
527   history ratios to describe length composition, spawning-per-recruit, and the spawning potential
528   ratio. *ICES Journal of Marine Science: Journal du Conseil* **72**, 204–216.
529 Iles, T.C. and Beverton, R.J.H. (1998) Stock, recruitment and moderating processes in flatfish. *Journal of*
530   *Sea Research* **39**, 41–55.
531 Jensen, O.P., Branch, T.A. and Hilborn, R. (2012) Marine fisheries as ecological experiments. *Theoretical*
532   *Ecology* **5**, 3–22.
533 Kass, R.E. and Steffey, D. (1989) Approximate bayesian inference in conditionally independent
534   hierarchical models (parametric empirical bayes models). *Journal of the American Statistical*
535   *Association* **84**, 717–726.
536 Kokkalis, A., Eikeset, A.M., Thygesen, U.H., Steingrund, P. and Andersen, K.H. (2017) Estimating
537   uncertainty of data limited stock assessments. *ICES Journal of Marine Science* **74**, 69–77.
538 Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H. and Bell, B.M. (2016) TMB: Automatic Differentiation
539   and Laplace Approximation. *Journal of Statistical Software* **70**, 1–21.
540 Levins, R. (1969) Some Demographic and Genetic Consequences of Environmental Heterogeneity for
541   Biological Control. *Bulletin of the ESA* **15**, 237–240.
542 Link, J.S., Ihde, T.F., Harvey, C.J., et al. (2012) Dealing with uncertainty in ecosystem models: The
543   paradox of use for living marine resource management. *Progress in Oceanography* **102**, 102–
544   114.
545 Mace, P.M. (1994) Relationships between Common Biological Reference Points Used as Thresholds and
546   Targets of Fisheries Management Strategies. *Canadian Journal of Fisheries and Aquatic Sciences*
547   **51**, 110–122.
548 Mangel, M., Brodziak, J. and DiNardo, G. (2010) Reproductive ecology and scientific inference of
549   steepness: a fundamental metric of population dynamics and strategic fisheries management.
550   *Fish and Fisheries* **11**, 89–104.
551 Marshall, K.N., Kaplan, I.C., Hodgson, E.E., et al. (2017) Risks of ocean acidification in the California
552   Current food web and fisheries: ecosystem model projections. *Global Change Biology* **23**, 1525–
553   1539.
554 Maunder, M.N. and Punt, A.E. (2013) A review of integrated analysis in fisheries stock assessment.
555   *Fisheries Research* **142**, 61–74.
556 McAllister, M.K., Pikitch, E.K. and Babcock, E.A. (2001) Using demographic methods to construct
557   Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock
558   rebuilding. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1871–1890.

559   Minto, C., Myers, R.A. and Blanchard, W. (2008) Survival variability and population density in fish
560   populations. *Nature* **452**, 344–347.
561   Morello, E.B., Plagányi, É.E., Babcock, R.C., Sweatman, H., Hillary, R. and Punt, A.E. (2014) Model to
562   manage and reduce crown-of-thorns starfish outbreaks. *Marine Ecology Progress Series* **512**,
563   167–183.
564   Myers, R. and Mertz, G. (1998) Reducing uncertainty in the biological basis of fisheries management by
565   meta-analysis of data from many populations: a synthesis. *Fisheries Research* **37**, 51–60.
566   Myers, R.A. (2001) Stock and recruitment: generalizations about maximum reproductive rate, density
567   dependence, and variability using meta-analytic approaches. *ICES Journal of Marine Science:
568   Journal du Conseil* **58**, 937–951.
569   Myers, R.A., Bowen, K.G. and Barrowman, N.J. (1999) Maximum reproductive rate of fish at low
570   population sizes. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 2404–2419.
571   Myers, R.A., Bridson, J. and Barrowman, N.J. (1995) Summary of worldwide spawner and recruitment
572   data. 2024. Department of Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, St.
573   Johns, Newfoundland.
574   Neill, W.H., Miller, J.M., Van Der Veer, H.W. and Winemiller, K.O. (1994) Ecophysiology of marine fish
575   recruitment: A conceptual framework for understanding interannual variability. *Netherlands
576   Journal of Sea Research* **32**, 135–152.
577   Osenberg, C.W., Sarnelle, O., Cooper, S.D. and Holt, R.D. (1999) Resolving ecological questions through
578   meta-analysis: goals, metrics, and models. *Ecology* **80**, 1105–1117.
579   Punt, A.E. (2008) Refocusing stock assessment in support of policy evaluation. In: *Fisheries for Global
580   Welfare and Environment*. (eds K. Tsukamoto, T. Kawamura, T. Takeuchi, T.D. Beard and M.J.
581   Kaiser). TerraPub, Tokyo, pp 139–152.
582   Roff, D.A. (1984) The evolution of life history parameters in teleosts. *Canadian Journal of Fisheries and
583   Aquatic Sciences* **41**, 989–1000.
584   Rose, K.A., Cowan, J.H., Winemiller, K.O., Myers, R.A. and Hilborn, R. (2001) Compensatory density
585   dependence in fish populations: importance, controversy, understanding and prognosis. *Fish
586   and Fisheries* **2**, 293–327.
587   Rudd, M.B. and Thorson, J.T. (2017) Accounting for variable recruitment and fishing mortality in length-
588   based stock assessments for data-limited fisheries. *Canadian Journal of Fisheries and Aquatic
589   Sciences*.
590   Sainsbury, K.J., Punt, A.E. and Smith, A.D.. (2000) Design of operational management strategies for
591   achieving fishery ecosystem objectives. *ICES Journal of Marine Science: Journal du Conseil* **57**,
592   731–741.
593   Shertzer, K.W. and Conn, P.B. (2012) Spawner-Recruit Relationships of Demersal Marine Fishes: Prior
594   Distribution of Steepness. *Bulletin of Marine Science* **88**, 39–50.
595   Skaug, H. and Fournier, D. (2006) Automatic approximation of the marginal likelihood in non-Gaussian
596   hierarchical models. *Computational Statistics & Data Analysis* **51**, 699–709.
597   Stewart, I.J. and Martell, S.J.D. (2015) Reconciling stock assessment paradigms to better inform fisheries
598   management. *ICES Journal of Marine Science* **72**, 2187–2196.
599   Thorson, Cope, J.M., Kleisner, K.M., Samhouri, J.F., Shelton, A.O. and Ward, E.J. (2015a) Giants'
600   shoulders 15 years later: lessons, challenges and guidelines in fisheries meta-analysis.
601   Thorson, Dorn, M. and Hamel, O.S. (In press) Steepness for West Coast rockfishes: Results from a
602   twelve-year experiment in iterative regional meta-analysis.
603   Thorson, Jensen, O.P. and Hilborn, R. (2015b) Probability of stochastic depletion: an easily interpreted
604   diagnostic for stock assessment modelling and fisheries management. *ICES Journal of Marine
605   Science: Journal du Conseil* **72**, 428–435.

606   Thorson, Jensen, O.P. and Zipkin, E.F. (2014) How variable is recruitment for exploited marine fishes? A
607   hierarchical model for testing life history theory. *Canadian Journal of Fisheries and Aquatic*
608   *Sciences* **71**, 973–983.
609   Thorson, J.T. and Minto, C. (2015) Mixed effects: a unifying framework for statistical modelling in
610   fisheries biology. *ICES Journal of Marine Science: Journal du Conseil* **72**, 1245–1256.
611   Thorson, J.T., Munch, S.B., Cope, J.M. and Gao, J. (2017) Predicting life history parameters for all fishes
612   worldwide. *Ecological Applications* **27**, 2262–2276.
613   Thorson, J.T., Rudd, M. and Winker, H. (In review) The case for estimating recruitment variation in data-
614   moderate and data-poor age-structured models.
615   Warton, D.I., Wright, I.J., Falster, D.S. and Westoby, M. (2006) Bivariate line-fitting methods for
616   allometry. *Biological Reviews* **81**, 259–291.
617   Winemiller, K.O. (1989) Patterns of variation in life history among South American fishes in seasonal
618   environments. *Oecologia* **81**, 225–241.
619   Zipkin, E.F., Rossman, S., Yackulic, C.B., Wiens, J.D., Thorson, J.T., Davis, R.J. and Grant, E.H.C. (2017)
620   Integrating count and detection–nondetection data to model population dynamics. *Ecology* **98**,
621   1640–1650.

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625 Table 1 – List of life-history parameters (including their name, symbol, the database used to
626 estimate them, and the type of parameter) that are predicted (along with estimated covariance)
627 for all fishes worldwide

Name	Symbol	Database	Type
Mortality rate	M	FishBase	Mortality
Maximum age	A_{max}	FishBase	Mortality
Growth coefficient	K	FishBase	Size
Asymptotic length	L_∞	FishBase	Size
Asymptotic mass	W_∞	FishBase	Size
Age at maturity	A_{mat}	FishBase	Maturity
Length at maturity	L_{mat}	FishBase	Maturity
Average temperature	T	FishBase	Environmental conditions
Marginal standard deviation of recruitment variability	σ_R	RAM	Recruitment
Autocorrelation of recruitment variability	ρ_R	RAM	Recruitment
Steepness	h	RAM	Recruitment
Fishing mortality rate at maximum sustainable yield	F_{msy}	FishBase, RAM	Management

628

629   Table 2 – Summary of the dominant axes of covariation for evolutionary covariance $\boldsymbol{\Sigma}$. The ratio
630   of two elements of a given eigenvector (columns) is interpreted as the "slope" between these two
631   variables (see text below Eq. 2 in main text for details), while the proportion of variance
632   explained by a given eigenvector (row "Proportion") measures what proportion of total variance
633   is explained by a given eigenvector.

	Eigenvectors		
	1	2	3
Variance decomposition			
Eigenvalues	59.918	11.959	1.298
Proportion	0.808	0.161	0.018
Cumulative proportion	0.808	0.97	0.987
Loadings			
$\log(M)$	0.055	-0.209	0.472
$\log(A_{max})$	-0.042	0.202	-0.505
$\log(K)$	0.046	-0.203	0.346
$\log(L_{\infty})$	-0.020	0.256	0.133
$\log(W_{\infty})$	-0.043	0.833	0.387
$\log(A_{mat})$	-0.037	0.219	-0.459
$\log(L_{mat})$	-0.025	0.237	0.087
T	0.994	0.084	-0.059
$\log(\sigma_R)$	-0.011	-0.039	-0.076
ρ_R	0.006	0.039	-0.085
h	0.010	-0.001	0.005

634

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636 Table 3 – Mode of the predictive distribution for steepness (h) and intrinsic growth rate (r) for bony fishes (Actinopyterygii) and
637 common taxonomic orders and families (with predictive standard deviation in parentheses). Also shown is the range of predictive
638 mean steepness (and range of predictive standard deviations) for West Coast rockfishes from six biannual meta-analyses compiled by
639 Thorson et al. (In press), the sample mean (and sample standard deviation) for steepness from all compiled data sets from Shertzer and
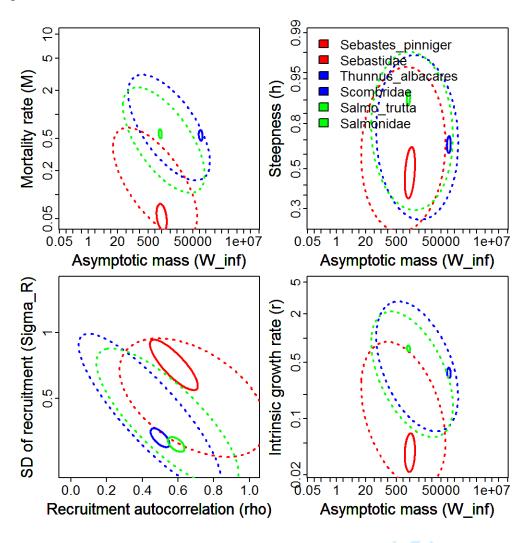640 Conn (2012).

| | Steepness (h) | | | Intrinsic growth rate (r) |
	This study	Thorson et al. (In press)	Shertzer and Conn (2012)	This study
Class				
Actinopterygii	0.69 (0.22)	-	0.75 (0.15)	1.91 (1.37)
Order				
Carcharhiniformes	0.50 (0.22)	-		0.10 (0.19)
Lamniformes	0.51 (0.22)	-		0.07 (0.12)
Clupeiformes	0.72 (0.21)	-		0.55 (0.66)
Gadiformes	0.63 (0.22)	-		0.23 (0.32)
Perciformes	0.71 (0.21)	-		0.41 (0.48)
Pleuronectiformes	0.76 (0.19)	-		0.50 (0.57)
Scorpaeniformes	0.62 (0.22)	-		0.26 (0.38)
Family				
Sebastidae	0.63 (0.18)	-		0.11 (0.12)
Salmonidae	0.74 (0.17)	-		0.36 (0.30)
Scombridae	0.69 (0.18)	-		0.45 (0.39)
Lutjanidae	0.77 (0.16)	-		0.40 (0.31)
Genus				
Sebastes	0.54 (0.13)	0.58-0.78 (0.15-0.20)		0.07 (0.05)

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642

643   Fig. 1 – Predictive distribution for selected life-history and stock-recruit parameters (see Table 1)
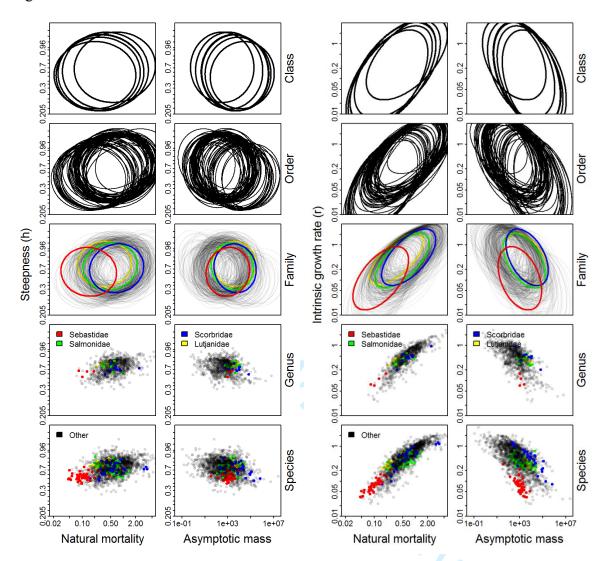
644   for three commercially important families (Sebastidae, Scombridae, and Salmonidae) and a

645   selected species from each family (*Sebastes pinniger, Thunnus albacares,* and *Salmo trutta*).

646

647   Fig. 2 – Visualization of the natural mortality rate (M, 1st and 3rd columns and plotted on x-axis

648   on log-scale) or asymptotic mass (W_∞, 2nd and 4th columns and plotted on x-axis on log-scale)

649   and steepness (h, 1st and 2nd columns and plotted on y-axis using logit-scale from 0.2 to 1.0) or

650   intrinsic growth rate (r, 2nd and 3rd columns and plotted on y-axis on log-scale) for every Class,

651   Order, Family, Genus, and Species in the database, while highlighting the predictive distribution

652   for commercially important families (Sebastidae, Salmonidae, Scombridae, and Lutjanidae). For

653   Class, Order and Family I show the 95% predictive distribution (an ellipse, given that the model

654   uses a multivariate normal distribution), while for Genus and Species I show the for each

655   modeled stock in that taxon.

656

657   Fig. 3 – Predictive probability (y-axis) for steepness h (left column) or intrinsic growth rate r

658   (right column) for every described class, order, family, genus, and species in FishBase (panels,

659   ordered top to bottom), with families Sebastidae, Salmonidae, Scombridae, and Lutjanidae

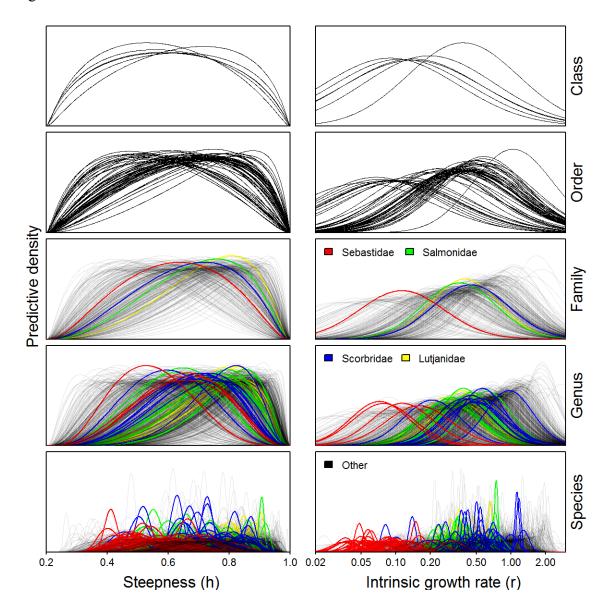660   highlighted to emphasize these particular, commercially-important species

661

662   Fig. 1

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664

665   Fig. 2

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667   Fig. 3

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Appendix 1: Computational details

1

2

3   I estimate parameters using Template Model Builder (Kristensen *et al.* 2016), which

4 applies automatic differentiation to calculate gradients of the joint likelihood with respect to

5 fixed and random effects, and uses an inner-optimize to optimize the joint likelihood with respect

6 to random effects. It then applies the Laplace approximation, and provides the gradient of the

7 marginal likelihood with respect to fixed effects. I use these gradients in a gradient-based

8 Nelder-Mead optimizer within the R statistical environment (R Core Team 2017) to identify

9 fixed effects that optimize the marginal likelihood, followed by two iterations of a Newton

10 optimizer step to ensure that remaining gradients are very low. I check convergence by ensuring

11 that the hessian matrix is positive definite, and that the gradient of the marginal log-likelihood is

12 within $\pm 10^{-6}$ for all fixed effects.

13   To improve convergence, I use the following numerical and analytical techniques:

14 1. I use a nonlinear generalization of restricted maximum likelihood (REML), which involves

15   treating non-variance fixed effects (e.g., density dependence β_i and expected values for

16   shared ancestor μ_x) as random effects with a "flat" hyperdistribution. This improves

17   calculation of gradients for combinations of fixed and random effects that are highly

18   correlated (e.g., density dependence β_i and recruitment compensation r_i for each stock-

19   recruit data set).

20 2. I add a small penalty to the objective function which favors plausible values for stock-recruit

21   parameters (α_i and β_i for each stock i). Specifically, I regularize density dependence towards

22   a shared mean, $\beta_i \sim Norm(0,10)$ for each stock i. I also add a penalty towards stock-recruit

23   fits where predicted recruitment is constant for all observations of a given stock, where

24   penalty $p_i = 0.5\log\left(Var_t(\hat{R}_{i,t})\right)$ is added to the log-likelihood function. This regularization

25   penalty on the variance of predicted recruitment was unnecessary in previous Bayesian

26   hierarchical models for stock-recruit meta-analysis (Thorson *et al.* 2014; Foss-Grant *et al.*

27   2016), but appears to be necessary when using the Laplace approximation for Empirical

28   Bayes estimation.

29 3. I have removed two stocks where the standard error for density dependence β_i approached

30   the regularization penalty (i.e., $\widehat{SE}(\beta_i)\rightarrow10$). Exploration showed that eliminating these

31   stocks improved model stability without noticeably impacting results. This decision resulted

32   in 151 stocks available for analysis.

33 These three techniques allow the model to converge with random starting values for different

34 complexities of evolutionary and measurement covariance (i.e., number of columns in $\mathbf{L_\Sigma}$ and $\mathbf{L_V}$
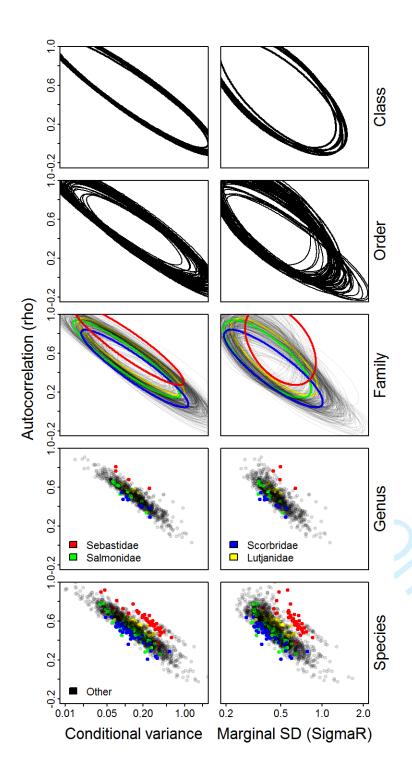
35).

36

37

Appendix 2: Visualizing other model results

38

39   Suppl. Fig. S1 – Fits to stock-recruit records for 151 stocks in the original RAM database. For

40   each stock (panel), I show recruitment (y-axis) for a given record of spawning biomass (x-axis),

41   visualizing the recruitment record (black point), predicted recruitment from the stock-recruit

42   relationship (blue point), or predicted recruitment from the stock-recruit relationship and the

43   impact of autocorrelated errors (red point). I also list the marginal standard deviation of

44   recruitment, the magnitude of autocorrelation, and the steepness parameter.

45

46   Suppl. Fig. S2 – Visualization of the conditional variance of recruitment (τ_i^2, x-axis left column)

47   or marginal standard deviation of recruitment (σ_R, x-axis right column) and the first-order

48   autocorrelation in recruitment (ρ_R, y-axis), see Fig. 2 caption for details.

51   Suppl. Fig. S3 – Visualization of stock-recruit parameters (y-axis) against maximum biomass (x-
52   axis on log-scale) for the 150 stocks that had available records of spawning biomass and
53   subsequent recruitment in the original RAM database, showing slope-at-the-origin of the stock-
54   recruit relationship (top-left panel), maximum annual spawners per spawner (top-right panel),
55   and steepness (bottom-left panel). Each panel also shows fits to a linear regression, and the p-
56   value for a two-sided Wald test in the bottom-right corner.

Fish and Fisheries

SigmaR = 0.52, Rho = −0.04, h = 0.69 (CHUMNBC); SigmaR = 0.40, Rho = 0.62, h = 0.58 (CHUMQCI); SigmaR = 0.57, Rho = 0.22, h = 0.48 (CHUMWVAN); SigmaR = 1.15, Rho = 0.53, h = 0.76 (CMACKCAL); SigmaR = 0.75, Rho = 0.82, h = 0.76 (COD2J3KL); SigmaR = 1.37, Rho = 0.66, h = 0.74 (COD3M3); SigmaR = 0.78, Rho = 0.76, h = 0.85 (COD3NO); SigmaR = 0.38, Rho = 0.38, h = 0.85 (COD3Ps); SigmaR = 0.49, Rho = 0.64, h = 0.83 (COD4TVn); SigmaR = 0.50, Rho = 0.76, h = 0.92 (COD4VsW); SigmaR = 0.37, Rho = 0.30, h = 0.82 (COD4X); SigmaR = 0.54, Rho = 0.14, h = 0.77 (COD5Z); SigmaR = 0.63, Rho = 0.38, h = 0.87 (CODBA2224); SigmaR = 0.49, Rho = 0.74, h = 0.87 (CODBA2532); SigmaR = 0.70, Rho = 0.18, h = 0.78 (CODCS); SigmaR = 0.59, Rho = 0.39, h = 0.87 (CODFAPL)

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