

Why we should not necessarily expect life history strategies to inform on sensitivity to environmental change

Letter

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Abstract

Speed of life and reproductive strategy form the two major axes that organise variation in life history strategies across plant and animal species. This cross-taxonomical structuring can inform on the sensitivity of species to environmental change. However, predictions based on broad cross-taxonomical patterns do not necessarily align with those from detailed research on a smaller range of species. Here, we use Dynamic Energy Budget Integral Projection Models (DEB-IPMs) to quantify the extent to which patterns in the life history strategies of a large and diverse taxonomic class of fish (*Actinopterygii*) inform on their sensitivity to environmental change. By accounting for additional complexity in individual life histories, the classical association between life history strategies and sensitivity to environmental change breaks down. We discuss which trait-based approach is best suited to tackle challenges in linking life histories to population responses to change, and summarise our perspective in a conceptual framework.

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Introduction

Populations are subject to temporal variation in environmental conditions that affects individual survival, growth, and reproduction in organisms (1, 2). Distinct combinations of these demographic rates comprise different life history strategies and different life history strategies are linked to population dynamics under environmental variation (3–5). Classifying a species by their life history strategy can therefore be useful in predicting population responses to environmental change (6). For example, in plants, the majority of life history variation is structured along (i) a fast-slow life history continuum including fast-growing, short-lived plant species at one extreme, and slow-growing, long-lived species at the other, and (ii) a reproductive strategy axis, with highly reproductive, iteroparous species at one extreme and poorly reproductive, semelparous plants with frequent shrinkage at the other (7). In animals, life history variation is also structured along the fast-slow life history continuum (8, 9), and a secondary axis defined by the distribution of age-specific mortality hazards and the spread of reproduction (10).

Demographic analyses across a wide range of plant and animal taxa have shown that the ranking of species across life history strategy axes informs on their sensitivity to environmental change. For example, species with slow life histories are less sensitive to environmental change than species with fast life histories (9, 11). The idea of structuring life history variation along one or two main axes is appealing, because it brings the high-dimensional complexity of life down to a more linear representation that allows for broad generalizations across different taxonomical groups. Also, this approach requires knowledge of only a few trait values to determine the position of a species along these main axes (e.g. six traits in (12)), allowing applications to a wide range of species that would be difficult to study in detail. However, the broad

cross-taxonomical predictions on sensitivity to environmental change obtained through this framework do not always align with those from more detailed life history analyses carried out on a narrow taxonomical range (e.g. (13, 14)). These latter findings can be interpreted as taxonomic oddities, but also call for a reflection on our current approach to life history structuring.

Currently, life history variation is most often structured using linear dimensionality reduction methods, such as Principal Component Analysis (PCA), after which post-hoc explanations describe which life history trade-offs likely underlie the structuring (e.g. (7, 9, 12)). This approach assumes that the underlying trade-offs align with patterns in life history traits across species (15). For example, from the fast-slow continuum we expect that larger-bodied animal species live longer and produce fewer offspring than smaller-bodied animals (16). Yet, this is not the case for all animals (17). In fish, for example, individuals of larger and longer-lived species can produce offspring numbers that are orders of magnitude higher than those of smaller, short-lived species (See, for example, differences in egg production between Atlantic cod (*Gadus morhua*), and zebrafish (*Danio rerio*) in Table 1). Such demographic details are not included in current, linearized accounts of life history variation, which are therefore unlikely to accurately predict how sensitive these species are to environmental change (18).

The question is whether additional life history details helps models predict accurately how sensitive species are to environmental change. One way to test this would be to explicitly account for underlying life history trade-offs a priori, and to examine whether this a priori classification is reflected in a post-hoc analysis of life history variation and the predicted sensitivity of species to environmental change. An important life history trade-off is that between energy investment into growth and/or survival, versus reproduction (6, 19); this trade-off is currently taken to post hoc explain the fast-slow life history speed axis (7). A second important trade-off is that between current and future reproduction (20), which is currently taken to post hoc explain the reproductive strategy axis (21). Here we test if explicitly accounting for trade-offs and reproductive decisions results in generalizable predictions on how sensitive life histories of different speed or reproductive strategy are to environmental change. To this end, we parameterised Dynamic Energy Budget Integral Projection Models (DEB-IPMs) (22) for 34 species of ray-finned fish (Actinopterygii) (Fig. 1); a taxonomic class of ~ 30.000 species that represent half of all known vertebrates today (23), and which comprises an exceptional range of reproductive strategies that are also found in other vertebrate groups. In each DEB-IPM, the demographic rates of growth and reproduction are based on a trade-off between energy investment into growth versus reproduction. We also explicitly account for different reproductive decisions (skip versus obligate breeding across iteroparous and semelparous species). We used the parameterised DEB-IPMs to investigate if (i) ray-finned fish life history variation is structured along axes that reflect the growth-reproduction trade-off and reproductive strategies, and (ii) if the main axes of life history variation inform on the sensitivity of ray-finned fish populations to shifts in environmental autocorrelation. We focus on shifts in environmental autocorrelation, because environmental fluctuations often show temporal autocorrelation (24, 25), that shifts towards more negative, or ‘blue’, autocorrelation in response to climate change (at least on a continental scale (26)).

We implemented each DEB-IPM into a stochastic model, from which we calculated the stochastic population growth rate,

IMS conceived the idea, IMS & MR designed the study, MR performed the research, all authors discussed results and contributed substantially to the writing and revising of the manuscript.

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53 $\log(\lambda_s)$, over the full range of the environmental autocorrelation ρ from $\rho = -1.0$, or blue noise, to $\rho = 0.0$, or white noise, and ρ
54 $= 1.0$, or red noise. We subsequently applied a perturbation analysis to identify the traits most strongly affecting $\log(\lambda_s)$. Next,
55 we took the difference in maximum and minimum $\log(\lambda_s)$ across $\rho = -1:1$, $\Delta \log(\lambda_s)$, as our measure of how sensitive a species
56 is to a shift in environmental autocorrelation. To answer question (i), we classified ray-finned fish according to their main life
57 history strategies using a phylogenetically informed principle component analysis (PCA) (27) on the DEB-IPM species-specific
58 trait values, and then assessed if main life history strategies were linked to our measure of sensitivity to environmental change,
59 $\Delta \log(\lambda_s)$, to answer question (ii). Finally, we used a combination of perturbation analysis, additive models and (non)linear
60 test statistics to determine if (iii) population responses to shifts in environmental autocorrelation can be linked to individual
61 life history traits and reproductive strategies in an informative way.

62 Materials and Methods

63 **General structure of a DEB-IPM.** We used a demographic modelling approach based on DEB-IPMs to compute the population
64 growth rate and sensitivity of ray-finned fish to environmental autocorrelation. A DEB-IPM is a population model that tracks
65 the survival, growth and reproduction of cohorts of individuals in a population (22). The model integrates over discrete time
66 and a continuous size distribution. Individual life history trajectories are captured in the DEB-IPM by four fundamental
67 functions: (1) The survival function $S(L(t))$ denotes the probability that an individual survives from time t to $t + 1$ given that
68 it is of length L . (2) The growth function $G(L(t))$ describes the probability that an individual grows from length L at time t
69 to L' at $t + 1$, conditional on survival. (3) The reproduction function $R(L(t))$ describes the number of offspring produced
70 from time t to $t + 1$ by a female of length L at time t . (4) The parent-offspring function $D(L', L(t))$ denotes the probability
71 that a female of length L at time t produces offspring of length L' at $t + 1$, conditional on reproduction. Together, the four
72 fundamental functions describe the dynamics of the number of female individuals in a population N , over the length domain Ω ,
73 from time t to $t + 1$ (28).

$$74 \quad N(L', L(t+1)) = \int_{\Omega} [D(L', L(t))R(L(t)) + G(L', L(t))]N(L, t)dL \quad [1]$$

75 We constructed three different DEB-IPMs to capture the different breeder types that occur among the ray-finned fish in our
76 dataset, and which reflect the three types of reproductive decisions that we explore: (1) iteroparous obligate breeders, which
77 have multiple reproductive events over their life cycle and reproduce every season irrespective of environmental conditions. (2)
78 Iteroparous skip breeders that also have multiple reproductive events over their life cycle, but pass up on the opportunity to
79 breed in bad environments, and (3) Semelparous skip breeders that have a single reproductive event in their life cycle, and pass
80 up on the opportunity to breed in bad environments. Based on these characteristics, we formulated different survival and
81 reproduction functions for the three breeder types, but maintained the same growth and parent-offspring functions.

82 **Growth.** Body growth of fish is typically indeterminate and food supply driven (29), following a von Bertalanffy growth curve:

$$83 \quad G(L', L(t)) = \frac{1}{\sqrt{2\pi\sigma_L^2(L(t+1))}} e^{\frac{-(L' - E(L(t+1)))^2}{2\sigma_L^2(L(t+1))}} \quad [2]$$

84 where $E(L(t+1))$ is the expected growth of individuals of length L :

$$E(L(t+1)) = \begin{cases} L(t)e^{-r_B} + (1 - e^{-r_B})L_m E(Y), & \text{if } L \leq L_m E(Y), \\ 0, & \text{otherwise.} \end{cases} \quad [3]$$

with r_B as the von Bertalanffy growth coefficient, L_m as the maximum length, $E(Y)$ as the expected feeding level, scaled between zero and one, and σ_L^2 the individual variance in length at $t+1$.

$$\sigma^2(L(t+1)) = \begin{cases} (1 - e^{-r_B})L_m \sigma^2(Y), & \text{if } L \leq L_m E(Y), \\ 0, & \text{otherwise.} \end{cases} \quad [4]$$

where $\sigma(Y)$ is the standard deviation of the expected feeding level

Parent-offspring association. The parent offspring association function describes the probability that the offspring of an individual of length L is of length L' at $t+1$.

$$D(L', L(t)) = \begin{cases} 0, & \text{if } L' < L_p, \\ \frac{1}{\sqrt{2\pi\sigma_{L_b}^2(L(t))}} e^{\frac{-(L' - E_{L_b}(L(t)))^2}{2\sigma_{L_b}^2(L(t))}}, & \text{otherwise.} \end{cases} \quad [5]$$

Where $E_{(L_b)}$ is the expected length at birth of the offspring, and $\sigma_{(L_b)}^2$ is the expected variation in offspring size, as measured at the next population census in the model at $t+1$.

Survival. The survival of individual fish is generally size-dependent, especially in the early life stages, with a decrease in predation mortality for increasing body sizes (30). Size-dependent survival is modelled using an exponential function. In iteroparous obligate and iteroparous skip breeders it takes the form:

$$S(L(t)) = \begin{cases} e^{-\left(\mu_p \frac{L_m}{L(t)}\right)}, & \text{if } L \leq \frac{L_m E(Y)}{k} \\ 0, & \text{otherwise.} \end{cases} \quad [6]$$

Where μ_p is the adult background mortality rate due to predation, and k denotes the fraction of assimilated energy allocated to metabolic maintenance and growth, following the Kooijman-Metz model (31). Semelparous skip breeders have two additional conditional statements on this survival function, that which ensures they die after having reproduced.

$$S(L(t)) = \begin{cases} e^{-\left(\mu_p \frac{L_m}{L(t)}\right)}, & \text{if } L \leq L_p \text{ \& } L \leq \frac{L_m E(Y)}{\kappa}, \\ e^{-\left(\mu_p \frac{L_m}{L(t)}\right)}, & \text{if } L > L_p \text{ \& } L \leq \frac{L_m E(Y)}{\kappa} \text{ \& } E(Y)_{t-1} = E(Y)_{low}, \\ 0, & \text{if } L > L_p \text{ \& } L \leq \frac{L_m E(Y)}{\kappa} \text{ \& } E(Y)_{t-1} = E(Y)_{high}, \\ 0, & \text{otherwise.} \end{cases} \quad [7]$$

With $E(Y)_{low}$ as the low expected feeding level and $E(Y)_{high}$ as the high expected feeding level.

Reproduction. Following the Kooijman-Metz model (31), we assume a quadratic scaling of reproductive output with female body size. In iteroparous obligate breeders, the reproduction function takes the form:

$$R(L(t)) = \begin{cases} 0, & \text{if } L_b < L < L_p, \\ \phi \left(E(Y) R_m \frac{L(t)^2}{L_m^2} \right), & \text{if } L_p < L < L_m E(Y) \\ \phi \left(\frac{R_m}{1-k} \left[E(Y) L(t)^2 - \frac{k L(t)^3}{L_m} \right] \right), & \text{if } L_m < L \leq \frac{L_m E(Y)}{k} \end{cases} \quad [8]$$

Where ϕ is the survival during the egg and larval phase, and R_m is the maximum reproduction in number of eggs of an individual of maximum size L_m . Iteroparous and semelparous skip breeders pass up on the opportunity to breed in bad environments. This imposes an additional restriction on the fundamental reproductive function as compared to iteroparous obligate breeders:

$$R(L(t)) = \begin{cases} 0, & \text{if } L_b < L < L_p, \\ 0, & \text{if } L_p < L < L_m E(Y) \text{ \& } E(Y) = E(Y)_{low}, \\ \phi \left(E(Y) R_m \frac{L(t)^2}{L_m^2} \right), & \text{if } L_p < L < L_m E(Y) \text{ \& } E(Y) = E(Y)_{high}, \\ \phi \left(\frac{R_m}{1-k} \left[E(Y) L(t)^2 - \frac{k L(t)^3}{L_m} \right] \right), & \text{if } L_m < L \leq \frac{L_m E(Y)}{k} \end{cases} \quad [9]$$

DEB-IPM parametrisation and implementation. We used a set of eight traits to parametrize the DEB-IPMs: Larval transformation length (L_b), variation in transformation length (σ_{L_b}), maturation length (L_p), maximum adult length (L_m), maximum number of eggs produced by adult of maximum length (R_m), egg and larval stage survival rate (ϕ), and natural mortality rate (μ_p). Parameter values for each of the model species are listed in Supplementary table S1, and additional life history information required to categorise species along different breeder types is listed in Supplementary table S2. We calculated six of the DEB-IPM parameters directly from literature, but computed the survival during the egg and larval phase, ϕ , and variation in offspring size, $\sigma_{L_b}^2$, manually:

$$\phi = 1 - e^{(-M \cdot n)} \quad [10]$$

Where M is the instantaneous mortality coefficient of the species during the egg and larval phase, and n is the duration of the egg and larval phase, both in unit days.

$$\sigma_{L_b}^2 = (c_i \cdot \left| \frac{\min_{L_b} - \mu_{L_b}}{3} \right|)^2 \quad [11]$$

In which \min_{L_b} represents the minimal larval or hatching size, μ_{L_b} is the mean of the distribution of larval size, assumed to follow a normal distribution, and c_i is a multiplier constant set to 0.1, 0.5 or 1.0 for species with low, medium and high spread in spawning, respectively. The rationale being that species releasing all eggs in a single event will have a lower variation in offspring size measured at the next population census compared to species that release eggs daily over an extended period of time. The equation itself is an adaptation of the z-score formula to calculate the standard deviation of a normal distribution (32).

Stochastic demographic model. We implemented the DEB-IPMs in the stochastic demographic model $\mathbf{p}(t+1) = \mathbf{A}(t) \cdot \mathbf{p}(t)$, to calculate population sensitivity to shifts in environmental autocorrelation, which we had defined as $\Delta \log(\lambda_s)$, the difference between maximum and minimum $\log(\lambda_s)$ across $\rho = -1 : 1$. The vector $\mathbf{p}(t)$ is the population vector at time t , and $\mathbf{A}(t)$ is a DEB-IPM at time t , defined by a two-state Markov chain habitat transition matrix \mathbf{H} (33):

$$H = \begin{bmatrix} 1-p & q \\ p & 1-q \end{bmatrix} \quad [12]$$

In the habitat transition matrix, p equals the probability of switching from the good to the bad environment, and q equals the probability of switching from the bad to the good environment. The autocorrelation equals $\rho = 1 - p - q$ (33). We defined good and bad environmental states as individuals experiencing either high feeding levels $E(Y)_{high}$, or low feeding levels $E(Y)_{low}$, respectively. The feeding levels were based on the feeding levels associated with population declines ($\log(\lambda_s) < 1.0$), and population increases ($\log(\lambda_s) > 1.0$). We set the feeding levels at $E(Y)_{high} = 1.0$, and $E(Y)_{low} = 0.7$, for all species. We accounted for variation in experienced feeding levels between individuals through the parameter $\sigma(Y)$, that was set at an intermediate level of $\sigma(Y) = 0.3$ (22).

We ran simulations for each of the 34 model species, across an autocorrelation range of $\rho = -1 : 1$, corresponding to a gradient of blue to white and red environmental noise, with a step size of 0.001, and a fixed frequency of good environments of $f = 0.5$. Each simulation consisted of 50,000 time steps, with an initial transient of 400 time steps, a starting population of one individual in each size bin, and a randomly chosen initial environmental state (34). At each time step, the DEB-IPM at time t , $\mathbf{A}(t)$ is calculated based on the experienced feeding level $E(Y)$ at time t , and stored. The log of the stochastic population growth rate, $\log(\lambda_s)$, could then be calculated for each of the simulations.

$$\log(\lambda_s) = \frac{1}{\tau} \sum_{\tau=0}^{\tau-1} \log \frac{\mathbf{p}(t+1)}{\mathbf{p}(t)} \quad [12]$$

PCA analysis. We used a phylogenetically informed principle component analysis (PCA)(27), to examine if the main life history strategies of ray-finned fish reflect the growth-reproduction trade-off and reproductive strategies (research question i), and if main life history strategies were linked to our measure of sensitivity to environmental change, $\Delta \log(\lambda_s)$ (research question ii). The input parameters of the phylogenetic PCA were the eight species traits values included as parameters in the DEB-IPMs (Table 1), and $\Delta \log(\lambda_s)$, calculated for each species. The trait and $\Delta \log(\lambda_s)$ values were log-transformed and scaled with a mean of one and standard deviation of zero to meet PCA assumptions of normality. We accounted for phylogenetic relatedness between the species in the PCA by constructing a species level phylogenetic tree using the phytools package (35). The phylogenetic relatedness of species, expressed as tree branch length, was linked to the life history traits and $\Delta \log(\lambda_s)$ values via a modified covariance matrix. Next, we calculated Pagel's λ , which functions as a scalar for the correlation observed between the values in the trait matrix and the phylogenetic relatedness matrix (36). A Pagel's λ value of zero indicates that the correlation in traits observed between species are independent of their shared evolutionary history, whereas a value of 1 suggests the correlation in traits is fully determined by it (37). We applied the Kaiser's criterion to select the number of PCA-axes to keep, retaining only those axes with an eigenvalue > 1 (38). Finally, we applied a K-means clustering to the PCA

162 results to evaluate and visualise how different groups of species varied in their loadings across the PCA axes. The optimal
163 amount of clusters in the data was determined using the NbClust package in R (39), which compares 30 different clustering
164 indices and uses the majority rule to decide the optimum amount of clusters. One species (*G. mirrabilis*), with outlier values
165 for sensitivity and mortality ($\Delta \log(\lambda_s) = 1.77$, $z_{\Delta \log(\lambda_s)} = 4.18$; $\mu_p = 4.76$, $z_{\mu_p} = 4.65$) was excluded from the PCA-analysis.

166 **Perturbation analysis.** We used a perturbation analysis to examine which of the eight life history traits listed in table 1 most
167 strongly affected ($\log(\lambda_s)$), and how trait importance might shift over the gradient of environmental autocorrelation; in partial
168 answer to research question iii. Each trait parameter was perturbed by 1% and the elasticity of $\log(\lambda_s)$ calculated.

169 **Additive modelling and (non)linear correlation metrics.** We used two separate measures of population responses, the previously
170 defined measure of sensitivity, $\Delta \log(\lambda_s)$, and the new measure of performance, to further statistically examine if individual
171 traits and reproductive strategies can be linked to population responses in an informative way (research question iii). The
172 measure of performance was defined as the complete time series of $\log(\lambda_s)$ for each value in the gradient of environmental
173 autocorrelation. We then used a generalised additive model (GAM) to fit a smoother trend to species performance data.
174 Each categorical variable from the life history table (Table 2), was included into the model as a separate ordered factor. We
175 accounted for the potential effect of related groups of species by including taxonomic order as an additional factor in the model.
176 Subsequently, we used a double penalty approach to get to a final selection of relevant factors (40) (Supplementary information
177 2). Significant differences in performance between the factor levels in the final model were visualised using difference smooths
178 (41). Next, we used the Wilcoxon ranked-sum test to assess whether there was any difference in sensitivity between the levels
179 of factors that had shown a significant difference in performance. Finally, we also examined the relationships between life
180 history traits and sensitivity to environmental variability on a trait-by-trait basis. We used a set of five linear and nonlinear
181 correlational metrics to account for the potentially varying nature of these relationships (1) Linear regression (2) Quadratic
182 regression (3) Distance correlation (4) Two-sample Kolmogorov-Smirnov test, and (5) Fisher's exact test.

183 Results

184 **Life history variation and sensitivity to environmental autocorrelation.** We found evidence that the main life history strategies
185 in ray-finned fish were analogous to the growth-reproduction trade-off and reproductive strategy axes (research question i). In
186 total, we found three main PCA axes that together explained 78 % of the total variation in the set of species life history traits
187 and sensitivity (PC1: 49%, PC2: 17%, PC3: 12%; Table 3). Phylogenetic relatedness had little effect on species trait and
188 sensitivity values (Pagel's $\lambda = 6.7 \cdot 10^{-5} \pm 5.4 \cdot 10^{-7}$); a finding that is reflected in species clustering of PCA-scores (Fig. 2),
189 where each of the four clusters found in the data contained species from across the phylogenetic tree. PC1 was most strongly
190 associated with traits relating to growth and survival, with the highest positive loadings for maximum length (L_m), maturation
191 size (L_p), and negative loadings for mortality rate (μ_p), variation in offspring size (σ_{L_b}), and growth rate (r_B). This reflects a
192 trade-off between growth and survival, i.e. larger, slow growing species with high survival, versus smaller, fast growing species
193 with lower survival. PC2 contained a high positive loading for egg-and larval survival (ϕ) and a high negative loading for the
194 maximum number of offspring produced (R_m); reflecting a trade-off between investing in a large number of offspring with
195 lowered survival and less offspring with increased survival.

196 We found that our measure of sensitivity to environmental change was not associated to PC1 and PC2 (research question

ii), but was most strongly linked to the third PCA axis. PC3 contained high negative loadings of both offspring size (L_b) and sensitivity to shifts in environmental autocorrelation $\Delta \log(\lambda_s)$; indicating that species with smaller offspring sizes also tended to have lower $\Delta \log(\lambda_s)$ to shifts in environmental autocorrelation. However, when examined individually, the relationship between L_b and $\Delta \log(\lambda_s)$ was found to be highly non-significant (Table 4). This indicates that rather than being strongly associated to each other, L_b and $\Delta \log(\lambda_s)$ have in common that they are strongly dissociated from the patterns in traits on PC1 and PC2. Furthermore, both variables are strongly separated from each other when including PC4 ($\Delta \log(\lambda_s)_{PC4} = 0.976$, $L_{b,PC4} = 0.057$). However, we dropped PC4 as it did not add substantial information in describing the complete set of traits based on the Kaiser criterion (Eigenvalue PC4= 0.817).

Links between sensitivity to environmental autocorrelation and individual life history traits and reproductive strategies. We did not find any significant linear or non-linear correlations between $\Delta \log(\lambda_s)$ and individual life history traits (research question iii; Table 4; Supporting plots in Supplementary Information 2). The $\Delta \log(\lambda_s)$ of species did differ significantly between several of the reproductive strategy variables. Specifically, marine species were found to have significantly lower $\Delta \log(\lambda_s)$ than freshwater species (Wilcoxon ranked sum test, $W = 109$, $p = 0.004$; Supplementary Figure S2a). Next to this, iteroparous breeders had significantly lower $\Delta \log(\lambda_s)$ than semelparous breeders (Wilcoxon ranked sum test, $W = 23$, $p = 0.013$; Supplementary Figure S2b), and obligate breeders significantly lower $\Delta \log(\lambda_s)$ than skip breeders (Wilcoxon ranked sum test, $W = 0$, $p < 0.001$; Supplementary Figure S2c). The $\log(\lambda_s)$ of species under environmental autocorrelation also differed significantly between reproductive strategy variables. These findings can be found in Supplementary Materials III.

Stochastic demographic model. Our stochastic demographic models captured the population growth rates of the 34 model species and showed different responses between models across the gradient of environmental autocorrelation (Supplementary Figure S10). The perturbation analysis of our demographic model revealed that $\log(\lambda_s)$ was most sensitive to perturbation of four traits related to growth and reproduction (research question iii; Fig. 3): Egg-larval survival (ϕ), maturation length (L_p), maximum length (L_m), and growth rate (r_B). In iteroparous obligate breeders, $\log(\lambda_s)$ of 94% of species was most sensitive to a single trait across the gradient of environmental autocorrelation, compared to 36% and 4% of species in iteroparous skip and semelparous breeders respectively. In the latter two models, trait importance across the gradient of environmental autocorrelation alternated between a maximum of two traits. The trait that was most influential to $\log(\lambda_s)$ in iteroparous obligate breeders was L_p (67%), followed by ϕ (22%). In iteroparous skip breeders, L_m (72%), and r_B (55%), were found to be most important. Finally, in semelparous species, ϕ (60%) was the most important trait, followed in equal terms by L_p , L_m , and r_B (all found in 40% of species). Changes in trait importance across the gradient of environmental autocorrelation did not follow changes in $\log(\lambda_s)$. For example, there was no observable shift in trait importance moving from white to red environmental autocorrelation in iteroparous skip breeders, or when moving from blue to white, and from white to red environmental autocorrelation in semelparous breeders.

Discussion

We used ray-finned fish as a model system to examine if explicitly accounting for life history trade-offs and reproductive decisions results in general patterns of how species of different life history speed and reproductive strategies respond to shifts in environmental autocorrelation. We found that the first two axes of life history variation in ray-finned fish were analogous to the

axes of life history speed and reproductive strategies found in previous cross-taxonomical analyses of plants and animals (Morris et al. 2008; Salguero-gomez et al. 2016; Paniw et al. 2018; Capdevilla et al. 2020; Healey et al. 2020). The next question is if these patterns in life history strategies relate to how sensitive species are to environmental autocorrelation. Unlike previous work that found that fast life histories were most sensitive to environmental autocorrelation, we found that our measure of sensitivity (the change in log stochastic population growth rate over the environmental autocorrelation gradient, $\Delta \log(\lambda_s)$), was unrelated to species position on the life history speed or reproductive strategy axes. Sensitivity occupied a separate axes on PC3, together with length at birth. However, although they occupied the same axis, we found no significant (non)linear relationship between the two variables, indicating they do not inform on each other. Moreover, we found no relationship between sensitivity and any of the other individual trait values, and no relationship between trait elasticities and population growth rates under environmental autocorrelation. We surmise that these results motivate a more in-depth investigation of the relations between traits and population performance under environmental autocorrelation. Our results question to what extent different trait based approaches are suited to address different types of life history research questions, including the application of traits as bio-indicators of species vulnerability to environmental change.

Life history traits are advocated to be used as bio-indicators of population performance to help inform conservation policy (42). One trait that is commonly associated with population performance is body size (43–45), and it has therefore been suggested as a useful bio-indicator (13, 46). Body-size as a trait is unspecified, but generally taken to be the average adult length or mass observed in a population. We were unable to link shifts in the values of any individual traits, including body-size related traits such as maximum length and length at birth, to shifts in stochastic population growth rates. We also found no statistically significant link between the values of individual traits and the values of sensitivity. Instead of using individual traits, specific groups of traits are sometimes suggested in the literature as bio-indicators of population performance. This approach is part of the continued search for the ‘holy-grail’ of cross-taxonomic functional traits (7, 47), whereby a single set of traits describes functions across the tree of life. Our PCA results indicate that there was no group of traits associated to sensitivity under environmental change. We suggest that this might be because the reproductive decisions included in our models more strongly affect population responses than specific trait combinations. This is supported by the fact that we found statistically significant differences in population growth rates between iteroparous and semelparous, and between skip and obligate breeding species, respectively (Supplementary information 3). It therefore seems that explicitly accounting for additional complexity in life history processes can disassociate trait values from measures of population performance, and this negates their use as bio-indicators of vulnerability to environmental change. It also raises the question on the type of method most suitable to answer certain types of life history research questions.

Our results highlight that patterns in trait values alone can be insufficient to inform on sensitivity to environmental change. When we accounted for additional life history complexity through the inclusion of an individual-level dynamic energy budget and reproductive decisions, the classical association between life history traits and population performance broke down. Informing on species sensitivity to environmental change therefore requires us to include relevant complexity in life history *a priori*. The challenge lies in determining what kind of life history processes should be accounted for. Apart from the processes within the individual organism, as explored in the current study, there are also important structuring processes external to the individual, such as feedbacks between populations and their environments and trophic interactions. Theoretical approaches accounting for those elements (while maintaining the mechanistic process description at the individual level) show detailed population

dynamics (48, 49). In a multi-species context, community structure and stability can be linked to underlying mechanisms and, for example, show multiple stable community states (49, 50). Process-based models can therefore be a useful tool to gain insights into the mechanisms of ecological communities and identifying the boundary conditions under which populations can be maintained. However, their computational expense and high output complexity quickly makes them unwieldy when aiming to examine broad cross-taxonomical responses.

We summarise our findings in a perspective that outlines which trait-based approach is most suitable in tackling different challenges in linking life histories to population responses to change (Fig. 4). We surmise that the biggest strength lies in combining different methods to address large and complex questions. For example, to know which species are most vulnerable to environmental change we can (1) use pattern based models to characterize the different life history strategies that have evolved across species, (2) a hybrid model, which combines patterns in traits in combination with a limited set of life history trade-offs and or processes, to identify which of these strategies and individual species show the highest sensitivity when exposed to environmental variation, and (3) a process model to study the responses of the most sensitive species to environmental change in a fuller ecological context, including feedbacks and accounting for trophic interactions. In this way, each approach acts as a focusing lens for the next one, and adds to their overall usefulness in addressing urgent conservation issues by combining their individual powers. We hope that our study can help pave the way towards a more integrative approach utilizing functional traits to understand complex demographic processes in an era of change (51).

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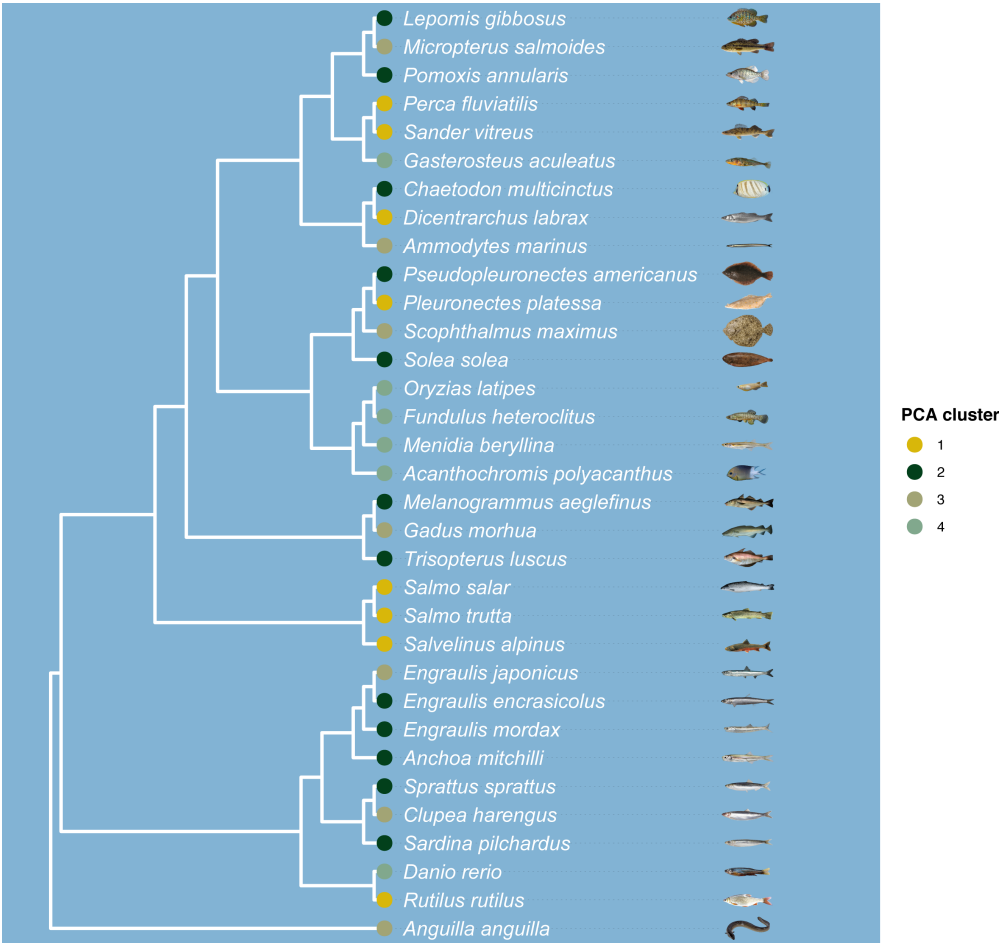


Fig. 1. Phylogenetic tree of the diversity of the ray-finned fish species included in the study. The colours of the end nodes represents cluster identities of species trait and sensitivity scores using a phylogenetically-informed PCA, further detailed in the Methods and Results sections.

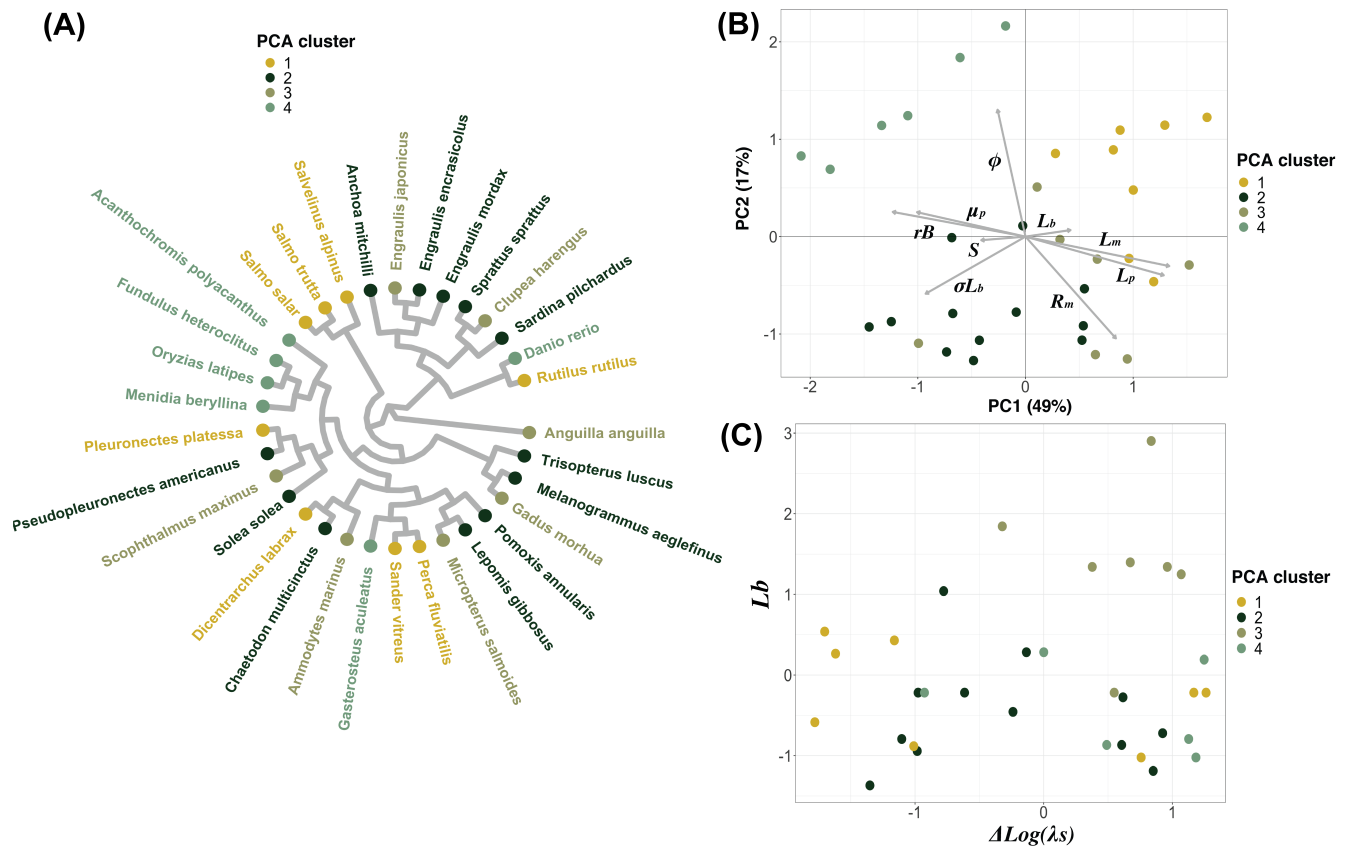


Fig. 2. phylogenetically informed PCA of species life history traits and sensitivity to environmental autocorrelation. (A) Clustering of species trait and sensitivity scores across the three principal components (B) PCA biplot of PC1, most strongly associated with growth and mortality traits, and PC2, associated with reproductive traits. (C) A biplot showing the scores of the two variables most strongly associated with PC3.

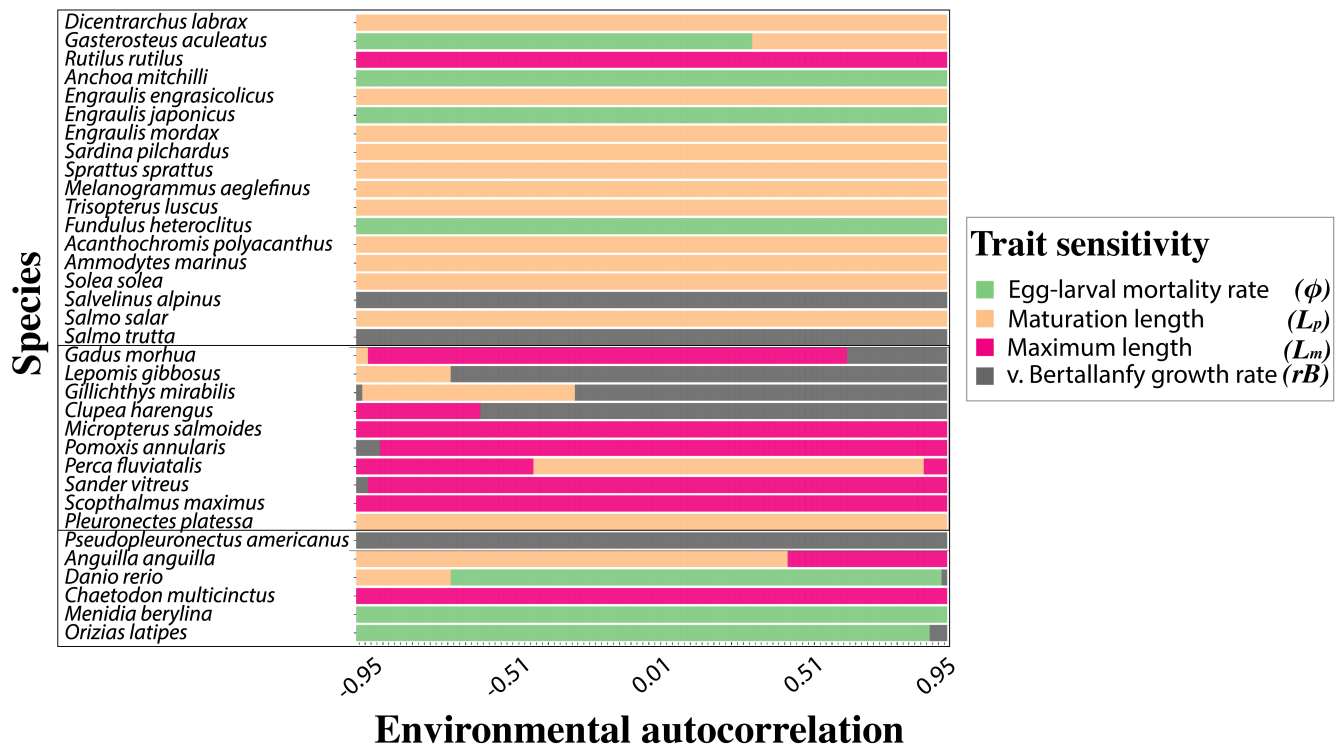


Fig. 3. Life history traits with the highest elasticity in relation to $\log(\lambda_s)$ as a function of environmental autocorrelation for all model species. The black boxes indicate species from the stochastic demographic models of Iteroparous obligate breeders (upper box), Iteroparous skip breeders (centre box) and Semelparous skip breeders (bottom box), respectively.

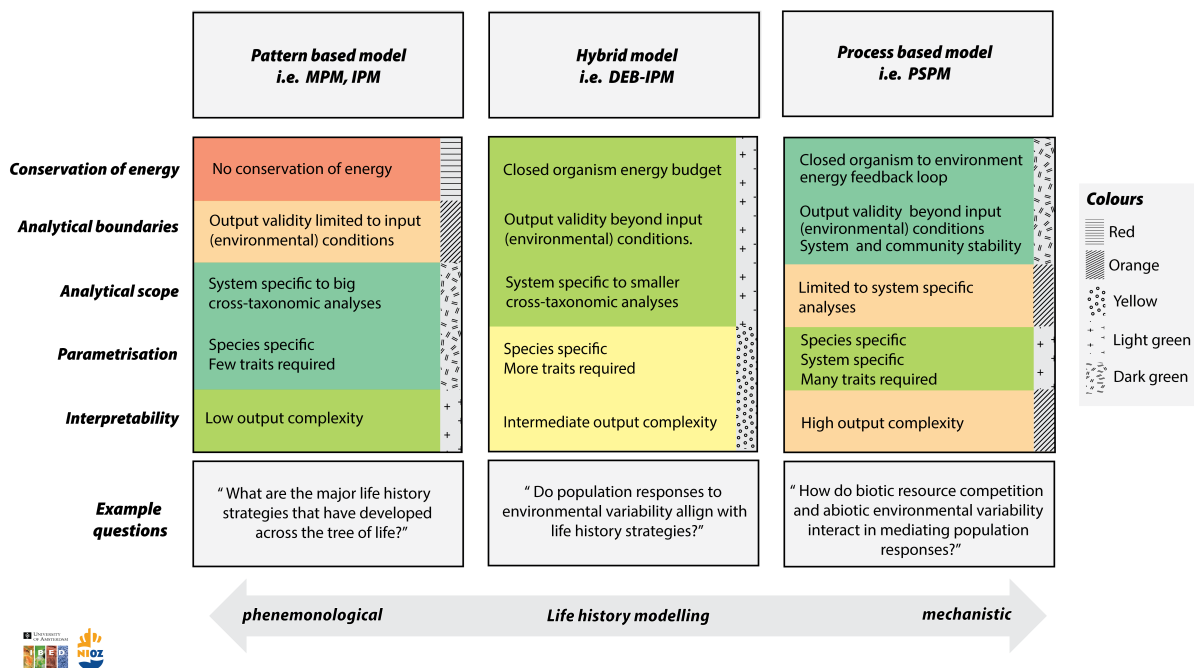


Fig. 4. Conceptual framework highlighting the characteristics of different kinds of modelling approaches in life history research. The framework can be used to identify the most appropriate approach based on research specifics. The columns list three different modelling approaches (pattern, hybrid, and process based models, respectively). The rows describe important modelling assumptions. The text in the row cells explains the limitation of each of the three modelling approaches in relation to these assumptions. This explanation is combined with both a 5-valued color scale that indicates how the different modelling approaches perform in relation to each assumption (Red: poor, Orange: bad, Yellow: average, Light green: good, Dark green: very good). Finally, the bottom row lists an example research question that each modelling approach is suited to address.

Table 1. Phylogenetic PCA loadings of life history traits and sensitivity to shifts in environmental variability on the first three principal components. Bold values indicate the principal component with which each trait is most strongly associated.

Life history traits	PC1 (Eigenvalue = 4.377)	PC2 (Eigenvalue = 1.546)	PC3 (Eigenvalue = 1.057)
1. μ_p	-0.710	0.177	0.055
2. L_p	0.905	-0.280	-0.057
3. ϕ	-0.183	0.918	-0.053
4. r_B	-0.869	0.179	-0.183
5. σ_{L_B}	-0.654	-0.413	-0.422
6. R_m	0.592	-0.736	0.067
7. L_b	0.295	0.047	-0.766
8. L_m	0.941	-0.213	-0.017
9. $\Delta \log(\lambda_s)$	-0.289	-0.026	-0.690

Table 2. Linear and non-linear test statistics of the relationship between $\Delta \log(\lambda_s)$ and log transformed life history traits. For the Kolmogorov-Smirnov test, distributions of trait values were compared between species classified as sensitive and insensitive. For Fischer's exact test, the trait values of species were classified into three quantile groups (low, medium and high values). Supporting plots for data grouping into classes and quantile groups are provided in Supplementary information III. There is no indication of significance, since none of these measures showed a significant correlation.

Life history traits	Pearson correlation	Distance correlation	Kolmogorov-smirnov test	Fischer's exact test
1. $\log_{10}(\mu_p)$	$r = 0.162, p = 0.366$	$dCor = 0.293, p = 0.285$	$D = 0.169, p = 0.972$	$p = 0.490$
2. $\log_{10}(L_p)$	$r = 0.139, p = 0.422$	$dCor = 0.282, p = 0.335$	$D = 0.287, p = 0.507$	$p = 0.240$
3. $\log_{10}(\phi)$	$r = 0.262, p = 0.140$	$dCor = 0.358, p = 0.076$	$D = 0.224, p = 0.801$	$p = 1.000$
4. $\log_{10}(r_B)$	$r = 0.250, p = 0.163$	$dCor = 0.328, p = 0.176$	$D = 0.290, p = 0.490$	$p = 0.092$
5. $\log_{10}(\sigma_{L_B})$	$r = 0.168, p = 0.431$	$dCor = 0.246, p = 0.467$	$D = 0.268, p = 0.593$	$p = 0.469$
6. $\log_{10}(R_m)$	$r = -0.042, p = 0.815$	$dCor = 0.279, p = 0.318$	$D = 0.290, p = 0.490$	$p = 0.735$
7. $\log_{10}(L_b)$	$r = 0.021, p = 0.909$	$dCor = 0.199, p = 0.880$	$D = 0.232, p = 0.768$	$p = 0.853$
8. $\log_{10}(L_m)$	$r = -0.145, p = 0.419$	$dCor = 0.259, p = 0.395$	$D = 0.235, p = 0.751$	$p = 0.295$