

# Ontogenetic specialism in predators with multiple niche shifts prevents predator population recovery and establishment

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**Abstract.** The effects of ontogenetic niche shifts on community structure and dynamics are underexplored, despite the occurrence of such shifts in the majority of animal species. We studied the form of niche shifts in a predator that exhibits multiple ontogenetic niche shifts, and analyzed how this life history complexity affects the size-structured predator–prey dynamics in the system. The predator represents either an ontogenetic generalist, exhibiting a partial shift to predation (in which case an alternative resource is also available) or an ontogenetic specialist, exhibiting a complete shift (in which case the predator depends entirely on predation). We showed two effects on community dynamics from accounting for a complete niche shift to predation: (1) occurrence of alternative stable community states (coexistence and a prey-only community state) and (2) occurrence of deterministic extinction following initially successful invasion (predators can invade an equilibrium with only prey, but are bound to go extinct after a few generations). Both phenomena are due to the match or mismatch in the timing of predators and suitably sized prey and the growth trajectory of the predator, which is plastic, due to the population feedback on available resources. In the case of persistence without invasion (alternative stable community states), slow growth during the pre-piscivorous life stage is necessary to stay in tune with the prey cycle; in the case of extinction following invasion, slow growth through the pre-piscivorous life stage causes the predator to reach the completely piscivorous stage when there is no prey available to feed upon. Somatic growth rates are directly coupled to food availability, which, in turn, is the result of density-dependent feedbacks in the system. Since they primarily determine these density-dependent feedbacks, the ontogenetic niche shifts in predator life history structure the community to a major extent.

*Key words:* alternative stable community states; community structure; complex life cycle; density dependent growth; diet shift; invasion; life history; ontogenetic niche shift; piscivory; predator extinction; predator–prey dynamics; size-structure mismatch.

## INTRODUCTION

Complex life cycles and ontogenetic niche shifts, where organisms change their usage of habitat or resources during ontogeny, occur in the majority of animal species (Werner and Gilliam 1984, Wilbur 1988). When organisms exploit separate niches in different life stages, they are faced with the problem of timing the ontogenetic niche shift. This timing may have to match the temporal presence of habitats, as with seasonal drying of ponds (Wilbur 1980, Podrabsky and Hand 1999), or should be synchronized with resources that fluctuate in time. The migration of Northeast Arctic cod that follows the spawning migration of capelin is a typical example where the timing of niche shifts and

matching of predator–prey spatial overlap both occur (Nakken 1994); other examples of matches and mismatches are reviewed in Parmesan (2006).

Theory predicts far-reaching impacts of ontogenetic niche shifts regarding community structure and stability. Food web stability may be significantly reduced when accounting for ontogenetic diet shifts, because many (also seemingly generalist) species actually turn out to be ontogenetic specialists (Rudolf and Lafferty 2011). Ontogenetic niche shifts in resource use and the consequent stage structure in consumer populations is predicted to give rise to bistability between alternative stable community equilibria, which itself may lead to hysteresis and regime shifts in ecosystems (Schreiber and Rudolf 2008, Guill 2009). Similarly, ontogenetic shifts in the exposure to predators may lead to predator–prey coexistence, while under the same conditions prohibiting predator recovery after a population collapse, a so-called emergent Allee effect (de Roos and Persson 2002).

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Intraguild predation occurs when predator species share a common resource with their prey species. If the predator exploits the shared resource in an early life history stage and subsequently switches to predation, the interaction is referred to as life history omnivory or life history intraguild predation. With life history omnivory, strong top-down control of the predator on the prey is necessary for predator persistence (Hin et al. 2011). When the ontogenetic niche shift is partial, in which case the predator can keep foraging on the shared resource throughout life (and predation is hence not necessary for reproduction), it is more likely that the prey population is excluded (van de Wolfshaar et al. 2006, Hin et al. 2011). These contrasting outcomes illustrate the importance of the shape of the niche shift, suggesting that it is essential whether the first resource remains accessible to predators switching to predation or not.

Most available studies of the effects of ontogenetic niche shifts assume that individuals go through only a single ontogenetic niche shift during their life history (de Roos et al. 2002, van de Wolfshaar et al. 2006, 2011, Schreiber and Rudolf 2008, Guill 2009), whereas the life history of many top predators is characterized by the occurrence of multiple ontogenetic niche shifts (Wine-miller 1989, Persson and Greenberg 1990, Stergiou and Fourtouni 1991, Flowers and Graves 1995, Lima 1998, Garcia-Berthou 2002, Martins et al. 2002, Galarowicz et al. 2006, Hammerschlag-Peyer and Layman 2012). The influence of two ontogenetic niche shifts in predator life history was studied in detail in a size-structured model analysis describing the life history of Atlantic cod (*Gadus morhua*; van Leeuwen et al. 2013; see Plate 1) and was shown to result in a bottleneck in the pre-piscivorous life stage (feeding on the intermediate resource), preventing predator population growth, and thereby also its top-down control of the prey fish species (van Leeuwen et al. 2013). Predators were assumed to only partially switch from (benthic) resource feeding to piscivory, but even for a well-studied and commercially important species such as cod, there is insufficient data to determine whether its diet shift to piscivory reflects a partial, or a complete shift, in which case individuals at some point become completely dependent on fish food.

Using a physiologically structured population model of a predator-prey system with multiple basic resources for the predator, we contrasted the effects on community structure and dynamics of two different predator life history strategies: The case with the predator as an ontogenetic generalist (Rudolf and Lafferty 2011), in which case the predator has a partial niche shift to piscivory, vs. the case with the predator as an ontogenetic specialist (Rudolf and Lafferty 2011), in which case the predator has a complete niche shift to piscivory. We studied this contrast in the same model system, thus illustrating two extremes of a continuous range of possibilities and providing an insight in the scope of consequences that niche shifts may have on

population and community dynamics. We show that the interplay between density dependence among predators with a complete niche shift and the temporal changes in prey availability may be beneficial as well as detrimental to predator persistence, and thus, determine possible community states, resulting in alternative stable community states and deterministic extinction following invasion.

#### MODEL DESCRIPTION

Our current study was based on the analysis of a discrete-continuous physiologically structured population model (PSPM; Metz and Diekmann 1986), which is for the most part identical to the model described in van Leeuwen et al. (2013, also see Persson et al. 1998 and Huss et al. 2013). The model accounts for a size-structured predator population (cod), a size-structured prey population (sprat), an unstructured resource exclusively preyed upon by large juvenile and adult predators (referred to as “intermediate resource,” macro-zoobenthos) and two unstructured basal resources (zooplankton): one exclusively accessible for small juvenile predators (referred to as “juvenile resource”) and one exclusively accessible for the prey species (referred to as “prey resource”; see Fig. 1 for a schematic representation of the modeling framework and an overview of the trophic interactions). In contrast with intraguild predation systems, we used two separate (non-competing) resources, with productivities that were assumed to be the same, to exclude all effects from competition between prey and predator and to focus our study on effects resulting from the different feeding scenarios in predators of larger sizes. Competition and cultivation effects were studied elsewhere (van Leeuwen et al. 2013). The definition of model functions and parameters can be found in Appendix A. We refer to Appendix A in van Leeuwen et al. (2013) for a full model description and justification of these functions; here we only provide a short overview of the main model components.

Individuals were characterized by their age, body size (structural mass, which represents essential body mass components such as bone and muscular tissue that cannot be starved away), and energy reserves (reversible mass, which represents nonessential parts of body mass such as fat and gonadal tissue that can be used and regained under starvation). The dynamics of the two size-structured populations result from the size-dependent feeding, growth, mortality, and reproduction of their individuals, whereas the three unstructured resources were assumed to follow semi-chemostat dynamics, reflecting a constant productivity in the absence of consumption (Persson et al. 1998).

Food intake by individual fish is modeled with Type II functional responses as a function of (size-dependent) attack and maximum ingestion rates, the density of different food sources and the fraction of time spent foraging on these resources, which depends on individ-

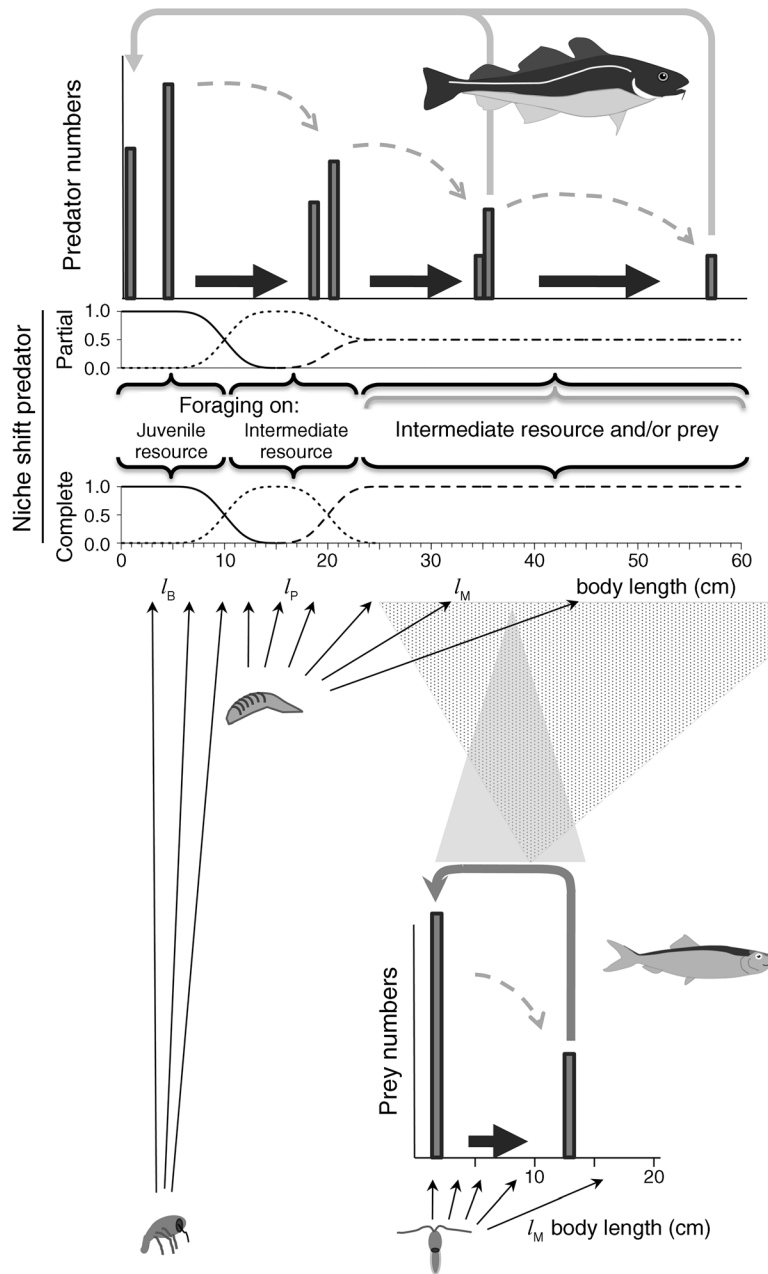


FIG. 1. The different levels of organization in the predator–prey model and the trophic connections between these levels are illustrated in two frequency distributions (prey shown on the bottom, and predator shown at the top) and by graphical illustrations for the unstructured resources. In the two frequency distributions, the x-axes depict individual length ( $l_B$  indicates the length at which benthivory starts,  $l_P$  the length at which piscivory starts, and  $l_M$  indicates the length at maturation). The y-axes in the upper and lower graphs show the cohort frequency distribution in the predator and prey populations. The individual level processes of growth and (discrete) reproduction are depicted in fat, solid arrows (growth in black, horizontal arrows and reproduction in gray curved arrows), whereas mortality is depicted in the dashed arrows. The thin, upward facing arrows indicate feeding interactions with prey or resources. The predation window of a predator individual of 35 cm is shown in the gray shaded triangle, and the vulnerability window of a prey individual of 11 cm is shown in the dotted inverted triangle. In the panel below the predator population distribution, the ontogenetic niche shifts in the two feeding scenarios of the predator are shown by the size-dependent functions of foraging time on the different resources: the panel above shows a partial shift, and the lower panel shows complete shift. The middle panels depict the foraging time on different resources in the partial niche shift scenario (upper panel) and complete niche shift scenario (lower panel): juvenile resource (solid line), intermediate resource (dotted line), prey (dashed line), and combination of intermediate resource and prey (dashed–dotted line). The upward- and downward-pointing gray and black brackets represent the major resource in the indicated ontogenetic niche (i.e., size range) of the predator. This figure is a modified version of Fig. 1 in van Leeuwen et al. 2013; used with permission from American Naturalist.

ual body size (Fig. 1; Appendix A; Appendix A in van Leeuwen et al. in 2013). Predator feeding leads to predation mortality of prey, the intensity of which depends on the body size of both prey and predator. Additionally, predator and prey experience size-dependent background mortality. We used a dynamic energy budget, modeled with a net production model (e.g., Persson et al. 1998), to describe growth in body size and reproduction as a function of the balance between the assimilated food intake and the size-dependent maintenance costs. When maintenance costs exceed food intake from resources and/or prey, body condition deteriorates, eventually leading to increased mortality and ultimately starvation. These dynamics are all modeled in continuous time, and referred to as within-season dynamics.

The model accounts for a discrete reproduction event at the start of the growing season, meaning that a single cohort is added to the prey and predator populations every year if reproduction occurs at all. When the reproduction event starts, adult individuals (individuals with length  $\geq l_M$  [length at maturation]) invest part of their reversible mass into egg production. We have investigated the sensitivity of results to a distributed production of offspring during a period of variable duration, in which case more than one cohort were added to the predator and prey populations each year. The qualitative model outcomes were robust against using a longer duration of the offspring production period with multiple offspring cohorts (Appendix B). Therefore, we present here only the outcomes from the setting with all reproduction occurring on the first day of the growing season (250 days). We assumed that the dynamics outside the growing season can be neglected.

Fig. 1 shows a schematic representation of the modeling framework and an overview of the trophic interactions accounted for in the model. In the two scenarios we analyzed, the life history of the predator is defined by two ontogenetic diet shifts: Early in life, predator individuals feed exclusively on the pelagic juvenile resource, which is followed by a demersal life stage feeding on the intermediate resource (starting at the minimum length  $l_B$  [the length at which benthivory starts]). Subsequently, predator individuals broaden their diet by the addition of piscivory (partial niche shift), or alternatively, they shift entirely to predation (complete niche shift; in both cases, piscivory starts at length  $l_P$ ; Fig. 1). We used a sigmoidal function to model the change in the fraction of time during which large predator individuals forage as piscivores, meaning that the shift takes place in a gradual manner, also in the case with a complete shift to piscivory. In the model with partial niche shift to predation, the sigmoid function has a maximum of  $1/2$ , while in the model with complete niche shift to predation, the maximum is 1 (Fig. 1). The rate at which individuals encounter food equals the product of the foraging time and the attack rate. The partial-shift scenario is completely identical to the model in van Leeuwen et al. (2013). The complete-shift

scenario results in the predator becoming energetically completely dependent on prey fish at a size of 25 cm (foraging time on the intermediate resource reaches zero at 25 cm; Fig. 1). The structured prey species is considered to feed on the same resource throughout its ontogeny.

We used the approach developed by De Roos et al. (1992) for the numerical analysis of model dynamics. Time integrations of the model either reflect stable attractors (as in Fig. 2) or transient dynamics (as in Figs. 4 and 5). We also report bifurcation analyses, which consist of sequential time integrations over periods of 400 years during which the asymptotic system dynamics are determined for a range of productivities of the intermediate resource (Fig. 3). We disregarded the first 350 years of each time integration as transient dynamics. The construction of the persistence and invasion boundaries of predator and prey were based on these time integrations. The resource productivity level below which a species is unable to sustain a population represents the persistence boundary. Since prey growth is independent from the intermediate resource, there is no minimum productivity level for its persistence. There is, nevertheless, a productivity threshold with maximum predation impact on the prey, above which it is unable to persist. These persistence boundaries were determined for both predator and prey both in the presence and the absence of the other species.

The invasion boundary was determined in absence of any population feedbacks, and therefore excludes the feedback from the invading population on the resources. The invasion boundary occurs exactly at the resource productivity combination for which an individual's average lifetime offspring production ( $R_0$ ) equals one, calculated in absence of any intraspecific density dependence (see Appendix A in Huss et al. 2012 for details). Differences between the persistence and invasion boundaries indicate a region of bistability in case persistence is possible for combinations of resource productivity that do not allow for invasion. The potential of the predator to invade was additionally assessed in single time integrations, where the dynamics immediately following introduction of the predator were studied. For this analysis, the regular prey-only dynamics were used as a starting point and five different densities of predator eggs were introduced in the prey-only state at the start of the year. In separate tests, we introduced the predator eggs in either year of the prey cycle (see Fig. 2C, D) to assess the potential for establishment under these different environmental conditions. Establishment was considered successful when the predator population persisted in at least one of the two years in the prey's cohort cycle.

We address the question whether the size-dependent predator-prey interactions between predator and prey can give rise to bistability in the system and how the shape of the ontogenetic niche shift in the predator influences the outcome.

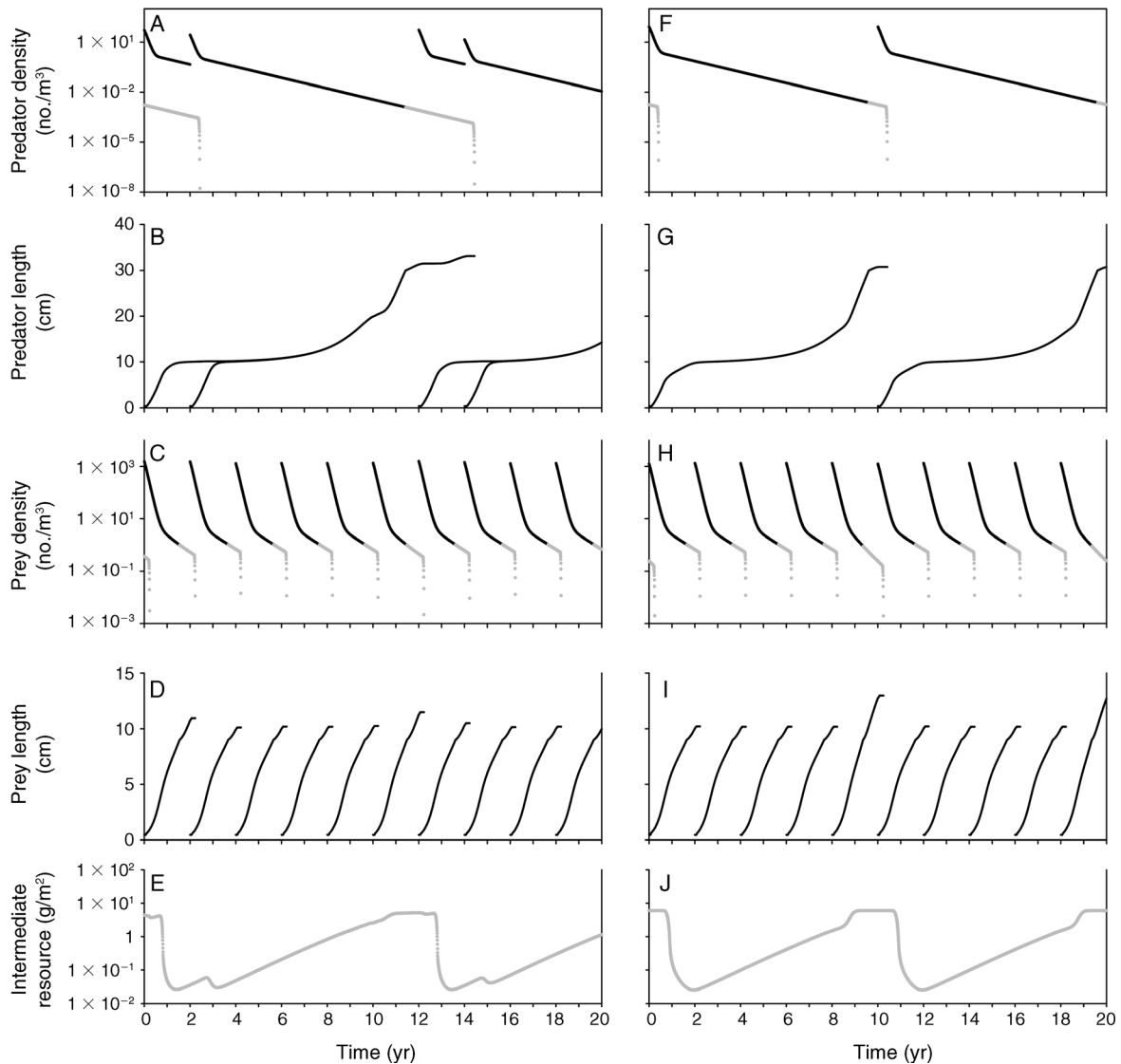


FIG. 2. Model dynamics at default productivity levels (prey resource and juvenile resource productivity,  $\beta_{\kappa_p}$ , is  $0.28 \text{ g}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ ; productivity of the intermediate resource,  $\beta_{\kappa_B}$ , is  $0.6 \text{ g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ), showing the predator–prey dynamics in the (A–E) partial-shift scenario and in the (F–J) complete-shift scenario: (A, F) juvenile (black) and adult (gray) densities in the predator population; (B, G) predator growth curves, showing predominantly single-cohort dynamics (either after convergence of the two juvenile cohorts up to the next reproduction event (partial-shift scenario in panel [B]), or continuously (complete-shift scenario in panel [G])); (C, H) juvenile (black) and adult (gray) densities in the prey population; (D, I) prey growth curves, showing consistent single-cohort dynamics in both scenarios; and (E, J) dynamics of the intermediate resource. Note that reproduction is a discrete process in predator and prey, taking place at the first day of the growing season.

## RESULTS

The predator–prey population dynamics in the scenario with a partial niche shift to piscivory represents our baseline case, the dynamics of which will be described in detail (a more extensive description of population dynamics in this scenario can be found in van Leeuwen et al. 2013).

Both predator and prey exhibited cyclic dynamics, but with different cycle lengths (Fig. 2A–E). The prey population dynamics were characterized by a so-called recruit-driven cohort cycle, with a dominant period of

two years (Persson et al. 1998). During this cycle, a newborn cohort grows and matures, produces a new cohort, and is subsequently outcompeted by the newborn individuals (Fig. 2C, D). This cyclic dynamics comes about due to the discrete reproduction event and the size-dependent scaling of net energy production (ingestion minus maintenance rate), which is more favorable for small individuals (Hjelm and Persson 2001, Huss et al. 2012). The prey growth curves show a 10-year pattern with some differentiation in the maximum size reached (Fig. 2D), which is due to predation,

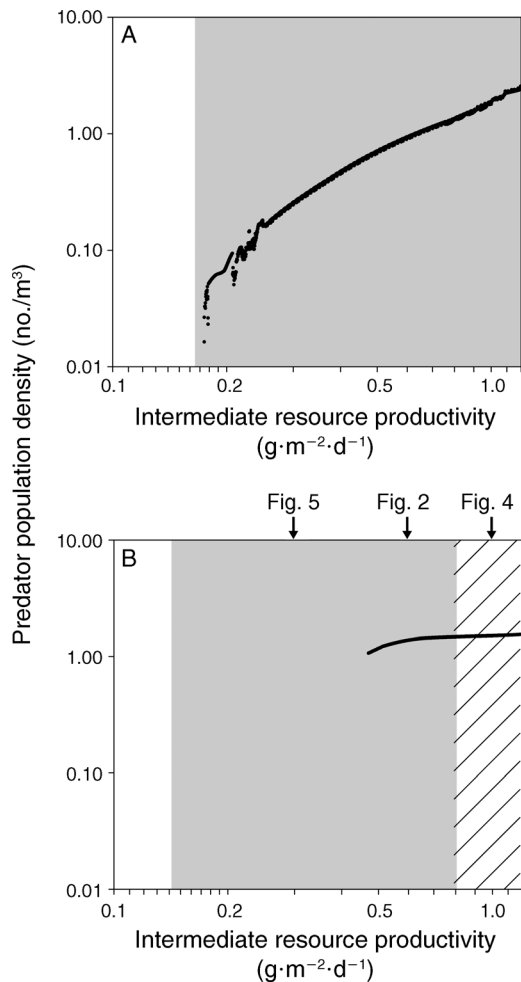


FIG. 3. Average total predator population density (black; average taken over the last 60% of the integration period, calculated for every productivity value) as a function of intermediate resource productivity ( $\beta_{\kappa_P}$ ) in the (A) partial niche shift scenario and the (B) complete niche shift scenario. The gray regions indicate the range of intermediate resource productivity levels where predator invasion is possible, i.e.,  $R_0 > 1.0$ . In panel (B), the parameter range where invasion is possible, but persistence is not, leads to extinction following invasion ( $\beta_{\kappa_B} \sim 0.14\text{--}0.45$ ); the parameter range where persistence is possible, but invasion is not, leads to bistability (hatched area,  $\beta_{\kappa_B} \sim 0.8\text{--}1.2$ ). The productivity levels as set in Figs. 2, 4, and 5 are indicated with arrows on top of the panel. (Productivity of the prey resource and juvenile resource,  $\beta_{\kappa_P}$ , is  $0.28 \text{ g}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ ).

but otherwise the prey dynamics are the same as in a single-species system (not shown).

Predator population dynamics showed a juvenile-driven cohort cycle, which has a period of 10 years (Fig. 2A). The predator dynamics were strongly regulated by the slow growth during the pre-piscivorous life stage (Fig. 2B). Adult predators went extinct after their second reproduction event, which was mainly due to resource competition for the intermediate resource with the juvenile cohorts. The moment that the first juvenile

cohort is foraging predominantly on the intermediate resource, there is a fast decrease in this resource's density (Fig. 2E, just before year 13). Adult predators survive this period because it coincides with a phase in the prey cycle where the prey cohort is of intermediate size (i.e., within the predation window of adult predators; Fig. 2D), but their energy intake is nonetheless too low to spawn. After adult predators spawn again the following year, their energy reserves (i.e., body condition), as well as densities of the intermediate resource and suitably sized prey (i.e., food intake) are insufficient for their survival (the cohort dies off through starvation mortality).

In the scenario with a complete switch to piscivory, the predator-prey dynamics were characterized by juvenile-driven cohort cycles, in a way similar to the scenario with partial niche shift (Fig. 2F–J). The predator dynamics were regular and reproduction occurred only one time during the cycle (Fig. 2F). Hence, the predator population continuously consists of a single cohort, like the prey population. Every 10 years, the predator cohort reaches the threshold of 25 cm, above which predators can no longer use the intermediate resource and individuals only feed on prey. Predation pressure is then more pronounced, resulting in a decrease of the prey density (Fig. 2H, year 10). The reduced prey densities allow for a higher prey resource biomass, which allows the surviving individuals in the prey cohort to grow fast and to a larger maximum length than in other years of the predator cycle (Fig. 2I, year 10).

The single cohort cycle in the prey leaves predators without available resource after adult prey die off following a reproduction event, since the size of the newborn cohort is not within the predation window of adult predators (Fig. 2I). The lack of suitably sized prey drives the predator cohort to extinction after one reproduction event.

Summarizing, the time integration in Fig. 2 shows that in both scenarios predator-prey dynamics follow cohort cycle dynamics. The major distinction between the dynamics in the two scenarios is the cause of the predator cohort extinction at the end of its cycle: In the partial niche shift scenario, predator cohort extinction is caused by starvation due to repressed levels of the intermediate resource. In the complete niche shift scenario, predator cohort extinction is caused by starvation due to the lack of sufficiently large prey individuals.

Whether the shift to piscivory is partial or complete does significantly affect how persistence varies with productivity of the intermediate resource. With a partial shift to piscivory, predator persistence is possible for the whole range of productivity levels for which  $R_0 > 1$  (Fig. 3A), and predator invasion is hence possible. Because the persistence and invasion boundaries coincide, there is no bistability in this scenario. This result was consistent for an extensive range of productivities of

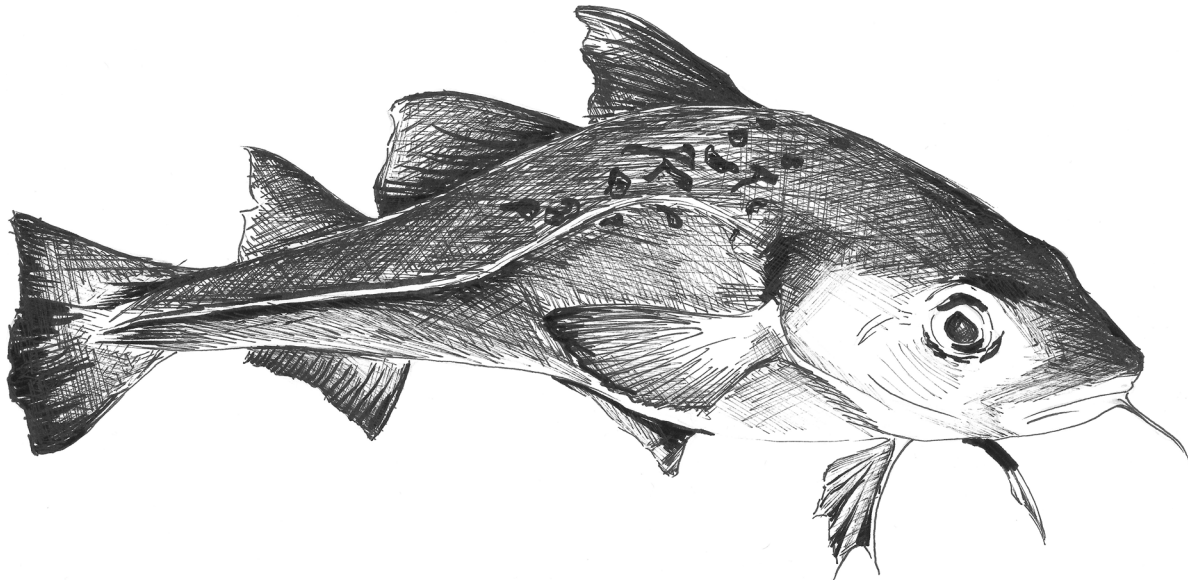


PLATE 1. Atlantic cod, *Gadus morhua*. Illustration credit: A. van Leeuwen.

the juvenile and prey resource. In contrast, when the shift to piscivory is complete, predator persistence depends on the productivity of the intermediate resource. For low productivity levels (approximately 0.14–0.45; Fig. 3B), predator persistence is not possible even though invasion is ( $R_0 > 1$ ), whereas for high productivity levels (approximately 0.8–1.2; Fig. 3B), persistence is possible while invasion is not ( $R_0 < 1$ ). That is, in case of a complete niche shift, bi-stability occurs at high productivity, between a coexistence state of predator and prey and a prey-only state from which the predator is absent and cannot establish a population when starting from a low density. At low productivity, there is a region where invasion by the predator is initially possible, but establishment is not.

To understand the processes underlying the alternative stable states and the failure of a predator to establish despite initial invasion in case of a complete niche shift, we analyzed the population dynamics during an attempted invasion of the predator.

At high productivity of the intermediate resource, the predator is unable to establish a population when it is initiated from low densities (Fig. 4, left column) and can only establish successfully when the initial density is sufficiently high (Fig. 4, right column). Predators go extinct at low densities because there is a mismatch in the timing of the shift of predators to complete piscivory (at a size of 25 cm) and the presence of suitably sized prey individuals (with sizes larger than 2 cm) that fall within the predation window of these predator individuals. Although this situation, where prey have sizes smaller than the lower boundary of the predation window, does not last very long, the predator cohort starves before the prey reaches vulnerable sizes, leading

to predator extinction (note that the predator cohort never reaches densities high enough to have a visible impact on the intermediate resource; Fig. 4E). In contrast, if the predator is invading in sufficiently high initial densities (Fig. 4, right column), the growth of the invading cohort slows down during the second, pre-piscivorous life stage (Fig. 4G) because the higher predator densities deplete the intermediate resource (Fig. 4J). At the moment when the prey availability for completely piscivorous individuals reaches a minimum (Fig. 4G, year 2), individuals in the invading predator cohort are still small enough to forage on the intermediate resource. These predator individuals hence shift to complete piscivory later, when suitably sized prey are present (Fig. 4G, after roughly 2.5 years). These aspects in the life history of the predator enable it to maintain itself during the low-energy phase (Fig. 4G) and to pick up fast growth again as soon as the prey cohort grows into the vulnerability window (Fig. 4I).

The effect from predation is visible in the prey growth curves, showing larger maximum sizes in every fifth prey cohort (Fig. 4I, starting in year 2 of the time series and coinciding with the piscivorous phase of the predator cohort), but predation does not become high enough to qualitatively affect the prey cohort cycle. In summary, resource competition and slow growth are necessary for the predator cohort to match its shift to complete dependence on the prey with the timing of the presence of suitable prey. Counterintuitively, the fast growth that is possible for predators at low population density turns out to be fatal for their persistence.

For low productivity levels of the intermediate resource, the predator can initially invade but cannot establish (i.e., invasibility is predicted on the basis of the

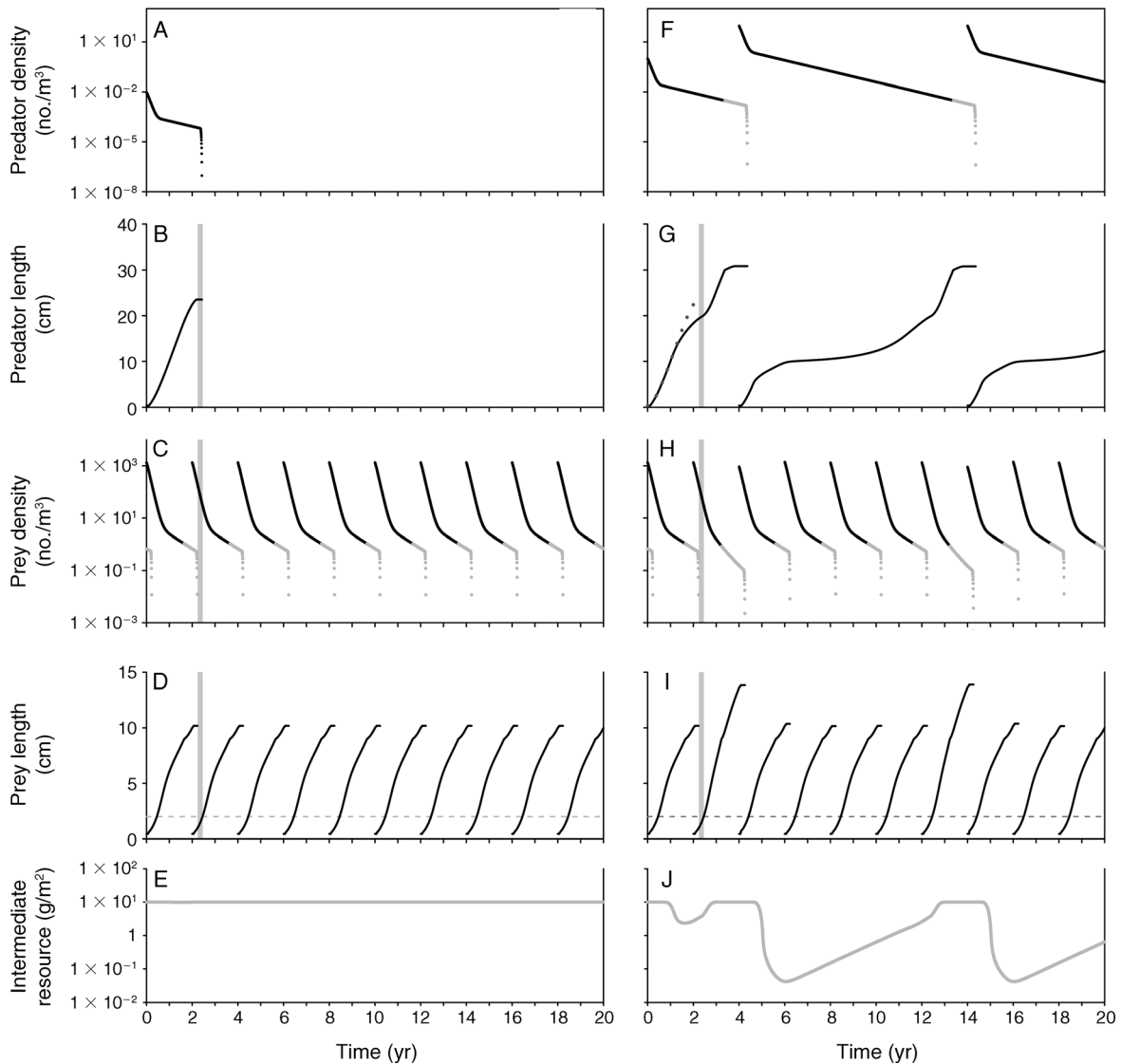


FIG. 4. Community dynamics after introduction of the predator in the system at high productivity of the intermediate resource ( $\beta_{K_B}$  is  $1.0 \text{ g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ; prey and juvenile resource productivity,  $\beta_{K_P}$ , is  $0.28 \text{ g} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ ) in the complete-shift scenario. The predator is introduced into the system with resources and prey: (A–E) dynamics after introduction of a low number of eggs ( $0.01 \text{ eggs/m}^3$  invading), and (F–J) dynamics after introduction of a high number of eggs ( $1 \text{ egg/m}^3$  invading): (A, F) Juvenile (black) and adult (gray) densities in the predator population; (B, G) predator growth curves (the vertical gray bar indicates the first period after predator introduction when no prey are available for predators in the completely predatory life stage. In panel [G], with a high number of eggs invading, the predator growth curve from panel [B] is drawn in gray dots for comparison.); (C, H) juvenile (black) and adult (gray) densities in the prey population (vertical gray bar as in panels [B, G]); (D, I) prey growth curves, (the gray dashed line indicates the minimum prey size for predators in the completely predatory life stage, vertical gray bar as in panels [B, G]); and (E, J) dynamics of the intermediate resource. Note that reproduction is a discrete process in predator and prey, taking place at the first day of the growing season.

$R_0$  calculation, but coexistence of predator and prey is not possible). In the invasion analysis, all density dependence among predators and their feedback on resource and prey populations is disregarded. Under these conditions, the predator population grows exponentially, regardless of its initial densities (Fig. 5F). Because all feedback from the predator is ruled out, the dynamics in the prey population are unaffected by

predation (Fig. 5H), and the basal and intermediate resources for the predator remain at their carrying capacity (Fig. 5J). Accounting for the feedback from the predator population on the system changes the picture (Fig. 5, compare left and right columns) and the predator population goes extinct after a few generations (Fig. 5A). Predation quantitatively affects the prey growth trajectories, as when productivity is low, but



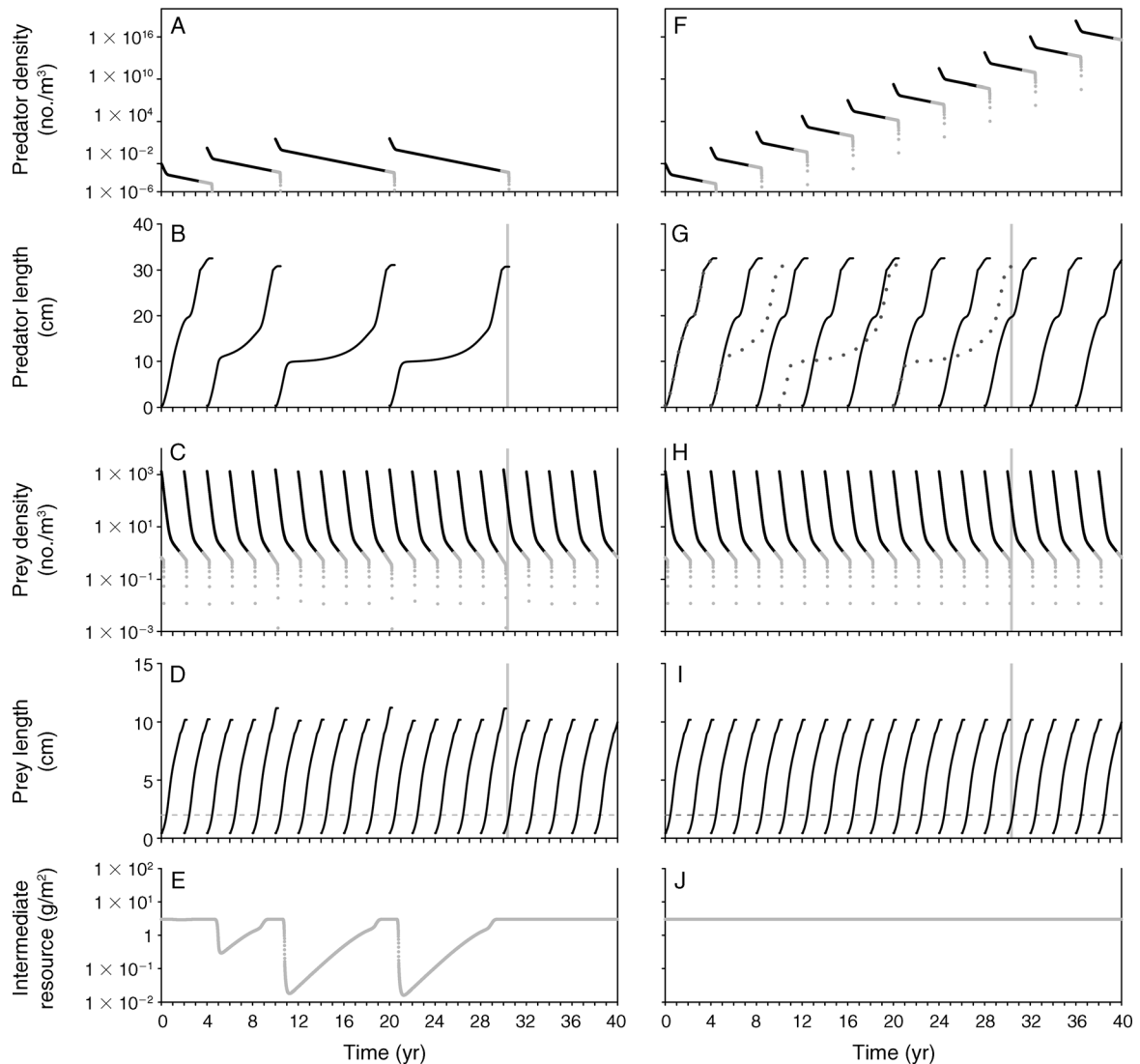


FIG. 5. Community dynamics after introduction of the predator in the system at low productivity of the intermediate resource ( $\beta_{KB}$  is  $0.3 \text{ g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ; prey and juvenile resource productivity,  $\beta_{Kp}$ , is  $0.28 \text{ g}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ ) in the complete-shift scenario. The predator is introduced into the system with resources and prey ( $0.01 \text{ eggs}/\text{m}^3$  invading in both columns): (A–E) Dynamics and invasion in the default setting with predator feedback on resources and prey, and (F–J) dynamics after predator introduction without predator feedback on the environment. (A, F) Juvenile (black) and adult (gray) densities in the predator population; (B, G) predator growth curves (the gray bar indicates the period when no prey are available for predators in the completely piscivorous life stage, leading to predator extinction in panel [B]). In panel [G], with no feedback, the predator growth curves from panel [B] are drawn in gray dots for comparison); (C, H) juvenile (black) and adult (gray) densities in the prey population (vertical gray bar as in panels [B, G]); (D, I) prey growth curves (the gray dashed line indicates the minimum prey size for predators in the completely piscivorous life stage, vertical gray bar as in panels [B, G]); and (E, J) dynamics of the intermediate resource. Note that reproduction is a discrete process in predator and prey, taking place at the first day of the growing season.

the difference with the non-feedback case is only minor (compare Fig. 5D with Fig. 5I). The growth trajectories of the predator cohorts, however, change significantly, since a growth bottleneck now develops in the pre-piscivorous life stage (Fig. 5B, E). The slow growth during this life stage, caused by intraspecific competition, causes a mismatch in time of obligate piscivores with the availability of suitably sized prey, resulting in

deterministic extinction following invasion (note that extinction is not due to random, stochastic events, but happens with certainty).

In summary, density-dependent growth of the predator allows for its persistence when intermediate resource productivity is high, because the feedback on the intermediate resource slows down predator growth in body size, and thus promotes the correct timing of the

switch to piscivory with the presence of suitably sized prey. At low population density, though, when the predator's growth in body size is density independent, individuals reach the piscivorous life stage before any suitably sized prey are available. In contrast, at low productivity of the intermediate resource population feedback on the intermediate resource has exactly the opposite effect: The timing of the switch to piscivory matches with the availability of suitably sized prey when growth in body size is density independent, whereas a mismatch occurs in case of density dependent growth. As a consequence, the predator cannot persist for more than a few generations, despite the fact that the environment allows for initial invasion, because the predator's own presence affects the environment and therewith the growth conditions. These results are robust against changes in several model assumptions, as discussed in Appendix B.

#### DISCUSSION

Our results clearly reveal how ontogenetic niche shifts can structure communities by determining the dynamics of interacting size-structured populations. We show that ontogenetic specialization of a predator with multiple ontogenetic niche shifts, which hence depends on different resources in different stages of its life history, gives rise to (1) alternative stable community states and (2) deterministic extinction following initially successful invasion. These phenomena are both caused by a mechanism that is related to the timing of occurrence of suitably sized prey for predators shifting to piscivory. In this process, the growth trajectory of the predator plays a determining role: In the case of persistence without invasion (alternative stable community states), slow growth during the pre-piscivorous life stage is necessary to stay in tune with the prey cycle; in the case of invasion without establishment, slow growth through this phase causes the predator to reach the completely piscivorous stage at a moment when there is no prey available to feed upon. The growth trajectories in the prey are mainly determined intraspecifically, where the dynamics show a classical cohort driven cycle, and there is only a minor, quantitative effect from predation on the maximum prey size reached. This means that the outcomes for invasion and persistence of the predator in the system are determined by the stage prior to the piscivorous phase.

The phenomena we report here result from the domination of a single cohort in the population dynamics of both prey and predator. As a result of the size-dependent parameterization of maintenance and food intake rates (see Appendix A), small individuals suppress the resource to lower levels than the minimum required for the maintenance of large individuals, which renders newborn individuals competitively superior to mature individuals.

This kind of dynamics have been shown to be common in natural systems, especially in fish commu-

nities (Townsend et al. 1990, Sanderson et al. 1999, Murdoch et al. 2002, White et al. 2014; also discussed in Huss et al. 2012). Furthermore, these single-cohort cycles are robust against distributing the reproductive phase over a prolonged period, when individuals born on different dates in the same year converge in size, resulting in similar single-cohort dominance (also see Appendix B). van Kooten et al. (2007) showed that single-cohort cycles are robust against moderate variability in somatic growth of individuals within the same year class. The latter conclusion agrees with the study of Ananthasubramaniam et al. (2011), who showed the robustness of cohort/generation cycles against stochastic variation in individual growth in a consumer–resource model.

In the size-structured predator–prey system that we analyzed, the predator experiences two ontogenetic niche shifts, which are both modeled in a continuous manner, assuming a size range over which the organism gradually switches between resources. When the second of these niche shifts involves a complete change to predation (piscivory), i.e., the predator is an ontogenetic specialist, the effects on community dynamics differ substantially from the effects of a partial shift in resource use, in which case the predator is an ontogenetic generalist (Rudolf and Lafferty 2011). Neither the ontogenetic generalist, nor the ontogenetic specialist exert top-down control on the prey, and the predator dynamics are determined by intraspecific competition and a growth bottleneck in the pre-piscivorous life stage. The lack of top-down control on the fish prey by the predator (regardless of its life history strategy) is related to the regulation of the predator population itself. There is no top-down control of the prey population because there is top-down control on the intermediate resource, and concomitantly, the predator population is regulated in the intermediate life stage. Schreiber and Rudolf (2008) described the potential for two modes of population regulation when consumers exploit different niches or habitats in the juvenile and adult phase. In the current situation, the predator exploits three different niches in its three life stages, which results in the potential for population regulation in either one of these. The production efficiency in the three life stages differs (an example of “ontogenetic asymmetry”; de Roos et al. 2013), and only for the situation where the piscivorous niche is the most energy limited, does the predator exert top-down control on the prey population (van Leeuwen et al. 2013).

Previously, it was shown that ontogenetic niche shifts have the potential to stabilize single-cohort dynamics in consumer resource systems (de Roos et al. 2002), cause bi-stability in stage-structured consumers with distinct population regulation in different stable attractors (Schreiber and Rudolf 2008, Guill 2009), and, in intraguild predation systems, lead to dynamics that can be dominated either by the prey (Hin et al. 2011) or by the predator (van de Wolfshaar et al. 2006). When a

predator exhibits multiple ontogenetic niche shifts, top-down control of the prey population by the predator occurs under limited conditions only, whereas coexistence of predator and prey occurs over wide ranges of conditions (van Leeuwen et al. 2013).

Previous analyses have mainly focused on the effects of transition in resource use consisting of a rather simple, single ontogenetic niche shift. Here we zoom in on the underlying processes, especially the form of niche shifts, and highlight the consequences of a partial vs. a complete shift on community structure.

The consequences of a complete niche shift are particularly important when considering the timing problems of species with metamorphosis, since metamorphosis is often associated with a shift in habitat. But also in the context of less stringent habitat changes, complete shifts are relevant, since ontogenetic niche shifts may involve a change in the energetic contribution of resources. For example, when predators switch from feeding on invertebrate prey to vertebrate prey, the latter may be required for maturation and reproduction, and thus represent an essential resource, whether the predator keeps foraging on the invertebrate resource or not. Dynamically, such a dependence pattern boils down to a complete ontogenetic niche shift. For cod, there is indeed evidence that fish (having high energy content) are an essential diet component that is associated with this species' reproductive potential (Kjesbu et al. 1998, Rose and O'Driscoll 2002, Rideout and Rose 2006). Similar examples include insects, which need protein-rich sources for reproduction, while being able to survive on water (e.g., Evans et al. 1999, Hodek and Honek 2009), and the Long-tailed Skua (*Stercorarius longicaudus*), a species that refrains from breeding altogether when prey (lemming) densities in the tundra breeding habitat provide insufficient energy, although adults can survive on berries and invertebrates like insects and spiders (Anderson 1981).

Our analysis focuses on the population and community dynamical consequences of differently shaped ontogenetic niche shifts. In contrast, the classical treatment of ontogenetic niche shifts by Werner and Gilliam (1984) focuses on the optimal size to switch between habitats. This approach considers the trade-off within habitats of minimizing predation risk while optimizing growth rate as a life history problem at the individual level, assuming a static environment, i.e., equilibrium conditions. By minimization of the ratio between mortality ( $\mu$ ) and growth rate ( $g$ ), individuals are supposed to maximize survival until maturation, which is summarized in the  $\mu/g$  rule. In contrast, our results show that the dynamical aspect of the environment and the feedback from density dependence in populations are central in the analysis of persistence and invasion in predator-prey communities. We show the importance of these dynamic connections between environment and organisms in a system where the predator experiences timing issues due to two ontoge-

netic niche shifts in its life history. Furthermore, our results demonstrate that consequences of individual-level life history processes for predator-prey dynamics cannot be understood by induction of individual-level processes alone, without regarding population feedbacks (de Roos et al. 2002, Persson and de Roos 2003).

#### *Alternative stable states*

The occurrence of alternative stable community states as we describe here, including a coexistence state and a prey-only state, resembles an Allee effect, because predators cannot establish a persistent population when initiated from low densities. An Allee effect is defined as a positive effect of increasing population densities on individual performance, in particular, at low population densities. The concept is classically ascribed to social behavior or increased success of egg fertilization with increasing population density (Rowe et al. [2004] proposed this as an explanation for the lack of recovery in cod), which are processes not included in our model. Instead, the alternative stable states emerge here as a system-level effect resulting from the form of the ontogenetic niche shift and the beneficial effect of intraspecific density dependence in the predator population, which leads to a match in timing of the presence of predator and prey in vulnerable size classes. The system is regulated bottom-up and, although predation pressure has a slight impact on cohort growth in the prey population, there is no top-down control of the prey by the predator. The absence of top-down control is notable, because de Roos and Persson (2002) previously described a so-called emergent Allee effect, which occurs specifically as a result of strong top-down control from a predator on a size- or stage-structured prey population. With strong top-down control, predation pressure changes the population size-structure of the prey to the benefit of the predator, whereas in the absence of strong predation pressure, the predator is not sustained on the available prey sizes (de Roos and Persson 2002). At the population level, the emergent Allee effect as reported by de Roos and Persson (2002) and the bi-stability between a consumer-only state and a predator-prey coexistence state in our model system resemble each other. Nevertheless, the underlying processes giving rise to the bi-stability have different origins: trophic restructuring of the prey population size distribution in the emergent Allee effect (de Roos and Persson 2002), and the beneficial effect of an intraspecific predator growth bottleneck in the current case.

The representation of the predator life history with two ontogenetic niche shifts in our model was based on the available descriptions of the life history of Atlantic cod (see van Leeuwen et al. 2013: Appendix A for detailed justification and parameterization). Although the occurrence of ontogenetic niche shifts is well recognized for cod (for example, Sparholt 1994, Hussy et al. 1997), as well as for many other marine and freshwater piscivores (e.g., Mittelbach et al. 1988,

Persson and Greenberg 1990, Hammerschlag-Peyer and Layman 2012), the form of these shifts is unclear. Even when the stomach contents of predators imply an omnivorous diet, there may be an energetic or stoichiometric dependence on particular diet components or prey types. In the Northwest Atlantic cod populations, for example, skipped spawning occurs more frequently in individuals containing less capelin in their diet (Marshall et al. 1998, Rose and O'Driscoll 2002, Rideout and Rose 2006). Analogously, the processes resulting in alternative stable community states in our model provide a tentative explanation for the changes in community structure and cod diet composition surrounding the collapse of the cod population in the early 1990s in the Baltic Sea. After the cod population collapsed and throughout the subsequent period without population recovery, the component of benthic invertebrate resources in the diet of cod, as estimated on the basis of a food web model, increased substantially (Tomczak et al. 2012). The concomitant decrease in fish intake could play a role in the reduced potential for cod population recovery. Nevertheless, the available data are insufficient to determine whether the continuous use of invertebrates as part of the overall piscivorous diet of cod represents a partial or a complete niche shift. It should be noted, though, that alternative community states do not occur in our model when large predator individuals keep foraging on the intermediate resource for ten percent of their time budget (see additional results in Appendix B: Fig. B4). Furthermore, on the basis of data available in the literature, it is impossible to conclude whether cod is able to reproduce and sustain a population on the basis of benthic invertebrate prey alone. At the same time, the occurrence of different alternative community states that we present here may contribute to the explanation of the prolonged period without recovery of Atlantic cod (Hutchings 2000, Frank et al. 2005).

#### *Deterministic extinction following invasion*

We found deterministic extinction following initially successful invasion to occur at low productivities of the intermediate resource, when invasion of predators in a system with only prey and resources is possible (since  $R_0 > 1$ ), but persistence is not, because of the feedback from the predator population itself on the resource environment following the increase in predator density. This phenomenon illustrates how ecological feedbacks can overrule predictions based on density-independent considerations. Density dependence is ignored in the calculation of  $R_0$ , since this is per definition a measure of the invasion potential in an environment without ecological feedback from the invading species. The concept of  $R_0$  plays a crucial role in, among others, conservation biology, epidemiology, and adaptive dynamics. In conservation biology, by its equivalence to the dominant eigenvalue of the next-generation matrix in matrix population models,  $R_0$  is used as indication for

population persistence (and growth, if  $R_0 > 1$ ), or extinction (if  $R_0 < 1$ ) (Heesterbeek 2002). In epidemiology,  $R_0$  is defined as the “expected number of new cases of an infection caused by a typical infected individual in a population consisting of susceptibles only” (Diekmann et al. 1990, Heesterbeek 2002). In the context of adaptive dynamics, but also in applications of life history evolution, the potential for invasion by a mutant of a resident population is given by the  $R_0$  of the invader, which is defined as the “expected number of female offspring born to one female during her entire life” (Roughgarden 1979, Yodzis 1989, Heesterbeek 2002). In all these applications, the condition  $R_0 > 1$  is assumed to have implications beyond the initial situation where the invading species lacks feedback on the environment (population persistence, disease outbreaks, or mutant invasion), leading to establishment, at least, and potentially to replacement. In the current study, it is shown that such extrapolation of the condition  $R_0 > 1$ , measured under ideal, density-independent environmental circumstances, may not be warranted, since ecological feedback may prevent persistence and lead to deterministic extinction after initial invasion. The phenomenon of extinction following invasion we describe provides the first ecological mechanism for a lack of persistence of an otherwise successful invader that does not involve a change in system dynamics (as in the “resident strikes back” phenomenon; Mylius and Diekmann 2001). This mechanism is solely based on two biologically realistic assumptions: that the predator is energetically dependent on prey for reproduction, and that there is temporal variation in the availability of suitably sized prey for maturing predators.

In summary, the two phenomena that we present in this study (alternative community states and deterministic extinction following invasion) come about as a result of three biological features: (1) a single cohort dominates both prey and predator population dynamics, (2) fish prey is an essential energy source for predator reproduction, and (3) the predator-prey interaction is size dependent. These features are biologically relevant for natural systems, with predominant evidence coming from freshwater and marine fish communities. Our findings show the importance of the form of ontogenetic niche shifts in determining how ecological communities are structured and call for empirical studies on the occurrence and form of ontogenetic niche shifts in natural predator-prey systems.

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#### SUPPLEMENTAL MATERIAL

##### Appendix A

A size-structured predator–prey model with two ontogenetic niche shifts in the predator: details of model variables, parameters, and functions ([Ecological Archives E095-214-A1](#)).

##### Appendix B

Additional robustness analyses and results ([Ecological Archives E095-214-A2](#)).