**­DRAFT**

**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 persist in its environment (Stearns 1992; Roff 1992). It is useful to view body size, fecundity, and offspring size as 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 lifetime fitness, or the average population growth rate over long time scales. Resources must also be allocated to maintenance, such as metabolic requirements. 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). 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).

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. As one 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 in analyses of aquatic ecosystems.

Promisingly, 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, consumption and predation rates, can be characterized in terms of 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 temperatures determine the evolutionarily advantageous strategy, given size-dependent metabolic requirements. In our model, consumption and mortality rates all 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, here we use the method of stochastic dynamic programming (Mangel and Clark 1988, Houston and McNamara 1999) to determine the optimal life history in different environments.

Our model framework is grounded in the unique consistency of aquatic size spectra across different body size classes, which connects the effect of changes in productivity (prey availability) to mortality risk (predator abundance). The consistent relationships that underlie the phenomenon of 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 species play interchangeable roles. 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 20014, 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 the richness of resources and temperature. Our model incorporates differences among individuals in two state variables (lipid stores and length) in an optimization of lifetime fitness, which emerges from the allocation of resources to growth and reproduction. A similar model of the evolution of migration behavior in bluefin tuna can be found in Chapman et al. (2011). Our approach is inspired by the diversity of market tuna life histories (Horswill et al. 2019), so we used parameters derived the physiological ecology of tunas to in our model of metabolic processes. We are able 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 and 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.* Following Andersen (2019) we can describe the biomass spectrum with an intercept parameter **and the spectrum exponent [[2]](#footnote-2)



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 can be used to describe the prey-preference window, as naturally most predators will accept a wider 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 based on these fundamental relationships can provide 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 an individual fish of size *w,* and solves for the expected biomass of available prey - either conspecifics or heterospecifics – based on its body size *w,* the ecosystem richness (the intercept of the size spectrum , the slope of the spectrum, and the quantity  which is an “abundance factor” encompassing the size spectrum slope, the PPMR, and the width of the prey preference window. The per unit time consumption of prey of mass *w* is . Ecosystems are dynamic, not static, so therefore we use a normal distribution for . The mean is estimated from parameters derived from empirical size spectra, reviewed in Andersen (2019, Table 2.2) and included in Table 1. This function therefore determines the expected energetic income of a given focal individual. For consistency between income and costs, we convert this quantity to joules using the coefficient of energy density *ρ* ( J/kg; estimate from Chapman et al. 2011). We further assume there are mass-dependent energetic costs to the focal individual, following the Metabolic Theory of Ecology (Gillooly et al 2001). Mass-dependent costs (in joules) paid over a season are modeled 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*:



We also can estimate mass-dependent predation risk per time. Andersen (2019, B2.7 and Eq. 2.11 on pp 82) derives the rate of mortality experienced by an individual of mass *w*, which encompasses the size preference window of predators , a consumption coefficient  and a scale coefficient *h,* and a metabolic exponent *n,*. This is the seasonal rate of mortality of a focal individual of mass *w.* Therefore, from size spectrum theory we can calculate net energetic income and the risk of predation for an individual of mass *w*. This risk will vary with the consumption coefficient  (representing how full predator stomachs are) and the scale coefficient *h,* which represents how likely a predator is to eat the focal individual*.* These are modeled independently in Andersen (2019) but are considered together here as one product *h*, which modify the risk of predation of an individual of mass *w.*

**Individual state dynamics**

To predict how allocation to growth and reproduction vary as a function of an individual’s age, size, and lipid reserves, we use a state-dependent modelling approach (Mangel and Clark 1988, Houston and MacNamara 1999, Clark and Mangel 2000). This method allows us to address how stochasticity in food consumption and risk of mortality interact to affect the evolution of size, maturation rate, and fecundity. We assume there is a finite period of time an individual can survive, , beyond which there is no opportunity for future reproduction. We consider decisions on monthly timescales. In each season  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 compare a model of constant environments with seasonal variation in temperature and the amount of food available. In the seasonal environment, for six months of the year the amount of available food in the ecosystem, determined by , doubles, representing winter (alternatively, the indivdual could migrate to temperate waters). The other half of the year, in summer, the water temperature 𝜏 increases by 4 degrees (e.g., from 290 K to 294 K).

We model energetic allocation to two dynamic state variables, length *L(t)* in cm and lipid stores *S(t)* in joules (a similar modeling approach to fish life-histories is described in 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 convert body length to mass to determine mass-dependent rates of income and mortality, which vary according to our assumptions about the size spectrum.

The structural mass of the individual (in kg) is a cubic function of its length in season *t,* with the coefficient *a* estimated from data



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 total mass  to calculate metabolic requirements  and net income.

In each time step, the individual encounters prey according to its position in the size spectrum (from Eq. 2) and the overall richness of the ecosystem **. Within a time step, lipid stores *S(t)* are mobilized to meet metabolic requirements, allocated to reproduction or growth, or saved for the future. There is a constraint on the maximum lipid mass that can be saved from *t* to *t+*1: it cannot exceed 75% of the structural mass *W1*(*t*); any lipid stores in excess of this are not carried over. Additionally, to survive from one season to the next, the lipid stores must be maintained above a critical mass threshold, which is a percentage of structural mass. An individual whose stores fall below this threshold starves and receives no current or future fitness. 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 . In the next season, the individual’s state will be



with the constraints that the mass of stored lipids must be less than 75% of structural mass, and stored lipids must exceed the critical threshold (. Reproductive effort (current fitness) in joules is . We assume that there is a constraint on the proportion of energetic mass that can be devoted to reproduction in a given time step (month), such that .

If the individual meets the critical threshold requirement in time *t,* but its future stores *S*(*t+1*)do not exceed the critical threshold for its future size (*W1*(*t+*1)), then the individual receives current fitness but no future fitness. If this energetic requirement is satisfied, then the individual will survive to the next time (*t*+1) according to the mortality risk given by Eq. 3 for its structural mass *.* The risk of predation is converted to survival *γ* by. Note that predation mortality depends only on structural mass, which is related directly to length; this assumes there is no variation in predation due to large differences in stored lipid mass. In practice, this assumption did not have a large effect on our results.

**Fitness and the Stochastic Dynamic Programming Equation**

We define  as the maximum expected accumulated reproduction between time *t* and  given size  and lipid stores of . We define . For *t < T*, satisfies the dynamic programming equation (Mangel 2015).



Changes in length depend on allocation of lipid stores to growth, such that. Changes in lipid stores depend on allocation to growth *g* and reproduction *r*, in addition to income and costs, such that *.* The solution of Eq. 5 generates both a fitness landscape and an optimal allocation , and for every combination of state and age. We used linear interpolation 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 (centimeter) 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. (This occurred when the size-based constraints we imposed on reproductive effort or stores that led to identical fitness outcomes from more than one proportional allocation amount.)

The solution of Eq. 5 provides allocation rules for every possible combination of stores and size, at every age. Some of these will not concur with nature (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 these optimal allocation rules, we next simulated the life history of an individual that starts its second year at a given size, with a given amount of lipid stores. We determined the body length and reproductive output at each time step of an individual allocating to growth and reproduction according to the optimal strategy given by Eq. 5. The cumulative survival of the individual was calculated 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.

***Environmental scenarios***

We are interested in how different environmental processes select for different growth and reproductive strategies of fish, and on isolating the effects of food, predation risk, and temperature, as those processes may change differentially in response to changes in climate. Although we explored many alternatives, in this paper we focus on comparing two environments of each type: high and low food, predation risk, and temperature. Environmental parameter values are given in Table 1. We also compared all of these factors in a constant environment with a seasonally varying scenario (described above), as we are motivated by tunas that migrate seasonally vs. those that remain in tropical waters year-round.

**Results**

|  |  |  |
| --- | --- | --- |
| **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 (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. Spectra are modeled as  [↑](#footnote-ref-2)