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The role of fish life histories in allometrically scaled food-web dynamics

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Running head: Life histories in allometrically scaled food webs

Abstract

1. Body size determines key ecological and evolutionary processes of organisms. Therefore, organisms undergo extensive shifts in resources, competitors and predators as they grow in

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28 body size. While empirical and theoretical evidence show that these size-dependent
29 ontogenetic shifts vastly influence the structure and dynamics of populations, theory on how
30 those ontogenetic shifts affect the structure and dynamics of ecological networks is still
31 virtually absent.

32 2. Here, we expand the Allometric Trophic Network (ATN) theory in the context of aquatic
33 food webs to incorporate size-structure in the population dynamics of fish species. We do this
34 by modifying a food web generating algorithm, the niche model, to produce food webs where
35 different fish life-history stages are described as separate nodes which are connected through
36 growth and reproduction. Then, we apply a bioenergetic model that uses the food webs and
37 the body sizes generated by our niche model to evaluate the effect of incorporating life-
38 history structure into food web dynamics.

39 3. We show that the larger the body size of a fish species relative to the body size of its
40 preys, the higher the biomass attained by the fish species and the greater the ecosystem
41 stability. We also find that the larger the asymptotic body size attained by fish species the
42 larger the total ecosystem biomass, a result that holds true for both the largest fish in the
43 ecosystem and each fish species in the ecosystem.

44 4. This work provides an expanded ATN theory that generates food webs with life-history
45 structure for chosen species. Our work offers a systematic approach for disentangling the
46 effects of increasing life-history complexity in food-web models.

47

48 **Keywords:** niche model, bioenergetics model, body size, life histories, aquatic ecosystems

49 **Introduction**

50 Body size determines key ecological and evolutionary processes during the ontogeny of
51 organisms (Werner & Gilliam 1984). Ecological interactions, diet breadth, foraging
52 efficiency, reproduction, mortality among other processes animating an organism's life
53 strongly depend on the organism's size (Werner & Gilliam 1984; Yodzis & Innes 1992; De
54 Roos et al. 2003). Given such dependency, organisms will undergo extensive shifts in
55 resources, competitors and predators as they grow (Werner & Gilliam 1984; Ramos-Jiliberto
56 et al. 2011). These size-dependent ontogenetic shifts vastly influence the structure and
57 dynamics of aquatic populations and communities (Werner & Gilliam 1984; De Roos et al.
58 2003). For example, 'juvenile bottlenecks' influences the structure and dynamics of fish
59 communities where prey populations compete with the juveniles of their predatory
60 populations exhibiting similar body sizes (Byström et al. 1998). Moreover, theoretical work
61 has shown that competitive and predatory (cannibalistic) interactions between different age
62 cohorts drive fish population dynamics (Persson 1988; van den Bosch et al. 1988; De Roos et
63 al. 2003). However, despite all the empirical and theoretical evidence of the vast impacts of
64 size-dependent ontogenetic shifts and stage-structured populations on the population
65 dynamics of interacting species, little theory has been developed on the effects of the size-
66 dependent ontogenetic shifts and population structure on the structure and dynamics of
67 ecological networks (but see Mougi 2017). Here, we contribute to develop such theory by
68 expanding the Allometric Trophic Network (ATN; Yodzis and Innes 1992; Williams &
69 Martinez 2004b; Williams et al. 2007) model to incorporate life-history structure for fishes
70 (to capture changes in body size across different ages) and evaluate its effect on the structure
71 and dynamics of aquatic food webs.

72 The study of ecological networks has recently achieved major breakthroughs by
73 recognizing that the ecological functionality of species can be largely attributed to their body
74 sizes (Brose et al. 2006a; Otto et al. 2007). Specifically, a large predator-prey body size ratio
75 appears to be key to stabilizing the dynamics of complex food webs (Brose et al. 2006b).
76 Through scaling by body size, ATN models have proven successful in explaining the
77 stability, structure and functioning of ecosystems (Williams & Martinez 2000; Brose et al.
78 2006b; Dunne 2006). Apart from model-based investigations on the role of body size in food
79 web dynamics, the theory has been further supported by Boit et al. (2012) who created a
80 remarkably accurate, empirically validated ATN model by incorporating body size that
81 explained 30-40% of the variation in the seasonal dynamics of the Lake Constance plankton
82 community.

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

95 Fishes constitute ideal study species because of their indeterminate growth, which
96 causes them to shift through several ecological niches as they grow (Wootton 1999). Their
97 body size, diet, exposure to predation, and general ecological functionality changes
98 tremendously from larvae through adult stages, resulting in many species transitioning from
99 the bottom of the food chain to the position of apex predator. For example, during their lives,
100 Atlantic cod (*Gadus morhua*) have the potential to change from being planktivores (as
101 <10mm, 1-2g larvae) to apex carnivores longer than 1m in length and tens of kg in mass
102 within 5-7 years (Brander 1994; Hutchings & Rangeley 2011). Another aspect that makes
103 fishes and aquatic food webs particularly interesting systems to study the role of life-history
104 structures in food web dynamics is the fact that contemporary life-history trends towards
105 smaller body sizes and earlier maturity have been documented in many fish species across the
106 world (Hutchings & Baum 2005; Audzijonyte et al. 2013). Understanding the impacts that
107 such life-history changes can have on interacting species, entire ecosystems and sustainable
108 fisheries management warrants for knowledge about the role of fish life-histories in food web
109 dynamics.

110 The present study has two primary objectives. The first is to expand the ATN
111 modelling approach by incorporating simple life-history structure for the fishes in a generic
112 aquatic ecosystem. The second objective is to evaluate the effect of life-history structure on
113 food web dynamics. This second objective includes disentangling the effect of increasing
114 food-web complexity by adding nodes representing the previously ignored life-history stages
115 from the effect of life-history dynamics, that is, ageing from one life-history stage to another
116 and reproduction (linkages between life-history stages). To this end, we use the generic

117 allometrically scaled niche model (Williams & Martinez 2000) adapted to aquatic food webs
118 (Martinez et al. 2012) to randomly generate scenarios for food webs, within which we
119 introduce life-history structure to fishes and split the species-level diets among the life-
120 history stages. Through systematic simulations, we disentangle the relative impacts of life-
121 history dynamics from adding life-history stages by analyzing three types of models: i)
122 'original' ATN model not including life-history stages within species, ii) ATN model with
123 'unlinked' life-history stages that incorporates new nodes but does not connect them via
124 growth and reproduction, and iii) ATN model incorporating life-history stages that are linked
125 together as a species through ageing (hereafter referred to as 'growth') and reproduction.
126 These analyses will provide broadly generalizable insights into the ways in which fish life-
127 histories affect their food webs.

128

129 **Materials and methods**

130 The theory we develop here consists of generating the topology of life-history structured food
131 webs which determines the trophic interactions among nodes (i.e., trophic species and fish
132 life-history stages) and coupling the population dynamics determined by those trophic
133 interactions with life-history dynamics (fish growth and reproduction). We first describe how
134 we generate the topology of the food webs and then how we link the population dynamics of
135 the species and fish life-history stages with the life-history dynamics.

136

137 *Generation of life-history structured food webs*

138 We expand the niche model (Williams & Martinez 2000) to generate networks that
139 incorporate life-history structures. The niche model uses as inputs the number of species and
140 connectance (i.e. fraction of potential feeding interactions that are realized) and randomly
141 assigns a 'niche value' (n_i) to each species from a uniform distribution. This value gives
142 species a hierarchical ranking where they fall relative to each other, which we interpret as
143 relative body size. Species with a low niche value are generally autotrophs, while species
144 with high niche values are more likely to be carnivores. Prey items are assigned to each
145 species from a range centered at a lower niche value, where a larger range indicates a more
146 varied diet. Range size (r_i) is chosen by first drawing a random variable, x_i , from a beta
147 distribution that has been weighted to reflect the desired connectance (C) of the web (see
148 Appendix for the derivation of β):

149 $x \sim \text{beta}(\alpha, \beta)$ with $\alpha = 1$
 $\beta = \frac{1-2c}{2c}$ (1)

150 A less connected web will have more specialists, such that the distribution will skew
 151 more towards smaller range values. The range width for each species is then scaled to fall in
 152 $(0, n_i)$ so that it will never exceed the niche index, which is obtained by:

153 $r_i = x_i n_i$ (2)

154 The predation range is then defined as $\left[c_i - \frac{r_i}{2}, c_i + \frac{r_i}{2} \right]$ Thus, we can center their
 155 predation range using a uniform distribution, limited only by the above assumptions ($c_i \in$
 156 $U\left(\frac{r_i}{2}, n_i\right)$), where c_i is the center of the species dietary range. Species are considered non-
 157 discriminatory beyond this as in they consume all species within their dietary range. We
 158 discarded webs failing to satisfy certain requirements of biological realism, including the
 159 conditions that (i) all species are connected to the web either by predating or being predated
 160 on by other species; (ii) every species has an autotroph in its food chain; (iii) the web is
 161 connected, which ensures that our food web is not composed of several smaller, distinct food
 162 webs. We also confirm that (iv) the generated web exhibits our desired level of connectance.

163 Once a food web has been created, the species are identified as autotrophs,
 164 invertebrates, or fishes (Yodzis & Innes 1992). Autotrophs are identified by looking for the
 165 species that have no prey (i.e. basal species). Invertebrates and fishes are identified depending
 166 on the species trophic position under the assumption that herbivores are more likely to be
 167 invertebrates and carnivores are more likely to be fishes (Romanuk et al. 2011). In particular,
 168 we assume that the three most apex predators are fish and that all the remaining species that
 169 are not autotrophs are invertebrates (following Tonin 2011 and Martinez et al. 2012). Trophic
 170 position of each species is calculated using the short-weighted trophic position (T ; Williams
 171 & Martinez 2000; 2004a), which is the average of two other trophic position metrics: the
 172 shortest trophic level to a basal species ($T1$) and the prey-averaged trophic position ($T2$; see
 173 electronic appendix for its calculation):

174 $T_i = \frac{T1_i + T2_i}{2}, \forall \text{ species } i.$ (3)

175 The shortest trophic level ($T1$) is defined as the shortest path to a basal species plus 1:

176
 177 $T1_i = 1 + \min_{j \in \{j | a_{ij}=1\}} T1_j$ (4)

178 where a_{ij} is a binary element from the species connection matrix.

179 Prey-averaged trophic position for species i is 1 plus the average trophic position of
180 all its prey:

$$\begin{aligned} T2_i &= 1 + \sum_{j \in S} a_{ij} \frac{T2_j}{P_i} \\ &= 1 + \sum_{j \in S_{\text{prey}, i}} \frac{T2_j}{P_i}. \end{aligned} \quad (5)$$

182 where P_i is the number of prey that species i consumes. We describe a computational shortcut
183 to calculate $T2_i$ for each species in the Appendix. The short-weighted trophic position has
184 been shown to be a better estimator of trophic position than $T1$ or $T2$ individually (Williams
185 and Martinez 2004a; Carscallen et al. 2012). Note that autotrophs (basal species) are assigned
186 a trophic position of 1 in every trophic position metric which is reflected in Eqs. 3 and 4.

187

188 *Coupling life-history and population dynamics in food webs*

189 The first step to define the population dynamics of each species within the generated food
190 webs is to determine how efficient species are at processing their food. We expand the
191 methods used by Brose et al. (2006b) to calculate species consumption rates based on species
192 metabolic rates that are approximated by relative body size. The body sizes (accounted as
193 body masses) of all species within the food web are related to the basal species. Therefore,
194 the relative body masses of all the basal species are assigned a value of 1. Then, the relative
195 body masses of the invertebrates and fishes are calculated assuming a constant body mass
196 ratio between consumers and resources (the so called allometric ratio, Z), set to $Z=100$ (Brose
197 et al. 2006b). Thus, the body mass is a simple function of trophic level $\text{Mass} = Z^{T-1}$, where
198 1 is subtracted from the trophic level to exclude basal species from the calculation (Brose et
199 al. 2006b).

200 Fish body mass is of importance not only because of dietary shifts but because
201 metabolic rate per unit mass decreases with size. A school of large fish is more efficient at
202 processing food than a school of small fish with the same biomass. In theory, this means that
203 an ecosystem would be able to support a larger biomass of fish if the fish were larger.
204 Kleiber's Law states that metabolic rates increase at a slower rate than body mass (Kleiber
205 1975). While this law has been revised and modified many times, the underlying principle
206 has held true (Smil 2000; Ballesteros et al. 2014). For instance, a predator may be 100 times
207 larger than its prey, but its metabolic rate is only 75 times that of its prey. Yodzis & Innes
208 (1992) took advantage of this relationship to approximate how efficient the hypothetical

209 organisms of this model convert energy from their food sources (Williams et al. 2007; Brose
 210 2008). Their calculations resulted in metabolic rate (x_i) per unit of body weight (M) as:
 211

$$212 \quad x_i = \begin{cases} 0, & \text{for autotrophs} \\ 0.314M^{-0.15}, & \text{for invertebrates} \\ 0.88M^{-0.11}, & \text{for fish} \end{cases} \quad (5)$$

213 We use a deterministic algorithm to find the weight for new life-history stages. From
 214 their weight, we can approximate their niche index so that we can fit them into the food web
 215 and their metabolic rates. We assign weights to three new, younger life-history stages
 216 ($t = 0,1,2$) with a von Bertalanffy isometric growth curve (Pauly 1980). Adults retain the
 217 original weight (W_{max}) we assigned to each species, and we assume that is the life-history
 218 stage ($t_{max} = 3$) and weight of maximum yield per recruit. The curvature of the von
 219 Bertalanffy curve is set as $K = \frac{3}{t_{max}}$ (Froese and Binohlan 2000), and we assume the adults
 220 reach $\frac{W_{max}}{W_{inf}} = 0.9$ of their asymptotic weight.

$$221 \quad W_t = W_{\infty}(1 - e^{-K(t-t_0)})^3 \quad (6)$$

222 The population dynamics of each species and life-history stages within the food web
 223 can be described with ordinary differential equations (ODEs), which we use to simulate the
 224 biomass of each species. We modified the ATN model (Williams & Martinez 2004b,
 225 Williams et al 2007) to accommodate life-history structure. The following equations from the
 226 ATN model show the growth for autotrophs (Eq.7) and consumers (Eq. 8) during the growing
 227 season:

$$228 \quad \dot{B}_i = \overbrace{r_i \left(1 - \sum_{j \in \text{Autotrophs}} \frac{B_j}{K}\right) B_i}^{\text{Intrinsic Growth}} - \overbrace{\sum_{j \in \text{Consumers}} x_j y_{ji} B_j \frac{F_{ji}}{e_{ji}}}^{\text{Loss to Grazing}} \quad \#(7)$$

$$\dot{B}_i = \underbrace{-f_m x_i B_i}_{\text{Metabolic Loss}} + \underbrace{\sum_{j \in \text{Resources}} f_a x_i y_{ij} B_j F_{ij}}_{\text{Dietary Intake}} - \underbrace{\sum_{j \in \text{Consumers}} x_j y_{ji} B_j \frac{F_{ji}}{e_{ji}}}_{\text{Loss to Predation}} \quad \#(8)$$

229 where r_i is the intrinsic growth rate for autotroph i , K is the carrying capacity, x_i is the
 230 metabolic rate (Eq. 5), y_{ij} is predator i 's maximum consumption rate for prey j , e_{ij} is the
 231 assimilation efficiency for i eating j , f_m is the fraction of assimilated carbon lost for

232 maintenance, and f_a is the fraction of assimilated carbon that contributes to growth. F_{ij} is the
 233 normalized functional response:

$$234 \quad F_{ij} = \frac{\omega_{ij} B_j^h}{B_{0_{ij}}^h + \sum_{k \in \text{consumer}} (c_{kj} p_{ik} B_k B_{0_{kj}}^h) + \sum_{l \in \text{resources}} (\omega_{il} B_l^h)} \quad (9)$$

235 where $\omega_{ij} = 1/P_i$ is the relative preference of species i on its prey j , P_i is the total number of
 236 species i 's prey, h is the Hill exponent, $B_{0_{kj}}$ is the half saturation density for k eating j , c_{kj} is
 237 the predator interference of species k eating j , and p_{ik} is the fraction of i 's resources that it
 238 shares in common with k . The values for these parameters are described in Table 1 and Fig. 1.
 239

240 At the end of each growth season, the ODEs (Eqs 7-8) are paused so that fish may
 241 grow and reproduce. The biomass (B_i) shifts between life-history stages according to the
 242 following Leslie matrix:

$$243 \quad \begin{pmatrix} \dot{B}_i \\ \dot{B}_{i+1} \\ \dot{B}_{i+2} \\ \dot{B}_{i+3} \end{pmatrix} = \begin{pmatrix} 0.1 & 0 & 0 & 0.9 \\ 0.9 & 0.1 & 0 & 0 \\ 0 & 0.9 & 0.1 & 0 \\ 0 & 0 & 0.9 & 0.1 \end{pmatrix} \begin{pmatrix} B_i \\ B_{i+1} \\ B_{i+2} \\ B_{i+3} \end{pmatrix} \quad (10)$$

244 Essentially, this means that 90% of biomass grows to the next life-history stage, while 10%
 245 remains in the previous stage. This choice was made to allow realistic phenotypic variability
 246 within the species, that is, most individuals growth from one age-specific average size to the
 247 next age-specific average size but a few individuals remain at the lower developmental stage
 248 (size) than expected based on their age. The highest (4th) life-history stage reproduces and
 249 90% of its biomass is transferred to the first life-history stage as newborns. Notably, our
 250 formulation of the Leslie matrix allows the model to be applied to a broad range of
 251 ontogenetic developments, not only the most obvious application, which is ageing from one
 252 age-class to another (100% biomass transfer from one stage to another).
 253

254 *Simulation design and analyses*

255 We investigated the model through systematic simulations to determine how inclusion
 256 of fish life-history stages affects the food web, its structure, dynamics, and stability. The
 257 addition of life-history structure for fishes changes multiple features of the food web.
 258

259 Introduction of life-history stages involves the addition of new nodes and feeding links to the

260 web; life-history dynamics (growth from one life-history stage to the next) alters the ways in
261 which biomass is transferred within the food web.

262 To tease apart the relative roles of these components involved with the life-history
263 structures, we run 3 sets of simulations (hereafter denoted as ‘model types’). The first model
264 type comprises an ‘original’ or baseline web that does not include life-history stages within
265 species. That is, each species, including fish, is described through one single node in the food
266 web. Model type 2 incorporates unlinked life-history stages within each fish species. That is,
267 each fish species is partitioned into life-history stages, but these stages are not linked with
268 one another through Leslie matrices. The new fish life stages are independent of each other
269 and biomass does not transfer through ageing from one life-history stage to another. In the
270 ATN modelling sense, they can be considered as new species. While this model type is not
271 biologically realistic, it is crucial for disentangling the effects of adding new nodes to the
272 food web from the effect of life-history dynamics. Model type 3 is an ATN model that
273 incorporates life-history stages that are linked to one another within each species using Eq.
274 10.

275 To compare the three model types, we begin the simulations (500 for each model
276 type) with the same initial conditions. In each simulation, the food web is allowed to stabilize
277 for 200 years, after which the food web is either accepted or rejected, based on the rules
278 detailed below. The dynamics of the food webs are then investigated across another 100-year
279 period. The chosen burn-in time and the investigated simulation period were chosen such that
280 the node biomasses reached dynamic equilibriums and to allow sufficient temporal
281 replication of the food web dynamics to capture short and long term oscillations. Each year
282 consists of 100 simulation time steps, representing a 100-day growing season. Because our
283 objective is to study the impact of fish life-history stages, we choose amongst the stabilized
284 food webs only those that contain at least one fish species or at least one fish life-history
285 stage (in model type 2). Life stages become extinct if their biomass is lower than $10^{-6}\mu\text{gCL}$,
286 although fish species can be revitalized through ageing, as biomass shifts from younger to
287 older age classes. Thus, the final analyzed food webs contained from one to three fish species
288 or, in the case of model 2, at least one fish life-history stage.

289 We initially conducted a preliminary analysis on the probability of fish extinctions for
290 each model type. For this preliminary analysis, we discarded only those food webs for which
291 all fish became extinct. The remaining analyses were subjected to a more stringent constraint;
292 at least one fish species must have persisted in every simulation run for a given model type
293 for the web to be included. The robustness of the results to the choice of $Z=100$ were

294 explored by replicating the analyses with the values of Z generated randomly from lognormal
295 distributions. The main difference was seen in the increased frequency of stable food webs
296 when $Z=100$, as compared to the scenario, where Z was randomly drawn from the lognormal
297 distribution (results not shown). We used R version 3.3.2 (R Core Team 2016) for all
298 analyses, and the R library tidyverse (Wickham 2017). We run the dynamic model with
299 MATLAB version 2016b (The MathWorks).

300

301 **Results**

302 One means of assessing the biological realism of the model was to examine the degree to
303 which the model produced biologically realistic results. In this regard, our model produced
304 realistic von Bertalanffy growth curves: mass is incomparable across simulations, but fish
305 species within a single simulation tended to be in the same size range, as the weight ranges
306 for fish species often overlap (Fig. 2). The youngest life stage of the largest fish species was
307 smaller than the oldest life stage of the smallest fish in 75.8% percent of the simulations.

308 A key criterion for the initial part of the analysis was to have the generic model
309 achieve stability in overall fish biomass. Most (81.0%) of the simulations met this criterion,
310 insofar as fish biomass stabilized in at least one of the experiments. A secondary criterion
311 was that at least one fish species must achieve stability in each of the specific models; 24.4%
312 of the simulations met this second criterion. Given that most simulations stabilized within
313 200 years, the initial 200 years were discarded and the remaining 100 years used for analysis.

314 Neither the CV for total ecosystem biomass or total fish biomass (Fig. 3) differed
315 between the three model types. This result is supported by the frequency of the consecutive
316 number of surviving fish species in each model (Fig. 4). The model types that included new
317 life stages were more likely to have at least one fish species survive, as well as having every
318 fish species survive. There does not appear to be a difference between the linked model
319 (model type 3) and unlinked model (model type 2). The unlinked model seems to have a
320 more intermediate outcome, while linking the life histories seems to steepen the probability
321 of consecutive extinctions.

322 Simulation outputs are illustrated for the fully linked model (model type 3) (Fig. 5;
323 but see Fig. S1 and S2 in the electronic supporting materials for the analogous figures for
324 model 1 and model 2). There is no correlation between fish size and mean total ecosystem
325 biomass ($t=0.61$, $df=1980$, $p=0.544$; Fig. 5a) or mean fish biomass ($t=1.64$, $df=1980$,
326 $p=0.102$; Fig. 5b). However, larger fish species are correlated with a higher CV for both the

327 total ecosystem biomass ($t=5.67$, $df=1980$, $p<0.001$; Fig. 5c), and the CV of fish biomass
328 ($t=3.13$, $df=1980$, $p=0.002$; Fig. 5d). Normality for each variable was confirmed using
329 qqplots.

330

331 **Discussion**

332 The present study opens new avenues of research in food web ecology by proposing a general
333 framework to integrate life histories into the analysis of complex food webs. This framework
334 extends the existing allometric trophic network (ATN) theory by incorporating life-history
335 structure. Using Williams & Martinez's (2000) niche model and the bioenergetics model
336 (Yodzis & Innes 1992) as starting points, we created life-history structured ATN models.
337 Firstly, we added additional life-history stages, i.e. nodes, to each species. Secondly, we
338 linked these stages together, such that juveniles grow into adults and then produce offspring.
339 Through these additional biological mechanisms, we are able to evaluate the effect of life-
340 history dynamics on the function and stability of food webs. While we chose aquatic
341 ecosystems, where fish species exhibit the life-history dynamics, our theory can easily
342 accommodate other types of systems and species exhibiting the life-history dynamics through
343 the broadly applicable Leslie matrix. Furthermore, our framework offers a systematic
344 approach for disentangling the effects of increasing life-history complexity in food-web
345 models.

346 Here, we find that the addition of life-history structure complexity significantly
347 influences model outcomes, but that the linking of the stages within each fish species through
348 a Leslie matrix alters the output of the unlinked model only marginally. For example, the
349 addition of life-history stages reduces variability in total ecosystem biomass, which we
350 interpret as reflecting increased stability. Given that new, unlinked life-history stages can be
351 treated as new individual species, this finding is essentially equivalent to the conclusion that
352 ecosystems which support greater numbers of fish species are more stable than ecosystems
353 that support fewer fish species.

354 One potential pathway leading to the increased stability is via linking multiple size-
355 varying life-history stages, which makes each species more dependent on a broader range of
356 prey. In a sense, we are creating a scenario for increased species generalism by linking all the
357 life stages and by making them less dependent on any one particular prey. On the other hand,
358 we might also increase the extinction probability of a predator species if any one of its life-
359 history stages goes extinct. These non-viable life-history stages may be partly responsible for

360 why we failed to find a strong effect of linking the life stages together. Perhaps if we ensured
361 life-history stage viability by assigning broader diets to each stage, we might have observed a
362 larger effect of stage linkage. The linking of life-history stages might also alleviate the
363 predator-induced mortality of certain prey species. If a fish predator is comprised of a wide
364 variation of cohort sizes in its life-history stages, the prey of any given stage may go through
365 phases of intense predation when it is targeted by the largest cohort followed by a recovery
366 period when the largest cohort is no longer preying on it.

367 The effects of increasing life-history complexity on ecosystems was recently explored
368 by Mougi (2017), who evaluated the effect of two life-history stages on food webs that were
369 randomly generated and which dynamics were described by Lotka-Volterra population
370 dynamics with linear functional responses. The author found that inclusion of two stages
371 (rather than only one stage per species) increased the probability of persistence of complex
372 food webs, while it decreased persistence for simpler food webs (Mougi 2017). Based on the
373 findings of the present study, we hypothesize that most of the effects that Mougi (2017)
374 documented when adding life-history structure might be attributable to an increase in food
375 web size resulting from the addition of non-random nodes, rather than any intrinsic effect of
376 life-history structure. That said, our methods were quite different. The structure of our food
377 webs were randomly generated by the niche model which has been demonstrated to generate
378 realistic structures when compared with empirical food webs (Williams & Martinez 2000).
379 Moreover, the parameters used in our population dynamics come from allometric relations
380 well supported by empirical studies (Enquist et al 1999; Brown et al 2004). Additionally, the
381 functional responses used in our model incorporates consumption saturation that has been
382 demonstrated to be much more biologically meaningful than linear functional responses
383 (Holling 1959). Therefore, we think our theory is a substantial advance after the contribution
384 of Mougi's (2017) work given that our theory is better supported empirically. Finally, we
385 applied an annual Leslie matrix to model growth from one life stage to the next, while Mougi
386 (2017) incorporated a continuous growth model directly into the differential equations. We
387 used four life stages for three species, while he used two life stages for various proportions of
388 the community.

389 Future research should deal with some of the limitations of the theory we present
390 here. Our application of the von Bertalanffy growth model lends increased biological realism
391 in terms of body mass and consequently metabolic rate. However, the species all have
392 identical life histories (exactly four life stages, identical age-specific probabilities of maturity,
393 and the same age-specific fecundity). It might be worth exploring alternative life spans and

394 life-history strategies in future model formulations. Moreover, our results suggest that it
395 would be instructive to increase life-history complexity in the models that explore the
396 impacts of fishing on the target ecosystems (e.g., Kuparinen et al. 2016). From an ecosystem-
397 based management perspective, it would be important to examine how size-selective fishing
398 mortality, which would differentially affect some species and life-history stages more than
399 others, influences species persistence and ecosystem functionality.

400 While the focus of our study was on aquatic food webs, several other applied
401 questions leveraging the relevance of life-history dynamics in food webs and ecological
402 networks in general can benefit from the theory developed here. Such applications of the
403 theory might include biological control, ecosystems services such as pollination, and
404 responses of ecosystems to various types of anthropogenic perturbations.

405

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411

412 **Author contributions**

413 SB, JAH and AK designed the study. SB, FSV and AK developed the model. SB conducted
414 the simulations with assistance from FSV. SB analyzed the results with assistance from AK
415 and JAH. SB, FSV, JAH and AK wrote the article.

416

417 **Data archiving**

418 Codes and simulation outputs can be found in Dryad
419 (<http://dx.doi.org/10.5061/dryad.1hd6dg7>).

420

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524

525 **Table 1.** Model parameters.

Variable	Description	Value	Unit	Reference
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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		Boit <i>et al.</i> 2012
f_m	fraction of assimilated carbon lost for maintenance	0.1		Boit <i>et al.</i> 2012

526

527

528 **Figure legends**

529

530 **Figure 1.** The half saturation constants (B_{0ij}) and competition coefficients (c_{ij}) for predator i
531 eating prey j . Figure and constants are reproduced from Tonin (2011) and Martinez et al.
532 (2012).

533

534 **Figure 2.** Von Bertalanffy growth curves for surviving fish in several simulated food webs.
535 Each colour represents a different food web simulation. Each species has four life stages.

536

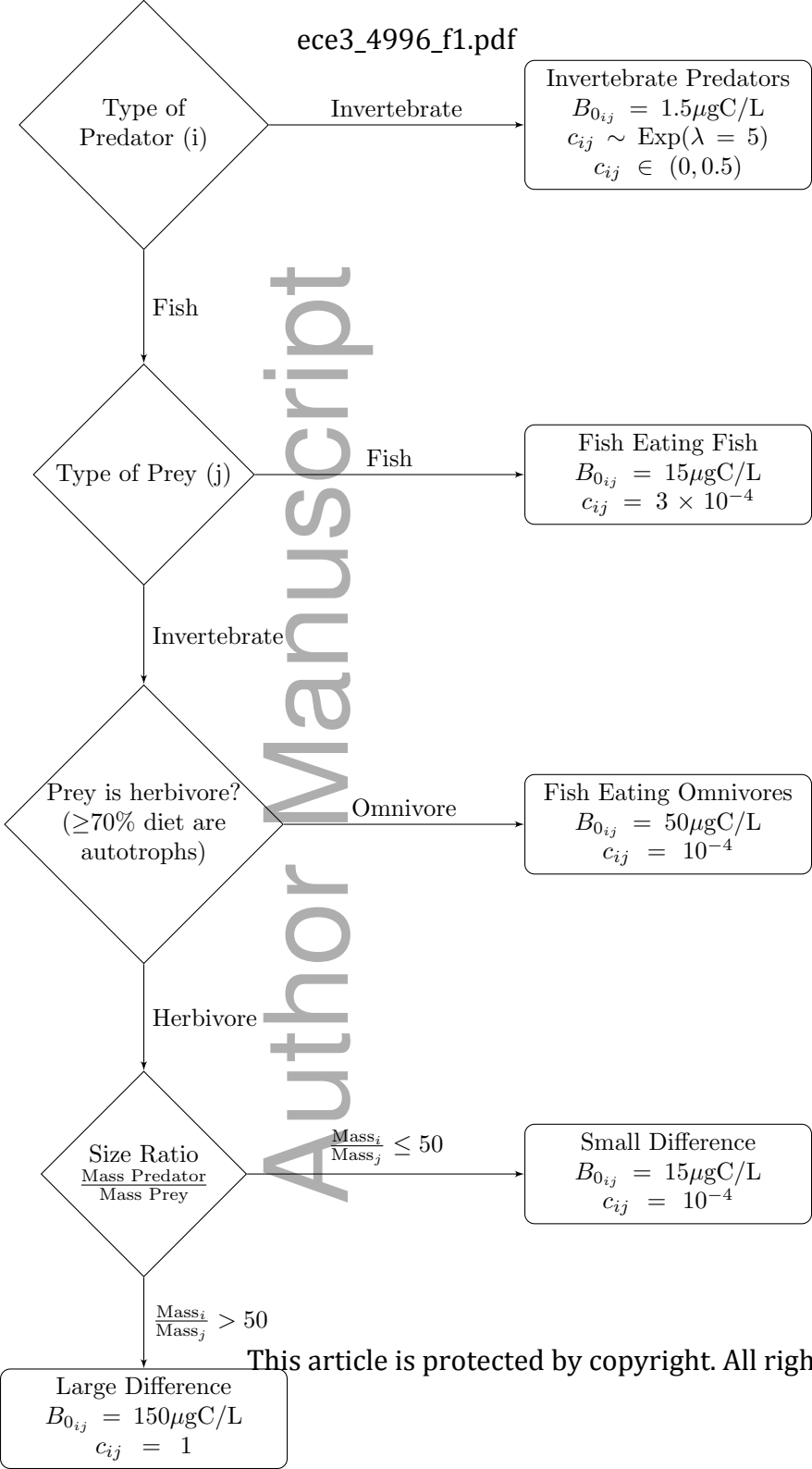
537 **Figure 3.** Boxplots of the coefficient of variation (CV) of the (a) total ecosystem biomass and
538 (b) total fish biomass for each model type (CV's greater than 100 are not shown for clarity).

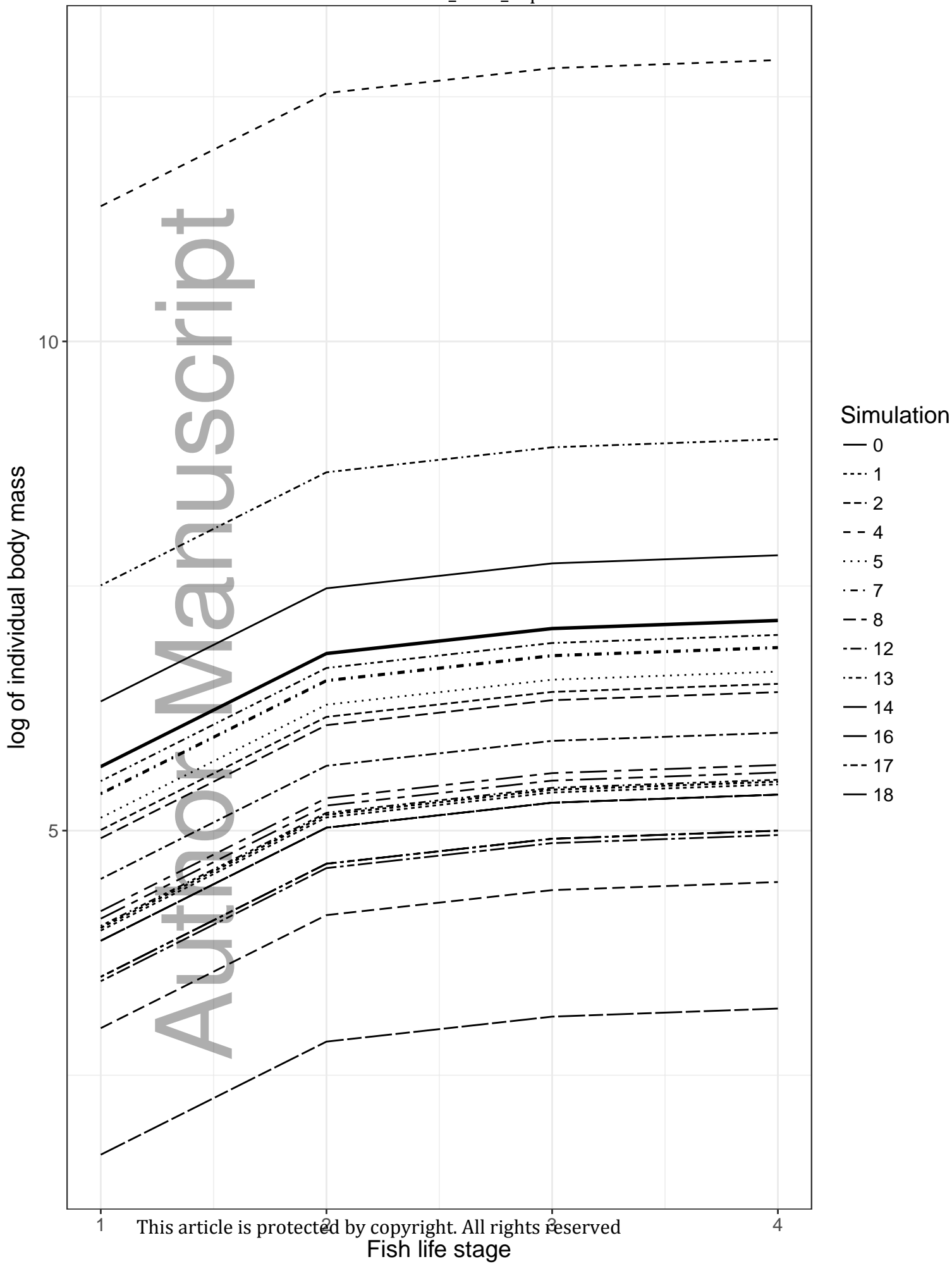
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540 **Figure 4.** The frequency of simulations with 0, 1, 2, or 3 surviving fish species in each
541 model. The different shapes indicate each model type: 1) The original ATN model (triangle),
542 2) Extended unlinked model (square), and 3) the linked model (circle).

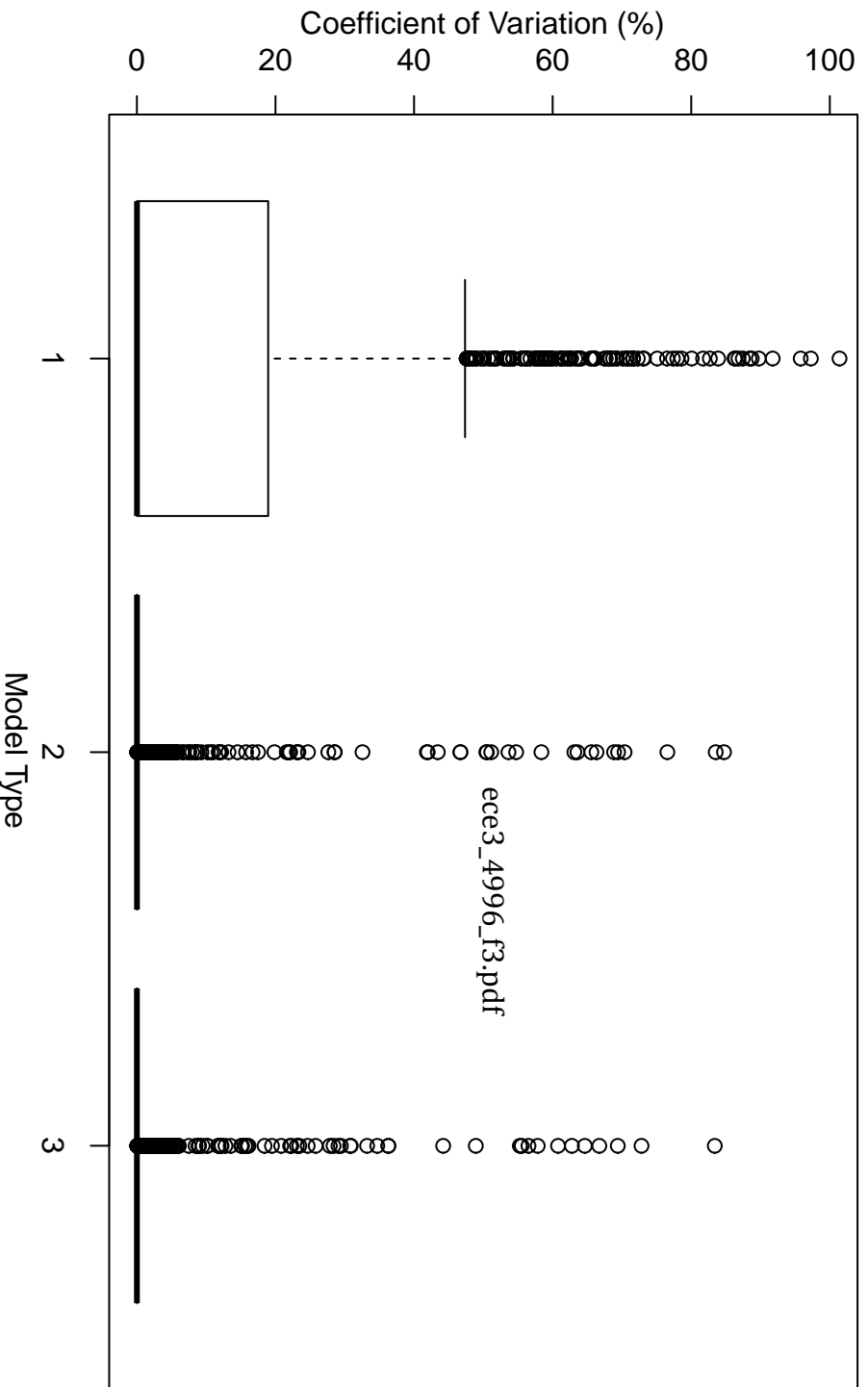
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544 **Figure 5.** Mean and CV of biomass as a function of the asymptotic individual body mass for
545 each surviving fish species. Panels (a) and (b) show the mean ecosystem biomass and mean
546 biomass of the 1982 fish species, respectively. Panels (c) and (d) show their respective CV's.
547 The blue lines represent linear regressions. These are significant for the CV of the total
548 ecosystem biomass (panel c; $t=5.67$, $df=1980$, $p<0.001$) and the CV of the fish biomass
549 (panel d; $t=3.13$, $df=1980$, $p=0.002$). Outliers with a mass larger than 10^{10} or CV greater than
550 800 were removed from the analysis.





Total Ecosystem Biomass



Total Fish Biomass

