

THE ROLE OF FISH LIFE HISTORIES IN ALLOMETRICALLY
SCALED FOOD-WEB DYNAMICS

by

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Abstract

Body size determines key ecological and evolutionary processes of organisms. Therefore, organisms undergo extensive shifts in prey, competitors and predators as they grow in body size. While empirical and theoretical evidence show that these size-dependent ontogenetic shifts vastly influence the structure and dynamics of populations, theory on how those ontogenetic shifts affect the structure and dynamics of ecological networks is still virtually absent. Here, we take a first step towards generating such theory by developing an Allometric Trophic Network (ATN) model that incorporates size-structure in the population dynamics of fish species within complex food webs. Our preliminary results show that fish with larger allometric ratios attain higher biomass and tend to be correlated with greater ecosystem stability. We also find that that fish with a larger asymptotic body mass tend to be correlated with a larger total ecosystem biomass, a result that holds true across models for both the largest fish in the ecosystem and each fish species in the ecosystem. The approach adopted here offers a potentially instructive means of disentangling the effects of increasing life-history complexity in food-web models.

List of Abbreviations and Symbols Used

a_{ij}	Interaction between predator i and prey j
$A_{S \times S}$	Food web matrix with S species
B_{0ij}	Half saturation density for i eating j
B_i	Biomass of species i
c_i	Center of dietary range for species i
c_{kj}	Predator interference of species k eating j
e_{ij}	Assimilation efficiency for i eating j
f_a	Fraction of assimilated carbon that contributes to growth
F_{ij}	Normalized functional response
f_m	Fraction of assimilated carbon lost for maintenance
n_i	Niche value for species i
p_{ik}	Fraction of i 's prey that it shares in common with k
r_i	Intrinsic growth rate for autotroph i
x_i	Metabolic rate
y_{ij}	Predator i 's maximum consumption rate for prey j
η_i	Number of prey that species i preys on
ω_{ij}	Relative inverse attack rate of species i on its prey j
ATN	Allometric Trophic Network
C	Connectance
CV	Coefficient of variation
h	Hill exponent
K	Carrying capacity
L	Number of links between species
m	Body mass mean
ODE	Ordinary Differential Equation
S	Number of species in the web
T	Short-weighted trophic position
T1	Shortest trophic level
T2	Prey-averaged trophic position
v	Body mass variance
Z	Allometric (predator-prey body mass) ratio

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Chapter 1: Introduction

Body size determines key ecological and evolutionary processes during the ontogeny of organisms (Werner & Gilliam 1984). Ecological interactions, diet breadth, foraging efficiency, reproduction, mortality among other processes animating an organism's life strongly depend on the organism's size (Werner & Gilliam 1984, Yodzis & Innes 1992, De Roos et al. 2003). Given such dependency, organisms will undergo extensive shifts in prey, competitors and predators as they grow (Werner & Gilliam 1984, Ramos-Jiliberto et al. 2011). These size-dependent ontogenetic shifts vastly influence the structure and dynamics of aquatic populations and communities (Werner & Gilliam 1984, De Roos et al. 2003). For example, 'juvenile bottlenecks' influences the structure and dynamics of fish communities where prey populations compete with the juveniles of their predatory populations exhibiting similar body sizes (Byström et al. 1998). Moreover, theoretical work has shown that competitive and predatory (cannibalistic) interactions between different age cohorts drive fish population dynamics (Persson 1988, van den Bosch et al. 1988, De Roos et al. 2003). However, despite all the empirical and theoretical evidence of the vast impacts of size-dependent ontogenetic shifts and stage-structured populations on the population dynamics of interacting species, little theory has been developed on the effects of the size-dependent ontogenetic shifts and population structure on the structure and dynamics of ecological networks. Here, we give the first step towards generating such theory by developing a general Allometric Trophic Network (ATN) model that incorporates size-structure in the population dynamics of fish species within complex food webs.

The study of ecological networks has recently achieved major breakthroughs

by recognizing that the ecological functionality of species can be largely attributed to their body sizes (Brose et al. 2006a; Otto et al. 2007). Specifically, large allometric (predator-prey body mass) ratios appears to be key to stabilizing the dynamics of complex food webs (Brose et al. 2006b). Through scaling by body size, so-called Allometric Trophic Network (ATN) models have proven successful in explaining the stability, structure and functioning of ecosystems (Williams and Martinez 2000; Brose et al. 2006b; Dunne 2006). Apart from model-based investigations on the role of body size in food web dynamics, the theory has been further supported by Boit et al. (2012) who created a remarkably accurate, empirically validated ATN model by incorporating body size that explained 30 to 40% of the variation in the seasonal dynamics of the Lake Constance plankton community.

Within the context of food web dynamics models in general, and ATN models in particular, species of similar body size have been traditionally lumped together in a single functional group, such that scaling by body size is done with respect to individual body size across the species' lifespan. This approach stemmed from a need to develop simple models to address generic questions, such as those related to species coexistence (Blondel 2003). However, for some species, an individual's body size can change by orders of magnitude throughout its life (e.g., fishes; Wootton 1999). As there are strong correlations between body size and key functional traits, such as metabolic rate (West et al. 1999), a species' ecological functionality is likely to change substantially from juvenile to adult life-history stages. Thus, incorporation of the life-history structure of species that experience substantial changes in their body size across their lifespan is likely to increase the structural realism of food webs and yield more biologically realistic predictions about their dynamics.

Fishes constitute ideal study species because of their indeterminate growth, which causes them to shift through several ecological niches as they grow (Wootton et al. 1999). Their body size, diet, exposure to predation, and general ecological functionality changes tremendously from larvae through adult stages, resulting in many species transitioning from the bottom of the food chain to the position of apex predator. For example, during their lives, Atlantic cod (*Gadus morhua*) have the potential to change from being planktivores (as <10mm, 1-2g larvae) to apex carnivores longer than 1m in length and tens of kg in mass within 5-7 years (Brander 1994; Hutchings and Rangeley 2011). Another aspect that makes fishes and aquatic food webs particularly interesting systems to study the role of life-history structures in food web dynamics is the fact that contemporary life-history trends towards smaller body sizes and earlier maturity have been documented in many fish species across the world (Hutchings and Baum 2005; Audzijonyte et al. 2013). Understanding the impacts that such life-history changes can have to interacting species and entire ecosystems warrants for knowledge about the role of fish life-histories in food web dynamics.

The present study has two primary objectives. The first is to expand the ATN modelling approach by incorporating simple life-history structure for the fishes in a generic aquatic ecosystem. The second objective is to then explore the role of life histories across a broad range of alternative scenarios for aquatic food webs. To this end, we use the generic allometrically scaled niche model (Williams and Martinez 2000) adapted to aquatic food webs (Martinez et al. 2012) to randomly generate scenarios for food webs, within which we introduce life-history structure to fishes and split the species-level diets among the life-history stages. Through systematic simulations, we disentangle the relative impacts of the following components

involved in the added life-history structure: i) extension of the food web to include additional nodes, ii) life-history dynamics moving biomass from previous life-history stages to subsequent ones and then into new larvae through reproduction, and iii) the role of different fish life-history types, characterized through traits such as species growth speed and body size, timing of maturity, and diet. These analyses will provide broadly generalizable insights into the ways in which fish life-histories affect their food webs.

Chapter 2: Methods

2.1 Food Web Creation

The backbone of our model is the generation of random food webs. Food webs can be described mathematically using graph theory, where nodes represent species and the links between them are feeding interactions. The ATN model generates random food webs based on the relative body size between hypothetical species (Williams and Martinez 2000). The ATN model creates hypothetical species and chooses prey items for each predator based on the size differences between the species. It is particularly good at representing the layered structure of ecological networks. Additionally, unlike other food web models, it does not have a strict trophic hierarchy, which allows the model to incorporate elements such as cannibalism and loops. The features of this model are explored in more depth elsewhere (Williams and Martinez 2000).

Food webs are commonly represented with matrices (Dunne 2006). In the present study, we use a binary directed matrix, where links indicate the presence of predator-prey interactions. For the sake of clarity, we will describe a model for which each node represents a species; the model can easily be extended to accommodate life stages within species. Here we create the niche model described by Williams and Martinez (2000), a food web with two main constraints: number of species and connectance (Figure 1).

The primary characteristic used to distinguish species from one another is the niche value, which is drawn from a uniform distribution $n_i \in U(0,1) \forall$ species i (Williams and Martinez 2000). This value is a rough proxy for trophic level; it gives species a hierarchical ordered ranking of where they fall relative to each other. Species are then assigned prey items from a range centred around a lower niche value

(Williams and Martinez 2000). Species with a low niche value are generally autotrophs, while species with high niche values are more likely to be carnivores (Williams and Martinez 2000).

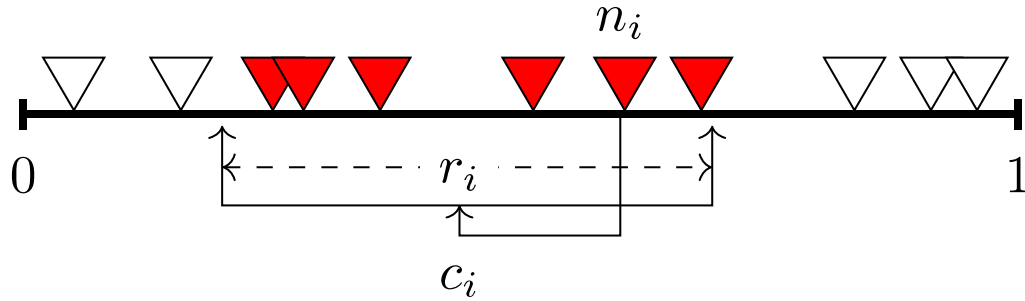


Figure 1. Niche creation model, reproduced from Williams and Martinez (2000), showing how diets are selected. A species with niche value n_i is assigned any prey with niche values that fall within the range of $r_i/2$ of the center of the predator's dietary range, c_i .

To control food web complexity (which determines how interconnected the web is), we can use a measure of connectance (C) that takes the fraction of actual links (L) between S species over all possible links (S^2) (Martinez 1991):

$$C = \frac{L}{S^2}$$

Complex webs, being more connected, have more predator-prey interactions.

Species are then assigned the degree to which they are specialists or generalists. This is represented by the width of their range of predation ($r_i \in (0, n_i)$), where a larger range indicates a more varied diet. Range size is chosen by first drawing a random variable, x_i , from a beta distribution that has been weighted to reflect the desired connectance (C) of the web (see Appendix for the derivation of β):

$$x \sim \text{beta}(\alpha, \beta) \text{ with } \begin{aligned} \alpha &= 1 \\ \beta &= \frac{1-2C}{2C} \end{aligned} \quad (1)$$

A less connected web will have more specialists, such that the distribution will skew more towards smaller range values (Figure 2). The range width for each species

is then scaled to fall in $(0, n_i)$ so that it will never exceed the niche index, which we do by multiplying it by n_i :

$$r_i = x_i n_i$$

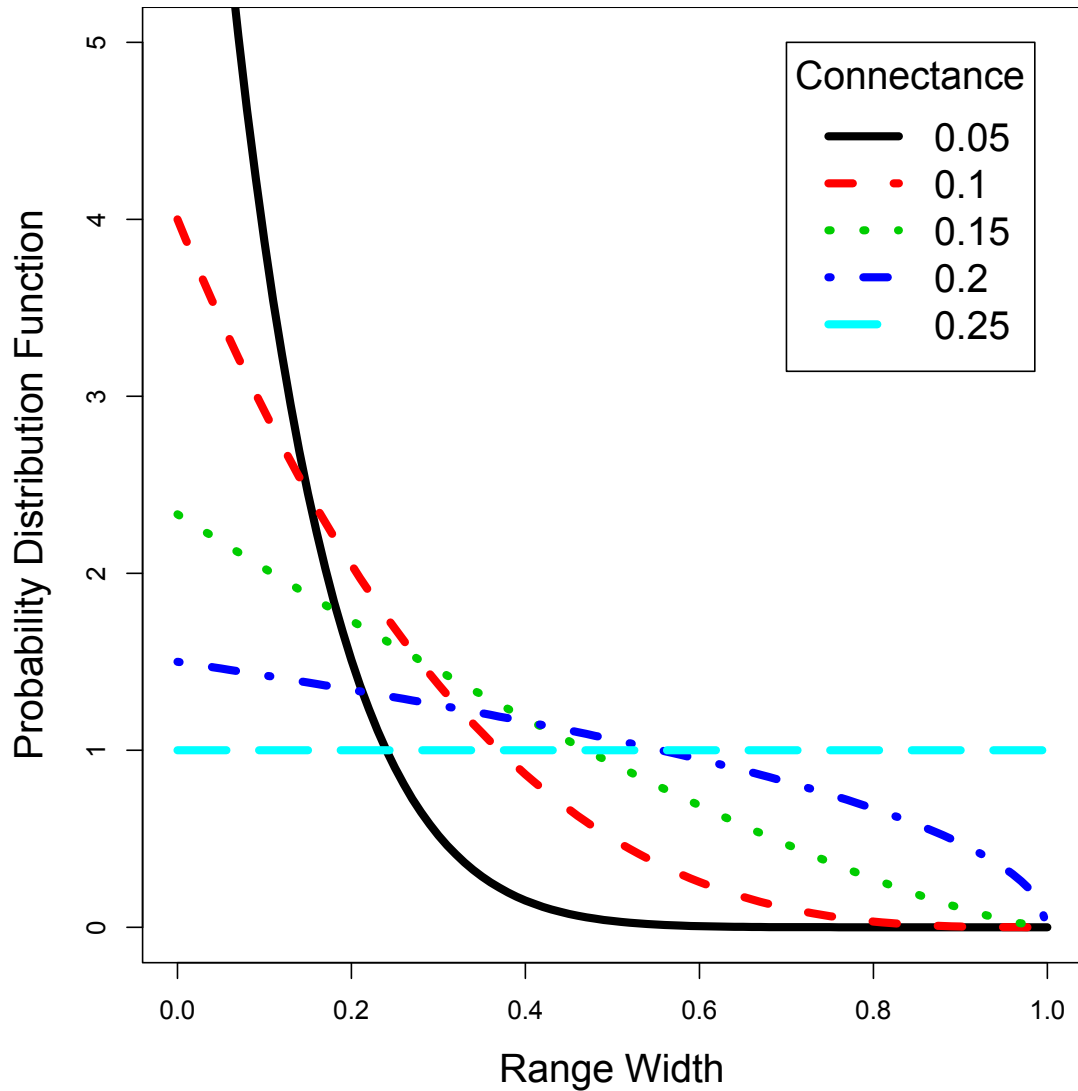


Figure 2. Example beta probability distribution functions for various levels of web connectance with $\alpha = 1$.

To determine the trophic level at which each species preys on other species, we assume that organisms mostly consume prey with smaller niche values than themselves, and that if they do eat species with a larger niche value, no more than half of their diet has a larger niche value. This reflects the non-strictly hierarchical nature of real food webs. Beyond these two rules, we assume they have no other innate

preferences. Thus, we can centre their predation range using a uniform distribution, limited only by the above assumptions ($c_i \in U\left(\frac{r_i}{2}, n_i\right)$), where c_i is the centre of their dietary range. Species are considered non-discriminatory beyond this such that they prey on all species within their dietary range $\left[c_i - \frac{r_i}{2}, c_i + \frac{r_i}{2}\right]$.

Matrices are a convenient and powerful way of compressing food web information (Dunne 2006). We create a matrix, $A_{S \times S}$, in which rows represent predators, columns represent prey, and element are assigned as:

$$a_{ij} = \begin{cases} 1, & \text{if predator } i \text{ eats prey } j \\ 0, & \text{if species } i \text{ does not eat species } j \end{cases} \quad (2)$$

$$= \begin{cases} 1, & c_i - \frac{r_i}{2} \leq n_j \leq c_i + \frac{r_i}{2} \\ 0, & \text{otherwise.} \end{cases}$$

2.2 Discarding Webs

Webs are discarded if they fail to satisfy certain requirements. They must represent biologically realistic webs, so (i) they must not have isolated species that are neither predator or prey, and (ii) every species must have an autotroph in its food chain. They should also (iii) be connected, which ensures that our food web is not composed of several smaller, distinct food webs. We also confirm that (iv) the generated web exhibits our desired level of connectance.

2.3 Calculating Trophic Level

Once a food web has been created, the question arises as to which type of species were created: autotrophs, invertebrates, or fish. Spotting the autotrophs is trivial; they are species that have no prey. The more complicated task is distinguishing between invertebrates and fish. A natural means of classifying organisms would be through their diet. In aquatic communities, an herbivore is more likely to be an

invertebrate, while a carnivore is more likely to be a fish (Romanuk et al. 2011).

Using trophic levels can be thought of as the iterative version of this process.

There are several ways of defining trophic position. Following Williams and Martinez (2000, 2004a), we use the short-weighted trophic position (T), which is the average of two other trophic metrics; the shortest trophic level (T1) and the prey-averaged trophic position (T2):

$$T_i = \frac{T1_i + T2_i}{2}, \forall \text{ species } i.$$

The resulting trophic metric proves to be a better estimator of trophic position than either individually (Williams and Martinez 2000; Carscallen et al. 2012). Autotrophs are assigned a trophic position of 1 in every trophic metric that we use. The shortest trophic level (T1), as shown in Figure 3a, is defined as the shortest path to a basal species plus 1:

$$T1_i = 1 + \min_{j \in \{j | a_{ij}=1\}} T1_j$$

where a_{ij} is a binary element from the species connection matrix (eq. 2); it is 1 when predator i feeds on prey j , and 0 elsewhere. In practice, we use Dijkstra's shortest path algorithm for directed unweighted graphs (Dijkstra 1959). This method progressively moves up the trophic levels, first identifying all the basal species, and iteratively finding the next level of predators.

Prey-averaged trophic position for species i , as shown in Figure 3b, is 1 plus the average trophic position of all its prey:

$$\begin{aligned} T2_i &= 1 + \sum_{j \in S} a_{ij} \frac{T2_j}{\eta_i} \\ &= 1 + \sum_{j \in S_{\text{prey}, i}} \frac{T2_j}{\eta_i}. \end{aligned} \tag{3}$$

where η_i is the number of prey that species i consumes. We can use a computational shortcut to solve this using our species connection matrix (described in further detail in the Appendix).

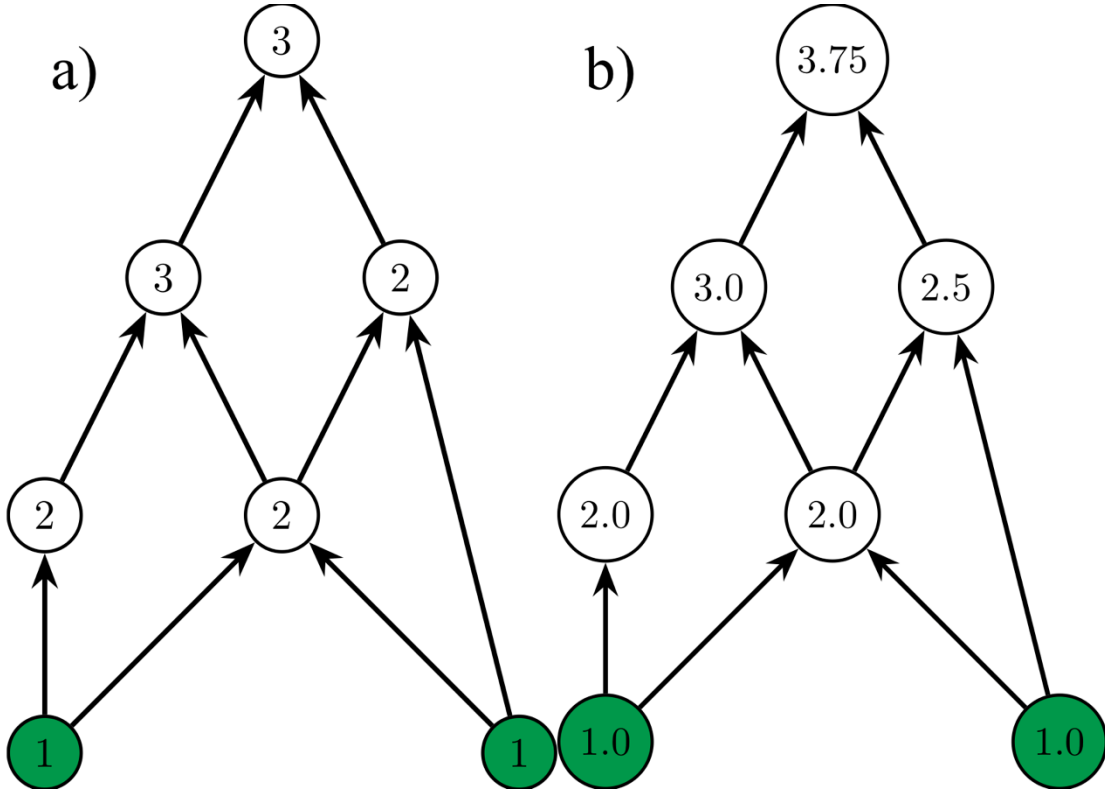


Figure 3. Trophic position for species in an example food web using the shortest trophic level, T1 (a); and prey averaged trophic position, T2 (b). The number in the nodes indicate the trophic position of each species, and directed arrows indicate the flow of energy from prey to predator. Green nodes represent autotrophs. Our model uses the short-weighted trophic position, which is the average of the two metrics.

2.4 Species Identification

As noted above, autotrophs are tautologically defined as any species with no prey:

$$\text{Autotrophs} = \left\{ i \mid \sum_{j \in \mathcal{S}} a_{ij} = 0 \right\}$$

while the remainder of the species are classified as either fish or invertebrates. Our focus is on ecosystems in which fish tend to be large and carnivorous (Bowman and Michaels 1984, Bowman et al. 2000), such that they have high trophic positions. To

simplify our model, we assume that the three most apex predators are fish. This means that the fish in our model are the three species with the highest trophic positions. This might seem like an unrealistic distribution, but we will partially correct for this later when we incorporate additional life stages, which are frequently smaller than invertebrate species. All remaining species are assumed to be invertebrates.

2.5 Estimating Mass

The next step in model development is to determine how efficient species are at processing their food. Here, we use their metabolic rate, an estimate of how energy flows through the system, as in Brose *et al.* 2006b. Rather than using trophic levels to estimate metabolic rates directly, Brose *et al.* uses body weight as a proxy for metabolic rate (2006b). This roundabout method is advantageous in two ways: (i) the relationships for both of these steps are well established, and (ii) we will later use fish body weights to infer life history properties.

Allometric properties are fundamentally important in our model. We want to establish the weight relationships between each predator and its prey. Invertebrates typically eat species of a similar body size, while fish tend to predate on much smaller prey. We use a lognormal distribution to establish the predator-prey body mass ratios (Z). The mean (m) values (variance v in parentheses) of Z for autotrophs, fish, and other species were 1(0), 5000(100), and 100(100), respectively, based on the following equations:

$$\mu = \log\left(\frac{m^2}{\sqrt{v + m^2}}\right)$$

$$\sigma = \sqrt{\log\left(\frac{v}{m^2} + 1\right)}$$

We use this distribution because most biological traits are lognormally distributed (Magurran 1988; Limpert *et al.* 2001).

We now have enough information to determine how much each species weighs, relative to the basal species, since we know what each species eats, and how much larger they are than their prey. The simplest approximation for body mass assumes that everything in a species food chain has the same predator-prey body mass ratios, such that body mass is a simple function of trophic level:

$$\text{Mass} = Z^{T-1}$$

We subtract 1 from the trophic level to exclude basal species from the calculation, as we are calculating the size relationship between species and the autotrophs.

The allometric ratios can be incorporated directly into the calculations for trophic level. Instead of assuming that everything in a species food chain has the same allometric ratio, we can go through each link, and scale the body mass by the correct allometric ratio. This method reduces apex predator's estimated body mass by several orders of magnitude to a more realistic weight. The first step is to disentangle the two different trophic position components:

$$\begin{aligned} M &= Z^T \\ &= Z^{\frac{T_1+T_2}{2}} \\ &= \sqrt{Z^{T_1}Z^{T_2}} \end{aligned}$$

The first component is the mass calculation associated with the shortest trophic level (T1). This can be thought of as finding the smallest prey that a predator eats and modifying the size ratio between the two so that the difference is less extreme. We can replace it with the smallest prey consumed by species *i*. However, since allometric ratios have similar orders of magnitude, this metric will be predominantly determined by trophic level. We can simplify our equations by finding the smallest prey among the prey with the shortest trophic levels. Thus, this calculation of body mass for species *i* is just its allometric ratio times the weight of its smallest prey in a shortest distance path:

$$m1_i = Z_i \times \min_j m1_j \quad \text{for } \{j | j \in S_{\text{prey } i} \text{ and } T1_j = T1_i - 1\}$$

We use a variation of the Floyd-Warshall algorithm to obtain the shortest multiplicative distance.

The second mass component is calculated using the prey-averaged trophic position (Levine 1980). This scales a species weight by its entire diet such that body mass, calculated using prey averaged trophic position, for species i , is:

$$m2_i = \prod_{j=1}^S Z_j^{c_{ij}}$$

where c_{ij} is an element of the matrix $C = (I - Q)^{-1}$ from the calculations for prey averaged trophic position, S is the number of species, and Z_j is the allometric ratio for species j . (The full proof can be found in the Appendix.)

2.6 Metabolic Rates

Fish weight is of importance not simply because of dietary shifts but because metabolic rate per unit mass decreases with size. A school of large fish is more efficient at processing food than a school of small fish with the same biomass. In theory this means that an ecosystem would be able to support a larger biomass of fish if the fish were larger.

Kleiber's Law states that metabolic rates increase at a slower rate than body mass (Kleiber 1975). While this law has been revised and modified many times, the underlying principle has held true (Smil 2000; Ballesteros et al. 2014). A predator may be 100 times larger than its prey, but its metabolic rate is only 75 times that of its prey. Yodzis & Innes (1992) took advantage of this relationship to approximate how efficient our hypothetical organisms are at converting energy from their food sources (Williams et al. 2007, Brose 2008).

The metabolic rate (x_i) per unit of body weight (M) is:

$$x_i = \begin{cases} 0, & \text{for autotrophs} \\ 0.314M^{-0.15}, & \text{for invertebrates} \\ 0.88M^{-0.11}, & \text{for fish} \end{cases} \quad (4)$$

2.7 New Life Stages

There are two key traits of new life history stages that will affect the simulation: how they fit into the food web and their metabolic rate. Everything else that we do to characterize these additional life stages is motivated by finding these two elements. For instance, body size in itself is not used to parameterize the time series simulation; it is merely a convenient stepping stone to find more important life history traits. But like most indirect solutions, each step will add noise to the model, and the cumulative noise has potential to spiral uncontrollably. We use a deterministic algorithm to find the weight for new life stages. From their weight, we can approximate their niche index so that we can fit them into the food web and their metabolic rates.

We assign weights to three new, younger life stages ($t = 0,1,2$) with a von Bertalanffy isometric growth curve (Pauly 1980). Adults retain the original weight (W_{max}) we assigned to each species, and we assume that is the age ($t_{max} = 3$) and weight of maximum yield per recruit. The curvature of the von Bertalanffy curve is set as $K = \frac{3}{t_{max}}$ (Froese and Binohlan 2000), and we assume the adults reach $\frac{W_{max}}{W_{inf}} = 0.9$ of their asymptotic weight.

$$W_t = W_{\infty}(1 - e^{-K(t-t_0)})^3$$

Ecosystem dynamics can be described with ordinary differential equations, which we use to simulate the biomass of each species in the ecosystem. We modified

the ATN model (Williams & Martinez 2004b, Williams et al 2007) to accommodate life history structure. The following equations from the ATN model show the growth for autotrophs (equation 5) and predators (equation 6) during the growing season:

$$\dot{B}_i = \overbrace{r_i \left(1 - \sum_{j \in \text{Autotrophs}} \frac{B_j}{K} \right) B_i}^{\text{Intrinsic Growth}} - \overbrace{\sum_{j \in \text{Predators}} x_j y_{ji} B_j \frac{F_{ji}}{e_{ji}}}^{\text{Loss to Grazing}} \quad (5)$$

$$\dot{B}_i = \underbrace{-f_m x_i B_i}_{\text{Metabolic Loss}} + \underbrace{\sum_{j \in \text{Prey}} f_a x_i y_{ij} B_j F_{ij}}_{\text{Dietary Intake}} - \underbrace{\sum_{j \in \text{Predators}} x_j y_{ji} B_j \frac{F_{ji}}{e_{ji}}}_{\text{Loss to Predation}} \quad (6)$$

where r_i is the intrinsic growth rate for autotroph i , K is the carrying capacity, x_i is the metabolic rate (eq. 4), y_{ij} is predator i 's maximum consumption rate for prey j , e_{ij} is the assimilation efficiency for i eating j , f_m is the fraction of assimilated carbon lost for maintenance, and f_a is the fraction of assimilated carbon that contributes to growth. F_{ij} is the normalized functional response:

$$F_{ij} = \frac{\omega_{ij} B_j^h}{B_{0ij}^h + \sum_{k=1}^S a_{kj} c_{kj} p_{ik} B_k B_{0kj}^h + \sum_{k=1}^S \omega_{ik} B_k^h}$$

$$\omega_{ij} = \frac{a_{ij}}{\eta_i} = \frac{a_{ij}}{\sum_{j=1}^S a_{ij}}$$

where ω_{ij} is the relative inverse attack rate of species i on its prey j , and where η_i total number of species i 's prey. h is the Hill exponent, B_{0ij} is the half saturation density for i eating j , c_{kj} is the predator interference of species k eating j , and p_{ik} is the fraction of i 's prey that it shares in common with k . The values for these parameters are shown in Table 1 and Figure 4.

Table 1. Model parameters.

Variable	Description	Value	Unit	Reference
S	Number of species in original niche web	30	-	Martinez <i>et al.</i> 2012
C	Connectance	0.15	-	Martinez <i>et al.</i> 2012
K	Autotroph carrying capacity	540	$\mu\text{gC}/L$	Boit <i>et al.</i> 2012; Martinez <i>et al.</i> 2012
r	Autotroph intrinsic growth rate	$r \sim N(0.9, 0.2)$ $r \in (0.6, 1.2)$	d^{-1}	
y_{ij}	Maximum consumption rate of predator i for prey j	10	d^{-1}	Boit <i>et al.</i> 2012
e_{ij}	Assimilation efficiency for i eating j	$\begin{cases} 0.45, & j \text{ is an autotroph} \\ 0.85, & \text{otherwise} \end{cases}$	-	Brose <i>et al.</i> 2006b
h	Hill Exponent	1.2	-	
f_a	fraction of assimilated carbon that contributes to growth	0.4		
f_m	fraction of assimilated carbon lost for maintenance	0.1		

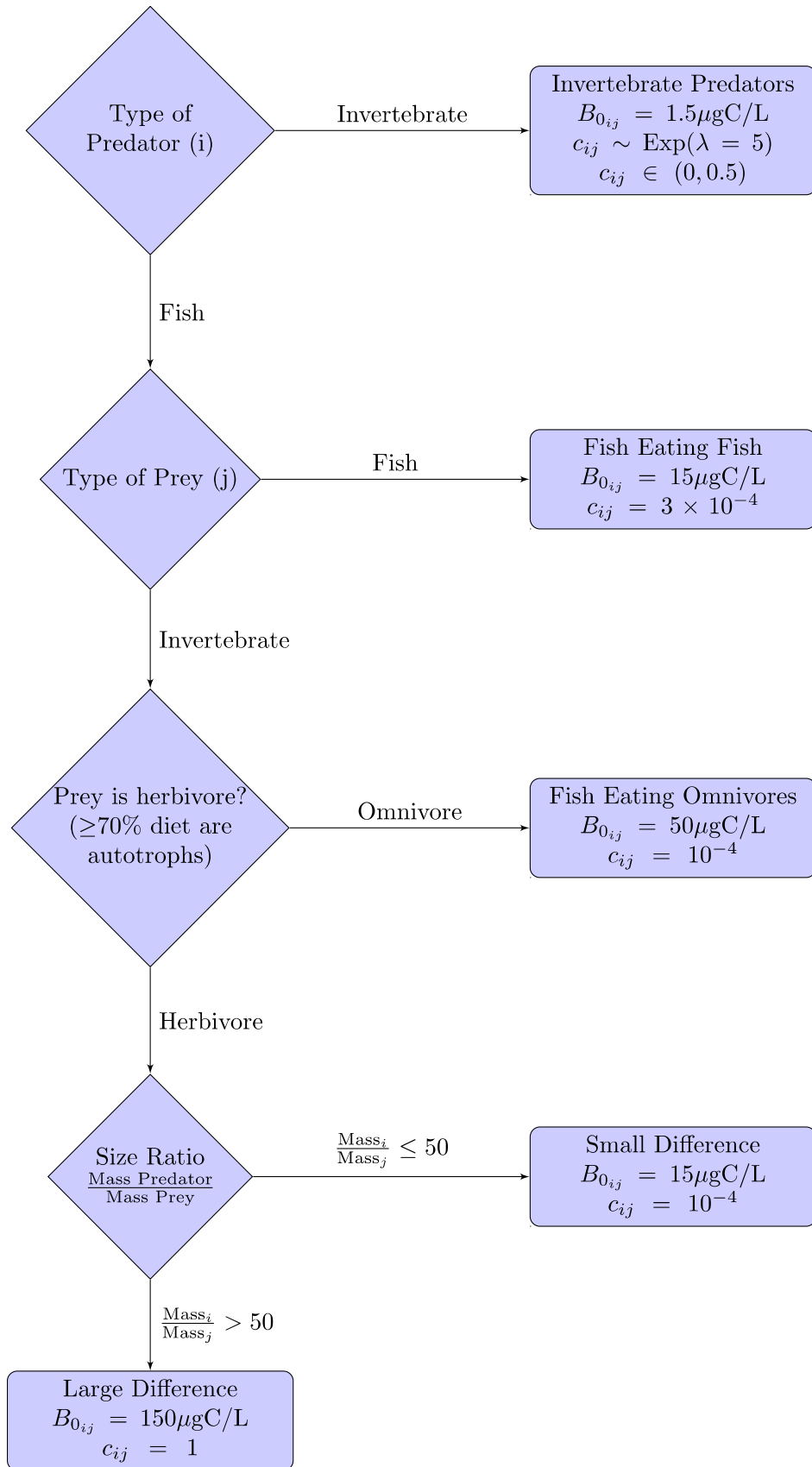


Figure 4. The half saturation constants ($B_{0_{ij}}$) and competition coefficients (c_{ij}) for predator i eating prey j . Figure and constants reproduced from Tonin (2011).

At the end of each growth season, the Ordinary Differential Equation (ODE) is paused so that fish may mature and reproduce. The cumulative growth dedicated to reproduction is also passed along to offspring through the second term of this equation, while the first term forces 50% of adult biomass to become offspring and life stages to mature. The biomass (B_i) shifts between life stages according to this Leslie matrix:

$$\begin{pmatrix} \dot{B}_i \\ \dot{B}_{i+1} \\ \dot{B}_{i+2} \\ \dot{B}_{i+3} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{pmatrix} \begin{pmatrix} B_i \\ B_{i+1} \\ B_{i+2} \\ B_{i+3} \end{pmatrix}$$

2.8 Simulation Design And Analyses

We investigated the model through systematic simulations to: (1) determine how inclusion of fish life-history structure affects the food web, its structure, dynamics, and stability; and (2) investigate how alternative fish life-history strategies are associated with various food-web properties. The addition of life-history structure for fishes changes multiple features of the food web. Introduction of life-history stages involves the addition of new nodes and feeding links to the web; life-history dynamics (growth from one life-history stage to the next) alters the ways in which biomass is transferred within the food web.

To tease apart the relative roles of these components involved with the life-history structures, we run 3 sets of simulations (hereafter denoted as ‘model types’). The first model type comprises an ‘original’ or baseline web that does not include life-history stages within species. That is, each species, including fish, is described through one single node in the food web. Model type 2 incorporates unlinked life-history stages within each fish species. That is, each fish species is partitioned into life-history stages, but these stages are not linked with one another through Leslie

matrices. The new fish life stages are independent of each other and biomass does not grow from one stage to another. In the ATN modelling sense, they can be considered as new species. While this model type is not biologically realistic, it is crucial for disentangling the effects of adding new nodes to the food web from the effect of life-history dynamics. Model type 3 is an ATN model that incorporates life-history stages that are linked to one another within each species.

To compare the three model types, we begin the simulations (500 for each model type) with the same initial conditions. In each simulation, the food web is allowed to stabilize for 200 years, after which the food web is either accepted or rejected, based on the rules detailed below. The dynamics of the food webs are then investigated across another 20-year period. Each year consists of 100 simulation time steps, representing a 100-day growing season. Because our objective is to study the impact of fish life-history stages, we choose amongst the stabilized food webs only those that contain at least one fish species or at least one fish life-history stage (in model type 2). Life stages become extinct if their biomass is lower than $10^{-6}\mu\text{gCL}$, although fish species can be revitalized from the maturation of other life stages.

We initially conducted a preliminary analysis on the probability of fish extinctions for each model type. For this preliminary analysis, we discarded only those food webs for which all fish became extinct. The remaining analyses were subjected to a more stringent constraint; at least one fish species must have persisted in every simulation run for a given model type for the web to be included. We used R version 3.3.2 (R Core Team, 2016) for all analyses, and the R library tidyverse (Wickham 2017). We modified the ATN model by Tonin (2011), and we run it with MATLAB version 2016b (The MathWorks).

Chapter 3: Results

3.1 Model Realism

One means of assessing the biological realism of the model was to examine the degree to which the model produced biologically realistic results. In this regard, our model produced realistic von Bertalanffy growth curves (Figure 5). Mass is incomparable across simulations. However, fish species within a single simulation tended to be in the same size range, as the weight ranges for fish species often overlap (Figure 5). The youngest life stage of the largest fish species was smaller than the oldest life stage of the smallest fish in 69.6% percent of the simulations.

Given that we are using an allometric trophic network model, mass is unitless, such that the only important characteristic is the relative ratio of predator to prey body mass within the same model. The growth curves for any given species were also realistic, as we defined the curve to follow a von Bertalanffy growth function (Figure 6a). The model produced fish species with realistic allometric ratios (Figure 6b), and fish extinctions were equally probable across the lognormal distribution of allometric ratios, such that none of our specific models favoured fish differentially by their body mass.

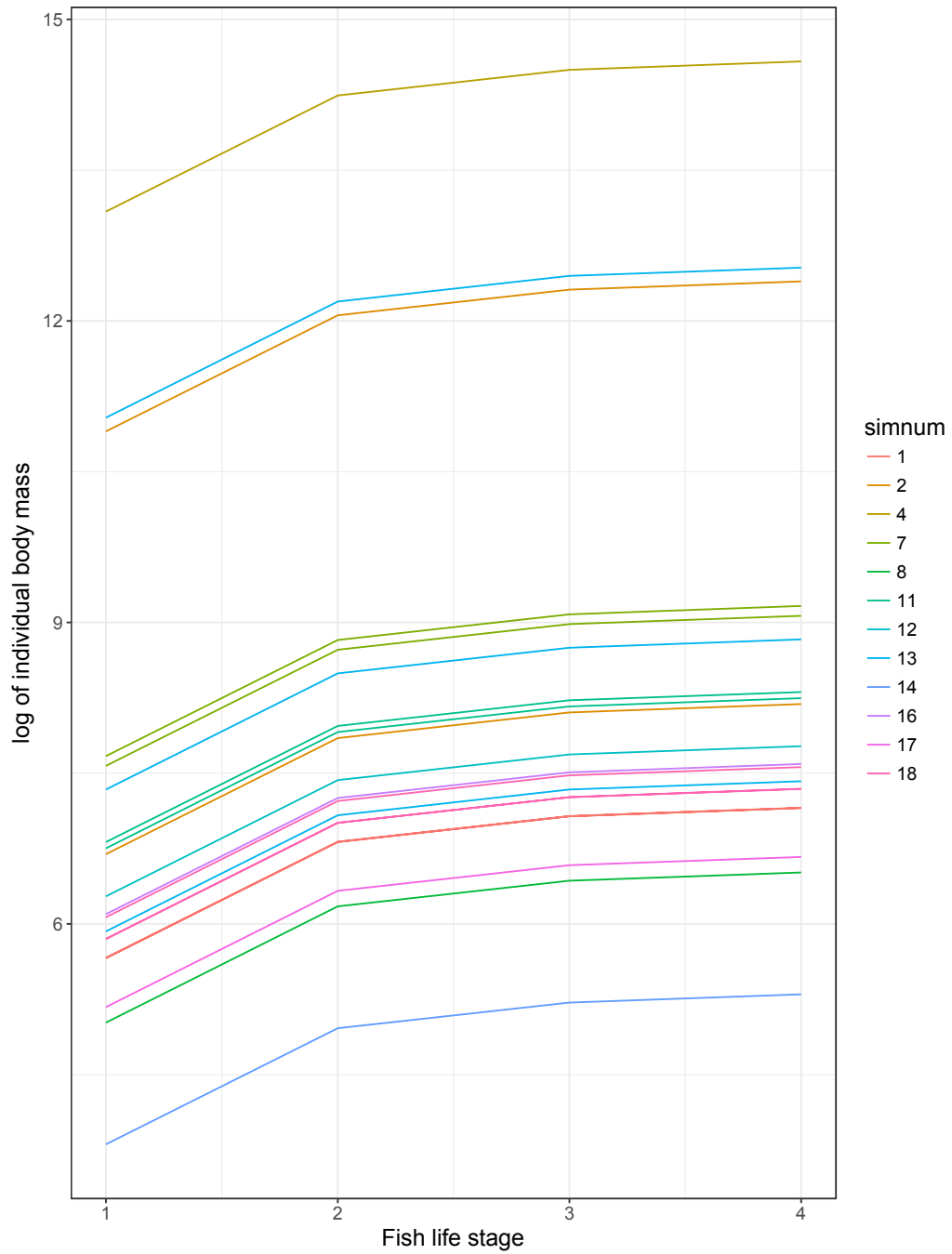


Figure 5. Von Bertalanffy growth curves for surviving fish in several simulated food webs. Each colour represents a different food web simulation ('simnum'). Each species has four life stages.

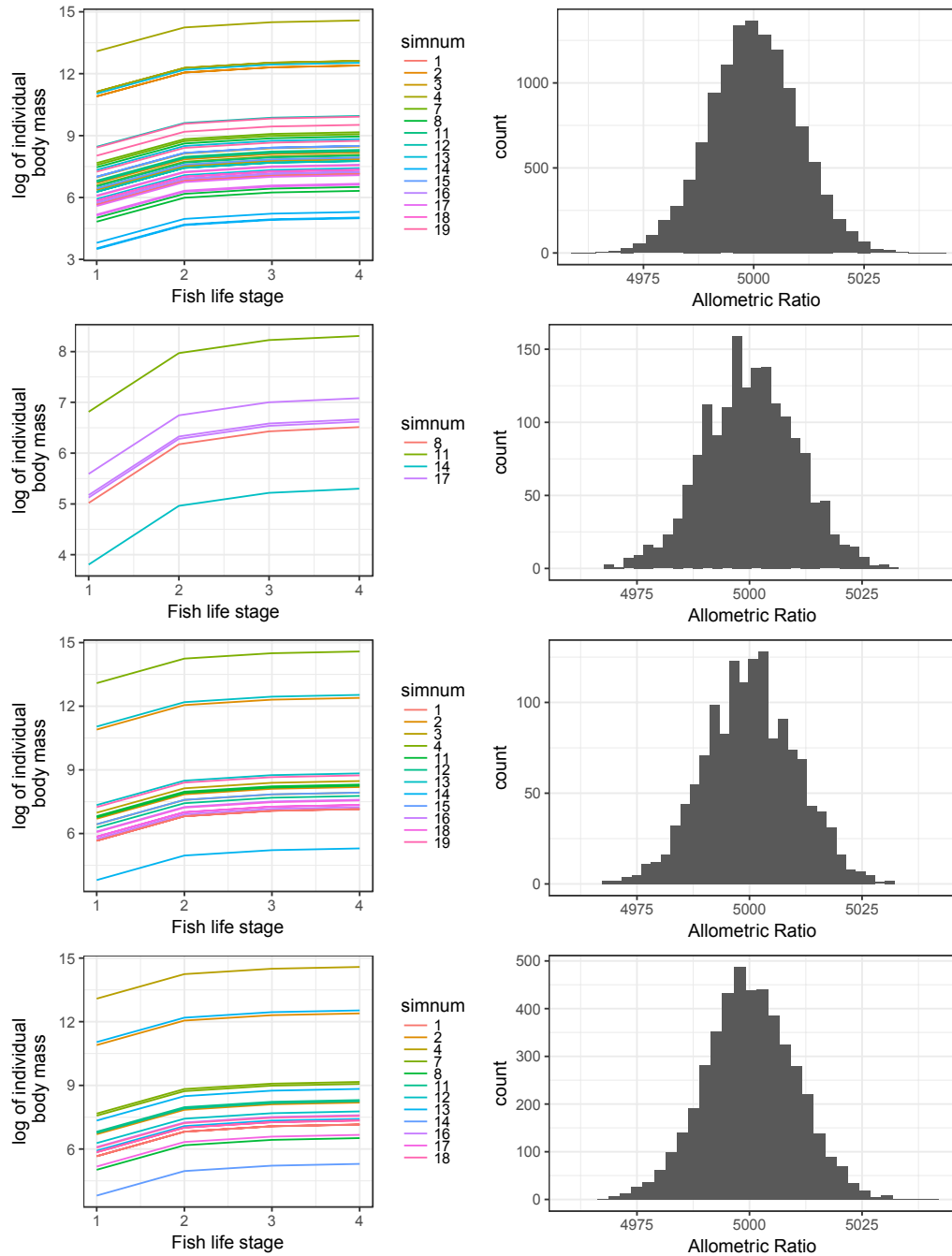


Figure 6. Life history growth curves and associated histograms of the allometric (predator:prey body mass) ratios for the four adult fish life stages. The rows, from top to bottom, show a) the initial ecosystem, including all species that go to extinction, and the surviving fish species in b) the original model, c) the extended model, and d) the linked model.

3.2 General Simulation Outputs

A key criterion for the initial part of the analysis was to have the generic model achieve stability in overall fish biomass. Most (80.2%) of the simulations met this criterion, insofar as fish biomass stabilized in at least one of the experiments. A secondary criterion was that at least one fish species must achieve stability in each of the specific models; 24.3% of the simulations met this second criterion. An illustrative time series of the simulation of a food web that eventually stabilized is shown in Figure 7. This time series shows annual recordings of the biomass for the three fish species, into four life stages, and the total biomass of all other species in the ecosystem. Given that most simulations stabilized within 200 years, the initial 200 years were discarded and the remaining 20 years used for analysis.

Neither the CV for total ecosystem biomass (Figure 8a) or total fish biomass (Figure 8b) differed between the three model types. This result is supported by the frequency of the consecutive number of surviving fish species in each model (Figure 9). The model types that included new life stages were more likely to have at least one fish species survive, as well as having every fish species survive. The difference between the linked model (model type 3) and unlinked model (model type 2) is more subtle. Linking the life stages seems to drive an “all or nothing” outcome; either all fish species survive or they all become extinct. The unlinked model seems to have a more intermediate outcome, while linking the life histories seems to steepen the probability of consecutive extinctions.

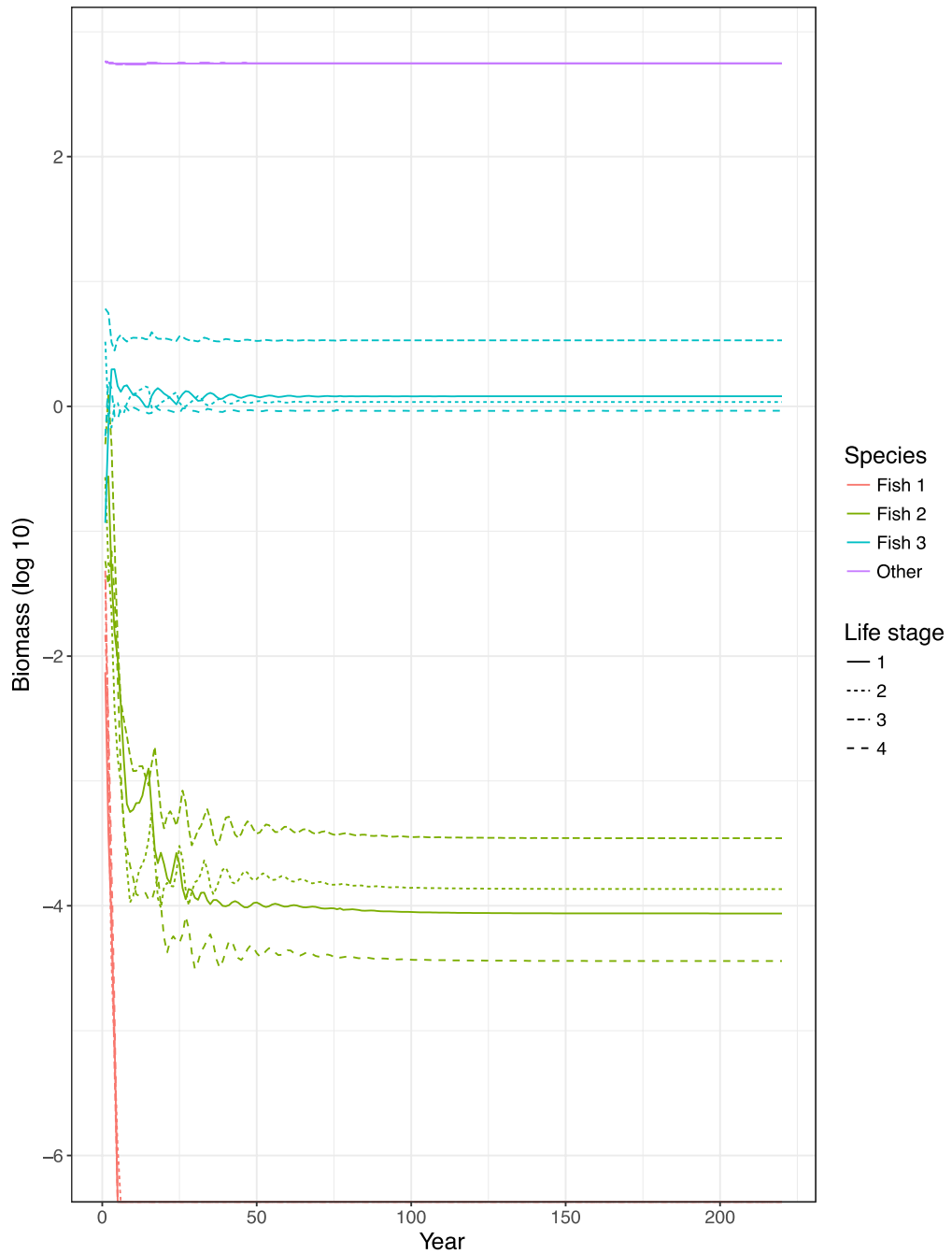


Figure 7. A time series of the biomass recorded at the end of each year for a linked model. The three fish species are represented with red, green, and turquoise lines, while the cumulative biomass of the rest of the ecosystem is shown as purple. Life stages are represented with different dashed lines.

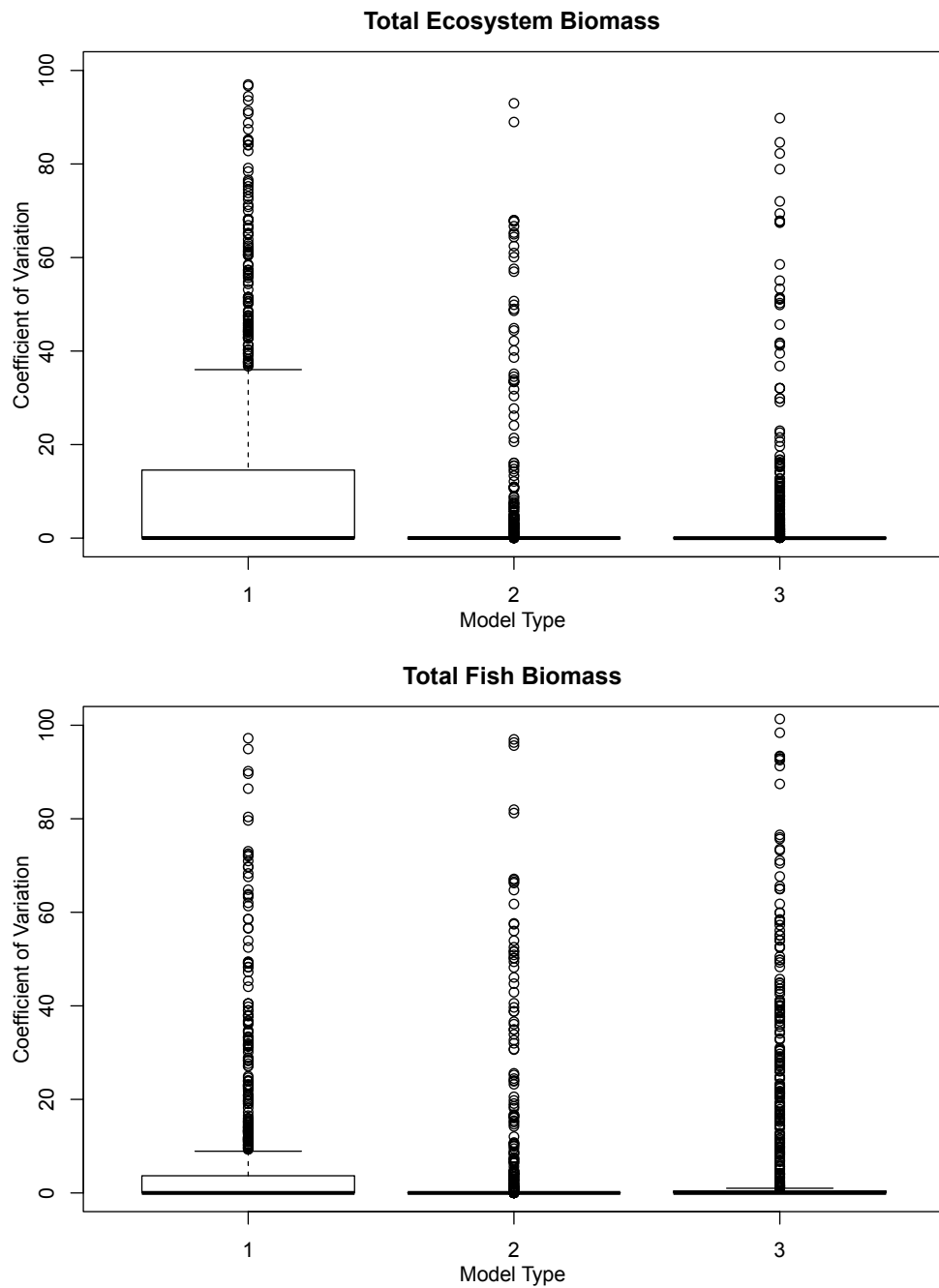


Figure 8. Boxplots of the coefficient of variation (CV) of the (a) total ecosystem biomass and (b) total fish biomass for each model type (CV's greater than 100 are not shown for clarity).

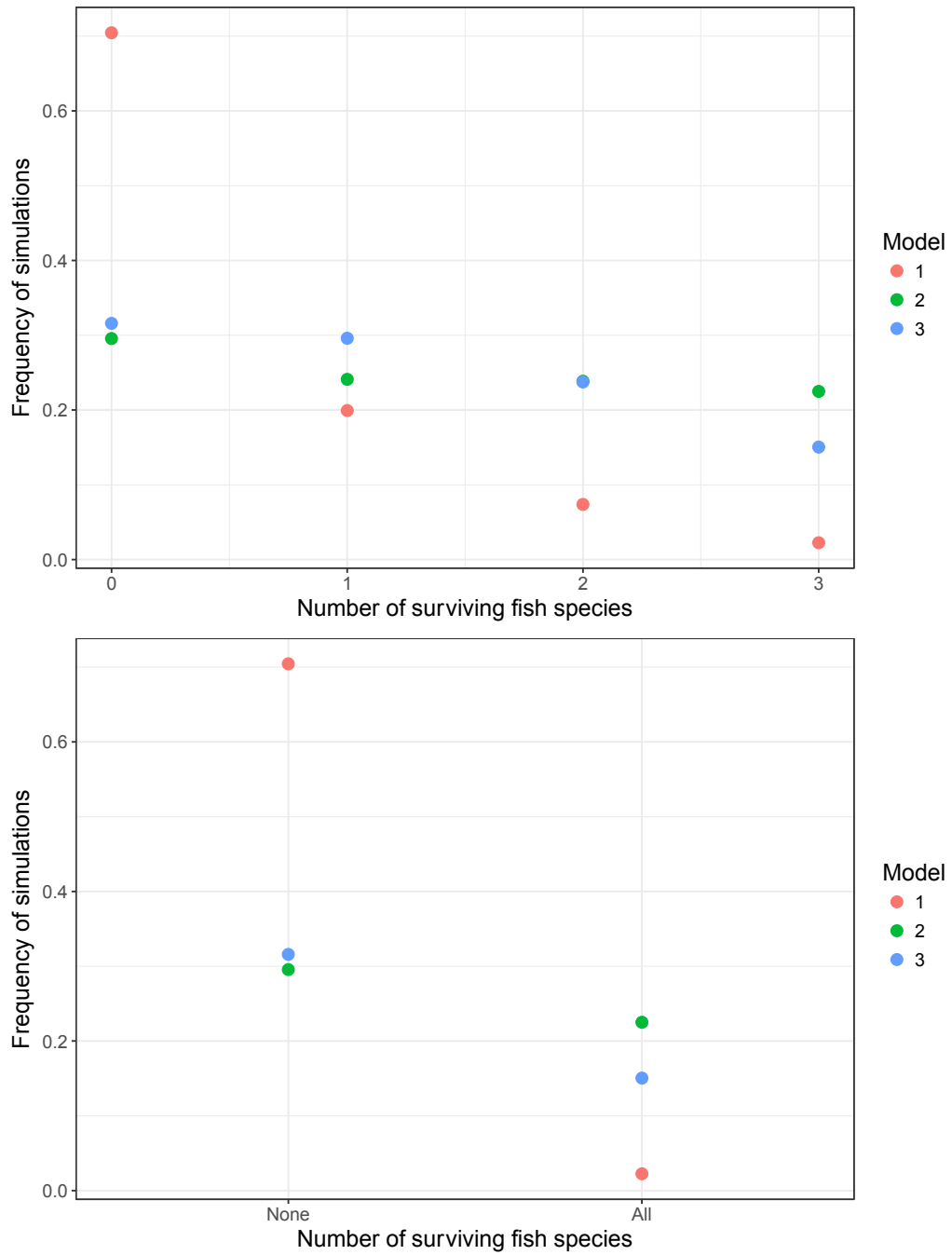


Figure 9. The frequency of simulations with a) 0, 1, 2, or 3 surviving fish species, and b) or no surviving fish versus all fish surviving, shown for each model. The different colours indicate each model type: 1) The original ATN model (red), 2) Extended unlinked model (green), and 3) the linked model (blue).

3.3 Output For The Linked Model

Simulation outputs are illustrated for the fully linked model (type 3) (Figure 10-Figure 12). The allometric ratio of surviving fish species is positively associated with mean fish biomass ($t=3.15$, $df=969$, $p=0.002$; Figure 10b) and negatively linked with the CV of mean total ecosystem biomass ($t=-2.55$, $df=969$, $p=0.011$; Figure 10c). This correlation is reversed in model 1 ($t=2.21$, $df=969$, $p=0.027$), but no trends were found in model 2 ($t=-0.52$, $df=969$, $p=0.601$).

The allometric ratio was not correlated with either mean total ecosystem biomass (Figure 10a) or the CV of fish biomass (Figure 10d). Fish size is positively associated with a higher total mean ecosystem biomass ($t=5.24$, $df=969$, $p<0.001$; Figure 11a) but is not correlated with fish biomass or the CV's in biomass (Figure 11b-d). Associations between the mean and CV of ecosystem and fish biomass and asymptotic individual body mass are presented in Figure 12. Larger fish species tend to increase mean ecosystem biomass across all 3 models ($t=8.3$, $df=1871$, $p<0.001$; Figure 12a). Normality for each variable was confirmed using qqplots.

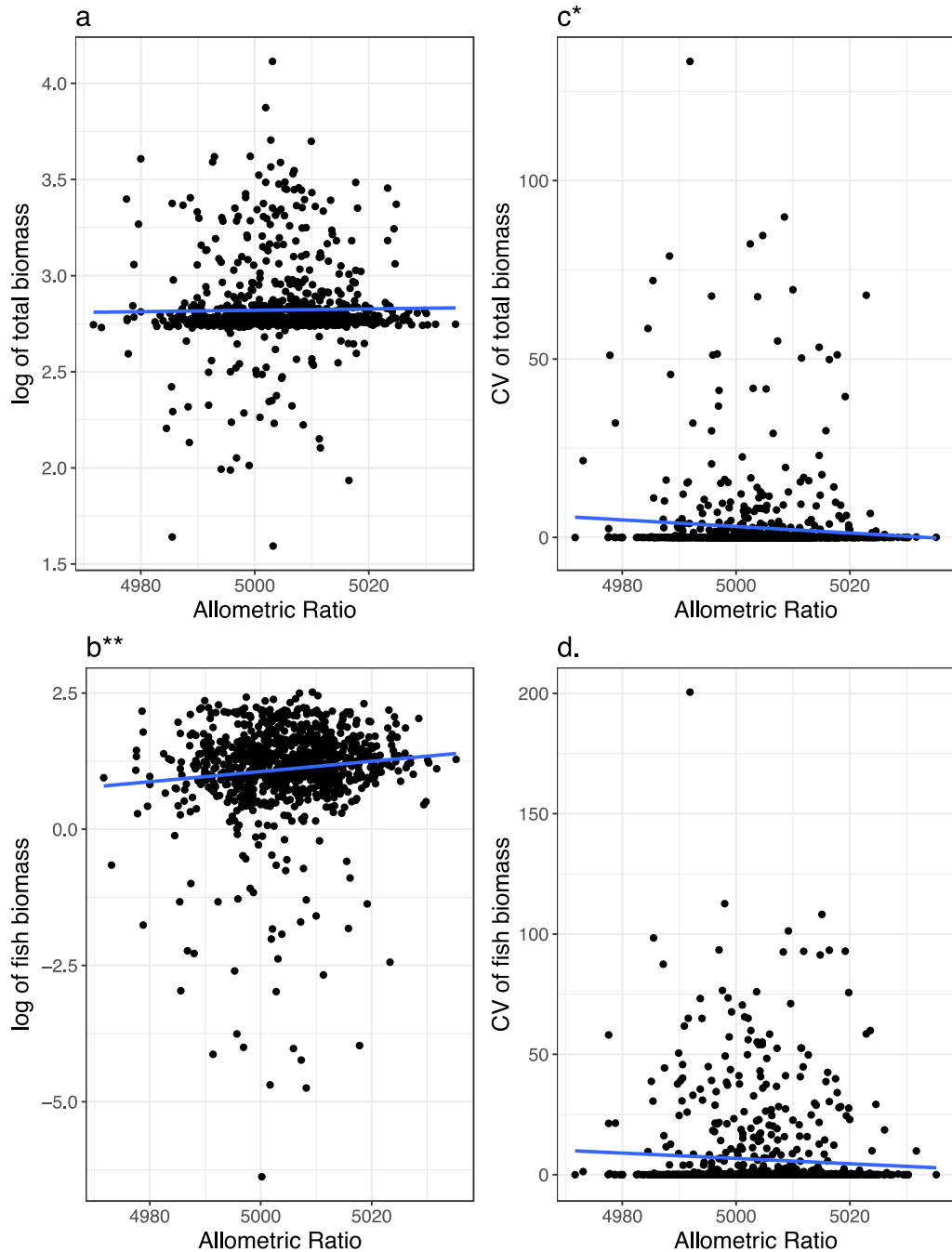


Figure 10. Mean and CV of biomass as a function of the allometric (predator:prey body mass) ratio of the largest surviving fish species for all simulations. Panels (a) and (b) show the mean ecosystem biomass and mean fish biomass of the 971 surviving fish species, respectively (N=971 fish species across all simulations). Panels (c) and (d) show their respective CV's. The blue lines represent linear regressions. These are significant for the log of fish biomass (panel b; $t=3.15$, $df=969$, $p=0.002$) and the CV of the total ecosystem biomass (panel c; $t=-2.55$, $df=969$, $p=0.011$).

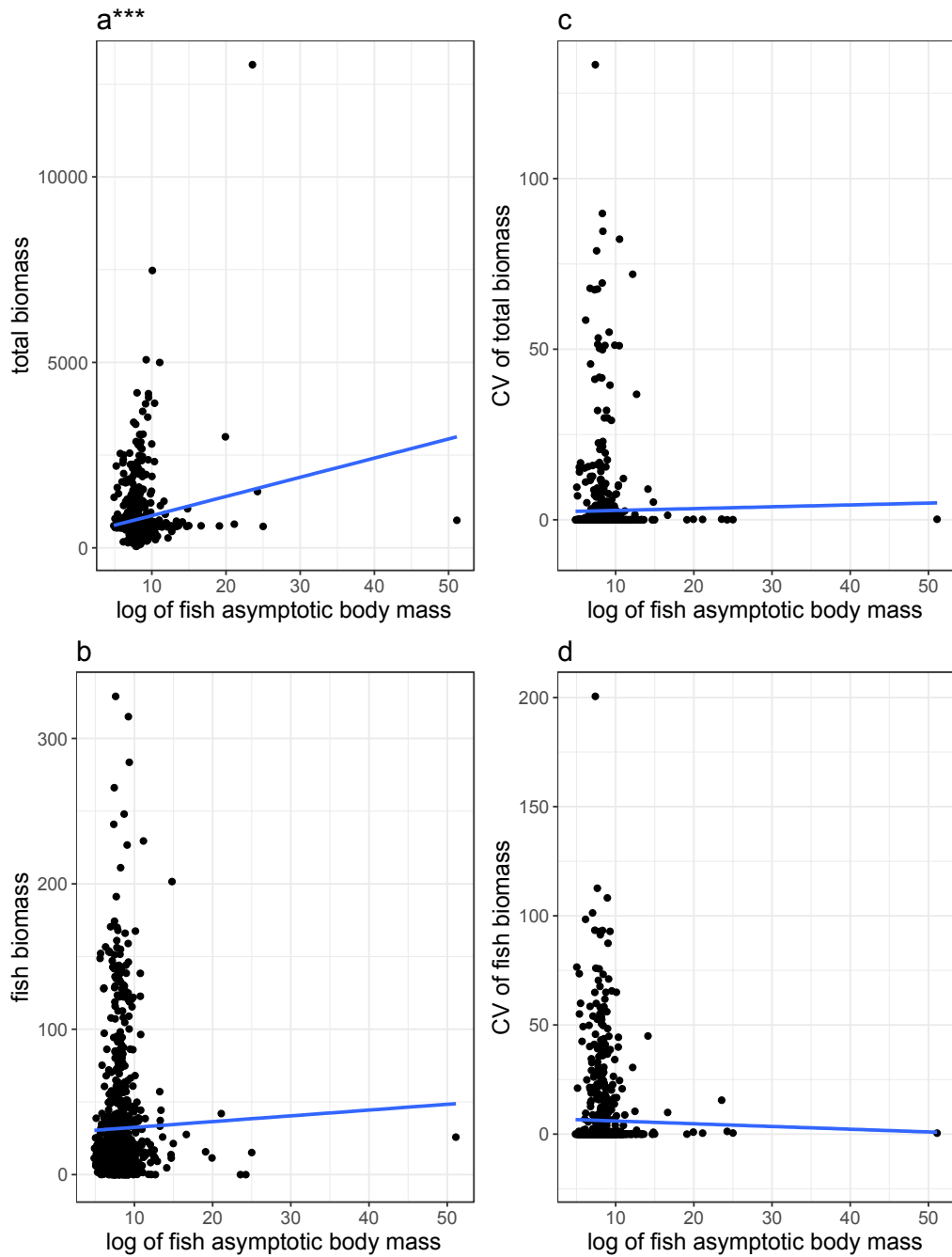


Figure 11. Mean and CV of biomass as a function of the logarithm of the asymptotic individual body mass for the largest surviving fish species. Panels (a) and (b) show the mean ecosystem biomass and mean biomass of the 971 fish species, respectively (N=971 fish species across all simulations). Panels (c) and (d) show their respective CV's. The blue lines represent linear regressions. These are significant for the log of the mean ecosystem biomass only (panel a; $t=5.24$, $df=969$, $p<0.001$).

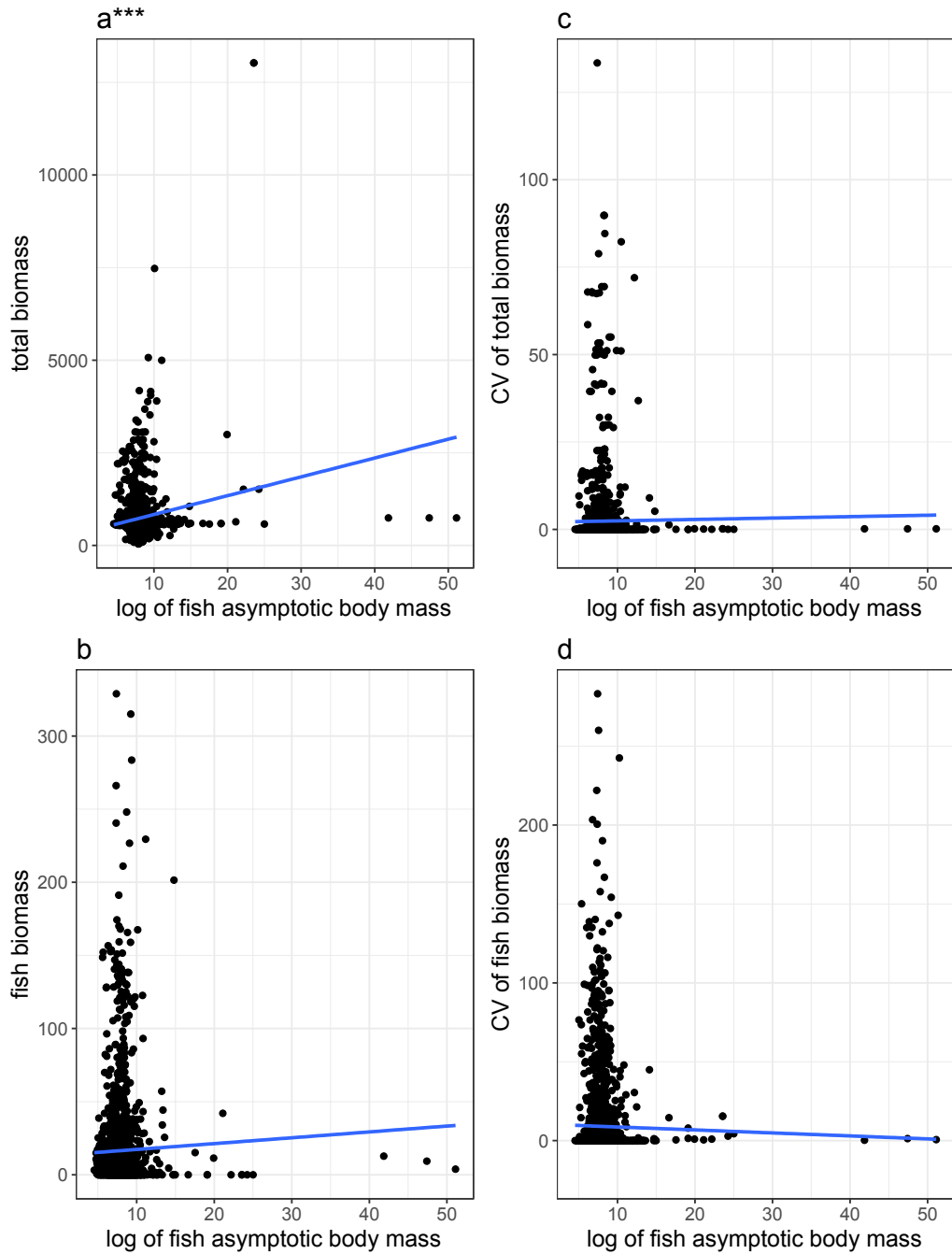


Figure 12. Mean and CV of biomass as a function of the asymptotic individual body mass for each surviving fish species. Panels (a) and (b) show the mean ecosystem biomass and mean biomass of the 971 fish species, respectively (N=971 fish species across all simulations). Panels (c) and (d) show their respective CV's. The blue lines represent linear regressions. These are significant for the log of the mean ecosystem biomass (panel a; $t=8.3$, $df=1871$, $p<0.001$).

Chapter 4: Discussion

The present study extends existing allometric trophic network (ATN) models by incorporating greater life-history complexity. Using Williams and Martinez' (2004b) ATN model as a starting point, we created two additional model formulations. Firstly, we added additional life stages, or nodes, to each species. Secondly, we linked these life stages together into a life history where juveniles mature into adults that then produce offspring. Through this additional complexity, we are able to explore the extent to which this increased biological realism, from a very basic life-history perspective, modifies the output and predictive capacity of traditionally formulated ATN models.

We find that the addition of life-stage complexity significantly influences model outcomes, but that the linking of life stages within each fish species alters the output of the unlinked model only marginally. For example, the addition of life stages reduces variability in total ecosystem biomass, which we interpret as reflecting increased stability. Given that new, unlinked life stages can be treated as new individual species, this finding is essentially equivalent to concluding that ecosystems which support greater numbers of fish species are more stable than ecosystems that support fewer fish species.

In theory, the linking of multiple size-varying life stages should make each species more dependent on a broader range of prey. In a sense, we are creating a bet-hedging scenario by linking all the life stages and by making them less dependent on any one particular prey. But we might also be increasing the extinction probability of a predator species if any one of its life stages becomes non-viable. These non-viable life stages may be partly responsible for why we failed to find a strong effect from linking the life stages together. Perhaps if we ensured life-stage viability by assigning

broader diets to each stage, we might have documented a larger effect of life-stage linkage. The linking of life stages might also alleviate the predator-induced mortality of certain prey species. If a fish predator is comprised of a wide variation of cohort sizes in its life stages, prey for any given life stage may go through phases of intense predation when it is being targeted by the largest cohort followed by a recovery period when the largest cohort is no longer preying on it.

An exploration of the effects of increasing life-history complexity on ecosystems was recently undertaken by Mougi (2017) who undertook simulations in which he assigned a certain proportion of species in an ecosystem a two-stage, rather than a single-stage, life history. He found that inclusion of moderately more complex life histories (two stages rather than one) increased the probability of persistence of complex ecosystems, while it decreased persistence for simpler ecosystems.

Based on the findings of the present study, we hypothesize that most of the effects that Mougi (2017) documented when adding life-history structure might be attributable to an increase in food web size resulting from the addition of non-random nodes, rather than any intrinsic effect of life-history structure. That said, our methods were quite different. We applied an annual Leslie matrix to model growth from one life stage to the next, while Mougi (2017) incorporated a continuous growth model directly into the differential equations. We used 4 life stages for 3 species, while he used 2 life stages for various proportions of the community. In addition, we used an ATN model while Mougi (2017) applied a continuous growth, two-life-stage model.

4.1 Allometric Ratio, Biomass, And Ecosystem Stability

The three model formulations differ in their predictions as to how allometric ratio is related to biomass and ecosystem stability. Across all simulations in models 1

and 3, fish with larger allometric ratios attain higher biomass; model 2 did not yield an association. This apparent link might be attributable to the fact that fish that are much larger than their prey have lower metabolic rates per unit biomass, thus they require less food to sustain them. The simulations in Model 3 produced a positive link between fish allometric ratio and ecosystem stability (we interpret ecosystems with a lower CV in total biomass to reflect greater stability). This is consistent with previous findings that high predator-prey body mass ratios tend to enhance ecosystem stability (Brose et al. 2006b; Kuparinen et al. 2016).

However, we find that model 1 yielded the opposite result: higher fish allometric ratios are associated with less stable ecosystems that exhibit greater fluctuations in total biomass (model 2 revealed no association between allometric ratio and ecosystem stability). If fish allometric ratio truly does affect the CV in total biomass, we might have expected it to also affect fish biomass, but such a link was not evident in our results. Alternatively, the absence of such a link could simply mean that allometric ratio has a higher impact on prey species than predator species, such that invertebrates are impacted more heavily by being preyed on by fish with lower allometric ratios than by the fish species themselves.

All three models were consistent in finding that fish with a larger asymptotic body mass tend to be correlated with a larger total ecosystem biomass, a result that holds true for both the largest fish in the ecosystem and every fish species in the ecosystem.

4.2 Model Considerations

There are merits to our modelling approach, but there are also caveats that warrant future attention. Our application of the von Bertalanffy growth model lends

increased biological realism in terms of body mass and consequently metabolic rate. However, the species all have identical life histories (exactly 4 life stages, identical probabilities of maturity and age-specific fecundity); this may not be an issue, although it might be worth exploring alternative life spans in future model formulations.

It is important to note, however, that when we incorporate these new nodes into the food web, we cannot apply the same methods that we used to generate the original web. This is because the original web generated the nodes and connections first and then assigned species characteristics based on their interactions. When we added new nodes, we reversed this process, such that the new nodes only approximately follow the species interaction patterns articulated by the original ATN web (Williams and Martinez 2000).

We anticipated that some of our simulations would not stabilize, given that we placed minimal constraints on the food webs during the web-creation stage. Thus, some of the webs would invariably end up being completely biologically unrealistic. This process of weeding out unstable webs might seem initially unintuitive, but it does mimic what is observed in nature; natural landscapes are eventually populated by stable ecosystems after a long process of species invasions and extinctions. Regarding species extinctions, if any of the life stages in our model survive, we treat the entire species as having survived. Model 1, having a single life stage per species, is more likely to produce fish extinctions than models 2 or 3, both of which incorporate four life stages per species.

Overall, our model produced relatively ‘noisy’ results, rendering it difficult to discern clear trends in our data. In part, this might have been caused by the variance associated with the model’s parameters. Although a reduction in parameter variances

might limit the range of ecosystems that our model can represent, it might provide clearer results for a subset of ecosystem types. Our model may be unduly sensitive to initial conditions, such that web stabilization web and probability of persistence is more dependent on the initial biomass of each species than the food web structure.

An interesting note is that our model does not selectively remove fishes based on their allometric ratios, meaning that fish are equally likely to survive regardless of their predator:prey body-mass ratios. This might contribute to excessive noise in our model outputs such that we are unable to discern an effect of allometric ratio on fish survival. Whatever the case, it means that our initial distribution of allometric ratio is not substantially disturbed by our simulations, such that all of our models are testing a similar ecosystem. It also means that our models are not differentially selecting for or against any particular body size.

Another caveat might relate to the fact that our measure of allometric ratio is very approximate. Although we use log-normal random distributions to assign ‘ideal’ allometric ratios to all species, the actual allometric ratio is distorted in two ways. Firstly, our ideal allometric ratios are used to establish initial body masses of all species; given that we cannot guarantee a perfect correspondence between allometric ratio and body mass, it will be an imperfect measure. Secondly, the ratio is further disturbed by species extinctions. When prey become extinct, the allometric ratio should ideally be adjusted to reflect this extinction.

To reduce model-output noise, it might be advantageous to approximate allometric ratios after the simulations have been completed, using only extant species. However, this approach might prove difficult to enact in practice. Not only is it computationally challenging, but issues can arise when not all life stages are connected to a basal species. This scenario is theoretically possible in our model.

Although we restrict our initial webs by forcing all nodes to be connected to a basal species, these chains can be broken during the simulations, resulting in life stages that obtain all their biomass growth from previous life stages but have no prey of their own. Under these circumstances, life stages survive solely by relying on a large biomass at the beginning of the year, but do not have any prey themselves.

Our model is severely limited by the amount of stochastic variation in webs produced. Since our model generates random webs using minimal constraints, it generates a lot of variability in outcome of the simulation. At the risk of decreasing generality of our model, it might be helpful to heavily constrain our parameters so that our model produces similarly structured webs with more consistent outcomes. This will be useful in detangling results. Even if we don't constrain our parameters, we could try subsetting our data set to a group of more similar webs. For instance, we could try only looking at webs with large fish species.

4.3 Future Considerations

The results of the present study suggest several avenues of future research. For example, a combination of the approach adopted here with that by Mougi (2017) offers a potentially instructive means of disentangling the effects of increasing life-history complexity in food-web models. There is also considerable scope to examine how increased life-history complexity might affect the influence of fisheries-induced evolution on ecosystems. Kuparinen et al. (2016) found that fisheries-induced evolution can destabilize an entire ecosystem (Lake Constance), with increased temporal fluctuations in fish biomass resonating down to basal species in the food web. Increasing life-history complexity might allow the well-parameterized Lake Constance model to be applied to a broader range of ecosystems.

Cannibalism is characteristic of many fish species, the consumption of conspecific individuals often comprising a sizable percent of the diet (Smith and Reay 1991). The effects of cannibalism on ecosystem stability are not well studied. If we allowed for cannibalism in our model, species would not be as dependent upon individual life stages because stages with less abundant prey would be able to persist by preying on younger life stages. Another consideration is that rare life stages may experience higher levels of predation, although this could probably be mitigated with a predation model that skews diet towards more abundant prey and relaxes predation on rare prey.

Our results suggest that it would be instructive to increase life-history complexity in ecosystem models that account for fisheries-induced evolution, a selection response that primarily affects large adults rather than a more balanced spectrum of life stages. It would be interesting to examine how such size-selective fishing mortality, which would differentially affect some life stages but not others, influences species persistence and ecosystem stability. If adults experience higher mortality, then most of the offspring production would depend on younger, less fecund life stages. Additionally, if adults do not reproduce till the end of the year, as in our model, they will be depleting prey by preying on species that might be more effectively used by younger life stages while failing to contribute significantly to the next generation.

An analytical approach might be enlightening. Our model is essentially a network where the links alternate between two states: a regular food web with weak links and a leslie life history growth matrix with strong and efficient links. Realistically, it would be a more continuous swap between the two matrices, and an even more accurate model would combine the two matrices into a single matrix with

link strength that varies on annual basis (for instance reproduction tends to be seasonal, so the fecundity links should be much stronger around that time). Hence, it would be worthwhile to use an analytical approach for a food web with seasonally variable interaction strength between the nodes.

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Appendix A: Math

A.1 Derivation Of β For The Beta Function

In order to get a beta distribution of the prey range values (r_i), we used a beta distribution with the parameters specified in equation 1. The value for β is set so that the expected value for a species range is the connectance (C):

$$\begin{aligned} C = E(r_i) &= E(n_i x_i) \\ &= E(n_i)E(x_i), \text{ since } x_i \text{ and } n_i \text{ are independent} \\ &= \frac{1}{2}E(x_i), \text{ since } n \sim U(0,1) \\ &= \frac{1}{2} \frac{\alpha}{\alpha + \beta}, \text{ since } x \sim \text{beta}(\alpha, \beta) \\ 2C(\alpha + \beta) &= \alpha \\ 2\beta C &= \alpha - 2\alpha C \\ \beta &= \frac{\alpha(1 - 2C)}{2C}, \text{ and since } \alpha = 1 \\ \beta &= \frac{1 - 2C}{2C} \end{aligned}$$

A.2 Prey-Averaged Trophic Position

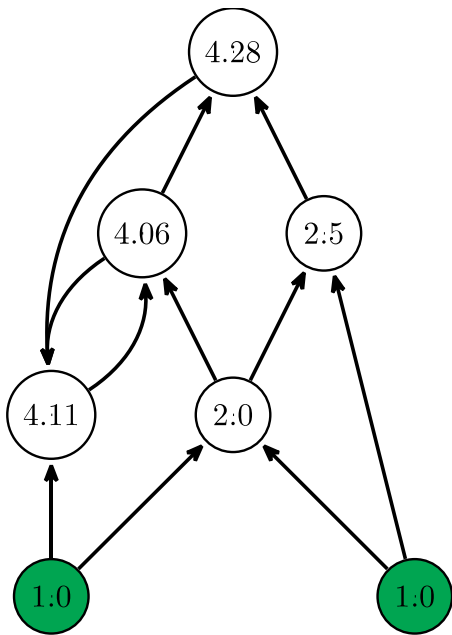
Prey averaged trophic position for a single species can easily be calculated using equation 3 if you have already established the trophic positions of all of its prey, but this is more complicated for webs with loops, as shown in supplementary figure 1. The earlier equation is certainly more intuitive, but for practical purposes I will present an equivalent way of solving for prey averaged trophic position using matrix algebra (Levine, 1980).

The species connection matrix (eq. 2) is the primary way of conveying food web information, but here we will use a transition matrix instead. As you may recall, the connection matrix has simple binary links between species, indicating the presence or absence of predation. Transition matrices, on the other hand, also convey how much a predator relies on each species in its diet.

Each element q_{ij} of the transition matrix, Q , is defined as the fraction that species j consists of in predator i 's diet:

$$q_{ij} = \begin{cases} \text{Fraction of predator } i\text{'s prey that is species } j, & \text{if species } i \text{ has prey;} \\ 0, & \text{if species } i \text{ is an autotroph.} \end{cases}$$

$$= \begin{cases} \frac{a_{ij}}{\sum_{j \in S} a_{ij}}, & \text{if } \sum_{j \in S} a_{ij} \neq 0; \\ 0, & \text{if } \sum_{j \in S} a_{ij} = 0. \end{cases}$$



Supplementary Figure 1. Prey-averaged trophic position (T2) of species in a food web with loops.

Transition matrices (Q) are powerful because they describe how energy flows through a food web. By taking the k th power of the matrix (Q^k), you can determine what proportion of a predator's diet came through exactly k trophic levels from each prey species. In other words, each element b_{ij} of $B=Q^k$ describes how much energy came through a food chain of length k from prey j for predator i . So element c_{ij} in the geometric series

$$C = \sum_{k=0}^{\infty} Q^k = I + Q + Q^2 + Q^3 + \dots$$

describes the average food chain length from prey j to predator i , weighted by its importance to the predator's diet (Orponen, 2005). So the sum of each row is equivalent to our desired prey-averaged trophic position (equation 3).

Conveniently, we can easily rearrange matrix geometric series:

$$(I - Q)^{-1} = I + Q + Q^2 + Q^3 + \dots \quad (7)$$

Which holds provided that $\lim_{k \rightarrow \infty} Q^k = 0$ (Watson, 2015). This is the case if all species have an autotroph in their food chain, so this calculation works for all biologically realistic food webs.

The end result is that we can use the following, computationally efficient, equation to solve for the prey averaged trophic position ($T2_i$) for species i :

$$T2 = \begin{bmatrix} T2_1 \\ T2_2 \\ \vdots \\ T2_S \end{bmatrix} = (I - Q)^{-1} \begin{bmatrix} 1 \\ 1 \\ \vdots \\ 1 \end{bmatrix}$$

A.3 Formal Proof

I will present a proof of the equivalence. See Levine (1980) for an alternative proof.

A.3.1 Proof Of Equation 7

This part of the proof is analogous to the convergence of the geometric series $\frac{1}{1-z} = \sum_{i=0}^{\infty} z^i$, for complex number z with $|z| < 1$ (Watson, 2015). Let:

$$C_k = \sum_{i=0}^k Q^i = I + Q + Q^2 + Q^3 + \dots + Q^k$$

So when you left-multiply by Q :

$$QC_k = \sum_{i=1}^{k+1} Q^i = Q + Q^2 + Q^3 + \dots + Q^k + Q^{k+1}$$

So

$$\begin{aligned} C_k - QC_k &= (I + Q + Q^2 + Q^3 + \dots + Q^k) - (Q + Q^2 + Q^3 + \dots + Q^k + Q^{k+1}) \\ (I - Q)C_k &= I - Q^{k+1} \end{aligned}$$

And similarly, if you right-multiply by Q:

$$C_k(I - Q) = I - Q^{k+1}$$

So if $\lim_{k \rightarrow \infty} Q^{k+1} = 0$, then:

$$\begin{aligned} C(I - Q) &= (I - Q)C = \lim_{k \rightarrow \infty} (I - Q^{k+1}) = I \\ C &= (I - Q)^{-1} \end{aligned}$$

A.3.2 Individual Body Mass

We want to find an equation equivalent to

$$m_2 = Z^{T-1}$$

but where the value of the allometric ratio, Z , is split into components that describe the allometric ratio for each species in a predator's direct or indirect food chain. Since basal species have an allometric ratio of 1, we no longer need to subtract one from the trophic level:

$$\begin{aligned} m_2 &= Z^{T-1} \\ m_{2_i} &= Z_i^{T-1} \\ m_{2_i} &= Z_i^{\sum_{j=1}^S \sum_{k=0}^{\infty} q_{ij}^{(k)}} \\ m_{2_i} &= \prod_{k=0}^{\infty} \prod_{j=1}^S Z_i^{q_{ij}^{(k)}} \end{aligned}$$

Where $q_{ij}^{(k)}$ is the element in the i^{th} row and j^{th} column of the matrix Q^k , the k^{th} power of the transition matrix (Levine 1980).

At this point we want to modify the equation to take into account the allometric ratio of each node that the food path passes through. So we can set the allometric ratio to Z_j instead of Z_i , to reflect the allometric ratio of the prey species rather than the predator:

$$m2_i = \prod_{k=0}^{\infty} \prod_{j=1}^S Z_j^{q_{ij}^{(k)}}$$

$$m2_i = \prod_{j=1}^S Z_j^{\sum_{k=0}^{\infty} q_{ij}^{(k)}}$$

$$m2_i = \prod_{j=1}^S Z_j^{c_{ij}}$$

This is equivalent to the row products of the hadamard power of the matrices:

$$M2 = \text{Row Product} \left[\left(\begin{array}{cccc} Z_1 & Z_2 & \cdots & Z_S \\ Z_1 & Z_2 & \cdots & Z_S \\ \vdots & \vdots & \ddots & \vdots \\ Z_1 & Z_2 & \cdots & Z_S \end{array} \right)^{\circ(l-Q)^{-1}} \right]$$

which is easy to implement in MATLAB.

Appendix B: Code

The following code has been uploaded to DalSpace as electronic supplementary material. Our analysis code was written in R version 3.3.2 (R Core Team, 2016) and the R library tidyverse (Wickham 2017).

B.1 Modified ATN Model

We modified a the ATN model from Tonin (2011) by extending it to include life history structure, as described in the thesis. We use MATLAB version 2016b (The MathWorks).

B.2 Reformatting Data For Analysis

This R code inputs the simulation output and reformats it into tidy data (Wickham 2014).

B.3 Analysis

This R code does all the analyses described in the main text.