

LETTER

Crossing habitat boundaries: coupling dynamics of ecosystems through complex life cycles

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Abstract

Ecosystems are often indirectly connected through consumers with complex life cycles (CLC), in which different life stages inhabit different ecosystems. Using a structured consumer resource model that accounts for the independent effects of two resources on consumer growth and reproductive rates, we show that such indirect connections between ecosystems can result in alternative stable states characterized by adult-dominated and juvenile-dominated consumer populations. As a consequence, gradual changes in ecosystem productivity or mortality rates of the consumer can lead to dramatic and abrupt regime shifts across different ecosystems, hysteresis and counterintuitive changes in the consumer abundances. Whether these counter intuitive or abrupt responses occur depend on the relative productivity of both habitats and which consumer life-stage inhabits the manipulated ecosystem. These results demonstrate the strong yet complex interactions between ecosystems coupled through consumers with CLC and the need to think across ecosystems to reliably predict the consequences of natural or anthropogenic changes.

Keywords

Apparent competition, consumer subsidies, ecosystem dynamics, food webs, life-history omnivory, metamorphosis, stage-structured interactions.

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INTRODUCTION

Ecologists increasingly recognize that the indirect coupling of different ecosystem types (e.g. ocean and coast communities, ponds and terrestrial communities, benthic and pelagic communities) through fluxes of organisms across ecosystem boundaries can have strong impacts on the dynamics and structure of communities (Polis *et al.* 1997; Polis *et al.* 2004). Werner (1988) estimated that more than 80% of all animals have complex life cycles, in which there is a major transition in the ecology between two ontogenetic life stages, i.e. an ontogenetic niche shift (Wilbur 1980). As a consequence, different stages within a species (e.g. juvenile and adults) often occupy different ecosystems or habitats and consume different resources (Werner & Gilliam 1984; Polis *et al.* 1989). Although the change in ecosystem or habitat use is obvious in holometabolous insects, amphibians or marine invertebrates (i.e. pelagic vs. sessile), it is also very common in organisms without metamorphosis such as marine (Dahlgren & Eggleston 2000), freshwater (Mittelbach & Osenberg 1993; Persson *et al.* 2000) and diadromous fish (Bond 1996), crustaceans (Leonardsson

1991; Childress & Herrnkind 2001), mammals (Adams 1996; Beck *et al.* 2007), reptiles (Law 1991; Keren-Rotem *et al.* 2006) and cephalopods (Hunt & Seibel 2000). Recent studies indicate that consumers with complex life cycles can promote strong trophic cascades, stretching across ecosystem boundaries (Knight *et al.* 2005). Together with the high frequency of such life histories (Werner 1988), this suggests that organisms with complex life cycles are one of the most common and important conduits linking the dynamics of seemingly different ecosystem types (Polis *et al.* 1997; Polis *et al.* 2004).

As a consequence of the complex consumer life cycle, different ecosystems that host different life stages of a consumer are connected through growth and reproduction of the consumer and can thus indirectly affect each other. Although the importance of one-way fluxes of species with complex life cycles across ecosystem boundaries has been a central research focus (e.g. Nakano & Murakami 2001; Knight *et al.* 2005; Marczak *et al.* 2007), the long-term effects of the reciprocal interactions between both ecosystems, resulting from consumers with complex life cycles, have been largely neglected (see, however, Mouquet *et al.*

2005b). Similarly, models on complex life cycles have usually not explicitly considered independent resources for the different life stages (see references in De Roos *et al.* 2003; De Roos *et al.* 2007). As the dynamics of stage/size-structured populations and communities are often fundamentally different from unstructured systems (Ebenman & Persson 1988; Schreiber *et al.* 2001, De Roos *et al.* 2003; Persson *et al.* 2003; Abrams & Quince 2005; van Kooten *et al.* 2005; Mouquet *et al.* 2005a,b; Rudolf 2006; Cameron *et al.* 2007; Persson *et al.* 2007; Rudolf 2007), our current knowledge of the dynamics of indirectly connected ecosystems might not be applicable to many natural systems. Thus, it remains a major challenge in community ecology to understand how changes in one ecosystem type indirectly affect others.

Resource productivity is a central factor determining reproduction and survival of consumers. Therefore, one might expect that an increase in productivity in one ecosystem resource will increase the consumer population and thus indirectly decrease the resource abundance in the other ecosystem [i.e. apparent competition (Holt 1977)]. Experiments and theoretical work suggest that this prediction is not quite so straightforward for systems with stage-structured consumers. Within species, intra-cohort competition for food generally determines growth and maturation rates in the juvenile stage and fecundity in the adult stage (e.g. Nicholson 1957; De Roos *et al.* 2003). Thus, although changes in resource productivity will lead to direct changes in the abundance of an unstructured species, the net effect of the resource change on the population of species with complex life cycles will depend on the dynamics of other stages within the population (De Roos *et al.* 2007). For example, Nicholson (1957) showed that adding an exclusive resource for adult blowflies to remove adult competition can result in a decrease of the adult population and an increase in larval abundance due to the resulting strong density-dependent competition in the larval stage. Mittlebach and Chesson (1987) showed in one of the few models that did not assume a shared resource for both stages that, at equilibrium, increasing adult fecundity will increase juvenile and adult abundance, but the authors also suggest that the dynamics could be different if the juvenile survival function is not monotonic. Unfortunately, their model did not explicitly include the resource dynamics, making it difficult to draw conclusions about the general dynamics. Thus, we still face the pressing question of how changes in productivity affect the dynamics of the resources indirectly connected by a stage-structured consumer.

In this study, we use a modelling approach to analyse the dynamics of two ecosystems that are indirectly connected through a species with a complex life cycle. In particular, we

examine how changes in the resource productivity in either ecosystem or changes in consumer mortality affect the dynamics of the abundance and distribution of consumers and resources. By accounting for the independent effects of the different resources on growth or reproduction of the consumer, we show that such systems can exhibit alternative stable states, which can lead to abrupt changes in the population structure and which can lead to hysteresis. In general, we show that the dynamics of the system depend on the relative productivity of both resources, demonstrating the importance of indirect interactions between different ecosystem types.

MODELS AND METHODS

We consider a population of consumers where juveniles and adults acquire resources in different habitats (Fig. 1). The abundances of the juveniles and adults are denoted C_J and C_A , respectively. The abundances of the resource species in the juvenile and adult habitats are R_J and R_A , respectively. In the absence of consumers who couple the habitats, the resource species exhibit logistic dynamics with r_i and K_i ($i = J$ or A), denoting their intrinsic rate of growths and carrying capacities. The consumer exhibits a type I functional response (Holling 1966), where a_i , e_i and m_i denote, respectively, the attack rates, energy conversion efficiencies and per-capita mortality rates of the consumer populations $i = J, A$. If the juvenile maturation rate is proportional to their consumption rate (Persson & de Roos 2006; De Roos *et al.* 2007), and the adult reproductive rate is proportional

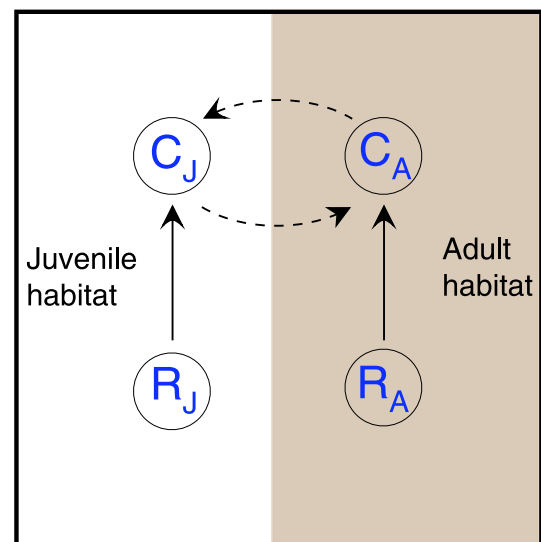


Figure 1 Flow of resources within habitats and consumers with ontogenetic niche shifts across habitat boundaries. Solid lines correspond to flow of individuals due to consumption and dashed lines correspond to flows due to reproduction and maturation.

their consumption rate (Yodzis & Innes 1992), then the consumer-resource dynamics are given by

$$\begin{aligned} \frac{dR_i}{dt} &= \underbrace{r_i R_i \left(1 - \frac{R_i}{K_i}\right)}_{\text{Logistic growth}} - \underbrace{a_i R_i C_i}_{\text{Consumption}} \quad i = J, A \\ \frac{dC_J}{dt} &= \underbrace{e_A a_A R_A C_A}_{\text{Reproduction}} - \underbrace{m_J C_J}_{\text{Mortality}} - \underbrace{e_J a_J R_J C_J}_{\text{Maturation}} \\ \frac{dC_A}{dt} &= \underbrace{e_J a_J R_J C_J}_{\text{Maturation}} - \underbrace{m_A C_A}_{\text{Mortality}}. \end{aligned} \quad (1)$$

To understand how resource productivity and mortality rates influence the structured consumer-resource dynamics, our analysis begins by deriving a criterion for persistence, i.e. all species abundances stay bounded away from extinction. When the consumer persists, we perform a nullcline analysis that permits us to understand the multiplicity of steady states for the system. Using the nullcline analysis in conjunction with numerical simulations, we examine the effects of varying habitat productivity and consumer mortality on the spatial and temporal distribution of consumer abundance and resource abundance. We conclude our analysis by examining the robustness of our results to the inclusion of consumer handling times.

RESULTS

Consumer persistence

In the absence of the consumer, the resources equilibrate at their respective carrying capacities. The consumer can invade this equilibrium if and only if the consumer reproductive number

$$R_0 = \frac{e_A a_A K_A}{m_A} \frac{e_J a_J K_J}{e_J a_J K_J + m_J}$$

is greater than 1. This reproductive number has a simple interpretation. When the adult resource is at its carrying capacity, the first term

$$\kappa = \frac{e_A a_A K_A}{m_A}$$

corresponds to the expected number of progeny produced by an adult during its lifetime. When the juvenile resource is at its carrying capacity, the second term $e_J a_J K_J / (e_J a_J K_J + m_J)$ corresponds to the probability of a juvenile surviving to adulthood. Hence, R_0 is the mean number of progeny produced by an adult that survive to adulthood. If the adult reproductive number is greater than 1, then we prove in Appendix A that the resources and the consumer coexist about a global attractor bounded away from extinction (i.e. the system is *permanent*; Hutson and Schmitt 1992; Schreiber

2000). If the adult reproductive number is less than 1, then the deterministic extinction of the consumer is unavoidable.

The adult reproductive number R_0 can be greater than 1 only if the mean number of progeny produced by an adult during its lifetime (κ) is greater than 1. As κ is proportional to the carrying capacity of the adult habitat, the consumers and resources coexist only if the adult's habitat is sufficiently enriched. Alternatively, the fraction of progeny that survive to adulthood ($e_J a_J K_J / (e_J a_J K_J + m_J)$) increases and saturates at 1, as the juvenile carrying capacity K_J increases. Therefore, when the carrying capacity of the juvenile habitat is low, the carrying capacities of the two habitats contribute in a multiplicative manner to the adult reproductive number: simultaneously increasing productivity of both habitats is more effective in mediating coexistence than increasing productivity in a single habitat. In contrast, when the juvenile habitat is highly productive (i.e. has a large carrying capacity), juveniles are likely to mature to adults and, consequently, increasing productivity of the adult habitat is the most effective means to mediate coexistence.

Nullcline analysis and alternative steady states

At an equilibrium for eqn 1, the growth rate of the resource in each habitat equals zero (i.e. $dR_J/dt = dR_A/dt = 0$). Consequently, at equilibrium, the resource and consumer abundances must satisfy $R_i = R_i^*(C_i)$, where

$$R_i^*(C_i) = K_i \left(1 - \frac{a_i C_i}{r_i}\right) \quad i = J, A.$$

Using this relationship between R_i and C_i at equilibrium, we examine the equilibria for eqn 1 via a graphical analysis in the consumer C_J – C_A plane. This analysis involves understanding the relative positions of the nullclines for the adult consumer and the total consumer population subject to the constraints $R_i = R_i^*(C_i)$.

The adult consumer nullcline is given by $dC_A/dt = 0$, which after solving for C_A and using the constraint $R_J = R_J^*(C_J)$ yields

$$C_A = \frac{e_J a_J}{m_A} C_J R_J^*(C_J).$$

As illustrated in Fig. 2a, the graph of this nullcline in the consumer plane is a downward facing parabola intercepting the juvenile consumer axis at zero and r_J/a_J , the ratio of the juvenile resource's intrinsic rate to the juvenile's searching efficiency. The maximum of this parabola occurs at an adult consumer abundance of

$$v_A = \frac{e_J r_J K_J}{4m_A}.$$

Subject to the constraints $R_i = R_i^*(C_i)$, the adults have a positive growth rate provided that (C_J, C_A) lies under

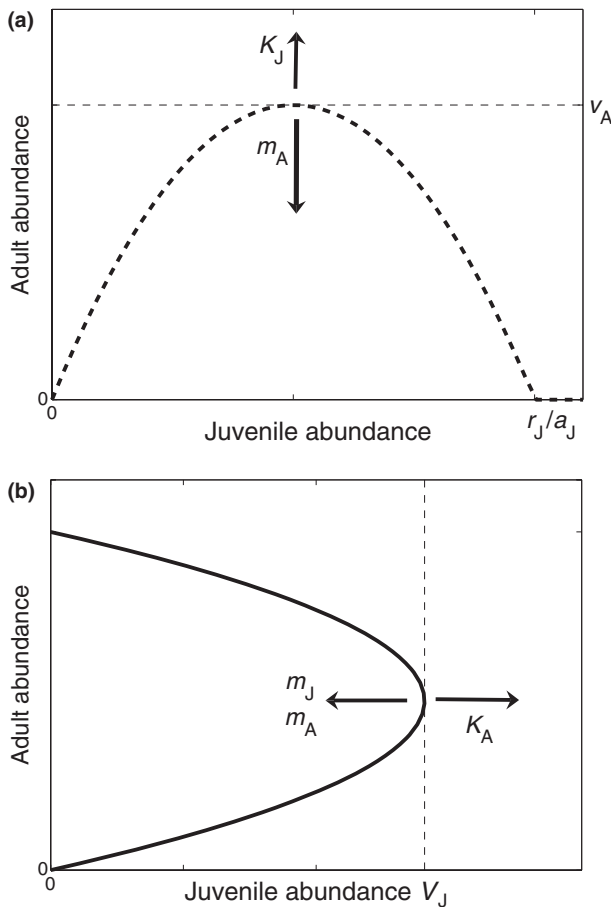


Figure 2 The nullclines for adults in (a) and for the entire consumer population in (b). The arrows show the effects of increasing productivity or consumer mortality in either habitat on the nullclines.

this parabola. The maximum of this parabola increases with productivity of the juvenile habitat and decreases with the per-capita mortality rate of the adult consumer. Intuitively, increasing juvenile habitat productivity or reducing adult mortality increases the range of conditions, supporting a positive growth rate for the adult consumers.

The nullcline for total consumer abundance is given by $dC_A/dt + dC_J/dt = 0$. Solving this expression for C_J and using the constraint $R_A = R_A^*(C_A)$ yields

$$C_J = \frac{C_A}{m_J} (e_A a_A R_A^*(C_A) - m_A).$$

Fig. 2b, the graph of this nullcline is a leftward facing parabola intercepting the adult consumer axis at zero and $(r_A/a_A)(1 - 1/\kappa)$. The maximum of this parabola occurs at a juvenile abundance of

$$v_J = \frac{1}{4} \frac{r_A}{a_A} \frac{m_A}{m_J} \left(\kappa - 2 + \frac{1}{\kappa} \right).$$

Subject to the constraints $R_i = R_i^*(C_i)$, the consumer population growth rate is positive in the region enclosed by the parabola. This expression for v_J implies that increasing the adult habitat productivity increases the maximum of the parabola and increasing adult or juvenile mortality decreases the maximum of the parabola. Intuitively, increasing adult habitat productivity or decreasing adult mortality increases the range of conditions supporting a positive growth rate for the consumer population.

As these nullclines are parabolas, they typically (i.e. for almost every parameter value) intersect at one, two or four equilibria. One of these equilibria always corresponds to extinction of the consumer. When the consumers and resources coexist (i.e. $R_0 > 1$), there are typically one or three equilibria supporting all populations. Thus, this system can exhibit alternative steady states. In the next two sections, we use the nullclines to examine how varying habitat productivity or consumer mortality rates influence the abundance and distribution of consumers and resources, and under what conditions these changes result in the creation or destruction of alternative steady states.

Varying productivities of habitats

To understand the impact of habitat productivity on the ecosystem dynamics, four scenarios are investigated. In the first two scenarios, the productivity in one habitat is varied whereas productivity in the other habitat is kept low. In the latter two scenarios, productivity in one habitat is varied whereas productivity in the second habitat is kept high. Our exploration of these scenarios combine our nullcline analysis with extensive numerical simulations of eqn 1.

Consider the case that the juvenile habitat has low productivity. The nullcline analysis implies that increasing the productivity of the adult habitat initially increases juvenile and adult abundances at equilibrium (Fig. 3a). Because the juvenile resource abundance $R_J^*(C_J^*)$ at equilibrium is a decreasing function of the consumer abundance C_J^* at equilibrium, the continual increase in juvenile abundance implies a continual decrease in juvenile resource abundance, as productivity of the adult habitat increases. With the decline of the juvenile resource, the fraction of juveniles successfully maturing declines. When the productivity of the adult habitat exceeds a threshold, the overexploitation of the juvenile resource results in such a low fraction of juveniles maturing that the adult equilibrium abundance decreases. Similar conclusions can be drawn for the case that the productivity of the adult habitat is kept low (Fig. 3b). Namely, increasing productivity of the juvenile habitat initially increases and then decreases juvenile

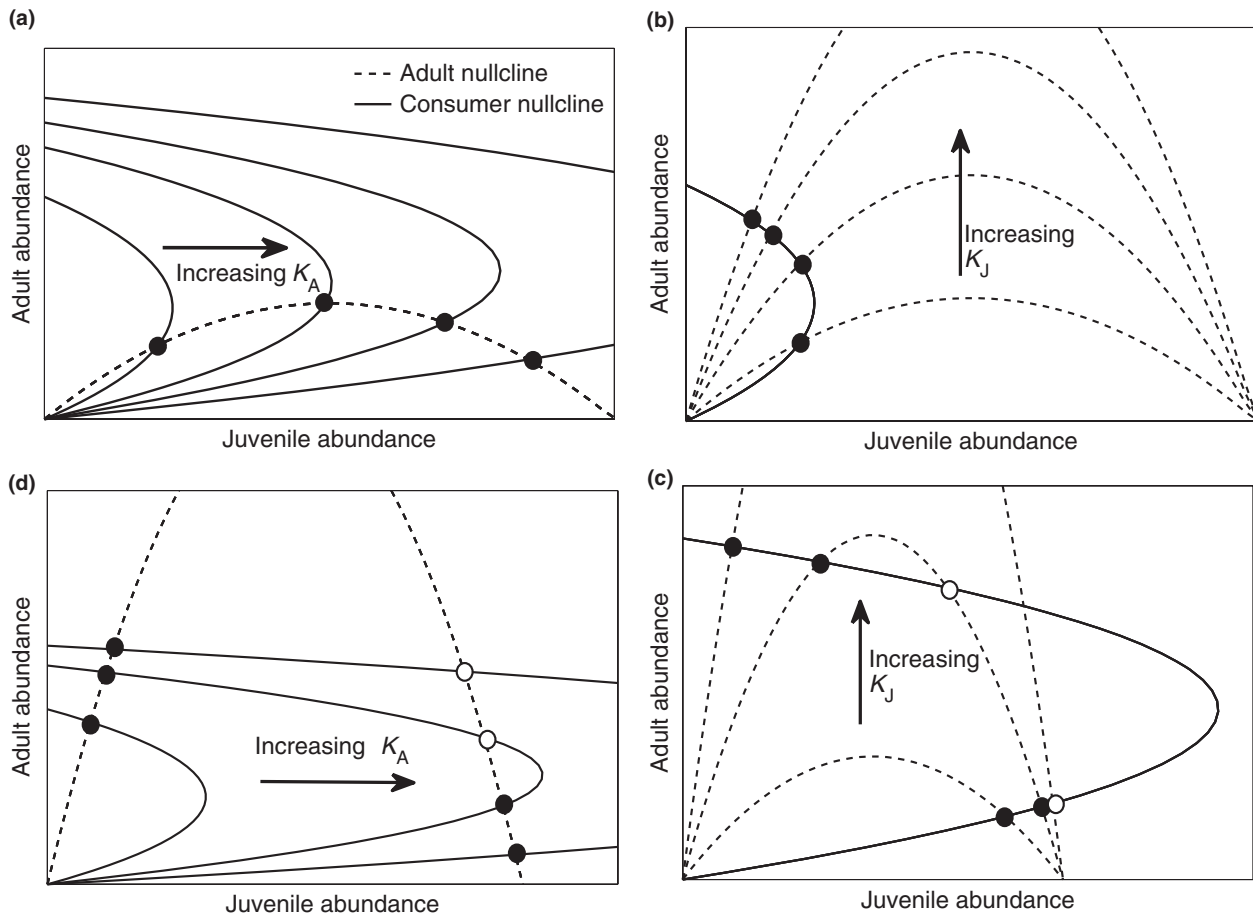


Figure 3 Effects of increasing productivity in one habitat. Solid lines correspond to the nullclines for the total consumer population and dashed lines correspond to the adult consumer nullcline. The intersection of the nullclines determine the consumer-resource steady states. Solid circles correspond to steady states associated with a stable state (e.g. stable equilibrium or periodic orbit). Open circles correspond to unstable steady states without a ‘nearby’ stable state. Plots are shown in a clockwise orientation. In (a) and (b), the productivity of the juvenile and adult habitats, respectively, is increased when the opposing habitat has a low carrying capacity. In (c) and (d), the productivity of the juvenile and adult habitats, respectively, is increased when the opposing habitat has a high carrying capacity.

abundance, continually increases adult abundance and continually decreases the abundance of the adult resource. Numerical simulations suggest that these trends occur for the mean abundances when the consumer-resource dynamics oscillate about a stable periodic orbit.

Next, assume that there is a high level of productivity in the adult habitat. Namely, $v_j > r_j/a_j$. When productivity of the juvenile habitat marginally supports the consumer population, the system exhibits a stable state with a juvenile-dominated consumer population. This stable state may be a stable equilibrium or a stable periodic orbit. At intermediate levels of productivity of the juvenile habitat, the nullclines cross (Fig. 3c) results (via a saddle node bifurcation) in two alternative stable states: the original stable state with a juvenile-dominated consumer population and a new stable state with an adult-dominated consumer

population. If the productivity of the adult habitat is pushed to sufficiently high levels, extensive simulations buttressed by the analysis presented in Appendix B imply that the juvenile-dominated stable state is lost. More precisely, increasing productivity in the juvenile habitat increases the amplitude of the consumer-resource cycle of the juvenile-dominated stable state. At a critical productivity level, the consumer-resource cycle collides with the basin boundary of the adult-dominated stable state. Following this basin boundary collision, almost all population trajectories converge to the adult-dominated stable steady state.

When enriching the juvenile habitat, the appearance and disappearance of stable states can lead to dramatic shifts in the distribution of the consumers and the availability of resources. With low productivity in the juvenile habitat, the consumer population is dominated by juveniles. Increasing

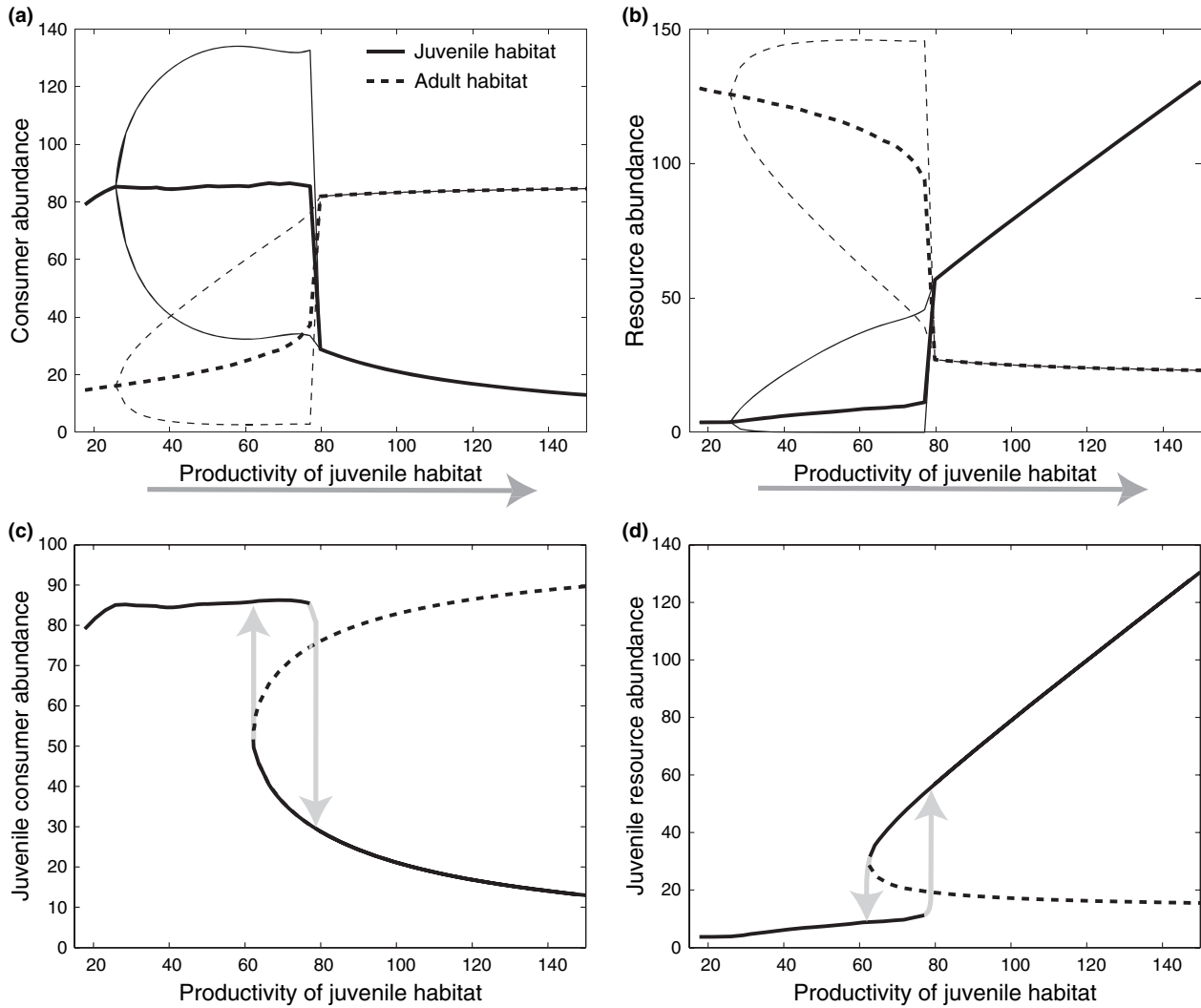


Figure 4 Altering juvenile habitat productivity when the adult habitat is productive. In (a) and (b), the juvenile habitat productivity is being increased. Mean abundances are plotted with thick lines and minimum/maximum abundances are plotted with thin dashed lines. In (c) and (d), the effects of increasing vs. decreasing juvenile habitat productivity on mean abundances (solid lines) in the juvenile habitat are shown. Dashed lines show the saddle equilibrium and grey lines indicate the directions of the bifurcations. Parameters values are $r_j = r_A = 1$, $a_j = a_A = 0.01$, $K_A = 150$, $e_j = e_A = 0.5$ and $m_j = m_A = 0.1$.

productivity of the juvenile habitat initially increases the mean abundance of all consumers (Figs 3c and 4a), which results in a decrease of adult resources (Fig. 4b). When the productivity of the juvenile habitat crosses a threshold, the community shifts to an alternative state dominated by adult consumers and juvenile resources. Crossing this productivity threshold reverses the relationship between productivity and total consumer abundance. After crossing this threshold, further increases in productivity decreases the total abundance of consumers and yields a corresponding increase in the total abundance of resources. Moreover, the consumer-resource dynamics exhibit hysteresis: the threshold necessary for the population to shift from the juvenile-dominated

stable state to the adult-dominated stable state is different from the threshold necessary for a transition back to the juvenile-dominated stable state (Fig. 4c and d).

Finally, assume that the juvenile habitat is highly productive. Namely, $v_A > r_A/a_A$. If initially the productivity of the adult habitat is low, then the consumer population consists primarily of adults. Enriching the adult habitat moves the nullcline for the consumer population to the right (Fig. 3d) and increases the equilibrium abundance of the juvenile and adult consumers. Corresponding to the increase in juvenile consumer abundance, the abundance of the juvenile resource decreases with enrichment of the adult habitat. If productivity of the adult habitat is increased

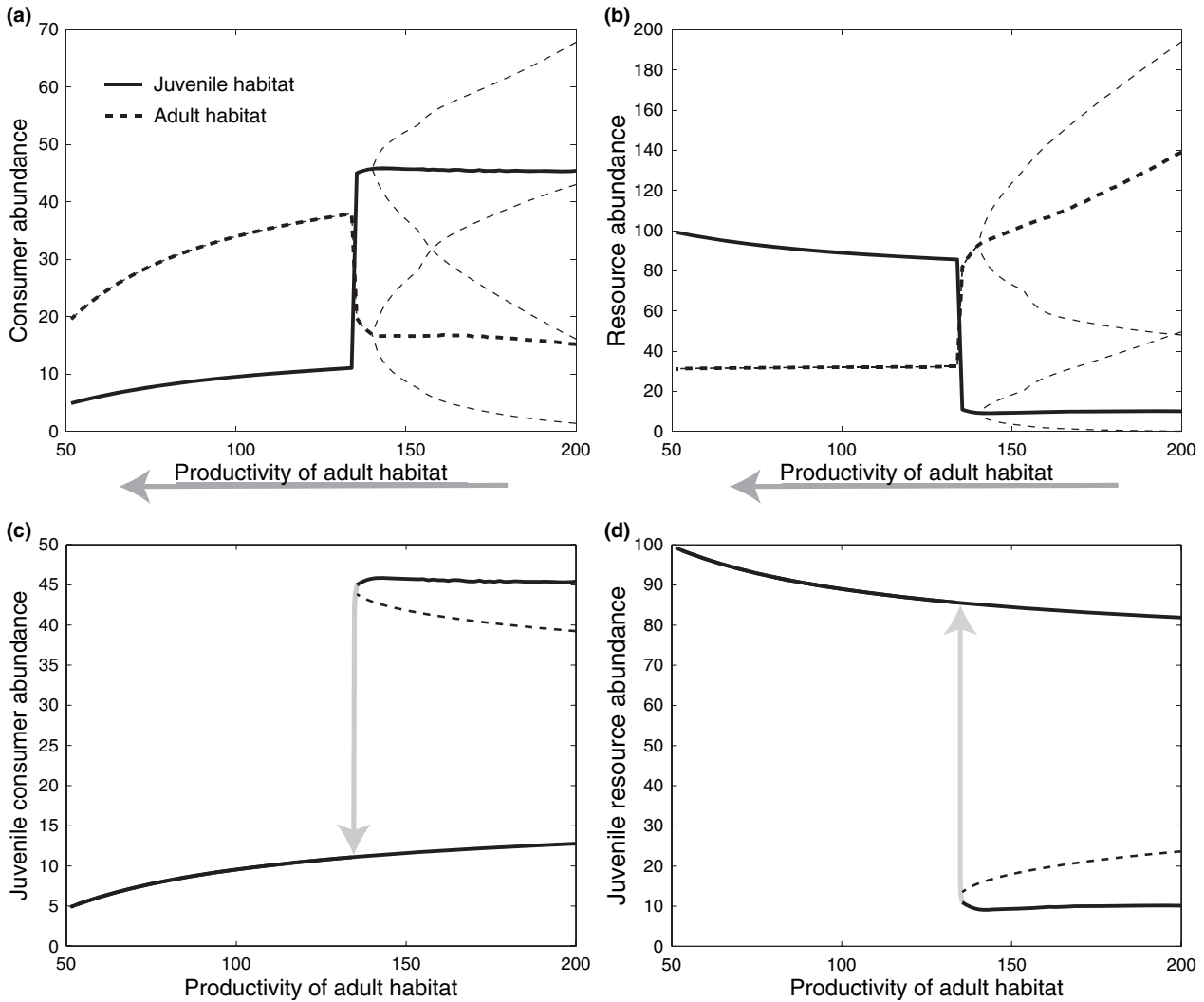


Figure 5 Altering adult habitat productivity when the juvenile habitat is productive. In (a) and (b), the adult habitat productivity is being decreased. Mean abundances are plotted with thick lines and minimum/maximum abundances are plotted with thin dashed lines. In (c) and (d), the effects of increasing vs. decreasing juvenile habitat productivity on mean abundances (solid lines) in the juvenile habitat are shown. Dashed lines show the saddle equilibrium and grey lines indicate the direction of the bifurcations. Parameter values are $r_j = r_A = 1$, $K_j = 110$, $a_j = a_A = 0.01$, $e_j = e_A = 0.4$ and $m_j = m_A = 0.1$.

sufficiently, then an alternative stable state dominated by juvenile consumers appears. However, unlike the case of enriching the juvenile habitat, numerical simulations suggest that enriching the adult habitat does not result in basin boundary collision. Consequently, without additional environmental perturbations, enriching the adult habitat does not result in a dramatic shift in the ecosystem dynamics (however, see Appendix C, which shows that such dramatic shifts can occur when the juvenile habitat has an intermediate level of productivity.)

Although increasing the productivity of the adult habitat does not lead to abrupt changes in consumer-resource dynamics, decreasing productivity can (Fig. 5a and b). These

abrupt changes occur whenever the adult habitat is initially productive and the consumer population is concentrated in the juvenile habitat. In this case, decreasing productivity of the adult habitat below a threshold results in a sharp fall in juvenile abundance and steep rise in adult abundance. Hence, there is a shift from a juvenile-dominated to adult-dominated consumer population. Corresponding to the abrupt changes in the distribution of consumers, there is a steep rise in the juvenile resource abundance and a sharp fall in the adult resource abundance. Moreover, the ecosystem exhibits an extreme form of hysteresis: increasing productivity of the adult habitat cannot return the system to its original juvenile dominated state (Fig. 5c and d). However,

as discussed in Appendix C, a less extreme form hysteresis occurs at intermediate levels of productivity in the juvenile habitat.

Effects of consumer mortalities

The previous section examined how bottom-up forces influence community dynamics across habitat boundaries. To understand how top-down forces influence patterns of abundance and ecosystem stability, we examine the effect of increasing consumer mortality in either habitat.

As observed in the nullcline analysis, increasing juvenile consumer mortality has the same effect on the nullclines as decreasing the productivity of the adult habitat (Fig. 2). For

instance, if the juvenile habitat is marginally productive and the adult habitat is highly productive, then increasing juvenile mortality can bring about a sudden shifts from an ecosystem with consumers concentrated in the juvenile habitat and resources concentrated in the adult habitat to an ecosystem where consumer and resource concentrations are reversed (Fig. 5). Moreover, this abrupt shift cannot be undone by the lowering juvenile mortality rates. In contrast to juvenile mortality, increasing adult mortality simultaneously effects the adult consumer nullcline and the total consumer nullcline: moving the former downward and the latter to the left (Fig. 2). Due to this combined effect, increasing adult mortality can have complex effects on consumer and resource abundance (Fig. 6). For instance,

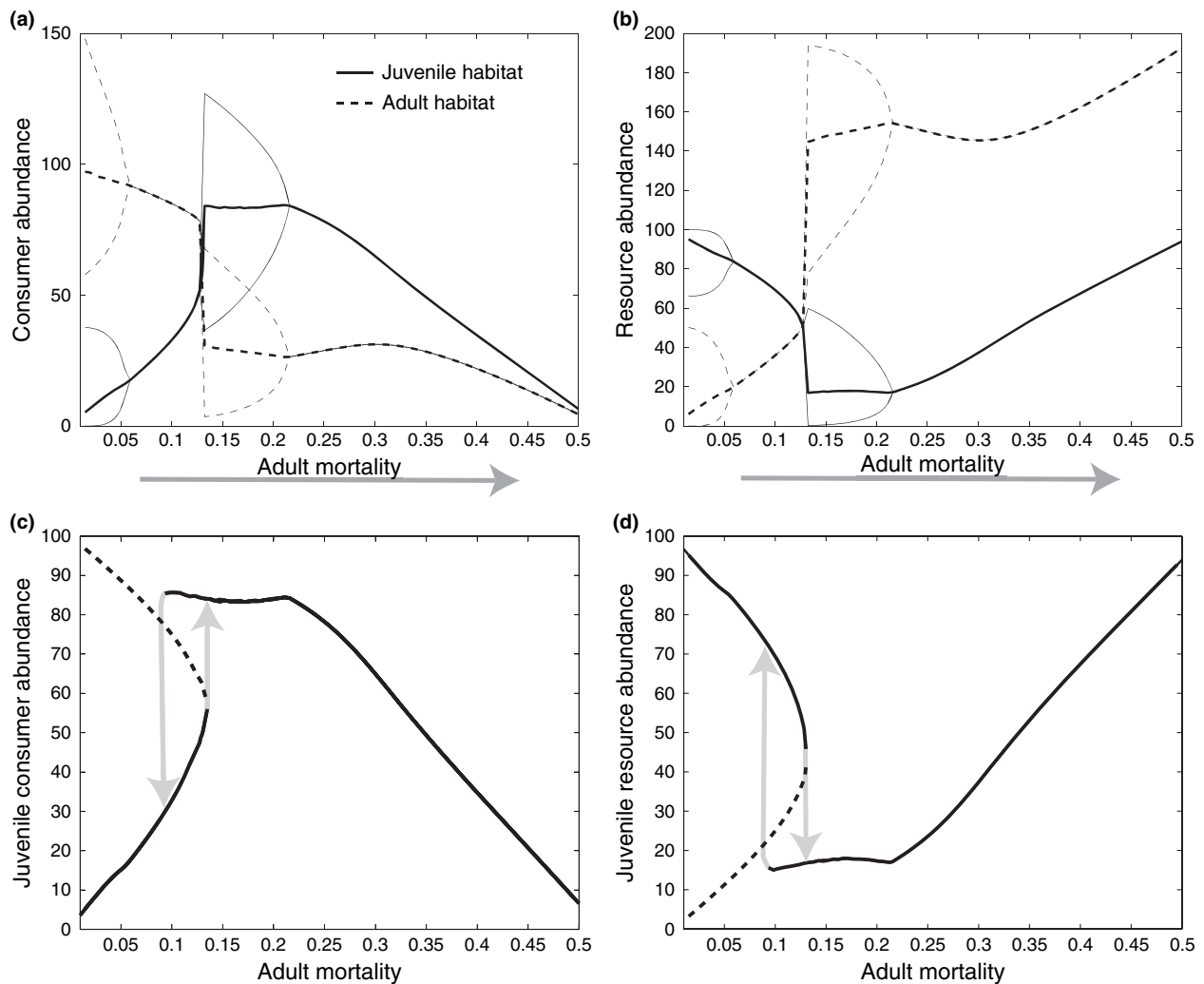


Figure 6 Effects of adult mortality. In (a) and (b), the effect of increasing the adult mortality is shown. Mean abundances are plotted with solid lines and minimum/maximum abundances are plotted with thin dashed lines. In (c) and (d), the effects of increasing versus decreasing juvenile habitat productivity on mean abundances (solid lines) in the juvenile habitat are shown. Dashed lines show the saddle equilibrium and gray lines indicate the directions of the bifurcations. Parameter values are $r_j = r_A = 1$, $K_j = 100$, $K_A = 200$, $a_j = a_A = 0.01$, $e_j = e_A = 0.4$, $b_A = b_j = 0$ and $m_j = 0.1$.

increasing adult mortality can increase juvenile consumer abundance when the ecosystem is in an adult-dominated state but decreases juvenile consumer abundance when the ecosystem has switched to a juvenile-dominated state.

Effects of handling times

In Appendix A, we describe how eqn 1 can be extended to include consumer handling times and show that longer consumer handling times decrease the reproductive number of consumers. Moreover, longer handling times make the reproductive number even more sensitive to adult consumer mortality than juvenile mortality. In Appendix D, we illustrate that although including short consumer handling times have little impact on the ecosystem dynamics, longer handling times can reduce the severity of shifts from juvenile-dominated to adult-dominated states or vice versa.

DISCUSSION

Here, we have shown that food-dependent life-history traits and an ontogenetic habitat switch that characterize the life history of many consumer species can couple the dynamics of otherwise independent ecosystems and lead to surprisingly complex dynamics, including alternative stable states and hysteresis. As a consequence, bottom-up or top-down effects in either ecosystem can lead to counterintuitive shifts in the abundances of the respective consumer stages and lead to dramatic regime shifts across different ecosystems.

Complex life cycles and regime shifts across ecosystems

There is increasing evidence of dramatic regime shifts in different ecosystems, and it has been suggested that this is due to a switch between different alternative stable states (ASS) of the system (Scheffer *et al.* 2001; Scheffer & Carpenter 2003; Schröder *et al.* 2005). Here, we have shown for the first time that enrichment in either resource or increasing the mortality of a consumer stage can lead to a shift between ASS in different ecosystems simultaneously. Once a critical threshold is reached, the consumer population shows a dramatic shift from an adult to a juvenile-dominated population [also referred to as reproduction and maturation limited populations, respectively (De Roos *et al.* 2007)] or vice versa, which results in equally dramatic but opposite shifts in their respective resources. Surprisingly, this leads to a counterintuitive collapse of the consumer stage of the enriched resource whereas the other stage dramatically increases. Additional analyses have shown that the general dynamics (including the presence of ASS) are similar if the resources have semi-chemostat dynamics (de Roos, pers. comm., Schreiber and Rudolf, unpublished data), indicating that the model predictions are robust to

specific assumptions about the resource dynamics. Previous studies that were restricted to organisms without ontogenetic diet shifts (De Roos *et al.* 2007) or did not explicitly account for the dynamics of the resources and food-dependent maturation rates (Mittelbach & Chesson 1987) did not find ASS. In our study, the presence of ASS result from two food-dependent life history traits and the complex life-cycle of the consumer, i.e. maturation and reproduction rate are dependent on two different resources.

Support for such dramatic changes comes from different field and laboratory systems. Pumpkinseed sunfish have a distinct ontogenetic diet shift from soft bodied invertebrates in the juvenile stage to snails in the adult stage (Osenberg *et al.* 1992). In ponds without Bluegill that compete for resources with juvenile Sunfish (i.e. high juvenile resource abundance), the snails (adult resource) abundance was 90% lower (Osenberg *et al.* 1992) than in ponds with the competitor (i.e. low juvenile resource abundance). Unfortunately, there is no data on the stage structure in the ponds with the competitor. However, in agreement with our model, growth rates and thus maturation rates of juveniles were much higher without the juvenile's competitors whereas the reproductive output of adults was reduced. Furthermore, a historical comparison within a pond documented that before the juvenile competitor was naturally eliminated, the abundance of snail (the adult resource) was 5–10 times more common and juvenile growth rates were four times lower and adult growth rates four times higher than after the elimination of the competitor (Osenberg *et al.* 1992). This dramatic change in the population structure of the consumer and its adult resource persisted for more than 15 years since the elimination of the competitor, suggesting a change between two stable alternative states as predicted by our model.

Additional support comes from Nicholson's (1957) seminal work on blowflies. He showed that increasing food for larvae actually decreased the survival and abundance of larvae and increased the abundance of the adult stage. Alternatively, increasing food for adults had the opposite effect and decreased the adult population by 50%. Overall, the changes in food supply for one stage lead to a sharp decrease in the abundance of that stage and sharp increase in the abundance of the other stage. These observations are consistent with our model when increasing productivity of the juvenile habitat with a sufficiently productive adult habitat, and when increasing productivity of the adult habitat with an intermediate level of productivity in the juvenile habitat (see Appendix C).

In general, these data support the predictions of our model and suggest that consumer with complex life cycles can create alternative stable states that can lead to dramatic regime shifts across completely different ecosystems. Interestingly, many of the documented regime shifts

occurred in coral reefs, lakes, ponds, marine and freshwater fish (reviewed in Scheffer *et al.* 2001; Scheffer & Carpenter 2003; Steele 2004; Persson *et al.* 2007), all of which are systems that include a large fraction of consumer species with ontogenetic habitat shifts. Unfortunately, researchers have generally focussed on one ecosystem and might thus have missed potential indirect impacts from connected ecosystems.

Coupling dynamics of ecosystem through complex life cycles

Although fluxes of species with complex life cycles are a major and important conduit connecting different ecosystems (Polis *et al.* 1996; Nakano & Murakami 2001; Knight *et al.* 2005; Marczak *et al.* 2007) little is known about the effects of the reciprocal interaction between both ecosystems that necessarily result from consumers with complex life cycles. Here, we have shown that changes in one ecosystem can indirectly and dramatically alter the community structure in the connected ecosystem if they are connected through consumers with complex life cycles.

The observed regime shifts are due to an ontogenetic diet shift and food-dependent maturation and reproduction rates. In some species such as mayflies, adults do not feed when they switch habitats. Thus, there is no ontogenetic diet switch, and the productivity in the juvenile stages is mostly driving population dynamics. However, given that the majority of organisms show some sort of ontogenetic diet shift (Werner & Gilliam 1984; Werner 1988; Polis *et al.* 1989) and food-dependent maturation and reproduction rates (De Roos *et al.* 2003), this poses the question of when such dramatic regime shifts are likely to occur. The model predicts that the effect of enrichment or changing the adult mortality depends on the relative productivity of the different resources. In general, regime shifts only occur if the carrying capacity of either the juvenile or the adult ecosystem is high relative to the adult mortality. Thus, regime shifts are unlikely if one of the ecosystems has a low net primary productivity (e.g. deserts, headwater streams, caves or oligotrophic lakes) or is relatively small compared with the other ecosystem, or if species have a relatively high adult mortality (e.g. semelparous species). Previous studies have shown that there is substantial variation in the relative difference between adult and juvenile carrying capacities across and within different species and ecosystems (Halpern *et al.* 2005). The results presented here indicate the importance of estimating and accounting for both carrying capacities to make reliable predictions on the dynamics of the two ecosystems and how environmental influences will affect the dynamics of both systems.

The model shows that increasing the resource in one habitat will generally have a predictable negative effect on

the other resource abundance and vice versa, similar to apparent competition (Holt 1977). The concurrent directions of changes in the consumer abundances, however, are dependent on the specific conditions (i.e. relative productivity) in both habitats and the distribution of the different consumer stages. Enrichment of a resource might initially increase the abundance of the respective consumer stage but can often lead to a counterintuitive gradual or dramatic (i.e. regime shift) reduction in the abundance of the consumer state as observed in Nicholson's blowflies (Nicholson 1957). This consumer decrease is caused by the corresponding decrease in the other resource, which in turn reduces the flow of individuals back into the focal habitat.

Furthermore, similar bottom-up or top-down changes in different ecosystem can lead to different dynamics depending on which life stage is present in the respective ecosystem. For example, shifts between ASS can occur when increasing the productivity of the juvenile habitat, but may not occur when increasing the productivity of the adult habitat. However, decreasing the productivity of the adult habitat can bring about a shift between ASS if the consumer population is initially dominated by juveniles. In a related study by Mouquet *et al.* (2005b), models of the complex life cycle of the butterfly *Maculinea* showed that increasing the resource of the first larval stages (plants) can either increase or decrease the adult population depending on the specific parameter conditions, whereas increasing the resource of the subsequent larval stages will always have an increase in the adult population. These results suggest that the indirect interactions between ecosystems through consumers with complex life cycles are often not symmetrical and that we need to account for the distribution of the consumer stages to predict how environmental changes will affect both ecosystems.

CONCLUSION AND IMPLICATIONS

Although there is ample evidence of ontogenetic shifts of consumers between ecosystems, there is surprisingly little information about these ontogenetic shifts for the long-term dynamics of coupled ecosystems, most likely due to the difficulties to monitor the different life stages of consumers with complex life cycles and their respective resource. Our results emphasize how reciprocal consumer fluxes across utterly different ecosystems can affect the structure and dynamics of local species interactions and emphasize the need to account for the resulting indirect interaction between ecosystems. This also indicates, however, that anthropogenic impacts such as eutrophication of lakes, or size-selective harvesting or stocking can indirectly lead to dramatic regime shifts, not only in the manipulated ecosystem but also in seemingly unrelated ecosystems, and the inability to restore the state of the system (i.e. hysteresis).

Furthermore, anthropogenic changes might lead to opposite outcomes than what was desired (i.e. collapse of the target population). These results emphasize the need to think across ecosystems when studying community dynamics and managing populations with complex life cycles or single ecosystems.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

A pdf file containing the following:

- **Appendix A** Permanence for the general model.
- **Appendix B** Increasing juvenile productivity.
- **Appendix C** Hysteresis at intermediate productivity levels.
- **Appendix D** Effects of handling time.
- **Figure B1** Loss of the juvenile-dominated state due to increasing productivity of the juvenile habitat.
- **Figure C1** Effects of increasing productivity in the adult habitat when the juvenile habit has intermediate levels of productivity.
- **Figure C2** Altering adult habitat productivity when the juvenile habitat is productive.
- **Figure D1** Effect of handling times on consumer-resource dynamics when the adult habitat is productive.

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