

**Community structure and collapses in multi-channel food webs: role of consumer body sizes and mesohabitat productivities.**

Samuel Dijoux<sup>a,b\*</sup>, David S. Boukal<sup>a,b</sup>

<sup>a</sup> Department of Ecosystem Biology, Faculty of Science, University of South Bohemia, Branišovská 1760, 370 05 České Budějovice, Czech Republic.

<sup>b</sup> Czech Academy of Sciences, Biology Centre, Institute of Entomology, Branišovská 31, 370 05 České Budějovice, Czech Republic

E-mail addresses: [dijoux.samuel@gmail.com](mailto:dijoux.samuel@gmail.com) (Dijoux S.); [boukal@entu.cas.cz](mailto:boukal@entu.cas.cz) (Boukal D. S.)

Short running title: Role of consumer body sizes and habitat productivities in multi-channel food webs

Key words: Apparent competition, size-dependent predation, emergent Allee effects, alternative stable states, limiting similarity.

Type of Article: Letter

Number of words in the abstract: 148

Number of words in the main text: 4995

Number of references: 56

Number of figures, tables and text boxes: 6

\* Corresponding author; [dijoux.samuel@gmail.com](mailto:dijoux.samuel@gmail.com) (+420 774 257 941)

Authorship statement: DSB and SD designed the study. SD performed all analytical and numerical stability analyses. Both authors discussed the results and made suggestion for their presentation. SD wrote the first draft of the manuscript and DSB revised it.

Data statement: no new data were used.

## **Abstract**

Multi-channel food webs are shaped by the ability of apex predators to link asymmetric energy flows in mesohabitats differing in productivity and community traits. While body size is a fundamental trait underlying life histories and demography, its implications for structuring multi-channel food webs are unexplored. To fill this gap, we develop a framework that links population responses to predation and resource availability to community-level patterns using a tri-trophic food web model with two populations of intermediate consumers and a size-selective top predator. We show that asymmetries in mesohabitat productivities and consumer body sizes drive food web structure, merging previously separate theory on apparent competition and emergent Allee effects (i.e., abrupt collapses of top predator populations). Our results yield theoretical support for empirically observed stability of asymmetric multi-channel food webs and discover three novel types of emergent Allee effects involving intermediate consumers, multiple populations or multiple alternative stable states.

## Introduction

Non-random distribution of trophic links underlies the persistence and stability of food webs (Otto *et al.* 2007; Rooney *et al.* 2006). Most food webs rely on the linkage of alternative, asymmetric energy sources by predators at higher trophic levels (Rooney *et al.* 2008; McCann & Rooney 2009; Barnes *et al.* 2018). Asymmetric energy flows strengthen the resilience of food webs (Rooney *et al.* 2006; Wolkovich *et al.* 2014), e.g., by reducing population fluctuations and subsequent extinction cascades due to the paradox of enrichment (Otto *et al.* 2007; Dolson *et al.* 2009). Asymmetric energy flows often arise in freshwater ecosystems when mobile generalist predators link different mesohabitats, such as the littoral, pelagic and benthic habitats in lentic systems (Schindler & Scheuerell 2002; Dolson *et al.* 2009; Marklund *et al.* 2018) or downstream and upstream areas in lotic systems (Lapointe *et al.* 2010; Rosenblatt & Heithaus 2011). Energy in these mesohabitats often comes from different sources and the flows differ in turnover and production rates (Rooney & McCann 2012). In lentic systems, energy flow driven by photosynthesis in the more productive ‘green’ pelagic mesohabitat is usually faster than the flow driven by decomposers that depend on detritus and dissolved organic carbon in the ‘brown’ benthic mesohabitat (Zou *et al.* 2016).

Asymmetries in regulatory processes within multi-channel food webs can influence the coexistence of competing species at intermediate trophic levels. Such asymmetries can arise in bottom-up regulatory processes from differences in basal productivity rate and prey biomass (Chesson & Kuang 2008; DeCesare *et al.* 2010) or in top-down processes stemming from differences in the feeding behaviour of the top predator (Post *et al.* 2000; Marklund *et al.* 2019) and hence asymmetric predation pressure (Rooney *et al.* 2006; Wolkovich *et al.* 2014). In particular, linkage by top predators may influence communities in different mesohabitats in a way that either permits their coexistence or makes the least resilient community vulnerable to extinctions as suggested by earlier work on apparent competition in simple food web modules (Holt *et al.* 1994; Chase 1999).

Asymmetric energy flows in multi-channel food webs relate to the limiting similarity hypothesis (MacArthur & Levins 1967), which posits that increasing niche overlap of co-occurring species diminishes their ability to coexist (Mészéna *et al.* 2006; Abrams & Rueffler 2009). For example, species competing for a common resource and sharing the same predator can only coexist if they differ

sufficiently in morphological or physiological traits, niche overlap and environmental requirements (Leibold 1996, 1998). Other studies, however, highlighted possible coexistence of similar species due to symmetric predation pressure (Holt *et al.* 1994) or due to varying fitness caused by variable phenotypes (Godoy *et al.* 2018; McPeck 2019) or variable body sizes.

Food webs can also undergo abrupt ecological regime shifts when they exceed their ecological stability boundaries, leading to a switch between alternative stable states (May 1977; Scheffer *et al.* 2001). These shifts occur in response to external perturbations such as eutrophication in freshwater (Folke *et al.* 2004; Scheffer & van Nes 2007) and marine habitats (Möllmann & Diekmann 2012; Muthukrishnan *et al.* 2016), or in response to intrinsic perturbations inherent to population dynamics such as Allee effects (de Roos & Persson 2002; Beisner *et al.* 2003; Oliver *et al.* 2015). Alternative stable states in food webs can be generated by various mechanisms including intraguild predation, apparent competition, prey size refugia, cannibalism and legacy effects during community assembly (reviewed in Schröder *et al.* 2005 and Gårdmark *et al.* 2015). For example, prey size refugia can lead to alternative stable states at intermediate nutrient levels in a food web consisting of two consumers sharing the same resource and predator (Chase 1999, 2003). However, the propensity of multi-channel food webs to ecological regime shifts has not yet been addressed.

Body size and resource productivity are ubiquitous drivers of community structure (Persson *et al.* 2014). Empirical data show that differences in community size spectra underlie the existence of fast- and slow-energy channels in aquatic food webs (Mehner *et al.* 2018). That is, pelagic habitats are dominated by small-bodied phytoplankton and zooplankton, while benthic habitats host mainly larger-bodied macroinvertebrates (McCann & Rooney 2009). Altogether, the combined asymmetries in consumer body size and energy partition across mesohabitats could stabilize multi-channel food webs (Rooney & McCann 2012) or promote population collapses (de Roos & Persson 2002) and alternative stable states (Chase 2003), but we lack quantitative theory to resolve these interacting roles of consumer body size and resource productivity in the structuring of multi-channel food webs.

To fill these gaps, we modelled the effect of varying body sizes and mesohabitat productivities on multi-channel food webs. We focused on a case in which a top predator integrates two tri-trophic chains with size-structured populations of intermediate consumers that differ in body size using a

modified tri-trophic chain model by de Roos & Persson (2002). This food chain model exhibits an emergent Allee effect due to predation-induced competitive release in the prey (Gårdmark *et al.* 2015) and the possibility of sudden predator collapse. Integrating two such food chains in different mesohabitats with a shared top predator opens the possibility for additional, qualitatively different community structures and steady state transitions. We thus examined how differences in productivity and consumer body sizes affect consumer life histories, the structure of each food chain, apparent competition between the intermediate consumers, and the persistence of the top predator. We were particularly interested in the combinations of consumer body sizes and habitat productivities that (1) enabled coexistence of the intermediate consumers when linked by the top predator and (2) lead to alternative stable states and possible collapses of top predator or intermediate consumer populations.

## Methods

### *Food web structure*

Our minimal multi-channel, tri-trophic food web includes seven possible communities differing in the presence of the intermediate consumers and the top predator (communities 0–6 in Fig. 1). For convenience, we refer to the mesohabitats as pelagic ( $i = 1$ ) and benthic ( $i = 2$ ), each with its own basal resource  $R_i$  and intermediate consumer species  $C_i$ , and apex predator  $P$  integrating both habitats. We begin by outlining expected transitions between these communities. Increasing productivity in each mesohabitat should lead to lengthening of the food chain and successful establishment of the consumer followed by the top predator (Oksanen *et al.* 1981; Fretwell 1987) (community state transitions 0→1→4 and 0→3→6 in Fig. 1). Benthic and pelagic consumers coexist in the absence of the top predator if each mesohabitat is sufficiently productive (community 2). Successful invasion of the top predator in this community (transition 2→5) may subsequently affect consumer coexistence and lead to the exclusion of the less resilient consumer due to apparent competition (transitions 5→4 or 5→6 in Fig. 1). Possible alternative stable states involving two or more of these communities are described in Results.

### *Population structure and dynamics*

In our model, the top predator  $P$  with a fixed body size feeds indiscriminately on the size-structured populations of intermediate consumers  $C_1$  and  $C_2$ , while each consumer population feeds on its own basal resource that follows a semi-chemostat dynamics with carrying capacity  $K_i$  and flow-through rate  $\rho_i$  ( $i = 1, 2$ ). We keep the parameter values used in de Roos & Persson (2002) as a baseline scenario for the benthic food chain  $R_2$ - $C_2$ - $P$  and modify them for the pelagic food chain  $R_1$ - $C_1$ - $P$  (see below and Appendix S1 for details). We also assume that the pelagic resource  $R_1$  has a faster turnover rate than the benthic resource  $R_2$  (Fortier *et al.* 1994) and set  $\rho_1 = 2 \rho_2$ .

Individual consumers are born at length  $l_{b,i}$ , mature at length  $l_{j,i}$  and can grow to the maximum length  $l_{m,i}$  under unlimited resources ( $i = 1, 2$ ). For simplicity, we assume that both consumers differ by a given size ratio in all three traits

$$\frac{l_{b,1}}{l_{b,2}} = \frac{l_{j,1}}{l_{j,2}} = \frac{l_{m,1}}{l_{m,2}} = \beta \quad (1)$$

(i.e., pelagic consumers are larger than benthic ones if  $\beta > 1$  and smaller if  $\beta < 1$ ) and that all processes regulating their populations are qualitatively identical, i.e., any differences arise only through their difference in body size and resource availability. Consumer individuals are characterized by size- and resource-dependent feeding rates  $I_i(R_i, l_i)$  growth rates  $g_i(R_i, l_i)$  and fecundities  $b_i(R_i, l_i)$  and size- and predator-dependent mortality rates  $\mu_i(P, l_i)$ . Their individual biomass scales with  $l^3$  with a proportionality constant  $\omega$ . Individuals of both consumers die with the same size-independent background mortality rate  $\mu_b$  and are further vulnerable to predation until reaching a vulnerability size threshold  $l_v$ . This vulnerability window provides a qualitatively correct description, e.g., for many fish population (Andersen & Beyer 2006). Ingestion rates of individual consumers with length  $l_i$  feeding on the respective basal resource  $R_i$  follow type II functional response,  $I_i(R_i, l_i) = I_m l_i^2 R_i / (R_h + R_i)$  with the proportionality constant  $I_m$  and half-saturation constant  $R_h$ . Individuals of both consumers follow a von Bertalanffy growth curve with resource-dependent asymptotic size,  $g_i(R_i, l_i) = k(l_{m,i} R_i / (R_h + R_i) - l_i)$ , where  $k$  is the growth rate coefficient. They produce offspring after maturation at a *per capita* rate  $b_i(R_i, l_i) = r_m l_i^2 R_i / (R_h + R_i)$ , with a proportionality constant  $r_m$ . Finally, the top predators feed indiscriminately on vulnerable individuals from both consumer populations when present and follow a Holling type II

functional response with constant attack rate  $a$  and handling time  $h$ . We assume constant conversion efficiency  $\epsilon$  of ingested prey biomass to predator biomass and background mortality rate  $\delta$  of the top predators.

In sum, both tri-trophic food chains in our model have identical properties except the mesohabitat productivity and the ratio of consumer body sizes, although the model could be easily modified to further explore the consequences of, e.g., consumer-specific functional response parameters. The five-species community dynamics is described by the following set of ordinary and partial differential equations ( $i = 1, 2$ ):

$$\begin{aligned}
\frac{dR_i}{dt} &= \rho_i (K_i - R_i) - \int_{l_{b,i}}^{l_{m,i}} I_i(R_i, l_i) c_i(t, l_i) dl \\
\frac{\partial c_i(t, l_i)}{\partial t} + \frac{\partial g_i(R_i, l_i) c_i(t, l_i)}{\partial l} &= -(\mu_b + dP) c_i(t, l_i) \\
g_i(R_i, l_i) &= \int_{l_{b,i}}^{l_{m,i}} b_i(R_i, l_i) c_i(t, l_i) dl \\
C_i &= \int_{l_{b,i}}^{l_v} \omega l_i^3 c_i(t, l_i) dl \\
\frac{dP}{dt} &= (\epsilon \frac{a(C_1 + C_2)}{1 + h(C_1 + C_2)} - \delta) P
\end{aligned} \tag{2}$$

We focus on three key properties that can affect the community structure and transitions including the emergent Allee effects: consumer size ratio  $\beta$  and the productivity in each mesohabitat, which we attribute to the resource carrying capacities  $K_1$  and  $K_2$ . We first quantify the impact of consumer body size and habitat productivity on its ontogeny including predation risk, population growth rate, and birth rate with and without predation. We then examine the effects of consumer body size and habitat productivity on the structure of each food chain and the whole food web to understand how asymmetries in consumer body size and mesohabitat productivity influence the apparent competition between intermediate consumers and the whole community structure (Fig. 1). We solve Eq. 2 numerically using the R package *PSPManalysis* version 3.1.2 (de Roos 2014, 2020) to track the system equilibria and detect thresholds associated with successful establishment or collapse of intermediate consumers and the top predator.

## Results

### *Effects of body size and habitat productivity on consumer life history*

Body size has a strong effect on nearly all aspects of the intermediate consumer life history (Fig. 2). Larger consumers take longer time to reach their asymptotic size but benefit from an earlier escape from predation, while very small consumers ( $\beta < 0.24$ ) stay vulnerable to predation even as adults (Fig. 2A). In the absence of predation, larger consumers have faster population growth rates (Fig. 2B) but lower birth rates than smaller consumers (Fig. 2C). Size-dependent predation releases the survivors from intraspecific competition and leads to higher birth rates relative to the non-predated population if some juvenile consumers are invulnerable to predation (ca.  $\beta > 0.24$ ; red vs. black lines in Fig. 2C). As expected, consumers birth rates and population growth rates increase with habitat productivity at any given body size (Fig. 2B-C). In what follows, we constrain our analyses to sufficiently large consumers for which the adults are not vulnerable to predation ( $\beta \geq 0.24$ ).

### *Tri-trophic chain: role of intermediate consumer body size and mesohabitat productivity*

For a wide range of consumer body sizes, the food chain lengthens as the habitat productivity increases and exhibits an emergent Allee effect in the top predator with two alternative stable states at intermediate habitat productivity levels (community state 1/4; Fig. 3A). That is, a relatively high habitat productivity is required for the top predator population to establish, but established top predators can sustain lower habitat productivity as they modify the stage structure of the consumer population (de Roos & Persson 2002; also Fig. 4A for  $\beta = 1.2$ ). The food chain collapses abruptly to a stable consumer-resource equilibrium when the habitat productivity decreases below the top predator persistence level (Fig. 4A). The productivity threshold required for consumer establishment is essentially independent of consumer body size, but those associated with top predator establishment and collapse are highly sensitive to consumer body size as top predators feeding on larger consumers require significantly higher resource productivity to survive (Fig. 3A). Finally, the top predator cannot survive when consumers become invulnerable to predation ( $\beta > \text{ca. } 3.8$ ; Fig. 3A).



*Multi-channel food web: role of asymmetries in intermediate consumer size and mesohabitat productivities*

Coexistence and exclusion of apparent competitors are determined by their relative ability to sustain predation pressure. Here we analyse the effects of varying mesohabitat productivities and consumer body size on the structure of the multi-channel food web, with emphasis on the coexistence of both intermediate consumers. We found surprisingly complex patterns of consumer body size ratios and habitat productivities required for their coexistence with the top predator. We first outline the range of habitat productivity levels that maintain both benthic and pelagic consumers of a given size ratio in the food web, and subsequently provide more detailed results on body size differences that enable consumer coexistence and top predator persistence at given productivity levels in one of the mesohabitats (community state 5 and states 2/5, 4/5, 5/6, 2/4/5 and 2/5/6 that include state 5 as one of the alternatives; see Fig. 1).

For a given consumer body size ratio  $\beta$ , the food web structure is driven by the ratio of the pelagic and benthic habitat productivity and the total effective productivity. The latter can be close to the sum of resource carrying capacities  $K_1+K_2$  (hereafter ‘total carrying capacity’, abbreviated as TCC) irrespective of the relative contribution of the pelagic habitat  $K_1/(K_2 + K_1)$  (hereafter abbreviated as PB ratio) as in Fig. 3B, or depend on both the PB ratio and TCC (see below). Resource carrying capacity in the given habitat determines the invasion threshold of each intermediate consumer (Fig. 5), while the total effective productivity determines the invasion and collapse thresholds of the top predator (Fig. S1). Competitive exclusion and coexistence of the two intermediate consumers when linked by the top predator is driven mainly by the PB ratio (Figs. 3B and S3).

Consumer coexistence along the habitat productivity gradients is promoted by larger body size differences. That is, the coexistence of all five species is constrained to a narrow range of PB ratios and sufficiently high TCC values for same-sized intermediate consumers ( $\beta \approx 1$ ; community states 5 and 2/5 in Figs. 5 and S3D). When one of the consumers is substantially larger ( $\beta \ll 1$  or  $\beta \gg 1$ ) and hence competitively superior (see above), all five species can coexist only if its habitat is moderately productive. Higher productivity values in that habitat lead to competitive exclusion of the smaller consumer, while lower productivity values cannot support the larger consumer. On the other hand,

coexistence is almost independent of the productivity in the smaller consumer's habitat as long as it can support the top predator (ca.  $K_1 > 1.5 \times 10^{-4}$  to  $4 \times 10^{-4}$  g.L<sup>-1</sup> in Fig. S4A-C and  $K_2 > 9 \times 10^{-5}$  g.L<sup>-1</sup> in Fig. S3E-I).

Unequal consumer body sizes also underpin asymmetric roles of habitat productivities in the fate of the top predator. TCC values required for top predator persistence are nearly independent of the PB ratio for most consumer body size ratios  $\beta$ , and increase with PB only when the pelagic consumers are much larger ( $\beta = 3$  in Fig. S1A). TCC thresholds associated with predator invasion are more sensitive to  $\beta$  and PB ratios: they decline with the PB ratio when  $\beta \leq 1$  and increase otherwise (Fig. S1B). This asymmetric role of the pelagic and benthic habitat productivities is caused by the habitat-specific consumer vulnerability to predation as both consumers are equivalent in terms of contribution to the critical prey biomass required by the top predator (Fig. S2). That is, a more productive pelagic habitat is required to sustain the top predator as  $\beta$  increases and the pelagic prey becomes less vulnerable (Fig. S1A).

At low benthic productivities  $K_2$ , all five species therefore coexist if pelagic consumers are sufficiently small and pelagic productivity sufficiently high (community state 5; ca.  $\beta < 0.66$  for  $K_1 > 10^{-4}$  g.L<sup>-1</sup> in Fig. 5A). Surprisingly, coexistence is also possible if the pelagic consumers are larger and pelagic productivity intermediate (community state 2/5; up to  $\beta = 1.5$  for  $K_1$  between ca.  $10^{-5}$  g.L<sup>-1</sup> and  $10^{-4}$  g.L<sup>-1</sup> in Figs. 3B and 5A; see also Figs. 4B and S4A-D). Coexistence at high benthic productivity  $K_2$  requires sufficiently large pelagic consumers (ca.  $\beta > 0.9$  in Fig. 5B) in a moderately productive pelagic mesohabitat; the range of pelagic productivity leading to possible coexistence increases with  $\beta$  (community states 5, 4/5 and 2/4/5; Figs. 5B and S4G-I; see also Fig. 4C). Intermediate benthic productivities  $K_2$  combine the outcomes for low and high  $K_2$ , i.e. all five species can coexist when sufficiently high pelagic productivity supports small pelagic consumers or when large pelagic consumers are constrained by intermediate pelagic productivity (community states 5, 2/5, 4/5 and 2/4/5, Fig. S4EF).

We observe similar patterns for fixed pelagic productivities  $K_1$ : coexistence is possible if benthic consumers are substantially larger and occupy a less productive habitat or if they are substantially smaller and live in a more productive habitat than the benthic consumers (community states 5, 2/5, 4/5,

5/6, 2/4/5 and 2/5/6; Figs. 5CD and S5). Coexistence is less likely, i.e. occurs for a smaller range of  $\beta$  and  $K_2$ , as the pelagic productivity becomes very low (Fig. S5A) or very high (Figs. 5D and S5G-I). At intermediate values of pelagic productivity, even similarly sized benthic and pelagic consumers may however coexist within a range of intermediate benthic productivity (community state 2/5 in Fig. 5C and states 5 and 2/5 in Fig. S5B-F).

### *Emergent Allee effects and alternative stable states in the multi-channel food web*

We identified nine possible alternative stable state configurations in the food web and classify them into four groups. First, they include the ‘classical’ *emergent Allee effect in the top predator* associated with its sudden collapse (de Roos & Persson 2002; Fig. 6A) when one or both consumer populations are present (community states 1/4, 3/6 and 2/5 in Figs. 1 and 5). Second, an *emergent Allee effect in an intermediate consumer* represents the collapse of a competitively inferior consumer population due to apparent competition when all other species are present (community states 4/5 and 5/6 in Fig. 1). Third, an *emergent two-species Allee effect* is associated with the invasion of the competitively inferior consumer species upon the sudden collapse of the top predator or its disappearance after the top predator establishes in the trophic food chain (community states 2/4 and 2/6 in Fig. 1). Finally, the community can have *three* alternative stable states: presence of the top predator with one or both consumer populations, or both consumer populations without the top predator (community states 2/5/4 and 2/5/6 in Fig. 1). This outcome combines the emergent Allee effects in the top predator and in an intermediate consumer; we call it a *cascading emergent Allee effect* characterised by consecutive (Fig. 6B) or nested (Fig. 6C) population collapses of the top predator and one or both consumers. While the consecutive collapses enable the food web structure pass through all three alternative stable states through gradual change of the environmental conditions alone, the nested collapses make one of the stable states unreachable by gradual change.

We observed emergent Allee effects across a wide range of habitat productivities (Figs. 3 and S3) and consumer size ratios (Figs. 5 and S4-S5). Emergent Allee effects in the top predator and the two-species Allee effects (community states 1/4, 2/4, 2/5, 2/6 and 3/6), occurred at all consumer size ratios  $\beta$  but were restricted to intermediate TCC levels; the exact TCC range varied with the PB ratio

when  $\beta$  deviated strongly from unity (Figs. 5 and S3). Emergent Allee effects in intermediate consumers (community states 4/5 and 5/6) occurred only when  $\beta$  deviated strongly from unity and TCC levels were high enough for the top predator to persist (Figs. 5B and S3-S5). Cascading emergent Allee effects (community states 2/5/4 and 2/5/6) appeared mainly for sufficiently dissimilar consumer body size ratios and intermediate TCC levels (Figs. 5AD, S3B, S3E-I, S4E-G and S5B and S5E-I). They almost always included consecutive population collapses (Figs. S6B and S7AC) and very rarely the nested collapse (community states 2/4 and 2/5/4 in Fig. S4CD).

Emergent Allee effects in our simulations predominately affected communities in which the top predator gained a feeding link to the pelagic or both consumers (community states 1/4, 2/4, 2/5 and 2/4/5) or in which apparent competition drove benthic consumers extinct (4/5; Fig. 5BD). We varied body size of pelagic consumers while keeping the size of benthic consumers constant in our analyses. Thus, the range of environmental conditions giving rise to the emergent Allee effect in the benthic food chain (community state 3/6) was independent of  $\beta$ , while the other emergent Allee effects in the top predator (1/4 and 2/5) and the two-species Allee effect associated with the loss of the benthic consumer (2/4) became more common as  $\beta$  increased (Figs. 3B, 4D and S4; see also Fig. 5AD). Alternative stable states in which the top predator could gain access to the benthic consumers (community states 2/6, 3/6 and 2/5/6) were less common and limited to sufficiently small pelagic consumers living in a moderately productive mesohabitat (states 2/6 and 2/5/6 in Figs. 5C, S3A-F, S4FG and S5A-D) and to food webs with intermediate benthic productivity  $K_1$  and pelagic productivity  $K_2$  below the pelagic consumer persistence threshold (state 3/6 in Figs. 3B, S3 and S4FG). Finally, we found the emergent Allee effect in which the top predator drove the pelagic consumers to extinction (community state 5/6) only for very small pelagic consumers ( $\beta < 0.5$ ) and a narrow range of moderate benthic productivity ( $K_2 \approx 10^{-4} \text{ g.L}^{-1}$ , Figs. 5CD, S3AB, S4FG, and S5).

## Discussion

Variation in predator-prey body size ratios underpins the structure and stability of food webs (Brose *et al.* 2006; Petchey *et al.* 2008). Furthermore, individual growth in size plays an important role in predator-prey interactions as large prey often become invulnerable to predation (de Roos & Persson 2002;

Andersen & Beyer 2006). However, the importance of varying body sizes in multi-channel food webs that arise in many aquatic and terrestrial ecosystems has not been explored. Here we provided theoretical support for the key role of asymmetric body sizes and resource productivities in the empirically observed stability of multi-channel food webs (Rooney *et al.* 2006). We also showed that alternative stable states in these food webs can go beyond the emergent Allee effect in the top predator (de Roos & Persson 2002) and mutual exclusion via apparent competition (Holt *et al.* 1994; Chase 1999) as we discovered three new types of emergent Allee effects affecting intermediate consumers or multiple populations, or involving multiple alternative stable states. Our results emphasize the need to jointly consider the strength of bottom-up regulatory processes, individual ontogeny and size-dependent interactions to improve our understanding of the responses of multi-channel food webs to environmental change.

#### *Multi-channel food webs and apparent competition*

We showed that intermediate consumer body sizes and energy partition between mesohabitats jointly determine the limits of species coexistence in multi-channel food webs. Classic theory of apparent competition between two consumers sharing a predator predicts that the prey resilient to the highest predation pressure prevails (Holt *et al.* 1994). Further extensions examining the combined roles of apparent and exploitative competition found that consumer coexistence requires a trade-off in the ability to dominate in each type of competition (Holt *et al.* 1994) and that habitat productivity drives the outcome (Leibold 1996; Chase 1999). That is, species dominating in exploitative competition should be gradually replaced by species resistant to predation as productivity increases, with coexistence possible at intermediate productivity levels (Leibold 1996). This will often mean that small and large species will respectively dominate at low and high habitat productivity if predators cannot feed on large prey (Chase 1999, 2003).

The lower vulnerability of larger consumers to predation was not traded off against higher resource requirements in our model. However, larger consumers did not always prevail as expected in apparent competition because of the additional role of bottom-up regulatory processes. That is, consumer coexistence in our model was primarily driven by the ratio of productivity in both linked mesohabitats when both consumers were similarly sized and by productivity in the larger consumer's

mesohabitat (i.e., similar to the findings by Chase (1999) and Leibold (1996)) when their sizes differed substantially. We conclude that a “symmetry in asymmetries” is required for consumer coexistence in multi-channel food webs: asymmetry in body size must compensate for a mirror asymmetry in energy partitioning such as smaller consumers living in a more productive mesohabitat.

These combination of asymmetries occur frequently between pelagic and benthic mesohabitats in freshwater systems (Rooney *et al.* 2006). The pattern of (i) smaller organisms and high photosynthetic-driven productivity in pelagic mesohabitats and (ii) larger organisms and low allochthonous productivity in benthic mesohabitat (Baird & Ulanowicz 1989; Rooney *et al.* 2008) corresponds to the observations for  $K_2 < K_1$  and  $\beta < 1$  in our model (Figs. S3–S5). This implies that these multi-channel food webs rely on the above compensatory asymmetries to ensure stable coexistence of apparent competitors in different food-web channels (Rooney *et al.* 2006). Interestingly, our model also predicts stable coexistence if the larger organisms and lower productivity occur in the pelagic mesohabitat, i.e. the observed coexistence patterns are not primarily driven by higher resource turnover rate in the pelagic mesohabitat ( $\rho_2 > \rho_1$ ).

#### *Emergent Allee effects, alternative stable states and catastrophic collapses*

Increasing anthropogenic pressure on fish stocks through eutrophication and harvesting (Möllmann & Diekmann 2012) has led to catastrophic declines of two thirds of freshwater and marine predatory fish, with an acceleration of 54% over the past 40 years (Christensen *et al.* 2014; Otto 2018). While these declines can be reversible (Hutchings 2000; Persson *et al.* 2007), they require disproportionately large efforts if the collapses associate with Allee effects that affect populations resilience and recovery, promote alternative stable states in the system (Scheffer *et al.* 2001; van Kooten *et al.* 2005), and make the food webs vulnerable to sudden collapse (Möllmann & Diekmann 2012; Gårdmark *et al.* 2015).

Here we demonstrated that multi-channel food webs can become disconnected not only by the loss of top predator, but also by the loss of populations at intermediate trophic levels in response to increased productivity in the other mesohabitat, e.g. due to eutrophication. Our results imply that multi-channel food webs show the highest propensity for alternative stable states at highly unequal consumer

body sizes and intermediate habitat productivity levels, which may guide future empirical studies on alternative stable states in such food webs. Intermediate levels of habitat productivity are also indispensable for alternative stable states in the diamond and intraguild predation food web modules (Chase 1999, 2003; Diehl & Feißel 2000), suggesting that this pattern is independent of food web topology.

Without exploitative competition, we did not observe alternative stable states affecting consumers via priority effects (Chase 1999, 2003). However, we identified other novel types of community transitions leading to the loss of the inferior consumer through an emergent Allee effect when (i) the top predator invades the system and the system shifts from separate consumer-resource pairs to a trophic chain, (ii) increased or decreased productivity in one mesohabitat disrupts the energy balance and the system changes from a multi-channel food web to a trophic chain, and (iii) cascading emergent Allee effects arise. In the latter case, we predict that the system can alternate between multiple stable states involving separate consumer-resource pairs, a trophic chain and the complete multi-channel food web. This additional complexity may contribute to the limited evidence of alternative stable states on whole-ecosystem level (Schröder *et al.* 2005; but see Möllmann & Diekmann 2012).

#### *Implications for food web resilience in a changing world*

Anthropogenic impacts now account for most perturbations of natural ecosystems (Schindler & Scheuerell 2002; Otto 2018). In particular, eutrophication (Oksanen *et al.* 1981; Otto *et al.* 2007) and removal or introduction of species (DeCesare *et al.* 2010) essentially impact food web and community structure (Möllmann & Diekmann 2012; Wollrab *et al.* 2012).

The impact of increased nutrient inputs on the structure of our multi-channel food web model was contingent on the consumer size ratio, which underpins the importance of differences in species traits between the energy channels. While increased nutrient loads in the mesohabitat occupied by the smaller consumers stabilized the food web, increased productivity in the other mesohabitat was potentially destabilizing as it disrupted the linkage between mesohabitats and excluded the weaker competitor. On the other hand, the loss of one consumer population did not necessarily lead to the

extinction of the top predator as long the total system productivity remained sufficiently high, thereby showing that multiple energy channels protect top predators.

To conclude, our predictions confirm empirical data on the resilience of natural systems due to asymmetric patterns between heterogeneous habitats, which enable faster recovery of the system after perturbation (Rooney *et al.* 2006; McCann & Rooney 2009). We have demonstrated that detailed understanding of species traits such as body size and their impact on trophic interactions are required to understand the structure and persistence of multi-channel, tri-trophic food webs when facing environmental stressors. Further studies of the role of species traits in multi-channel food webs could help identify communities and species vulnerable to regime shifts (Gårdmark *et al.* 2015) and suggest possible restoration approaches.

## Acknowledgements

We thank Andrea Landeira-Dabarca for comments on an earlier version of the manuscript. This research was supported by the Grant Agency of the Czech Republic, project nr. 14-29857S.

## References

- Abrams, P.A. & Rueffler, C. (2009). Coexistence and limiting similarity of consumer species competing for a linear array of resources. *Ecology*, 90, 812–822.
- Andersen, K.H. & Beyer, J.E. (2006). Asymptotic size determines species abundance in the marine size spectrum. *Am. Nat.*, 168, 54–61.
- Baird, D. & Ulanowicz, R.E. (1989). The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr.*, 59, 329–364.
- Barnes, A.D., Jochum, M., Lefcheck, J.S., Eisenhauer, N., Scherber, C., O'Connor, M.I., *et al.* (2018). Energy flux: The link between multitrophic biodiversity and ecosystem functioning. *Trends Ecol. Evol.*, 33, 186–197.
- Beisner, B.E., Haydon, D.T. & Cuddington, K. (2003). Alternative stable states in ecology. *Front. Ecol. Environ.*, 1, 376–382.
- Brose, U., Williams, R.J. & Martinez, N.D. (2006). Allometric scaling enhances stability in complex



423 food webs. *Ecol. Lett.*, 9, 1228–1236.

424 Chase, J.M. (1999). Food web effects of prey size refugia: Variable interactions and alternative stable  
 425 equilibria. *Am. Nat.*, 154, 559–570.

426 Chase, J.M. (2003). Experimental evidence for alternative stable equilibria in a benthic pond food  
 427 web. *Ecol. Lett.*, 6, 733–741.

428 Chesson, P. & Kuang, J.J. (2008). The interaction between predation and competition. *Nature*, 456,  
 429 235–238.

430 Christensen, V., Coll, M., Piroddi, C., Steenbeek, J., Buszowski, J. & Pauly, D. (2014). A century of  
 431 fish biomass decline in the ocean. *Mar. Ecol. Prog. Ser.*, 512, 155–166.

432 DeCesare, N.J., Hebblewhite, M., Robinson, H.S. & Musiani, M. (2010). Endangered, apparently: The  
 433 role of apparent competition in endangered species conservation. *Anim. Conserv.*, 13, 353–362.

434 Diehl, S. & Feiße, M. (2000). Effects of enrichment on three-level food chains with omnivory. *Am.*  
 435 *Nat.*, 155, 200–218.

436 Dolson, R., McCann, K., Rooney, N. & Ridgway, M. (2009). Lake morphometry predicts the degree  
 437 of habitat coupling by a mobile predator. *Oikos*, 118, 1230–1238.

438 Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., *et al.* (2004). Regime  
 439 shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.*, 35,  
 440 557–581.

441 Fortier, L., Le Fèvre, J. & Legendre, L. (1994). Export of biogenic carbon to fish and to the deep  
 442 ocean: The role of large planktonic microphages. *J. Plankton Res.*, 16, 809–839.

443 Fretwell, S.D. (1987). Food chain dynamics: the central theory of ecology? *Oikos*.

444 Gårdmark, A., Casini, M., Huss, M., van Leeuwen, A., Hjelm, J., Persson, L., *et al.* (2015). Regime  
 445 shifts in exploited marine food webs: Detecting mechanisms underlying alternative stable states  
 446 using sizestructured community dynamics theory. *Philos. Trans. R. Soc. B Biol. Sci.*, 370, 1–10.

447 Godoy, O., Bartomeus, I., Rohr, R.P. & Saavedra, S. (2018). Towards the integration of niche and  
 448 network theories. *Trends Ecol. Evol.*, 33, 287–300.

449 Holt, R.D., Grover, J. & Tilman, D. (1994). Simple rules for interspecific dominance in systems with  
 450 exploitative and apparent competition. *Am. Nat.*, 144, 741–774.

451 Hutchings, J.A. (2000). Collapse and recovery of marine fishes. *Nature*, 406, 882–885.

452 van Kooten, T., De Roos, A.M. & Persson, L. (2005). Bistability and an Allee effect as emergent  
 453 consequences of stage-specific predation. *J. Theor. Biol.*, 237, 67–74.

454 Lapointe, N.W.R., Corkum, L.D. & Mandrak, N.E. (2010). Macrohabitat associations of fishes in  
 455 shallow waters of the Detroit River. *J. Fish Biol.*, 76, 446–466.

456 Leibold, M.A. (1996). A graphical model of keystone predators in food webs: Trophic regulation of  
 457 abundance, incidence, and diversity patterns in communities. *Am. Nat.*, 147, 784–812.

458 Leibold, M.A. (1998). Similarity and local co-existence of species in regional biotas. *Evol. Ecol.*, 12,  
 459 95–110.

460 MacArthur, R.H. & Levins, R. (1967). The limiting similarity, convergence, and divergence of  
 461 coexisting species. *Am. Nat.*, 101, 377.

462 Marklund, M.H.K., Svanbäck, R., Faulks, L., Breed, M.F., Scharnweber, K., Zha, Y., *et al.* (2019).  
 463 Asymmetrical habitat coupling of an aquatic predator—The importance of individual  
 464 specialization. *Ecol. Evol.*, 9, 3405–3415.

465 Marklund, M.H.K., Svanbäck, R., Zha, Y., Scharnweber, K. & Eklöv, P. (2018). The influence of  
 466 habitat accessibility on the dietary and morphological specialisation of an aquatic predator.  
 467 *Oikos*, 127, 160–169.

468 May, R.M. (1977). Thresholds and breakpoints in ecosystems with a multiplicity of stable states.  
 469 *Nature*, 269, 471.

470 McCann, K.S. & Rooney, N. (2009). The more food webs change, the more they stay the same.  
 471 *Philos. Trans. R. Soc. B Biol. Sci.*, 364, 1789–1801.

472 McPeck, M.A. (2019). Limiting similarity? The ecological dynamics of natural selection among  
 473 resources and consumers caused by both apparent and resource competition. *Am. Nat.*, 193, 92–  
 474 115.

475 Mehner, T., Lischke, B., Scharnweber, K., Attermeyer, K., Brothers, S., Gaedke, U., *et al.* (2018).  
 476 Empirical correspondence between trophic transfer efficiency in freshwater food webs and the  
 477 slope of their size spectra. *Ecology*, 99, 1463–1472.

478 Meszéna, G., Gyllenberg, M., Pásztor, L. & Metz, J.A.J. (2006). Competitive exclusion and limiting

479 similarity: A unified theory. *Theor. Popul. Biol.*, 69, 68–87.

480 Möllmann, C. & Diekmann, R. (2012). Chapter 4 - Marine ecosystem regime shifts induced by climate  
 481 and overfishing: A review for the Northern Hemisphere. *Adv. Ecol. Res.*, 47, 303–347.

482 Muthukrishnan, R., Lloyd-Smith, J.O. & Fong, P. (2016). Mechanisms of resilience: empirically  
 483 quantified positive feedbacks produce alternate stable states dynamics in a model of a tropical  
 484 reef. *J. Ecol.*, 104, 1662–1672.

485 Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981). Exploitation ecosystems in gradients of  
 486 primary productivity. *Am. Nat.*

487 Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F., *et al.* (2015).  
 488 Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.*, 30, 673–684.

489 Otto, S.B., Rall, B.C. & Brose, U. (2007). Allometric degree distributions facilitate food-web stability.  
 490 *Nature*, 450, 1226–1229.

491 Otto, S.P. (2018). Adaptation, speciation and extinction in the Anthropocene. *Proc. R. Soc. B*, 285,  
 492 20182047.

493 Persson, L., Amundsen, P.-A., de Roos, A.M., Klemetsen, A., Knudsen, R. & Primicerio, R. (2007).  
 494 Culling prey promotes predator recovery - Alternative states in a whole-lake experiment. *Science*  
 495 (80-. ), 316, 1743–1746.

496 Persson, L., van Leeuwen, A. & de Roos, A.M. (2014). The ecological foundation for ecosystem-  
 497 based management of fisheries: mechanistic linkages between the individual-, population-, and  
 498 community-level dynamics. *ICES J. Mar. Sci.*, 71, 2268–2280.

499 Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008). Size, foraging, and food web  
 500 structure. *Proc. Natl. Acad. Sci. U. S. A.*, 105, 4191–4196.

501 Post, D.M., Connors, M.E. & Goldberg, D.S. (2000). Prey preference by a top predator and the  
 502 stability of linked food chains. *Ecology*, 81, 8–14.

503 Rooney, N., McCann, K., Gellner, G. & Moore, J.C. (2006). Structural asymmetry and the stability of  
 504 diverse food webs. *Nature*, 442, 265–269.

505 Rooney, N. & McCann, K.S. (2012). Integrating food web diversity, structure and stability. *Trends*  
 506 *Ecol. Evol.*, 27, 40–45.

- Rooney, N., McCann, K.S. & Moore, J.C. (2008). A landscape theory for food web architecture. *Ecol. Lett.*, 11, 867–881.
- de Roos, A. (2020). A general approach for analysis of physiologically structured population models: The R package ‘PSPManalysis.’ *bioRxiv*, 2020.06.27.174722.
- de Roos, A.M. (2014). PSPManalysis: A Matlab/C package for numerical analysis of Physiologically structured population models.
- de Roos, A.M. & Persson, L. (2002). Size-dependent life-history traits promote catastrophic collapses of top predators. *Proc. Natl. Acad. Sci. U. S. A.*, 99, 12907–12912.
- Rosenblatt, A.E. & Heithaus, M.R. (2011). Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *J. Anim. Ecol.*, 80, 786–798.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591–596.
- Scheffer, M. & van Nes, E.H. (2007). Shallow lakes theory revisited: Various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia*, 584, 455–466.
- Schindler, D. & Scheuerell, M. (2002). Habitat coupling in lake ecosystems. *Oikos*, 98, 177–189.
- Schröder, A., Persson, L. & De Roos, A.M. (2005). Direct experimental evidence for alternative stable states: A review. *Oikos*, 110, 3–19.
- Wolkovich, E.M., Allesina, S., Cottingham, K.L., Moore, J.C., Sandin, S.A. & De Mazancourt, C. (2014). Linking the green and brown worlds: The prevalence and effect of multichannel feeding in food webs. *Ecology*, 95, 3376–3386.
- Wollrab, S., Diehl, S. & de Roos, A.M. (2012). Simple rules describe bottom-up and top-down control in food webs with alternative energy pathways. *Ecol. Lett.*, 15, 935–46.
- Zou, K., Thébault, E., Lacroix, G. & Barot, S. (2016). Interactions between the green and brown food web determine ecosystem functioning. *Funct. Ecol.*, 30, 1454–1465.

## Legends

**Fig. 1: Classification of all possible scenarios of community assembly in the multi-channel food web.** Populations and trophic links: top predator (black circle), consumers (diamonds) and resources (circles) linked by stable (solid lines) or bistable (dotted lines) trophic links; pelagic species in green, benthic species in brown. Transitions between possible community states (numbered rectangles) correspond to the invasion/extinction threshold of one consumer (dark green or brown arrows), or top predator (black arrows). Dotted arrows = transitions between communities with 2–3 alternative stable states (multiple numbers separated by slashes). Grey arrows illustrate gradients of energy partitioning among mesohabitats and total system productivity.

**Fig. 2: Influence of consumer relative body size  $\beta$  on key life history events (A), population growth rate (B) and birth rate (C).** (A) Grey area: consumers vulnerable to predation (daily resolution); black dotted line = maturation time; black solid line = time to reach maximum size, defined as age when individual growth rate declines below  $0.01 \text{ mm day}^{-1}$ ; resource level  $R$  fixed at ca.  $3 \times 10^{-4} \text{ g.L}^{-1}$ . (B and C) Population-level rates without predation (black lines, B and C) and with predation (red lines, C); resource carrying capacity fixed at  $K = 3 \times 10^{-5} \text{ g.L}^{-1}$  (thin lines),  $8 \times 10^{-5} \text{ g.L}^{-1}$  (medium lines), and  $3 \times 10^{-4} \text{ g.L}^{-1}$  (thick lines). Other parameters as in Table S1. Community structure in panel C: solid lines = stable equilibria dashed lines = unstable equilibria of the tri-trophic chain; black points = predator invasion thresholds, red points = predator persistence thresholds; dash-dotted line = adult predation vulnerability threshold.

**Fig. 3: Changes in community structure of the tri-trophic food chain (A) and the multi-channel food web (B) along gradients of mesohabitat productivity and consumer body size.** Community structures, numbered as in Fig. 1: resource-only equilibrium (0, white), consumer-resource equilibria (green, 1–3), four-species equilibria (blue, 4 and 6), and coexistence of all five species (blue, 5). Solid lines: invasion thresholds of pelagic ( $C_1$ , dark green) and benthic ( $C_2$ , brown) consumers and the top predator (black). Dashed lines: invasion thresholds of pelagic (dark green) and benthic (brown)

consumers in an unstable equilibrium with top predator, and extinction threshold of top predator with one or both consumers present (black). Parameters: (A)  $K_2 = 5 \times 10^{-6} \text{ g.L}^{-1}$ , (B)  $\beta = 1.2$ , other values as in Table S1. Dotted lines: (A),  $\beta$  and  $K_2$  values used in Fig. 4; (B),  $K_1$  and  $K_2$  values used in Fig. 5.

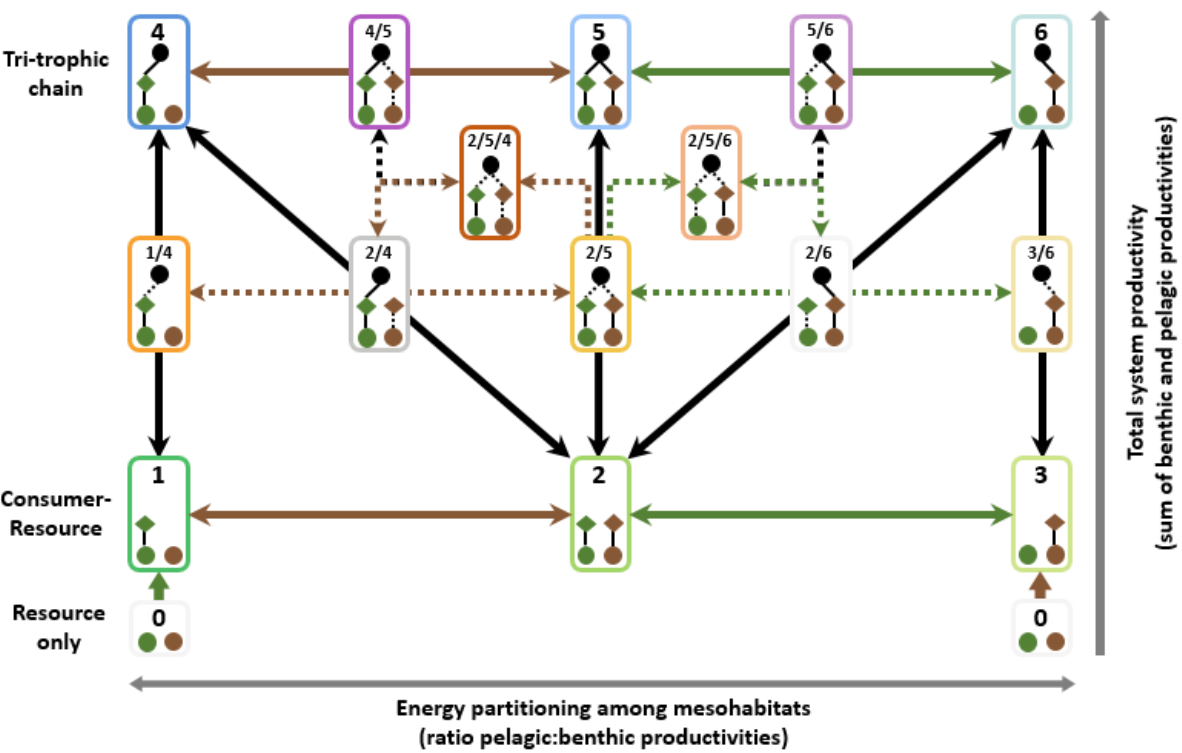
**Fig. 4: Emergent Allee effects in tri-trophic chain (A) and multi-channel food web (B), and community transition between consumer coexistence and exclusion (C) along the pelagic productivity gradient.** Parameter values:  $\beta = 1.2$ ;  $K_2 = 5 \times 10^{-6} \text{ g.L}^{-1}$  (A),  $3 \times 10^{-5} \text{ g.L}^{-1}$  (B) and  $3 \times 10^{-4} \text{ g.L}^{-1}$  (C), i.e. benthic resource productivity increasing from A to C. Other parameters as in Table S1. Solid lines: stable equilibria; dotted lines: unstable equilibria. Threshold productivity values marked by vertical dotted lines: consumer invasion (blue points), top predator invasion (black points), top predator collapse (red points). Top predator panel duplicated in (B) and (C) to enable comparison within each mesohabitat. Community structures numbered as in Fig. 1. Axes scaling: x axis transformed as  $\log_{10}(x+10^{-5})$ ; y axis transformed as  $\log_{10}(y+10^{-8})$  for juvenile and adult consumers and as  $\log_{10}(y+10^{-6})$  for resources and top predator.

**Fig. 5: Dependence of community structure of the multi-channel system on resource productivity and consumer relative body size  $\beta$ .** Resource carrying capacity always fixed in one habitat:  $K_2 = 3 \times 10^{-5} \text{ g.L}^{-1}$  (A) and  $3 \times 10^{-4} \text{ g.L}^{-1}$  (B);  $K_1 = 3 \times 10^{-5} \text{ g.L}^{-1}$  (C) and  $3 \times 10^{-4} \text{ g.L}^{-1}$  (D). Other parameters as in Table S1. Community structures numbered as in Fig. 1; coexistence of all five species denoted by '5'. Line type and colour as in Fig. 3. Dotted lines ( $\beta = 1.2$ ): results shown in Fig. 3B. Dash-dotted lines ( $\beta = 3.8$ ): predation vulnerability limit of the pelagic consumer.

**Fig. 6: Diagram of (A) emergent Allee effect and (B and C) cascading emergent Allee effects along a productivity gradient.** Dashed arrows = sudden community transitions between alternative system states; stable states (solid blue lines) separated by unstable equilibria (dotted lines). In cascading emergent Allee effect, sudden community transitions follow in succession (B; e.g., community state 2/5/6 in Figs. S3B and S5B) or in a single event (C; community state 2/5/4 in Fig S4CD). Note that stable state 2 cannot be reached by gradual changes in (C).

588    **Figures**

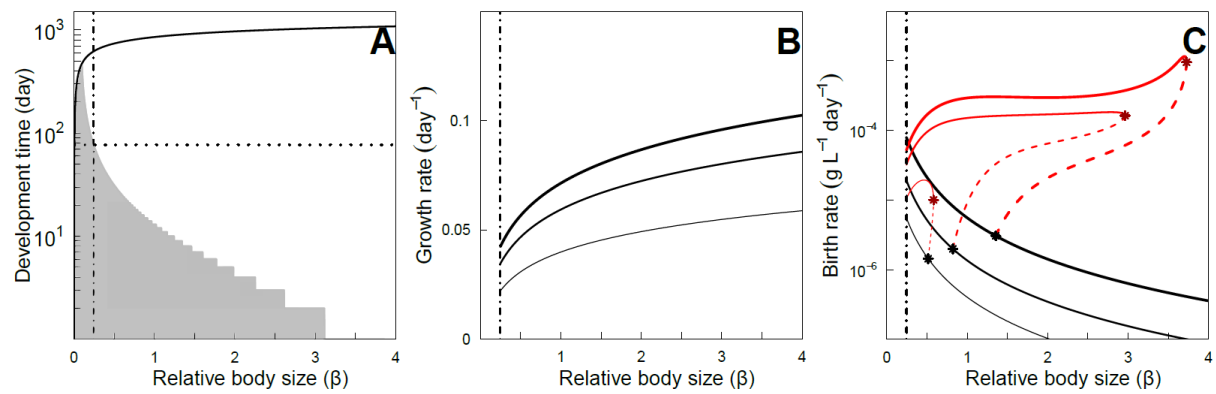
589    **Fig. 1**



590

591 **Fig. 2**

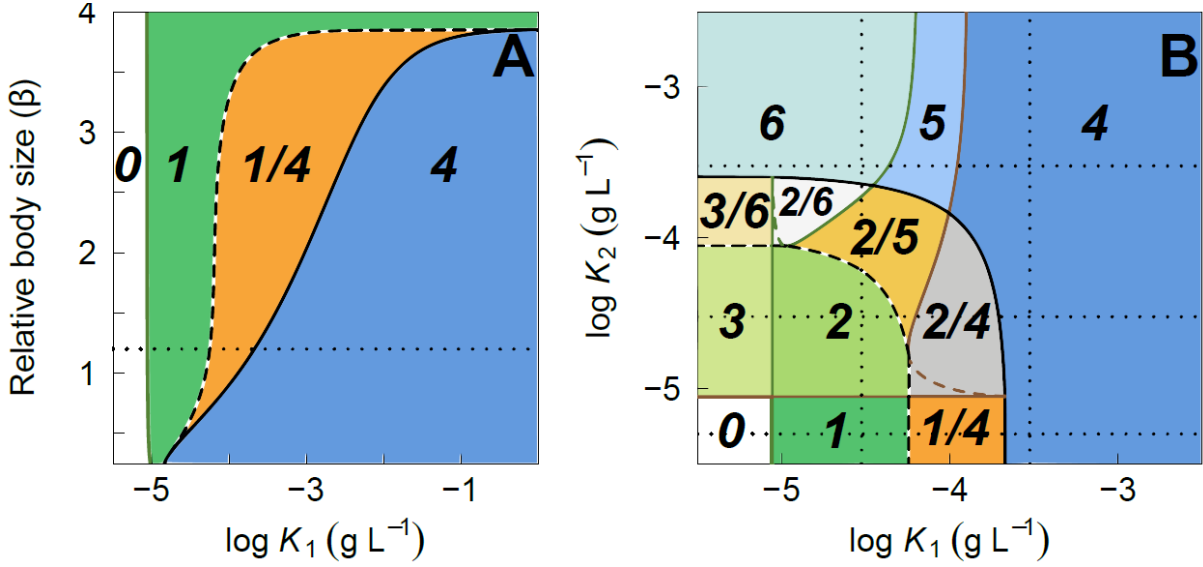
592



593

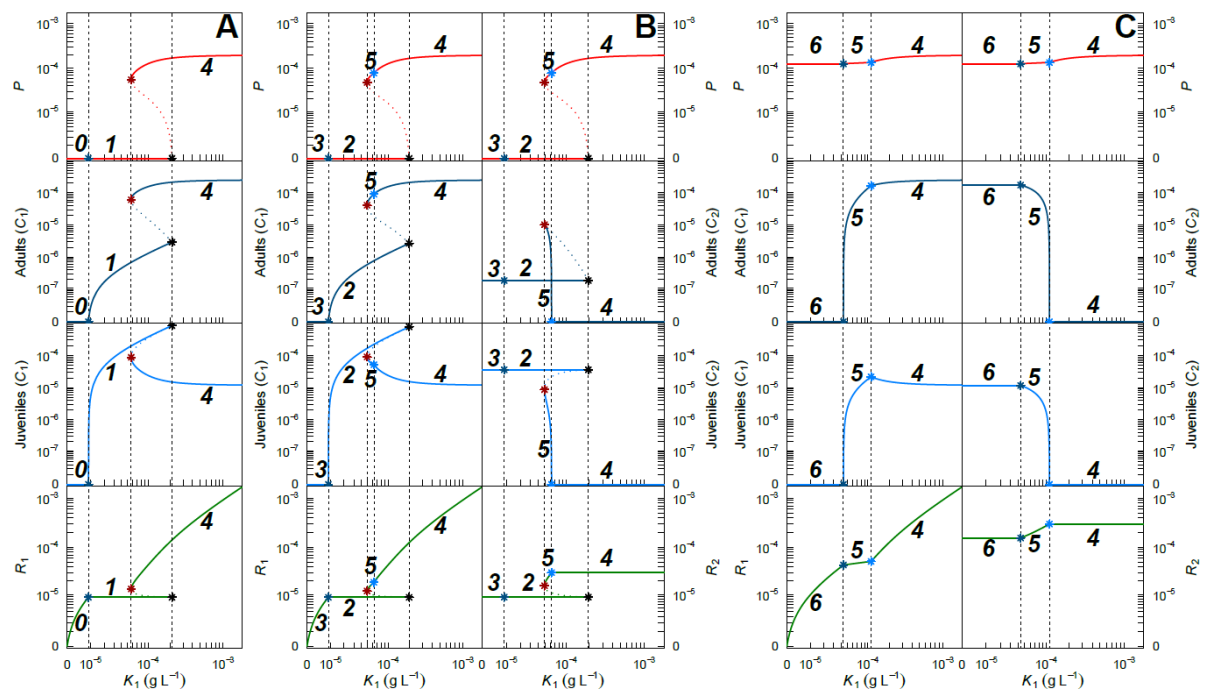


**Fig. 3**



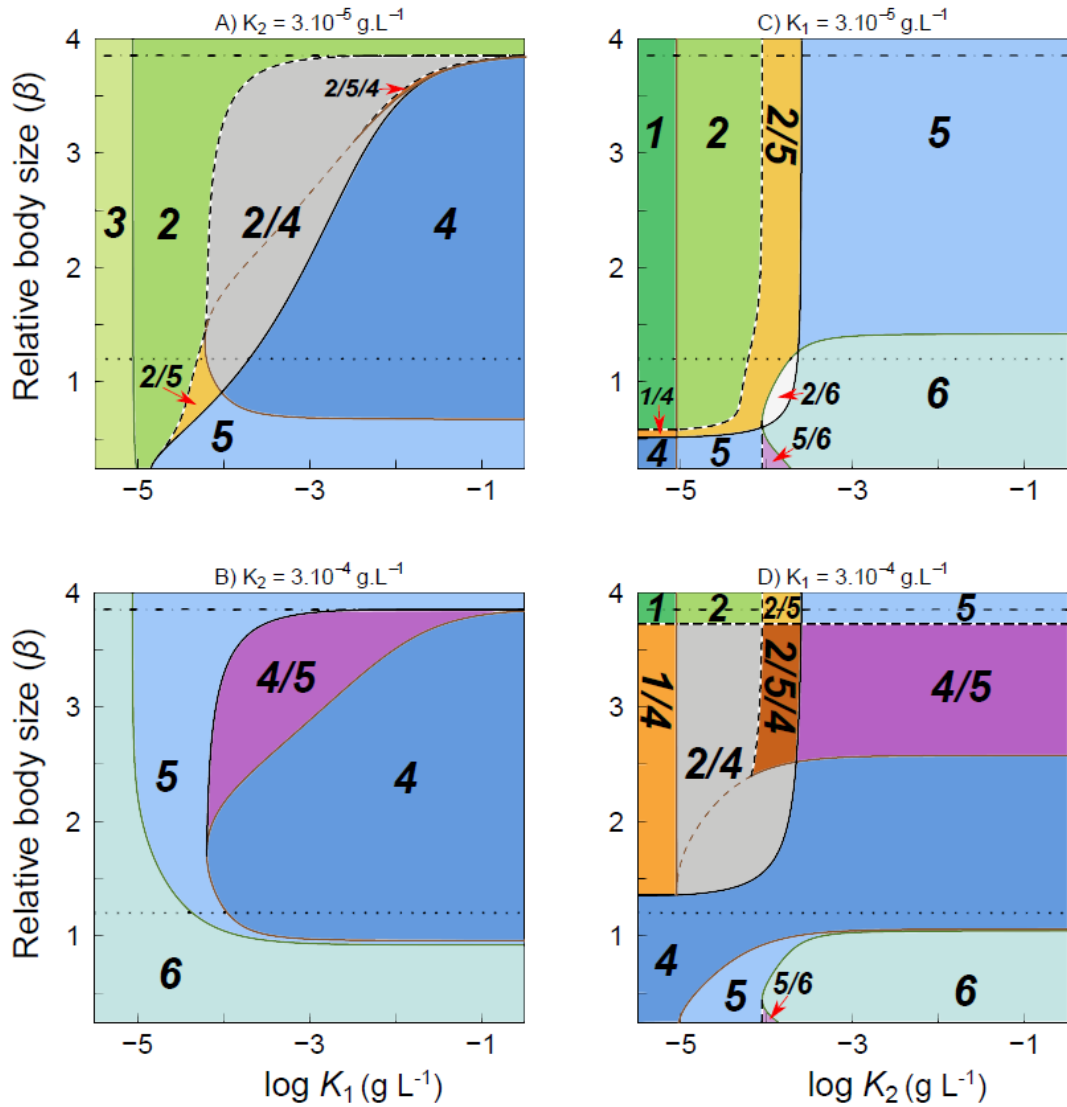
597 **Fig. 4**

598



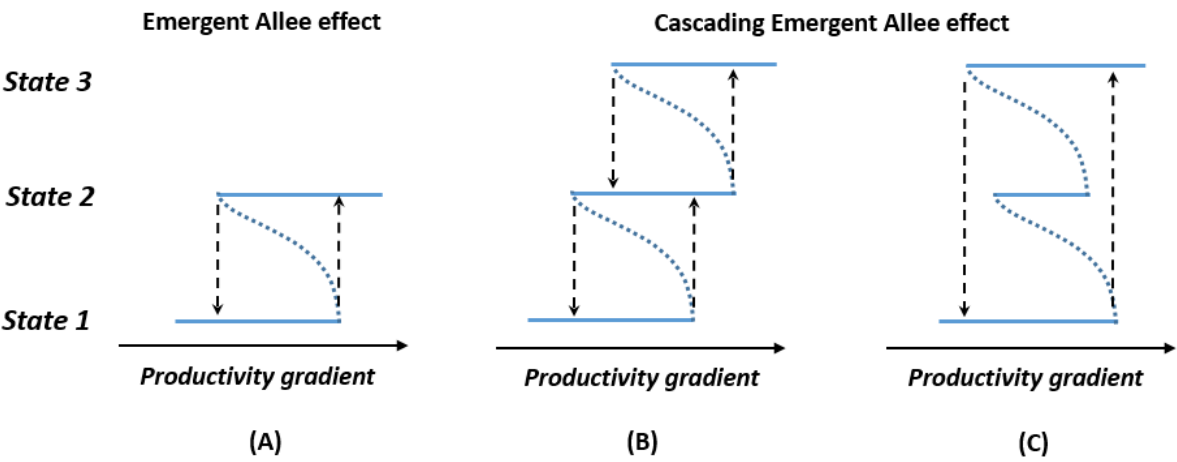
599

**Fig. 5**



603 **Fig. 6**

604



605