

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

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Abstract

Fisheries scientists use biological models to determine sustainable fishing rates and forecast future dynamics. These models require both life-history parameters (mortality, maturity, growth) and stock-recruit parameters (juvenile production). However, there has been little research to simultaneously predict life-history and stock-recruit parameters. I develop the first data-integrated life-history model, which extends a simple model of evolutionary dynamics to field measurements of life-history parameters as well as historical records 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 steepness and either natural mortality or asymptotic maximum size (W_{∞}). However, it does reveal taxonomic patterns, where family Sebastidae has lower steepness (mean=0.72) and Salmonidae has elevated steepness (mean=0.79) relative to the prediction for bony fishes (class Actinopterygii, mean=0.74). Similarly, genus *Sebastes* has growth rate r (0.09) approaching that of several shark families (Lamniformes: 0.02; Carcharhiniformes: 0.02). A cross-validation experiment confirms that the model is accurate, explains a substantial portion of variance (32%–67%), but generates standard errors that are somewhat too small. Predictive intervals are tighter for species than for higher-level organizations (e.g. families), and predictions (including intervals) are available for all 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 modeling and strategic management.

KEYWORDS

life-history theory, meta-analysis, recruitment, Steepness, stock assessment, taxonomy

1 | 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 poorly- 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” to distinguish them from “stock-recruit parameters” as defined below. There is an extensive literature regarding the expected relationship among life-history parameters in fishes (Beverton, 1992; Charnov & Berrigan, 1990; Roff, 1984; Winemiller, 1989). 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, Thorson, & Reyes, 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 uncertainty from the quantity and quality of records for a given taxon and its relatives (Thorson, Munch, Cope, & Gao, 2017). Improved documentation and access to these meta-analytic results can presumably improve fisheries management for species that currently have little direct biological information.

Despite progress in predicting adult life-history parameters for fishes, these parameters are insufficient to predict population dynamics. In fact, fisheries scientists have recognized for nearly 100 years that fish populations are often composed of a single or few small cohorts (Hjort, 1926) and that fluctuations in population size are largely driven by the production of juveniles. Recruitment is typically predicted as a function of spawning output, and parameters governing the expected relationship between spawning output and recruitment are rarely included in classical life-history theory. Instead, stock-recruit parameters have historically been predicted using meta-analyses (e.g. Myers, 2001) applied to a database of spawning biomass and subsequent recruitment (termed “stock-recruit data”) or via ecological theories of marine community structure (Andersen & Beyer, 2006) or demography (Mangel, Brodziak, & DiNardo, 2010). The stock-recruit relationship has received a great deal of research attention over the past thirty years both using theoretical arguments (Charnov, Berrigan, & Beverton, 1991; Iles & Beverton, 1998; Mangel et al., 2010; Neill, Miller, Veer, & Winemiller, 1994) and empirical methods (Britten, Dowd, & Worm, 2016; Foss-Grant, Zipkin, Thorson, Jensen, & Fagan, 2016; Minto, Myers, & Blanchard, 2008; Rose, Cowan, Winemiller, Myers, & Hilborn, 2001;

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Thorson, Jensen, & Zipkin, 2014) to predict variation in stock-recruit parameters. These previous theoretical investigations have linked stock-recruit parameters to life-history categories (Rose et al., 2001) and predicted stock-recruit parameters based on ecological theory regarding community dynamics (Andersen & Beyer, 2015), population persistence (He, Mangel, & MacCall, 2006) and demography (Mangel et al., 2010). However, there have been surprisingly few empirical studies that simultaneously analyse variation in stock-recruit and adult life-history parameters.

Ecologists increasingly use models combining data from multiple collection protocols (termed “integrated models”) to estimate ecological parameters. These integrated models are useful to estimate processes that are not identifiable using one data set in isolation and are common, for example, when estimating population dynamics for assessing stock status (Maunder & Punt, 2013), when estimating growth from tagging and length sampling data (Eveson, Laslett, & Polacheck, 2004) or when estimating population density using encounter and count data (Zipkin et al., 2017). However, data-integrated modelling has not to my knowledge been used in life-history analysis (which typically analyses databases of field measurements of population rates) or stock-recruit analysis (which typically analyses stock-recruit data while assuming that population-dynamics parameters are known and fixed exogenously). Combining these two analyses is sufficient to describe adult fish dynamics (e.g. spawning biomass per recruit without fishing) and recruit dynamics (e.g. recruits per spawning biomass) and therefore is sufficient to describe the entire life cycle under alternative scenarios regarding fishing effort and selectivity (e.g. Thorson, Jensen, & Hilborn, 2015a).

In this study, I develop the first data-integrated model for life-history analysis and demonstrate this approach by combining data from life-history and stock-recruit databases. By combining life-history and stock-recruit information, I am able to generate predictions of life-cycle dynamics for all described fishes. I specifically modify the evolutionary model used by *FishLife* to fit both adult life-history parameters and stock-recruit measurements for over 150 fish

populations worldwide and use this integrated model for population-dynamics parameters to estimate the strength of recruitment compensation for all fishes. I then use these predictions to generate a full life-cycle model and estimate the intrinsic growth rate r for all fishes. This parameter is widely used in theoretical and applied studies, for example, as one of two key parameters in the surplus production models that are taught in introductory fisheries science classes (Haddon, 2010). In the discussion, I compare resulting estimates with previous studies to evaluate plausibility of model results. Finally, I distribute predictions of recruitment density dependence and intrinsic growth rate (and associated uncertainty) as an updated version of the fully documented, publicly available R package *FishLife* (<https://github.com/James-Thorson/FishLife>), so that future users can generate multivariate predictions of life-history and stock-recruit parameters for any described fish species.

2 | METHODS

I seek to predict stock-recruit parameters (the strength of recruitment compensation and the variance and autocorrelation in recruitment variation) and use results to describe life-cycle dynamics (i.e. intrinsic growth rate) for all fishes worldwide. To do so, I integrate two previous meta-analytic models:

1. An evolutionary model of life-history parameters (Thorson et al., 2017) fitted to field measurements of size, growth, mortality and maturity for thousands of species worldwide as compiled by FishBase (Froese, 1990);
2. A hierarchical model for stock-recruit parameters (Thorson et al., 2014) fitted to stock and recruitment measurements from the original RAM database (Myers, Bridson, & Barrowman, 1995).

By fitting an evolutionary model to both data sets simultaneously, I am able to characterize uncertainty arising from estimates of individual life-history parameters as well as stock-recruit processes. I then distribute results using an R package *FishLife*, release 2.0.0 (<https://github.com/James-Thorson/FishLife/releases/tag/2.0.0>).

For this analysis, I draw heavily upon previous advice regarding good practices in fisheries meta-analysis (Thorson, Cope, et al., 2015b). Specifically, I address both experimental variability, for example, errors in field measurements of life-history parameters, and parametric variability, for example, differences in larval and adult survival rates, following definitions of experimental and parametric variability from Osenberg, Sarnelle, Cooper, and Holt (1999). To account for both types of variability, I apply a hierarchical model that explicitly estimates the magnitude of measurement versus process variability (Thorson & Minto, 2015). Hierarchical models automatically implement “shrinkage,” that is, the tendency for parameter estimates for each species to be shrunk towards both (a) the average of available data and (b) the prediction given other model components (Gelman & Hill, 2007). Shrinkage permits parameter estimates even for species with no field records. Shrinkage will also bias estimates for a given taxon towards estimates for related species, but theory

suggests that it will minimize expected errors even in cases when some species are mis-categorized or otherwise greatly different from other taxa (Efron & Morris, 1977).

2.1 | Evolutionary model for life-history parameters

I first summarize *FishLife* (Thorson et al., 2017), an evolutionary model for size, growth, mortality and maturity parameters for all fishes worldwide. This model adapts the coalescent model for molecular evolution (Felsenstein, 1973) to predict a vector \mathbf{x}_g of life-history values $x_{g,j}$ for taxon g and parameter j (of G and J modelled taxa and parameters). Parameters \mathbf{x}_g that are estimated in the model are described in detail below (see Table 1 for list).

According to this model, life-history parameters \mathbf{x}_g for taxon g evolve to deviate from the parameters $\mathbf{x}_{p(g)}$ for their taxonomic parent $p(g)$, where this deviation follows a multivariate normal distribution:

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

for example, if $\mathbf{x}_{p(g)}$ is the average value of life-history parameters for family Sebastidae, then \mathbf{x}_g is the average life-history values genus *Sebastes*. $\Sigma_{l(g)}$ is the evolutionary covariance among life-history parameters:

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

where \mathbf{L}_Σ is a lower-diagonal matrix that approximates covariance among parameters, \mathbf{D}_Σ is a diagonal matrix representing additional variance for the evolution of each trait (where each element of the

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

Name	Symbol	Database	Type
Mortality rate	$\log(M)$	FishBase	Mortality
Maximum age	$\log(A_{\max})$	FishBase	Mortality
Growth coefficient	$\log(K)$	FishBase	Size
Asymptotic length	$\log(L_\infty)$	FishBase	Size
Asymptotic mass	$\log(W_\infty)$	FishBase	Size
Age at maturity	$\log(A_{\text{mat}})$	FishBase	Maturity
Length at maturity	$\log(L_{\text{mat}})$	FishBase	Maturity
Average temperature	T	FishBase	Environmental conditions
Conditional standard deviation of recruitment variability	$\log(\tau_R)$	RAM	Recruitment
Autocorrelation of recruitment variability	ρ_R	RAM	Recruitment
Maximum annual spawners per spawner in excess of replacement	γ	RAM	Recruitment

diagonal is estimated separately), and $l(g)$ represents the taxonomic level of taxon g (e.g. Class, Order, Family, Genus or Species) such that $\lambda_{l(g)}$ represents the proportion of evolutionary covariance occurring at taxonomic level $l(g)$. This specification is completed by specifying the mean traits for the top of the fish taxonomy (phylum Chordata) as fixed effects with expected value μ_x . The evolutionary covariance from phylum Chordata to any fish species can be calculated as $\Sigma = \sum_{l=1}^5 \Sigma_l$. This model approximates many different evolutionary mechanisms, for example, by assuming that evolution rates of life-history and stock-recruit parameters are identical for all evolutionary lineages despite likely differences in evolutionary mechanisms and effective population size, and future research could expand the model by incorporating additional information regarding evolutionary rates and divergence times within the fish taxonomic tree.

The association of one trait (e.g. natural mortality M) and another trait (e.g. asymptotic mass W_∞) can be interpreted using major axis regression (Warton, Wright, Falster, & Westoby, 2006). Major axis regression (MAR) involves calculating the eigen-decomposition of evolutionary covariance Σ , and the ratio of elements in a given eigenvector is interpreted as the regression “slope” between two variables. MAR is useful given that the slope does not require defining which variable is “dependent” or “independent”, and an estimated slope of β can be interpreted as “a 1% change in variable X_1 is associated with a $\beta\%$ change in variable X_2 ” whenever both variables have been log-transformed prior to analysis (see Thorson et al., 2017 for an example). By contrast, conventional linear modelling (e.g., a regression of natural mortality M on growth coefficient K) requires specifying a dependent and independent variable, and estimates of the slope will depend upon that choice.

The evolutionary model in *FishLife* is completed by specifying a distribution for life-history measurements \tilde{y}_i for study i :

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

where $g(i)$ is the taxon for study i , such that $\mathbf{x}_{g(i)}$ is the expected value for each field measurement for that study, and \mathbf{V} represents covariance among studies for a given taxon (resulting from a combination of field-measurement errors and biological variation among stocks for a given species, years for a given stock, etc). However, most studies do not measure all life-history parameters simultaneously, so I use a “missing-data” model under the assumption that data are missing at random:

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

where ε_{ij} is assigned a uniform prior distribution, $\varepsilon_{ij} \sim \text{Uniform}(LB, UB)$ (where the lower bound LB and upper bound UB are chosen such that further changes in their values have no effect on model results).

This model was previously fitted to seven life-history parameters and average environmental temperature (which I collectively call “life-history parameters”; Table 1), where all were log-transformed

prior to analysis (except for average temperature Temp). Results from Thorson et al. (2017) showed:

1. Well-known life-history patterns, for example, a positive association between observed values for growth coefficient (K) and natural mortality rate (M) and the close-to-cubic relationship between asymptotic length (L_∞) and asymptotic mass (W_∞).
2. Major axes of evolution in life-history parameters, wherein the first axis is associated with temperature, the second with body size and the third represents a non-linear relationship between mortality rate and growth coefficient (M/K) and the timing of maturation (L_{mat}/L_∞).
3. Useful predictions of uncertainty for both well-studied species and poorly studied species, where predicted life-history parameters for individual species are more precise (smaller predictive intervals) than predictions for higher-level taxa.

However, that analysis could not predict population dynamics because it did not include parameters governing recruitment.

2.2 | Hierarchical model for stock-recruit parameters

I next extend the existing *FishLife* model to predict stock-recruit parameters by fitting to records of spawning stock size $S_{i,t}$ and subsequent recruitment $R_{i,t}$ for stock-recruit study i in year t . Previous research has predicted stock-recruit parameters based on ecological mechanisms drawn from population (e.g. Mangel et al., 2010) and community theory (e.g. Andersen & Beyer, 2015), whereas I instead approach the problem by estimating correlations between stock-recruit parameters either across related taxa or with life-history parameters. I use notation from Thorson et al. (2014), but modify this model by (a) embedding it within the evolutionary model for life-history parameters and (b) defining a hyper-distribution for maximum recruits per spawning biomass for each stock. I note that the original RAM database records the age at recruitment for each stock i , and I align data such that $\hat{R}_{i,t}$ is the record of recruitment arising from spawning that occurs given spawning biomass $S_{i,t}$. I specifically associate each stock-recruit study i with a corresponding vector of life-history and stock-recruit measurements \tilde{y}_i . Vector \tilde{y}_i is defined such that all life-history measurements are missing for stock-recruit study i ; these values are instead predicted based on life-history estimates $\mathbf{x}_{g(i)}$ for species $g(i)$ corresponding to study i (see Equation 3). Similarly, stock-recruit parameters for study i are extracted from vector \tilde{y}_i and are then used to calculate the likelihood of stock-recruit records $S_{i,t}$ and $R_{i,t}$ for all years t available in study i ; the fit to this likelihood is then used to predict stock-recruit parameters in vector \mathbf{x}_g for all taxa $g(i)$ corresponding to study i .

I specify one parameterization of the Beverton–Holt model for expected recruitment $\hat{R}_{i,t}$ for study i in year t :

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

where α_i is maximum recruits per spawning biomass for stock-recruit study i (i.e. extracted from $\hat{\gamma}_i$), and β_i represents the density-dependent decrease in recruits per spawning biomass with increasing $S_{i,t}$. I then specify a distribution for process variability around this assumed relationship:

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

where ρ_i is the first-order autocorrelation coefficient for study i , and residual errors are normally distributed, $\delta_{i,t} \sim N(0, \tau_i^2)$, where τ_i^2 is the conditional variance for recruitment deviations. This model involves estimating four parameters for every each study i : α_i , β_i , τ_i^2 and ρ_i .

I apply a hierarchical model that shrinks α_g , τ_g^2 and ρ_g towards expected values for a given taxon. I assume that carrying capacity varies greatly among species (e.g. because spawning biomass and recruits are expressed in different units among different studies, or mechanisms differ among species), so I treat $\beta_{g(i)}$ as a fixed effect for every study i such that it is not shrunk towards a common value (and it is not included for species g for which no study). By contrast, I specify a hierarchical model for maximum recruits per spawning biomass α_i in the following way. First, I use the observation that maximum annual spawners per spawner is less variable than other measures of density dependence (Myers, Bowen, & Barrowman, 1999). I then convert this value to maximum lifetime spawners per spawner in excess of replacement p_i for each study i :

$$p_i = 1 + \frac{\gamma_i}{1 - \exp(-M_i^*)} \quad (7)$$

where $\exp(-M_i^*)$ is the annual survival fraction given adult natural mortality rate M_i^* . The right-hand-side of Equation 7 ensures that $p_i > 1$ for all values of $\log(\gamma_i)$, which is a necessary condition for persistence of the population in the absence of fishing, such that γ_i is defined as maximum annual spawners per spawner *in excess of replacement*. Given that maximum annual recruits per spawning biomass (α_i) times lifetime spawning biomass per recruit in the absence of fishing ($SPR_{F=0}$) must equal maximum lifetime spawners per spawner (p_i) (Myers & Mertz, 1998), it then follows that $\alpha_i = p_i / SPR_{F=0}^*$. In summary, I specify a hierarchical model for $\log(\gamma_i)$, convert γ_i to p_i (Equation 7) and then convert p_i to α_i , where α_i and β_i are used to predict recruitment $\hat{R}_{i,t}$ for the levels of spawning biomass $S_{i,t}$ that have been observed for each population. In this analysis, I use values $SPR_{F=0}^*$ and M_i^* compiled by Ram Myers in the original stock-recruit database.

Given this model, I then define the variables used in the evolutionary model as the set of life-history parameters that are comparable across different fish species worldwide (see Table 1 for list).

$$\mathbf{x}_g \equiv \{\log(M_g), \log(A_{\max,g}), \log(K_g), \log(L_{\infty,g}), \log(W_{\infty,g}), \log(A_{\text{mat},g}), \log(L_{\text{mat},g}), T_i, \log(\tau_g), \log(\rho_{R,g}), \log(\gamma_g)\} \quad (8)$$

where the vector of life-history parameters \mathbf{x}_g includes γ_g such that maximum annual spawners per spawner in excess of replacement is shrunk towards a value that is correlated both taxonomically and with other life-history parameters.

Given predicted values for life-history parameters \mathbf{x}_g for each taxon g , I calculate derived quantities that are useful for other models or management purposes (see list in Table 2). I discuss several in detail here:

1. **Intrinsic growth rate:** Many theoretical and applied studies in ecology have used the intrinsic growth rate (r) as an integrated measure of population resilience (Levins, 1969), and the parameter arises in fisheries science in the Schaeffer production model (Schaefer, 1954). I calculate r as the dominant eigenvalue for a Leslie matrix representing population growth in numbers and reproductive output, and it represents the instantaneous rate of population growth at asymptotically low population sizes; it is identical if expressed as growth rate in numbers or biomass (McAllister, Pikitch, & Babcock, 2001). The calculation requires the parameters predicted by *FishLife* (Table 1), as well as several that are not available including: the allometric scaling of asymptotic biomass and length (fixed at 3.04 based on the average from Froese et al. (2014)), the extrapolated age at zero length in the von Bertalanffy growth curve (fixed at -0.1) and the slope of the maturity ogive at 50% maturity (fixed at 25% of age at maturity). I recommend future research to incorporate these parameters into *FishLife*, although sensitivity analysis suggested that results are relatively insensitive to small changes in these values.
2. **Steepness:** Many stock assessment models use the steepness parameterization of the Beverton-Holt stock-recruit model (Mace, 1994), where steepness h_g for taxon g is defined as the proportion of unfished recruitment expected to occur when spawning biomass declines to 20% of its unfished average:

$$h_g = \frac{p_g}{4 + p_g} \quad (9)$$

where this calculation is derived, for example, by Myers and Mertz (1998) and has been re-derived with small differences elsewhere (Mangel et al., 2010 Equation 26).

TABLE 2 List of population-dynamics parameters that are predicted as a function of one or more life-history and stock-recruit parameters (listed in Table 1) for each fish species

Name	Symbol	Database
Steepness	h	FishBase + RAM
Marginal standard deviation of recruitment variability	σ_R	FishBase + RAM
Intrinsic growth rate	r	FishBase + RAM
Generation time	G	FishBase + RAM
Fishing mortality ratio at MSY	F_{MSY}/M	FishBase + RAM

3. Standard deviation for recruitment: the marginal (pointwise) standard deviation of recruitment is calculated as

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

where this standard deviation (and its standard error) can be used, for example, when fitting an age-structured surplus production model in data-poor assessments (Thorson, Rudd, & Winker, 2018).

I calculate these derived quantities for each taxon g , append them to the vector of estimated parameters, $\hat{\mathbf{x}}_g = (\mathbf{x}_g, h_g, \sigma_g^2, r_g, G_g)$, and calculate the expectation and covariance of $\hat{\mathbf{x}}_g$ using Monte Carlo sampling based on the predictive covariance of both life-history (adult) and stock-recruit (early life) parameters.

2.3 | Parameter estimation

I estimate parameters for this evolutionary model of life-history and stock-recruit parameters given life-history measurements y_{ij} in FishBase (Froese, 1990) as downloaded using *rfishbase* (Boettiger, Chamberlain, Lang, & Wainwright, 2015) on 25 August 2016 and stock-recruit data R_{ij} and S_{ij} from the Myers stock-recruit database (Myers & Mertz, 1998). Parameters are estimated using maximum marginal likelihood as implemented using Template Model Builder (Kristensen, Nielsen, Berg, Skaug, & Bell, 2016), while using the Laplace approximation (Skaug & Fournier, 2006) to integrate the joint likelihood of data and random effects with respect to random effects \mathbf{x}_g for all taxa. Further details are available in Appendix S1: Computational details.

I run this model with different degrees of complexity for evolutionary covariance Σ , and use the Akaike information criterion (AIC) to select the rank of \mathbf{L}_Σ . I then present results for the AIC-selected model, and distribute reproducible software, input data, and resulting estimates as a publicly available R package *FishLife* version 2.0.0 (<https://github.com/James-Thorson/FishLife>). I specifically provide predicted values $\hat{\mathbf{x}}_g$ for every described fish species, as well as the predictive covariance $\widehat{\text{Cov}}(\hat{\mathbf{x}}_g)$ derived using a combination of Monte Carlo sampling and a generalization of the delta method (Kass & Steffey, 1989). By publicly providing access to the code, I hope to facilitate future studies using simulation experiments to test model performance, for example, when identifying the true rank of \mathbf{L}_Σ .

2.4 | Assessment of model performance

Finally, I seek to evaluate model performance by addressing three questions:

1. Does the model accurately predict stock-recruit parameters (i.e. are predictions unbiased)?

2. Does the model precisely predict stock-recruit parameters (i.e. do predictions explain a substantial portion of among-stock variability)?
3. Does the model accurately measure its own uncertainty (i.e. are standard errors well calibrated, such that confidence intervals are likely to include the true value at a desired rate)?

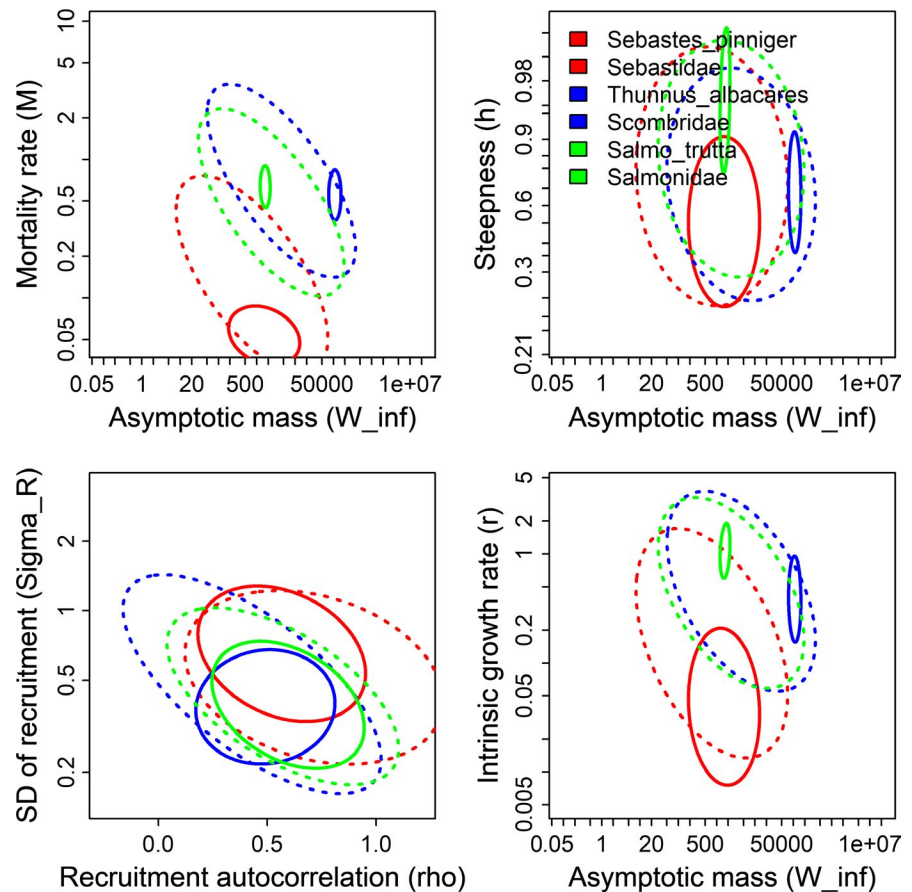
To address these three questions, I conduct a 5-fold cross-validation experiment. This experiment involves dividing the set of stocks with stock-recruit data into five equally sized partitions. I then fit the model five times: the first to stocks in partition 2–5; the second to stocks in partition 1 and 3–5, etc. For each fit, I record the predicted stock-recruit parameters (and associated standard errors), and compare these “out-of-sample” predictions with “in-sample” estimates that arise from fitting all stocks simultaneously. I then measure accuracy (question #1) by comparing out-of-sample predictions with in-sample estimates; I measure precision by calculating the variance explained by out-of-sample predictions; and I measure standard error calibration by calculating the quantile of in-sample estimates within the out-of-sample predictive distribution. This cross-validation experiment mimics the scenario of adding additional stock-recruit data from the same “data-generating process” as was used to generate the original data; if the original stock-recruit data are biased or otherwise not representative of unmeasured stocks, then this cross-validation experiment will not uncover bias arising from this issue. I therefore recommend additional model evaluation using new and/or updated stock-recruit records (e.g. extending Patrick, Cope, & Thorson, 2014), but leave this as a topic for future research.

3 | RESULTS

I first illustrate the predictive intervals for life-history and recruitment parameters for three commercially important species, canary rockfish (*Sebastes pinniger*, Sebastidae), yellowfin tuna (*Thunnus albacares*, Scombridae), and brown trout (*Salmo trutta*, Salmonidae) and the taxonomic family for each species (Figure 1). AIC selects a model that has a rank of six (i.e. \mathbf{L}_Σ has six columns), although the first three explain almost 99% of the covariance (Table 3). As expected, predictions for each individual species are much more precise (have smaller confidence interval width) than predictions for a given family, and predictions for species generally fall within the 95% confidence interval for a given family.

I next present the relationship between parameters using major axis regression (Table 3). This shows that the model fitted to life-history and stock-recruit records preserves the life-history relationships documented by Thorson et al. (2017). For example, the association with the 3rd axis of variation differs between $\log(M)$ and $\log(K)$, and also between $\log(L_{\text{inf}})$ and $\log(L_{\text{mat}})$ (see Table 3 caption for details). This then results in a negative and non-linear association between the ratio of mortality and growth rates (M/K) and the timing of maturation ($L_{\text{mat}}/L_{\text{inf}}$) as predicted originally by Holt (1958). However, *FishLife* also now fits stock-recruit records, and there is no

FIGURE 1 Predictive distribution for selected life-history and stock-recruit parameters (see Table 1) for three commercially important families (Sebastidae, Scombridae and Salmonidae) and a selected species from each family (*Sebastes pinniger*, *Thunnus albacares* and *Salmo trutta*)



evidence that the model fits these data poorly (Appendix 2: Fig. S1). By fitting to both data sets simultaneously, FishLife is able to estimate the relationship between stock-recruit and life-history parameters. The 1st axis (temperature) indicates that a 1°C increase in temperature is associated with a 0.004 increase in steepness on average and a 1% decrease in the standard deviation of recruitment. Similarly, the 2nd axis (body size) indicates that a 10% increase in asymptotic body size (W_∞) is associated with a 0.6% ($\frac{0.057}{0.828} = 0.06$) increase in recruitment autocorrelation (ρ_R), but has an essentially negligible effect on steepness. Finally, the 3rd axis (timing of maturation) shows that a 10% increase in the ratio of mortality and growth (and resulting decrease in $\frac{L_{mat}}{L_\infty}$) is associated with a 3% increase in recruitment variation ($\frac{0.052}{0.476-0.310} = 0.31$). In summary, steepness has a weak-to-non-existent relationship with body size and timing of maturity, and recruitment autocorrelation (ρ_R) has a positive association with age at maturity (A_{mat}) via axes representing increased body size and the timing of maturation.

I next visualize the predictive relationships between steepness (h) or intrinsic growth rate (r) and both natural mortality and asymptotic mass (Figure 2). This shows that steepness has a weakly positive relationship with natural mortality (Figures 2, 1st column), and a weakly negative relationship with asymptotic mass (Figures 2, 2nd column), resulting from the net effect of temperature, body size and timing of maturation patterns. Although steepness does not have a strong association with either mortality or body size, there does appear to be

some taxonomic clustering in both natural mortality and steepness values. For example, Sebastidae generally has lower values for natural mortality and steepness while Scombridae has elevated values of natural mortality and steepness. By contrast, intrinsic growth rate has a strong positive relationship with natural mortality (Figures 2, 3rd column) and a strong negative relationship with asymptotic body size (Figures 2, 4th column). Again, there is strong taxonomic clustering along this axis of variation, where Sebastidae has relatively low natural mortality and intrinsic growth rate, and is somewhat of an outlier in having a asymptotic body size in the middle range of predicted values. Finally, there is also some taxonomic signal in recruitment variance and autocorrelation (Appendix 2: Figure S2), where Sebastidae has somewhat higher recruitment variation than other taxa.

Exploring these taxonomic patterns for steepness in detail (Figure 3, left column), I find that the mode of the predictive distribution for Salmonidae is higher (0.79) than Sebastidae (0.72), Lutjanidae (0.73) or Scombridae (0.69). By contrast, intrinsic growth rate for Sebastidae is on the low-end (0.15) and genus *Sebastes* is particularly low (0.09); these values are still above those for selected Chondrythian families (Carcharhiniformes: 0.02; Lamniformes: 0.02). Meanwhile, Scombridae (0.45) and Salmonidae (0.44) have relatively high intrinsic growth rates among the fish families explored here, and Lutjanidae (0.33) is intermediate.

Finally, the 5-fold cross-validation experiment suggests that the out-of-sample predictions are an unbiased and precise measurement

TABLE 3 Summary of the dominant axes of covariation for evolutionary covariance Σ . Each value indicates the association between an axis of variation (columns) and a given parameter (rows), while the ratio of two elements of a given eigenvector is interpreted as the “slope” between these two variables (see text below Equation 2 in main text for details). For example, an increase in the 3rd eigenvector results in a smaller increase in $\log(L_{\text{mat}})$ than $\log(L_{\infty})$, suggested that movement along this axis results in a decreasing ratio of $L_{\text{mat}}/L_{\infty}$. Similarly, movement along this 3rd axis results in a larger increase in $\log(M)$ than $\log(K)$, thus resulting in a increasing ratio of M/K . Therefore, this axis represents a negative linear association between $\log(L_{\text{mat}}/L_{\infty})$ and $\log(M/K)$, and a negative and non-linear relationship between $L_{\text{mat}}/L_{\infty}$ and M/K . Finally, a slope of X between two variables that are both calculated in log-space (i.e. all variables except T , ρ_R and h) indicates that a 1% increase in one variable is associated with an approximately X% increase in the other variable. The proportion of variance explained by a given eigenvector (row “Proportion”) measures what proportion of total variance is explained by a given eigenvector

	Eigenvectors		
	1	2	3
Variance decomposition			
Eigenvalues	72.58	15.238	1.457
Proportion	0.802	0.168	0.016
Cumulative proportion	0.802	0.970	0.986
Loadings			
$\log(M)$	0.054	-0.212	0.476
$\log(A_{\text{max}})$	-0.043	0.202	-0.483
$\log(K)$	0.046	-0.214	0.310
$\log(L_{\infty})$	-0.019	0.263	0.124
$\log(W_{\infty})$	-0.044	0.828	0.397
$\log(A_{\text{mat}})$	-0.041	0.210	-0.492
$\log(L_{\text{mat}})$	-0.026	0.235	0.090
T	0.994	0.086	-0.058
$\log(\sigma_R)$	-0.013	-0.053	0.052
ρ_R	0.006	0.057	-0.116
h	0.004	-0.011	0.030

of in-sample estimates (Figure 4). In particular, the model explains 32%–57% of among-stock variance in log-marginal variance of recruitment, autocorrelation and log-maximum annual spawners per spawner. This then translates to 59%–67% reduction in variance in logit-steepness, log-Fmsy and log-intrinsic growth rate. However, estimated standard errors generally are too small, resulting in a quantile distribution that has excess mass near zero and one (Figure 5). This is particularly true for autocorrelation, which presumably has a highly skewed predictive distribution, and standard errors are best for logit-transformed steepness and log-maximum annual spawners per spawner.

4 | DISCUSSION

In this study, I have developed the first integrated life-history model for population-dynamics parameters in fishes, which simultaneously fits to public life-history and stock-recruit databases. The analysis specifically builds upon a simple model for evolution along phylogenetic lineages to reconcile both data sets, and results can be used to predict parameters for species that otherwise have no known information (Thorson et al., 2017). Importantly, this model estimates the uncertainty for each parameter (including the correlation between parameters) in a logical way that has three useful characteristics: (a) species with many life-history records are more precise than those with few or no records; (b) species are shrunk towards related species that are well-studied; and (c) uncertainty is greater for poorly studied species that have few well-studied relatives than those with many well-studied relatives.

This analysis shows that the strength of recruitment compensation (“steepness”) is not strongly correlated with the major axes of life-history variation in fishes (temperature, body size or timing of maturation), but does cluster taxonomically (e.g. with lower steepness for family Sebastidae and higher for Scombridae). By contrast, intrinsic growth rate has strong correlations with body size, as expected given the dependence of intrinsic growth rate upon natural mortality rates. By using a simple evolutionary model, I am able to predict a unique value for life-history parameters for every species in either data set, as well as all higher-level taxonomic groups of those species. This contrasts with previous attempts to estimate steepness and intrinsic growth rate, which have typically estimated a single, average value for these quantities for all species (e.g. Jensen, Branch, & Hilborn, 2012) or within a given taxonomic grouping (Shertzer & Conn, 2012).

I evaluate results by comparing predictions of steepness for higher-level taxa (e.g. for a given genus, family or order) with those from previous studies to look for differences with previously published studies (see Table 4). For example, the mode of the predictive distribution of steepness for bony fishes (Actinopterygii) is 0.74 in this study, compared with the predictive mean of 0.75 for all data sets analysed by Shertzer and Conn (2012). The current analysis did not observe the strong, positive association between steepness and asymptotic size that is predicted from size-structured community theory (Andersen & Beyer, 2015). Instead, results were consistent with Shertzer and Conn (2012), who found no strong life-history predictor for steepness. Exploring this in more detail, FishLife predictions of the slope-at-the-origin of the stock-recruit relationship (α) shows a strong negative correlation with asymptotic biomass (Appendix S2: Figure S3) as previously shown by Hall et al. (2006 Figure 1). However, this negative relationship is counter-balanced by a strong positive correlation with unfished spawning biomass per recruit ($\text{SPR}_{F=0}^*$), as previously shown by Goodwin, Grant, Perry, Dulvy, and Reynolds (2006), such that FishLife identifies little correlation of body size with either maximum lifetime spawners per spawner ($p = \alpha \times \text{SPR}_{F=0}^*$) or steepness ($h = \frac{p}{4+p}$). Furthermore, residual variability in any relationship between steepness and any single life-history parameter

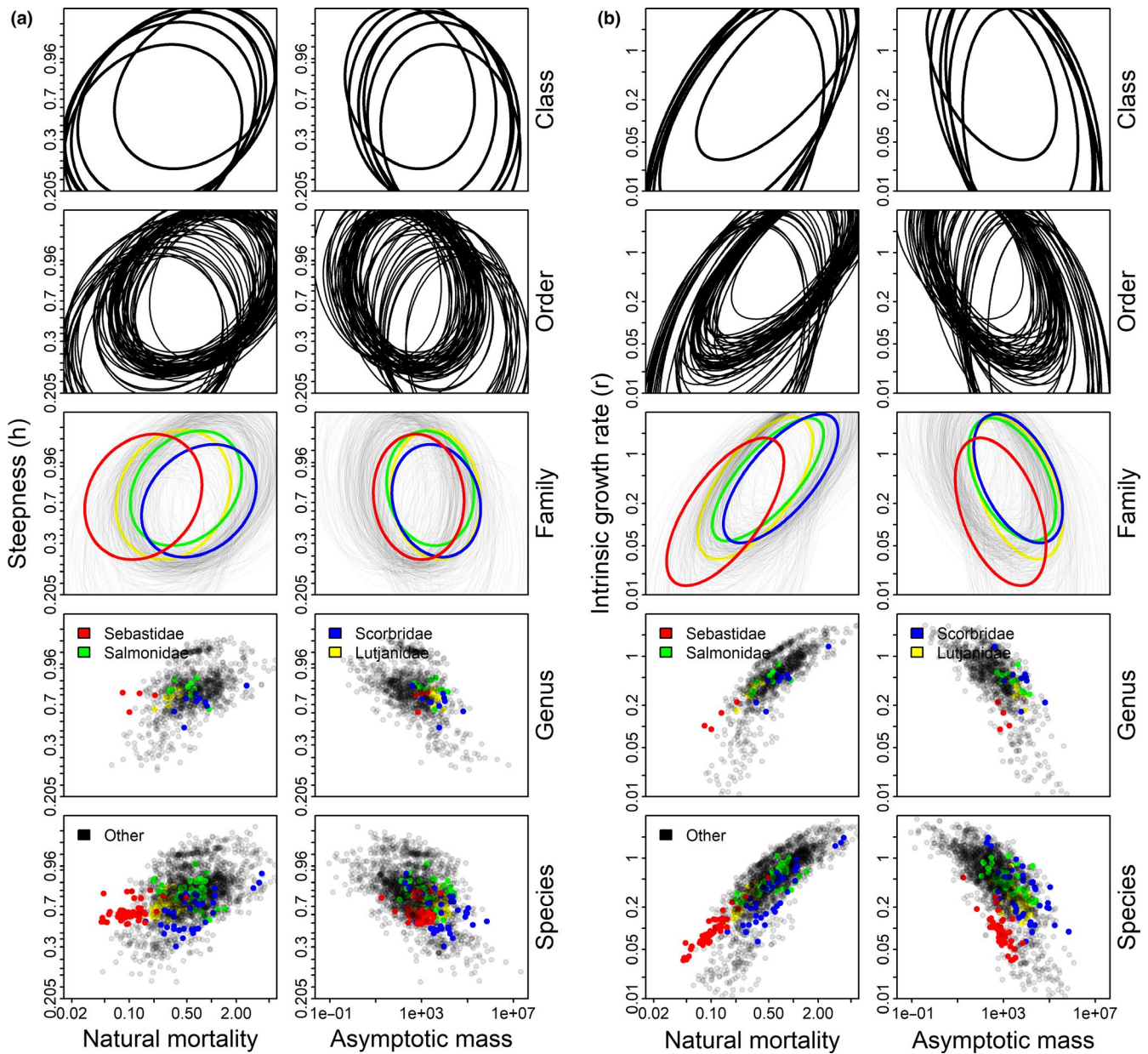


FIGURE 2 Visualization of the natural mortality rate (M , 1st and 3rd columns and plotted on x-axis on log-scale) or asymptotic mass (W_{∞} , 2nd and 4th columns and plotted on x-axis on log-scale) and steepness (h , 1st and 2nd columns and plotted on y-axis using logit scale from 0.2 to 1.0) or intrinsic growth rate (r , 3rd and 4rd columns and plotted on y-axis on log-scale) for every Class, Order, Family, Genus and Species in the database, while highlighting the predictive distribution for commercially important families (Sebastidae, Salmonidae, Scombridae and Lutjanidae). For Class, Order and Family I show the 95% predictive distribution (an ellipse, given that the model uses a multivariate normal distribution), while for Genus and Species I show the for each modelled stock in that taxon

(e.g. body size) is predictable given that steepness is a function of both slope-at-the-origin α and unfished spawning biomass per recruit ($SPR_{F=0}^*$). This is because $SPR_{F=0}^*$ is a non-linear function of many life-history parameters including growth rate, asymptotic weight, age at maturity and natural mortality, and there are three biologically interpretable axes of variation among these life-history parameters (Thorson et al., 2017), such that projecting $SPR_{F=0}^*$ or steepness onto any single parameter will not control for variation in those remaining axes of life-history variation (see also Mangel et al., 2013). I recommend further comparison of results from this integrated life-history

model with mechanistic predictions of steepness (Andersen & Beyer, 2015; Mangel et al., 2010), in particular to compare predictions of the relationship between steepness and life-history parameters under different mechanistic assumptions.

The predictive mode for steepness of genus *Sebastes* (Pacific rockfishes) is 0.61 in this study, compared with 0.58–0.78 obtained from six biannual iterations of a regional meta-analysis for these species on the US West Coast (Thorson, Dorn, & Hamel, 2019). Steepness predictions from that biannual regional meta-analysis rose sharply between 2007 and 2011, likely reflecting improved

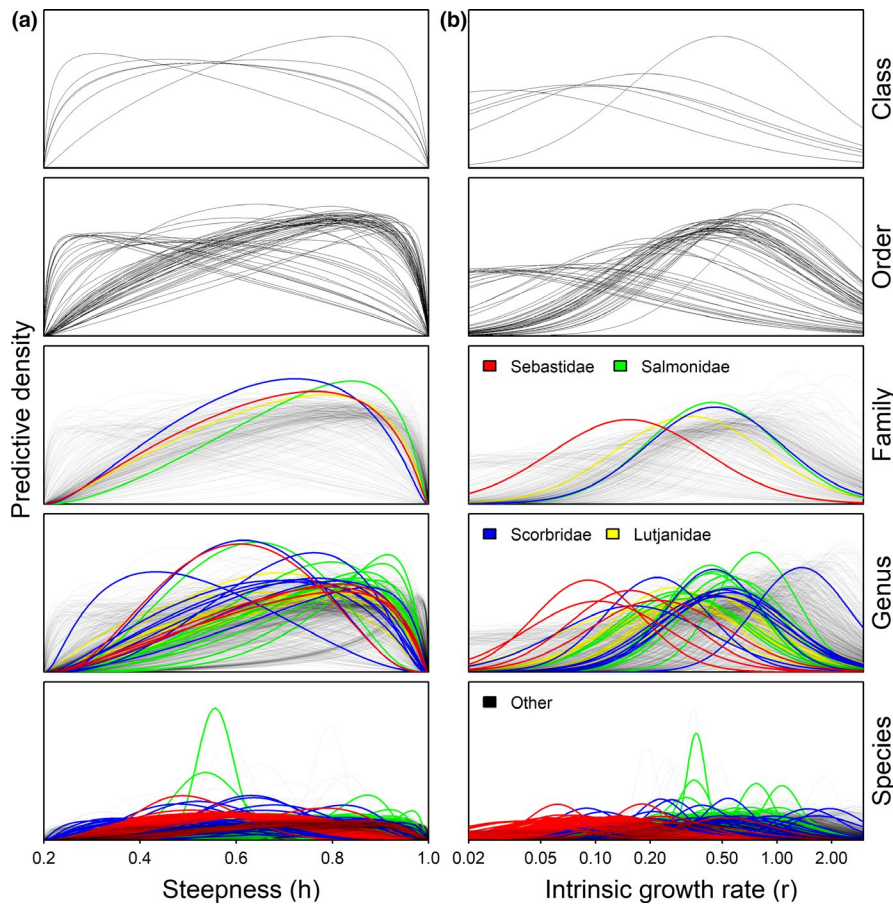


FIGURE 3 Predictive probability (y-axis) for steepness h (left column) or intrinsic growth rate r (right column) for every described class, order, family, genus and species in FishBase (panels, ordered top to bottom), with families Sebastidae, Salmonidae, Scorbridae and Lutjanidae highlighted to emphasize these particular, commercially important species

environmental conditions for West Coast rockfishes in the mid-2000s. Predictions in this paper, by contrast, are based on data from the Myers and Mertz (1998) database, prior to these years of good recruitment. Different steepness predictions from these two meta-analyses emphasize that meta-analytic results are reflective of stock-recruitment parameters during an historical period that might differ from current environmental conditions. Finally, the current analysis shows that family Sebastidae has higher recruitment variance and autocorrelation than Salmonidae (Supporting Information S1), and this is consistent with results from Thorson et al. (2014) for orders Scorpaeniformes and Salmoniformes. The low value for steepness for genus *Sebastes*, combined with unusually low mortality for their body size, causes *Sebastes* species to have an intrinsic growth rate (0.09) that is closer to several shark families (Lamniformes: 0.02; Carcharhiniformes: 0.02) than other bony fishes. Large differences in productivity among different fish genera suggest the importance of predicting life-history parameters using taxonomic information in addition to life-history theory.

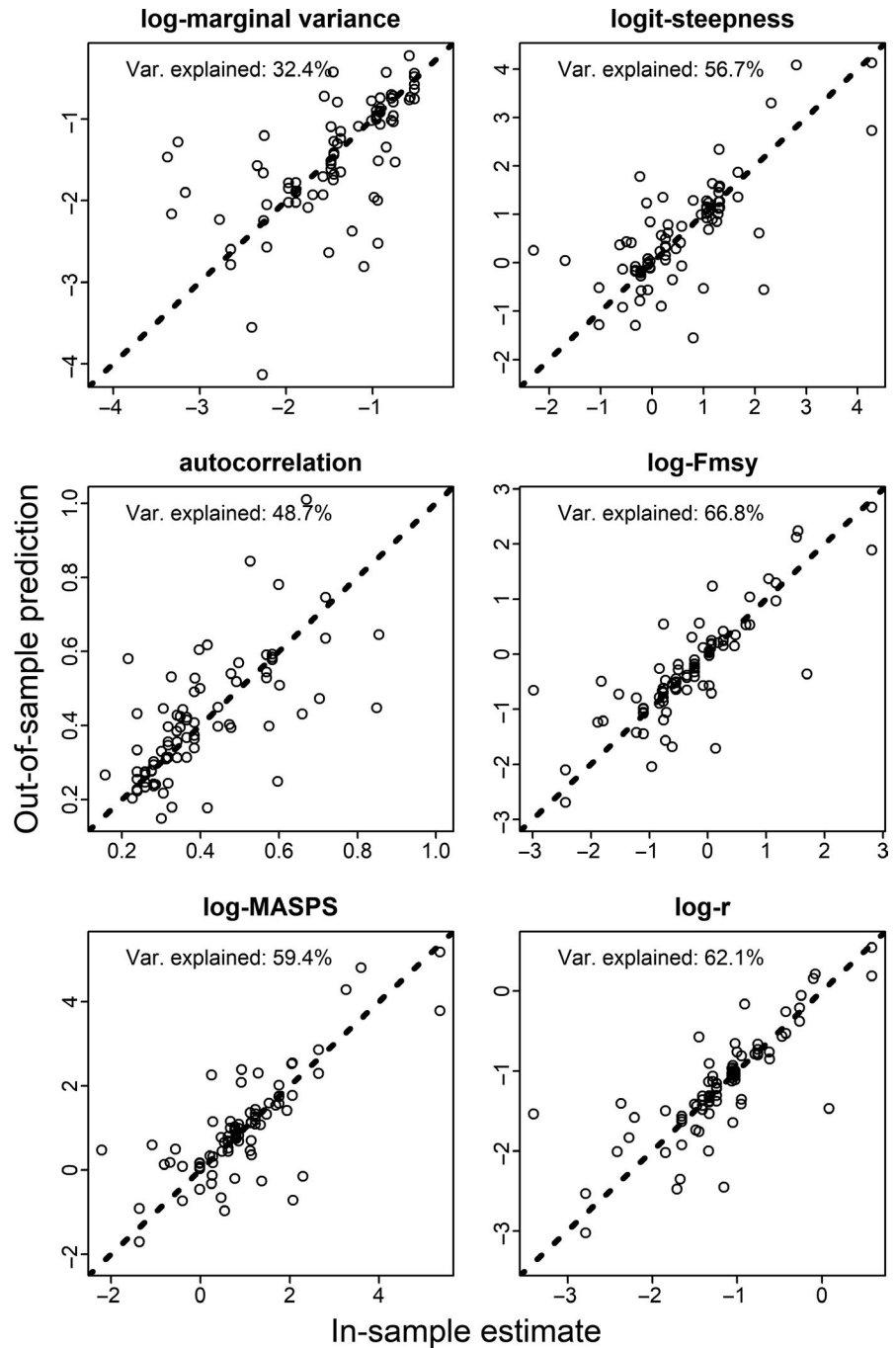
I note that any meta-analysis is confronted with a trade-off between using aggregated data (e.g. output from an assessment model) for many stocks, or using lower-level data (e.g. output from an index standardization model) for a small number of stocks (Thorson, Cope, et al., 2015b). In this study, I have fitted to the largest data sets available for both life-history parameters (FishBase) and stock-recruit estimates (the RAM database), and results are therefore sensitive to the biases that arise from using model output as “data” (Brooks

& Deroba, 2015; Dickey-Collas, Payne, Trenkel, & Nash, 2014). Although it is possible to conduct a meta-analysis for steepness using lower-level data, this has been done previously for only a small number of species (Thorson et al., 2019). I therefore recommend ongoing research to use lower-level data (e.g. individual records of size and age to estimate growth parameters) within future data-integrated life-history models to eliminate the potential bias arising from analysing model output as data in a meta-analysis.

I believe that multivariate predictions for multiple population-dynamics parameters will be useful for stock assessment, decision theory, ensemble modelling, and strategic decision-making, and discuss each of these briefly:

1. *Stock assessment*: These multivariate predictions can be used to define a joint prior distribution (or penalty) for parameters used in a Bayesian (or maximum likelihood) stock assessment model. For example, a recent data-poor assessment model using length-composition data to estimate stock status requires values for maturity, mortality, size, steepness and recruitment variability (Rudd & Thorson, 2017), and a joint prior for all of these parameters can be generated using the results. Using a joint prior distribution prevents assessments from estimating a combination of life-history parameters that are highly unlikely (Brandon, Breiwick, Punt, & Wade, 2007; Kindsvater et al., 2018), for example, by estimating high mortality M in combination with large maximum body size W_{∞} . The concern with biologically

FIGURE 4 Model performance for estimating stock-recruit parameters, assessed using a 5-fold cross-validation experiment for three estimated parameters (log-marginal variance, autocorrelation and log-maximum annual spawners per spawner) and three derived quantities (steepness, log-fishing mortality rate at maximum sustainable yield and log-intrinsic growth rate), showing the out-of-sample prediction when excluding each of the stocks with available stock-recruit data (y-axis) versus estimates when fitting to all stocks with available stock-recruit data (x-axis); each panel also lists the percentage of variance explained (one minus the variance of the difference between x-axis and y-axis values divided by the variance of y-axis values)



implausible life-history values has motivated development of data-poor assessment models that employ life-history invariants to restrict parameter inputs to plausible values (Hordyk, Ono, Sainsbury, Lonergan, & Prince, 2015; Kokkalis, Eikeset, Thygesen, Steingrund, & Andersen, 2017). Similarly, using multivariate predictions as a joint prior distribution would restrict parameter estimates to plausible life-history strategies for any assessment model that can use multivariate prior distributions. However, I note that using a prior distribution for life-history information creates a trade-off between bias (if using information from other stocks) and imprecision (if ignoring information from other stocks). I therefore recommend further simulation

testing to explore this bias-variance trade-off for steepness and other life-history parameters.

2. *Operating model development:* Similarly, a multivariate distribution for life-history parameters can guide the design of simulation experiments that are widely used to evaluate likely performance for ecological models or management procedures (Sainsbury, Punt, & Smith, 2000). In particular, analysts could use predictions to generate plausible population-dynamics parameters for different life-history types, for example, by using the predictive distribution for all parameters for genus *Sebastes* to evaluate harvest strategies given simulated dynamics for Pacific rockfishes (Punt, 2008). This would allow researchers to link management

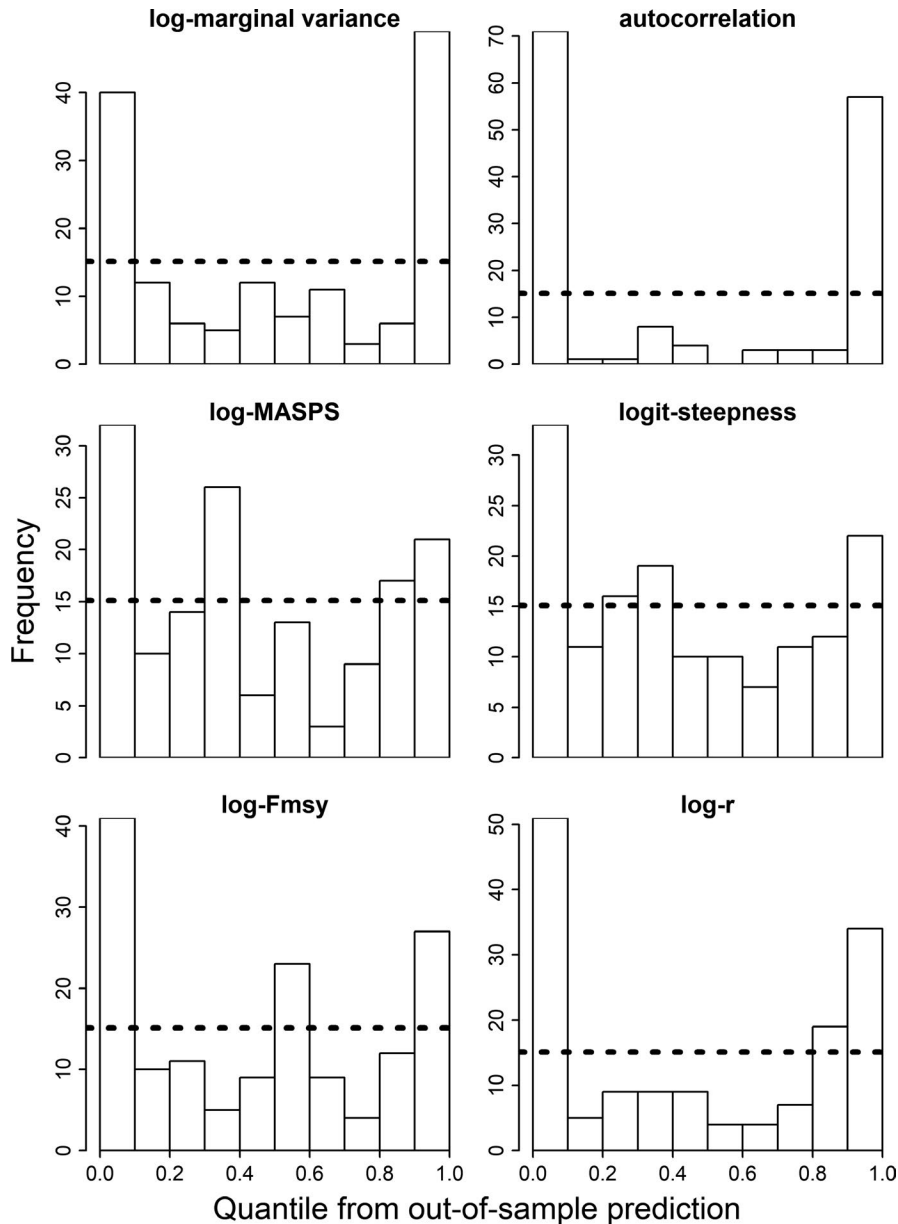


FIGURE 5 Model performance for estimating the standard error of stock-recruit parameters, assessed using a 5-fold cross-validation experiment (see Figure 4 caption), showing the quantile of estimates when fitting to all stocks with available stock-recruit data, compared against the predictive distribution when excluding each of the stocks. A well-performing predictive distribution will be approximately uniform (dashed horizontal line), while a model with too small of standard errors will have excess mass near 0 and 1, while a model with too large of standard errors will have excess mass near 0.5

decision theory to the likely population dynamics for all species worldwide.

3. *Ensemble modelling*: Stock assessment will generally be more robust if management advice is based on an ensemble of alternative life-history assumptions (Stewart & Martell, 2015). Results from a model ensemble can be presented using a decision table (Hilborn, Pikitch, & Francis, 1993) or via ensemble weighting of model results (Anderson et al., 2017), but either presentation requires some objective method for determining the weight of different unknown "states of nature." I therefore recommend that stock assessments increasingly present results using an ensemble of life-history values, where model weights can be obtained from the multivariate distribution for these parameters.
4. *Strategic decisions*: Finally, strategic decision-making in ecosystem-based management is increasingly informed by models that include dynamics for multiple species and physical drivers (Fulton et al.,

2011). For example, ecosystem models have been used to forecast likely impacts of ocean acidification, temperature changes or invasive species on fisheries potential (Cheung, Lam, & Pauly, 2008; Marshall et al., 2017; Morello et al., 2014). However, these models often require values for population-dynamics parameters for several to hundreds of species simultaneously, and there is increased interest in characterizing uncertainty in ecosystem model predictions given uncertainty about population-dynamics parameters (Collie et al., 2016; Link et al., 2012). One source of uncertainty is fixing biological parameters (and their associated standard errors), and this uncertainty could be dealt with uniformly across different species or taxonomic groups using results from this analysis.

For these reasons and more, I encourage continued research regarding data-integrated life-history modelling. These models lie at the intersection of evolutionary, life-history and stock-recruit

TABLE 4 Mode of the predictive distribution for steepness (h) and intrinsic growth rate (r) for bony fishes (Actinopterygii) and common taxonomic orders and families (with predictive standard deviation for a species with no data in a given taxon listed in parentheses). Also shown is the range of predictive mean steepness (and range of predictive standard deviations) for West Coast rockfishes from six biannual meta-analyses compiled by Thorson et al. (2019), the sample mean (and sample standard deviation) for steepness from all compiled data sets from Shertzer and Conn (2012)

	Steepness (h)			Intrinsic growth rate (r)
	This study	Thorson et al. (2019)	Shertzer and Conn (2012)	This study
Class				
Actinopterygii	0.74 (0.23)	–	0.75 (0.15)	0.49 (0.83)
Order				
Carcharhiniformes	0.36 (0.20)	–		0.02 (0.19)
Lamniformes	0.36 (0.20)	–		0.02 (0.14)
Clupeiformes	0.74 (0.23)	–		0.61 (0.96)
Gadiformes	0.63 (0.23)	–		0.21 (0.46)
Perciformes	0.73 (0.22)	–		0.46 (0.71)
Pleuronectiformes	0.76 (0.21)	–		0.49 (0.79)
Scorpaeniformes	0.74 (0.23)	–		0.39 (0.63)
Family				
Sebastidae	0.72 (0.21)	–		0.15 (0.20)
Salmonidae	0.79 (0.18)	–		0.44 (0.43)
Scombridae	0.69 (0.20)	–		0.45 (0.48)
Lutjanidae	0.73 (0.21)	–		0.33 (0.41)
Genus				
Sebastes	0.61 (0.16)	0.58–0.78 (0.15–0.20)		0.09 (0.07)

theory and can translate insights from these theories into tools for applied ecologists and fisheries managers. For this purpose, I distribute the predictions of life-history and stock-recruit parameters (and associated confidence intervals) within R package *FishLife* version 2.0.0 and interested users can read the vignette to learn more.

ACKNOWLEDGEMENTS

I give a huge thanks to H. Winker, who contributed ideas and example code for calculating intrinsic growth rate from adult and juvenile life-history parameters. I also thank K. Kristensen, H. Skaug, and the developers of Template Model Builder, without which this analysis would not be feasible. The analysis is possible due to the pioneering work R. Myers in assembling the RAM stock-recruit database, and I thank D. Hively and C. Minto for preserving and maintaining it. I also thank R. Froese, D. Pauly and others for assembling and maintaining the FishBase life-history archive; the RAM and FishBase databases are a tremendous asset for fisheries scientists worldwide. Finally, I think K. Shertzer, J. Hastie, M. McClure, J. Munyandorero, M. Mangel, H. Winker, and three anonymous reviewers for comments on an earlier draft.

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DATA AVAILABILITY STATEMENT

All data used are publicly available. FishBase life-history information is available from www.FishBase.org, as accessed using R package

rfishbase. Stock-recruit data are from the RAM stock-recruit database, as maintained by D. Hively and C. Minto. Both data sets are available in R package *FishLife* release 2.0.0 at <https://github.com/James-Thorson/FishLife>.

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SUPPORTING INFORMATION

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