

RESEARCH ARTICLE

Why we cannot always expect life history strategies to directly inform on sensitivity to environmental change

Mark Rademaker¹  | Anieke van Leeuwen¹ | Isabel M. Smallegange² 

¹Department of Coastal Systems, Royal NIOZ and Utrecht University, Texel, The Netherlands

²School of Natural & Environmental Sciences, Newcastle University, Newcastle upon Tyne, UK

Correspondence

Mark Rademaker

Email: mark.rademaker@nioz.nl

Handling Editor: Marlène Gamelon

Abstract

1. Variation in life history traits in animals and plants can often be structured along major axes of life history strategies. The position of a species along these axes can inform on their sensitivity to environmental change. For example, species with slow life histories are found to be less sensitive in their long-term population responses to environmental change than species with fast life histories.
2. This provides a tantalizing link between sets of traits and population responses to change, contained in a highly generalizable theoretical framework.
3. Life history strategies are assumed to reflect the outcome of life history tradeoffs that, by their very nature, act at the individual level. Examples include the trade-off between current and future reproductive success, and allocating energy into growth versus reproduction. But the importance of such tradeoffs in structuring population-level responses to environmental change remains understudied.
4. We aim to increase our understanding of the link between individual-level life history tradeoffs and the structuring of life history strategies across species, as well as the underlying links to population responses to environmental change.
5. We find that the classical association between life history strategies and population responses to environmental change breaks down when accounting for individual-level tradeoffs and energy allocation.
6. Therefore, projecting population responses to environmental change should not be inferred based only on a limited set of species traits.
7. We summarize our perspective and a way forward in a conceptual framework.

KEYWORDS

dynamic energy budget, fast-slow continuum, functional traits, integral projection model, reproductive strategies

Anieke van Leeuwen and Isabel M. Smallegange shared senior authors.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2024 The Authors. *Journal of Animal Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

The wide diversity in life history traits observed across plant and animal species can be summarised by two main axes reflecting different strategies in speed of life and reproduction (Capdevila et al., 2020; Gaillard et al., 1989; Salguero-Gómez, Jones, Jongejans, et al., 2016). This is typically reflected by the ranking of fast-growing, short-lived species with high fecundity at one extreme of the speed of life axis (also referred to as the fast-slow continuum) and slow-growing, long-lived species with low fecundity at the other (in the next paragraph, we discuss in more detail the processes that shape these life history strategies). Similarly, highly semelparous species with a single reproductive event in their lifespan and high mortality are ranked at one extreme of the reproductive strategy axis, and iteroparous species with high spread in reproduction and low mortality on the other (Healy et al., 2019). When looking at only a particular group of living beings, the nature of the second axis might be variable depending on the traits considered, for example in mammals the second axis can relate to development rather than reproduction (Stearns, 1983). Early demographic modelling studies predicted that the long-term population responses of plant and animal species with slow life histories are buffered against increasing environmental variation (Morris et al., 2008) because the long-lasting adult stage typical of slower life histories allows these populations to better tolerate changes in the year-to-year variation expected under increasing environmental variation than faster ones. The degree of environmental variation is a useful proxy in demographic models to assess the potential impacts of climate change on populations (Stireman et al., 2005); where certain regions are expected to experience higher variability in climatic conditions, and others less (Lewis & King, 2017; van der Wiel & Bintanja, 2021). However, predictions from more recent demographic analyses regarding the sensitivity of faster versus slower populations to increasing environmental variation are inconclusive. When the vital rates of growth and reproduction are described more mechanistically using the trade-off between growth and reproduction, populations of species with fast life-histories are less sensitive in their long-term population responses (Smallegange et al., 2020; Smallegange & Berg, 2019), and when vital rates are described phenomenologically, based on random variation of statistical averages, populations of species with slow life-histories are less sensitive in their long-term population responses to environmental variation (Paniw et al., 2018). Furthermore, the timescale considered matters. Populations of species with slow life histories have been found to be more sensitive in their short-term responses to disturbances than populations of species with fast life histories (Gamelon et al., 2014), and to be generally more sensitive to increases in mortality (Lebreton, 2006, 2011). These contrasting findings highlight the need to improve our mechanistic understanding of how the structuring of life history variation and population responses to environmental variation link together.

The historical foundation of the speed of life axis, also referred to as the fast-slow continuum, is based on the concept of life history trade-offs (Gaillard et al., 2016). Empirical studies using traits

measured at the population or species level find that there are general trade-offs underlying the structuring life history variation. A range of vertebrate-specific studies showed that underlying the speed of life axis is a trade-off in the value of traits related to reproduction and survival (reviewed in table 1 in Gaillard et al., 2016). Here, species range from high adult survival and low fecundity on one extreme of the speed of life axis, and low adult survival and high fecundity on the other. The existence of a speed of life axis was also found to depend on the selection of traits included and confounding factors accounted for (Jeschke & Kokko, 2009); with body size and phylogenetic relatedness considered the most important confounding factors. Many recent studies structured life history variation across vertebrates, invertebrates and plant species, in both terrestrial and aquatic systems. These studies still find speed of life as the primary axis of life history variation (Capdevila et al., 2020; Healy et al., 2019; Paniw et al., 2018). However, both fecundity and survival, important components of the speed of life axis in previous vertebrate-specific studies, are no longer consistently loaded on the main axis of life history variation. This means that the life history trade-offs inferred from the structuring of traits can also be slightly different. However, structuring population or species-level traits does not represent the only way to account for life history trade-offs.

Life history trade-offs reflected by species or population traits are shaped by limitations in energy allocation that fundamentally operate at the level of the individual organism (Cody, 1966; Stearns, 1989). Organisms have a limited amount of time or energy available and therefore allocating more energy to one biological function, such as growth, will leave less energy available to allocate to other functions (Gaillard et al., 2016). Primary examples are the life history trade-off in energy allocation between growth and reproduction (Gadgil & Bossert, 1970; Reznick, 1983), and between allocating energy to current versus future reproduction (Williams, 1966a, 1966b). Accounting for energy allocation processes at the individual organismal level is important as it allows for emergent differences in dynamics between populations or species even if they have similar traits. Such emergent differences, for example, might help explain the different life history strategies that may be observed between populations of the same species (Gamelon et al., 2021; Nilsen et al., 2009). It also ensures that the law of energy conservation is not violated, and therefore prevents the creation of 'free' biomass in model projections. This is important as it limits any extrapolation biases that might otherwise occur when projecting population responses based on life history strategies. Extending previous studies of life history variation by explicitly accounting for energy allocation at the individual organismal level might therefore lead to new insights on the links between life history trade-offs, traits, strategies, and population responses to environmental variation.

In this study, we aim to assess if life history trade-offs in energy allocation link to the structuring of life history strategies and how they inform on population responses to environmental change. To this end, we parameterised dynamic energy budget integral projections models (DEB-IPMs) (Smallegange et al., 2017)

for 34 species of ray-finned fish *Actinopterygii*. We choose ray-finned fish as our biological model system as they represent the most numerous group of vertebrates (Near et al., 2012) and display a particularly wide range of life history strategies also found in other species groups (Beukhof et al., 2019), that can also be found in other animal groups. In DEB-IPMs, the demographic rates of growth and reproduction are based on an individual-level trade-off between energy allocation into growth versus reproduction (Kooijman & Metz, 1984). Additionally, we extended these DEB-IPMs by incorporating skip and obligate breeding decisions at the individual level across semelparous and iteroparous species. These decisions represented the individual-level trade-off between allocating energy in current versus future reproduction. We used the parameterised DEB-IPMs to answer (i) how life history traits structure into life history strategies when applying a demographic modelling approach explicitly accounting for energy allocation trade-offs at the individual level, and (ii) if individual-level life history trade-offs align with the patterning of traits along the life history strategy axes when using this approach. These two questions help elucidate the links between life history trade-offs in energy allocation operating at the individual organismal level, population-level traits, and life history strategies across populations of different species. We then tested if (iii) population sensitivity to environmental variation covaries with either of the primary life history strategy axes, and also if (iv) population sensitivity to environmental variation covaries with individual life history traits. Finally, we used a perturbation analysis to assess (v) if trait importance might shift over the gradient of environmental variation. Together, these results help improve our understanding of how life history trade-offs, traits, and strategies, link together to shape population responses to environmental variation.

2 | MATERIALS AND METHODS

2.1 | Brief summary of the DEB-IPM

A DEB-IPM is a population model that tracks the survival, growth, and reproduction of cohorts of individuals in a population (Smallegange et al., 2017). The individuals in the population are exposed to environmental variation, affecting their feeding level, and, consequently, the energy available for individual growth and reproduction. Individuals within a certain cohort are exposed to the same sequence of environmental conditions over time, but do not necessarily experience the exact same feeding level at each time step; with some individuals being slightly more successful in gathering resources than others given a certain environment. This means that the life history trajectory of each individual in the model is unique. The individual-level life history functions used to model growth, reproduction and survival in the DEB-IPM are parametrised using a set of life history traits derived from demographic studies at the population level. The individual-level life history functions are then integrated over discrete time and a

continuous size distribution, to yield population-level outcomes, such as projections of population size and population growth rates. The population-level outcomes of the DEB-IPM are therefore an emergent property of individual-level processes and trade-offs. We use a selection of 34 ray-finned fish species as model organisms in the DEB-IPM. These species were selected because their life histories have been studied in particular detail and together they represent the full range of life history strategies observed in this species group (McBride et al., 2015). As many important life history processes such as growth, maturation, reproduction, and survival in ray-finned fish are dependent on body size, rather than age (Kozłowski, 1996; Peters, 1986; Stige et al., 2019), we express the individual level life history functions in our DEB-IPM as a function of individual body size.

2.2 | Brief summary of environmental variation

We model environmental variation over time by exposing individuals in the population to a temporal sequence of good and bad environments. This translates into individuals experiencing high $E(Y)_{\text{high}}$ or low $E(Y)_{\text{low}}$ feeding levels, with individual variation in feeding level $\sigma(Y)$. Feeding level is a relative measure that captures the level of satiation of an organism from empty (feeding level = 0) to completely satiated (feeding level = 1). The ordering of the temporal sequence of environments experienced by individuals is determined by the level of environmental autocorrelation (ρ). We use environmental autocorrelation to express environmental variability because real-world environmental variation often shows temporal autocorrelation (Garca-Carreras & Reuman, 2011; Inchausti & Halley, 2002; Ruokolainen et al., 2009). Specifically, ρ expresses the level of correlation between the environments experienced at subsequent time steps. Positive values ($0 < \rho < 1$) mean environmental conditions at the next time step are likely to be similar to those experienced at the current time step. Negative values ($-1 < \rho < 0$) mean that environmental conditions at the next time step are more likely to be different from those experienced at the current time step. We examine population responses over the entire gradient of $-1 < \rho < 1$, thus exposing populations to a gradient from highly variable to highly invariable environments.

2.3 | Individual level life history functions

Individual life history trajectories are captured in the DEB-IPM by four fundamental functions: (1) The growth function $G(L(t))$ describes the probability that an individual grows from length L at time t to L' at $t + 1$, conditional on survival. (2) The survival function $S(L(t))$ denotes the probability that an individual survives from time t to $t + 1$ given that it is of length L . (3) The reproduction function $R(L(t))$ describes the number of offspring produced 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 that a female of length

L at time t produces offspring of length L' at $t + 1$, conditional on reproduction. We adjusted the reproduction and survival functions to approximate the individual-level trade-off of allocating energy into current versus future reproduction for the different types of breeders that occur in our dataset: Iteroparous obligate breeders, which have multiple reproductive events over their life cycle and reproduce every season irrespective of environmental conditions. Iteroparous skip breeders that also have multiple reproductive events over their life cycle, but pass up on the opportunity to breed in bad environments. Finally, semelparous skip breeders that have a single reproductive event in their life cycle followed by death, and pass up on the opportunity to breed in bad environments.

2.3.1 | Growth function

Body growth of fish is typically indeterminate and food supply driven (Sebens, 1987), following a von Bertalanffy growth curve:

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

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

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

with r_B as the von Bertalanffy growth coefficient (dimensionless), 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 $t + 1$.

$$\sigma^2(L(t+1)) = \begin{cases} (1 - e^{-r_B})L_m \sigma^2(Y), & \text{if } L \leq L_m E(Y), \\ 0, & \text{otherwise} \end{cases} \quad (3)$$

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

2.3.2 | Survival function

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 (Stige et al., 2019). Size-dependent survival is modelled using an exponential function. In iteroparous obligate and iteroparous skip breeders it takes the form:

$$S(L(t)) = \begin{cases} e^{-\left(\mu_p \frac{L_m}{L(t)}\right)}, & \text{if } L \leq \frac{L_m E(Y)}{k}, \\ 0, & \text{otherwise} \end{cases} \quad (4)$$

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 (Kooijman & Metz, 1984). Semelparous skip breeders have two additional conditional statements on this survival function, which ensures they die after having reproduced.

$$S(L(t)) = \begin{cases} e^{-\left(\mu_p \frac{L_m}{L(t)}\right)}, & \text{if } L \leq L_p \text{ \& } L \leq \frac{L_m E(Y)}{\kappa}, \\ e^{-\left(\mu_p \frac{L_m}{L(t)}\right)}, & \text{if } L > L_p \text{ \& } L \leq \frac{L_m E(Y)}{\kappa} \text{ \& } E(Y)_{t-1} = E(Y)_{\text{low}}, \\ 0, & \text{if } L > L_p \text{ \& } L \leq \frac{L_m E(Y)}{\kappa} \text{ \& } E(Y)_{t-1} = E(Y)_{\text{high}}, \\ 0, & \text{otherwise} \end{cases} \quad (5)$$

with $E(Y)_{\text{low}}$ as the low expected feeding level, $E(Y)_{\text{high}}$ as the high expected feeding level, and L_p is the size at maturation.

2.3.3 | Reproduction function

Following the Kooijman-Metz model (Kooijman & Metz, 1984), we assume a quadratic scaling of reproductive output with female body size. In iteroparous obligate breeders, the reproduction function takes the form:

$$R(L(t)) = \begin{cases} 0, & \text{if } L_b < L < L_p, \\ \phi \left(E(Y) R_m \frac{L(t)^2}{L_m^2} \right), & \text{if } L_p < L < L_m E(Y), \\ \phi \left(\frac{R_m}{1-k} \left[E(Y) L(t)^2 - \frac{k L(t)^3}{L_m} \right] \right), & \text{if } L_m < L \leq \frac{L_m E(Y)}{k}, \end{cases} \quad (6)$$

where ϕ is the survival during the egg and larval phase, R_m is the maximum reproduction in number of eggs of an individual of maximum size L_m , and L_b is the size at birth. 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:

$$R(L(t)) = \begin{cases} 0, & \text{if } L_b < L < L_p, \\ 0, & \text{if } L_p < L < L_m E(Y) \text{ \& } E(Y) = E(Y)_{\text{low}}, \\ \phi \left(E(Y) R_m \frac{L(t)^2}{L_m^2} \right), & \text{if } L_p < L < L_m E(Y) \text{ \& } E(Y) = E(Y)_{\text{high}}, \\ \phi \left(\frac{R_m}{1-k} \left[E(Y) L(t)^2 - \frac{k L(t)^3}{L_m} \right] \right), & \text{if } L_m < L \leq \frac{L_m E(Y)}{k}, \end{cases} \quad (7)$$

2.3.4 | Parent-offspring association function

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

$$D(L', L(t)) = \begin{cases} 0, & \text{if } L_b < L < L_p, \\ \frac{1}{\sqrt{2\pi\sigma_{L_b}^2(L(t))}} e^{-\frac{(L' - E_{L_b}(L(t)))^2}{2\sigma_{L_b}^2(L(t))}}, & \text{otherwise} \end{cases} \quad (8)$$

TABLE 1 Species life history trait table including references for the parametrization of the DEB-IPM models. Parameter values were obtained from published studies and the references are listed in parentheses behind the trait values. Units are listed in the top row. L_b = larval transformation length, $\sigma(L_b)$ = variation in transformation length, R_m = maximum number of eggs produced by adult of maximum length L_m , ϕ = fraction egg and larval survival, r_B = von Bertalanffy growth coefficient (dimensionless), L_p = maturation length, L_m = maximum length and μ_p = Natural mortality rate.

Species	L_b (mm)	$\sigma(L_b)$ (mm)	R_m (no. eggs)	ϕ (t^{-1})
1. <i>Acanthochromis polyacanthus</i>	25.0 (Kavanagh, 2000)	0.327 id	225 (Thresher, 1985)	0.195 (Kavanagh, 1996)
2. <i>Ammodytes marinus</i>	50.0 (Jensen et al., 2003)	0.767 id	13,133 (Froese & Pauly, 2002)	0.005 (Wright & Bailey, 1997)
3. <i>Anchoa mitchilli</i>	20.0 (Fahay, 1983; Mansueti & Hardy, 1967)	3.033 id	21,006 (Froese & Pauly, 2002)	0.001 (Houde & Zastrow, 1993)
4. <i>Anguilla anguilla</i>	80.0 (Ayala et al., 2018; Fahay, 2007; Munk & Nielsen, 2005)	1.228 id	2,500,000 (Froese & Pauly, 2002)	0.002 (Bonhommeau et al., 2009)
5. <i>Chaetodon multicinctus</i>	19.5 (Degidio et al., 2017; Leis, 1989)	3.050 id	14,509 (Tricas, 1986)	0.001 (Paris et al., 2009; Tricas, 1986)
6. <i>Clupea harengus</i>	41.0 (Munk & Nielsen, 2005)	0.600 id	141,075 (Froese & Pauly, 2002)	0.001 (Houde & Zastrow, 1993)
7. <i>Danio rerio</i>	14.0 (Singleman & Holtzman, 2014)	1.667 id	500 (Riehl & Baensch, 1973)	0.033 (Houde, 1994; Wilson, 2012)
8. <i>Dicentrarchus labrax</i>	17.0 (Munk & Nielsen, 2005)	0.225 id	520,228 (Froese & Pauly, 2002)	0.001 (Houde & Zastrow, 1993)
9. <i>Engraulis engrasicolus</i>	14.5 (Morote et al., 2010)	1.867 id	226,500 (Froese & Pauly, 2002)	0.001 (Houde & Zastrow, 1993)
10. <i>Engraulis japonicus</i>	40.0 (Takahashi & Watanabe, 2004; Zenitani et al., 2007)	6.167 id	160,000 (Jung et al., 2008)	0.001 (Houde & Zastrow, 1993)
11. <i>Engraulis mordax</i>	35.0 (Hunter, 1977; O'Connell, 1981)	0.536 id	21,006 (Froese & Pauly, 2002)	0.002 (Houde & Zastrow, 1993)
13. <i>Gadus morhua</i>	20.0 (Fahay, 2007)	1.392 id	5,900,000 (Froese & Pauly, 2002; Wiedmann et al., 2014)	0.001 (Houde & Zastrow, 1993)
14. <i>Gasterosteus aculeatus</i>	15.0 (Fahay, 2007)	2.000 id	470 (Froese & Pauly, 2002)	0.139 (Kraak et al., 1997; Swarup, 1958)
15. <i>Gillichthys mirabilis</i>	15.0 (Moser, 1996)	1.000 id	27,000 (Moser, 1996; Shanks & Eckert, 2005)	0.013 (Brothers, 1975)
16. <i>Lepomis gibbosus</i>	15.0 (Auer, 1982)	2.100 id	5000 (Carbine, 1939; Scott & Crossman, 1973)	0.008 (Houde & Zastrow, 1993)
17. <i>Melanogrammus aeglefinus</i>	20.0 (Fahay, 2007)	1.392 id	969,000 (Froese & Pauly, 2002)	0.001 (Houde & Zastrow, 1993)
18. <i>Menidia beryllina</i>	24.0 (Fahay, 2007)	3.417 id	223 (Froese & Pauly, 2002)	0.113 (Gleason & Bengtson, 1996)
19. <i>Micropterus salmoides</i>	40.0 (Heidinger, 1976)	6.167 id	82,000 (Kelley, 1962)	0.016 (Houde & Zastrow, 1993)
20. <i>Oryzias latipes</i>	15.5 (Iwamatsu, 2004)	1.950 id	141 (Leaf et al., 2011)	0.033 (Houde, 1994; Lee et al., 2014)
21. <i>Perca fluviatilis</i>	20.0 (Auer, 1982)	0.255 id	157,594 (Brazo et al., 1975)	0.041 (Houde & Zastrow, 1993)
22. <i>Pleuronectes platessa</i>	14.0 (Houde & Zastrow, 1993)	0.667 id	552,000 (Pecuchet et al., 2017)	0.007 (Houde & Zastrow, 1993)
23. <i>Pomoxis annularis</i>	16.0 (Auer, 1982)	1.233 id	325,677 (Morgan, 1954)	0.002 (Houde & Zastrow, 1993)
24. <i>Pseudopleuronectes americanus</i>	13.0 (Fahay, 2007)	0.177 id	648,836 (Froese & Pauly, 2002)	0.001 (Houde & Zastrow, 1993)
25. <i>Rutilus rutilus</i>	14.9 (Copp, 1990)	0.132 id	190,000 (Lappalainen et al., 2008)	0.033 (Houde, 1994)
26. <i>Salmo salar</i>	26.7 (Kazakov, 1981; Pearlstein et al., 2007)	0.145 id	10,794 (Froese & Pauly, 2002)	0.013 (Houde & Zastrow, 1993)
27. <i>Salmo trutta</i>	28.0 (Réalis-Doyelle et al., 2016)	0.200 id	8616 (Froese & Pauly, 2002)	0.013 (Houde & Zastrow, 1993)
28. <i>Salvelinus alpinus</i>	24.8 (Pavlov & Osinov, 2008)	0.165 id	5400 (Tallman et al., 1996)	0.013 (Houde & Zastrow, 1993)
29. <i>Sander vitreus</i>	20.0 (Auer, 1982)	0.237 id	600,000 (Wolfert, 1969)	0.017 (Houde & Zastrow, 1993)
30. <i>Sardina pilchardus</i>	15.5 (Morote et al., 2010)	1.667 id	169,000 (Froese & Pauly, 2002)	0.001 (Houde & Zastrow, 1993)
31. <i>Scophthalmus maximus</i>	38.4 (Al-Maghazachi & Gibson, 1984; Russell, 1976)	3.022 id	5,000,000 (Pecuchet et al., 2017)	0.001 (Houde & Zastrow, 1993)
32. <i>Solea solea</i>	12.0 (Munk & Nielsen, 2005)	0.750 id	300,000 (Froese & Pauly, 2002)	0.001 (Houde & Zastrow, 1993)
33. <i>Sprattus sprattus</i>	25.0 (Munk & Nielsen, 2005)	3.583 id	14,630 (Froese & Pauly, 2002)	0.001 (Houde & Zastrow, 1993)
34. <i>Trisopterus luscus</i>	18.0 (Rodríguez et al., 2018; Russell, 1976)	2.500 id	521,738 (Froese & Pauly, 2002)	0.001 (Houde & Zastrow, 1993)

$r_B(-)$	$L_p(\text{cm})$	$L_m(\text{cm})$	$\mu_p(t^{-1})$
1.392 (Kingsford et al., 2019)	9.07 (Kavanagh, 2000)	15.3 (Kavanagh, 1996)	0.477 (Kingsford et al., 2019)
0.490 (Froese & Pauly, 2002)	14.0 (Bergstad et al., 2001)	21.0 (Froese & Pauly, 2002)	0.600 (Cook, 2004; ICES, 1998)
0.480 (Froese & Pauly, 2002)	3.69 (Luo, 1991)	11.0 (Hildebrand, 1963)	2.360 (Newberger & Houde, 1995)
0.140 (Froese & Pauly, 2002)	54.00 (Tesch, 1977)	145.0 (Froese & Pauly, 2002)	0.230 (Svedäng, 1999)
1.330 (Tricas, 1986)	7.10 (Tricas, 1986)	9.5 (Tricas, 1986)	0.518 (Goatley & Bellwood, 2016)
0.320 (Froese & Pauly, 2002)	16.70 (Froese & Pauly, 2002)	51.0 (Froese & Pauly, 2002)	0.168 (Beverton, 1963; Cushing, 1959)
1.200 (Froese & Pauly, 2002)	2.50 (Froese & Pauly, 2002)	3.8 (Froese & Pauly, 2002)	1.515 (Weyl & Booth, 1999)
0.120 (Froese & Pauly, 2002)	42.00 (Spitz et al., 2013)	103.0 (Froese & Pauly, 2002)	0.240 (ICES, 2018)
0.470 (Froese & Pauly, 2002)	11.50 (ICES, 2016)	21.0 (Froese & Pauly, 2002)	0.900 (Brandhorst, 1974; Iversen et al., 1993; Schaefer, 1967)
1.700 (Froese & Pauly, 2002)	8.18 (Funamoto et al., 2004)	18.0 (Froese & Pauly, 2002)	0.630 (Iversen et al., 1993)
0.380 (Froese & Pauly, 2002)	13.50 (Richardson, 1980)	24.0 (Froese & Pauly, 2002)	0.970 (Hanan, 1981)
0.160 (Froese & Pauly, 2002)	68.30 (Froese & Pauly, 2002)	123.0 (Froese & Pauly, 2002)	0.216 (Dickie, 1963; Jones, 1966; Pinhom, 1975; Sinclair, 2001)
2.237 (Froese & Pauly, 2002)	5.50 (Froese & Pauly, 2002)	10.0 (Froese & Pauly, 2002)	1.060 (Jones & Hynes, 1950)
0.790 (McGourthy et al., 2009)	10.00 (Barlow, 1963)	21.0 (Eschmeyer & Herald, 1999)	4.761 (Fonds, 1973; Hernaman & Munday, 2005)
0.395 (Copp et al., 2004)	7.00 (van Kleef & Jongejans, 2014)	20.0 (Holtan, 1998)	0.540 (Goedde & Coble, 1981)
0.220 (Froese & Pauly, 2002)	34.90 (Froese & Pauly, 2002)	110.0 (Froese & Pauly, 2002)	0.430 (Jones & Shanks, 1990)
1.140 (Froese & Pauly, 2002)	4.50 (Gleason & Bengtson, 1996)	15.0 (Page & Burr, 1991)	0.993 (Hubbs, 1982)
0.245 (Jackson et al., 2008)	25.00 (Heidinger, 1976)	70.0 (Lee, 1980)	0.450 (Mueller et al., 2005)
3.650 (Leaf et al., 2011)	2.20 (Dhillon & Fox, 2004)	4.5 (Leaf et al., 2011)	1.515 (Weyl & Booth, 1999)
0.332 (Jackson et al., 2008)	19.20 (Froese & Pauly, 2002)	40.0 (Page & Burr, 1991)	1.170 (Goedde & Coble, 1981)
0.130 (Froese & Pauly, 2002)	30.80 (Froese & Pauly, 2002)	100.0 (Nielsen, 1986)	0.140 (Beverton, 1964; Siddeek, 1989)
0.246 (Jackson & Hurley, 2005)	20.50 (Edwards, 1982)	51.0 (Carlander, 1997)	0.84 (Allen et al., 1998)
0.310 (Froese & Pauly, 2002)	27.40 (Froese & Pauly, 2002)	64.0 (Robins & Ray, 1986)	0.300 (Dickie & McCracken, 1955)
0.107 (Sandlund et al., 2013)	10.27 (Paull et al., 2008)	50.2 (Verreycken et al., 2011)	0.400 (Britton, 2007)
0.270 (Froese & Pauly, 2002)	73.10 (Froese & Pauly, 2002)	150.0 (Froese & Pauly, 2002)	0.740 (Chaput, 2012)
0.240 (Froese & Pauly, 2002)	20.20 (Taube, 1976)	94.0 (Froese & Pauly, 2002)	0.670 (Carline, 2006)
0.075 (Loewen et al., 2010)	38.98 (Loewen et al., 2010)	107.0 (Froese & Pauly, 2002)	0.170 (Moore, 1975)
0.266 (Quist et al., 2003)	42.90 (Froese & Pauly, 2002)	107.0 (Scott & Crossman, 1973)	0.440 (Kocovsky & Carline, 2001)
0.360 (Froese & Pauly, 2002)	14.30 (Silva et al., 2013)	27.0 (Froese & Pauly, 2002)	0.667 (Bedairia & Djebbar, 2009; Erdoğan et al., 2010)
0.250 (Froese & Pauly, 2002)	34.70 (Froese & Pauly, 2002)	100.0 (Nielsen, 1986)	0.246 (Chen & Xiao, 2006; Pitt, 1973; Wilderbuer & Turnock, 2009)
0.320 (Froese & Pauly, 2002)	24.60 (Mollet et al., 2007)	70.0 (Froese & Pauly, 2002)	0.100 (Lorenzen, 2005)
0.600 (Froese & Pauly, 2002)	10.00 (Glover et al., 2011; Peck et al., 2012)	16.0 (Whitehead, 1988)	0.377 (Bentley et al., 2019)
0.430 (Froese & Pauly, 2002)	19.20 (Alonso-Fernández et al., 2008)	46.0 (Froese & Pauly, 2002)	1.330 (Bauey & Kunzlik, 1984; Menon, 1950)

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 $t + 1$.

2.4 | Parametrisation of individual-level life history functions

A set of eight traits are used to parameterise the individual level life history functions in the DEB-IPM: Larval transformation length (L_b), variation in transformation length (σ_{L_b}), von Bertalanffy growth coefficient (r_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). We collected the values of these traits from scientific literature (values and references in Table 1). Where multiple studies were available, for example from studies of different populations, an average was taken. The trait values in Table 1, therefore, represent a generalised life history of a species based on combining information from multiple populations where available. We were able to collect species-specific values for six of these DEB-IPM parameter traits directly from scientific literature. We calculated two of the traits, survival during the egg and larval phase, ϕ , and variation in offspring size, $\sigma_{L_b}^2$, manually:

$$\phi = 1 - e^{(-M \cdot n)} \quad (9)$$

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. M and n values were collected from scientific literature (values and references in Table 1).

$$\sigma_{L_b}^2 = \left(c_i \cdot \left\| \frac{\min_{L_b} - \mu_{L_b}}{3} \right\| \right)^2 \quad (10)$$

in which \min_{L_b} represents the minimal larval or hatching size, collected from scientific literature, 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 (Abdi, 2007).

2.5 | Population level integration and outcome variables

The individual-level growth, survival, reproduction, and parent-offspring association functions in the DEB-IPM are integrated over the length domain Ω to describe the dynamics of the total number of

female individuals in a population N , from time t to $t + 1$ (Easterling et al., 2000).

$$N(L', L(t + 1)) = \int_{\Omega} [D(L', L(t))R(L(t)) + G(L', L(t))S(L(t))]N(L, t)dL \quad (11)$$

Given a simulation of τ steps, the log of the stochastic growth rate of the population, $\log(\lambda_s)$ can then be calculated

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

We define the sensitivity of the population to variation in the environment as the difference between maximum and minimum $\log(\lambda_s)$ across simulated environments.

$$\Delta \log(\lambda_s) = \log(\lambda_{s_{\text{Max}}}) - \log(\lambda_{s_{\text{Min}}}) \quad (13)$$

The population-level outcome variables of growth rates and sensitivity to environmental variation are therefore an emergent property of individual-level processes and trade-offs included in the DEB-IPM.

2.6 | DEB-IPM implementation and simulations

2.6.1 | Stochastic demographic model simulations

We implemented the parametrised DEB-IPMs into a stochastic demographic model using *Matlab* (version R2021a) to calculate stochastic population growth rates ($\log(\lambda_s)$) and sensitivity to environmental variation ($\Delta \log(\lambda_s)$). We ran simulations for each of the 34 model species, across an environmental autocorrelation range of $\rho = -1:1$, with a step size of 0.001. 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 (see also Smallegange et al., 2014; Tuljapurkar et al., 2003).

2.6.2 | Stochastic demographic model details

The stochastic demographic model was defined as $p(t + 1) = A(t) \cdot p(t)$. The vector $p(t)$ is the population vector at time t , and $A(t)$ is a DEB-IPM at time t , defined by a two-state Markov chain habitat transition matrix H (Caswell, 2001).

$$H = \begin{bmatrix} 1-p & q \\ p & 1-q \end{bmatrix} \quad (14)$$

In the habitat transition matrix, p equals the probability of switching from a good to a bad environment, and q equals the probability of switching from a bad to a good environment. The autocorrelation level in the model equals $\rho = 1 - p - q$ (Caswell, 2001).

TABLE 2 Phylogenetically informed principal component analysis (pPCA) loadings of life history traits and sensitivity to shifts in environmental variation on the first three principal components for three different models: Full model (FM) with all traits and phylogeny, FM without phylogeny, and model with phylogeny and body size corrected traits. Bold values indicate the principal component with which each trait is most strongly associated. Definitions of the descriptions of the PCA axes on the bottom bar: *fast-slow* fast slow continuum, *reprod.*, reproductive strategy axes; *sens.*, sensitivity to shifts in environmental variation.

pPCA	FM			FM—phylogeny			FM—body size residuals		
Eigenvalue >1	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Cum. variance explained	0.486	0.658	0.775	0.486	0.658	0.775	0.285	0.480	0.615
$\Delta\log(\lambda_s)$	0.289	-0.025	-0.690	-0.090	-0.042	-0.604	0.065	0.699	-0.135
r_B	-0.868	0.178	-0.183	-0.426	0.006	-0.149	-0.093	0.529	-0.624
ϕ	-0.182	0.918	-0.052	-0.005	0.729	-0.123	-0.922	0.033	0.023
R_m	0.591	-0.736	-0.066	0.250	-0.504	-0.013	0.901	0.106	0.081
μ_p	-0.709	0.176	0.055	0.364	0.022	0.058	-0.145	0.001	-0.299
L_p	0.905	-0.279	-0.057	0.458	-0.073	-0.058	0.442	-0.011	-0.769
$\sigma(L_b)$	-0.653	-0.413	-0.422	-0.344	-0.435	-0.316	0.446	0.678	0.296
L_b	0.294	0.047	-0.766	0.232	0.121	-0.699	-0.072	0.626	-0.050
L_m	0.941	-0.213	-0.016	-0.480	-0.014	-0.028	-	-	-
	fast-slow	reprod.	sens.	fast-slow	reprod.	sens.	reprod.	sens.	fast-slow

We used a fixed frequency of good environments of $f = 0.5$ for all levels of environmental autocorrelation examined. The feeding levels of individuals in good and bad environments are associated with positive ($\log(\lambda_s) > 1$), and negative ($\log(\lambda_s) < 1$), population growth rates, respectively. We set the feeding levels associated with good and bad environmental states at $E(Y)_{\text{high}} = 1.0$, and $E(Y)_{\text{low}} = 0.7$, for all species, and the variation in experienced feeding levels between individuals $\sigma(Y)$ at an intermediate level of $\sigma(Y) = 0.3$ (Smallegange et al., 2017). Summarising, at each time step in the stochastic demographic model, the DEB-IPM at time t , $A(t)$ is calculated based on the experienced feeding level $E(Y)$ at time t , determined by the habitat transition matrix, and subsequently stored.

2.7 | PCA analysis

We used a varimax rotated, phylogenetically informed PCA (pPCA; Revell, 2009) to structure species life history traits into life history strategies, following the procedure outlined in (Capdevila et al., 2020; Paniw et al., 2018; Salguero-Gómez, Jones, Jongejans, et al., 2016), implemented using R (version 4.2.1). The life history traits included in this analysis were the eight DEB-IPM parameters and sensitivity to environmental variation $\Delta\log(\lambda_s)$. Trait values were log-transformed and scaled with a mean of one and a standard deviation of zero to meet pPCA assumptions. We constructed a species-level phylogenetic tree prior to performing the pPCA using data from the Open Tree of Life (<https://tree.opentreeoflife.org>, Hinchliff et al., 2015), and the R package ROTL (Michonneau et al., 2016). We used branch lengths as the measure of phylogenetic relatedness between species. Branch lengths were computed using the *compute.brlen* function, and polytomies resolved using the *multi2di* function, from the R package *ape* (Paradis et al., 2004).

We then checked that the constructed tree was rooted and there were no branches with zero length before implementing the pPCA. We implemented the pPCA using the *phyl.pca* function from the R package *phytools* (Revell, 2012). The pPCA linked the phylogeny to the life history traits using a modified covariance matrix, and simultaneously estimated Pagel's λ with maximum likelihood methods (Capdevila et al., 2020; Revell, 2009). Pagel's λ expresses the phylogenetic signal strength in trait evolution under a Brownian motion model (Blomberg & Garland Jr, 2002). 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 one indicates the correlation in traits is fully determined by it (Meireles et al., 2020; Revell, 2010). We applied the Kaiser's criterion to select the number of PCA-axes to keep, retaining only those axes with an eigenvalue > 1 (Kaiser, 1960). One species with outlier values for sensitivity and mortality, as determined based on z -scores (*Gillichthys mirabilis*; $\Delta\log(\lambda_s) = 1.77$, $z_{\Delta\log(\lambda_s)} = 4.18$; $\mu_p = 4.76$, $z_{\mu_p} = 4.65$) was excluded from the pPCA-analysis. Finally, we checked for the influence of phylogeny and body size on the final structuring of life history strategies (see Jeschke & Kokko for a detailed discussion; Jeschke & Kokko, 2009), by running pPCA analyses with and without phylogeny, and with and without a correction for body size. Body size was corrected for by using the residuals of linear regressions of \log_{10} -transformed values of traits versus \log_{10} -transformed adult body mass (Bielby et al., 2007; Gaillard et al., 1989). The resulting pPCA analyses allowed us to examine if the observed life history strategies differ when explicitly accounting for individual-level life history trade-offs (research question i), whether life history trade-offs align with the patterning of traits into life history strategies (research question ii), and if sensitivity to environmental variation covaries with either of the primary life history strategy axes (research question iii), or individual life history traits (research question iv).

2.8 | Perturbation analysis

We used a perturbation analysis to examine which of the eight life history traits listed in Table 1 most strongly affected $\log(\lambda_s)$, and how trait importance might shift over the gradient of environmental autocorrelation (research question v). Each trait parameter i was perturbed by 1% and the elasticity of $\log(\lambda_s)$ calculated.

$$e_i^{(\log(\lambda_s))} = \frac{\log(\lambda_{\gamma_i}) - \log(\lambda_s)}{\gamma_i}, \quad (15)$$

where the elasticity of $\log(\lambda_s)$ to perturbation of trait i by fraction γ_i , equals the difference in population growth rate with and without perturbation, divided by the fraction perturbed. This approach adds detailed insights into the sensitivity to environmental variation at the individual species level.

3 | RESULTS

3.1 | Life history strategies sensitivity to environmental variation

We find that species life history traits in ray-finned fish structure along three separate pPCA axes that cumulatively explain 78% of the total variation in life histories (Table 2: Full Model [FM], pPC1: 48.6%, pPC2: 17.2%, pPC3: 11.7%). Phylogenetic relatedness has little effect on species trait values in this analysis (Pagel's $\lambda = 6.7 \cdot 10^{-5} \pm 3.5 \cdot 10^{-7}$). Trait loadings indicate pPC1 and pPC2 are

analogous to the fast-slow and reproductive strategy axes observed in previous studies (Figure 1). Specifically, pPC1 shows the coupling of traits relating to growth and survival, with the highest positive loadings for maximum length (L_m), maturation size (L_p), and negative loadings for mortality rate (μ_p), variation in offspring size ($\sigma(L_b)$), and growth rate (r_B). This reflects a trade-off between growth and survival, i.e. larger, slow-growing species with high survival, versus smaller, fast-growing species with lower survival. Trait patterning on pPC2 shows a negative coupling between egg-and larval survival rate (ϕ), and the maximum number of offspring produced (R_m). This reflects a trade-off between allocating energy in many offspring with lowered survival versus fewer offspring with increased survival.

Sensitivity to environmental variation, ($\Delta \log(\lambda_s)$), was only very weakly correlated with pPC1 and pPC2, and instead most strongly loaded onto pPC3 (Table 1: FM). Checking for the effect of phylogeny and body size does not alter this result (Table 1: FM—phylogeny; FM—body size residuals). When phylogeny is excluded, the loading of $\Delta \log(\lambda_s)$ is further reduced on pPC1, while remaining similarly weak on pPC2, and strongly loaded on pPC3. Correcting for body size changes the ordering of the principal components, but $\Delta \log(\lambda_s)$ remains strongly loaded on a separate axis with offspring size, and weakly loaded on the fast-slow and reproductive axes. Therefore, across our three pPCA models, we find no evidence of $\Delta \log(\lambda_s)$, i.e. sensitivity covarying with either the fast-slow axis or the reproductive strategy axis.

Next, we examined a potential interaction effect between the fast-slow and reproductive strategy axes on sensitivity, by excluding $\Delta \log(\lambda_s)$ from the pPCA and modelling it as a function of pPCA scores using multiple linear regression (Table 3). pPC1, pPC2, pPC3,

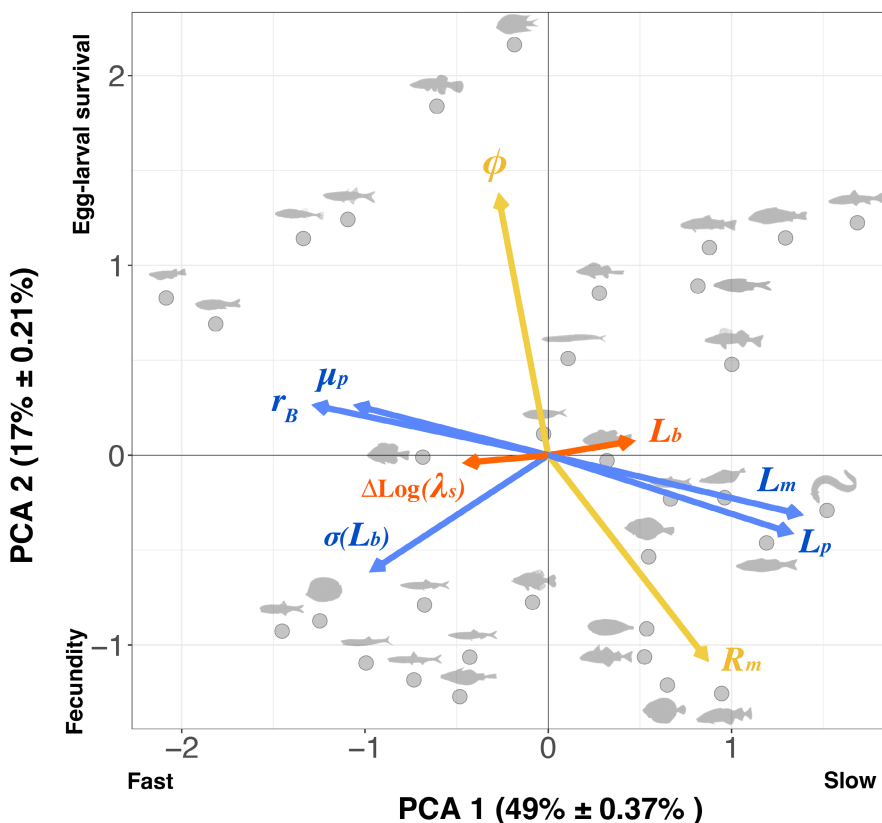


FIGURE 1 Biplot of phylogenetically corrected principal component analysis (pPCA), with the percentage of variance explained in brackets ($\hat{\lambda} \pm \text{SE}$) for the 8 life history traits included as parameters in the dynamic energy budget integral projections models (DEB-IPMs), and the DEB-IPM derived trait of sensitivity ($\Delta \log(\lambda_s)$). Arrow lengths indicate mean loading of each trait, and arrow colour indicates to which pPCA axis it is most strongly associated (blue: pPC1, yellow: pPC2, and orange: pPC3). pPC1 is most strongly associated with growth and mortality traits, pPC2 most strongly with reproductive traits, and pPC3 with sensitivity and size at birth. Points represent the pPCA scores of the sample species on this two-dimensional space, which can be further identified by their silhouettes.

and pPC1 \times pPC2 scores only explained 7.5% of the variation observed in sensitivity across species. The model's F -statistic and associated p -value indicate there is no relationship between any of the predictors and sensitivity, and that it does not perform better than an intercept-only model. Finally, the residual standard error almost equals the intercept effect size, and is much larger than the other estimated effects, further indicating the poor predictive power of the PCA scores in terms of predicting $\Delta(\log(\lambda_s))$. Visually examining sensitivity values across the pPC1-pPC2 gradient also does not indicate a clear PC1-PC2 interaction pattern to be present (Figure S1). Therefore, we find no evidence of $\Delta(\log(\lambda_s))$ covarying with the interaction between the fast-slow and reproductive strategy axis in our study. Examples of species with similar life history strategies and contrasting responses to environmental variation are provided in Figure 2.

3.2 | Life history traits and sensitivity to environmental variation

In the pPCA analysis, $\Delta(\log(\lambda_s))$ consistently negatively loaded on a separate axis together with offspring size L_p , indicating that species

with smaller offspring sizes also tended to have lower sensitivity to environmental variation. However, when examined individually, the relationship between L_b and $\Delta(\log(\lambda_s))$ was found to be highly non-significant (Table S1). 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 trait loadings on pPC1 and pPC2. Additional testing confirmed no statistically significant relationship between $\Delta(\log(\lambda_s))$ and any of the eight life history traits included in the study (Table S1). Although we did not find a clear relationship between sensitivity and traits across species, our perturbation analysis did show differences in trait importance in driving the population growth rates of individual species (Figure 3). Furthermore, there was a clear influence of reproductive decisions on these results. In 70% of iteroparous obligate breeders, maturation length L_p is the most important trait driving population growth rate, and there is generally no shift in trait importance depending on the degree of environmental autocorrelation. In iteroparous skip breeders, however, maximum length L_m (72%), and von Bertalanffy growth rates r_B (55%), are more important than L_p in driving population growth rates. Finally, in semelparous species, egg-larval survival rate ϕ is the most important trait driving population growth

TABLE 3 Main and interaction effects of phylogenetically informed principal component analysis (pPCA) scores on sensitivity to environmental change $\Delta(\log(\lambda_s))$. For this analysis $\Delta(\log(\lambda_s))$ was excluded from the pPCA analysis and subsequently modelled as a function of the pPCA scores using Multiple Linear Regression. The model terms explained little of the observed variation in sensitivity (R^2_{adj}). The insignificant and low-valued F -statistic indicates no predictor has a significant relationship with sensitivity and adds value to an intercept-only model. Finally, the Residual standard error almost equals the intercept effect size, and is much larger than the other estimated effects, indicating poor model fit.

Model terms	Coefficients	SE	p-Value	t-Value	F-statistic	p-Value	df	Residual SE	R^2_{adj}
Intercept	0.23773	0.04065	<0.001	5.849	1.645	0.1895	28	0.2335	0.075
pPC (fast-slow)	-0.02073	0.04251	0.6279	-0.490					
pPC2 (repr. strategy)	-0.012368	0.04171	0.7634	0.304					
pPC3 (offspring size)	-0.02388	0.04138	0.5685	-0.577					
pPC1 \times pPC2	-0.10097	0.04550	0.0348*	-2.219					

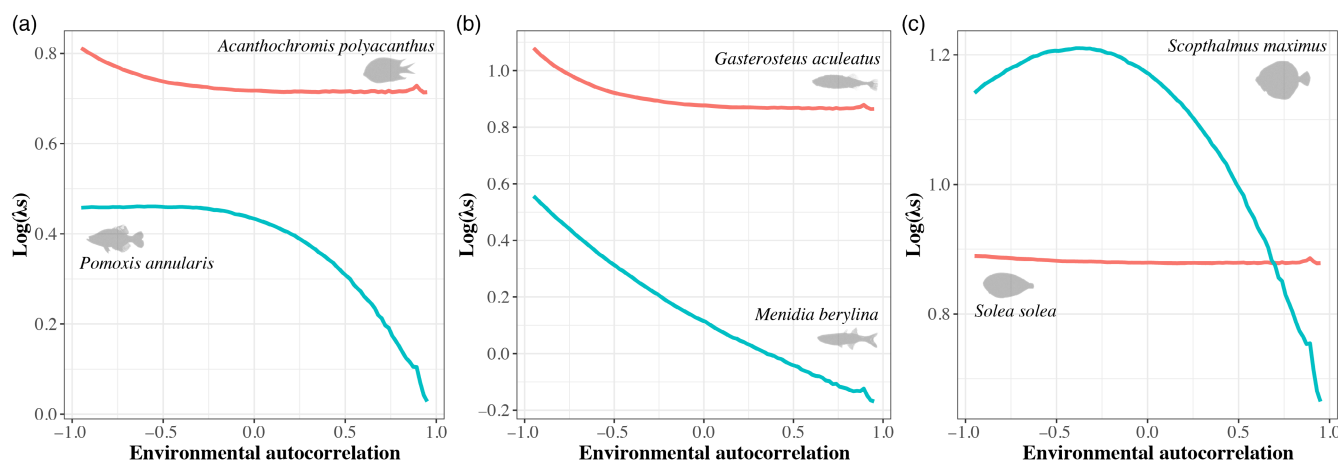


FIGURE 2 Examples of species with similar life history strategies and contrasting population growth rates ($\log(\lambda_s)$) in response to environmental autocorrelation. (a) Species with similar position on PC-1 only and dissimilar responses. (b) Species with similar low PC1 and high PC2 scores (top-left Figure 1) and dissimilar responses. (c) Species with similar high PC1 and low PC2 scores (bottom-left) and dissimilar responses.

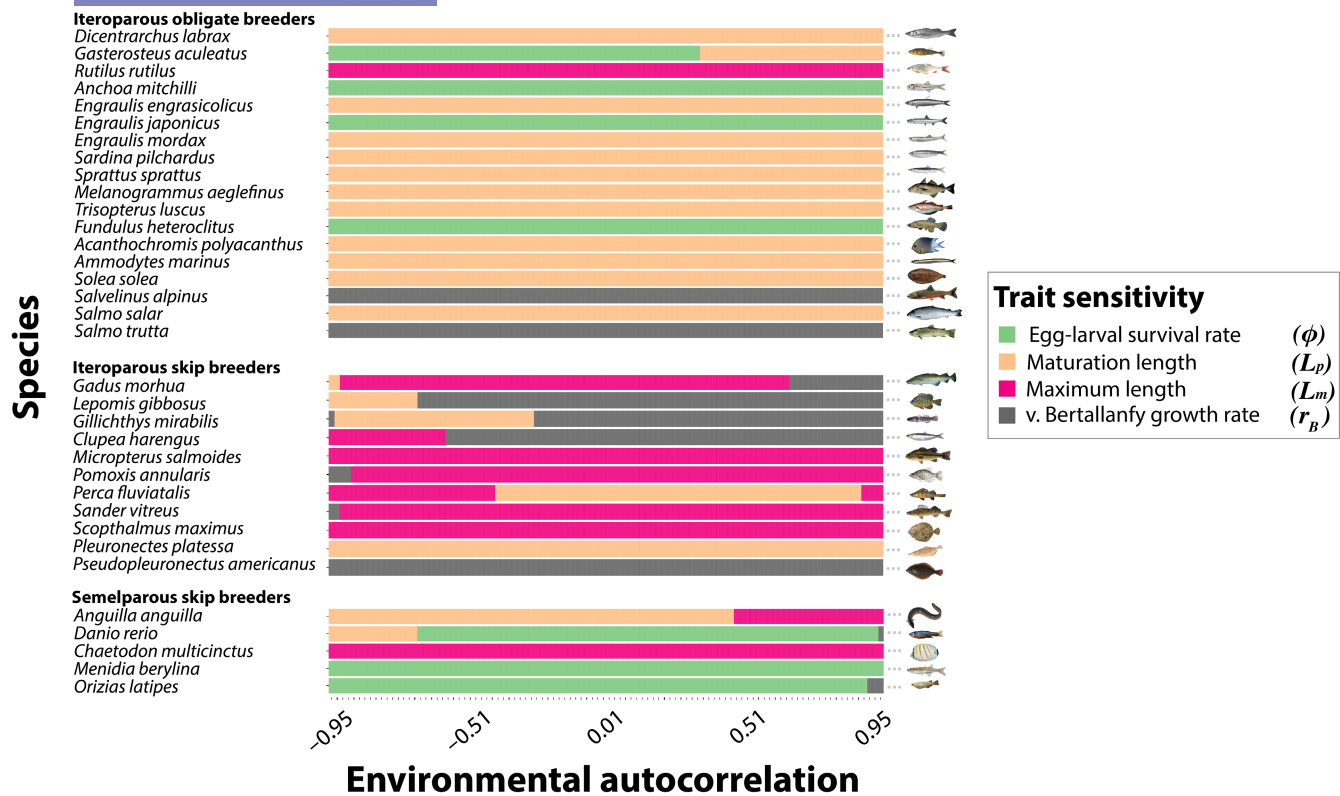


FIGURE 3 Species level perturbation plot highlighting the life history traits most strongly affecting population growth rate $\log(\lambda_s)$ across the gradient of environmental autocorrelation. In the underlying perturbation analysis each trait was perturbed by 1% and the elasticity of $\log(\lambda_s)$ calculated. Model species are grouped depending on the reproductive decisions included in the dynamic energy budget integral projections model: (top) iteroparous obligate breeders (centre), iteroparous skip breeders and (bottom) semelparous skip breeders, respectively.

rates (60%), followed by r_B and L_p (both found in 40% of species). The variation in trait importance across the gradient of autocorrelation is generally inconsistent, that is specific traits can be important drivers of population growth rates both when environments are highly variable, or highly invariable. Notably, there is a pattern in the importance of egg-larval survival, which was only observed in species with relatively small adult body sizes (*Gasterosteus aculeatus*, *Anchoa mitchilli*, *Engraulis engrasicolus*, *Engraulis japonicus*, *Fundulus heteroclitus*, *Danio rerio*, *Menidia beryllina*, *Oryzias latipes*).

4 | DISCUSSION

4.1 | Life history trade-offs, traits and strategies

We find three primary life history strategy axes when explicitly accounting for energy allocation trade-offs at the individual level (research question i). This includes the classical fast-slow axis and the often-reported secondary reproductive strategy axis (Capdevila et al., 2020; Healy et al., 2019; Morris et al., 2008; Paniw et al., 2018; Stearns, 1992), and a third axis for population sensitivity to environmental variation. Our results show differences between the life history trade-offs in energy allocation that we incorporated at the individual level (growth vs. reproduction, future vs. current

reproduction) and the life history trade-offs reflected by the patterning of species traits along our fast-slow and reproductive strategy axes (research question ii). This indicates that individual-level life history trade-offs do not necessarily apply to the population and species level. The assumption that the structure of individual differences in life history traits resembles in important ways the structure of variation across species underpins the pace of life syndrome (POLS), in which behavioural and physiological differences between individuals are postulated to covary with the slow-fast life-history continuum (Réale et al., 2010). Our results provide one explanation for why we lack robust empirical support for the predictions of the POLS framework (Laskowski et al., 2021). We argue we do not find an alignment because the general trade-offs in energy allocation faced by all individual organisms do not necessarily reflect the potential selective pressures and opportunities posed by the environment in which populations occur. For example, in marine systems, species can realise relatively high fecundity through a combination of oviparity and external fertilisation (Benun Sutton & Wilson, 2019; Gross & Shine, 1981). This strategy is not available to terrestrial species and comes at a cost of increased mortality when depositing undeveloped eggs in the external environment. This can for example explain why many marine species groups such as large ray-finned fish can combine the slow growth, longevity and low adult mortality rates typical of slow life histories with the high fecundity and

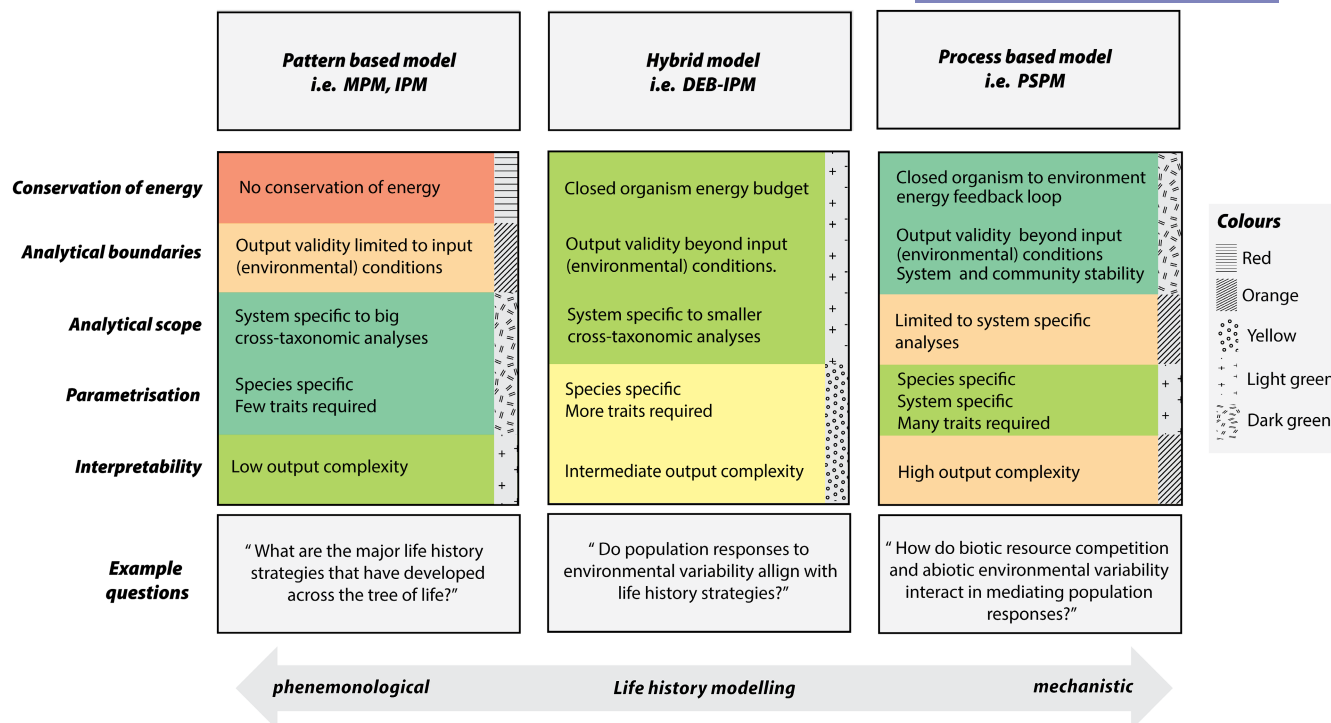


FIGURE 4 Conceptual framework highlighting the characteristics of different kinds of demographic modelling approaches in life history research. The framework can be used to identify the most appropriate approach based on research specifics. The columns list three different modelling approaches (pattern, 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 colour 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. DEB-IPM, dynamic energy budget integral projections model.

high offspring mortality rates typical of fast life histories (Beukhof et al., 2019). Differences in selective pressures and opportunities between environments might also explain why populations of the same species can exhibit very different life history strategies in different areas (Gamelon et al., 2021). It is still important to account for the individual-level trade-offs in energy allocation when examining life history variation even if they don't reflect the trade-offs in traits at the population or species level. This is because they impose critical energetic constraints on individual development and reproduction that translate through in population dynamics (Karjalainen et al., 2016). Without such energetic constraints, the law of conservation of energy would be violated and biomass freely created in demographic model studies, affecting projected population production, structure and responses to the environment. Although demographic vital rates in our study are dependent on the energy.

4.2 | Responses to environmental variation

We failed to find a significant link between life history traits and strategies in ray-finned fish, and their sensitivity to environmental variation (research questions iii, iv). The implications of these results extend beyond the immediate species modelled. The large range of environmental conditions that were simulated (~50,000 scenarios

per species), in combination with the range in trait combinations across species, and the reproductive decisions incorporated in our models, provide broad insights into the idiosyncrasy of population responses to environmental variation. Part of the wide range of environmental variation that was simulated, e.g. extremely negative autocorrelation, might not generally be expected to occur in nature. However, recent studies show, for example, how terrestrial arctic species are already facing increasingly high interannual variability in environmental conditions (Schmidt et al., 2023), leading to very unpredictable feeding environments between years. The absence of a general link between population responses and species life history strategies also aligns with other demographic studies in terrestrial systems that have shown different populations of the same species can display highly different life history strategies and therefore different population responses (Gamelon et al., 2021; Nevoux et al., 2010; Nilsen et al., 2009). This intraspecific variation in life history strategies also highlights a potential limitation concerning the comprehensiveness of our current study. For example, different populations of *Salmo salar* can display different life history strategies, where some populations migrate to sea and others remain fully resident (Fleming, 1996; MacCrimmon & Gots, 1979). Both types even exist sympatrically in some populations (Verspoor & Cole, 1989). Because our study used life history trait values averaged across multiple populations, we therefore overlook this potentially important

source of intraspecific variation in life histories between populations. However, we believe that this does not negate, but rather strengthens and adds to the general message of our results: a need to study and account for individual-level life history complexity in order to examine complex population responses. If included, population responses might have been reasonably expected to be more idiosyncratic rather than more general. This strongly aligns with other recent findings. For example, Van de Walle et al. (2023) show that although across species a slow-fast continuum could be identified as the main axis of life history variation, there is no alignment to this pattern when examining the populations of a species individually. The authors therefore conclude that individual life-history variation is likely idiosyncratic across species. The importance of accounting for individual-level life history complexity to understand population level outcomes is also not an altogether new perspective. For example, a long line of ecological research shows that populations accounting for size-structure and individual growth have very different dynamics than those in which individuals are all assumed to be identical (de Roos & Persson, 2013). However, added complexity comes at a cost. Studies accounting for successively more individual-level complexity typically can examine fewer species, lowering sample size (34 in our study), and the outcomes are more system specific. This contrasts with the statistical power of broad cross-taxonomical approaches to use big functional-trait datasets to derive general inferences across large groups of species and systems (Kissling et al., 2018; Salguero-Gómez et al., 2015; Salguero-Gómez, Jones, Archer, et al., 2016), that in turn come at the cost of reduced mechanistic insight.

4.3 | Perspective

Our results show that the classical association between life history strategies and responses to environmental variation breaks down when explicitly accounting for individual-level life history trade-offs. Contributing factors are that (i) trade-offs can differ between levels of organisation, and (ii) we must account for individual-level trade-offs in order to have a link between individual processes and population-level responses that is based on first principles, such as the conservation of energy. We postulated that the assumed alignment between individual, population, and species-level trade-offs depends on the specific selective pressures and opportunities posed by the environment. This alludes to another important level of organisation that is not always included in demographic models, including our own: feedback with the environment. Population modelling approaches accounting for both individual life-history mechanisms and environmental feedbacks show complex population dynamics, including alternative stable states (de Roos & Persson, 2013; Persson et al., 1998). Crucially, such complex dynamics are usually directly dependent on individual-level processes, such as size-dependent differences in mortality rates or feeding efficiency. We already highlighted how the gains from additional mechanistic insight

when accounting for individual-level complexity comes at the cost of being able to examine fewer species when we wish to examine population responses to environmental variation. This leaves the question of how to best move forward in the future. We summarise our perspective in a conceptual framework (Figure 4), listing the strengths and weaknesses of varying demographic modelling approaches using functional traits to model population responses. We find that this framework actually points towards the potential of combining different methods to address large and complex questions, such as which species are most vulnerable to environmental change. For example, we can use (1) pattern based models to characterise 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 utility in addressing urgent conservation issues by combining their individual powers. We hope that this perspective can help pave the way towards a more integrative approach utilising functional traits to understand complex demographic processes in an era of change (Salguero-Gómez et al., 2018).

AUTHOR CONTRIBUTIONS

Isabel M. Smallegange conceived the idea; Isabel M. Smallegange and Mark Rademaker designed methodology; Mark Rademaker collected the data; Mark Rademaker analysed the data; Mark Rademaker led the writing; Anieke van Leeuwen and Isabel M. Smallegange contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.2ngf1vhsh> (Rademaker et al., 2023).

ORCID

Mark Rademaker  <https://orcid.org/0000-0001-9210-1164>

Isabel M. Smallegange  <https://orcid.org/0000-0001-6218-7358>

REFERENCES

- Abdi, H. (2007). Z-scores. In N. J. Salkind (Ed.), *Encyclopedia of measurement and statistics* (pp. 1055–10158). Sage Publishing.
- Allen, M., Miranda, L., & Brock, R. (1998). Implications of compensatory and additive mortality to the management of selected sportfish populations. *Lakes & Reservoirs: Research & Management*, 3(1), 67–79.
- Al-Maghazachi, S. J., & Gibson, R. (1984). The developmental stages of larval turbot, *Scophthalmus maximus* (L.). *Journal of Experimental Marine Biology and Ecology*, 82(1), 35–51.

- Alonso-Fernández, A., Domínguez-Petit, R., Bao, M., Rivas, C., & Saborido-Rey, F. (2008). Spawning pattern and reproductive strategy of female pouting *Trisopterus luscus* (Gadidae) on the Galician shelf of north-western Spain. *Aquatic Living Resources*, 21(4), 383–393.
- Auer, N. A. (1982). *Identification of larval fishes of the Great Lakes basin with emphasis on the Lake Michigan drainage* (Vol. 82). Great Lakes Fishery Commission.
- Ayala, D. J., Munk, P., Lundgreen, R. B., Traving, S. J., Jaspers, C., Jørgensen, T. S., Hansen, L. H., & Riemann, L. (2018). Gelatinous plankton is important in the diet of European eel (*Anguilla anguilla*) larvae in the sargasso sea. *Scientific Reports*, 8(1), 1–10.
- Barlow, G. W. (1963). Species structure of the gobiid fish *Gillichthys mirabilis* from coastal sloughs of the eastern pacific. *Pacific Science*, 17, 47–72.
- Bauey, R., & Kunzlik, P. (1984). *Ices technical report: Variation in growth and mortality rates of Norway pout Trisopterus esmarkii* (Nilsson). ICES Technical Report.
- Bedairia, A., & Djebbar, A. B. (2009). A preliminary analysis of the state of exploitation of the sardine, *Sardina pilchardus* (Walbaum, 1792), in the gulf of Annaba, East Algerian. *Animal Biodiversity and Conservation*, 32(2), 89–99.
- Bentley, J., Bartolino, V., Kulatska, N., Vinther, M., Gaichas, S., Kempf, A., Lucey, S., Baudron, A., Belgrano, A., & Bracis, C. (2019). *Working Group on Multispecies Assessment Methods* (WGSAM). Technical report, ICES.
- Benun Sutton, F., & Wilson, A. B. (2019). Where are all the moms? External fertilization predicts the rise of male parental care in bony fishes. *Evolution*, 73(12), 2451–2460.
- Bergstad, O. A., Høines, Å. S., & Krüger-Johnsen, E. M. (2001). Spawning time, age and size at maturity, and fecundity of sandeel, *Ammodytes marinus*, in the north-eastern North Sea and in unfished coastal waters off Norway. *Aquatic Living Resources*, 14(5), 293–301.
- Beukhof, E., Dencker, T. S., Palomares, M. L., & Maureaud, A. (2019). A trait collection of marine fish species from North Atlantic and Northeast Pacific continental shelf seas. <https://doi.org/10.1594/PANGAEA.900866>
- Beverton, R. (1964). Differential catchability of male and female plaice in the north sea and its effect on estimates of stock abundance. *Rapport et Proces Verbaux du Conseil International Pour l'Exploration de la Mer*, 155, 103–112.
- Beverton, R. J. (1963). Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. *Rapports et Procès-Verbaux des Réunions*, 154, 44–67.
- Bielby, J., Mace, G. M., Bininda-Emonds, O. R., Cardillo, M., Gittleman, J. L., Jones, K. E., Orme, C. D. L., & Purvis, A. (2007). The fast-slow continuum in mammalian life history: An empirical reevaluation. *The American Naturalist*, 169(6), 748–757.
- Blomberg, S. P., & Garland, T., Jr. (2002). Tempo and mode in evolution: Phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology*, 15(6), 899–910.
- Bonhommeau, S., Le Pape, O., Gascuel, D., Blanke, B., Tréguier, A. M., Grima, N., Vermard, Y., Castonguay, M., & Rivot, E. (2009). Estimates of the mortality and the duration of the trans-Atlantic migration of European eel *Anguilla anguilla* leptocephali using a particle tracking model. *Journal of Fish Biology*, 74(9), 1891–1914.
- Brandhorst, W. (1974). Evaluación de los recursos de anchota (*Engraulis anchoita*) frente a la Argentina y Uruguay. VIII. Desove, crecimiento, mortalidad y estructura de la población. *Physis, Buenos Aires, Sección A*, 33, 37–58.
- Brazo, D. C., Tack, P. I., & Liston, C. R. (1975). Age, growth, and fecundity of yellow perch, *Perca flavescens*, in lake Michigan near Ludington, Michigan. *Transactions of the American Fisheries Society*, 104(4), 726–730.
- Britton, J. (2007). Reference data for evaluating the growth of common riverine fishes in the UK. *Journal of Applied Ichthyology*, 23(5), 555–560.
- Brothers, E. B. (1975). *The comparative ecology and behavior of three sympatric California gobies*. University of California, San Diego.
- Capdevila, P., Beger, M., Blomberg, S. P., Hereu, B., Linares, C., & Salguero-Gómez, R. (2020). Longevity, body dimension and reproductive mode drive differences in aquatic versus terrestrial life-history strategies. *Functional Ecology*, 34(8), 1613–1625.
- Carbine, W. F. (1939). Observations of the spawning habits on centrarchid fishes in Deep Lake, Oakland county, Michigan. *The Progressive Fish-Culturist*, 6(44), 33–34.
- Carlander, K. D. (1997). *Handbook of freshwater fishery biology* (Vol. 3). Iowa State University Press.
- Carline, R. F. (2006). Regulation of an unexploited brown trout population in spruce creek, Pennsylvania. *Transactions of the American Fisheries Society*, 135(4), 943–954.
- Caswell, H. (2001). *Matrix population models: Construction, analysis, and interpretation*. Sinauer Associates.
- Chaput, G. (2012). Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, 69(9), 1538–1548.
- Chen, D.-G., & Xiao, Y. (2006). A general model for analyzing data from mark-recapture experiments with an application to the pacific halibut. *Environmental and Ecological Statistics*, 13(2), 149–161.
- Cody, M. L. (1966). A general theory of clutch size. *Evolution*, 20, 174–184.
- Cook, R. (2004). Estimation of the age-specific rate of natural mortality for Shetland sandeels. *ICES Journal of Marine Science*, 61(2), 159–164.
- Copp, G. (1990). Recognition of cohorts and growth of larval and juvenile roach *Rutilus rutilus* (L.), using size-class ordination of developmental steps. *Journal of Fish Biology*, 36(6), 803–819.
- Copp, G. H., Fox, M. G., Przybylski, M., Godinho, F. N., & Vila i Gisbert, A. (2004). Life-time growth patterns of pumpkinseed *Lepomis gibbosus* introduced to Europe, relative to north American populations. *Folia Zoologica: International Journal of Vertebrate Zoology*, 53(3), 237–254.
- Cushing, D. (1959). On the effect of fishing on the herring of the southern north sea. *ICES Journal of Marine Science*, 24(2), 283–307.
- de Roos, A. M., & Persson, L. (2013). *Population and community ecology of ontogenetic development*. Princeton University Press.
- Degidio, J.-M. L., Yanong, R. P., Watson, C. A., Ohs, C. L., Cassiano, E. J., & Barden, K. (2017). Spawning, embryology, and larval development of the milletseed butterflyfish *Chaetodon miliaris* in the laboratory. *North American Journal of Aquaculture*, 79(3), 205–215.
- Dhillon, R. S., & Fox, M. G. (2004). Growth-independent effects of temperature on age and size at maturity in Japanese Medaka (*Oryzias latipes*). *Copeia*, 2004(1), 37–45.
- Dickie, L. (1963). Estimation of mortality rates of Gulf of St. Lawrence cod from results of a tagging experiment. *Special Publication—International Commission for the Northwest Atlantic Fisheries*, 4, 71–80.
- Dickie, L., & McCracken, F. (1955). Isopleth diagrams to predict equilibrium yields of a small flounder fishery. *Journal of the Fisheries Board of Canada*, 12(2), 187–209.
- Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size-specific sensitivity: Applying a new structured population model. *Ecology*, 81(3), 694–708.
- Edwards, E. A. (1982). *Habitat suitability index models: white crappie*. Western Energy and Land Use Team, Office of Biological Services, Fish and Wildlife Service, US Department of the Interior.
- Erdoğan, Z., Koç, H. T., Gicili, S., & Ulunehir, G. (2010). Age, growth and mortality of European pilchard, *Sardina pilchardus* in Edremit bay (Northern Aegean Sea, Turkey). *Cybiurn*, 34(2), 185–193.
- Eschmeyer, W. N., & Herald, E. S. (1999). *A field guide to Pacific coast fishes: North America*. Houghton Mifflin Harcourt.
- Fahay, M. P. (1983). Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. *Journal of Northwest Atlantic Fishery Science*, 4, 3–423.

- Fahay, M. P. (2007). *Early stages of fishes in the Western North Atlantic Ocean*. Northwest Atlantic Fisheries Organization.
- Fleming, I. A. (1996). Reproductive strategies of Atlantic salmon: Ecology and evolution. *Reviews in Fish Biology and Fisheries*, 6, 379–416.
- Fonds, M. (1973). Sand gobies in the Dutch Wadden Sea (Pomatoschistus, Gobiidae, Pisces). *Netherlands Journal of Sea Research*, 6(4), 417–478.
- Froese, R., & Pauly, D. (2002). *Fishbase: A global information system on fishes*. World Wide Web Electronic Publication. www.fishbase.org
- Funamoto, T., Aoki, I., & Wada, Y. (2004). Reproductive characteristics of Japanese anchovy, *Engraulis japonicus*, in two bays of Japan. *Fisheries Research*, 70(1), 71–81.
- Gadgil, M., & Bossert, W. H. (1970). Life historical consequences of natural selection. *The American Naturalist*, 104(935), 1–24.
- Gaillard, J.-M., Lemaître, J.-F., Berger, V., Bonenfant, C., Devillard, S., Douhard, M., Gamelon, M., Plard, F., & Lebreton, J. (2016). Life histories, axes of variation in. In R. Kliman (Ed.), *Encyclopedia of evolutionary biology* (pp. 312–323). Oxford Academic Press.
- Gaillard, J.-M., Pontier, D., Allaine, D., Lebreton, J., Trouvilliez, J., & Clobert, J. (1989). An analysis of demographic tactics in birds and mammals. *Oikos*, 56, 59–76.
- Gamelon, M., Gimenez, O., Baubet, E., Coulson, T., Tuljapurkar, S., & Gaillard, J.-M. (2014). Influence of life-history tactics on transient dynamics: A comparative analysis across mammalian populations. *The American Naturalist*, 184(5), 673–683.
- Gamelon, M., Touzot, L., Baubet, É., Cachelou, J., Focardi, S., Franzetti, B., Nivois, É., Veylit, L., & Sæther, B.-E. (2021). Effects of pulsed resources on the dynamics of seed consumer populations: A comparative demographic study in wild boar. *Ecosphere*, 12(5), e03395.
- Garca-Carreras, B., & Reuman, D. C. (2011). An empirical link between the spectral colour of climate and the spectral colour of field populations in the context of climate change. *Journal of Animal Ecology*, 80(5), 1042–1048.
- Gleason, T. R., & Bengtson, D. A. (1996). Growth, survival and size-selective predation mortality of larval and juvenile inland silversides, *Menidia beryllina* (Pisces: Atherinidae). *Journal of Experimental Marine Biology and Ecology*, 199(2), 165–177.
- Glover, K. A., Skaala, Ø., Limborg, M., Kvamme, C., & Torstensen, E. (2011). Microsatellite DNA reveals population genetic differentiation among sprat (*Sprattus sprattus*) sampled throughout the north-east Atlantic, including Norwegian fjords. *ICES Journal of Marine Science*, 68(10), 2145–2151.
- Goatley, C. H. R., & Bellwood, D. R. (2016). Body size and mortality rates in coral reef fishes: A three-phase relationship. *Proceedings of the Royal Society B: Biological Sciences*, 283(1841), 20161858.
- Goedde, L. E., & Coble, D. W. (1981). Effects of angling on a previously fished and an unfished warmwater fish community in two Wisconsin lakes. *Transactions of the American Fisheries Society*, 110(5), 594–603.
- Gross, M. R., & Shine, R. (1981). Parental care and mode of fertilization in ectothermic vertebrates. *Evolution*, 35, 775–793.
- Hanan, D. (1981). *Update of the estimated mortality rate of Engraulis mordax in southern California*. California Fish and Game.
- Healy, K., Ezard, T. H., Jones, O. R., Salguero-Gómez, R., & Buckley, Y. M. (2019). Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. *Nature Ecology & Evolution*, 3(8), 1217–1224.
- Heidinger, R. C. (1976). *Synopsis of biological data on the largemouth bass Micropterus salmoides (Lacepede) 1802*. FAO fisheries synopses (FAO) no. 115.
- Hernaman, V., & Munday, P. (2005). Life-history characteristics of coral reef gobies. I. Growth and life-span. *Marine Ecology Progress Series*, 290, 207–221.
- Hildebrand, S. F. (1963). *A review of the American anchovies (family Engraulidae)* (Vol. 8). Bingham Oceanographic Laboratory.
- Hinchliff, C. E., Smith, S. A., Allman, J. F., Burleigh, J. G., Chaudhary, R., Coghill, L. M., Crandall, K. A., Deng, J., Drew, B. T., Gazis, R., Gude, K., Hibbett, D. S., Katz, L. A., Laughinghouse, H. D., IV, McTavish, E. J., Midford, P. E., Owen, C. L., Ree, R. H., Rees, J. A., ... Cranston, K. A. (2015). Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proceedings of the National Academy of Sciences of the United States of America*, 112(41), 12764–12769.
- Holtan, P. (1998). *Pumpkinseed*. Wisconsin Department of Natural Resources, Bureau of Fisheries Management.
- Houde, E. (1994). Differences between marine and freshwater fish larvae: Implications for recruitment. *ICES Journal of Marine Science*, 51(1), 91–97.
- Houde, E. D., & Zastrow, C. E. (1993). Ecosystem-and taxon-specific dynamic and energetics properties of larval fish assemblages. *Bulletin of Marine Science*, 53(2), 290–335.
- Hubbs, C. (1982). Life history dynamics of *Menidia beryllina* from Lake Texoma. *American Midland Naturalist*, 107, 1–12.
- Hunter, J. R. (1977). *Behavior and survival of northern anchovy Engraulis mordax Larvae*. Calif. Coop. Oceanic Fish. Invest. Rep. 19:138–146.
- ICES. (1998). *Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak*. Technical report, ICES.
- ICES. (2016). *Report of the workshop on age estimation of European anchovy (Engraulis encrasicolus); 28 November–2 December 2016*. Technical report, ICES.
- ICES. (2018). *Report of the Benchmark Workshop on Seabass (WKBASS)*. Technical report, ICES.
- Inchausti, P., & Halley, J. (2002). The long-term temporal variability and spectral colour of animal populations. *Evolutionary Ecology Research*, 4(7), 1033–1048.
- Iversen, S., Zhu, D., Johannessen, A., & Toresen, R. (1993). Stock size, distribution and biology of anchovy in the yellow sea and east China sea. *Fisheries Research*, 16(2), 147–163.
- Iwamatsu, T. (2004). Stages of normal development in the medaka *Oryzias latipes*. *Mechanisms of Development*, 121(7–8), 605–618.
- Jackson, J. J., & Hurley, K. L. (2005). Relative growth of white crappie and black crappie in the United States. *Journal of Freshwater Ecology*, 20(3), 461–467.
- Jackson, Z., Quist, M., & Larscheid, J. (2008). Growth standards for nine North American fish species. *Fisheries Management and Ecology*, 15(2), 107–118.
- Jensen, H., Wright, P. J., & Munk, P. (2003). Vertical distribution of pre-settled sandeel (*Ammodytes marinus*) in the North Sea in relation to size and environmental variables. *ICES Journal of Marine Science*, 60(6), 1342–1351.
- Jeschke, J. M., & Kokko, H. (2009). The roles of body size and phylogeny in fast and slow life histories. *Evolutionary Ecology*, 23(6), 867–878.
- Jones, B. (1966). *Cod and the cod fishery at Faroe. Fishery investigations series II* (Vol. 24). FAO.
- Jones, J., & Hynes, H. (1950). The age and growth of *Gasterosteus aculeatus*, *Pygosteus pungitius* and *Spinachia vulgaris*, as shown by their otoliths. *The Journal of Animal Ecology*, 19, 59–73.
- Jones, R., & Shanks, A. (1990). An estimate of natural mortality for north sea haddock. *ICES Journal of Marine Science*, 47(1), 99–103.
- Jung, S., Hwang, S.-D., & Kim, J. (2008). Fecundity and growth-dependent mortality of pacific anchovy (*Engraulis japonicus*) in Korean coastal waters. *Fisheries Research*, 93(1–2), 39–46.
- Kaiser, H. F. (1960). The application of electronic computers to factor analysis. *Educational and Psychological Measurement*, 20(1), 141–151.
- Karjalainen, J., Urpanen, O., Keskinen, T., Huuskonen, H., Sarvala, J., Valkeajärvi, P., & Marjomäki, T. J. (2016). Phenotypic plasticity in growth and fecundity induced by strong population fluctuations affects reproductive traits of female fish. *Ecology and Evolution*, 6(3), 779–790.
- Kavanagh, K. D. (1996). *The early life history of the brooding damselfish Acanthochromis polyacanthus: Effects of environment and ancestry* [PhD thesis, James Cook University of North Queensland].
- Kavanagh, K. D. (2000). Larval brooding in the marine damselfish *Acanthochromis polyacanthus* (Pomacentridae) is correlated with

- highly divergent morphology, ontogeny and life-history traits. *Bulletin of Marine Science*, 66(2), 321–337.
- Kazakov, R. (1981). The effect of the size of Atlantic salmon, *Salmo salar* L., eggs on embryos and alevins. *Journal of Fish Biology*, 19(3), 353–360.
- Kelley, J. W. (1962). Sexual maturity and fecundity of the largemouth bass, *Micropterus salmoides* (Lacepede), in Maine. *Transactions of the American Fisheries Society*, 91(1), 23–28.
- Kingsford, M. J., Welch, D., & O'Callaghan, M. (2019). Latitudinal and cross-shelf patterns of size, age, growth, and mortality of a tropical damselfish *Acanthochromis polyacanthus* on the great barrier reef. *Diversity*, 11(5), 67.
- Kissling, W. D., Walls, R., Bowser, A., Jones, M. O., Kattge, J., Agosti, D., Amengual, J., Basset, A., Van Bodegom, P. M., Cornelissen, J. H., Denny, E. G., Deudero, S., Egloff, W., Elmendorf, S. C., García, E. A., Jones, K. D., Jones, O. R., Lavorel, S., Lear, D., ... Guralnick, R. P. (2018). Towards global data products of essential biodiversity variables on species traits. *Nature Ecology & Evolution*, 2(10), 1531–1540.
- Kocovsky, P. M., & Carline, R. F. (2001). Dynamics of the unexploited walleye population of Pymatuning Sanctuary, Pennsylvania, 1997–1998. *North American Journal of Fisheries Management*, 21(1), 178–187.
- Kooijman, S., & Metz, J. (1984). On the dynamics of chemically stressed populations: The deduction of population consequences from effects on individuals. *Ecotoxicology and Environmental Safety*, 8(3), 254–274.
- Kozłowski, J. (1996). Optimal allocation of resources explains interspecific life-history patterns in animals with indeterminate growth. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 263(1370), 559–566.
- Kraak, S., Bakker, T., & Mundwiler, B. (1997). How to quantify embryo survival in nest-building fishes, exemplified with three-spined sticklebacks. *Journal of Fish Biology*, 51(6), 1262–1264.
- Lappalainen, J., Tarkan, A. S., & Harrod, C. (2008). A meta-analysis of latitudinal variations in life-history traits of roach, *Rutilus rutilus*, over its geographical range: Linear or non-linear relationships? *Freshwater Biology*, 53(8), 1491–1501.
- Laskowski, K. L., Moiron, M., & Niemelä, P. T. (2021). Integrating behavior in life-history theory: Allocation versus acquisition? *Trends in Ecology & Evolution*, 36(2), 132–138.
- Leaf, R. T., Jiao, Y., Murphy, B. R., Kramer, J. I., Sorensen, K. M., & Wooten, V. G. (2011). Life-history characteristics of Japanese Medaka *Oryzias latipes*. *Copeia*, 2011(4), 559–565.
- Lebreton, J.-D. (2006). Dynamical and statistical models of vertebrate population dynamics. *Comptes Rendus Biologies*, 329(10), 804–812.
- Lebreton, J.-D. (2011). The impact of global change on terrestrial vertebrates. *Comptes Rendus Biologies*, 334(5–6), 360–369.
- Lee, D. (1980). *Micropterus salmoides* (Lacepede), Largemouth Bass. *Atlas of North American Freshwater Fishes*. North Carolina State Museum of Natural History.
- Lee, S.-H., Kim, C.-C., Koh, S.-J., Shin, L.-S., Cho, J.-K., & Han, K.-H. (2014). Egg development and morphology of larva and juvenile of the *Oryzias latipes*. *Development & Reproduction*, 18(3), 173–178.
- Leis, J. M. (1989). Larval biology of butterflyfishes (Pisces, Chaetodontidae): What do we really know? In P. J. Motta (Ed.), *The butterflyfishes: Success on the coral reef* (pp. 87–100). Springer.
- Lewis, S. C., & King, A. D. (2017). Evolution of mean, variance and extremes in 21st century temperatures. *Weather and Climate Extremes*, 15, 1–10.
- Loewen, T. N., Gillis, D., & Tallman, R. F. (2010). Maturation, growth and fecundity of Arctic charr, *Salvelinus alpinus* (L.), life-history variants co-existing in lake systems of Southern Baffin Island, Nunavut, Canada. *Hydrobiologia*, 650(1), 193–202.
- Lorenzen, K. (2005). Population dynamics and potential of fisheries stock enhancement: Practical theory for assessment and policy analysis. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 360(1453), 171–189.
- Luo, J. (1991). *Life history of the bay anchovy, Anchoa mitchilli*, in Chesapeake Bay. The College of William and Mary.
- MacCrimmon, H. R., & Gots, B. L. (1979). World distribution of Atlantic salmon, *Salmo solar*. *Journal of the Fisheries Board of Canada*, 36(4), 422–457.
- Mansueti, A., & Hardy, J. (1967). *Development of fishes of the Chesapeake Bay region: An atlas of egg, larval, and juvenile stages*. Natural Resources Institute, University of Maryland.
- McBride, R. S., Somarakis, S., Fitzhugh, G. R., Albert, A., Yaragina, N. A., Wuenschel, M. J., Alonso-Fernández, A., & Basilone, G. (2015). Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish and Fisheries*, 16(1), 23–57.
- McGourthy, C., Hobbs, J., Bennet, W., Green, P., Hwang, H., Ikemiyagi, N., & Cope, J. (2009). Likely population-level effects of contaminants on a resident estuarine fish species: Comparing *Gillichthys mirabilis* population static measurements and vital rates in San Francisco and Tomales Bays. *Estuaries and Coasts*, 32(6), 1111–1120.
- Meireles, J. E., O'Meara, B., & Cavender-Bares, J. (2020). Linking leaf spectra to the plant tree of life. In J. Cavender-Bares & J. A. Gamon (Eds.), *Remote sensing of plant biodiversity* (pp. 155–172). Springer.
- Menon, M. D. (1950). Bionomics of the poor-cod (*Gadus minutus* L.) in the Plymouth area. *Journal of the Marine Biological Association of the United Kingdom*, 29(1), 185–239.
- Michonneau, F., Brown, J. W., & Winter, D. J. (2016). rotI: An R package to interact with the open tree of life data. *Methods in Ecology and Evolution*, 7(12), 1476–1481.
- Mollet, F. M., Kraak, S. B., & Rijnsdorp, A. D. (2007). Fisheries-induced evolutionary changes in maturation reaction norms in North Sea Sole *Solea solea*. *Marine Ecology Progress Series*, 351, 189–199.
- Moore, J. (1975). Distribution, movements, and mortality of anadromous arctic char, *Salvelinus alpinus* L., in the Cumberland sound area of Baffin Island. *Journal of Fish Biology*, 7(3), 339–348.
- Morgan, G. D. (1954). The life history of the white crappie (*Pomoxis annularis*) of Buckeye Lake, Ohio. *Journal of the Scientific Laboratories of Denison University*, 43, 113–144.
- Morote, E., Olivar, M. P., Villate, F., & Uriarte, I. (2010). A comparison of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) larvae feeding in the Northwest Mediterranean: Influence of prey availability and ontogeny. *ICES Journal of Marine Science*, 67(5), 897–908.
- Morris, W. F., Pfister, C. A., Tuljapurkar, S., Haridas, C. V., Boggs, C. L., Boyce, M. S., Bruna, E. M., Church, D. R., Coulson, T., Doak, D. F., Forsyth, S., Gaillard, J. M., Horvitz, C. C., Kalisz, S., Kendall, B. E., Knight, T. M., Lee, C. T., & Menges, E. S. (2008). Longevity can buffer plant and animal populations against changing climatic variability. *Ecology*, 89(1), 19–25.
- Moser, H. (1996). *The early stages of Fishes in the California current region. California cooperative oceanic fisheries investigations, Atlas no. 33*. University of Chicago.
- Mueller, K. W., Brouwer, N. L., & Congdon, B. D. (2005). Characteristics of unexploited black bass populations from a remote lake in the San Juan Archipelago, Washington. *Northwest Science*, 79(2/3), 131–140.
- Munk, P., & Nielsen, J. G. (2005). *Eggs and larvae of North Sea fishes*. Biofolia.
- Near, T. J., Eytan, R. I., Dornburg, A., Kuhn, K. L., Moore, J. A., Davis, M. P., Wainwright, P. C., Friedman, M., & Smith, W. L. (2012). Resolution of ray-finned fish phylogeny and timing of diversification. *Proceedings of the National Academy of Sciences of the United States of America*, 109(34), 13698–13703.
- Nevoux, M., Forcada, J., Barbraud, C., Croxall, J., & Weimerskirch, H. (2010). Bet-hedging response to environmental variability, an intra-specific comparison. *Ecology*, 91(8), 2416–2427.

- Newberger, T., & Houde, E. (1995). Population biology of bay anchovy *Anchoa mitchilli* in the mid Chesapeake bay. *Marine Ecology Progress Series*, 116, 25–37.
- Nielsen, J. (1986). Scopthalmidae. In P. Whitehead, M. Bauchot, J. Hureau, J. Nielsen, & E. Tortonese (Eds.), *Fishes of the North-eastern Atlantic and the Mediterranean* (pp. 1287–1293). UNESCO.
- Nilsen, E. B., Gaillard, J.-M., Andersen, R., Odden, J., Delorme, D., Van Laere, G., & Linnell, J. D. (2009). A slow life in hell or a fast life in heaven: Demographic analyses of contrasting roe deer populations. *Journal of Animal Ecology*, 78(3), 585–594.
- O'Connell, C. P. (1981). Development of organ systems in the northern anchovy, *Engraulis mordax*, and other teleosts. *American Zoologist*, 21(2), 429–446.
- Page, L. M., & Burr, B. M. (1991). *A field guide to freshwater fishes: North America north of Mexico*. Houghton Mifflin Harcourt.
- Paniw, M., Ozgul, A., & Salguero-Gómez, R. (2018). Interactive life-history traits predict sensitivity of plants and animals to temporal autocorrelation. *Ecology Letters*, 21(2), 275–286.
- Paradis, E., Claude, J., & Strimmer, K. (2004). Ape: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20(2), 289–290.
- Paris, C. B., Kingsford, M., & Leis, J. (2009). Fate of reef fish larvae through ontogeny: Advection or true mortality. Death in the sea: Proceedings of the 2009 annual science conference, Berlin, 21–25.
- Paull, G. C., Lange, A., Henshaw, A., & Tyler, C. (2008). Ontogeny of sexual development in the roach (*Rutilus rutilus*) and its interrelationships with growth and age. *Journal of Morphology*, 269(7), 884–895.
- Pavlov, D., & Osinov, A. (2008). Reproduction and development in the dwarf form of Arctic charr *Salvelinus alpinus* from lake Davatchan, Transbaikalia. *Journal of Ichthyology*, 48(1), 96–113.
- Pearlstein, J. H., Letcher, B. H., & Obedzinski, M. (2007). Early discrimination of Atlantic salmon smolt age: Time course of the relative effectiveness of body size and shape. *Transactions of the American Fisheries Society*, 136(6), 1622–1632.
- Peck, M. A., Baumann, H., Bernreuther, M., Clemmesen, C., Herrmann, J.-P., Haslob, H., Huwer, B., Kanstinger, P., Köster, F. W., Petereit, C., Temming, A., & Voss, R. (2012). Reprint of: The ecophysiology of *Sprattus sprattus* in the Baltic and North Seas. *Progress in Oceanography*, 107, 31–46.
- Pecuchet, L., Lindgren, M., Hidalgo, M., Delgado, M., Esteban, A., Fock, H. O., Gil de Sola, L., Punzón, A., Sólmundsson, J., & Payne, M. R. (2017). From traits to life-history strategies: Deconstructing fish community composition across European seas. *Global Ecology and Biogeography*, 26(7), 812–822.
- Persson, L., Leonardsson, K., de Roos, A. M., Gyllenberg, M., & Christensen, B. (1998). Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theoretical Population Biology*, 54(3), 270–293.
- Peters, R. H. (1986). *The ecological implications of body size* (Vol. 2). Cambridge University Press.
- Pinhom, A. (1975). Estimates of natural mortality for the cod stock complex in ICNAF divisions 2J, 3K AND 3L. *International Commission*, 6, 31.
- Pitt, T. (1973). Assessment of American plaice stocks on the Grand Bank, ICNAF divisions 3L and 3N. *ICNAF Research Bulletin*, 10, 63–77.
- Quist, M. C., Guy, C. S., Schultz, R. D., & Stephen, J. L. (2003). Latitudinal comparisons of walleye growth in north America and factors influencing growth of walleyes in Kansas reservoirs. *North American Journal of Fisheries Management*, 23(3), 677–692.
- Rademaker, M., van Leeuwen, A., & Smallegange, I. (2023). Data from: Why we cannot always expect life history strategies to directly inform on sensitivity to environmental change. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.2ngf1vhsh>
- Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 365(1560), 4051–4063.
- Réalès-Doyelle, E., Pasquet, A., De Charleroy, D., Fontaine, P., & Teletchea, F. (2016). Strong effects of temperature on the early life stages of a cold stenothermal fish species, brown trout (*Salmo trutta* L.). *PLoS One*, 11(5), e0155487.
- Revell, L. J. (2009). Size-correction and principal components for inter-specific comparative studies. *Evolution*, 63(12), 3258–3268.
- Revell, L. J. (2010). Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, 1(4), 319–329.
- Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3(2), 217–223.
- Reznick, D. (1983). The structure of guppy life histories: The tradeoff between growth and reproduction. *Ecology*, 64(4), 862–873.
- Richardson, S. L. (1980). Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. *Fishery Bulletin*, 78, 855–876.
- Riehl, R., & Baensch, H. (1973). *FAquarien Atlas. Band. 1*. Verlag für Natur- und Heimtierkunde.
- Robins, C. R., & Ray, G. C. (1986). *A field guide to Atlantic coast fishes: North America* (Vol. 32). Houghton Mifflin Harcourt.
- Rodríguez, J. M., Alemany, F., & Garcia, A. (2018). *A guide to the eggs and larvae of 100 common Western Mediterranean Sea bony fish species*. Food and Agriculture Organization of The United Nations.
- Ruokolainen, L., Lindén, A., Kaitala, V., & Fowler, M. S. (2009). Ecological and evolutionary dynamics under coloured environmental variation. *Trends in Ecology & Evolution*, 24(10), 555–563.
- Russell, F. S. (1976). *The eggs and planktonic stages of British marine fishes*. Academic Press.
- Salguero-Gómez, R., Jones, O. R., Archer, C. R., Bein, C., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Ruoff, T., Sommer, V., Wille, J., Voigt, J., Zeh, S., Viereg, D., Buckley, Y. M., Che-Castaldo, J., ... Vaupel, J. W. (2016). Comadre: A global data base of animal demography. *Journal of Animal Ecology*, 85(2), 371–384.
- Salguero-Gómez, R., Jones, O. R., Archer, C. R., Buckley, Y. M., Che-Castaldo, J., Caswell, H., Hodgson, D., Scheuerlein, A., Conde, D. A., Brinks, E., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Runge, J., Ruoff, T., ... Vaupel, J. W. (2015). The COMPADRE plant matrix database: An open online repository for plant demography. *Journal of Ecology*, 103(1), 202–218.
- Salguero-Gómez, R., Jones, O. R., Jongejans, E., Blomberg, S. P., Hodgson, D. J., Mbeau-Ache, C., Zuidema, P. A., de Kroon, H., & Buckley, Y. M. (2016). Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, 113(1), 230–235.
- Salguero-Gómez, R., Violle, C., Gimenez, O., & Childs, D. (2018). Delivering the promises of trait-based approaches to the needs of demographic approaches, and vice versa. *Functional Ecology*, 32(6), 1424–1435.
- Sandlund, O. T., Haugerud, E., Rognerud, S., & Borgström, R. (2013). Arctic charr (*Salvelinus alpinus*) squeezed in a complex fish community dominated by perch (*Perca fluviatilis*). *Fauna Norvegica*, 33, 1–11.
- Schaefer, M. B. (1967). Dynamics of the fishery for the anchoveta *Engraulis ringens* off Peru. *Boletín Instituto del Mar del Perú*, 1, 189–304.
- Schmidt, N. M., Kankaanpää, T., Tiusanen, M., Reneerkens, J., Versluijs, T. S., Hansen, L. H., Hansen, J., Gerlich, H. S., Høye, T. T., Cirtwill, A. R., Zhemchuzhnikov, M. K., Peña-Aguilera, P., & Roslin, T. (2023). Little directional change in the timing of arctic spring phenology over the past 25 years. *Current Biology*, 33(15), 3244–3249.
- Scott, W., & Crossman, E. (1973). *Freshwater fishes of Canada; bulletin 184*. Fisheries Research Board of Canada.

- Sebens, K. P. (1987). The ecology of indeterminate growth in animals. *Annual Review of Ecology and Systematics*, 18(1), 371–407.
- Shanks, A. L., & Eckert, G. L. (2005). Population persistence of California current fishes and benthic crustaceans: A marine drift paradox. *Ecological Monographs*, 75(4), 505–524.
- Siddeek, M. (1989). The estimation of natural mortality in Irish Sea plaice, *Pleuronectes platessa* L., using tagging methods. *Journal of Fish Biology*, 35, 145–154.
- Silva, A., Faria, S., & Nunes, C. (2013). Long-term changes in maturation of sardine, *Sardina pilchardus*, in Portuguese waters. *Scientia Marina*, 77(3), 429–438.
- Sinclair, A. (2001). Natural mortality of cod (*Gadus morhua*) in the Southern Gulf of St Lawrence. *ICES Journal of Marine Science*, 58(1), 1–10.
- Singleman, C., & Holtzman, N. G. (2014). Growth and maturation in the zebrafish, *Danio rerio*: A staging tool for teaching and research. *Zebrafish*, 11(4), 396–406.
- Smallegange, I. M., Avilés, M. F., & Eustache, K. (2020). Unusually paced life history strategies of marine megafauna drive atypical sensitivities to environmental variability. *Frontiers in Marine Science*, 7, 597492.
- Smallegange, I. M., & Berg, M. P. (2019). A functional trait approach to identifying life history patterns in stochastic environments. *Ecology and Evolution*, 9(16), 9350–9361.
- Smallegange, I. M., Caswell, H., Toorians, M. E., & de Roos, A. M. (2017). Mechanistic description of population dynamics using dynamic energy budget theory incorporated into integral projection models. *Methods in Ecology and Evolution*, 8(2), 146–154.
- Smallegange, I. M., Deere, J. A., & Coulson, T. (2014). Correlative changes in life-history variables in response to environmental change in a model organism. *American Naturalist*, 183(6), 784–797.
- Spitz, J., Chouvelon, T., Cardinaud, M., Kostecki, C., & Lorange, P. (2013). Prey preferences of adult sea bass *Dicentrarchus labrax* in the northeastern Atlantic: Implications for bycatch of common dolphin *Delphinus delphis*. *ICES Journal of Marine Science*, 70(2), 452–461.
- Stearns, S. C. (1983). The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, 41, 173–187.
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, 3(3), 259–268.
- Stearns, S. C. (1992). *The evolution of life histories* (Vol. 249). Oxford University Press.
- Stige, L. C., Rogers, L. A., Neuheimer, A. B., Hunsicker, M. E., Yaragina, N. A., Ottersen, G., Ciannelli, L., Langangen, Ø., & Durant, J. M. (2019). Density- and size-dependent mortality in fish early life stages. *Fish and Fisheries*, 20(5), 962–976.
- Stireman, J. O., Dyer, L. A., Janzen, D. H., Singer, M., Lill, J., Marquis, R. J., Ricklefs, R. E., Gentry, G., Hallwachs, W., Coley, P. D., Barone, J. A., Greeney, H. F., Connahs, H., Barbosa, P., Morais, H. C., & Diniz, I. R. (2005). Climatic unpredictability and parasitism of caterpillars: Implications of global warming. *Proceedings of the National Academy of Sciences of the United States of America*, 102(48), 17384–17387.
- Svedäng, H. (1999). Vital population statistics of the exploited eel stock on the Swedish west coast. *Fisheries Research*, 40(3), 251–265.
- Swarup, H. (1958). Stages in the development of the stickleback *Gasterosteus aculeatus* (L.). *Journal of Embryology and Experimental Morphology*, 6, 373–383.
- Takahashi, M., & Watanabe, Y. (2004). Staging larval and early juvenile Japanese anchovy based on the degree of guanine deposition. *Journal of Fish Biology*, 64(1), 262–267.
- Tallman, R. F., Saurette, F., & Thera, T. (1996). Migration and life history variation in arctic charr, *Salvelinus alpinus*. *Ecoscience*, 3(1), 33–41.
- Taube, C. M. (1976). Sexual maturity and fecundity in brown trout of the Platte River, Michigan. *Transactions of the American Fisheries Society*, 105(4), 529–533.
- Tesch, F. (1977). *The eel: Biology and management of anguillid eels* (J. Greenwood, Trans.). Chapman and Hall.
- Thresher, R. E. (1985). Distribution, abundance, and reproductive success in the coral reef fish *Acanthochromis polyacanthus*. *Ecology*, 66(4), 1139–1150.
- Tricas, T. C. (1986). *Life history, foraging ecology, and territorial behaviour of the Hawaiian butterflyfish, Chaetodon multicinctus* (territoriality, coral reef) [PhD thesis, University of Hawai'i at Manoa].
- Tuljapurkar, S., Horvitz, C. C., & Pascarella, J. B. (2003). The many growth rates and elasticities of populations in random environments. *American Naturalist*, 162(4), 489–502.
- Van de Walle, J., Fay, R., Gaillard, J.-M., Pelletier, F., Hamel, S., Gamelon, M., Barbraud, C., Blanchet, F. G., Blumstein, D. T., Charmantier, A., Delord, K., Larue, B., Martin, J., Mills, J. A., Milot, E., Mayer, F. M., Rotella, J., Saether, B.-E., Teplitsky, C., ... Jenouvrier, S. (2023). Individual life histories: Neither slow nor fast, just diverse. *Proceedings of the Royal Society B*, 290(2002), 20230511.
- van der Wiel, K., & Bintanja, R. (2021). Contribution of climatic changes in mean and variability to monthly temperature and precipitation extremes. *Communications Earth & Environment*, 2(1), 1–11.
- van Kleef, H. H., & Jongejans, E. (2014). Identifying drivers of pumpkin-seed invasiveness using population models. *Aquatic Invasions*, 9(3), 315–326.
- Verreycken, H., Van Thuyne, G., & Belpaire, C. (2011). Length-weight relationships of 40 freshwater fish species from two decades of monitoring in Flanders (Belgium). *Journal of Applied Ichthyology*, 27(6), 1416–1421.
- Verspoor, E., & Cole, L. (1989). Genetically distinct sympatric populations of resident and anadromous Atlantic salmon, *Salmo salar*. *Canadian Journal of Zoology*, 67(6), 1453–1461.
- Weyl, O. L., & Booth, A. J. (1999). On the life history of a cyprinid fish, *Labeo cylindricus*. *Environmental Biology of Fishes*, 55(3), 215–225.
- Whitehead, P. (1988). An annotated and illustrated catalogue of herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. *Clupeoid Fishes of the World (Suborder Clupeoidei)*. FAO Fisheries Synopsis, 125(2), 305–579.
- Wiedmann, M., Primicerio, R., Dolgov, A., Ottesen, C., & Aschan, M. (2014). Life history variation in Barents Sea fish: Implications for sensitivity to fishing in a changing environment. *Ecology and Evolution*, 18(4), 3596–3611.
- Wilderbuer, T. K., & Turnock, B. J. (2009). Sex-specific natural mortality of arrowtooth flounder in Alaska: Implications of a skewed sex ratio on exploitation and management. *North American Journal of Fisheries Management*, 29(2), 306–322.
- Williams, G. C. (1966a). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton University Press.
- Williams, G. C. (1966b). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist*, 100(916), 687–690.
- Wilson, C. (2012). Aspects of larval rearing. *ILAR Journal*, 53(2), 169–178.
- Wolfert, D. R. (1969). Maturity and fecundity of walleyes from the eastern and western basins of Lake Erie. *Journal of the Fisheries Board of Canada*, 26(7), 1877–1888.
- Wright, P., & Bailey, M. (1997). Timing of hatching in *Ammodytes marinus* from Shetland waters and its significance to early growth and survivorship. *Oceanographic Literature Review*, 7(44), 735.
- Zenitani, H., Kono, N., & Tsukamoto, Y. (2007). Relationship between daily survival rates of larval Japanese anchovy (*Engraulis japonicus*) and concentrations of copepod nauplii in the Seto Inland Sea, Japan. *Fisheries Oceanography*, 16(5), 473–478.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Histogram showing the distribution of sensitivity values across species.

Figure S2. Distribution of log-transformed trait values between species classified as sensitive or insensitive to shifts in environmental autocorrelation used for Kolmogorov–Smirnov test.

Table S1. Linear and non-linear test statistics of the relationship between $\Delta\log(\lambda_s)$ and log transformed life history traits.

Appendix S1. Sensitivity and individual traits.

How to cite this article: Rademaker, M., van Leeuwen, A., & Smallegange, I. M. (2024). Why we cannot always expect life history strategies to directly inform on sensitivity to environmental change. *Journal of Animal Ecology*, 93, 348–366. <https://doi.org/10.1111/1365-2656.14050>