**­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). Therefore, if we imagine maximum body size (the corollary of somatic growth) and lifetime fecundity (the outcome of rates of maturation and reproductive effort) as axes of trait values, we can calculate an associated likelihood for each combination of life-history traits, in a given habitat. Some combinations are inviable , and will not persist in the long term. In this paper, we describe mass-specific consumption and mortality rates in an evolutionary model of allocation to growth and reproduction, using tunas as an example. 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. We do so by solving a dynamic state-variable model, in which the states are energetic resources (lipid stores) and size (body length). Chapman et al. (2011) used a similar approach to model the migration of bluefin tunas to spawning grounds, although our method differs in that we explicitly model mass-specific consumption and predation as a function of an individual’s position in the size spectrum.

A trait-by-environment map ca be used to predict demographic rates, which are determined by life-history traits. Such a map would present a major advance in our ability 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). Additionally, there are also 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).

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 posits 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 an individual life history 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 can thus 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. In this paper, our model incorporates differences among individuals in two state variables (lipid stores and length). After finding the optimal allocation strategy in a given environment for all possible values of these states, we can simulate a population of individuals experiencing stochastic prey and predator encounter rates to determine emergent rates of births and mortality. We explicitly merge the fundamental ideas in evolutionary ecology that species’ traits emerge from individual allocation decisions and physiological costs with the mass-specific predator and prey interactions that define observed size spectra.

**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 depend on 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 . Empirical estimates for these parameters are summarized in Andersen (2019, Table 2.2) and included in Table 1. This function therefore determines the expected income (in mass) of a given focal individual of a body size. Income in kg can be converted 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) 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 next consider mass-dependent predation. Andersen (2019, B2.7 and Eq. 2.11 on pp 82) also 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 per unit time rate of mortality of a focal individual of mass *w.* Thus from size spectrum theory we can calculate net energetic income and the risk of predation for 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 seasonal timescales, assuming four seasons in a year. 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 (a similar modeling approach to fish life-histories is described in Jorgensen and Fiksen 2006).

We model two dynamic state variables, length *L(t)* in cm and lipid stores *S(t)* in joules*.* We assume 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 . We also can convert lipid stores to lipid mass . We then use total mass  to calculate mass-specific 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, although the mass of saved energy cannot exceed structural mass. To survive from one season to the next, lipid stores must be maintained above a critical mass threshold, which is a percentage  of structural mass. 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 structural mass, and stored lipids must exceed the minimum threshold requirement (. In this individual, reproductive effort in this season is . If the energetic requirements are satisfied, then the individual will survive to the next season according to the mortality risk given by Eq. 3 for its structural mass  *.*

Risk of predation is converted to survival γ by. Note that predation depends only on structural mass, which is related directly to length; this assumption minimizes 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).



Where 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 units (centimeters) were 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 mean allocation behavior as the optimum.

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, it is 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 a population of 10,000 individuals that start their second year at a given size, with a given amount of lipid stores. This allowed us to investigate the range of expected life history outcomes, and measure properties of a population of individuals that are stochastically encountering food and dying. Initially we assumed recruits’ sizes have a mean of 50 cm, and a standard deviation of 5. Initial stores were 95% of the maximum stores allowed for the individual’s body size. We followed the fates of individuals that behave according to the optimal allocation strategy given by Eq. 5. Individuals in the cohort found food of stochastically varying quantities, and encountered predators, again according to the mass-dependent probabilities determined by the size spectrum. Mortality from predationis calculated after reproduction but before growth. Itwas determined by drawing a number uniformly distributed between 0 and 1 and comparing this number to an individual’s survival probability.We then measured the demographics of our simulated population, including realized mortality rates (which reflect both predation and starvation), size-at-age distributions, maturation rates, and reproductive output at the population level.

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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 (2018) 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- 30 |
|  | 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 a complement to (value derived from mechanistic principles regarding predator preferences in Andersen 2019; reported Ch. 2 Table 2.2) | 0.07 |
|  | Prey consumption coefficient based on predator satiation estimates (estimated from gut contents) that modulates predation risk (Andersen 2019 Ch. 2 Table 2.2) | 0.6 |
| *h* | Predator consumption coefficient that scales metabolic requirements with body mass (value estimated in Andersen 2019; Ch. 2 Table 2.2) | 17.2 |
| *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) | 293-296 |
| *C* | Metabolic requirements (costs) that scale with mass and temperature | - |
| *c* | Normalization constant scaling metabolic costs, adjusted according to Clarke and Portner 2010) | 1.2 × 1011 |
| *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 seasons in the dynamic model | - |
| *Tmax* | Maximum possible time over which an individual can accrue fitness (maximum lifespan) | 80 |
| *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 required amount of structural mass needed for survival; if  the individual starves (and ) | 0.1 |
| γ | Survival from one time step 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)