**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 almost all cases, even when increased temperature incurs high metabolic costs. Seasonality also favors larger body sizes so larger individuals can consume more food in the high-nutrient season. We predict that rates of maturation rates 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**

**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 (Stearns 1992; Roff 1992). Body size, fecundity, and offspring size are the outcomes of a series of decisions about the allocation of resources to growth and reproduction (Gadgil and Bossert 1970). These decisions have evolved to maximize the long-term representation of genes in a population, or a proxy such as the average population growth rate over long time scales. Resources must also be allocated to maintenance (i.e., metabolic requirements; Jorgensen 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 (West et al. 1997; Clarke and Johnston 1999; Brown 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 and Rose 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) 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 (Gilloly et al. 2001, Kingsolver and Huey 2008). However, whether increasing temperatures will lead to a decrease in body size is currently debated (Neubauer and Andersen 2019). The outcome likely depends on simultaneous changes in productivity and predator abundance, but these processes are difficult to disentangle.

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 (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 flow 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 (Sprules and Barth 2016, Andersen et al. 2015).

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 live 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) to determine 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. 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 (Olsen et al. 2015). For example, some studies of anchovy and sardine diets have found 30% of their stomach contents are conspecific eggs. 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. We are motivated by the range of life histories that are observed in the six market tunas (*Thunnus spp.* Horswill et al. 2019), so 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 *T. orientalis*, Pacific bluefin (which mature around four years) and *T.* *maccoyii* , Southern bluefin (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. They 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. These trait covariances strongly suggest that mortality rates, as well as how reproductive outputs are portioned out over the lifespan, vary among these species, but we cannot predict these patterns *a priori.* Here, we aim to produce a spectrum of patterns of growth and reproduction in different environmental scenarios, as well as predict the response of these life history traits to changes in environmental temperature overall and seasonally, as well as changes in the abundance of predators and prey.

**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 (Kiorboe 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 (Kjorboe 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 (West et al. 1997; Kjorboe and Hirst 2014; Andersen 2019). 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 (e.g. Reum et al. 2018). 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. Jorgensen and 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 **. In each month, 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 <* 1*- r* of stores to growth, it will grow by

 (6)

The derivation for Eq. 6 is in the Supplemental Material. 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 after the current time step). 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 allocaiton to gonads imposed by the size of the body cavity.

**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 combination of state 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.

The solution of Eq. 8 provides allocation rules for every possible combination of stores and size, at every age. Some of these 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).

***Forward simulation***

Given the optimal allocation rules 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). We determined the body length and reproductive output at each subsequent month for an individual investing in growth and reproduction according to the optimal allocation behaviors. 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 and multiplied the slope by 12 to estimate annual mortality rates. Although all slopes are expected to be negative, we report the absolute value, as is customary in fisheries science.

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. 2014; Marshall et al. 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 for batch spawners in different environments, given metabolic scenarios, is currently unknown. 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). The notable exceptions were the scenarios with high food and low predation, in which individuals began to reproduce at very low levels, but delayed growth to their eventual maximum body size (which varied with seasonality; Figure 2c). Sensitivity analyses revealed that the age to which individuals deferred growth to their maximum body size varied with *T* (the maximum lifespan possible), which interacted with predation (*h).*  We can interpret this secondary growth pattern as an effect of changing reproductive value due to senescence (and predation risk). We can conclude that 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*.

Based on Figure 2, we conclude that in general, selection favored the evolution of larger maximum body sizes in seasonal environments. In the high food scenarios (Figure 2a,c), the quantity of food is very high in the seasonal environment (Figure 1a), explaining the evolution of very large body sizes with seasonality (Figure 2). From a close analysis of the results presented in Figure 2, we can infer that seasonality itself is important to the evolution of body size. The maximum body sizes of individuals in the low-food seasonal scenarios were comparable to maximum body sizes evolving in the high-food constant environments at both base temperatures (Figure 2). This is surprising, because food availability was greater 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). At the same time, 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). Additionally, in the high predation scenarios (Figure 2, top row) somatic growth rates (measured by the age at which individuals reached their maximum body sizes) were slower in low-food seasonal environments than in high-food constant environments, despite growth to the same maximum body size in both cases. This difference can be attributed to seasonality, not the food abundance.

*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. Many iteroparous fishes do mature by reproducing at very low levels, 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 temperature. In sensitivity analyses, we found that with very low food in constant environments, individuals matured at a small size shortly after their first year and did not invest in somatic growth afterwards (result not shown). In the environmental scenarios presented here, maturation age was between 1.9 and 4 years, except when predation was low and food was abundant (discussed below). Seasonality 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.

Late age at maturation evolved in high-food, low-predation scenarios; individuals matured between ages 13 (constant) and 14 (seasonal) years. This timing coincides with the onset of secondary growth (Figure 2c). Despite this dramatic effect of predation on age, the size of maturation did not vary between high- and low-predation scenarios (Supplemental figure). In our model, late maturing individuals can and do reproduce at very low levels for a long time prior to our metric of their maturation age, because we do not constrain them from doing so (described above). Sensitivity analyses showed that very late maturation ages decreased predictably with earlier onset of senescence (lower *T*) and with increased predation risk *h* (results not shown).

*Fecundity*

Our model allowed the timing of maturation to vary independently of maximum reproductive output per month (i.e., total batch fecundity), 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). Because the optimal pattern of somatic growth differed between constant and seasonal environments (described above), and growth and our metric of the age of maturation are related, we did not find a consistent relationship between food or temperature, maturation, and monthly reproductive output.

In Figure 3c we show the fecundity exponent for each environmental scenario. Values greater than three indicate hyperallometry of the fecundity-length relationship (Barneche et al 2018). This limit is most important at small body sizes, when individual growth from one month to the next is limited by the amount of energy individuals could take in and store (a function of current structural mass), and excess energy can be devoted to reproduction. As mass increases, income itself becomes naturally limiting, due to the increase in metabolic costs and diminishing shape of the prey availability curve, which is a result of the size spectrum (Figure 1). Therefore, the slope of the fecundity-length relationship in log-log space decreased at higher values of , because higher values allowed small fish to have relatively high reproductive output. Sensitivity analyses revealed that the size-based limit on the total amount of reproductive effort  (which depended on structural mass) affected this metric .After these exploratory analyses, we chose to focus on the scenarios where reproductive effort was limited 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 (156 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: they were perfectly adapted to their environment, which did not vary unpredictably. In other words, 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 (Figure 3d), and high-food individuals had lower mortality than low-food individuals (because they were larger). The exception was the low-predation seasonal environment, 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. Baseline temperature affected mortality, especially in low-food scenarios, but did not have a consistent directional effect (Figure 3d). However, the highest mortality rate emerging from our analyses was in the constant, warm, low-food, high-predation scenario.

*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). In seasonal scenarios, with warmer temperatures a slightly larger body size was advantageous, accompanied by either faster growth and larger size of maturation (low-food, high-predation, seasonal scenario; Supplemental Figure) or slower growth and delayed age of maturation, but no difference in size of maturation (low-food, low-predation seasonal scenario; Supplemental Figure). In other cases, faster growth to a slightly smaller maximum body size and size at maturation evolved (high-food seasonal scenario at both levels of predation).

Individuals in constant warm environments were similar in size or slightly smaller than individuals in cool environments. Age or size at maturity did not vary dramatically with temperature or food except in the high food scenario, when maturation at a larger size was advantageous in both predation scenarios (supplemental figure).

**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.

Our analyses 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. To achieve this growth pattern, in seasonal environments individuals matured slightly later, at a larger size, than individuals in the constant environment, sacrificing some of their reproductive output.

Predation did not strongly affect the maximum body size predicted by our model, but it did affect growth patterns. Higher predation rates favored the evolution of larger body sizes, fast growth, and early maturation, but optimal body size and size at maturity also depended largely on food availability. In low food environments, the evolution of very large body sizes was simply not possible. Mortality rates also differed among scenarios, but primarily varied with maximum body size and maturation rates (Figure 3d), not with the predation, *h*. This result provides a theoretical justificaiton for the common practice of using body size and age at maturity (a proxy for generation time) to estimate mortality rates in different environments, but it also highlights the complex interactions between food, predation, growth, and reproduction that affect mortality rate.

Our comparison of two base temperatures suggest that the increased metabolic costs associated with a higher baseline temperature do not prohibit that the evolution of large body sizes, despite their increased metabolic requirements, as the advantages (increased prey availability and decreased predation risk) outweigh the costs. However, this result could vary if individuals cannot adapt their allocation strategy according to changes in environmental temperature, which might occur if temperatures are unexpectedly warm, and larger individuals cannot take in enough food to meet their metabolic budgets.

We found that age at maturation was not strongly affected by temperature; instead it was largely related to body size (length). The exception ocurred in low predation, high food environments. In this scenario, the optimal strategy involving a period of initial growth, followed by many years of reproduction at 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. Also consistent with life history expectations for batch spawners, reproductive output (analogous to batch fecundity) varied predictably according to the interacting effects of body size, food availability, and seasonality.

We predict that the fecundity exponent, which reflects how reproductive output changes with an individual’s size, is consistently higher in low-food scenarios, and in constant scenarios (also when maximum lengths were 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 in cases like this one. If we had sampled the population without perfect knowledge and overestimated this difference, our estimate of the exponent would have decreased. 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.

**References**

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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 | 5,15 |
|  | 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 ouput 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)