**Combining size spectra and state dependent life history theory to understand the diversity of tuna growth and reproduction**

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**Abstract**

Life history traits are central to both individual fitness and population growth. Theory explains how the evolution of traits depends on age-specific survival rates, and also predicts trade-offs among key traits such as growth, reproduction, and survival. Bioenergetic models of fish have been used to explain allocation to these traits according to food availability and metabolic processes. We connect life history theory to models of ecosystem and community dynamics described by size spectra. Size spectra suggest that aquatic systems are structured predictably by size-based rates of consumption. We develop an energetically based model of lifetime fitness that merges these two areas of aquatic ecology to predict the evolution of life history traits and emergent mortality rates. We thus link the interactions between predation, food availability, seasonality, and temperature and apply the model to characterize the growth of tunas. Larger body size is predicted to be advantageous in seasonal environments, although increased temperature incurring high metabolic costs leads to the evolution of smaller fish. We predict that rates of maturation rate will not vary with temperature, although mortality rates, and to a lesser extent, the allometry of reproduction and body length, can. We conclude that the complexity of the interactions between predation, metabolism, and food availability preclude simple predictions for changes in growth and based on increases in temperature alone.

**Keywords**

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

**Introduction**

Explaining the evolution of diverse life histories and understanding their consequences for population dynamics remains a fundamental challenge for ecologists seeking to manage human interactions with wild populations and predict their responses to future global change. Life -history traits such as body size, maturation timing, and schedule of reproductive output, comprise a strategy that allows an individual to achieve successful reproduction its environment (Roff 1992; Stearns 1992). Body size, fecundity, and offspring size are the outcomes of a series of decisions about the allocation of resources to growth and reproduction (Beverton and Holt 1959; Gadgil and Bossert 1970; Kozlowski 1996). These decisions have evolved to maximize the long-term representation of genes in a population, or a proxy for fitness such as the average population growth rate. Resources must also be allocated to maintenance (i.e., metabolic requirements; (Jørgensen et al. 2016)). Metabolic demands consume energy in a predictable way according to environmental variables, such as temperature and biophysical variables, arising from the fractal transport network of blood vessels in tissue (Clarke and Johnston 1999; Brown et al. 2004). After these maintenance requirements are satisfied, allocation to growth and reproduction, as well as other behavioral and physical traits, such as sexual ornaments or weapons, will generate covariances among traits ( Winemiller & Rose, 1992; Winemiller, 1992). We expect these covariances to map predictably onto environmental factors.

A trait-by-environment map can be used to predict demographic rates, which are determined by life-history traits. The map can then be used to infer the trajectories of understudied populations. This idea has roots in fundamental ecological theory (Charnov and Krebs 1974; Southwood 1977; Charnov et al. 1991; Gislason et al. 2010) but the search for “rules” for predicting ecological assemblages based on functional traits continues (Ferraro 2013; Winemiller et al. 2015). In some cases, strong correlations between life history traits, in particular body size, and aspects of the environment or community have been observed. For example, the temperature-size rule is a well-documented phenomenon in which body sizes of ectotherms are larger in colder temperatures (Gillooly et al. 2001; Kingsolver and Huey 2008). However, whether increasing temperatures will lead to a decrease in body size of ectotherms is currently debated (Daufresne et al. 2009; Neubauer and Andersen 2019). The outcome likely depends on simultaneous changes in productivity and predator abundance, which are difficult to disentangle.

Another approach to understanding the link between traits and the environment are size-spectra relationships. There are well-established examples of consistent relationships among body size, trophic level, and abundance across species in the same environment, notably in aquatic communities (Law et al. 2009; Trebilco et al. 2013; Sprules and Barth 2016). These predictable relationships between individual size, abundance, and biomass in aquatic ecosystems are known as size spectra (Sheldon et al. 1977, Andersen 2019). In a community size spectrum, energy flows between trophic levels and consumption and predation rates are characterized by individual mass, instead of species identity (Blanchard et al. 2017, Andersen 2019). Variation among species in consumption and predation risk is expected due to differences in resource richness in different environments, but differences among species in the same group (e.g., fish) in the same environment are minimized when traits are measured across large scales (Andersen et al. 2016; Sprules and Barth 2016).

In this paper, we use an evolutionary model of allocation to growth and reproduction to predict how variation in environmental productivity (food), predators, and temperature determine the emergent evolutionarily strategy, given size-dependent metabolic requirements. In our model, consumption and mortality rates scale with body size according to size-spectra theory (Andersen 2019). 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. To do so, we use state dependent life history theory implemented by stochastic dynamic programming (Mangel and Clark 1988, Houston and McNamara 1999, Clark and Mangel 2000). We predict the optimal life history in environments characterized by size spectra for food availability and the rate of predation.

Our model is grounded in aquatic size spectra across different body size classes, which connect the effect of changes in productivity (prey availability) to mortality risk (predator abundance). The consistent relationships that underlie community size spectra can be explained by the allometric scaling relationships that are consistent among ectotherms in aquatic ecosystems (Benoît and Rochet 2004; Blanchard et al. 2009, 2017). Aquatic predators are usually generalist consumers with a preference for prey in a given size range. The lower limit of prey size preference depends on the profitability of the prey, and the upper limit of prey size preference depends on 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 obtain a general relationship between predator mass and prey mass, the Predator-Prey Mass Ratio (PPMR). The PPMR of aquatic predators is surprisingly predictable, despite differences in predator biology, and can be used to understand the fundamental regularities in body size and abundance that lead to community size spectra (Andersen 2019).

The interactions between predators and prey that lead to community size spectra in aquatic ecosystems also apply to interactions within size-structured populations of the same species: individuals are born small and grow through the size spectrum over their lifetime, eventually consuming conspecifics that are a fraction of its own size. This is the case for many bony fishes that have small progeny and grow through several orders of magnitude in mass over their life. For example, some studies of anchovy and sardine diets have found 30% of their stomach contents are conspecific egg (Smith et al. 1989). Even if other prey and predator species are present, size-spectra 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, because it is size rather than species that determines the rates of consumption and predation (see Eqs 1, 2, and 4 below). Given this assumption, the predation and consumption rates defined by a size spectrum can 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).

The evolution of a species’ life history traits can be related to its position in the size spectrum, since its mass determines the resources (prey) available for growth and reproduction and its predation risk. We use this idea to predict how traits such as body size, age of maturation, and fecundity evolve in an aquatic environment that is characterized by its richness of resources, seasonal variability, and temperature, as those are primary drivers of fish life history variation (Kamler 2005). We are motivated by the range of life histories that are observed in the genus *Thunnus,* the largest market tunas (Horswill et al. 2019). We used parameters derived the physiological ecology of tunas to in our model of metabolic processes. The market tunas vary in body size, but also in growth rates, maturation, spawning frequency and duration of the spawning season, as well as batch fecundity. These tunas display unexpected variability in traits such as maturation, survival, and growth among stocks. For example, the average age at maturation diverges between Pacific bluefin (*T. orientalis*, which mature around four years) and Southern bluefin (*T.* *maccoyii,* which mature around 10 years), although these species have similar maximum body size, and both inhabit temperate waters for a significant portion of each year (Horswill et al., 2019). Two more distantly related species, *T. albacares,* yellowfin tuna, and *T. obesus,* bigeye tuna, remain in tropical waters year-round. The tropical species tend to grow faster and mature earlier than bluefin, spawning for a sustained period each year, and potentially achieving higher annual fecundity (Horswill et al., 2019). These two species can reach comparable body sizes to bluefin tunas, although their lifespans are shorter, and on average they are smaller. These trait covariances indicate that mortality rates, as well as how reproductive outputs are portioned out over lifetimes, vary among these species, but it is difficult to predict these patterns *a priori.* To address this gap, we aim to produce a spectrum of patterns of growth and reproduction in different environmental scenarios, as well as predict the responses of these life history traits to changes in environmental temperature overall and seasonally, as well as changes in the abundance of predators and prey. We can then compare the predicted trait covariances with those found in extant tuna species, and simultaneously produce a trait-by-environment map to understand how species will adapt to environmental change.

**METHODS**

**The size spectrum**

Biomass size spectra are defined as the absolute biomass *B(w)* as a function of body mass *w.* We can describe the biomass spectrum with an intercept parameter **and the spectrum exponent [[2]](#footnote-2) Andersen (2019)



To understand why the biomass in each trophic level is unrelated to the body mass of species in that trophic level, theory invokes mass-dependence in prey encounter rates, consumption limits, and prey preferences (prey (Andersen 2019; Benoit and Rochet 2004, Blanchard et al. 2017). The encounter rate between aquatic predators and prey, also called the clearance rate, is typically measured in units of volume per time, as we are considering organisms that occupy a three-dimensional habitat (Kiørboe and Hirst 2014). This rate is frequently modeled as a function of mass in which the volume of prey differs among species with different feeding modes in aquatic environments (Kiørboe and Hirst 2014). After encounter, consumption rates of predators will be limited by the digestive capacity, which scales with body size because digestive tissue is a fractal delivery network (Brown et al. 2004; Kiørboe and Hirst 2014). Finally, empirical evidence on prey size preferences (e.g., Ursin 1973) suggest they can be described by a log-normal distribution of the predator-prey mass ratio (PPMR), which is usually estimated from diet studies (Reum et al. 2019). This distribution describes the prey-preference window: most predators will accept a range of prey sizes close to their preferred size. As long as the PPMR does not vary with predator mass, *i.e.,* it is independent of *w,* size spectra theory provides us with a clear link between consumption and predation rates (Andersen 2019).

In a thorough review of these scaling relationships, Andersen (2019, Eq. B2.2) considers a focal individual of size *w,* and computes the expected biomass of available prey - either conspecifics or heterospecifics – based *w,* the ecosystem richness (the pre-exponential parameter of the size spectrum), the slope of the spectrum, and an “abundance factor” that combines the PPMR and the width of the prey preference window. The per-unit-time consumption of prey of mass *w* is

 (2)

We assume that average individual consumption is given by Eqn 2, with parameters estimated from empirical size spectra, reviewed in Andersen (2019, Table 2.2) and included in Table 1 here. This function therefore determines the expected energetic income of a focal individual according to its size. For consistency between income and costs, we convert consumption to joules, assuming that the energy density *ρ* = 4.2 MJ/kg (Chapman et al. 2011).

We assume that mass-dependent energetic costs to the focal individual follow the Metabolic Theory of Ecology (Gillooly et al. 2001). Thus, we model mass-dependent costs (in joules) as a function of temperature 𝜏in Kelvin, depending on the allometric exponent θ, the activation energy *E,* Boltzmann’s constant **, and a normalization coefficient *c*. The per unit time cost of metabolism is then

 (3)

The normalization coefficient is adjusted according to taxon. 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 rate of bluefin tuna (Kitchell et al. 1978). Due to the considerable uncertainty in this parameter, we varied it in sensitivity analyses.

Andersen (2019, B2.7 and Eq. 2.11 on pp 82) also derives the rate of mortality experienced by an individual of mass *w*. This result depends on the size preference window of predators , a consumption coefficient  (representing how full predator stomachs are), a scale coefficient *h* (representing how likely a predator is to eat the focal individual), anda metabolic exponent *n.* The parameters  and *h* are modeled independently in Andersen (2019) but are considered together here as one product *h*, that modifies the risk of predation of an individual of mass *w.*

The per unit time rate of mortality is

 (4)

In summary, we use results of size spectrum theory to calculate net energetic income and the risk of predation for an individual of mass *w*.

**Dynamics of Individual States**

To predict how allocation to growth and reproduction vary as a function of an individual’s age, size, and lipid reserves, we use state-dependent life-history theory (Mangel and Clark 1988, Houston and MacNamara 1999, Clark and Mangel 2000). We assume a time horizon of months beyond which there is no opportunity for future reproduction, either because of senescence or because survival to *T* is essentially 0. In each month  the individual acquires energy from food, which it can use to grow, allocate to reproduction within the same season, or store for future allocation.

We model both a constant environment and an environment with seasonal variation in temperature and the amount of food available, determined by . We modeled two constant environments with different average temperatures, 290 K and 295 K. We also modeled two seasonal environments. In both seasonal environments, for six months of the year the amount of available food in the ecosystem doubled. The other half of the year, the water temperature 𝜏 increases by 4 degrees from the baseline (i.e., from 290 to 294 K and from 295 to 299 K). Figure 1 shows how varying and temperature change the relationship between food availability, costs, and body size.

We characterize individuals by two dynamic state variables: length *L(t)* in cm and lipid stores (reserves) *S(t)* in joules (cf. Jørgensen & Fiksen, 2006)*.* We use joules as the common currency of every process in the model (temperature-dependent metabolic costs, reproductive output, body length, and lipid stores).We use the standard von Bertlanffy assumption (Mangel 2006)of a cubic relationship between length and associated structural (vs. reserve) mass to convert body length to mass in kg to determine mass-dependent rates of income and mortality, which vary according to our assumptions about the size spectrum. We do not distinguish between reproductive allocation of males and females; therefore all reproductive output is quantified in joules. We consider this output to represent investment in the form of gametes of either sex, although it could also include investment in courtship behaviors, mate guarding, or intra-sexual aggression (particularly in males).

Since prey availability, predation risk, physiological constraints, and metabolic costs are all a function of mass, we make the simplifying assumption that predation, income, 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 structural mass of an individual (in kg) with length *L*(*t*) is

 (5)

where the parameter *a* is empirically determined (Table 1). Structural mass in joules is, where is the average energy density of structural tissue, and can be estimated empirically (Chapman et al. 2011). We also can convert lipid stores to lipid mass . We then use structural mass to calculate metabolic requirements  and income.

In each month, the individual encounters prey according to its position in the size spectrum (from Eq. 2) and the overall richness of the ecosystem **. Lipid stores *S(t)* are mobilized to meet metabolic requirements, allocated to reproduction or growth, or saved for the future. 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

(6)

The derivation for Eq. 6 is in Appendix 1. Consequently, the dynamics from one month to the next are

 (7)

There are several physiological conditions 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 . An individual whose stores fall below this threshold starves (and receives no current or future fitness). 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. 4 for its structural mass *.* 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 1992).

**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 . Because there is no reproduction at or after *T,*  .

For *t < T*, satisfies the dynamic programming equation (Mangel 2015).

 (8)

Changes in length depend on allocation of lipid stores to growth, so that , where the growth component is given by Eqn 6. 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.*

The solution of Eq. 8 generates both a fitness landscape and an optimal allocation , and for every possible combination of states (length and stores) and age. We used linear interpolation when computing future fitness in Eq. 8 for values of lipid stores to minimize the effects of discontinuities when calculating expected fitness, which arise because lipid stores must take an integer value (Clark and Mangel 2000). We did not interpolate length, as 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 behavior was tied, we recorded the minimum allocation as the optimal behavior. 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 proportional allocation amount. It was also possible some combinations of states and age will not occur naturally (for example, individuals are unlikely to be both old and small) and some will be inviable (some states will not be viable with some sizes, given the energetic requirements of large individuals). Therefore, to understand the expected combinations of states and ages we simulated the expected fates of individuals that recruit to the population after their first year of life.

***Forward simulation***

We simulated the life history of an individual that starts its second year at 50 cm in length, with 3675000 J of stores (equivalent to 70% of the structural mass of a 50 cm individual). The individual allocates to growth and reproduction according to the rules given in Eq. 8. We determined the body length and reproductive output at each subsequent month. We computed the cumulative survival of the individual from its size-based risk of predation, which was determined after reproduction but before growth. From this survival curve we calculated the annual mortality rate. We did so by calculating the expected proportion of the population that survived to each age, taking the natural log of this metric of abundance. We fit a linear model to these data. The slope, which is always negative, is an approximation of the monthly mortality rate *Mmonthly*. We then calculated the annual mortality rate *M* as

We also calculated the exponent of the size-fecundity relationship. Traditionally, fecundity of fishes has been assumed to be proportional to mass, and modeled as a cubic function of length. However, recent work has suggested the relationship between size and fecundity is hyperallometric in ectotherms with indeterminate growth, including fishes (Dick et al. 2017; Marshall and White 2019). This relationship assumes that fecundity is not strictly proportional to size, but rather grows as older individuals allocate an increasing proportion of their energy budget to reproduction (rather than growth or metabolic maintenance). How this exponent is expected to vary in different environments is currently unknown, although some research suggests for multiple spawners in seasonal environments, variability in individual size can have important consequences for fecundity and future growth (Lowerre-Barbieri et al. 1998; Farley et al. 2015). We calculated the fecundity exponent by plotting reproductive output as a function of length in log-log space, and calculating the slope of the shortest line connecting minimum and maximum reproductive output. This allowed us to determine if there are age-based differences in reproductive output consistent with the pattern of hyperallometric reproduction.

***Environmental scenarios***

In this paper we focus on comparing two environments of each type: high and low food, predation risk, and base temperature, which was either the temperature of the constant environment or the temperature of the cold season (Figure 1). Since we are motivated to understand life-history strategies of tunas, such as bluefin, that migrate seasonally among environments, relative to those that remain in tropical waters year-round, such as yellowfin, we also compared all of these factors in a constant environment with a seasonally varying scenario (dashed lines, Figure 1). Environmental parameter values for the functions in Figure 1 are given in Table 1. Individuals in our cool-baseline scenario experience seasonal warming to temperatures that approach the warm-baseline scenario (Figure 1b).

**Results**

*Body size and growth patterns*

Varying the metabolic scaling coefficient *c* had only minor effects on our results, so we present analyses for only one value of *c.* Individuals largely allocated to growth early in life, and shifted to reproduction later, so that an asymptotic growth pattern naturally emerged from the model (Figure 2). There were some exceptions to this asymptotic growth pattern. With high food and low predation, and with low food at higher seasonal temperatures, individuals delayed growth to their eventual maximum body size (Figure 2, panels c and d). In these cases, sensitivity analyses revealed that in high-food environments, the age to which individuals deferred growth to their maximum body size varied with *T* (the maximum lifespan possible) (Supplemental Figure 1). The pattern disappeared as predation risk (*h)* increased (Figure 2, top row)*.*  We interpret this secondary growth pattern as an effect of changing reproductive value due to senescence (and predation risk). When extrinsic and intrinsic mortality are low, large body sizes and early reproductive investment are less advantageous (food is abundant and survival is high, even for mid-size individuals). In other scenarios, the evolutionarily optimal strategy did not vary with *T*.

In general, selection favored the evolution of larger maximum body sizes in seasonal environments (Figure 2), although with low food levels and low predation risk individuals delayed growth (described above). We observed the evolution of larger body sizes in seasonal environments, especially with cooler base temperatures in all predation and food scenarios (Figure 2). We infer seasonality itself also contributed to the evolution of larger body sizes, because the maximum body sizes of individuals in the low-food seasonal environment were larger than the maximum body sizes evolving in the high-food constant environment, especially at the lower base temperature (Figure 2). This pattern emerged in spite of greater food availability at every body size in the high-food constant environment (Figure 1a, thick solid red line) than in the low-food seasonal environment (Figure 1a, thin dashed blue line) and the fact that size-dependent metabolic costs in the seasonal environment were higher or comparable to the constant environment (Figure 1b, dashed red lines are higher or comparable to solid blue lines).

*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 3b). Our model structure allowed young individuals to reproduce (although output was constrained to a percentage of body size), and allocation of a small amount of energy to reproduction early on was optimal in every scenario. This pattern occurred because we did not model physiological constraints or costs preventing low levels of spawning *per se,* and because small fish were also limited in how many resources they could store to use for growth (so any excess energetic income could be devoted to reproduction without trading off with somatic growth). In nature, behavioral, developmental and hormonal mechanisms likely prevent this pattern of maturation in fish with large asymptotic size. Detailed studies on cod, tunas and other teleosts suggest that iteroparous fishes do show substantial variation in size-specific fecundity, which may be explained by age differences (Rijnsdorp 1991; Trippel et al. 1997; Kjesbu et al. 1998; McIntyre and Hutchings 2003; Farley et al. 2013) so we do not consider this outcome of our model to be wildly inconsistent with reality.

Age at maturation varied with predation, seasonality, food, and, to a lesser extent, temperature. In the environmental scenarios presented here, our metric of maturation age ranged from 1.9 to 16.2 years. However, with delayed secondary growth (Fig. 2c), individuals were able to reproduce at very low levels for a long period before reaching the age of maturation calculated with our method (Supplemental Figure 2). Maturation age decreased as predation risk increased, and also varied with food and temperature. With low predation and high food, individuals matured later (Figure 3b), with the exception of the seasonal, low-food environment with a warm base temperature, where individuals remained small and matured later (16.2 years) than in every other case (Figure 3b, Supplemental Figure 2). This timing of maturation coincided with the onset of secondary growth (Figure 2c). Seasonality itself also delayed the age of maturation, especially with warmer base temperatures (Figure 3b), but these effects were small relative to the interacting effects of food and predation. Similar to the patterns in maximum body size, the size of maturation was also larger in seasonal environments and in high food environments, and did not vary strongly with predation (Supplemental Figure 3). Sensitivity analyses showed that with low food, maturation ages decreased predictably with earlier onset of senescence (lower *T*) (following the growth trends in Supplemental Figure 1).

*Fecundity*

Our model allowed the timing of maturation to vary independently of maximum reproductive output per month (i.e., total batch fecundity and oocyte size), although total reproductive output each month was constrained by body length. We found reproductive output varied over the lifetime of mature individuals according to the growth pattern, seasonality, and temperature-dependent metabolic costs of each environmental scenario. In seasonal environments, reproduction occurred in both seasons, but increased in the cold season (when food was abundant and metabolic costs lower than in the warm season). This seasonal variation in reproductive output was much greater in high food than low food environments (an example is given in Supplemental Figure 2).

In Figure 3c we show the fecundity exponent for each environmental scenario. Values greater than three indicate hyperallometry of the fecundity-length relationship (Marshall and White 2019). Sensitivity analyses revealed that the size-based limit on reproductive effort  (which depended on structural mass) affected this metric, as it indirectly affected growth as well as fecundity (Supplemental Figures 4 and 5). Varying  had stronger effects on growth in low food scenarios. At higher values of  (0.3 and greater) delayed growth, smaller body sizes, and earlier reproduction were advantageous (Supplemental Figure 4, top row). This difference disappeared at higher food levels (Supplemental figure 4, bottom row). Varying  also affected the fecundity exponent (Supplemental Figure 6). After these exploratory analyses, we chose to limit reproductive effort to a maximum of 20% of structural mass (= 0.2), because this value generates fecundity exponents that were consistently equal to or greater than the cubic (Figure 3c). Constant environments had higher exponents than seasonal, and low food environments had higher exponents than high food. This is largely the inverse of the pattern in maximum body size. The largest exponent (indicating the greatest hyperallometry) emerged in the smallest fish (160 cm), which evolved in a constant, cool environment with low predation and low food (Figure 3c). In this case, individuals matured early at a small size, and grew very little after beginning to reproduce, but their monthly reproductive output increased once they finished growing (at age three).

*Mortality rate*

Annual mortality rates were strongly affected by the overall predation curve of the size spectrum, as well as food and temperature (Figure 3d). Although individuals faced starvation if their reserves fell below a critical threshold, because we used a deterministic model, individuals did not starve, because allocation strategies evolved to ensure individual energy stores were above this threshold and were sufficient to meet the size-based metabolic costs.

The individuals in seasonal environments had, in general, lower mortality rates than those in constant environments (with similar food and predation risk) (Figure 3d). High-food individuals had lower mortality than low-food individuals (because they were larger) except in low-predation environments, where high-food individuals had higher mortality, on average, than low-food individuals, because they remained small for a significant proportion of their life before the onset of secondary growth (the one case where secondary growth was also advantageous with low food, the warm seasonal environment, also had higher mortality). Baseline temperature affected mortality, especially in low-food environments, but did not have a consistent directional effect (Figure 3d). However, the highest mortality rates emerging from our analyses came from constant low-food, high-predation environments, and the warm, seasonal low-food environment, as these conditions all favored the evolution of the small maximum body sizes.

*Temperature*

In Figures 2 and 3, comparing the blue and red lines and symbols shows that individuals responded to the increased metabolic requirements of warmer environments in several ways, with the result that mortality rates did not vary consistently with temperature, because of the factors that drove the evolution of body size (seasonality, food, and predation). With seasonality in food and temperature, warmer base temperatures often led to the evolution of smaller body sizes (Figure 2). In constant warm environments, individuals were similar in size or even slightly larger than individuals in cool environments. Temperature affected size and age at maturation most in the seasonal environment. In warm environments, size at maturation increased relative to cool environments with high food and low predation, and decreased with low food and both levels of predation (Supplemental Figure 3). Age at maturation not strongly affected by temperature except in the warm low predation, low-food environment, which favored secondary growth and delayed maturation relative to the cool environment (Figure 2d).

**Discussion**

Motivated by understanding the diversity of life histories of the tunas, we developed a model for the evolution of body size, maturation, and reproductive output from which schedules of mortality and the length-fecundity relationship also emerge. We used size spectra theory to incorporate mechanistic functions describing the relationship between body size, prey availability (food), predation, and metabolic costs, which also depended on 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 predict that seasonality in food availability favors larger body sizes, despite increased metabolic costs during the warm season. We infer this is because larger individuals can better take advantage of high food conditions during the cold season. Furthermore, our comparison of two base temperatures suggest that the increased metabolic costs associated in with warmer baseline temperatures do lead to the evolution of smaller body sizes (Daufresne et al. 2009). However, this difference was only evident when occurred when food was seasonally abundant, and large body sizes were advantageous. In constant environments, warmer base temperatures lead to slightly larger body sizes than cool, but smaller body sizes were favored overall.

Predation risk alone did not strongly affect the maximum body size predicted by our model, but it did affect growth patterns. As expected, higher predation rates favored the evolution of larger body sizes and earlier maturation, a trend which has been demonstrated empirically (Conover and Munch 2002) and using fisheries datasets (Kuparinen and Merilä 2007; Enberg et al. 2009). However, optimal body size and size at maturity also 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 with environmental conditions, but primarily varied with maximum body size (Figure 3d), 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 found that age at maturation was not directly affected by temperature. Instead it was strongly related to body size (length), and the growth pattern. Maturation was delayed when individuals adopted a secondary growth pattern. In these cases, the optimal strategy was a period of initial growth, followed by many years of reproduction at very low levels, followed by a period of secondary growth, accompanied by maturation. This pattern of delayed growth and maturation in environments with low intrinsic and extrinsic mortality is highly consistent with expectations from life-history theory (Stearns 1992). However, it is less clear whether some fish remain small, reproducing at low levels, although there are examples of small, old fish that appear to have delayed growth (Rijnsdorp et al. 1991; Hunter et al. 2015).

Our results suggest that the fecundity exponent, which indicates how reproductive output changes with an individual’s size, is consistently higher when maximum lengths are smallest. This highlights one drawback of our method of using the slope of the shortest line to calculate the fecundity exponent, because the size difference between the individual producing the minimum non-zero level of output, and the youngest individual producing the maximum output is small when the maximum body size is small. If we had sampled the population without perfect knowledge and overestimated this difference, our estimate of the exponent would decrease. For this reason, seasonality and higher food led to lower fecundity exponents than those measured in constant, low food environments, because increased body size was advantageous in these scenarios. Larger body sizes naturally take longer to reach, thereby increasing the x-axis distance used in calculating the slope.

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 1994). 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 and can potentially explain the diversity of fish life histories beyond scombrids (tunas). Along with this diversity is the fact that mortality rate is influenced by many factors other than body size, and using trait-based proxies to estimate mortality rates are likely to be unsuccessful (Thorson et al. 2017). We also demonstrated that an increase in mortality, which could be due to fishing pressure, can influence the life history in several dimensions. When food is low, especially in constant environments, optimal growth patterns may not change as much as fecundity (Supplemental Figure; see also Rijnsdorp et al. 1991).

Our model adresses the diversity of market tuna species. The largest tunas (e.g., *T. orientalis, T. thunnus*)experience seasonal variation in temperature and food availability (Chapman et al. 2011, Juan Jorda et al. 2013), which is consistent with our model predictions. Their large body sizes may be an adaptation to take advantage of seasonal fluctuations in resources. Our model suggests that for these species, warming oceans may lead to the evolution of smaller maximum body sizes. By contrast, for species (e.g., *T. macoyii*) that do not experience seasonal fluctuations in food and temperature, but have intermediate body sizes, the optimal body size may not change, or could increase slightly. For species that currently inhabit nutrient-poor waters that vary seasonally, but where predation risk is relatively low, increased temperatures could favor the evolution of a slow-growing, late maturing strategy, reaching a much smaller body size.

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**Appendix 1**

Derivation of Eq. 6.

As stated in Eq. 5 in the main text, 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 first have to convert the energy to mass

(A2)

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

(A3)

The growth increment depends on the allocation and the energetic stores *S(t),* so we write it as

**References**

Andersen, K. H., N. S. Jacobsen, K. D. Farnsworth, and J. Baum. 2016. The theoretical foundations for size spectrum models of fish communities 1. Canadian Journal of Fisheries and Aquatic Sciences 73:575–588.

Benoît, E., and M. J. Rochet. 2004. A continuous model of biomass size spectra governed by predation and the effects of fishing on them. Journal of Theoretical Biology.

Beverton, R. J. H., and S. J. Holt. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Pages 142–177 *in*CIBA Foundation Colloquium on Ageing.

Blanchard, J. L., R. F. Heneghan, J. D. Everett, R. Trebilco, and A. J. Richardson. 2017. From Bacteria to Whales: Using Functional Size Spectra to Model Marine Ecosystems. Trends in Ecology and Evolution.

Blanchard, J. L., S. Jennings, R. Law, M. D. Castle, P. McCloghrie, M. J. Rochet, and E. Benoît. 2009. How does abundance scale with body size in coupled size-structured food webs? Journal of Animal Ecology.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology.

Chapman, E. W., C. Jørgensen, and M. E. Lutcavage. 2011. Atlantic bluefin tuna ( *Thunnus thynnus* ): a state-dependent energy allocation model for growth, maturation, and reproductive investment. (R. Hilborn, ed.)Canadian Journal of Fisheries and Aquatic Sciences 68:1934–1951.

Charnov, E. L., D. Berrigan, and R. J. H. Bevertron. 1991. Dimensionless numbers and the assembly rules for life histories. Philosophical Transactions: Biological Sciences 332:41–48.

Charnov, E. L., H. Gislason, and J. G. Pope. 2013. Evolutionary assembly rules for fish life histories. Fish and Fisheries 14:213–224.

Charnov, E. L., and J. R. Krebs. 1974. ON CLUTCH‐SIZE AND FITNESS. Ibis.

Clarke, A., and N. M. Johnston. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. Journal of Animal Ecology.

Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. Science.

Daufresne, M., K. Lengfellner, and U. Sommer. 2009. Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences of the United States of America 106:12788–12793.

Dick, E. J., S. Beyer, M. Mangel, and S. Ralston. 2017. A meta-analysis of fecundity in rockfishes (genus Sebastes). Fisheries Research 187:73–85.

Enberg, K., C. Jørgensen, E. S. Dunlop, M. Heino, and U. Dieckmann. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. Evolutionary Applications 2:394–414.

Farley, J. H., T. L. O. Davis, M. V. Bravington, R. Andamari, and C. R. Davies. 2015. Spawning dynamics and size related trends in reproductive parameters of southern bluefin tuna, Thunnus maccoyii. PLoS ONE 10.

Farley, J. H., A. J. Williams, S. D. Hoyle, C. R. Davies, and S. J. Nicol. 2013. Reproductive Dynamics and Potential Annual Fecundity of South Pacific Albacore Tuna (Thunnus alalunga). PLoS ONE 8.

Ferraro, S. P. 2013. Ecological periodic tables: in principle and practice. Oikos 122:1541–1553.

Gadgil, M., and W. H. Bossert. 1970. Life Historical Consequences of Natural Selection. The American Naturalist.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science 293:2248–2251.

Gislason, H., N. Daan, J. C. Rice, and J. G. Pope. 2010. Size, growth, temperature and the natural mortality of marine fish. Fish and Fisheries 11:149–158.

Horswill, C., H. K. Kindsvater, M. J. Juan‐Jordá, N. K. Dulvy, M. Mangel, and J. Matthiopoulos. 2019. Global reconstruction of life‐history strategies: A case study using tunas. (R. Arlinghaus, ed.)Journal of Applied Ecology 56:855–865.

Jørgensen, C., K. Enberg, and M. Mangel. 2016. Modelling and interpreting fish bioenergetics: a role for behaviour, life-history traits and survival trade-offs. Journal of Fish Biology 88:389–402.

Jørgensen, C., and Ø. Fiksen. 2006. State-dependent energy allocation in cod ( *Gadus morhua* ). Canadian Journal of Fisheries and Aquatic Sciences 63:186–199.

Kamler, E. n.d. Parent-egg-progeny relationships in teleost fishes: an energetics perspective.

Kingsolver, J. G., and R. B. Huey. 2008. Size , temperature , and fitness : three rules. Evolutionary Ecology Research 10:251–268.

Kiørboe, T., and A. G. Hirst. 2014. Shifts in Mass Scaling of Respiration, Feeding, and Growth Rates across Life-Form Transitions in Marine Pelagic Organisms. The American Naturalist 183:E118–E130.

Kjesbu, O. S., P. R. Witthames, P. Solemdal, and M. Greer Walker. 1998. Temporal variations in the fecundity of arcto-Norwegian cod (Gadus morhua) in response to natural changes in food and temperature. Journal of Sea Research.

Kozlowski, J. 1996. Optimal Allocation of Resources Explains Interspecific Life-History Patterns in Animals with Indeterminate Growth.

Kuparinen, A., and J. Merilä. 2007. Detecting and managing fisheries-induced evolution. Trends in Ecology and Evolution.

Law, R., M. J. Plank, A. James, and J. L. Blanchard. 2009. Size-spectra dynamics from stochastic predation and growth of individuals. Ecology 90:802–811.

Lowerre-Barbieri, S. K., J. M. Lowerre, and L. R. Barbieri. 1998. Multiple spawning and the dynamics of fish populations: Inferences from an individual-based simulation model. Canadian Journal of Fisheries and Aquatic Sciences 55:2244–2254.

Mangel, M. 2006. The theoretical biologist’s toolbox : quantitative methods for ecology and evolutionary biology. Cambridge University Press.

Mangel, M. 2015. Stochastic Dynamic Programming Illuminates the Link Between Environment, Physiology, and Evolution. Bulletin of Mathematical Biology 77:857–877.

———. 2017. The inverse life-history problem, size-dependent mortality and two extensions of results of Holt and Beverton. Fish and Fisheries.

Marshall, D. J., and C. R. White. 2019. Have We Outgrown the Existing Models of Growth? Trends in Ecology and Evolution. Elsevier Ltd.

McIntyre, T. M., and J. A. Hutchings. 2003. Small-scale temporal and spatial variation in Atlantic cod (Gadus morhua) life history. Canadian Journal of Fisheries and Aquatic Sciences.

Neubauer, P., and K. H. Andersen. 2019. Thermal performance of fish is explained by an interplay between physiology, behaviour and ecology. (N. Fangue, ed.)Conservation Physiology 7.

Reum, J. C. P., K. K. Holsman, K. Y. Aydin, J. L. Blanchard, and S. Jennings. 2019. Energetically relevant predator–prey body mass ratios and their relationship with predator body size. Ecology and Evolution 9:201–211.

Rijnsdorp, A. D. 1991. Changes in fecundity of female north sea plaice (Pleuronectes platessa l.) between three periods since 1900. ICES Journal of Marine Science.

Roff, D. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York.

Southwood, T. R. E. 1977. Habitat, the Templet for Ecological Strategies? The Journal of Animal Ecology.

Sprules, W. G., and L. E. Barth. 2016. Surfing the biomass size spectrum: some remarks on history, theory, and application. (H. Giacomini, ed.)Canadian Journal of Fisheries and Aquatic Sciences 73:477–495.

Stearns, S. 1992. The Evolution of Life Histories. Oxford University Press, New York.

Trebilco, R., J. K. Baum, A. K. Salomon, and N. K. Dulvy. 2013. Ecosystem ecology: Size-based constraints on the pyramids of life. Trends in Ecology and Evolution.

Trippel, E. A., O. S. Kjesbu, and P. Solemdal. 1997. Effects of adult age and size structure on reproductive output in marine fishes. Early Life History and Recruitment in Fish Populations.

Winemiller, K. O. 1992. Life-History Strategies and the Effectiveness of Sexual Selection. Oikos.

Winemiller, K. O., D. B. Fitzgerald, L. M. Bower, and E. R. Pianka. 2015. Functional traits, convergent evolution, and periodic tables of niches. (H. Arita, ed.)Ecology Letters 18:737–751.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences.

|  |  |  |
| --- | --- | --- |
| **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 | 4.16, 12.5 |
|  | 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 in Andersen 2019; reported Ch. 2 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 *h* (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)