**Gigantism and dwarfism of fish body sizes arises from state-dependent life history theory within an ecosystem context**

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**Abstract**

Theory explains how the evolution of body size depends on age-specific survival rates and trade-offs among growth, reproduction. State-dependent life history models explain allocation of energy resources to these traits according to food availability and metabolic costs. Yet, these models rarely include seasonal variation and realistic predator-prey interactions. We use size-dependent relationships defined by community size spectra to model the risk of predation (fearscape) and availability of prey (foodscape) as a fish grows throughout its life. Our energetic model of lifetime fitness embedded predicts the evolution of body size and reproduction, as well as emergent mortality rates in a given ecosystem. We use this general framework how the foodscape and fearscape vary with abiotic features of seasonality and temperature to determine the growth, reproduction and death of tunas. We show that larger body sizes are advantageous in seasonal environments, and to a lesser extent, in warm constant environments. In our deterministic model framework, we do not predict the range of maturation timing that is observed in nature, but we do fine that it consistently increases with environmental richness. We predict that mortality rates will vary with temperature driven by patterns of growth in different thermal environments, but rates of maturation will be consistent in constant scenarios. We conclude that the complexity of the interactions between predation risk, metabolism, and food availability preclude simple predictions for changes in growth based on climate-driven increases in temperature alone. Further our results reveal the roles of food, fear, growth, and reproduction in determining emergent mortality rates. We conclude by discussing the implications of our results for understanding macroecological relationships of tunas.

**Keywords -** Size spectra, state-dependent models, energy budgets, life history, tunas, metabolic theory, body size evolution

**Introduction**

***The need to understand mechanisms driving the evolution of body size in aquatic vertebrates***

Body size is correlated with survival, foraging success, and reproductive output in aquatic vertebrates with indeterminate growth. Explaining the evolution of body size is a challenge for ecologists seeking to manage human interactions with wild populations and predict their responses to future global change. Correlations between temperature and body size have been documented for a variety of species ((Gillooly et al. 2001, Kingsolver and Huey 2008). Accumulating evidence suggests that the body sizes and population biomass of aquatic species are responding strongly to human-induced environmental change, but not all species are responding the same ways (Free et al. 2019, Audzionte et al 2020). For aquatic taxa, the demographic consequences of changing ocean productivity and predatory abundance are difficult to disentangle from effects of temperature and seasonality. We still do not fully understand the mechanisms driving body size or their consequences for reproductive output and survival (Daufresne et al. 2009, Neubauer and Andersen 2019) Audzujonte and Richards 2019.

***Going from environment to traits to demography***

The search for “rules” determining ecological assemblages according to species’ traits can be traced to fundamental ecological theory (Charnov and Krebs 1974, Southwood 1977, Charnov et al. 1991, Gislason et al. 2010), but trait-based predictions of population dynamics under continued environmental changes continue to be challenging. In fishes, growth, reproduction and maintenance, along with other behavioral and physical traits - including sexual ornaments or weapons - covary among species and environments (Winemiller & Rose, 1992; Winemiller, 1992). This phenomenological perspective on life histories offers insight into the role of environmental context in revealing trade-offs among traits and driving both the evolution of body size and demographic rates. Classic theory recognized that demography arises from individuals trading off the allocation of energetic resources to growth and reproduction (Beverton and Holt 1959, Gadgil and Bossert 1970, Kozlowski 1996), while meeting their metabolic requirements (Jørgensen et al. 2016), which can vary according to temperature (Clarke and Johnston 1999, Brown et al. 2004). However, mechanistic predictions of changes in growth have struggled to explain latitudinal and temporal trends in body size among species (reviewed in Audizionte et al. 2020). Many mechanistic models lack consistent, general relationships between body size and energy availability when predicting growth, reproduction, and survival over the individual’s lifetimes.

***Size-spectra can specify consumption and mortality of individuals (thus shaping life histories)***

An intriguing possibility is that the size-dependence in energy budgets of aquatic vertebrates can be informed by the allometric relationships underlying community size-spectra. Community size spectra are predictable relationships among body size, trophic level, and abundance across species in aquatic ecosystems (Sheldon et al. 1977; Law et al. 2009, Trebilco et al. 2013, Sprules and Barth 2016). In a community size spectrum, energy flows between trophic levels and consumption and predation rates are characterized by individual mass, instead of species identity (Benoît and Rochet 2004, Blanchard et al. 2009, Blanchard et al. 2017, Andersen 2019). For example, aquatic predators are usually generalist consumers with a preference for prey in a given size range rather than of a particular identity. Size spectra theory assumes the lower limit of prey size preference depends on the profitability of the prey, and the upper limit depends on the maximum gape size of the predator. When prey preference is combined with the other physical and physiological processes that scale with mass[[1]](#footnote-1) we can predict a general relationship between predator mass and prey mass, known as the Predator-Prey Mass Ratio (PPMR; Barnes et al. 2010). PPMR emerges because individuals are born small and grow through the size spectrum over their lifetime, consuming prey that are a fraction of their own size. The interactions between predators and prey underlying community size spectra equally apply to interactions within size-structured populations of the same species. In other words, even if other prey and predator species are present, size-spectrum theory assumes the availability of resources and the mortality risk experienced by an individual fish of a given size are indistinguishable from the case where all individuals in the community are also the same species. Therefore, predation and consumption rates defined by a size spectrum could be used to simultaneously characterize the mass-specific resource availability and risk of predation experienced by an individual as it grows (Benoit and Rochet 2014, Andersen 2019).

***Tunas as an ideal case study of our general model***

To understand how size-dependent consumption rates and predation risk interact with different ecosystem contexts to determine the evolution of body sizes, we focus on market tunas (members of the genus *Thunnus*)*,* as a specific case of our general model. We have chosen tunas as a clade with species that are some of the best-studied fish families due to their high value (Juan Jordá et al. 2013) and widely distributed in tropical and temperate oceans and coastal and pelagic habitats, which vary in seasonality and productivity. Members of the genus *Thunnus* represent a range of body sizes (Horswill et al. 2019), corresponding to diverse life histories adapted to different environments, ranging from the bluefin tuna (*Thunnus thunnus*), which occupies temperate waters and reach sizes of more than 600 kg, to the blackfin tuna (*T. atlanticus*), which is tropical, and weighs less than 21 kg. The larger tunas are notable for their endothermic adaptations, which allow them to migrate great distances, dive into cooler waters to forage, and to efficiently chase down their prey. However, even among the largest *Thunnus* species, variation in traits such as maturation, survival, and growth cannot be explained by environmental temperature and foraging habits alone. For example, *T. albacares,* yellowfin tuna, and *T. obesus,* bigeye tuna, remain in tropical waters year-round, but can reach comparable body sizes to bluefin tunas, although their lifespans are shorter. These tropical species tend to grow faster and mature earlier than the three species of temperate bluefin tunas (*T. thunnus, T. orientalis, and T. maccoyii*), spawning for a sustained period each year, and potentially achieving higher annual fecundity (Horswill et al., 2019). These interspecific trait covariances indicate that reproductive patterns and mortality rates vary among these species, but it is difficult to predict these patterns *a priori* from macroecological phenomena such as the temperature-size rule*.*

***Mission statement of paper***

In this paper, we develop a general state-dependent life history model of energy allocation to growth and reproduction to predict how variation in ecosystem richness, seasonality, and temperature determine the emergent evolutionary strategy of life histories (Mangel and Clark 1988, Houston and McNamara 1999, Clark and Mangel 2000). We use stochastic dynamic programming to find the optimal strategy of allocation to growth and reproduction (Mangel and Clark 1988). From this strategy, we can calculate the relationship between size and age, and the mortality risk that emerges as a consequence of the individual’s body size in the size spectrum. Although models of aquatic food webs using size spectra have a rich history in ecosystem ecology, they have not been connected with models of aquatic life-history evolution before now. We consider how the size spectrum governing consumption and predation rates changes with environmental richness, temperature, and seasonality, as these are primary drivers of fish life history variation (Kamler 2005). We can thereby predict a range of patterns of growth and reproduction in different predator-prey scenarios, as well as compare differences in life history in constant and seasonally varying environments. We can then compare the predicted trait covariances with those found in extant tuna species to refine our understanding of the mechanisms underlying changes in life history due to climate change. Our framework is general and flexible, and could be applied to other taxa in other environmental scenarios.

**METHODS**

To find the optimal life history strategy in different environments, we develop a dynamic state variable model, which is solved with stochastic dynamic programming.This is a powerful method that allows us to consider differences in individual physiological state (energetic reserves and body size) affect the trade-off between growth and reproduction in the context of lifetime fitness. We then parameterize our model with values consistent with the metabolic rates estimated for tunas from eco-physiological research (Kitchell et al. 1979; Clarke and Johnston 1999) in order to illustrate its potential to provide mechanistic explanations for the evolution of body size and life-history diversity of tunas.

***The size spectrum***

A biomass size spectrum is defined as the distribution of total ecosystem biomass *B(w)* across body size classes (bins) of equal width*.* Size spectra have parametric definitions as power functions, parameterized (in log space) in terms of an intercept parameter and a spectrum exponent[[2]](#footnote-2) (Figure 1).

This function arises from the key observation by Sheldon (1972) and colleagues that the total biomass of individuals *B* in each size bin *w* is roughly constant (flat) across logarithmic intervals of body size (Sprules and Barth 2016; Andersen 2019). This phenomenon emerges from three size-dependent eco-physiological processes: 1) the encounter rate of predators and prey; 2) the preference of predators for prey of a given size; and 3) the limit to prey consumption imposed by the size of the predator’s stomach (Benoît and Rochet 2004, Blanchard et al. 2017, Andersen 2019). The phenomenon of size spectra allows us to characterize the prey available to an individual (foodscape) and its risk of predation (fearscape) simultaneously as a given individual grows from small to large. We can thereby calculate net prey biomass (energetic income) and the risk of predation for an individual of mass *w*. We assume the prey biomass available to the focal individual can be defined as a constant proportion of predator mass because the Predator-Prey Mass Ratio usually does not vary with predator size (*i.e.,* it is independent of *w;* Anderson 2019). An exception to the consistency of PPMR across body sizes occurs among species with different feeding modes, such as large-bodied filter feeders including baleen whales and planktivorous sharks and rays (Trebilco et al. 2013). These species also consume greater volumes of prey than otherwise predicted by size-spectra theory (Kiørboe and Hirst 2014).

For gape-limited taxa like fishes, a given predator encounters a prey field (foodscape) according to its encounter rate with prey in its preferred size range. This encounter rate (which is sometimes called the clearance rate) is typically measured in units of volume per time, as aquatic species forage in a three-dimensional habitat (Kiørboe and Hirst 2014). We can describe the preference for prey of different sizes with a log-normal distribution of the PPMR, which is usually estimated from diet studies or stable isotope analyses of size fractions of whole ecosystems (Jennings et al. 2008, Reum et al. 2019). We assume this distribution describes the range of acceptable prey sizes. Finally, the limit to prey consumption imposed by the size of the prey’s stomach contributes to the overall risk of predation (the fearscape).

***The foodscape***

For a focal individual of size *w* the expected biomass of available prey – which can be either conspecifics or heterospecifics – involves integrating over all prey sizes in the spectrum. The details are given in Box 2 of Andersen (2019), but the solution of this integral gives the per-unit-time consumption of prey in units of mass:

(2)

Therefore, energetic income from eating prey depends on the ecosystem richness (the exponentiated intercept of the size spectrum), the slope of the spectrum, and an “abundance factor” Φ*a* that represents the density of prey in each bin, given the PPMR and the width of the prey preference window (Andersen 2019, Eq. B2.2). Parameters estimated from empirical size spectra, reviewed in Andersen (2019, Table 2.2) and included in Table 1 here. For consistency between income and costs (below), we convert consumption *Bprey* in mass to joules with a conversion factor *ρ* .

***The fearscape***

The probability of survival (over a unit of time) is modeled as a negative exponential function. The exponent of this function – often referred to as a rate of mortality – is a proxy for the risk of predation faced by an individual as it grows through the size spectrum. It changes concordantly with changes in density of individuals in each size class, as this will affect encounter rates. The risk of predation requires an integration over all size classes, and depends on the volume of water cleared by predators of size *w*, weighted by the PPMR, and multiplied by the density of individuals of size *w* (Andersen 2019). From this, the mortality risk per unit time is:

(3)

The constant represents prey vulnerability, given predator preferences, and is estimated from eempirical distributions of prey sizes in predator guts (Ursin 1973)*.* The other parameters are the scale coefficient *h,* representing how likely a predator is to capture the focal individual[[3]](#footnote-3), anda metabolic exponent *n* Andersen (2019, B2.7 and Eq. 2.11). These parameters are reviewed in Andersen (2019, Table 2.2) and included in Table 1 here. In our model, the probability of dying at a given size (given by Eq. 3) is factored in to the calculation of expected future fitness, so it affects the fitness associated with allocation to growth vs. reproduction at every age (or size). In this way, we are able to evaluate the non-consumptive effects of predation on the evolution of life histories.

***Metabolic costs***

All individuals experience metabolic costs that increase with their body size and environmental temperature (Clarke 2006). We model mass-dependent costs (in joules) as a function of temperature 𝜏in Kelvin. The specific equation is given in the section *Functional forms motivated by tunas,* below.

***Dynamics of individual states: age, size, and stored energy***

We used a general state-dependent life-history model (Houston et al. 1988, Houston and McNamara 1999, Clark and Mangel 2000) to find the allocation strategy that maximizes the expected lifetime survival and reproductive success (fitness) of an individual (or genotype) in a range of environmental scenarios, given the individual’s age, size, and condition (energetic state). This modeling method solves for the optima of a complex fitness landscape that involves trade-offs among multiple traits, and can address how an organism’s energetic state, body size or other state variables affect behavior, growth and reproduction (Jørgensen and Fiksen 2006, Chapman et al. 2011). Unlike other models of energetic allocation (such as Dynamic Energy Budget theory (Kooijman 2000)) this method incorporates time-dependent changes in fitness, so that the trade-off between current and future fitness is factored in to allocation decisions. Solving such complex optimization problems is possible because the method uses backward iterations of a numerical search (a process known as stochastic dynamic programming) to find the allocation decisions that maximize lifetime fitness at every age, starting from an endpoint when fitness is known. In other words, by assuming a finite lifespan *T* after which there is no opportunity for future reproduction, we can use dynamic programming to evaluate the effects of different allocation strategies in light of their effects on expected lifetime fitness.

In each month (*t < T*) the individual acquires energy from food, which it can use to grow, allocate to reproduction within the same month, or store for future allocation. Expected future fitness will decrease as the individual ages, and approaches *T.*

We characterize individuals by two dynamic state variables: length *L(t)* in cm and lipid stores *S(t)* in joules (cf. Jørgensen & Fiksen, 2006)*.* These variables correspond to the *structural* mass , which depends on as well as the varying mass of the energy *storage* component (Mangel 2006)). Structural mass in joules is. We use structural mass to calculate metabolic requirements and income. Lipid mass is . These conversions allow us to compare structural mass and stored energy in joules, the common currency of every process in the model (temperature-dependent metabolic costs, reproductive output, body length, and lipid stores).All reproductive output is quantified in joules, so is comparable to Gonadal Somatic Investment, a common metric of reproductive output.

Since prey availability, predation risk, physiological constraints, and metabolic costs are all a function of mass, we make the simplifying assumption that predation, food availability, metabolic costs, and physiological constraints (described below) are a function of *structural* mass, determined by length. This means for individuals of a given length there is no variation in predation risk arising from differences in stored lipid mass. In practice, this assumption did not have a large effect on our results because we allowed individuals to reproduce every month (and they did), so the mass of stored lipids was generally small relative to structural mass.

The state variables (energy stores and body length) vary dynamically over time. In each month, the individual encounters prey according to its position in the size spectrum (from Eq. 2) and the richness of the ecosystem. Lipid stores *S(t)* are mobilized to meet metabolic requirements, allocated to reproduction or growth, or saved for the future.

Consequently, the dynamics from one month to the next are

(4)

There are several physiological constraints that determine whether an individual survives from time *t* to *t* + 1. Lipid stores must be maintained above a critical threshold, which is a percentage of structural mass (in joules), so that . The maximum lipid mass that can be saved from *t* to *t+*1 cannot exceed 75% of the structural mass *W1*(*t*); any lipid stores in excess of this are not carried over. If, after allocation to growth and reproduction, an individual’s expected future stores *S*(*t+1*)do not exceed the critical threshold for its future structural mass *W1*(*t+*1), then the individual has no future fitness (i.e., it starves). If the physiological constraints are satisfied, then the individual will survive to the next time according to the mortality risk given by Eq. 3 for its structural mass in the current time *.* We convert the risk of predation to the probability of survival *γ* by. Reproductive output in each month is limited to be a fraction of structural mass (in joules), so that . This represents a constraint on allocation to gonads imposed by the size of the body cavity (Wootton 1993).

***Fitness and the Stochastic Dynamic Programming Equation***

We define , the fitness function, to be the maximum expected accumulated reproduction between time *t* and given size and lipid stores of . The consequences of allocation to growth *g* and reproduction *r* affect both current fitness (current reproduction and survival) and the potential size and lipid stores in the next time step (future states). We denote potential future states as and , and use these values to calculate the expected future fitness of every combination of *g* and *r*. Because there is no reproduction at or after *T,* . For *t < T*, *V*(*l,s,t*)satisfies the dynamic programming equation (Mangel 2015).

(5)

Changes in length depend on allocation of lipid stores to growth, so that . Changes in lipid stores depend on allocation to growth *g* and reproduction *r*, in addition to income and costs, so that , where is the structural mass of an individual of length *l.*

*Functional forms motivated by tunas*

Following the Metabolic Theory of Ecology, we defined costs as

(6)

Studies of the physiological ecology of tunas have estimated the allometric exponent *θ* is 0.66 (Clarke and Johnston 1999). The remaining parameters of this function have been discussed thoroughly in the scientific literature on the Metabolic Theory of Ecology, or MTE (Gillooly et al. 2001, Brown et al. 2004), which suggests that metabolic requirements increase allometrically with mass, such that the relationship is linear in log-space. Evidence for the MTE suggests that Boltzmann’s constant *k0* and the activation energy *E* (the energy required for the reactions of respiration and other metabolic processes) do not vary appreciably among taxa (O’Conner and Bernhardt 2018). The normalization coefficient *c* was introduced to account for differences among taxonomic groups in the intercepts of the linear relationship (more attention has been focused on the slope of this relationship (*θ*), which is strikingly similar among taxa). As we have little information on *c* for tunas, we adjusted it so that the range of costs experienced over an individual’s lifetime were comparable to estimates obtained in physiological experiments on metabolic rates of tunas (Kitchell et al. 1978). Due to the uncertainty in this parameter, we explore variation in *c* in sensitivity analyses.

The structural mass of an individual (in kg) with length *L*(*t*) is

(7)

where the parameter *a* was estimated for Atlantic bluefin tuna (Table 1). If an individual of size *L*(*t*) with stores *S(t)* allocates a fraction *r* of its energy stores to reproduction, and a fraction *g* of stores to growth, where *g*, it will grow by

(8)

The derivation for Eq. 6 is in Appendix 1.

*Solving the for the optimal allocation at each age, using backward iteration*

For all scenarios discussed in the main text, we assume the maximum lifespan of *T =* 216 months (18 years). We considered alternative values of *T* in the supplemental material to ensure our choice of *T* value did an influence on our results.

The solution of Eq. 5 generates both a fitness landscape and an optimal allocation rule , and for every possible combination of length, lipid stores, and age (Fig. 2b), given the food, risk of predation, and metabolic cost functions (Fig. 2c). We used linear interpolation when computing future fitness in Eq. 5 to minimize the effects of discontinuities on the fitness landscape arising from the step size of the proportional allocation decisions in our model, which varied in increments of 0.1 (Clark and Mangel 2000). We did not interpolate length, since its unit (centimeters) was sufficiently fine-grained that there were minimal effects of discontinuities. When, in rare cases, the fitness of more than one allocation decision was tied, we recorded the minimum allocation as the optimum. For example, this occurred when the size-based constraints we imposed on reproductive effort or lipid stores led to identical fitness outcomes from more than one allocation level.

***Forward simulation***

The solution of Eq. 5 provides the optimal allocation for all possible combinations of size, lipid stores, and age, but some combination will not occur naturally (for example, individuals are unlikely to be both old and small) and some will be inviable. For example, some states will not be viable with some sizes, given the energetic requirements of large individuals. Therefore, to predict combinations of states and ages that will be observed in nature, we use the solution of Eq. 5 to the expected fates of individuals that recruit to the population after their first year of life, given an arbitrary initial size and lipid stores. We simulated the life history of an individual that starts its second year at 50 cm in length, with 3.675 MJ of stores (equivalent to 70% of the structural mass of a 50 cm individual). This individual allocated proportions of its energy stores to growth and reproduction according to the decision rules that emerged from the solution of Eq. 5 for each environmental scenario. We recorded the body length and reproductive output in each subsequent month of the focal individual’s life. We also calculated the size-dependent risk of predation, given the individual’s growth trajectory. This chance of mortality was computed each month after reproduction, but before the individual grew to the next size. We then plotted the individual’s probability of survival to each age. We fit a linear model to the logarithm of survival probability. Following conventions for mortality rates in fisheries science, we used the absolute value of the slope as an approximation of the monthly mortality rate *Mmonthly*. We then calculated the annual mortality rate *M* as

(9)

This realized mortality emerges from individual decisions to allocate to growth at every age, which varies according to the prey availability in the ecosystem and the size-dependent decrease in predation.

***Environmental scenarios***

We modeled the optimal life history in 12 different environmental scenarios, to include a spectrum of past, present, and potential future environments in Earth’s oceans. We considered environmental scenarios that varied in temperature, food availability, and metabolic costs. We modeled two constant environments with different average temperatures, 290 K and 295 K, which we will call the cool and warm scenarios. In both temperature scenarios, we considered three levels of food richness (*c* = 1, 2.5, and 5). We present a single value of the predator efficacy parameter *h* in Eq. 3 (*h* = 4) which represent differences in overall predation risk, but we considered the interaction with a higher level of predation (*h* = 8) in sensitivity analyses.

We also considered environments which varied in both seasonal temperature and food availability. In summer, the water temperature 𝜏 increases by 4 degrees above the base temperature for six months of the year (from 290 to 294 K in the cool scenario, and from 295 to 299 K in the warm scenario). In these seasonal environments, during winter the food available in the ecosystem (*c*) doubles but the temperature is identical to the constant environments (Figure 1) An individual in the cool seasonal scenario experiences summer temperatures that approach the constant warm scenario (Figure 1b; Table 1). The inclusion of seasonality in our factorial combinations means that we can compare warm “tropical” scenarios (which may be constant or vary seasonally in coastal upwelling zones in the tropics) with seasonal cool “temperate” scenarios. The constant cool scenario could represent “deep ocean” conditions. The factorial combinations are designed to reveal the interacting affects of seasonality in metabolic demands and food availability on top of the interacting effects of the foodscape and fearscape.

**Results**

*Body size and growth patterns*

In the majority of the environmental scenarios that we considered, individuals allocated to growth early in life, and shifted to reproduction later, so that an asymptotic growth pattern naturally emerged from the model (Figure 3). For purposes of illustration, we plot the growth pattern emerging for an individual that survives until the final time, *T,* even though the chances of an individual living this long are essentially zero. With increasing richness of the size spectrum, body size increased. Although not presented graphically here, under extremely rich size spectra – environments with very high productivity – staying small was advantageous in all environmental scenarios suggesting that when bathed in food, there is no reason to grow larger, even though lifespan is extremely short (due to high mortality of small individuals). We chose not to include these results in our analysis as individuals were very short lived (essentially, they were semelparous).

Increased body sizes were observed in warm, constant environments (discussed further below in *Warm vs. cool environments*). Additionally, we consistently observed the evolution of larger body sizes in seasonally varying environments. The strong effect of seasonality on the evolution of body size in our model is partially due to that fact that in seasonal environments, twice as much food is available during the winter season (Figure 1). This means that on average there is 50% more food available to an individual as it grows (but it must pay higher metabolic costs during the low-food seasons, which is a disadvantage of growing larger). To understand the effect of seasonality apart from the effect of increased food, it is useful to compare the body sizes that evolve in constant environments with greater richness () with the body sizes that are favored in seasonal environments of lesser richness (Figure 4). Body sizes in seasonal scenarios are similar or greater than body sizes in constant environments offering much greater richness and lower metabolic costs (Figure 4). We can infer that the large body sizes in seasonal environments are not simply due to the increased food available, but comes from the temporal aspects of food availability and metabolic costs.

*Age and size of maturation*

We defined the age of maturation in each scenario to be the youngest age that individuals produce at least 50% of their maximum reproductive output (Figure 5a,b). Age at maturation varied with seasonality, food, and, to a lesser extent, between warm and cool scenarios. In the model scenarios presented here, individuals matured between one and two years, and surprisingly, this did not change in sensitivity analyses in which we varied predator gut fullness across the size spectrum, represented by parameter *h*. Greater environmental richness and seasonal environments both led to later maturation, as the optimal growth pattern required that reproduction be put off in favor of early growth and larger body size. The effect of temperature alone was weak, although in seasonal environments, there was an interaction with temperature; at lower richness (), individuals in the colder seasonal environment had late maturation, but at intermediate richness, this pattern reversed (Figure 5b). Our definition of maturity as the age at which females produce 50% of their eventual maximum reproductive output has minimized differences in the steepness of the maturation ogive – a function describing how quickly reproductive investment increases with maternal body size – that are apparent in the pattern of reproductive investment over an individual’s life (Supplemental Figure 1).

Maturation was slightly delayed in seasonal environments, relative to corresponding constant environments (Figure 5b), but these effects were small overall. In constant environments, size at maturity increased with environmental richness, closely following the pattern of age at maturity. As with age at maturity, there was no effect of varying predation risk in the size spectrum (by varying predator gut fullness; Figure 5c,d). There was a minor effect of temperature, which was associated with smaller size at maturity in warmer environments, if they were constant). All else being equal, in seasonal scenarios with low and intermediate richness, size at maturity occurred at a larger size in warmer environments than cooler environments (Figure 5d; recall age at maturity was either the same, or earlier in warmer environments). In seasonal environments, we found an unexpected pattern where size at maturation was smaller at the highest level of richness (monthly = 0.42) than intermediate environments, even though the age of maturity was slightly later. We infer that with plentiful food, the ability to take advantage of seasonally abundant resources is less important to fitness, so early growth is not prioritized over reproduction to the same degree. Inspection of the pattern of reproductive investment in seasonal environments suggests that the maturation ogive is less steep.

*Reproductive output*

Our model allowed the timing of maturation to vary independently of monthly reproductive output (i.e., total batch fecundity and oocyte size), although total reproductive output was constrained by body length. We specified that reproductive output was limited to a proportion of structural mass. We chose to limit reproductive effort to a maximum of 20% of structural mass (= 0.2) for all other scenarios. Sensitivity analyses revealed this choice affected allocation to growth as well as body size (FIGURE), but it does not affect the general conclusions of our model. Reproductive output varied over the lifetime of mature individuals according to the growth pattern, seasonality, and temperature-dependent metabolic costs of each environmental scenario (An example for both seasonal and constant cool environments is plotted in Supplemental Figure 1). In seasonal environments, reproduction occurred in both seasons, but increased during winter (when food was abundant and metabolic costs lower than in the summer). This seasonal variation in reproductive output was much greater in high food than low food environments (e.g., Figure 4).

*Mortality rate*

Annual rates of mortality were strongly affected by food and varied between warm and cool environments (Figure 6). Variation in natural mortality emerged through predation, not starvation, because the optimal allocation strategies ensured individual energy stores were above the critical threshold and were sufficient to meet the size-based metabolic costs. Therefore, we can think of the mortality rates discussed here as *extrinsic* mortality.

Following the patterns observed for body size, the mortality rate depended on environmental richness as well as seasonality. Emergent mortality rates were inversely related to body size, which is to be expected, given the size-dependent nature of predation in our model of size-spectra, and thus primarily correlated to richness. Therefore, due to their body size, the individuals in seasonal environments had, in general, lower mortality rates than those in constant environments (Figure 6). Individuals in higher food environments were also larger and had lower mortality than individuals in low-food environments. Warm and cool environments did not have a consistent directional effect on mortality (Figure 6). However, the highest mortality rates emerging from our analyses came from constant low-food environments, since these conditions favored the evolution of small maximum body sizes.

*Warm vs. cool environments*

Comparing the blue and red lines and symbols in Figures 3 and 4 shows that the response to the increased metabolic requirements of warmer environments differed in several ways, with the result that extrinsic mortality rates did not vary consistently with temperature, because multiple factors drove the evolution of body size (seasonality, food, and fear). Warmer environments generally favored larger body sizes, *especially* constant conditions. In general, seasonality favors larger body sizes, so the minor effect of temperature is understandable. An exception occurred at intermediate food levels, in seasonal environments, when cooler temperature led to a delayed growth strategy, where older individuals had a period of secondary growth, eventually reaching larger body sizes than individuals in warmer environments. This difference in growth trajectory was less pronounced in sensitivity analyses where we varied the parameters associated with mortality risk at each size (predator gut fullness, *h*). This exception to the general pattern of larger body sizes in warmer environments illustrates that the effect of temperature on growth is sensitive to the trade-off between reproduction and the increased metabolic costs associated with larger sizes, as well as the seasonality of the environment.

The effect of temperature on growth was greatest at intermediate food levels. Both nutrient poor or nutrient rich conditions lead to similar strategies in both thermal environments. There is one outlier, in high food, cold seasonal environments, individuals are favored to have a terminal growth investment to even larger body sizes (over three meters). We don’t focus on that here, as very few individuals survive to that ages (Recall Fig. 3 presents the growth pattern for the rare individual that does survive the full lifespan).

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**Discussion**

Our primary motivation was to develop a model of energetic allocation to life-history traits. We embedded the life history model within a realistic ecosystem context to explain potential mechanism for a range of macroecological phenomena pertinent to understanding global change, such as the temperature-size rule. We were motivated to explain the diversity of life histories of tunas as a key group representative of the fundamental challenge to understand the diversity of life body sizes and life histories on earth. We developed a model for the evolution of body size, maturation, and reproductive output from which mortality rate could emerge. We used size spectra theory to embed mechanistic functions describing the relationship between body size, prey availability (food), predation, and metabolic costs, which also varied between ecosystems that differed in average temperature. Finally, we considered seasonal variation in food and temperature. This allowed us to determine how life history traits are shaped by environmental conditions.

We found that the forces shaping body size and reproductive patterns interact in complex ways. One of the most unexpected results of the model is the finding that seasonality in temperature and food availability favors larger body sizes, despite increased metabolic costs during summer. We infer this because larger individuals can better take advantage of high food conditions during the cool season. Furthermore, our comparison of warm and cool environments suggest that the increased metabolic costs associated in with the tropics do lead to the evolution of smaller body sizes (Daufresne et al. 2009). However, this difference only occurred when food was seasonally abundant.

*Connections between our results and extant scombrid life histories*

Our model structure was primarily motivated by the biogeography of scombrids (tunas and their relatives). The largest tunas (e.g., *T. orientalis, T. thunnus, T. maccoyii*)reach larger body sizes than predicted by our model (Chapman et al. 2011, Juan-Jordá et al. 2013), but we note that the largest body sizes in our model were also found in environments with variation in temperature and food availability. This result suggests their large body sizes may be an adaptation to take advantage of seasonal fluctuations in resources, in addition to allowing them to migrate long distances and dive to deep water (Wilson and Block 2009). Our model suggests that for these species, warming oceans may not change their growth patterns unless environmental productivity also changes, restructuring the size spectrum such that smaller body sizes are advantageous in warmer environ,ents (Figure 3b,c). By contrast, for tropical tuna species (e.g., *Katsuwonus pelamis*, *T. albacares*) that do not experience seasonal fluctuations in food and temperature, the outcome of increased temperature for growth is unclear; growth may increase in some cases (Figure 3b). For smaller scombrids, a change in temperature is not predicted to affect growth patterns much unless productivity also changes the size spectrum.

We also can derive general insights into the evolution of body sizes in aquatic communities. In sensitivity analyses varying the predator satiation parameter (*h*) we found that predation risk alone did not strongly affect the maximum body size or age at maturation predicted by our model. The optimal body size depended largely on food availability and seasonality (which also affected food availability). In low-food environments, the evolution of very large body sizes was simply not possible. Mortality rates also differed between cool and warm scenarios, but primarily varied with maximum body size (Figure 6), which depended on growth patterns that were driven by seasonality, temperature, and food. This result provides a theoretical justification for the common practice of using body size to estimate mortality rates in different environments (Beverton and Holt 1959, Gislason et al. 2010, Charnov et al. 2013, Mangel 2017), but it also highlights the complex interactions between food, predation, growth, and reproduction that affect mortality rate. We emphasize mortality rate could be influenced by many factors other than body size, and using trait-based proxies to estimate mortality rates are likely to miss key determining factors (Thorson et al. 2017).

Our model predicted a very narrow range of maturation ages, and did not predict the range of maturation ages observed in nature, but the trend of increasing maturation age with body size is consistent with the expected trends in scombrids. Furthermore, both the timing of maturation and the size of maturation were unchanged by increasing the risk of predation at every body size (in our sensitivity analysis, where predator satiation, *h*, varied across the size spectrum). This suggests that in our model it is the relative difference in predation risk at different sizes - the fearscape - that is driving the timing of maturation, not absolute levels of predation.

The result that size at maturation is larger in seasonal warmer environments (unless food is super-abundant), combined with the positive effects of seasonality and temperature on body size, suggests that warmer environments favor increased growth over reproduction in early life for species where resources vary temporally (seasonal changes in environmental richness). Warmer environments also led to larger body sizes, but did not affect the optimal size at maturity, in constant environments. However, the importance of thermal conditions on growth and size is weaker than the effect of seasonality itself, which has a consistently strong directional effect on body size evolution. This result persists despite the increased metabolic costs (which are increased again for larger individuals) during the warmer season. We interpret the fact that seasonality favors larger body size - despite increased costs - because they are able to acquire and store a larger quantity of resources in a short amount of time. Without the temporal variation in resource availability, organisms grow more slowly.

Our study follows in the steps of previous work linking energy budgets and the scaling of metabolic requirements with body size evolution (e.g., Kozlowski 1996, Kooijman 2000). However, ours is the first to incorporate the size-specific changes in prey availability and predation risk that underlie the phenomenon of aquatic size spectra (Anderson 2019). By synthesizing these two conceptual frameworks, we are able to predict a greater diversity of life histories than previous models. This approach to further environmental scenarios to explore and predict the consequences of expected future changes in temperature and productivity.

**Acknowledgements**

This work was supported by NSF DEB-1556779 to HKK. We thank Christian Jørgensen and Ken H. Andersen for discussion of early drafts.

**Appendix 1**

Derivation of Eq. 8, the length-weight relationship for tunas.

We assume that structural mass is a cubic function of length.

(A1)

To calculate the equivalent change in length arising from the allocation of a fraction of stores to structural masswe convert the energy *gS(t)* to mass by dividing by the energetic mass conversion coefficient , and add it to existing mass:

(A2)

We then combine Eqs. A1 and A2 to calculate the new length:

(A3)

If and then the growth increment is

(A4)

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|  |  |  |
| --- | --- | --- |
| **Parameter** | **Description** | **Value** |
| *w* | Body mass in kg | varies |
| *B* | Absolute biomass in a trophic level (prey or predators) when considering a community size spectrum | - |
| 𝜆 | The exponent that defines the shape of a biomass size spectrum, or its slope on a log-log plot of biomass as a function of body mass. Its value depends on the way the size spectrum is characterized, here the value in Eq. 2 is reported (following Andersen 2019). | 1.95 |
|  | The intercept of a biomass size spectrum, which defines the total biomass of organisms of the smallest body size *w*  in a given ecosystem; Andersen (2019) gives an estimate of 10 gained by averaging over all PPMR estimates measured from gut contents. We vary it to represent ecosystem differences in overall ecosystem richness | 5,10 |
|  | Size spectrum “abundance factor” that integrates prey encounter rates, predator prey mass ratios, and prey preferences (value derived from mechanistic principles in Andersen 2019; Ch. 2 Table 2.2). | 3 |
| *Bprey* | Biomass of prey expected by a focal individual | - |
|  | Risk of mortality due to predation, which depends on body mass and position in the size spectrum | - |
|  | Size spectrum “predation factor” that is an anology to (value derived from mechanistic principles regarding predator preferences reported in Andersen 2019 Table 2.2) | 0.07 |
|  | Predation risk, comprised of predator satiation estimates (estimated from gut contents) and predator preference (or effectiveness) for consuming prey of a given mass (Andersen 2019) | 15,20 |
| *n* | Predator consumption exponent that determines how metabolic requirements increase with body mass (estimated in Andersen 2019; Ch. 2 Table 2.2) | 0.75 |
| 𝜏 | Temperature of the environment (in degrees Kelvin) | 290,295 |
| *C* | Metabolic requirements (costs) that scale with mass and temperature | - |
| *c* | Normalization constant scaling metabolic costs (in J), based on metabolic rate data from tunas (Kitchell et al. 1978) | 1.67 × 1016,  5× 1016 |
| *k* | Boltzmann constant, relating particle energy to temperature in units of m2 kg s-2 K-1 | 1.3 × 10-23 |
| *E* | The average activation energy for the rate limiting enzymes in metabolism in units of joules; from the metabolic theory of ecology (Gilooly et al. 2001). | 1.04 × 10-19 |
| 𝜃 | Metabolic scaling exponent; values vary among clade, here we use a value reported for tunas (Clarke and Johnston 1999) | 0.66 |
| 𝜌 | The energy density of tuna body mass in our model in J/kg (estimated empirically and reported in Chapman et al. 2011) | 4.2 × 106 |
| *t* | Time in monthly time steps in the dynamic model | - |
| *Tmax* | Maximum lifespan in years | 18 |
| *l* | Body length (in cm) – this is a dynamic state variable but can only increase with time. The maximum value is 375 cm. | - |
| *s* | Lipid stores (in joules) – this is a dynamic state variable representing energy stores that can be used for metabolism, growth, and reproduction. | - |
|  | Structural mass of the individual (in kg); a cubic function of length | - |
| *a* | Scale coefficient relating length to structural mass, estimated empirically for bluefin tuna and reported in ICCAT (2015) | 1.0 × 10-5 |
|  | Lipid mass of the individual (in kg); cannot exceed | - |
|  | Total mass of the individual (in kg) | - |
|  | The fraction of structural mass that determines the critical threshold of energetic mass needed for survival; if the individual starves | 0.1 |
|  | The fraction of structural mass that determines the maximum limit on reproductive output in a monthly time step. | 0.2 |
| γ | Survival from one month to the next, which is a function of predation risk |  |
| *g* | Proportion of lipid stores allocated to growth (this allocation decision is optimized by the dynamic programming equation); can take values between 0 and 1 |  |
| *r* | Proportion of lipid stores allocated to reproduction (this allocation decision is optimized by the dynamic programming equation); can take values between 0 and 1 and the sum of *g* and *r* cannot exceed one. |  |
| *V* | Expected lifetime fitness for an individual of a given state at a given time. |  |

1. Such as encounter rates between predators and prey, respiration and ingestion, and metabolism. [↑](#footnote-ref-1)
2. In light of Eq. 1 which in log-log space is a line with slope and intercept . [↑](#footnote-ref-2)
3. Andersen (2019) models predator gut fullness *f0* as a separate component of mortality risk from prey capture success *h*, but in Eq. 3 we model stomach size (which determines gut fullness) and capture success together in one parameter *h* that represents the expected chance of being eaten by a predator once it is encountered. [↑](#footnote-ref-3)