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Citation for the published paper:

van Leeuwen, A., Huss, M., Gardmark, A., Casini, M., Vitale, F. et al. (2013)
"Predators with Multiple Ontogenetic Niche Shifts Have Limited Potential for
Population Growth and Top-Down Control of Their Prey"
American Naturalist, 182(1): 53-66

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Source: *The American Naturalist*, Vol. 182, No. 1 (July 2013), pp. 53-66

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/670614>

Accessed: 29/07/2013 08:21

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Predators with Multiple Ontogenetic Niche Shifts Have Limited Potential for Population Growth and Top-Down Control of Their Prey

Anieke van Leeuwen,^{1,*} Magnus Huss,^{2,†} Anna Gårdmark,² Michele Casini,³ Francesca Vitale,³ Joakim Hjelm,³ Lennart Persson,⁴ and André M. de Roos¹

1. Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands; 2. Institute of Coastal Research, Department of Aquatic Resources, Swedish University of Agricultural Sciences, Skolgatan 6, SE-742 42 Öregrund, Sweden; 3. Institute of Marine Research, Department of Aquatic Resources, Swedish University of Agricultural Sciences, Turistgatan 5, 453 30 Lysekil, Sweden; 4. Department of Ecology and Environmental Sciences, Umeå University, SE-901 87 Umeå, Sweden

Submitted May 14, 2012; Accepted February 6, 2013; Electronically published May 15, 2013

Online enhancements: appendixes.

ABSTRACT: Catastrophic collapses of top predators have revealed trophic cascades and community structuring by top-down control. When populations fail to recover after a collapse, this may indicate alternative stable states in the system. Overfishing has caused several of the most compelling cases of these dynamics, and in particular Atlantic cod stocks exemplify such lack of recovery. Often, competition between prey species and juvenile predators is hypothesized to explain the lack of recovery of predator populations. The predator is then considered to compete with its prey for one resource when small and to subsequently shift to piscivory. Yet predator life history is often more complex than that, including multiple ontogenetic diet shifts. Here we show that no alternative stable states occur when predators in an intermediate life stage feed on an additional resource (exclusive to the predator) before switching to piscivory, because predation and competition between prey and predator do not simultaneously structure community dynamics. We find top-down control by the predator only when there is no feedback from predator foraging on the additional resource. Otherwise, the predator population dynamics are governed by a bottleneck in individual growth occurring in the intermediate life stage. Therefore, additional resources for predators may be beneficial or detrimental for predator population growth and strongly influence the potential for top-down community control.

Keywords: ontogenetic niche shifts, life-cycle complexity, mixed interactions, predator-prey dynamics, *Gadus morhua*, size-structured population.

* Corresponding author. Present address: Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544; e-mail: aleeuwen@princeton.edu.

† Present address: Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06520.

Am. Nat. 2013. Vol. 182, pp. 53–66. © 2013 by The University of Chicago. 0003-0147/2013/18201-53844\$15.00. All rights reserved.

DOI: 10.1086/670614

Introduction

The ecological importance of top predators structuring lower trophic levels by top-down control is increasingly acknowledged, as illustrated by the numerous studies and examples of trophic cascades in diverse ecosystems (reviewed in, e.g., Pace et al. 1999; Shurin et al. 2002; Estes et al. 2011). The majority of examples of the structuring role of predators is, however, found in marine and freshwater systems (e.g., Scheffer et al. 1993; Persson et al. 2003, 2007; Daskalov et al. 2007; Myers et al. 2007; Casini et al. 2008; Möllmann et al. 2008; Baum and Worm 2009). Trophic cascades in natural systems are often revealed following the collapse of a top predator, which is in many cases due to anthropogenic influences, such as overexploitation by fishing and hunting, habitat destruction, and disturbances (Strong and Frank 2010). If a community restructuring and inverted dominance occurs after a top-predator collapse, this may represent an irreversible system state and hence indicate that a regime shift has occurred (Carpenter et al. 2008; but see Frank et al. 2011 for a different perspective). The potential for spontaneous predator recovery is then diminished even when exploitation is reduced to levels below the situation preceding the collapse. Evidence for such alternative stable states in whole ecosystems is present in freshwater and marine systems (Frank et al. 2005; Persson et al. 2007; Casini et al. 2008; Möllmann et al. 2008).

Proposed mechanisms for stabilization of alternate states after a predator collapse often involve life-history omnivory in the predator (Pimm and Rice 1987), which refers to a trophic configuration with predators feeding on different resources at different stages in life. Life-history

omnivory may lead to mixed interactions between predator and prey species, when predators compete in early life stages with species on which they feed in later life stages. Life-history omnivory has been suggested to be a driver of juvenile bottlenecks (limitation of individual growth during the juvenile phase) in predator life history (Persson 1988; Olson et al. 1995; Byström et al. 1998). This occurs when competition with prey species slows down individual growth and decreases survival through early juvenile predator stages, thus limiting recruitment to the adult life stage. As a consequence, juvenile bottlenecks may limit predator population recovery from low densities and can lead to alternative stable community states in predator-prey systems (Neill 1975; Persson 1986). At high abundance, predators have been suggested to suppress the competitors of their own juveniles and lift the bottleneck in that stage ("cultivation"; Walters and Kitchell 2001). On the other hand, when the predatory life stages are removed from the system (e.g., by harvesting), the increased competition from abundant prey may induce a bottleneck in juvenile predator development and prevent the predator population rebuilding from low densities ("depensation"; Walters and Kitchell 2001). The cultivation/depensation hypothesis is often invoked to explain lack of recovery of collapsed cod stocks (Olson et al. 1995; Bax 1998; Swain and Sinclair 2000; Walters and Kitchell 2001; Bundy and Fanning 2005; Baskett et al. 2006; Casini et al. 2009).

Life history and population structure are explicitly considered in the theory regarding mixed interactions, life-history omnivory, and cultivation/depensation effects, as exemplified by studies that have analyzed the effect of an ontogenetic diet shift in predators (van de Wolfshaar et al. 2006; Hammerschlag-Peyer et al. 2011; Hin et al. 2011). These analyses have significantly expanded the understanding of community dynamics and underlie general predictions about community properties, such as coexistence potential, stability, and invasion success, in both theoretical and experimental settings (Olson et al. 1995; Polis and Strong 1996; Swain and Sinclair 2000; Walters and Kitchell 2001; Schroder et al. 2009; Rudolf and Lafferty 2011). In these studies, two aspects in predator life history are considered: competition with prey in the juvenile stage and foraging on prey in the adult stage. In many cases, however, the life history of predators is more complicated than that, including multiple diet shifts and more than two life stages. For example, piscivorous fish, such as perch and cod, forage on zooplankton in their earliest feeding stage and switch to benthic organisms before actually becoming piscivorous (Olson et al. 1995; Hussy et al. 1997; Lomond et al. 1998). Although known in particular from examples in piscivorous fish species (Winemiller 1989; Stergiou and Fourtouni 1991; Garcia-Berthou 2002; Galarowicz et al. 2006), the phenomenon of multiple onto-

genetic niche shifts is general, occurring in anurans and vipers as well (Flowers and Graves 1995; Lima 1998; Martins et al. 2002). The ecological effects for community stability and structure of this added complexity in the predator life cycle are unclear (but see Rudolf and Lafferty 2011).

In this study, we explicitly address this issue and analyze the implications for community dynamics of an additional diet shift in predator life history during an intermediate life stage, in which predators forage on an alternative resource. For analysis of this question, we use a size-structured predator-prey model that is based on the Baltic Sea cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) predator-prey system. Population abundance data from this ecosystem have revealed a regime shift in the late 1980s and early 1990s, marking a change in species dominance from cod to sprat and discriminating two system states with different drivers of community dynamics (Casini et al. 2008, 2009; Möllmann et al. 2008). Increased competition between zooplanktivorous prey species (such as sprat) and early cod stages following reduced predation pressure after the cod population collapse is thought to play an important role for the continuously low cod population densities in several regions (Bax 1998; Swain and Sinclair 2000; Walters and Kitchell 2001; Bundy and Fanning 2005; Casini et al. 2009). In this hypothesis, competition between prey and early cod stages forms the major limiting factor for individual predator growth (i.e., competition then results in a juvenile bottleneck). Such a juvenile bottleneck in individual growth can be the underlying cause for the lack of predator population recovery. We formulate and analyze a physiologically structured population model (Metz and Diekmann 1986) for this predator-prey system based on the size-dependent processes and interactions between cod and its prey species. Three ontogenetic foraging stages in the predator are explicitly accounted for. We study how increased life-history complexity resulting from the intermediate foraging stage influences the possibility for top-down control and the scope of juvenile predator bottlenecks. The results are compared to those from previous theoretical studies especially with respect to the effects of the additional niche shift, the discreteness of the niche shifts, and the extent to which the predator can mature on nonprey resources.

Model Description

We formulate a physiologically structured population model (Metz and Diekmann 1986) to study increased complexity in the predator life cycle in the form of an additional ontogenetic niche shift and a second nonpredatory life stage. The life-history scenario in the predator-prey system used for this analysis was based on the Baltic

Sea cod-sprat system. The full model description is given in appendix A (app. A and B are available online), but the main model components are summarized below. The model accounts for a size-structured predator population, a size-structured prey population, an unstructured predator-exclusive resource (referred to as “intermediate resource” because the intermediate predator life stage depends on this resource; this resource is, however, also preyed upon by adult predators, and it represents benthic organisms), and two unstructured basal resources (referred to as “basal resources,” consumed by prey and small juvenile predators, representing zooplankton). We refer to the basal resource that is used exclusively by small juvenile predators as “juvenile resource.” The overlap in use of the basal resources by prey and small juvenile predators is varied (see below and app. A for more details).

Figure 1 shows a schematic representation of the modeling framework and an overview of the trophic interactions accounted for in the model. The predator experiences two niche shifts during its ontogeny: after hatching it starts out feeding on only the juvenile resource, after which it gradually switches to the intermediate resource (starting at the minimum length l_B ; fig. 1; note the difference with van de Wolfshaar 2006, where the second resource is available to predators of all sizes), and subsequently it broadens its diet by the addition of piscivory (starting at length l_P ; fig. 1; this coincides with the size where juvenile predators completely stop foraging on the juvenile resource). It is important to note that the modeled diet shifts do not occur as discrete changes but that in both cases there is overlap in resource use over a range of body sizes (see the fraction of foraging time per resource in fig. 1).

In the framework of physiologically structured population models, the individual state (*i*-state) is distinguished from the population state (*p*-state): the *i*-state constitutes the physiological characteristics of an individual, and the *p*-state constitutes the distribution of these characteristics in the population. In the model, size-dependent processes and interactions between species are defined at the *i*-state level, with the dynamics of the *p*-state level emerging from those processes. The *i*-state is defined by (1) age; (2) body size (or structural mass), representing the part of body mass that is essential and cannot be starved away (i.e., bone and muscular tissue); and (3) energy reserves (or reversible mass), representing the part of body mass that is not essential and can be used and regained under starvation (i.e., fat and gonadal tissue). Structural body mass is directly related to length, whereas the ratio between reversible and structural body mass determines the condition of an individual. Total body mass is the sum of body size (structural mass) and energy reserves (reversible mass; see app. A for details).

Attack and maximum ingestion rates are defined as func-

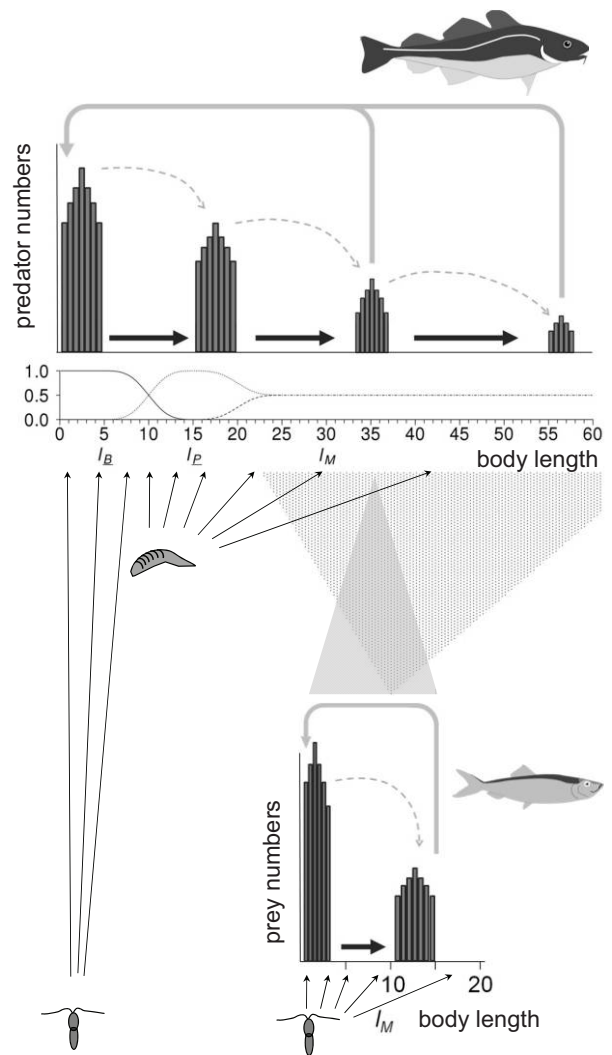


Figure 1: The three levels of trophic organization and connections between these levels in the predator-prey model. The X-axes in the two frequency distributions represent individual length (l_B and l_P indicate the length at which benthivory and piscivory start in the predator, and l_M indicates the length at maturation). The Y-axes show the cohort frequency distribution in the predator (*upper graph*) and prey (*lower graph*) populations. The individual-level processes of growth and reproduction are indicated by thick arrows (black and gray, respectively), whereas mortality is indicated by the gray dashed arrows. Note that reproduction is a discrete event, leading to a discontinuous frequency distribution. Feeding interactions are indicated by thin arrows, representing the biomass flows from resources to consumers. The predation window of a predator individual of 35 cm is shown in the shaded area. The vulnerability window of a prey individual of 11 cm is shown in the dotted area. Below the predator frequency distribution the ontogenetic niche shifts in predator life history are shown as the size-dependent functions of foraging time on the different resources.

tions of individual body length. The prey is considered to feed on the basal resource throughout its ontogeny. Its attack rate is defined as a hump-shaped function of length. The attack rates of the predator on the juvenile and intermediate resources are described as power functions of its length. The piscivorous attack rate follows a tent-shaped function with a maximum at an optimal prey-predator length ratio and lower attack rates on suboptimal prey sizes within the predation window. Apart from the attack rates, the encounter rate with different resources is a function of the fraction of time spent foraging for these resources, which depends on individual body size (fig. 1; see the model formulation in app. A for more details and parameterization).

The density of different food sources, the attack rates, the foraging time, and the maximum ingestion rates together determine the food intake of individual fish, following type II functional responses. Ingested food is assimilated with constant efficiency. A net production model (as in Persson et al. 1998) is used to describe the dynamic energy budget of individuals as a balance between assimilated food and costs for metabolism (Kooijman 2000). Metabolism is modeled as a power function of the total body mass of an individual. When assimilated energy from food consumption exceeds the costs for metabolism (and net energy is hence positive), the net energy is used for growth and reproduction. When maintenance costs exceed the energy gains from feeding, the individual starves (and uses biomass from fat reserves and gonads as energy source), eventually leading to an increase in mortality when energy reserves are depleted below a threshold level (see app. A for the exact functions and dependence of mortality on body condition). When an individual can recover after a period of starvation, the buildup of reversible body mass takes priority over growth in length, which ensures a relatively high body condition. Apart from starvation mortality, both predator and prey suffer from size-dependent mortality, which decreases with body size, and from size-independent background mortality. Prey furthermore experience predation mortality by the predator. Cannibalism is not included in the model, so predators do not experience predation mortality.

We have analyzed two different versions of the model, one in which reproduction takes place in a discrete event at the start of the growing season and another in which offspring production follows a normal distribution over a spawning period of 90 days. When the reproduction event starts, adult individuals (individuals with length $\geq l_{\text{ad}}$; fig. 1) invest part of their reversible mass in egg production, bringing their body condition down to a baseline level. Since both model variants lead to qualitatively equivalent results (see details in app. A), we present only results of the model with reproduction as a discrete event. We assume that the growing season lasts 250 days and that dynamics outside

this growing season can be neglected. The dynamics of the prey and predator populations arise from the processes taking place at the individual level—that is, feeding, growth, and survival—while reproduction at the start of each season leads to an increase in these populations. The three unstructured resources are characterized by a constant productivity in the absence of predation and hence follow semi-chemostat growth dynamics (Persson et al. 1998).

The population dynamics resulting from the individual-level processes described above are studied with numerical simulations using the integration method developed by de Roos et al. (1992). Community dynamics are studied over a broad range of basal resource productivities. For each productivity value the asymptotic dynamics of the system is determined using time integrations over periods of 400 years, of which the first 350 years of transient dynamics are disregarded. These time integrations are used to construct both the persistence and the invasion boundary of predator and prey. The persistence boundary of a species is located at the resource productivity level for which it cannot sustain itself any longer and is lost from a community (see app. A for a more detailed definition). For the predator, this boundary hence reflects the productivity threshold below which resource availability (juvenile resource biomass or prey biomass) is too low or prey competition is too high for predator persistence. The prey has a similar minimum productivity level for persistence (albeit at lower resource productivity than the predator) in addition to an upper persistence boundary at the productivity threshold above which predation becomes too high for prey persistence. We determine these persistence boundaries for predator and prey in both the presence and the absence of the other species.

In contrast to the persistence boundary, which reflects the performance of a population under conditions that include feedback on its resources, the invasion boundary reflects individual performance in the absence of population feedbacks. More specifically, the invasion boundary represents the resource productivity combination for which the average lifetime offspring production of a single individual in the absence of any intraspecific density dependence equals exactly 1. We calculate this boundary for predator and prey while assuming no feedback from the focal species itself. In other words, we use the baseline dynamics of the environment in which a species would invade to determine whether the species has the potential for population expansion under these environmental conditions in the absence of any direct or indirect density dependence (see app. A for a more detailed description). Differences between the persistence and invasion boundaries indicate a region of bistability where persistence is possible for combinations of resource productivity that do not allow for invasion. For example, if the predator can

persist but cannot invade a prey-only community for particular resource productivities, coexistence of prey and predator is possible, but the predator will not be able to recover after a collapse.

In this study we focus on two aspects of community dynamics: how does life-cycle complexity in the top predator affect the potential for top-down control of the prey population, and how does life-cycle complexity affect the scope for juvenile predator bottlenecks to limit predator population recovery? To answer these questions, we study the community dynamics in two scenarios: (1) the intermediate resource is modeled assuming a constant resource level on which feeding by the predator has no effect and (2) feedback from predator foraging on the intermediate resource is taken into account. The maximum density of the intermediate resource is the same in both scenarios and is assumed to provide a feeding level >85% for individuals larger than 15 cm. The two scenarios represent the cases where the intermediate resource is excluded from intraspecific density dependence or where it may be limiting for predator growth. The former situation may represent the scenario where benthic organisms are continuously available in high supply for an omnivorous predator like cod. Alternatively, it may represent a scenario where the turnover of these organisms is sufficiently high such that depletion of their abundance is irrelevant for food limitation of predators.

In both scenarios, we analyze the consequences of including competition from prey for top-down control and prey-induced juvenile bottlenecks in the predator. Competition is modeled as an overlap in use of the basal resources, which are exploited exclusively by one species in the default scenario without competition. Because we focus primarily on the issue of whether the predator can recover from low densities, we vary the foraging effort of small juvenile predators on the basal resource and the juvenile resource. Juvenile predators are assumed either to feed only on their exclusive juvenile resource (default scenario) or to spend part of their foraging time on the basal resource that otherwise is exclusively fed upon by prey. This leaves the baseline dynamics of the prey population in the absence of the predator unaffected, independent of possible overlap in the feeding niche between prey and juvenile predators. Tests and findings regarding the generality of results and robustness of the major outcomes are described in more detail in "Discussion" and in appendix B.

Results

Including Feedback on the Intermediate Resource, No Competition

The dynamics of the prey population are characterized by a so-called single cohort cycle with a 2-year period (fig.

2A). Throughout this cohort cycle the population is constituted by a single cohort, due to the pulsed nature of reproduction and the size scaling of resource intake. Because small individuals have a more energy-efficient balance between maintenance and intake rates, the newborns depress the resource below the minimum level needed by adults to cover their maintenance requirements. The newborn cohort therefore outcompetes the adult individuals immediately following a reproduction event. The juvenile cohort declines in abundance as a result of size-dependent and background mortality, which allows the individuals to grow to maturation size and subsequently reproduce, after which they are outcompeted by their own offspring (Persson et al. 1998; fig. 2A). Predation has little impact on prey population dynamics, regardless of the productivity level of the basal resource (see app. B). Predation only leads to some differentiation in the maximum length reached by prey over a period of 10 years (fig. 2A, bottom panel).

Predator dynamics at high basal resource productivity are regulated bottom-up by the availability of the intermediate resource. In the first life stage, when foraging on the juvenile resource, predators experience ample food and fast growth (fig. 2B, bottom panel). When the intermediate resource becomes relatively more important in the diet than the juvenile resource (at a length of 10 cm), growth slows down. During the following 4 years, the juvenile cohorts that are born in consecutive years converge in size. When the piscivorous niche is reached (at 15 cm), their growth speeds up again (fig. 2B, bottom panel). After two or three reproduction pulses, the adults die from starvation when the juvenile cohorts they have produced as offspring have converged in size and are in the niche feeding on the intermediate resource, suppressing its biomass to levels lower than the minimum needed for adults to sustain themselves (fig. 2C). Clearly, the slow growth during the intermediate life stage regulates the predator dynamics, resulting in a cohort-driven cycle with a period of 10 years.

Excluding Feedback on the Intermediate Resource, No Competition

At high basal resource productivity, excluding feedback on the intermediate resource leads to top-down control of the prey by the predator (see app. B for the dynamics at low basal resource productivity). The high predation pressure on prey leads to a change in its cycle that is now characterized by an alternation between two types of cohorts (fig. 2D), which have different growth patterns (fig. 2D, bottom panel; a detailed description of prey cohort dynamics is given in app. B).

The predator experiences most growth limitation in its first life stage. After every reproduction pulse the juvenile

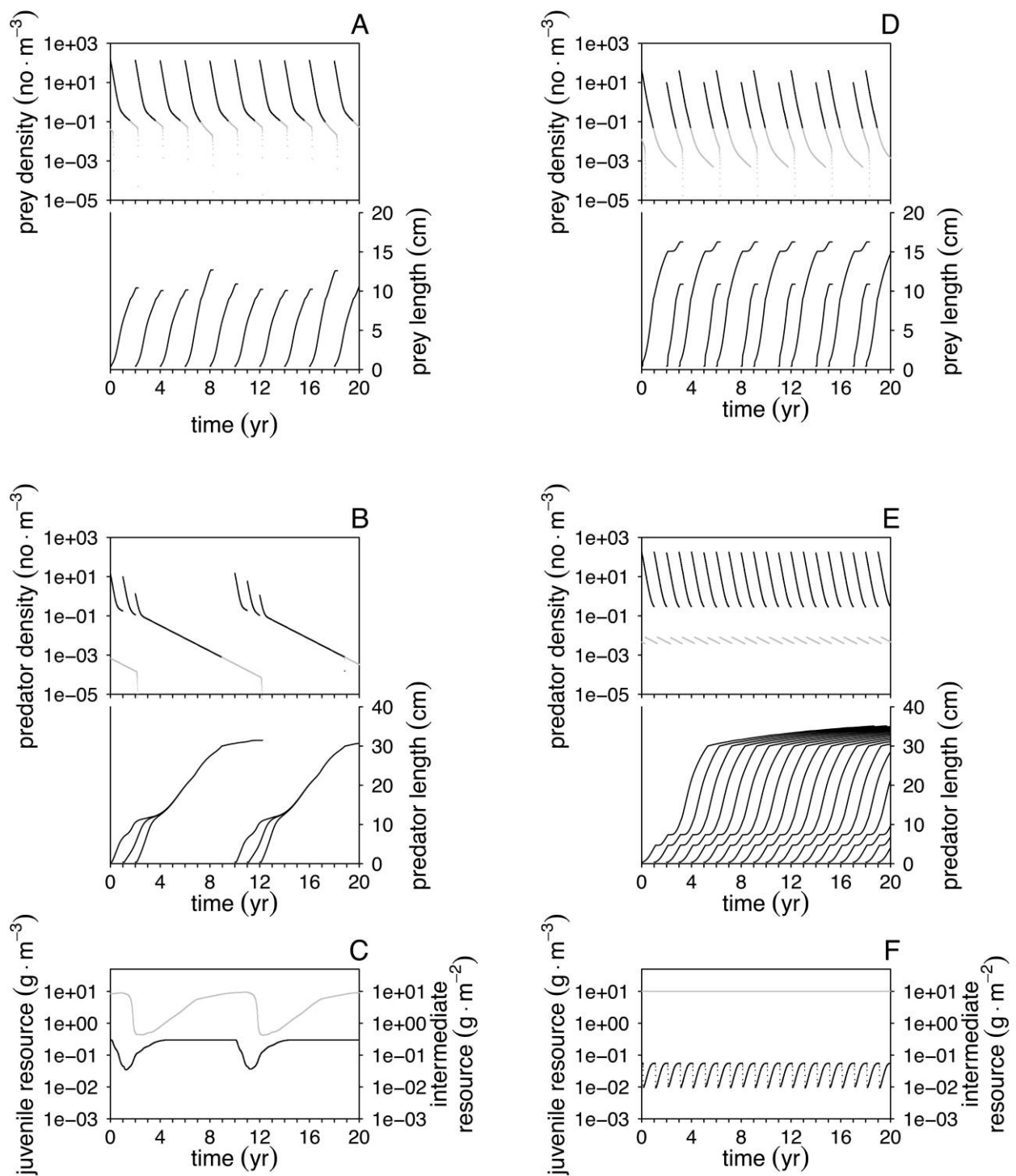


Figure 2: Coexistence dynamics of prey (A, D) and predators (B, E) over a 20-year period at high basal resource productivity ($0.03 \text{ g m}^{-3} \text{ d}^{-1}$). The dynamics are shown for two scenarios: including feedback on the intermediate resource (A–C), and excluding feedback on the intermediate resource (D–F). In the scenario including feedback the predator experiences density-dependent effects from foraging on the intermediate resource, whereas in the second scenario the intermediate resource is available at a constant level. The upper panels of A, B, D, and E show the densities of juveniles (young-of-year and one-plus juveniles summed; black) and adults (gray) in the populations, and the bottom panels in A, B, D, and E show the length at age of cohorts of individuals that are born in different years. C and F show the juvenile (black) and intermediate resource (gray) density available for predators. Productivity of the intermediate resource is $1.0 \text{ g m}^{-2} \text{ d}^{-1}$.

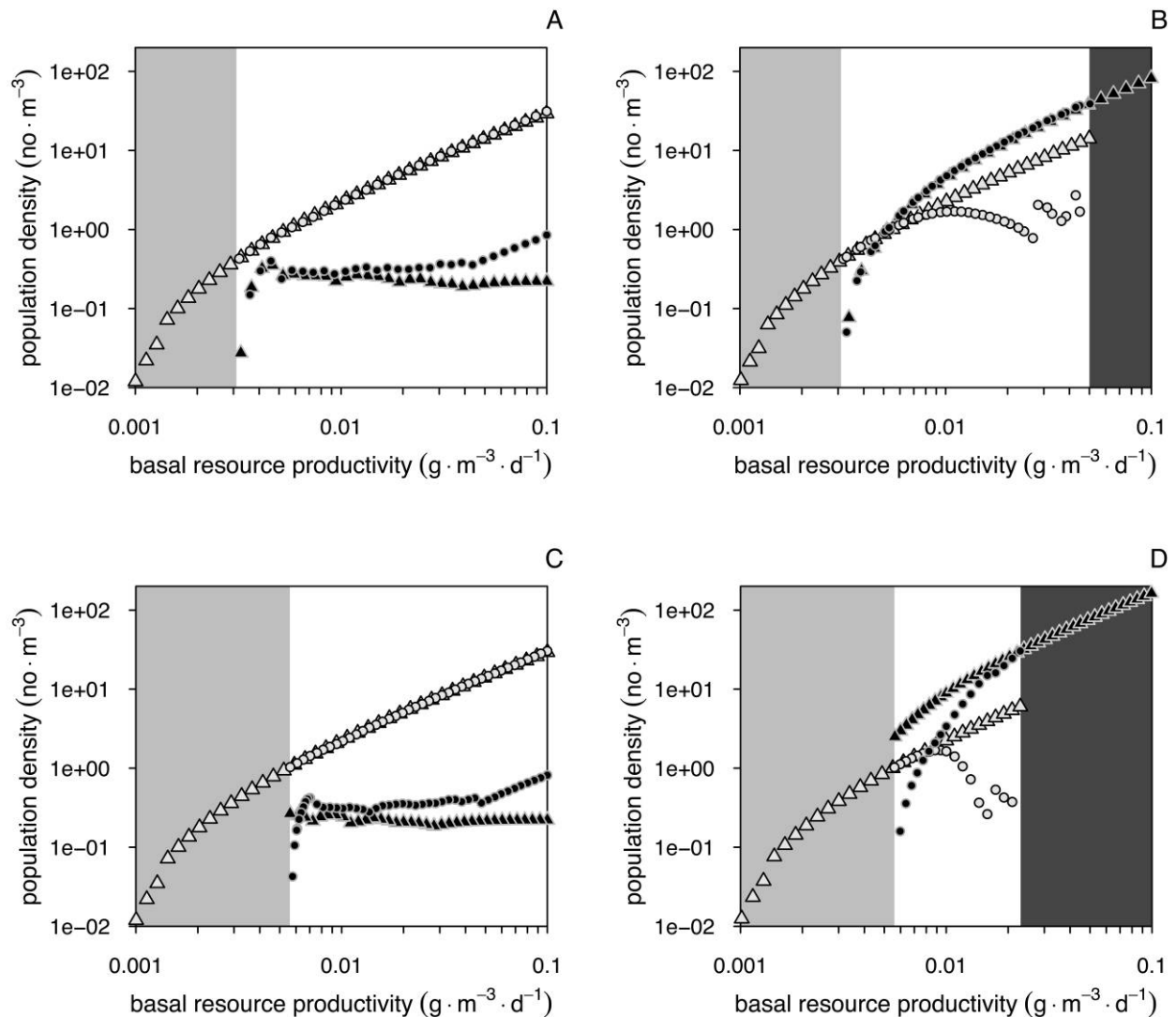


Figure 3: Average total population densities (young-of-year, one-plus juveniles, and adults, averaged over the last 60% of the integration period at every productivity value) of the predator (black symbols) and prey (gray symbols) for varying levels of basal resource productivity in the two feedback scenarios: including feedback on the intermediate resource (A, C), and excluding feedback on the intermediate resource (B, D). In the scenario including feedback the predator experiences density-dependent effects from foraging on the intermediate resource, whereas in the second scenario the intermediate resource is available at a constant level. The dynamics in both scenarios are shown without (A, B) and with (C, D) competition (where juvenile predators spend 50% of their time foraging on the zooplankton [basal] resource otherwise exclusive for the prey). Circles represent average densities of predator and prey when coexisting, and triangles represent densities in single-species community states. Note that for clarity not all points are shown. Light gray regions indicate a prey-only system, white regions indicate coexistence of predator and prey, and dark gray regions indicate a predator-only system. Productivity of the intermediate resource is $1.0 \text{ g m}^{-2} \text{ d}^{-1}$.

resource is depressed (fig. 2F), which slows down the growth through the first life stage (fig. 2E, bottom panel). Once the intermediate resource is the major foraging component, growth continues without any significant slowing until the maturation length is reached, followed by a small length increase in the adult phase (fig. 2E, bottom panel). The predator population dynamics are characterized by a

cycle with yearly reproduction and limitation by growth through the first life stage due to an intraspecific developmental bottleneck.

Basal Resource Productivity Gradient: No Competition

Figure 3 summarizes the asymptotic dynamics of predator and prey in the two cases with and without feedback on

the intermediate resource as a function of basal resource productivity. At low productivity the predator cannot persist (productivity $<0.0031 \text{ g m}^{-3} \text{ day}^{-1}$; fig. 3A, 3B), whereas at intermediate productivities prey and predator coexist, independent of whether there is feedback on the intermediate resource. At these intermediate productivities, predators foraging on the basal resource—in particular, individuals with a length between 5 and 10 cm—experience slow growth and low survival (mainly because of size-dependent mortality) due to the low resource availability, whereas individuals in the intermediate and piscivorous stage (for which size-dependent mortality is zero) manage to survive for a long period (app. B). These intermediate resource productivities only support predators at such low densities that their feedback on the resources is invariably small, explaining the absence of an effect of excluding this feedback.

At high basal resource productivity, however, the dynamics do depend on the inclusion or exclusion of feedback on the intermediate resource (fig. 3A vs. 3B). Excluding feedback on the intermediate resource allows for top-down control of prey by the predator, which leads to prey extinction above a threshold productivity level (upper persistence boundary at $0.05 \text{ g m}^{-3} \text{ day}^{-1}$ in fig. 3B). The continuous availability of the intermediate resource for adult predators leads to apparent competition between the prey and the intermediate resource that eventually causes the extinction of the prey. Because of the constant intermediate resource availability, adult predators can be present continuously (fig. 2E, 2F) and impose predation on the prey whenever individuals with sizes in the predation window are present. The resultant thinning of the prey cohort in combination with the high basal resource productivity allows prey individuals to reach a large maximum size and high reproductive output (fig. 2D). Without the feedback on the intermediate resource, strong predation pressure leads to top-down control of the prey population. We find predator-prey coexistence with decreased prey population densities for intermediate to high basal resource productivity levels (fig. 3B). Because there is no difference in the average total predator population density between the coexistence and single predator situations, the coexistence dynamics are clearly top-down regulated (fig. 3B).

When feedback on the intermediate resource is included, top-down control of the prey population by the predator is not possible, since limited food availability in the second niche imposes a developmental bottleneck. This bottleneck results in the occurrence of cohort cycle dynamics in the predator population and limits the density of piscivorous predators (figs. 2B, 3A), such that piscivorous predators never reach densities that are sufficient for strong predation pressure on the prey. The prey dy-

namics are then qualitatively unaffected by predation (fig. 3A; note that the average prey densities in a prey-only equilibrium are the same as the average densities in the coexistence state). This is characteristic for a bottom-up-regulated system.

Irrespective of the feedback of the predator on the intermediate resource, the predator persistence boundary always exactly coincides with its invasion boundary, such that all productivity levels that allow for predator invasion also allow for predator persistence and vice versa. Hence, bistability of alternative stable states with and without predators does not occur.

Basal Resource Productivity Gradient: With Competition

Diet data show an overlap in the zooplankton species that cod larvae and sprat forage on, although the overlap is not complete (Voss et al. 2003). The asymptotic model system dynamics including competition (50% overlap in resource use of small juvenile predators and the prey species) are shown in figure 3C and 3D. Coexistence is limited to a smaller productivity region than in a system without competition (fig. 3C, 3D; compare with fig. 3A, 3B). Regardless of including or excluding the feedback on the intermediate resource, the predator persistence and invasion boundary occurs at a higher basal resource productivity level when competition is accounted for than in the system without competition (fig. 3C, 3D). This is mostly due to the fact that juvenile predators spend less time foraging on their exclusive juvenile resource and hence need a higher productivity of it to persist (details not shown). In fact, the contribution of the shared resource to the diet of juvenile predators is negligible.

In the scenario excluding feedback on the intermediate resource, competition between prey and juvenile predators shifts the prey persistence boundary to a basal resource productivity level lower than where it occurs in the system without competition (fig. 3D; compare with fig. 3B). This shift in the prey persistence boundary as a consequence of competition between prey and juvenile predators is actually much more pronounced than the change in the predator persistence boundary. The basal resource productivity region for which the predator and prey coexist is therefore mainly dependent on whether feedback of predator foraging on the intermediate resource occurs (fig. 4). With feedback on the intermediate resource, only a threshold productivity level has to be exceeded to ensure predator persistence, resulting in a large coexistence region up to high competition levels. This outcome is largely independent of the intermediate resource productivity and occurs over a broad range of productivity levels (see app. B, fig. B1). In the absence of feedback on the intermediate resource, prey persistence—and hence coexistence—in ad-

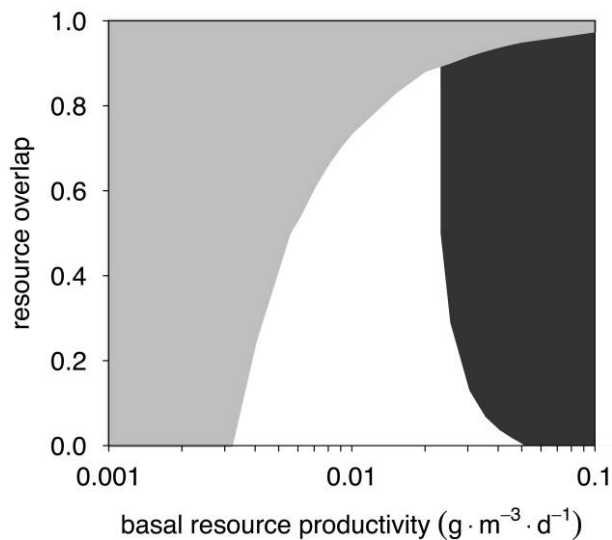


Figure 4: Possible community states at different levels of basal resource productivity and levels of competition between prey and juvenile predators. The region boundaries represent persistence and invasion thresholds, which are completely identical. Different shadings indicate the potential communities: light gray indicates prey only, white indicates coexistence of predator and prey, and dark gray indicates predator only. The dark gray region occurs only in the scenario excluding population feedback of predator foraging on the intermediate resource, but otherwise the figure is equivalent for both scenarios. Note that the rows in figure 3 can be considered as two cross sections through this two-parameter plot: at resource overlap 0 and 0.5 for the top (*A*, *B*) and bottom (*C*, *D*) panels of figure 3, respectively. Productivity of the intermediate resource is $1.0 \text{ g m}^{-2} \text{ d}^{-1}$.

dition requires the basal resource productivity to be below the prey persistence boundary. The coexistence region is in this case restricted, especially for high levels of competition (fig. 4). The two-parameter plane of competition and basal resource productivity furthermore shows that regardless of the degree of competition and feedback on the intermediate resource, the persistence boundaries always exactly coincide with the invasion boundaries. This means that irrespective of the level of competition experienced in the first life stage of the predator, there is no bistability between stable community states with and without the predator; neither is there any bistability at the higher range of basal resource productivity, around the prey persistence boundary.

Discussion

We have shown how an additional resource for adult predators, which also constitutes the main food source in an intermediate life stage preceding the predatory life stage, affects the interplay between top-down control of the prey and the competition pressure imposed by the prey on

juvenile predators. First, bistability of community states monopolized by either the predator or the prey does not occur. Second, the potential for top-down control of the prey species by the predator is limited to the condition that feedback from predators foraging on the intermediate resource is negligible. Third, overlap in resource use by juvenile predators and prey does limit predator persistence but limits persistence of prey even more.

Bistability and Juvenile Bottlenecks

The interaction between size-structured predators and their prey has been claimed to be of major importance in size-structured communities because it may give rise to mixed competition–predation interactions and role reversals (Werner and Gilliam 1984; Persson 1988; Wilbur 1988; Olson et al. 1995; Polis and Strong 1996). Mixed interactions occur when small predators compete with the consumer for a shared resource while adult predators feed on the consumers. Prey are considered competitively superior to the juvenile predators when foraging on the shared resource because juvenile predators are thought to be more adapted to their predatory lifestyle later in life. Mixed interactions potentially allow prey populations to suppress the growth of juvenile predators, imposing a developmental bottleneck in predator life history, and hence limit their recruitment to the adult predator stage. Through these bottlenecks in predator development, prey populations can thus reduce the predation pressure they are exposed to.

In line with these earlier ideas, Walters and Kitchell (2001) postulated the compelling idea that mixed interactions promote the occurrence of two alternative stable community states in which either the prey limits predator population growth through intense competition for resources with juvenile predators (depensation) or adult predators crop down the prey abundance through top-down control and thereby facilitate growth and development of juvenile predators (cultivation). This mechanism has been claimed to explain the lack of recovery of various overexploited fish stocks (Bax 1998; Swain and Sinclair 2000; Walters and Kitchell 2001; Bundy and Fanning 2005; Baskett et al. 2006; Casini et al. 2009).

Figure 5 summarizes the results from earlier theoretical studies of life-history omnivory systems with respect to bistability, cultivation/depensation, and juvenile bottlenecks in the top predator. These results highlight the importance of the extent to which adult predators forage on the shared resource as well (discussed below) and show how the results of this study fit in the context of theory on life-history omnivory.

In accordance with the cultivation/depensation theory, life-history omnivory results in bistability between a co-

Life history omnivory and cultivation/depensation effects in models with a shared resource for predator and prey species.

Predator ontogenetic niche shift scenario	Coexistence	Types of ASS	Top-down control	Cultivation/depensation effects under same conditions	Main juvenile bottleneck in predator	Ref
Classical IGP (no stage- or size-structure considered)	Yes	RP/ RCP RC/ RP	Yes	No; cultivation only	-	1, 2
Non-predatory life stage added to classical IGP model	Yes	RP/ RCP	Yes	No; cultivation only	Interspecific	2
Discrete shift from shared resource to predation (predation is required for reproduction)	Yes	RC/ RCP	Yes	Yes	Interspecific	3, 4, 5
Continuous use of shared resource; diet broadening with predation	No	RC/ RP	Yes prey exclusion	Yes	Interspecific	6
Same as above, plus continuous use of additional resource	Yes	RP/ RCPi RCi/ RPi	Yes (prey exclusion)	Yes	Interspecific	7
Complete shift from shared resource to non-dynamic, intermediate resource (no feedback); diet broadening with predation	Yes	None	Yes (prey exclusion)	No; cultivation or depensation	Intraspecific (in intermediate life stage)	8
Same as above, with dynamic intermediate resource (including feedback)	Yes	None	No	No; depensation only	Intraspecific (in juvenile life stage)	8

existence state and a prey-only state in stage-structured systems (fig. 5). Nevertheless, prey exclusion from the coexistence state results when adult predators can feed on the shared resource to an extent that is sufficient for them to reproduce (fig. 5; see van de Wolfshaar et al. 2006). In this scenario, bistability occurs between community states in which either the prey (dominant at low to intermediate productivities) or the predator (dominant at intermediate to high productivities) monopolizes the community state (van de Wolfshaar et al. 2006). This bistability and the absence of coexistence result from the positive feedback between predator density and their food availability (the basal shared resource). As a result of suppression of the prey, predators relax the prey's grazing pressure on the shared resource, giving rise to such positive feedback. The absence of both types of bistability in the current model system is explained below.

Occurrence of Top-Down Control

Prey exclusion indicates dominance of predator over prey, which is intuitively expected to increase when predators have additional resources to forage upon (fig. 5; see Walters and Kitchell 2001; van de Wolfshaar et al. 2006). Instead of increased predator dominance, in this study we found that when predators depend on an intermediate resource before they switch to predation, their potential for top-down control of prey abundance is limited. Top-down control by the predator now occurs only under the condition of negligible feedback from the predator on the intermediate resource. When feedback from predators foraging on the intermediate resource is present, recruitment to the adult predator stage is limited by a developmental bottleneck in the intermediate predator life stage. This bottleneck is induced by intraspecific competition among predators for the intermediate resource, in contrast to the juvenile bottleneck in predator development that may be imposed by competition with prey for the shared resource (Werner and Gilliam 1984; Persson and Greenberg 1990; Byström et al. 1998; see also fig. 5).

The juvenile bottleneck described here is absent in the case where the second resource is available throughout the life of the predator (fig. 5; see van de Wolfshaar 2006). Therefore, an additional resource for the predator may have a negative impact on the prey when predators can

start feeding on this resource from the earliest life stage onward and the attack rate increases gradually with increasing body size. The additional resource is in this case just an energy boost for the predator and increases the predator's potential for top-down control of prey.

In contrast, an additional resource for the predator may have a negative impact on the predator itself, as is shown in this study. The two factors determining this negative impact are (1) that the additional resource is accessible only above a fixed predator size and (2) that the additional resource forms the main resource in a specific predator life stage (i.e., the intermediate life stage). By these factors the potential for a threshold in the energy or biomass flow through predator life stages is created.

Competition between Prey and Early Life-Stage Predators

When juvenile predators experience resource competition from the prey species fed upon by adult predators, models accounting for simpler predator life histories predict alternative community states due to cultivation/depensation (fig. 5). In our model, including overlap in resource use by juvenile predators and prey in the case of top-down control by the predator (i.e., feedback from predator foraging on the intermediate resource is negligible) restricts most significantly the possibility for prey persistence. Because predators in the piscivorous life stage do not feed on the shared basal resource, the positive feedback between strong predation pressure and resource availability does not arise. In addition, interspecific competition plays only a very minor role in the food limitation of juvenile predators.

It may seem straightforward that limitation in the first-feeding life stage disappears when an intermediate life stage is included, but in this context it should be noted that this is not merely due to the bottleneck in the intermediate life stage. In the system where feedback on the intermediate resource is negligible (and the growth bottleneck in the intermediate life stage is absent), there is also no bistability due to a growth bottleneck in the first-feeding life stage.

Robustness of Results

The result that top-down control of the prey population by the predator is limited to conditions where feedback

Figure 5: ASS = alternative stable states; IGP = intraguild predation; R = basal resource; C = intermediate consumer; P = predator; P_j = juvenile predator stage; P_a = adult predator stage; i = intermediate resource. Parentheses indicate that prey exclusion is possible but not necessary. In diagrams, circles indicate species stages in stage-structured models, rectangles indicate population size distributions in continuously size-structured models, solid arrows indicate feeding relations, and dotted arrows indicate growth. Sources are as follows: 1 = Holt and Polis 1997; 2 = Mylius et al. 2001; 3 = Walters and Kitchell 2001; 4 = Baskett et al. 2006; 5 = Hin et al. 2011 ($\Phi < 0.3$); 6 = van de Wolfshaar 2006; 7 = van de Wolfshaar et al. 2006; 8 = this study.

on the intermediate resource is negligible is a fundamental outcome of this study. We tested the sensitivity of this outcome to model parameterization. Therefore, we studied a broad range of resource productivity levels and different levels of size-dependent mortality, the latter being a factor that is known to affect cohort cycle dynamics (van Kooten et al. 2007). We found the same qualitative system dynamics as described here over a large range of productivity levels (fig. B1) as well as when predators and prey experience size-dependent mortality twice as high as that under default conditions.

Besides being robust against changes in parameter values, the fundamental model outcome is also robust against changes in model formulation: we have formulated and analyzed a model with different assumptions regarding the shape of the ontogenetic niche shift to predation, where the shift is complete and predators become energetically dependent on the prey. Also in this model, the system dynamics are characterized by the intraspecific bottleneck in predator growth during its intermediate life stage, as described here, and top-down control does not occur when the feedback from predator foraging on the intermediate resources is included (van Leeuwen 2012).

Moreover, we formulated a stage-structured biomass model along the lines of the model described in van Leeuwen et al. (2008) but in addition included a subadult intermediate life stage foraging on a second resource, thus accounting for two ontogenetic niche shifts in predator life history. In this model, top-down control of the prey population by the predator was possible only under the condition that the feedback on the resource used by the subadult stage was negligible (results not shown). This confirms the dynamics found in the continuously size-structured population model reported in "Results." The fundamental outcome of our study is therefore reproducible in a simplified model formulation. At the same time, the more detailed formulation of the continuously size-structured model is necessary to completely understand the origin of the dynamics found and explain the system dynamics.

Implications for Predator Recovery

Our results call into question a popular view that the lack of recovery of marine top predators after a collapse represents an alternative stable state induced by competition with prey for shared resources. We show that due to the additional niche shift, community structuring by interspecific competition is not possible under the same conditions that give rise to top-down control by the predator.

With regard to the observed field data on Atlantic cod, the prolonged period without rebound of cod stocks to earlier high levels is often ascribed to negative effects from

their prey species, for example, through predator-prey reversal or competition for zooplankton (e.g., Swain and Sinclair 2000; Walters and Kitchell 2001; Casini et al. 2009). Observational evidence for individual-level processes, which reveals that cod population growth in the Baltic Sea is limited by negative interactions with prey, is, however, scarce and inconclusive (Sparholt 1994; Köster and Möllmann 2000; Minto and Worm 2012). Earlier studies, both theoretical and empirical (Hin et al. 2011; Persson and de Roos 2012), have also shown that the realized interaction network in a food web may be simpler than the network of potential interactions that can be inferred from diet overlap data.

Top-down control of prey by the predator and structuring of the community by predation occurs in our results with high benthic profitability, whereas this is impossible under limited benthic resource availability. This conclusion is supported by the analysis of long-term dynamics of perch and roach: when lake productivity is dominated by benthic production (an alternative resource for perch), predation is the major structuring interaction (Persson and de Roos 2012). In that situation, there is no evidence for a competitive effect of roach on perch. It is hypothesized that when the pelagic productivity dominates, predation is less likely to be the predominant interaction structuring the community.

Currently the sprat population in the Baltic Sea seems to be released from the strong top-down control exerted by cod before its population collapsed (Casini et al. 2009). With the results presented here, we offer a mechanistic explanation for this situation. The differences in dynamics under the two feedback scenarios suggest that at present cod in the Baltic Sea system may experience poor feeding conditions in the benthic environment that limit its potential for top-down control of the sprat population. An analysis of the biomass flows through different trophic levels of the food web in the Baltic Proper indeed shows a prominent change from benthic to pelagic flows in the periods before and after the cod population collapse (Tomczak et al. 2012). The estimated diet composition of adult cod in this study shows a pattern that is consistent with our explanation: prior to the collapse the diet of cod contained roughly 40%–50% benthic resources, whereas after the collapse this diet component is estimated at around 15%–20% (see fig. 10A in Tomczak et al. 2012), which means a halving of the benthic component in adult cod diets. After its collapse, the Baltic cod population has not recovered for 2 decades, and this has been tentatively explained by the occurrence of alternative stable states driven by competition for plankton prey between the abundant sprat population and cod early life stages (Möllmann et al. 2008; Casini et al. 2009). The cultivation/depensation hypothesis gives an intuitive explanation for community

dynamics as seen following cod stock collapses. Nevertheless, the hypothesis is based on assumptions that are at odds with the pattern of ontogenetic niche shifts that cod experience throughout their life history. This study shows that the occurrence of a life stage in which cod depend on the benthic resource before switching to piscivory can explain the lack of top-down control by cod as a result of an intraspecific bottleneck. In contrast to explanations involving alternative stable community states, this study therefore points at changes in relative habitat profitability of the benthic and pelagic resources as the major cause for delayed stock recovery.

In conclusion, in predator-prey systems with competitive and predatory interactions in different life-history stages, the competitive advantage of prey foraging on resources cannot be balanced with predation pressure if the predatory individuals themselves do not forage on the shared resource. Instead of a balance, we find that either competition or predation dominates the community dynamics. When predators do not switch directly from the stage experiencing competition to the predatory stage, the predator population tends to be regulated through intraspecific density dependence. This leads to bottom-up structuring of the community and a lack of top-down control. The supposed bistability between a predator-dominated and a prey-dominated state is difficult to explain if adult predators, in addition to feeding on prey, also have an alternative resource to forage on.

Acknowledgments

We thank two anonymous reviewers for their valuable comments on an early version of the manuscript. This study is part of the PLAN FISH project, financially supported by the Swedish Environmental Protection Agency and the Swedish Board of Fisheries.

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Associate Editor: Volker Grimm
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