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Complete List of Authors:	Nadon, Marc; Joint Institute for Marine and Atmospheric Research; NOAA, Pacific Islands Fisheries Science Center; University of Miami, Rosenstiel School of Marine and Atmospheric Science Ault, Jerald; University of Miami, Rosenstiel School of Marine and Atmospheric Science
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A stepwise stochastic simulation approach to estimate missing life history parameters for data-poor fisheries

Running headline: Life history parameters for data-poor fisheries

Marc O. Nadon^{1, 2, 3} and Jerald S. Ault³

¹ Joint Institute for Marine and Atmospheric Research, 1000 Pope Road, Honolulu, HI 96822 U.S.A.
² Pacific Island Fisheries Science Center, NOAA Fisheries, 1845 Wasp Boulevard, Honolulu, HI 96818 U.S.A.
³ University of Miami, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, FL 33149 U.S.A.

Corresponding author:
Marc Nadon – marc.nadon@noaa.gov
1845 Wasp Boulevard, Honolulu, HI 96816, USA
Phone: 808-725-5317

Abstract

Coastal fisheries are typically characterized by species-rich catch compositions and limited management resources which typically leads to notably data-poor situations for stock assessment. Some parsimonious stock assessment approaches rely on cost-efficient size composition data, but these also require estimates of life history parameters associated with natural mortality, growth, and maturity. These parameters are unavailable for most exploited stocks. Here, we present a novel approach that uses a local estimate of maximum length and statistical relationships between key life history parameters to build multivariate probability distributions that can be used to parameterize stock assessment models in the absence of species-specific life history data. We tested this approach on three fish species for which empirical length-at-age and maturity data were available (from Hawaii and Guam) and calculated probability distributions of spawning potential ratios (SPR) at different exploitation rates. The life history parameter and SPR probability distributions generated from our data-limited analytical approach compared well with those obtained from bootstrap analyses of the empirical life history data. This work provides a useful new tool that can greatly assist fishery stock assessment scientists and managers in data-poor situations, typical of most of the world's fisheries.

Key words: coral reef fish, Beverton-Holt invariants, stock assessment, Bayesian priors, growth, maturity, longevity, natural mortality, spawning potential ratio

Introduction

Coastal fisheries provide livelihoods and sustenance for hundreds of millions of people worldwide, particularly in poorer tropical countries (Pauly et al. 2005). These fisheries are often characterized by highly diverse catch compositions, sometimes reaching hundreds of species, and are mostly managed with limited financial and human resources, if managed at all. For most of these fisheries, limited information exists on historical catches, fishing effort, and baseline population abundances (Fenner 2012). These issues make assessing these fisheries highly problematic. Recently, methods have been proposed for data-poor situations that rely mainly on cost-effective size composition data and some basic demographic knowledge of growth, maturity, and longevity (Ault et al. 1998, 2008, 2014, Gedamke and Hoenig 2006, Hordyk et al. 2015). However, even these simple data requirements are often unmet due to a lack of life history (LH) information for either a particular region or even globally. Specifically, Froese and Binohlan (2000) have estimated that only 1200 out of 7000 (about 17%) of exploited species worldwide have some life history data. Here, we propose a novel, standardized approach to obtain probability distributions of LH parameters for under- and un-studied species by employing a stepwise Monte Carlo simulation approach based on a meta-analysis of published parameters and some relatively well-known relationships between individual parameters.

Beverton and Holt (1959) and Beverton (1963) were the first to identify fundamental linkages between LH parameters in fishes. They observed that: (1) natural mortality rate M is positively correlated to von Bertalanffy's Brody growth coefficient K , such that the ratio of M/K is typically close to 1.5 (i.e., whereas longer lived fishes tend to grow more slowly); (2) length at 50% maturity (L_{mat}) is positively correlated to asymptotic length L_{inf} where the ratio $L_{\text{mat}}/L_{\text{inf}}$ is generally around 0.66 (i.e., species tend to mature at a specific fraction of their maximum size);

and, (3) von Bertalanffy growth model coefficients L_{inf} and K are negatively correlated following a general power function of the form $L_{\text{inf}} \sim K^{-h}$; where h is typically about 0.5. These ratios, generally referred to as Beverton-Holt (BH) invariants (Charnov 1993), have been shown to be related to the maximization of reproductive output (Jensen 1996, 1997, Charnov 2008). As a consequence, these relationships have likely been conserved through natural selection, as originally theorized by Beverton and Holt (1959). Some recent studies (e.g., Prince et al. 2015) noted that these “invariants” may actually differ significantly between taxonomic groups, and thus are better retained within taxa.

One important interest in studying these relationships is their potential use in the estimation of elusive LH parameters such as M by relating these to more tractable ones, such as L_{inf} , K , and perhaps water temperature (see Kenchington 2014 for a review of other empirical M relationships). Recent studies have proposed other relationships related to maximum length and optimum length (Froese and Binohlan 2000, 2003, Jarić and Gačić 2012). These studies were mainly concerned with imputing estimates for individual unavailable parameters. However, it is not clear how these relationships might be used to generate complete multivariate distributions for all key LH parameters (e.g., L_{inf} , K , L_{mat} , M) given that these are all typically correlated to some degree. Standard multivariate distributions (e.g., multivariate normal) can describe the variance-covariance structure of multiple parameters, but preclude the use of more complex relationships between parameters (e.g., power, exponential, polynomial) and non-normal error distributions (e.g., log-normal, gamma).

As a solution, we propose using a stepwise stochastic simulation approach that seeks to preserve the inherent correlation structure between these parameters, an approach analogous to the “sequence of regressions” (or fully conditional specification - FCS) method used for multiple

imputation of missing data (Raghunathan et al. 2001, van Buuren 2007, Ellington et al. 2015). To accomplish this, we first reviewed the literature on the life history of six commonly targeted families of coral reef fishes to generate family-specific models linking the four main LH parameters: $L_{\text{inf}} \sim L_{\text{max}}$, $K \sim L_{\text{inf}}$, $M \sim K$, and $L_{\text{mat}} \sim L_{\lambda}$ where L_{max} is a local estimate of maximum length and L_{λ} is the expected length at oldest recorded age (i.e., the length predicted by a specific growth curve for the oldest age; see Table 1 for definitions). With these models, it is theoretically possible to generate the underlying complex multivariate probability distributions for these parameters by taking successive random samples from the estimated regression models, starting with a local estimate of L_{max} . Here, we tested this approach for three well-studied species for which empirical data on lengths, ages, and maturity were available. We used bootstrap analyses to generate probability distributions of LH parameters from biological studies and compared these distributions to those obtained through our stepwise approach. Finally, we derived spawning potential ratios (SPRs) at various fixed exploitation rates using these imputed life history distributions and compared the two resulting datasets.

Methods

The approach presented here only requires a local estimate of L_{max} to generate probability distributions of missing LH parameters. To do so, it is first necessary to model the family-level relationships between these parameters using published estimates from growth and maturity studies.

Life history parameter datasets

We obtained LH parameters from a synthesis of the literature for 6 commonly exploited families of coral reef fishes: surgeonfishes (Acanthuridae), jacks (Carangidae), emperors (Lethrinidae), snappers (Lutjanidae), goatfishes (Mullidae), and parrotfishes (Scaridae) (see

Supplementary Material S1 for sources). Unfortunately, we could not assemble a dataset comprised of raw length, age, and maturity data given that such information is rarely published and generally difficult to obtain for the large number of species that we targeted. These data could have been useful in a hierarchical meta-analysis modeling context (Helser et al. 2007, Thorson et al. 2014, 2015). Instead, we obtained fitted parameter estimates for growth (L_{inf} , K , a_0) and maturity (L_{mat}), in addition to longevity (a_{λ}) and L_{max} (see Table 1 for definitions). In all of these studies, length dependent on age data were fitted using the von Bertalanffy growth equation,

$$(1) \quad L_a = L_{\text{inf}}(1 - e^{-K(a-a_0)})$$

where L_a is the expected length at age a . Although we could have potentially taken L_{max} values from other local data sources (e.g., visual surveys, catch records), we had limited access to such datasets. We also avoided using reported “world-record” lengths as L_{max} since these can represent anomalous individuals and are not reported for all species. If multiple studies existed for a single species, we kept the parameters from the most in-depth and recent studies, with the exception of longevity, for which we kept the greatest value found in any study. If an individual study provided separate parameters for different localities, we averaged these parameters (if the study had not already provided the averaged values). Most growth studies either did not attempt to separate sexes (67%) or did not identify differences in growth between sexes (28%). Only 5% of studies reported some differences in growth between sexes. For these, growth parameters fitted separately for males and females were averaged together. On the other hand, maturity studies were generally sex-specific: for species with different length-at-maturity between sexes, the female L_{mat} was retained (since spawning potential ratio is related to female spawning biomass, see details further down). Parameters L_{inf} , L_{mat} , and L_{max} reported in standard or fork

lengths were converted to total length (TL, mm) using published conversion factors. Time-based parameters (K , a_0 , a_λ) expressed in units other than years were converted to that time unit. Finally, natural mortality rates M were estimated from longevity by applying the procedure of Alagaraja (1984), similar to Hoenig (1983) and Hewitt and Hoenig (2005), assuming that 5% of a cohort survives to the observed maximum age (a_λ) :

(2)
$$M = \frac{-\ln(0.05)}{a_\lambda}$$

We used the 5% cohort survivorship value based on the analyses of Nadon et al. (2015) which showed that this is an appropriate survivorship value for coral reef fishes. We did not have independent estimates of M *per se* and had to rely on this longevity-based approach. Although there are other data-poor methods for estimating natural mortality, involving other parameters (e.g., K , L_{inf} , L_{mat} , water temperature), two recent comprehensive reviews on the subject clearly suggest that longevity-only methods are the best performing (Kenchington 2014, Then et al. 2015). These studies also raised two important points concerning this approach: (1) the importance of selecting an appropriate survivorship parameter; and (2) the potential difficulty in obtaining a representative longevity value in heavily exploited stocks. Regarding the first point, although we selected a survivorship value of 0.05, for the reason explained above, the M estimates obtained using our data-poor approach can easily be converted to M estimates based on a different survivorship value by simply converting M to longevity (by inverting equation 2) and re-calculating M from longevity using a different survivorship value. Regarding the second point, we tried to alleviate this concern as much as possible by selecting the oldest recorded age, regardless of location, as our measure of longevity. It was, unfortunately, impossible to only select longevity estimates from un-exploited stocks given that these are, of course, extremely rare.

We rejected studies where growth parameters came from length-frequency or mark-recapture analyses (i.e., we only kept studies based on hard structure ageing, which are generally considered more reliable), a_0 was very negative (< -2 years), the authors expressed concerns about their results, or parameter estimates were derived from empirical relationships. We also rejected life history studies from regions with annual mean sea surface temperatures below 20 °C due to the well-known effects of water temperature on growth and longevity (Pauly 1980, Jobling 1994, Choat and Robertson 2002). We decided not to add temperature as a variable in our regression models since the families targeted in this current study were mostly tropical, resulting in only a few studies that were discarded (15 out of 167, mostly jacks). However, we did retain growth and maturity information from 2 goatfish studies from colder water ($< 20^{\circ}\text{C}$) regions (i.e., Mediterranean Sea) because of a low sample size for this family, but we did not retain their longevity values. It is also important to note that we did not attempt to control for intra-specific regional differences in LH parameters, thus we analyzed all parameters globally. This was due mainly to the limited number of growth and maturity studies, where most species have one set of LH parameters from a single location. Intra-specific regional variability in LH parameters are thus simply added to the overall error variability in our models, in addition to inter-specific variability (where most of the variability in LH parameters is likely to be found).

After completing the literature review described above, we found growth information for 167 of the 560 species that are currently listed for the 6 families included in our analyses (Table 2). Of those 167, we found size-at-maturity information for 97 species. A total of 15 species were discarded because their growth and longevity information came from regions where mean SST was below 20°C. Furthermore, 6 species were discarded in some of the models for being clear outliers. The L_{mat} values for *Lethrinus laticaudis* (Ayvazian et al. 2004) and *Lutjanus*

190 *campechanus* (White and Palmer 2004) corresponded to very low $L_{\text{mat}}/L_{\text{inf}}$ ratios (0.46 and 0.37,
191 respectively) which were far lower than for other species in their family. These ratios were also
192 far lower than the predicted ratio based on the theoretical maximization of reproductive output
193 (~ 0.66 ; Jensen 1996). We removed the L_{inf} and K values for the goatfish *Mulloidichthys*
194 *vanicolensis* since they were clear outliers; the ageing for this species was done using un-
195 validated annual otoliths rings, which may be a reason for this discrepancy (Cole 2009).
196 Similarly, we discarded growth and longevity parameters for the surgeonfish *Acanthurus*
197 *tristegus*, since Longenecker et al. (2008) used (presumed) daily growth rings that resulted in a
198 lifespan estimate much lower than anything previously recorded for surgeonfishes (3 years vs. 20
199 years for the next surgeonfish species with the shortest reported lifespan). We removed the small
200 parrotfish *Sparisoma atomarium* from our meta-analysis since this is an extremely small species
201 ($L_{\text{inf}} = 110$ mm) with very fast growth ($K=1.8$) and short lifespan (3 years) that could not be
202 properly modeled with other parrotfishes and was a clear outlier. Finally, we removed a very low
203 (and unlikely) longevity estimate for the parrotfish *Calotomus carolinus* from a study in Guam
204 (Taylor and Choat 2014). Other parrotfish longevity estimates in this study were low compared
205 to values reported elsewhere. For example, the parrotfish *Scarus rubroviolaceus* has a maximum
206 lifespan estimate of 22 years around Oahu, Hawaii (Howard 2008), and 20 years in the
207 Seychelles (Grandcourt 2002), while the estimate for the same species around Guam was only 6
208 years (Taylor and Choat 2014).

209 **Life history parameter models**

210 A preliminary look at the distribution of LH parameters and Beverton-Holt invariants
211 (Charnov 1993) revealed important differences in the distributions and ranges of certain
212 parameters between families (Table 2), which is consistent with observations from previous

studies (Beverton and Holt 1959, Choat and Robertson 2002, Prince et al. 2015). We therefore conducted all analyses at the family level.

We built statistical regression models for the empirical relationships between pairs of LH parameters for each of the 6 families (Bolker 2008, Fox 2008). These models were built using total fish lengths (TL) reported in millimeters. We fitted maximum-likelihood models to the parameter pairs with the closest relationships: $L_{\text{inf}} \sim L_{\text{max}}$, $L_{\text{mat}} \sim L_{\text{inf}}$, $K \sim L_{\text{inf}}$, and $M \sim K$ (Beverton and Holt 1956, Pauly 1980, Beverton 1992, Jensen 1996, Stamps et al. 1998, Froese and Binohlan 2000, 2003, Binohlan and Froese 2009, Gislason et al. 2010). We also tested the use of a 2-variable model to predict M which included the L_{max} variable (in addition to K , similarly to the model described in Pauly 1980). Additionally, we tested L_{λ} (expected length at the oldest measured age) as a replacement for L_{inf} as a predictor of L_{mat} (Fig. 1). For all four models, we tested three deterministic functions (linear, power, and exponential) and two error probability distributions (normal and lognormal). We selected the best model based on an in-depth review of scatterplots and other diagnostics (to select an adequate linear or non-linear function) and residual error distributions (to select an appropriate probability distribution). Based on published empirical and theoretical results, we did expect certain relationships to be linear ($L_{\text{inf}} \sim L_{\text{max}}$ and $L_{\text{mat}} \sim L_{\text{inf}}$ or L_{λ}) and others to be curvilinear ($K \sim L_{\text{inf}}$ and $M \sim K$) and these relationships were typically explored first. However, we did not assume *a priori* any model structure (i.e., functional form or error distribution), we simply let the data and diagnostics determine the most appropriate model. For curvilinear relationships, we log-transformed the response variable (K or M) and fitted either an exponential or power function with a lognormal error distribution. The a_0 parameter was originally described using a triangular probability distribution independently from the other parameters, as we did not observe any significant

correlation between this parameter and L_{inf} or K (as opposed to Helser et al. 2007). However, after running some preliminary analyses, we found no measurable impact of a_0 variability on L_λ and L_{mat} and we simply fixed this parameter to -0.3 (the overall average for the species in our dataset).

Once these four LH parameter models were established for each family, we used the iterative approach described in Figure 1 to build multivariate probability distributions of the four principal LH parameters (L_{inf} , K , M , and L_{mat} ; referred to as the “data-poor” approach in the rest of the document). The first step in this process was to draw a random L_{max} and use the $L_{\text{inf}} \sim L_{\text{max}}$ model (step A in Fig. 1) to draw a random L_{inf} . From this random L_{inf} , a K value was drawn from the $K \sim L_{\text{inf}}$ model (step B) which was then used to draw a random M from the $M \sim K + L_{\text{max}}$ model (step C). Finally, we tested two models to draw a random L_{mat} : the $L_{\text{mat}} \sim L_{\text{inf}}$ and $L_{\text{mat}} \sim L_\lambda$ models (step D). For the second model, we had to first calculate L_λ using the von Bertalanffy equation from the L_{inf} , K , a_0 , and longevity parameters drawn during the same iteration (longevity being derived back from M using equation 2). We tested both model fits (using the coefficient of determination r^2) and ultimately decided on the $L_{\text{mat}} \sim L_\lambda$ model, which is the reason why it is presented as step D in Figure 1 (see Results for more details). It is important to note that the error distributions do not include the uncertainty in the regression coefficients (Fox 2008). To do so, we used the regression coefficient variance-covariance matrix to draw random sets of coefficients from a multivariate normal distribution and then calculated expected values at each iteration. This entire process (Fig. 1) was repeated for 5000 iterations to build multivariate distributions describing the variance and covariance of all 4 LH parameters. At each iteration, we also calculated spawning potential ratios (SPRs, see next section).

Testing the data-poor approach

We evaluated the precision and accuracy of the data-poor approach by comparing the probability distributions of LH parameters obtained in this way versus the probability distributions originating from well-conducted growth and maturity studies (referred to as the “data-rich situation” in the rest of the text). We selected 3 growth and maturity studies from Hawaii and Guam for which we had access to empirical length, age, and maturity data: *Scarus rubroviolaceus* (Howard 2008), *Naso unicornis* (Eble et al. 2009), and *Lethrinus harak* (Taylor and McIlwain 2010). We first used the approach described above to obtain “data-poor” probability distributions of LH parameters for those 3 species. The $L_{\max}$ values used for this approach came from an extensive underwater visual census dataset collected by the National Oceanic and Atmospheric Administration in Hawaii and Guam (Williams et al. 2011). We used the 99th percentile of lengths in this dataset to obtain $L_{\max}$ to reduce the risk of using spurious length measurements from divers. Furthermore, since there was uncertainty associated with $L_{\max}$ estimates derived from our survey dataset, we used a bootstrapping approach to estimate the $L_{\max}$ probability distributions from which random values could be sampled.

To generate probability distributions for the “data-rich” situation, we bootstrapped the empirical length, age, and maturity observations for the 3 selected studies since these did not report the error associated with their fitted parameter estimates. Fish collected for growth/maturity studies are typically selected to be representative of an entire species’ size range (i.e., once researchers have sufficient average-sized specimens, they shift their focus to capturing small and large individuals until they have a representative size range). To reflect this, we stratified the bootstrapping of the raw dataset for each species in three size categories (small – bottom 30% of length range, medium, and large – top 30% of length range). We ran the

bootstrapping procedure for 5000 iterations to obtain probability distributions of the LH parameters presented in these studies.

We compared the probability distributions of all 4 LH parameters obtained in the way described above with the ones obtained using our novel data-poor approach. To assess precision, we compared the widths of the data-poor distributions (using standard deviations - SD) with those of the data-rich distributions (SD ratio = $SD_{\text{data-poor}} / SD_{\text{data-rich}}$). To assess accuracy, we calculated the standardized distance between the medians of the data-poor and data-rich distributions where relative error (RE) = $(\text{median}_{\text{data-poor}} - \text{median}_{\text{data-rich}}) / \text{median}_{\text{data-rich}} \times 100$.

For both the data-poor and data-rich situations we calculated SPR, a measure of stock sustainability status, at various fishing mortality rates ranging from close to zero to $4 \times M$ where M was derived from the oldest measured age for all 3 species (12 years for *L. harak* Taylor and McIlwain 2010; 54 years, *N. unicornis*, A. Andrews pers. comm.; 22 years, *S. rubroviolaceus*, Howard 2008). We used an age-structured numerical population model to make these calculations. In this model, numerical abundance at age a was estimated through the use of an exponential mortality function. Length at age was derived using the von Bertalanffy growth equation. This numerical model was used to obtain spawning stock biomass (SSB) by summing over individuals in the population between the age of sexual maturity (a_m ; age where 50% of individuals are mature, with knife-edge assumption) and 1.5 times the oldest recorded age (a_λ),

$$(3) \quad SSB = \sum_{a_m}^{1.5a_\lambda} \bar{N}_a \bar{W}_a$$

where $\bar{N}_a$ is the average abundance at age a and $\bar{W}_a$ is the mean weight of individuals at age a .

The model was run using weekly timesteps. Average abundance at age was modeled using the following equation:

$$(4) \quad \bar{N}_{a+\Delta a} = \bar{N}_a e^{-(S_a \cdot F + M) \Delta a},$$

where F and M are fishing and natural mortality, respectively. S_a , proportional selectivity at age a , was treated as “knife-edged” selectivity and was derived from a specific length based on the size composition of the catch and the translation of length to age via the von Bertalanffy growth relationship (similarly to Nadon et al. 2015). We used data from the Hawaii commercial trip report and Marine Recreational Information Program for *S. rubroviolaceus* and *N. unicornis*, and the Guam creel survey data for *L. harak* to look for a clear jump in selectivity in the smaller size bins (i.e., a disproportionate increase in abundance from the previous size bin) to select an appropriate size at first capture. These size-at-first capture values were 260 mm for *S. rubroviolaceus* and *N. unicornis*, and 160 mm for *L. harak* (total lengths). We examined the sensitivity of our model comparisons to different selectivity values and did not find important differences. Weight (W) dependent on length (L) relationship parameters (α, β , where $W = \alpha \cdot L^\beta$), necessary for SPR calculations, were obtained from the literature (e.g., Kulbicki et al. 2005). These values are easily calculated and are typically available from local studies. We obtained these values from the same studies that provided growth and maturity information for our 3 test species. Finally, a stock’s theoretical maximum reproductive biomass occurs when there is no fishing (i.e., $F=0$). SPR at various fishing mortality rates F was computed as the ratio of the SSB at a given F relative to that of an unexploited stock:

$$(5) \quad SPR_F = \frac{SSB_F}{SSB_{F=0}}$$

We compared the SPR distributions between the data-poor and data-rich scenarios with the same approach used for the LH parameter distribution comparisons.

Finally, due to concerns with biased $L_{\max}$ values in heavily fished stocks, we tested the effect of using $L_{\max}$ values 10%, 20%, and 30% smaller than the “true” value on LH parameters and SPR estimates.

Results

Life history parameter models

Maximum size in a representative local sample ($L_{\max}$) was generally a good predictor of $L_{\inf}$, with a reasonably small standard error of about 20 mm for most families (Table 3). We used a normal error distribution for most families except for jacks where we used a log-normal distribution to take into account increasing $L_{\inf}$ variability with $L_{\max}$ (i.e., the variance of the log-normal distribution is proportional to the square of its mean). We also had to use a size break point in our models for jacks and snappers, as there was an important increase in variability in $L_{\inf}$ beyond certain $L_{\max}$ values that could not be taken into account by the properties of the log-normal distribution (900 mm TL for jacks and 500 mm TL for snappers; Fig. 2). The growth parameter K followed a decreasing, curvilinear trend with increasing $L_{\inf}$ which was described using either an exponential or power function, depending on the family (Fig. 2). Variability in K generally decreased with increasing $L_{\inf}$ which was properly described by a log-normal error distribution (Table 3). Goatfishes were an exception with no clear trend between $L_{\inf}$ and K or increases in variability with $L_{\inf}$. K values for this family were simply described by their mean (0.47) with a normal error distribution (SD=0.17; Table 3). Natural mortality (M) generally followed a weak increasing curvilinear trend with higher K values and a weak negative curvilinear trend with $L_{\max}$ (i.e., larger species in general grew slower and lived longer; Fig. 2). This was true for jacks, snappers, emperors, and parrotfishes (Fig. 2; Table 3). However, there was no clear relationship between M and K or $L_{\max}$ for either surgeonfishes or goatfishes (i.e.,

species in these families had a similar range of longevity regardless of size). Surgeonfishes were all fairly long-lived, with lifespans between 20 years (*Acanthurus chirurgus*, a Caribbean species) and 54 years (*Naso unicornis*, a widespread Indo-Pacific species). Conversely, goatfishes were all short-lived (longest lifespan of 6 years, or 11 years if colder water species are included). Lastly, L_{λ} (expected size at maximum age) was an equal or better predictor of L_{mat} for all families compared to L_{inf} , especially for jacks and goatfishes (Table 4). The r^2 value for the $L_{\text{mat}} \sim L_{\lambda}$ regression was 0.91 vs. 0.83 for the $L_{\text{mat}} \sim L_{\text{inf}}$ regression for all families combined. We therefore selected L_{λ} as our predictor of L_{mat} , instead of the typical L_{inf} . A simple linear equation with a normal error distribution fitted the $L_{\text{mat}} \sim L_{\lambda}$ data for all families, except surgeonfishes and snappers, where a log-normal error distribution was used due to the increasing variance with larger L_{mat} values (Table 3; Fig. 2). The variance-covariance matrices for all model parameters are available online in the supplementary material (Supplementary Material S2) and an R code example of our approach is also available online (Supplementary Material S3).

Test of the data-poor approach

For all 3 test species, we compared LH parameter and SPR probability density distributions obtained through the data-poor approach with those from the data-rich situation. Figures 3 and 4 present these distributions for these species, and Table 5 presents the descriptive statistics associated with these distributions. The LH parameter estimates were all more variable in the data-poor situation compared to the data-rich situation (on average 6 times larger SD; Table 5). This was especially true for the growth parameter K (8 times larger SD, on average, especially for *L. harak*) and L_{mat} parameter (8 times larger SD on average). The data-poor approach provided estimates of the L_{inf} and M parameters that were generally close to the data-rich estimates in terms of variability and accuracy, although the M estimates for *L. harak* were

fairly variable (Fig. 3; Table 5). In general, the data-poor parameter estimates for the parrotfish *Scarus rubroviolaceus* were the most accurate and precise, with probability distributions closer to those originating from the data-rich situation for all parameters (average SD ratio ~ 3 and average RE $\sim 8\%$). The estimates for the surgeonfish *Naso unicornis* were slightly less precise and accurate than for *S. rubroviolaceus* when compared to the data-rich situation (average SD ratio ~ 5 and average RE $\sim 40\%$; Table 5), especially for the growth parameter K . Both the L_{mat} estimates and M estimates were slightly higher than the data-rich estimates. Finally, the life history comparisons from the data-poor approach fared worst compared to the data-rich situation for the emperor *Lethrinus harak* (average SD ratio ~ 11 and average RE $\sim 25\%$), mainly due to the K parameter (Table 5). It is important to note that the SD from data-rich situations were smaller for this species, likely due to the high sample sizes used in the growth/maturity study ($n=409$), and this makes the data-poor results for this species appear worse than for the other two species.

The medians of the data-poor SPR distributions for both the emperor *L. harak* and the parrotfish *S. rubroviolaceus* were fairly close to those of data-rich distributions (RE $\sim 15\%$). The median value of the data-poor SPR distributions for the surgeonfish *N. unicornis* were less accurate, being larger than those for data-rich distributions, especially at $F=M$ (median SPR of 0.51 vs. 0.38, respectively; RE $\sim 34\%$; Fig. 4, Table 5). The variability of the SPR probability density distributions for both the data-poor and data-rich approaches varied with fishing mortality, with lower variability at low ($0.1M$) and high ($2M$) fishing mortality rates (Table 5). The probability density distributions at moderate fishing mortality rates ($F=M$) were the most variable (Fig. 4). The SD from the data-poor approach were, on average, 7 times as wide as those from the data-rich approach which is a similar average ratio than for the LH distributions (6

times wider on average). The data-poor and data-rich SPR distributions for the emperor *L. harak* were generally less precise than those from the other 2 species, similarly to the LH parameter comparisons (Fig. 4; Table 5).

Finally, the effects of negatively biased $L_{\max}$ values were strongest on K and M estimates and led to these parameters being positively biased (Table 6). The obvious exception was the surgeonfish *N. unicornis*, where M was modeled as a simple mean, independent of K and $L_{\max}$ (Table 6). For $L_{\inf}$ and L_{mat} , the biases were negative and directly proportional to the $L_{\max}$ bias (i.e., a 20% bias in $L_{\max}$ lead to a 20% bias in these parameters). This pattern was expected given the linear relationship between these parameters. It is interesting to note that the simulated negative bias in $L_{\max}$ consistently led to a positive bias in SPR. The positive bias in K and negative bias in L_{mat} will push SPR values lower, as both age-at-first capture and age-at-maturity are reached more quickly (i.e., a greater portion of the mature population is exposed to fishing). However, the negative bias in $L_{\inf}$ and positive bias in M will result in higher SPR values, as age-at-first capture is reached more slowly and the relative contribution of F to total mortality is reduced. From the results shown in Table 6, it seems that biased $L_{\inf}$ and M parameters have a greater influence on SPR than biased K and L_{mat} parameters, thus leading to an overall positive bias in SPR. This is also evident from the smaller impact of biased $L_{\max}$ values on SPR for *N. unicornis* due to M being independently estimated for surgeonfishes (Table 6).

Discussion

This study presents a novel way of obtaining probability distributions for key LH parameters ($L_{\inf}$, K , L_{mat} , and M) in data-poor situations where the only available information for a stock is taxonomic group (i.e., family) and a local estimate of maximum size. It is well-known that these parameters are correlated to varying degrees (Beverton and Holt 1959, Beverton 1992, Charnov

1993) and therefore that their probability distributions should not be described independently (e.g., species with large L_{inf} typically have large L_{mat} , but small K and M values). The relatively intuitive stepwise approach presented here allows researchers to build relatively complex multivariate probability distributions for these parameters that preserve their correlative structure and associated benefits (Pulkkinen et al. 2011). These distributions can be used to parameterize population models or provide prior information for Bayesian analyses. Although our study was focused on 6 families found in tropical coastal areas, this approach is quite flexible and can be easily extended to other families in other geographical regions (e.g., groupers, Pacific rockfishes, etc.).

Our stepwise approach is analogous to the fully conditional specification method (FCS; Raghunathan et al. 2001, van Buuren 2007) used for multiple imputation. Multiple imputation seeks to generate missing values in an incomplete dataset by calculating the posterior distribution of the variables and then drawing samples at random from this distribution (Rubin 1987). This can be accomplished through joint modeling (JM) under the multivariate normal distribution (or other distributions) which is theoretically elegant, but inflexible to important data features such as non-linearity, censoring, and non-normal distributions (van Buuren 2007). FCS removes this important limitation by imputing missing data variable-by-variable using a specific model for each variable. This allows complex models to be built for each variables (Raghunathan et al. 2001). In our stepwise approach, we do not regress individual variables against all others, but rather focus on the key relationships between variables (i.e. life history invariants). One reason for doing so was that it is unlikely that modeling a variable such as L_{mat} using variables beyond L_{λ} would improve our predictions given that L_{λ} explained up to 96% percent of the variability in L_{mat} . Another difference was that our approach did not seek to fill all missing values in a dataset

in order to run further analyses on this completed dataset, but instead attempted to build missing parameter probability distributions for an individual set of observations (i.e., a species' LH parameters).

The first step in our stepwise approach was to build statistical models describing four key relationships connecting LH parameters with one another. These models allowed for an intercept similarly to Froese and Binohlan (2000) and so are not directly comparable to the BH invariants which are typically calculated as ratios (e.g., M/K vs. $M = b_0 + b_1 \cdot K$). However, we did calculate two BH invariants (M/K and $L_{\text{mat}}/L_{\text{inf}}$), as well as the $L_{\text{max}}/L_{\text{inf}}$ ratio, as a first step comparison of the families in our study, as well as to compare these values with those from previous studies (Table 2). First, it was clear that these ratios varied by taxonomic group, in this case family, as reported in previous studies (Beverton 1992, Prince et al. 2015). The families fell into two broad categories characterized by determinate or indeterminate growth. Individuals from families with mostly determinate growth do not grow as adults and will, on average, reach lengths close to L_{inf} before dying. Individuals from families with mostly indeterminate growth will continue growing as adults, usually at a decreasing rate, and will not, on average, reach lengths near L_{inf} . Jacks and goatfishes had relatively high M/K ratios (1.6 vs. < 1 for other families) which corresponded to an indeterminate growth curve (i.e., high M coupled with slow growth; Prince et al. 2015). This type of growth curve typically leads to maximum observed sizes (L_{max}) being smaller than L_{inf} , as indicated in the average $L_{\text{max}}/L_{\text{inf}}$ ratios for these families which is < 1 (Table 2). The other 4 families followed the more typical determinate growth patterns, with lower average M/K ratios (0.3 to 0.8) and $L_{\text{max}}/L_{\text{inf}}$ ratios > 1 .

The distinction between these two type of growth curves was also apparent for the reproductive load values as usually defined ($L_{\text{mat}}/L_{\text{inf}}$) with low ratios of ~ 0.55 for the jacks and

462 goatfishes (i.e., indeterminate growth). These estimates were well below the theoretical value of
463 0.66 that maximizes reproductive output (Jensen 1996). However, we believe these low
464 reproductive load ratios for families with indeterminate growth curves are actually an artifact of
465 L_{inf} not being representative of the expected size at the oldest age (L_{λ}). In the case of highly
466 indeterminate growth, L_{inf} plays more of a fitting parameter role, rather than having any
467 biological meaning. For example, L_{inf} for the giant trevally *Caranx ignobilis* equaled 1840 mm,
468 while L_{λ} was only 1260 mm (as compared with the world-record size of ~1800 mm TL). As a
469 consequence, we found that, for families with indeterminate growth, L_{λ} was a better predictor of
470 L_{mat} and the $L_{\text{mat}}/L_{\lambda}$ ratio was closer to 0.66 (i.e., 0.63). This observation likely explains the
471 previously reported negative relationship between $L_{\text{mat}}/L_{\text{inf}}$ and M/K ratios (see Prince et al.
472 2015): as M/K increases there is concomitant decrease in the biological significance of L_{inf} as a
473 representation of the expected mean length at oldest age (L_{λ}), and thus, the $L_{\text{mat}}/L_{\text{inf}}$ ratio
474 decreases accordingly. Beverton (1992) showed a similar relationship between $L_{\text{mat}}/L_{\text{inf}}$ and
475 $K \cdot a_{\text{max}}$ that is likely related to this artifact as well. Support for this conjecture was apparent in our
476 dataset when using L_{inf} but disappeared when we replaced L_{inf} with L_{λ} . For this reason, we
477 selected L_{λ} to infer L_{mat} in our model, and further, we suggest replacing the $L_{\text{mat}}/L_{\text{inf}}$ LH invariant
478 with $L_{\text{mat}}/L_{\lambda}$, when possible.

479 Although we looked at the BH-LH ratios as a preliminary source of information, our primary
480 focus was to go beyond these relatively simple ratios and explore more flexible statistical
481 models, an approach similar to Froese and Binohlan (2000). In general, these relationships
482 followed similar patterns to those previously published, with linear relationships between $L_{\text{inf}} \sim$
483 L_{max} and $L_{\text{mat}} \sim L_{\text{inf}}$ (or L_{λ}), and curvilinear relationships between $K \sim L_{\text{inf}}$ and $M \sim K$, with a few
484 notable exceptions. For example, there was no clear $K \sim L_{\text{inf}}$ and $M \sim K$ relationships for

goatfishes, although this may be simply related to the small sample size and narrow L_{inf} range. The $K \sim L_{\text{inf}}$ relationship for jacks was linear, but this is likely due to the lack of smaller species in our dataset. The clearest departure from the expected relationship was the flat trend between $M \sim K$ (and L_{max}) for surgeonfishes, despite a wide range of K and L_{max} values. Choat and Robertson (2002) also reported a lack of significant relationship between K or L_{max} and longevity for surgeonfishes (note: M was directly derived from longevity in our study). It is not clear why surgeonfishes seem to so clearly violate the M/K LH invariant. However, a lack of pattern between M and K has also been observed for other fishes, such as walleye (Beverton 1987) and brown trout (Vøllestad et al. 1993). Despite the lack of a predictor variable for M , the range of longevity (and associated M) values found in these families was consistent and fairly limited: surgeonfishes had the longest maximum age range (20-54 years) and goatfishes had a low longevity range (3-6 years). For these families, taxonomic group was the sole predictor of longevity (and thus M). Consequently, biases in L_{max} had no impact on M estimates for surgeonfishes and goatfishes, as shown in Table 5 for *N. unicornis*.

For the three selected test species, the precision of the data-poor stepwise approach compared reasonably well with the data-rich situation, especially for *S. rubroviolaceus* and *N. unicornis* (i.e., SDs about 3 times larger on average). However, the data-poor to data-rich SD ratios were significantly larger for *L. harak* due in part to the much larger sample size used in the *L. harak* study (n=409 vs. n=180 for the two other species) which resulted in narrower distributions for the data-rich situation for this species. Furthermore, the emperor (Lethrinidae) family life history relationships were generally less precise than for other species, contributing to wider data-poor parameter distributions and higher average SD ratios (~11 vs. 4 for the other species). In terms of accuracy, the LH parameter and SPR medians were, on average, about 22% off the “true”

median values of the data-rich situation, although this varied between species. *S. rubroviolaceus* median values were off the true median by about 8% on average compared to ~35% for *N. unicornis*. The median M for *N. unicornis* was 67% larger than the data-rich median which likely explains the positive bias in SPR median values as well (a higher M leads to increased resilience to high fishing mortality rates and higher SPR values). The larger M estimate is explained by the fact that the growth study used for this species reports the oldest recorded age for any surgeonfish (54 years vs. 45 years for the next oldest species). The natural mortality of *N. unicornis* is thus slightly over-estimated by our simple model for surgeonfishes, which only uses an average M value for this family (since K and $L_{\max}$ were independent from M for this family). In general, life history and SPR parameter distributions were surprisingly accurate, with data-poor median values only about 20% off their “true” values, on average.

The stepwise stochastic simulation approach presented here provides relatively accurate and precise life history parameter estimates which allows for first-step stock assessments in data-poor situations where perhaps only size structure information is available. The probability distributions generated by our approach can also be used as prior information in a Bayesian statistical analysis framework. Although this study presented the models necessary to run this approach for 6 families, other important families could easily be added through extended meta-analyses (e.g., groupers, rockfishes, etc.). It is important to note that this study presented a way of obtaining SPR when fishing mortality rates have been quantified, which is generally not the case for data-poor situations. However, it is possible to estimate fishing mortality rates through the use of length-based methods (Ehrhardt and Ault 1992, Ault et al. 2005, Gedamke and Hoenig 2006). We plan on extending and integrating these concepts in future studies.

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Tables

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Table 1 – List of life history parameters with definitions. All lengths are total lengths.

Parameter	Definition
L_{λ}	Expected length at the oldest recorded age
L_{mat}	Length at which 50% of females reach maturity
L_{max}	Longest length in a growth study or 99 th percentile of lengths in a population survey
L_{inf}	Expected length at infinite age
K	Brody growth coefficient of the von Bertalanffy growth curve
a_0	Theoretical age at which length equals zero
a_{λ}	Oldest recorded age (i.e., longevity)
M	Instantaneous natural mortality rate

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686 Table 2 – Summary of life history parameter datasets by family (L_{inf} , K , and a_λ show the ranges
 687 of these parameters). See Table 1 for parameter definitions. All lengths are TL. SST < 20°C
 688 refers to studies where annual sea surface temperature was lower than 20°C on average.

	Acanthuridae (surgeonfish)	Carangidae (jack)	Lethrinidae (emperor)	Lutjanidae (snapper)	Mullidae (goatfish)	Scaridae (parrotfish)	All families
Species count	81	148	38	110	82	100	559
Growth studies	27	40	22	39	12	27	167
Maturity studies	11	20	14	22	11	19	97
SST < 20°C	0	10	0	0	3 ^a	2	15
Excluded outliers	1	0	1	1	1	2	6
L_{inf} (mm)	142-619	255-2170	180-712	216-1264	187-547	116-818	116-2170
K (yr ⁻¹)	0.2-1.2	0.1-0.4	0.1-0.9	0.1-1.0	0.2-0.8	0.1-1.8	0.1-1.8
a_λ (yr)	20-53	5-23	7-36	8-55	3-11 ^b	5-33	3-55
L_{max} (mm)	1.1(0.1)	0.9(0.2)	1.2(0.1)	1.1(0.1)	0.9(0.1)	1.2(0.1)	1.1(0.2)
M/K	0.3(0.1)	1.6(0.7)	0.5(0.3)	0.8(0.6)	1.6(0.6)	0.5(0.3)	0.8(0.7)
L_{mat} / L_λ	0.79(0.08)	0.63(0.08)	0.78(0.07)	0.67(0.12)	0.63(0.11)	0.69(0.07)	0.70(0.11)
L_{mat} / L_{inf}	0.79(0.08)	0.55(0.11)	0.78(0.07)	0.64(0.13)	0.55(0.09)	0.68(0.08)	0.66(0.13)

689 ^a Kept for growth and L_{mat} , but not longevity estimate

690 ^b Includes cold water species.

Table 3 – Model functional form, error probability distribution, and variance-covariance matrix of regression coefficients for models relating various life history parameters. For each family, the first line presents model functional forms and error distributions in brackets. Functional forms are I = intercept-only ($Y=b_0$), L = linear ($Y=b_0+b_1 \cdot X$), E = exponential ($\log Y= b_0+b_1 \cdot X$), P = power ($\log Y= b_0+b_1 \cdot \log X$). Error distribution types are N = normal and LN = log-normal. The first line also shows regression coefficients followed by the standard deviation parameter for each distribution in parentheses. The second line presents the variance-covariance matrix of the regression parameters for one-variable models (b_0 variance, b_1 variance, b_0 - b_1 covariance) and two-variable models (b_0 variance, b_1 variance, b_2 variance, b_0 - b_1 covariance, b_0 - b_2 covariance, b_1 - b_2 covariance).

Family	(A) $L_{inf} \sim L_{max}$	(B) $K \sim L_{inf}$	(C) $M \sim K + L_{max}$	(D) $L_{mat} \sim L_{\lambda}$
Acanthuridae	[L,N] -39.4, 1.02, (18.1)	[E,LN] -0.278, -1.80e-3, (0.420)	[I,N] 9.77e-2, (2.28e-2)	[L,LN] -12.6, 0.828, (0.102)
	137, 1.04e-3, -0.345	3.63e-2, 2.42e-7, -8.49e-5	1.99e-5	194, 3.05e-3, -0.693
Carangidae Small	[L,LN] 28.0, 1.00, (0.130)	[E,LN] -1.10, -4.60e-4, (0.359)	[P,LN] 2.27, 3.02e-2, -0.515, (0.307)	[L,N] 33.6, 0.573, (44.0)
	1.65e+3, 8.12e-3, -3.38	1.77e-2, 2.21e-8, -1.72e-5	0.764, 2.20e-2, 1.94e-2, -2.14e-3, -0.118, 5.21e-3	542, 8.60e-4, -0.612
Carangidae Large	[L,LN] -27.9, 1.20, (0.242)	-	-	-
	8.62e-9, 1.15e-2, 9.94e-6	-	-	-
Lethrinidae	[L,N] -1.44, 0.872, (17.1)	[P,LN] 4.66, -0.930, (0.439)	[P,LN] 0.541, 0.538, -0.284, (0.297)	[L,N] 36.0, 0.672, (21.3)
	162, 7.53e-4, -0.334	3.13, 8.87e-2, -0.526	2.12, 2.49e-2, 6.24e-2, -9.77e-2, -0.362, 1.94e-2	396, 2.86e-3, -1.02
Lutjanidae Small	[L,N] -5.08, 0.912, (21.3)	[P,LN] 5.23, -1.06, (0.397)	[P,LN] 2.04, -8.64e-3, -0.631, (0.393)	[L,LN] 63.9, 0.519, (0.148)
	952, 7.72e-3, -2.65	0.760, 1.90e-2, -0.120	1.72, 2.51e-2, 5.32e-2, -0.139, -0.300, 2.73e-2	423, 2.16e-3, -0.853
Lutjanidae Large	[L,N] -81.8, 1.06, (85.9)	-	-	-
	6711, 1.08e-2, -8.30	-	-	-
Mullidae	[L,N] -9.34, 1.16, (16.7)	[I,N] 0.467, (0.173)	[I,LN] 0.674, (0.348)	[L,N] 49.3, 0.415, (22.1)
	519, 7.94e-3, -1.97	2.71e-3	6.90e-3	345, 4.36e-3, -1.14
Scaridae	[L,N] 0.191, 0.849, (23.2)	[E,LN] 0.681, -3.54e-3, (0.331)	[P,LN] -0.769, 0.646, -3.95e-2, (0.242)	[L,N] -7.97, 0.714, (22.0)
	379, 2.09e-3, -0.848	2.68e-2, 1.93e-7, -6.59e-5	3.47, 3.70e-2, 0.105, -0.258, -0.602, 4.64e-2	183, 1.15e-3, -0.425

Table 4 – Family and overall coefficient of determination (r^2) values for the linear models relating length-at-maturity (L_{mat}) dependent on either expected length at infinite age (L_{inf}) or expected length at oldest recorded age (L_{λ}).

Family	$L_{\text{mat}} \sim L_{\text{inf}}$	$L_{\text{mat}} \sim L_{\lambda}$
Acanthuridae (surgeonfish)	0.95	0.95
Carangidae (jack)	0.85	0.95
Lethrinidae (emperor)	0.93	0.93
Lutjanidae (snapper)	0.79	0.77
Mullidae (goatfish)	0.77	0.84
Scaridae (parrotfish)	0.94	0.96
All families	0.83	0.91

Table 5 – Descriptive statistics for the probability distributions of life history parameters and SPR values for the data-rich and data-poor situations. The median $L_{\max}$ used to run the models are presented with SD in parentheses. SD ratio is the ratio of the data-poor to data-rich standard deviations, and RE (relative error) is the standardized distance between the data-poor and data-rich medians.

Parameter	<i>S. rubroviolaceus</i>		<i>N. unicornis</i>		<i>L. harak</i>	
	Data-rich	Data-poor	Data-rich	Data-poor	Data-rich	Data-poor
$L_{\max}$ (mm)	-	653 (12)	-	558 (35)	-	312 (3)
$L_{\inf}$ (mm)						
Median	574	555	530	528	293	271
SD	22	28	8	40	6	18
SD ratio	-	1.3	-	5	-	3.0
RE (%)	-	-3	-	1	-	-8
K (yr ⁻¹)						
Median	0.25	0.28	0.17	0.29	0.31	0.58
SD	0.04	0.11	0.02	0.14	0.02	0.30
SD ratio	-	2.8	-	7	-	15
RE (%)	-	12	-	70	-	87
L_{mat} (mm)						
Median	368	384	361	420	222	218
SD	5	31	10	56	2	26
SD ratio	-	6.2	-	5.6	-	13
RE (%)	-	4	-	16	-	-2
M (yr ⁻¹)						
Median	0.14	0.16	0.06	0.10	0.24	0.25
SD	0.02	0.06	0.01	0.02	0.01	0.11
SD ratio	-	3.0	-	2.0	-	11
RE (%)	-	14	-	67	-	4
SPR $F=0.1M$						
Median	0.92	0.90	0.89	0.93	0.95	0.89
SD	0.01	0.03	0.01	0.02	0.002	0.04
SD ratio	-	3.0	-	2.0	-	20
RE (%)	-	-2	-	4	-	-6
SPR $F=M$						
Median	0.35	0.38	0.38	0.51	0.29	0.36
SD	0.03	0.11	0.03	0.08	0.01	0.13
SD ratio	-	3.7	-	3.0	-	13
RE (%)	-	9	-	34	-	24
SPR $F=2M$						
Median	0.16	0.18	0.19	0.29	0.11	0.16
SD	0.02	0.08	0.02	0.08	0.01	0.10
SD ratio	-	4.0	-	4.0	-	10
RE (%)	-	13	-	53	-	36

Table 6 – Life history parameter estimates from the data-poor approach at various levels of negative bias in $L_{\max}$ (percentage reduction in $L_{\max}$ compared to “true” value). F was set to M for SPR calculations in this table.

Species	Bias in $L_{\max}$ (%)	$L_{\max}$ (mm)	$L_{\inf}$ (mm)	K (yr ⁻¹)	M (yr ⁻¹)	L_{mat} (mm)	SPR
<i>S. rubroviolaceus</i>	0	653	555	0.28	0.16	384	0.38
	-10	588	499	0.36	0.19	347	0.42
	-20	522	443	0.44	0.22	307	0.49
	-30	457	388	0.53	0.25	268	0.56
<i>N. unicornis</i>	0	558	528	0.29	0.10	420	0.51
	-10	502	472	0.36	0.10	376	0.52
	-20	446	415	0.38	0.10	329	0.54
	-30	391	358	0.42	0.10	284	0.58
<i>L. harak</i>	0	312	271	0.58	0.25	218	0.36
	-10	281	244	0.71	0.30	198	0.37
	-20	250	218	0.77	0.33	179	0.43
	-30	218	190	0.88	0.35	158	0.53

Figures

Figure 1– Diagram presenting one iteration of the stepwise simulation chain used to obtain a single spawning potential ratio (SPR) estimate. Solid arrows represent steps that are derived using the four modeled relationships (represented by a letter). Dashed arrows represent deterministic steps where certain values are used to calculate others.

Figure 2 – Modeled statistical relationships between 4 life history parameter pairs (columns) for 6 fish families (rows). Gray areas are 95% confidence intervals; open circles represent removed outliers (see text for justifications). Model C also includes the $L_{\max}$ variable for most families but only the one-variable $M \sim K$ models are presented here. Vertical dotted lines represent model break points between size categories.

Figure 3 – Probability distributions of life history parameters from the data-rich (red areas; solid lines) and data-poor (blue areas; dashed lines) situations, for the 3 selected fish species.

Figure 4 – Spawning potential ratio (SPR) at various fishing mortality rates (F) using life history parameters from the data-rich (red areas; solid lines) and data-poor (blue areas; dashed lines) situations. Fishing mortality rates ranged from zero to four times natural mortality (M). Lines represent median values and shaded areas represent 95% confidence intervals.

87x120mm (150 x 150 DPI)

160x165mm (300 x 300 DPI)

160x127mm (300 x 300 DPI)

117x160mm (300 x 300 DPI)

Supplementary material S1 - Source of life history parameters for the reef fish species included in the meta-analysis.

Family	Scientific name	Longevity source	Growth source	Maturity source
Acanthuridae	<i>Acanthurus auranticavus</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	<i>Acanthurus bahianus</i>	(Mutz 2006)	(Mutz 2006)	
Acanthuridae	<i>Acanthurus blochii</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	<i>Acanthurus chirurgus</i>	(Mutz 2006)	(Mutz 2006)	
Acanthuridae	<i>Acanthurus coeruleus</i>	(Mutz 2006)	(Mutz 2006)	
Acanthuridae	<i>Acanthurus dussumieri</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	<i>Acanthurus lineatus</i>	(Choat & Axe 1996)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	<i>Acanthurus maculiceps</i>	(Newman et al. 2000b)	(Choat & Robertson 2002)	
Acanthuridae	<i>Acanthurus mata</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	<i>Acanthurus nigricans</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	<i>Acanthurus nigrofuscus</i>	(Hart & Russ 1996)	(Hart & Russ 1996)	
Acanthuridae	<i>Acanthurus olivaceus</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	<i>Acanthurus pyroferus</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	<i>Acanthurus xanthopterus</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	<i>Ctenochaetus striatus</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	<i>Ctenochaetus strigosus</i>	(Langston et al. 2009)	(Langston et al. 2009)	(Langston et al. 2009)
Acanthuridae	<i>Naso annulatus</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	<i>Naso brachycentron</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	<i>Naso brevirostris</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	<i>Naso hexacanthus</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	<i>Naso lituratus</i>	NOAA-CRED unpublish.	(Kitalong & Dalzell 1994)	NOAA-CRED unpublish.
Acanthuridae	<i>Naso tuberosus</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	<i>Naso unicornis</i>	A. Andrews - p. comm.	(Eble et al. 2009)	(DeMartini et al. 2014)
Acanthuridae	<i>Naso vlamingii</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	<i>Zebrasoma flavescens</i>	(Claisse et al. 2009)	(Claisse et al. 2009)	(Bushnell 2007)
Acanthuridae	<i>Zebrasoma scopas</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	<i>Zebrasoma veliferum</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Carangidae	<i>Alectis indica</i>		(Edwards & Shaher 1991)	

Family	Scientific name	Longevity source	Growth source	Maturity source
Carangidae	<i>Alepes djedaba</i>		(El-Sayed 2005)	(Reuben et al. 1992)
Carangidae	<i>Carangoides chrysophrys</i>	(Al-Rasady et al. 2013)	(Al-Rasady et al. 2013)	(Al-Rasady et al. 2012)
Carangidae	<i>Carangoides ferdau</i>		(Edwards et al. 1985)	
Carangidae	<i>Caranx caballus</i>	(Cruz-Romero et al. 1993)	(Gallardo-Cabello. et al. 2007)	
Carangidae	<i>Caranx caninus</i>	(Espino Barr et al. 2008)	(Espino Barr et al. 2008)	
Carangidae	<i>Caranx crysos</i>	(Goodwin & Johnson 1986)	(Goodwin & Johnson 1986)	(Goodwin & Finucane 1985)
Carangidae	<i>Caranx ignobilis</i>	(Fry et al. 2006)	(Sudekum et al. 1991)	(Sudekum et al. 1991)
Carangidae	<i>Caranx lugubris</i>	(Fry et al. 2006)	(Fry et al. 2006)	(Garcia-Cagide et al. 1994)
Carangidae	<i>Caranx melampygus</i>	(Sudekum et al. 1991)	(Sudekum et al. 1991)	(Sudekum et al. 1991)
Carangidae	<i>Caranx rhonchus</i>	(CECAF 1979)	(CECAF 1979)	(Do Chi 1994)
Carangidae	<i>Caranx ruber</i>	(Garcia-Arteaga & Reshetnikov 1985)	(Garcia-Arteaga & Reshetnikov 1985)	(Garcia-Cagide et al. 1994)
Carangidae	<i>Caranx sexfasciatus</i>	(Fry et al. 2006)	(Munro & Williams 1985)	(Whitfield 1998)
Carangidae	<i>Caranx tille</i>	(Fry et al. 2006)	(Fry et al. 2006)	
Carangidae	<i>Chloroscombrus chrysurus</i>	(Cergole et al. 2005)	(Cergole et al. 2005)	(Cergole et al. 2005)
Carangidae	<i>Decapterus macarellus</i>	(Shiraishi et al. 2010)	(Shiraishi et al. 2010)	(Shiraishi et al. 2010)
Carangidae	<i>Gnathanodon speciosus</i>	(Koob 2011)	(Koob 2011)	(Koob 2011)
Carangidae	<i>Parastromateus niger</i>	(Tao et al. 2012)	(Tao et al. 2012)	(Tao et al. 2012)
Carangidae	<i>Pseudocaranx dentex</i>	(Williams & Lowe 1997)	(Williams & Lowe 1997)	(Seki 1986)
Carangidae	<i>Scomberoides commersonnianus</i>	(Griffiths et al. 2006)	(Griffiths et al. 2006)	(Griffiths et al. 2006)
Carangidae	<i>Seriola dumerili</i>	(Manooch III & Potts 1997)	(Harris 2004)	(Harris 2004)
Carangidae	<i>Trachinotus carolinus</i>	(Murphy et al. 2008)	(Murphy et al. 2008)	(Garcia-Cagide et al. 1994)
Carangidae	<i>Trachinotus falcatus</i>	(Crabtree et al. 2002)	(Crabtree et al. 2002)	(Crabtree et al. 2002)
Carangidae	<i>Trachurus capensis</i>	(Hecht 1990)	(Hecht 1990)	(Hecht 1990)
Carangidae	<i>Trachurus indicus</i>	(Edwards & Shaher 1991)	(Edwards & Shaher 1991)	
Carangidae	<i>Trachurus japonicus</i>	(Kim et al. 1969)	(Kim et al. 1969)	
Carangidae	<i>Trachurus lathami</i>	(Saccardo & Katsuragawa 1995)	(Saccardo & Katsuragawa 1995)	
Carangidae	<i>Trachurus picturatus</i>	(Vasconcelos et al. 2006)	(Vasconcelos et al. 2006)	(Vasconcelos et al. 2006)
Carangidae	<i>Trachurus</i>	(Wengrzyn 1975)	(Wengrzyn 1975)	(Kerstan 1995)
Carangidae	<i>Trachurus trecae</i>	(Do Chi 1994)	(Do Chi 1994)	

Family	Scientific name	Longevity source	Growth source	Maturity source
Lethrinidae	<i>Gymnocranius audleyi</i>	(Laursen et al. 1999)	(Laursen et al. 1999)	
Lethrinidae	<i>Gymnocranius euanus</i>	(Loubens 1980a)	(Loubens 1980a)	(Loubens 1980b)
Lethrinidae	<i>Gymnocranius grandoculis</i>	(Loubens 1980a)	(Loubens 1980a)	
Lethrinidae	<i>Lethrinus atkinsoni</i>	(Currey et al. 2013)	(Currey et al. 2013)	
Lethrinidae	<i>Lethrinus borbonicus</i>	(Grandcourt et al. 2010)	(Grandcourt et al. 2010)	(Grandcourt et al. 2010)
Lethrinidae	<i>Lethrinus enigmaticus</i>	(Lebeau & Cueff 1975)	(Lebeau & Cueff 1975)	
Lethrinidae	<i>Lethrinus erythracanthus</i>	(Fry et al. 2006)	(Fry et al. 2006)	
Lethrinidae	<i>Lethrinus genivittatus</i>	(Loubens 1980a)	(Loubens 1980a)	(Loubens 1980b)
Lethrinidae	<i>Lethrinus harak</i>	(Lasi 2003)	(Lasi 2003)	(Lasi 2003)
Lethrinidae	<i>Lethrinus laticaudis</i>	(Ayvazian et al. 2004)	(Ayvazian et al. 2004)	(Ayvazian et al. 2004)
Lethrinidae	<i>Lethrinus lentjan</i>	(Currey et al. 2013)	(Currey et al. 2013)	Grandcourt 2011
Lethrinidae	<i>Lethrinus mahsena</i>	(Grandcourt 2002)	(Grandcourt 2002)	
Lethrinidae	<i>Lethrinus microdon</i>	(Grandcourt et al. 2010)	(Grandcourt et al. 2010)	(Grandcourt et al. 2010)
Lethrinidae	<i>Lethrinus miniatus</i>	(Williams et al. 2007)	(Williams et al. 2007)	(Ebisawa 2006)
Lethrinidae	<i>Lethrinus nebulosus</i>	(Andrews et al. 2011)	(Ebisawa & Ozawa 2009)	(Ebisawa & Ozawa 2009)
Lethrinidae	<i>Lethrinus obsoletus</i>	(Lasi 2003)	(Lasi 2003)	(Lasi 2003)
Lethrinidae	<i>Lethrinus olivaceus</i>	(Currey et al. 2013)	(Currey et al. 2013)	
Lethrinidae	<i>Lethrinus ornatus</i>	(Ebisawa & Ozawa 2009)	(Ebisawa & Ozawa 2009)	(Ebisawa & Ozawa 2009)
Lethrinidae	<i>Lethrinus ravus</i>	(Ebisawa & Ozawa 2009)	(Ebisawa & Ozawa 2009)	(Ebisawa & Ozawa 2009)
Lethrinidae	<i>Lethrinus rubrioperculatus</i>	(Ebisawa & Ozawa 2009)	(Trianni 2011)	(Trianni 2011)
Lethrinidae	<i>Lethrinus variegatus</i>	(Loubens 1980a)	(Loubens 1980a)	(Loubens 1980b)
Lethrinidae	<i>Wattsia mossambica</i>	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	<i>Aphareus rutilans</i>	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	<i>Aprion virescens</i>	(Loubens 1980a)	(Loubens 1980a)	(Everson et al. 1989)
Lutjanidae	<i>Etelis carbunculus</i>	(Andrews et al. 2011)	(Ralston & Williams 1988)	(DeMartini & Lau 1998)
Lutjanidae	<i>Etelis coruscans</i>	(Ralston & Williams 1988)	(Ralston & Williams 1988)	(Everson et al. 1989)
Lutjanidae	<i>Lutjanus adetii</i>	(Newman et al. 1996)	(Newman et al. 1996)	(Loubens 1980b)
Lutjanidae	<i>Lutjanus analis</i>	(Burton 2002)	(Burton 2002)	(Garcia-Cagide et al. 1994)
Lutjanidae	<i>Lutjanus argentimaculatus</i>	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	<i>Lutjanus argentiventris</i>	(García-Contreras et al. 2009)	(García-Contreras et al. 2009)	

Family	Scientific name	Longevity source	Growth source	Maturity source
Lutjanidae	<i>Lutjanus bohar</i>	(Marriott et al. 2007)	(Marriott et al. 2007)	(Marriott et al. 2007)
Lutjanidae	<i>Lutjanus boutton</i>	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	<i>Lutjanus buccanella</i>	(Espinosa & Pozo 1982)	(Espinosa & Pozo 1982)	(Garcia-Cagide et al. 1994)
Lutjanidae	<i>Lutjanus campechanus</i>	(White & Palmer 2004)	(White & Palmer 2004)	(White & Palmer 2004)
Lutjanidae	<i>Lutjanus carponotatus</i>	(Newman et al. 2000a)	(Newman et al. 2000a)	
Lutjanidae	<i>Lutjanus cyanopterus</i>	(Baisre & Paez 1981)	(Baisre & Paez 1981)	
Lutjanidae	<i>Lutjanus ehrenbergii</i>	(Grandcourt et al. 2011)	(Grandcourt et al. 2011)	(Grandcourt et al. 2011)
Lutjanidae	<i>Lutjanus erythropterus</i>		(Newman et al. 2000b)	
Lutjanidae	<i>Lutjanus fulviflamma</i>	(Grandcourt et al. 2006)	(Grandcourt et al. 2006)	(Grandcourt et al. 2006)
Lutjanidae	<i>Lutjanus gibbus</i>	(Nanami et al. 2010)	(Nanami et al. 2010)	
Lutjanidae	<i>Lutjanus griseus</i>	(Fischer et al. 2005)	(Fischer et al. 2005)	(Garcia-Cagide et al. 1994)
Lutjanidae	<i>Lutjanus guttatus</i>	(Amezcuca et al. 2006)	(Amezcuca et al. 2006)	
Lutjanidae	<i>Lutjanus jocu</i>	(Previero et al. 2011)	(Previero et al. 2011)	(Garcia-Cagide et al. 1994)
Lutjanidae	<i>Lutjanus kasmira</i>	(Loubens 1980a)	(Morales-Nin & Ralston 1990)	(Allen 1985)
Lutjanidae	<i>Lutjanus malabaricus</i>	(Newman et al. 2000b)	(Newman et al. 2000b)	
Lutjanidae	<i>Lutjanus peru</i>	(Rocha-Olivares 1998)	(Rocha-Olivares 1998)	
Lutjanidae	<i>Lutjanus purpureus</i>	(Manickchand-Heileman & Phillip 1996)	(Manickchand-Heileman & Phillip 1996)	(Manickchand-Heileman & Phillip 1996)
Lutjanidae	<i>Lutjanus quinquelineatus</i>	(Newman et al. 1996)	(Newman et al. 1996)	(Loubens 1980b)
Lutjanidae	<i>Lutjanus russellii</i>	(Sheaves 1995)	(Sheaves 1995)	(Sheaves 1995)
Lutjanidae	<i>Lutjanus sebae</i>	(Loubens 1980a)	(Newman et al. 2000b)	
Lutjanidae	<i>Lutjanus synagris</i>	(Johnson et al. 1995)	(Johnson et al. 1995)	(Manickand-Dass 1987)
Lutjanidae	<i>Lutjanus timoriensis</i>	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	<i>Lutjanus vitta</i>	(Newman et al. 2000a)	(Newman et al. 2000a)	(Loubens 1980b)
Lutjanidae	<i>Ocyurus chrysurus</i>	(Manooch III & Drennon 1987)	(Manooch III & Drennon 1987)	(Garcia-Cagide et al. 1994)
Lutjanidae	<i>Paracaesio kusakarii</i>	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	<i>Paracaesio stonei</i>	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	<i>Pristipomoides filamentosus</i>	(Andrews et al. 2012)	(DeMartini et al. 1994)	(Mees 1993)
Lutjanidae	<i>Pristipomoides flavipinnis</i>	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	<i>Pristipomoides multidens</i>	(Newman & Dunk 2003)	(Newman & Dunk 2003)	(Lokani et al. 1990)

Family	Scientific name	Longevity source	Growth source	Maturity source
Lutjanidae	<i>Pristipomoides sieboldii</i>	(Ralston & Williams 1988)	(Ralston & Williams 1988)	(DeMartini & Lau 1998)
Lutjanidae	<i>Pristipomoides zonatus</i>	(Ralston & Williams 1988)	(Ralston & Williams 1988)	
Lutjanidae	<i>Rhomboplites aurorubens</i>	(Potts et al. 1998)	(Potts et al. 1998)	(Boardman & Weiler 1980)
Mullidae	<i>Mulloidichthys flavolineatus</i>		(Holland et al. 1993)	(Cole 2009)
Mullidae	<i>Mulloidichthys vanicolensis</i>	(Cole 2009)	(Cole 2009)	(Cole 2009)
Mullidae	<i>Mullus barbatus</i>	(Stergiou et al. 1997)	(Stergiou & Karachle 2006)	(Stergiou et al. 1997)
Mullidae	<i>Mullus surmuletus</i>	(Stergiou et al. 1997)	(Mehanna 2009)	(Morales-Nin 1992)
Mullidae	<i>Parupeneus barberinus</i>	(Wahbeh & Ajiad 1985)	(Wahbeh & Ajiad 1985)	(Vijay Anand & Pillai 2002)
Mullidae	<i>Parupeneus heptacanthus</i>	(Al-Absy & Ajiad 1988)	(Al-Absy & Ajiad 1988)	
Mullidae	<i>Parupeneus multifasciatus</i>	(Pavlov et al. 2013)	(Longenecker & Langston 2008)	(Longenecker & Langston 2008)
Mullidae	<i>Parupeneus porphyreus</i>	(Moffitt 1979)	(Moffitt 1979)	(Moffitt 1979)
Mullidae	<i>Pseudopeneus maculatus</i>	(Santana et al. 2006)	(Santana et al. 2006)	(Munro 1976)
Mullidae	<i>Upeneus pori</i>	(Ismen 2006)	(Ismen 2006)	(Ismen 2006)
Mullidae	<i>Upeneus tragula</i>	(Sabrah & El-Ganainy 2009)	(Sabrah & El-Ganainy 2009)	(Sabrah & El-Ganainy 2009)
Mullidae	<i>Upeneus vittatus</i>	(Sabrah & El-Ganainy 2009)	(Sabrah & El-Ganainy 2009)	(Sabrah & El-Ganainy 2009)
Scaridae	<i>Bolbometopon muricatum</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Hamilton et al. 2008)
Scaridae	<i>Calotomus carolinus</i>	Taylor & Choat 2014)	Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	<i>Calotomus japonicus</i>	(Kume et al. 2010)	(Kume et al. 2010)	
Scaridae	<i>Cetoscarus bicolor</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Scaridae	<i>Chlorurus frontalis</i>	(Taylor & Choat 2014)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	<i>Chlorurus gibbus</i>	(Choat et al. 1996)	(Choat et al. 1996)	(Page 1998)
Scaridae	<i>Chlorurus japanensis</i>	(Page 1998)		
Scaridae	<i>Chlorurus microrhinos</i>	(Choat & Robertson 2002)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	<i>Chlorurus sordidus</i>	(Taylor & Choat 2014)	(Taylor & Choat 2014)	(Page 1998)
Scaridae	<i>Hipposcarus longiceps</i>	(Choat & Robertson 2002)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	<i>Scarus altipinnis</i>	(Taylor & Choat 2014)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	<i>Scarus chameleon</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Scaridae	<i>Scarus forsteni</i>	(Taylor & Choat 2014)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	<i>Scarus frenatus</i>	(Choat et al. 1996)	(Choat et al. 1996)	(Taylor & Choat 2014)
Scaridae	<i>Scarus ghobban</i>	(Grandcourt 2002)	(Grandcourt 2002)	

Family	Scientific name	Longevity source	Growth source	Maturity source
Scaridae	<i>Scarus iseri</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Scaridae	<i>Scarus niger</i>	(Choat et al. 1996)	(Choat et al. 1996)	(Choat & Robertson 2002)
Scaridae	<i>Scarus oviceps</i>	(Page 1998)		(Page 1998)
Scaridae	<i>Scarus psittacus</i>	(Taylor & Choat 2014)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	<i>Scarus rivulatus</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Barba 2010)
Scaridae	<i>Scarus rubroviolaceus</i>	(Howard 2008)	(Howard 2008)	(Howard 2008)
Scaridae	<i>Scarus schlegeli</i>	(Taylor & Choat 2014)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	<i>Sparisoma atomarium</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Scaridae	<i>Sparisoma aurofrenatum</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Garcia-Cagide et al. 1994)
Scaridae	<i>Sparisoma chrysopterum</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Scaridae	<i>Sparisoma cretense</i>	(Pallaoro & Dulcic 2004)	(Pallaoro & Dulcic 2004)	
Scaridae	<i>Sparisoma rubripinne</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Garcia-Cagide et al. 1994)
Scaridae	<i>Sparisoma strigatum</i>	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Scaridae	<i>Sparisoma viride</i>	(Paddack et al. 2009)	(Paddack et al. 2009)	(Garcia-Cagide et al. 1994)

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Appendix S2. Life history model parameters for 6 fish families followed by variance-covariance matrices of the regression coefficients.

Acanthuridae

Linf model: $\text{Linf} \sim N(E, sd)$ $E = b_0 + b_1 * L_{\max}$
 Estimate
 b0 -39.421486
 b1 1.018236
 sd 18.073072

	b0	b1
b0	136.5050105	-0.345017509
b1	-0.3450175	0.001037638

K model: $K \sim LN(\log E, sd_{\log})$ $\log E = b_0 + b_1 * \text{Linf}$
 Estimate
 b0 -0.27823534
 b1 -0.00179617
 sdlog 0.41955247

	b0	b1
b0	3.628268e-02	-8.492274e-05
b1	-8.492274e-05	2.423078e-07

M model: $M \sim N(E, sd)$ $E = b_0$
 Estimate
 b0 0.0976836
 sd 0.0227706

	b0
b0	1.994236e-05

Lmat model: $L_{\text{mat}} \sim LN(\log E, sd_{\log})$ $E = b_0 + b_1 * L_{\lambda}$
 Estimate
 b0 -12.551248
 b1 0.827516
 sdlog 0.102111

	b0	b1
b0	1.944283e+02	-6.928236e-01
b1	-6.928236e-01	3.050065e-03

Carangidae

Linf model $\leq 900\text{mm}$: $\text{Linf} \sim LN(\log E, sd_{\log})$ $E = b_0 + b_1 * L_{\max}$
 Estimate
 b0 27.997851
 b1 1.003558
 sdlog 0.130156

	b0	b1
b0	1.650201e+03	-3.3814631668
b1	-3.381463e+00	0.0081213854

Linf model > 900mm: Linf~LN(logE,sdlog) E = b0+b1*Lmax

Estimate
b0 -2.7938e+01
b1 1.1961e+00
sdlog 2.4161e-01

	b0	b1
b0	8.624730e-09	9.937220e-06
b1	9.937220e-06	1.145423e-02

K model: K~LN(logE,sdlog) logE = b0+b1*Linf

Estimate
b0 -1.10386285
b1 -0.00045998
sdlog 0.35885624

	b0	b1
b0	1.772833e-02	-1.721886e-05
b1	-1.721886e-05	2.206721e-08

M model: M~LN(logE,sdlog) logE=b0+b1*logK+b2*logLmax

Estimate
b0 2.267174
b1 0.030239
b2 -0.515081
sdlog 0.307207

	b0	b1	b2
b0	7.638689e-01	-2.137078e-03	-1.179220e-01
b1	-2.137078e-03	2.197155e-02	5.211300e-03
b2	-1.179220e-01	5.211300e-03	1.939093e-02

Lmat model: Lmat~N(E,sd) E = b0+b1*Llambda

Estimate
b0 33.576092
b1 0.572904
sd 43.957894

	b0	b1
b0	542.3375676	-0.611514575
b1	-0.6115146	0.000859941

Lethrinidae

Linf model: Linf~N(E,sd) E = b0+b1*Lmax

Estimate
b0 -1.441152
b1 0.872423
sd 17.105324

	b0	b1
b0	161.8062667	-0.333560243
b1	-0.3335602	0.000752506

K model: $K \sim \text{LN}(\log E, \text{sdlog})$ $\log E = b_0 + b_1 \cdot \log \text{Linf}$

Estimate
 b0 4.658581
 b1 -0.930113
 sdlog 0.438728

	b0	b1
b0	3.124779e+00	-5.257665e-01
b1	-5.257665e-01	8.871238e-02

M model: $M \sim \text{LN}(\log E, \text{sdlog})$ $\log E = b_0 + b_1 \cdot \log K + b_2 \cdot \log \text{Lmax}$

Estimate
 b0 0.54085
 b1 0.53750
 b2 -0.28432
 sdlog 0.29714

	b0	b1	b2
b0	2.115091e+00	-9.768916e-02	-3.619241e-01
b1	-9.768916e-02	2.494511e-02	1.944466e-02
b2	-3.619241e-01	1.944466e-02	6.240972e-02

Lmat model: $\text{Lmat} \sim \text{N}(E, \text{sd})$ $E = b_0 + b_1 \cdot \text{Llambda}$

Estimate
 b0 36.013807
 b1 0.671787
 sd 21.307974

	b0	b1
b0	395.5265340	-1.0156028933
b1	-1.0156029	0.0028603607

Lutjanidae

Linf model $\leq 500\text{mm}$: $\text{Linf} \sim \text{N}(E, \text{sd})$ $E = b_0 + b_1 \cdot \text{Lmax}$

Estimate
 b0 -5.077514
 b1 0.912436
 sd 21.314440

	b0	b1
b0	952.051969	-2.651956402
b1	-2.651956	0.007722089

Linf model $> 500\text{mm}$: $\text{Linf} \sim \text{N}(E, \text{sd})$ $E = b_0 + b_1 \cdot \text{Lmax}$

Estimate
 b0 -81.77184
 b1 1.05954
 sd 85.86606

	b0	b1
b0	6711.302438	-8.30116144
b1	-8.301161	0.01076043

K model: $K \sim \text{LN}(\log E, \text{sdlog})$ $\log E = b_0 + b_1 \cdot \log \text{Linf}$

Estimate
b0 5.225192
b1 -1.056897
sdlog 0.397114

b0 b1
b0 7.595088e-01 -1.196958e-01
b1 -1.196958e-01 1.896458e-02

M model: $M \sim \text{LN}(\log E, \text{sdlog})$ $\log E = b_0 + b_1 \cdot \log K + b_2 \cdot \log L_{\max}$

Estimate
b0 2.0379245
b1 -0.0086432
b2 -0.6306451
sdlog 0.3929242

b0 b1 b2
b0 1.723808e+00 -1.386993e-01 -3.004497e-01
b1 -1.386993e-01 2.507150e-02 2.729170e-02
b2 -3.004497e-01 2.729170e-02 5.317334e-02

Lmat model: $L_{\text{mat}} \sim \text{LN}(\log E, \text{sdlog})$ $E = b_0 + b_1 \cdot L_{\lambda}$

Estimate
b0 63.875705
b1 0.519023
sdlog 0.148013

b0 b1
b0 423.325388756 -8.530914e-01
b1 -0.853091438 2.161344e-03

Mullidae

Linf model: $L_{\text{inf}} \sim N(E, \text{sd})$ $E = b_0 + b_1 \cdot L_{\max}$

Estimate
b0 -9.340027
b1 1.158293
sd 16.720210

b0 b1
b0 518.672234 -1.967218231
b1 -1.967218 0.007936577

K model: $K \sim N(E, \text{sd})$ $E = b_0$

Estimate
b0 0.466636
sd 0.172700

b0
b0 2.711398e-03

M model: $M \sim \text{LN}(\log E, \text{sdlog})$ $E = b_0$

Estimate
b0 0.674379
sdlog 0.348307

b0
b0 6.896719e-03

Lmat model: $Lmat \sim N(E, sd)$ $E = b0 + b1 * Llambda$
Estimate
b0 49.326576
b1 0.414815
sd 22.093625

b0 b1
b0 344.831162 -1.135673725
b1 -1.135674 0.004357041

Scaridae

Linf model: $Linf \sim N(E, sd)$ $E = b0 + b1 * Lmax$
Estimate
b0 0.190650
b1 0.849181
sd 23.231003

b0 b1
b0 378.6815365 -0.848459796
b1 -0.8484598 0.002086915

K model: $K \sim LN(logE, sdlog)$ $logE = b0 + b1 * Linf$
Estimate
b0 0.68111900
b1 -0.00353955
sdlog 0.33085776

b0 b1
b0 2.681769e-02 -6.586431e-05
b1 -6.586431e-05 1.933287e-07

M model: $M \sim LN(logE, sdlog)$ $logE = b0 + b1 * logK + b2 * logLmax$
Estimate
b0 -0.768542
b1 0.646086
b2 -0.039457
sdlog 0.241926

b0 b1 b2
b0 3.465647e+00 -2.579116e-01 -6.015445e-01
b1 -2.579116e-01 3.699427e-02 4.640341e-02
b2 -6.015445e-01 4.640341e-02 1.046714e-01

Lmat model: $Lmat \sim N(E, sd)$ $E = b0 + b1 * Llambda$
Estimate
b0 -7.967278
b1 0.713637
sd 22.000253

b0 b1
b0 183.0398307 -0.42502341
b1 -0.4250234 0.00114699

Draft

```

library(MASS)

# INPUT LMAX
VALUE-----
lmax          <- 653      # This is the lmax estimate for S. rubroviolaceus
in Hawaii (mm)
lmax.error    <- 12

# PARAMETERS FOR
PARROTFISHES-----
linf.coef     <- c(0.191,0.849)                # Linf ~ Lmax
linear model coefficients
linf.error    <- 23.2                          # Standard
deviation of error distribution
linf.cov      <- rbind(c(379,-0.848),c(-0.848,2.09e-3) ) #
Variance-covariance matrix of model coefficients

K.coef        <- c(0.681,-3.54e-3)
K.error       <- 0.331
K.cov         <- rbind( c(2.68e-02,-6.59e-05),c(-6.59e-05,1.93e-07) )

M.coef        <- c(-0.769,0.646,-3.95e-2)
M.error       <- 0.242
M.cov         <- rbind(
c(3.47,-0.258,-0.602),c(-0.258,3.70e-02,4.64e-02),c(-0.602,4.64e-02,0.105) )

lmat.coef     <- c(-7.97,0.714)
lmat.error    <- 22
lmat.cov      <- rbind(c(183,-0.425),c(-0.425,1.15e-3) )

a0            <- -0.3

iterations    <- 5000

# STEPWISE STOCHASTIC
MODEL-----
Results <- matrix(nrow=iterations, ncol=5)
colnames(Results) <- c("Linf","K","M","Lmat","Longevity")
for(i in 1:iterations)
{
  # Draw a random Lmax value
  lmax.r <- rnorm(n=1,mean=lmax,sd=lmax.error)

  # Draw a random set of coefficients from a multivariate normal distribution
  aCoef <- mvrnorm(n=1,linf.coef,linf.cov)

  # Use these coefficients to generate one expected Linf value from the random
  Lmax value
  linf.e <- aCoef[1]+lmax.r*aCoef[2]

  # Generate a random Linf value from the normal error distribution using the
  expected Linf value
  linf.r <- rnorm(n=1,mean=linf.e,sd=linf.error)

  aCoef <- mvrnorm(n=1,K.coef,K.cov)

  # Use the random Linf value from previous step as predictor for K
  K.e <- aCoef[1]+aCoef[2]*linf.r

```

```
# Generate a random K value from the log-normal error distribution using the
expected K value
K.r      <- rlnorm(n=1,meanlog=K.e, sdlog=K.error)

aCoef    <- mvrnorm(n=1,M.coef,M.cov)

# Note: power function form. Use random K from previous step and random Lmax
to generate expected M value
M.e      <- aCoef[1]+aCoef[2]*log(K.r)+aCoef[3]*log(lmax.r)

# Generate random M value
M.r      <- rlnorm(n=1,meanlog=M.e, sdlog=M.error)

# Calculate longevity from M
longevity.r <- -log(0.05)/M.r

# Use longevity (and other previous parameters) in von Bertalanffy equation
to calculate Llambda
llambda   <- linf.r*(1-exp(-K.r*(longevity.r-a0)))

# Draw a random set of coefficients for Lmat
aCoef     <- mvrnorm(n=1,lmat.coef,lmat.cov)

# Calculate expected Lmat from Llambda
lmat.e    <- aCoef[1]+llambda*aCoef[2]

# Generate a random Lmat value
lmat.r    <- rnorm(n=1,mean=lmat.e, sd=lmat.error)

Results[i,1] <- linf.r
Results[i,2] <- K.r
Results[i,3] <- M.r
Results[i,4] <- lmat.r
Results[i,5] <- longevity.r

}

# PLOT RESULTS
Results <- data.frame(Results)

par(mfrow=c(2,2))
hist(Results$Linf)
hist(Results$K)
hist(Results$M)
hist(Results$Lmat)
```