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Symmetry breaking in ecological systems through different energy efficiencies of juveniles and adults

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Abstract. Ontogenetic development is a fundamental aspect of the life history of all organisms and has major effects on population and community dynamics. We postulate a general conceptual framework for understanding these effects and claim that two potential energetics bottlenecks at the level of the individual organism—the rate by which it develops and the rate by which it reproduces—form a fundamental route to symmetry-breaking in ecological systems, leading to ontogenetic asymmetry in energetics. Unstructured ecological theory, which ignores ontogenetic development, corresponds to a limiting case only, in which mass-specific rates of biomass production through somatic growth and reproduction, and biomass loss through mortality, are independent of body size (ontogenetic symmetry). Ontogenetic symmetry results in development and reproduction being limited to the same extent by food density. In all other cases, symmetry-breaking occurs. Ontogenetic asymmetry results in increases in juvenile, adult, or even total biomass in response to mortality. At the community level, this gives rise to alternative stable states via predator-induced shifts in prey size distributions. Ontogenetic asymmetry furthermore leads to two distinct types of cycles in population dynamics, depending on whether development or reproduction is most energy limited. We discuss the mechanisms giving rise to these phenomena and the empirical support for them. We conclude that the concepts of ontogenetic symmetry and ontogenetic asymmetry form a novel and general organizing principle on which future ecological theory should be developed.

Key words: *alternative stable states; biomass overcompensation; cohort cycles; food-dependent development; individual energetics; ontogenetic asymmetry; population size structure.*

INTRODUCTION

Ontogenetic development characterizes the life history of all organisms on Earth (Bonner 1965, Werner and Gilliam 1984, 1988, Miller and Rudolf 2011). In fact, next to mortality, ontogenetic development is the second most certain life history process, given that only few individuals survive until reproduction. Even in unicellular organisms such as yeast and phytoplankton, individual cells necessarily undergo an increase in body mass from their “birth” through cell division up to mitosis (Pascual and Caswell 1997, Massie et al. 2010). All multicellular organisms, except for some birds and mammals, generally increase at least an order of

magnitude in body mass from the moment they become independent of their parents and have to search for food themselves until they mature (de Roos and Persson 2013). This increase in size during ontogeny inevitably involves major changes in the individual’s ecological role and performance as a result of the relative body size scaling of intake and maintenance rates (de Roos et al. 2008), changes with increasing body size in mortality rate, resource and habitat use (Werner and Gilliam 1984, Dahlgren and Eggleston 2000), and role changes between competitive and predator–prey relationships during ontogeny (Wilbur 1988).

Especially during the last two decades, empirical and theoretical studies have revealed major consequences of size-dependent interactions on populations and communities after first having been considered primarily at the individual level (cf. Werner and Gilliam 1984). These consequences include effects on population processes (Townsend et al. 1990, Sait et al. 1994, McCauley et al.

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1999, Sanderson et al. 1999, Coulson et al. 2012), community structure (Persson et al. 2007, Schreiber and Rudolf 2008, Miller and Rudolf 2011, de Roos and Persson 2013), and food webs (Hartvig et al. 2011, Rudolf and Lafferty 2011). Moreover, modeling as well as empirical studies have by now revealed a number of generic outcomes of size-dependent interactions, such as generation cycles, stage-specific biomass overcompensation, and alternative stable states through stage-specific biomass redistributions (Murdoch et al. 2003, de Roos et al. 2007, Schreiber and Rudolf 2008, Ohlberger et al. 2011). The fact that these outcomes have been found in models with very different structures and in organisms of very different taxa suggests the existence of generic processes that underlie these outcomes.

Here we postulate that the common root to all these outcomes is body size dependence in mass-specific biomass production. More specifically, we argue that the rate at which the individual organism develops and the rate at which it reproduces form two potential energetics bottlenecks in its life history and that the ratio of these rates constitutes a fundamental route to a particular type of symmetry-breaking in ecological systems. Only under the very limited condition in which mass-specific rates of biomass production through somatic growth and reproduction and biomass loss through mortality are independent of individual body size (a condition we refer to as *ontogenetic symmetry*) are the ecological dynamics of a population independent of its body size structure. In contrast, whenever the mass-specific rate of biomass production differs between different body sizes, ontogenetic symmetry-breaking occurs (*ontogenetic asymmetry*), resulting in two distinctly different dynamical regimes, depending on whether juveniles or adults have greater energy efficiency.

In the following, we first discuss how basic energy balance relationships at the level of individuals may lead to symmetry or symmetry-breaking in ecological systems. Subsequently, we consider how the two dynamic regimes with ontogenetic asymmetry translate into distinct consequences for both community structure and population dynamics. Our aim is to provide a synthetic perspective on the core consequences of ontogenetic asymmetry for ecological communities. The mathematical underpinning of our arguments regarding ontogenetic asymmetry and symmetry is provided by de Roos et al. (2013), while de Roos and Persson (2013) provide an extensive treatment that also adds different details to the core theory presented here.

ONTOGENETIC SYMMETRY AND ASYMMETRY IN INDIVIDUAL ENERGETICS

Standard ecological textbooks literally define population dynamics as the variation in time and space in the *number* of individuals in a population (Begon et al. 1996, Turchin 2003). This definition implies that reproduction and mortality are the only processes giving rise to

population dynamics and that biological populations are conceptually similar to many-particle systems in other disciplines (physics, chemistry), with dynamics resulting from the balance between synthesis (reproduction) and destruction (mortality) of particles. Differences between individuals within a population are thereby completely ignored. Two recent reviews (Bolnick et al. 2011, Miller and Rudolf 2011) call attention to this neglect of intraspecific variability and argue for developing a general framework to understand the consequences of intraspecific trait variation. In this context, differences between individuals in age and size are unique because these characteristics change throughout life in predictable ways as a result of ontogenetic development. Population size structure is furthermore fundamentally different from age structure, because growth in body size necessarily depends on energy and, hence, food availability. Compared to the age structure of a population, this dependence significantly increases the scope for feedback of environmental conditions on its size structure.

For size-structured populations of individuals with the same use of resources, de Roos et al. (2013) recently showed that any model that accounts for growth in body size, size-dependent foraging, reproduction, and mortality simplifies to a model in terms of just the total population biomass if (1) individual mortality rate and (2) the *mass-specific* rate, with which new biomass is produced through either somatic growth or reproduction, are independent of body size. Furthermore, the impact of the population on its resources also depends only on its total population biomass if (3) the *mass-specific* food ingestion rate is independent of body size. When these three invariance principles hold, the dynamics of total population biomass and population size structure decouple and become independent of one another, such that the system dynamics are described by two ordinary differential equations for resource and total population biomass that could also be interpreted as an unstructured model. In line with the role of invariance principles in symmetry concepts in physics, we define a situation in which the aforementioned three invariance principles hold, as a condition of *ontogenetic symmetry in energetics*.

The pioneering bioenergetics model introduced by Yodzis and Innes (1992), which in recent years has been used to an increasing extent in theoretical analyses (Shurin and Seabloom 2005, Brose et al. 2006), provides a specific model example that is an *exact* representation of the biomass dynamics of a fully size-structured population model under conditions of ontogenetic symmetry in energetics. The underlying size-structured model, which is presented in detail in the Appendix, assumes that resource ingestion by an individual consumer (juvenile or adult) is proportional to its body size, with the mass-specific ingestion rate by consumers, $\omega_c(R)$, following a Type II functional response as a function of resource density R :

$$\omega_c(R) = M_c \frac{R}{H_c + R} \quad (1)$$

where M_c is the maximum intake rate per unit of biomass, H_c is the half saturation constant, and subscript “c” represents consumer. Furthermore, ingested resource is converted into new biomass with constant efficiency σ_c , and maintenance requirements of an individual consumer are also proportional to its body size with proportionality constant T_c . Under these conditions, the net production of new biomass by consumers is proportional to body size and to the mass-specific net production rate, $v_c(R)$:

$$v_c(R) = \sigma_c \omega_c(R) - T_c. \quad (2)$$

Note that to arrive at this equation, we have assumed a closed energy budget for individual consumers and assumed that the conversion efficiencies for growth (of juveniles) and reproduction (by adults) are identical. These conditions ensure that mass-specific ingestion of resources and mass-specific production of new biomass are independent of body size and that, hence, the last two of the invariance principles are satisfied. If now, in addition, all consumers experience the same mortality rate d_c , satisfying the first invariance principle, the dynamics of the size-structured consumer–resource system is captured completely by the following, seemingly unstructured model, in terms of the resource biomass R and the total consumer biomass C :

$$\frac{dR}{dt} = G(R) - \omega_c(R)C \quad (3a)$$

$$\frac{dC}{dt} = v_c(R)C - d_c C. \quad (3b)$$

The function $G(R)$ in these equations represents the rate at which the resource biomass increases due to input or autonomous growth. Clearly, at the level of individual consumers, the rates of ingestion, maintenance, and biomass production scale with body size, which determines the dynamics of the population size structure (following a partial differential equation, as shown in the Appendix). The population size structure is not constant, but nonetheless does not affect the total biomass dynamics of the consumer–resource dynamics.

The Yodzis and Innes model is thus at the same time analogous to unstructured, Lotka–Volterra type predator–prey models based on numbers (also having the same dynamical properties), as well as being an *exact* representation of the biomass dynamics of a fully size-structured population that fulfills the conditions of ontogenetic symmetry in energetics. This dualistic character makes the Yodzis and Innes model the perfect starting point to judge any ecological consequences of the intraspecific variation in body size that arises as a consequence of ontogenetic development. Furthermore, because the conditions of ontogenetic symmetry, strictly speaking, also characterize all unstructured models

based on numbers that ignore differences among individuals altogether, we argue that contemporary ecological theory that is based on unstructured models represents only the limiting case of ontogenetic symmetry within a more general theory, which encompasses the complete spectrum of dependence of biomass production and mortality on body size.

Ontogenetic symmetry in energetics implies that individuals in different stages of development are limited in their life history processes to the same extent by food availability and mortality. In particular, the effects of food availability on juvenile development (i.e., growth in juvenile body size) and adult reproduction are, by and large, equally strong. The most important consequence of ontogenetic symmetry in energetics, however, is the fact that the dynamics of the population size structure and the total population biomass decouple, such that changes in environmental conditions (e.g., changes in resource productivity and mortality) do not change the population size structure (de Roos et al. 2013). In other words, the relative composition of the population in terms of differently sized individuals is always the same.

In contrast, whenever the rates of biomass production or mortality differ between different body sizes, ontogenetic asymmetry occurs in one of two possible forms. In one form, juveniles have greater energy efficiency, because their net biomass production is higher and/or their mortality is lower than that of adults. At equilibrium, the system will then ultimately be limited by reproduction. Alternatively, if adults have greater energy efficiency, the system will ultimately be limited by development. If we assume the same mortality rate for juveniles and adults and that both stages use the same resource, intrinsic properties of the individual (*i*-state; sensu Metz and Diekmann 1986) solely determine whether or not ontogenetic symmetry or asymmetry occurs. However, ontogenetic asymmetry also may occur when juveniles and adults have intrinsically identical energetics but feed on different resources, and the productivities of these resources differ (de Roos and Persson 2013). In this case, whether symmetry or asymmetry is present is affected by factors extrinsic to the individual (*E*-condition; sensu Metz and Diekmann 1986).

As we discuss next, the most important consequence of ontogenetic symmetry and asymmetry for ecological processes pertains to the response of consumer populations to increased mortality. For illustrative purposes, we use a size-structured population model that is analogous to the Yodzis and Innes model discussed previously, except that juvenile and adult mass-specific ingestion rates are assumed to equal $(2 - q)\omega_c(R)$ and $q\omega_c(R)$, respectively, whereas juvenile and adult mortality rates are assumed to be $(2 - p)\mu$ and $p\mu$, respectively (see Appendix for model details). We model potential asymmetries in biomass production and mortality phenomenologically using the two compound param-

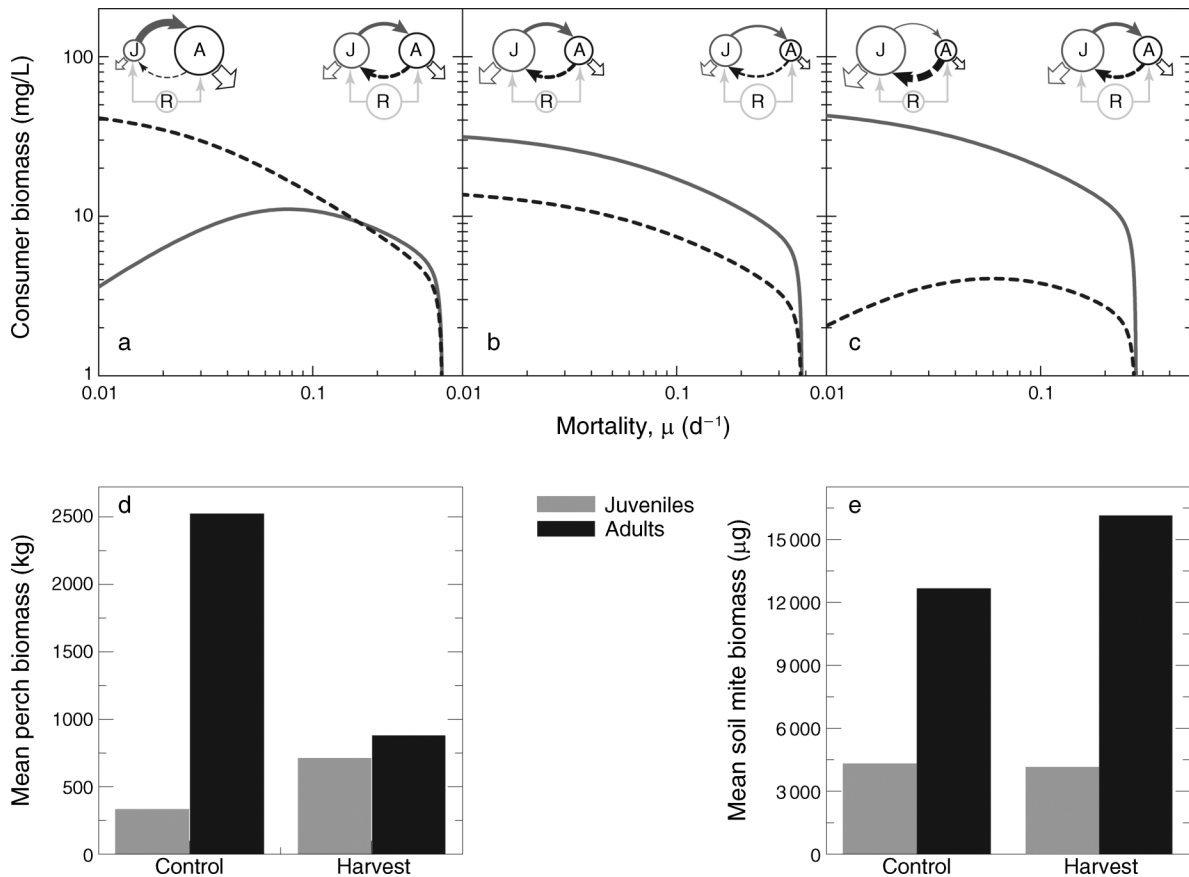


FIG. 1. (a–c) Modeled biomass responses of juveniles (solid line) and adults (dashed line) to increased random mortality (increasing mortality rate μ) (a) when juveniles have a superior energy balance (ontogenetic asymmetry in net biomass production, $q = 0.65$, $p = 1.0$, where q is a factor scaling juvenile and adult ingestion, and p is a factor scaling juvenile and adult mortality); (b) when juveniles and adults have identical energetics (ontogenetic symmetry, $q = 1.0$, $p = 1.0$); and (c) when adults have a superior energy balance (ontogenetic asymmetry in net biomass production, $q = 1.35$, $p = 1.0$). Feeding modules at the top of each panel reflect approximate biomass densities of juveniles (J), adults (A), and resource (R), and development (dark gray solid arrows), reproduction (black dashed arrows), and maintenance rates (open arrows) for conditions of low mortalities (left modules) and intermediate mortalities (right modules). Light gray arrows represent food intakes. Other model parameter values are: $H_c = 3.0$, $M_c = 1.0$, $T_c = 0.1$, $\sigma_c = 0.5$, $z = 0.1$, $\rho = 0.1$, and $R_{max} = 100$, where H_c is ingestion half-saturation resource density, M_c is mass-specific maximum ingestion rate, T_c is mass-specific maintenance rate, σ_c is conversion efficiency, z is newborn–adult consumer size ratio, ρ is resource turnover rate, and R_{max} is resource maximum biomass density. See the Appendix for model formulation. (d, e) Experimental examples of stage-specific overcompensation are shown in either (d) juvenile biomass (reproduction control, Eurasian perch) or (e) adult biomass (development control, soil mites). Note that adult biomass decreases with harvesting (no overcompensation) in panel (d) and increases with harvesting (overcompensation) in panel (e). Data were generously provided by T. Cameron and J. Ohlberger (Cameron and Benton 2004, Ohlberger et al. 2011).

ters q and p , respectively, as it makes the mathematics simpler and more intuitive. For a more mechanistic handling of size-dependent competitive ability, see Persson et al. (1998). For $q = 1$ and $p = 1$, the model is identical to the Yodzis and Innes (1992) biomass model and ontogenetic symmetry occurs, whereas ontogenetic asymmetry is present when $q \neq 1$ and/or $p \neq 1$. As it turns out, asymmetry in mortality has significantly less effect than asymmetry in net biomass production (Appendix: Fig. A1); see de Roos et al. (2013). We therefore will focus on the case that juveniles and adults only differ in net biomass production rate.

OVERCOMPENSATION IN BIOMASS AS A RESULT OF ONTOGENETIC ASYMMETRY

Under ontogenetic symmetry, an increase in consumer mortality in a consumer–resource system leads to a monotonic decrease in biomass of both juveniles and adults, whereas the juvenile/adult biomass ratio remains constant (Fig. 1b). In other words, the population structure is irrelevant for the system response. Consumption by both juveniles and adults increases with increased mortality as a result of increased resource availability, leading to larger mass-specific growth rates of juveniles and reproduction rates of adults. Still, these

TABLE 1. Overcompensatory/compensatory responses in biomass of different organisms to harvesting (D, developmental control; R, reproduction control).

Species	Juvenile response	Adult response	Control	Source	Notes
<i>Sancasania berlisi</i>	decrease	increase	D	Cameron and Benton (2004)	eggs, juveniles, or adults
<i>Lucilla cuprina</i>	decrease/ increase	increase/ decrease	D/R	Nicholson (1957)	resource levels for juveniles and adults varied
<i>Daphnia</i>	increase	decrease	R	Slobodkin and Richman (1956)	newborns harvested
<i>Daphnia pulex</i>	unaffected	decrease	R	Nilsson et al. (2010)	random harvesting
<i>Holopedium gibberum</i>	increase	decrease	R	Huss and Nilsson (2011)	large individuals harvested
<i>Heterandria formosa</i>	increase	decrease	R	Schröder et al. (2009)	juveniles or adults harvested
<i>Perca fluviatilis</i>	increase	decrease	R	Ohlberger et al. (2011)	massive pathogen outbreak, adult mortality > juvenile mortality

increases in mass-specific rates do not compensate for the decreases in juvenile and adult biomasses. Overall, the monotonic decrease in biomass with increased mortality corresponds to well-known patterns observed in unstructured consumer–resource models.

With ontogenetic asymmetry, either the juvenile or the adult stage forms the bottleneck in the population. If juveniles are more energy efficient, the population is at low mortality characterized by a high maturation rate of juveniles into adults and a low adult reproduction rate, leading to a biomass dominance of adults and high biomass loss through maintenance in the adult compared to the juvenile stage (Fig. 1a). An increase in mortality in this case will lead to a decrease in adult biomass, whereas juvenile biomass first increases and thereafter decreases. Thus the juvenile/adult biomass ratio is no longer constant but changes with mortality, despite the fact that both stages experience the same increase in mortality. This type of ontogenetic asymmetry leads to *reproduction control*. Increased mortality will then increase per capita fecundity of adults to such an extent that total population fecundity goes up, leading to an increased inflow of recruiters into the population. This overcompensatory increase in fecundity arises because adults experience a very high resource limitation at low mortality, and most of the food ingested is lost to maintenance. An increase in food availability will then lead to a disproportional increase in net energy gain that can be allocated to reproduction. Juvenile performance also increases, but proportionally less, as juveniles are less resource limited at low mortality. As a consequence, juvenile biomass will increase. Fig. 1a–c illustrates the case in which mortality affects all individuals equally (random mortality). However, overcompensation occurs irrespective of whether mortality is random or targeted at juveniles or adults, although the magnitude of the overcompensation will differ (de Roos and Persson 2013).

If adults are more energy efficient than juveniles, the reverse pattern emerges. This type of ontogenetic asymmetry leads to *development control*. The population is at low mortality now characterized by a low maturation rate of juveniles into adults, a high

reproduction rate, a biomass dominance of juveniles, and high biomass loss through maintenance in the juvenile compared to the adult stage (Fig. 1c). An increase in mortality, in this case, will lead to a decrease in juvenile biomass, whereas adult biomass first increases and thereafter decreases. In this case, an increase in food availability will have a positive effect on the transition of juvenile biomass into adults. Like juvenile biomass overcompensation, adult biomass overcompensation occurs irrespective of whether mortality is random or targeted at juveniles or adults, although the magnitude will differ.

Stage-specific biomass overcompensation is the single most important consequence of ontogenetic asymmetry, which as we will discuss in the next section has major consequences for community structure. When juveniles and adults share a resource, total biomass will still show a monotonic decrease with mortality. In contrast, if juveniles and adults feed on different resources, an increase in mortality may actually lead to an overcompensatory increase in *total population biomass* if the productivities of the two resources differ (de Roos and Persson 2013). Moreover, when juveniles and adults use different resources, overcompensation can also occur when, intrinsically, juveniles and adults have identical energetics. It should be noted that the two-stage representation that we have used here is, in many cases, an idealized view of more complex representations involving several stages or even continuous size distributions. Still, stage-specific overcompensation and positive biomass–mortality relationships occur as generic aspects of ontogenetic asymmetry also in more complex stage- and size-structured settings, as long as development and reproduction both depend on resource availability and ontogenetic asymmetry in net biomass production prevails (de Roos and Persson 2013).

In view of the theoretical expectation that overcompensation is common, the empirical evidence is so far relatively limited, possibly because the theoretical insights about biomass overcompensation are relatively recent (de Roos and Persson 2002), and thus researchers may not have looked for empirical evidence yet. This interpretation is supported by the substantial increase in

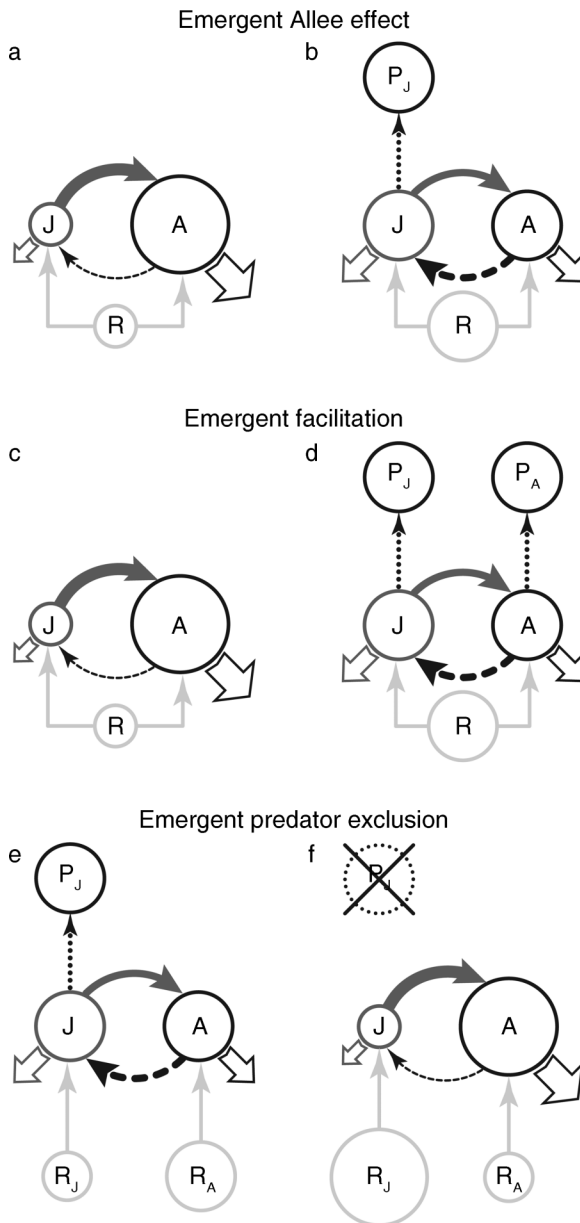


FIG. 2. Community consequences of biomass overcompensation. (a, b) Feeding modules showing the alternative stable community states occurring under the same conditions in a food web module including a stage-structured consumer and (in panel b) a predator feeding on juveniles (P_J), which exhibits an emergent Allee effect. (c, d) Modules illustrating emergent facilitation between predators where the presence of a facilitating predator feeding on adults (P_A) is necessary for a predator feeding on juveniles to be able to invade. (e, f) Modules showing a food web module including a stage-structured consumer with juveniles and adults feeding on separate resources and a predator feeding on juveniles, which goes extinct at high productivities of the juvenile consumer's resource (emergent predator exclusion). A consumer–resources state and a predator–consumer–resources state occur here as alternative stable community states for intermediate productivities of the juvenile consumer resource. For consumer and resources, biomass relationships within trophic levels, food intake (light gray arrows) and relative mass flows between

the number of empirical studies providing evidence for biomass overcompensation in recent years (Table 1). Another reason is that, due to the hump-shaped overcompensatory response, overcompensation may be missed, although present, if imposed mortality rates are too high. Nevertheless, the classical population studies by Nicholson (1957) on the Australian sheep blowfly (*Lucilla cuprina*) already provide substantial evidence for stage-specific overcompensation. By manipulating resource limitations of larvae and adults, respectively, Nicholson induced conditions in which either juvenile or adult overcompensation is expected (Table 1). Overall, he showed a strong overcompensation in larval density to adult harvesting under high adult competition, and overcompensation in adult density to adult harvesting under high larval competition. Furthermore, his results show that the form of resulting overcompensation is clearly affected by differential resource productivities for juveniles and adults, irrespective of intrinsic individual energy efficiency.

Besides an experimental study by Slobodkin and Richman (1956), the rest of the empirical evidence for overcompensation mainly comes from studies published during the last decade (Table 1). The most complete evidence is provided by Schröder et al. (2009), who showed (1) the actual existence of a hump-shaped relationship between (juvenile) biomass and mortality for the first time, and who showed that (2) overcompensation in juveniles was present when either adults and juveniles were exposed to increased mortality. The empirical studies on biomass overcompensation have almost all been carried out in laboratory or field mesocosm experiments. However, Ohlberger et al. (2011) recently demonstrated that stage-specific overcompensation in a fish population occurred in a whole lake, showing that overcompensatory responses are not restricted to laboratory or mesocosm systems (Fig. 1d).

Overcompensatory responses to mortality have been demonstrated in both juvenile and adult biomass (Fig. 1d, e). Still, existing empirical evidence suggests that ontogenetic asymmetry with reproduction control might be more common than ontogenetic asymmetry with development control. More data are obviously needed to evaluate the generality of this pattern, but the pattern is in line with the circumstance that the body size scaling of metabolic demands, on average, has a higher scaling exponent than the scaling of food ingestion (Glazier 2005, Basset et al. 2012). Correspondingly, the system with an overcompensatory response in line with development control (Cameron and Benton 2004) was characterized by substantial interference from larger mites against smaller mites (Fig. 1e).

← compartments due to development (dark gray arrows), and reproduction (dashed black arrows) are also shown. For specific model formulations and results, see de Roos and Persson (2013).

ONTOGENETIC ASYMMETRY AND COMMUNITY STRUCTURE

As we have seen in the previous section, ontogenetic asymmetry leads to overcompensation in stage-specific (or even total) biomass in response to increased mortality. When it occurs in prey populations, this overcompensatory response has major implications for community structure because it gives rise to positive feedbacks between predators and their prey, leading to the presence of alternative stable states or facilitation among predators that are not present under ontogenetic symmetry. These positive feedbacks thus lead to predictions that are quite distinct from existing unstructured theory about basic trophic modules. Consider first a three-link food chain, the behavior of which is well-known in the unstructured, symmetrical case (i.e., Oksanen et al. 1981). In this case, food chain length depends on the productivity of the basic resource, and the invasion and persistence thresholds of the top predator coincide (no alternative stable states are present). If the intermediate consumer exhibits ontogenetic asymmetry, however, such that juveniles have greater energy efficiency than adults (reproduction control), the situation becomes very different. In the absence of predators, the consumer population is dominated by adults, as shown in the previous section, and juvenile biomass is relatively low due to low adult population fecundity (Fig. 2a feeding module; emergent Allee effect). In contrast, if a predator feeding selectively on juveniles is present, its predation pressure causes an overcompensatory increase in juvenile consumer biomass such that this biomass is *higher* with predators present, despite the fact that predators feed selectively on juveniles (Fig. 2b; emergent Allee effect). This shift in consumer population size structure induced by predation mortality allows the community states with and without predators to occur as alternative stable states, such that the predator may persist at lower productivity levels than those at which it can invade by promoting its feeding condition through predation (compare juvenile consumer biomasses in the upper two modules; Fig. 2a, b). The fact that predators through predation promote their own food availability has been termed an *emergent Allee effect* because, in contrast to most mechanisms causing Allee effects, it is based on purely exploitative predation of prey (de Roos and Persson 2002).

The presence of an emergent Allee effect was demonstrated in a long-term whole-lake experiment involving the consumer species Arctic char (*Salvelinus alpinus*) and the predator brown trout (*Salmo trutta*) (Persson et al. 2007). At the start of the experiment, the system was totally dominated by a stunted population of Arctic char, and brown trout was almost absent. An intensive harvesting on Arctic char during 1986–1990 resulted in increased individual growth of the remaining Arctic char, but also an increase in the number of small size classes of Arctic char that brown trout feed on. This increase in small size classes of Arctic char allowed

brown trout to recover and increase to large numbers. Subsequently, the brown trout has, through its own predation on small size classes of Arctic char, sustained the Arctic char population size structure for more than two decades in a condition with high numbers of small and large size classes.

As another type of community effect of biomass overcompensation in prey populations, it also may lead to positive effects among predators sharing the same prey (emergent predator facilitation). A predator feeding on one stage of a consumer population may then facilitate the presence of another predator feeding on another consumer stage. For example, a predator feeding on adult consumers in a reproduction-controlled system will increase juvenile consumer biomass, allowing a predator that feeds on juveniles to invade under conditions that do not allow for its invasion in the absence of adult-specialized predators (Fig. 2c, d). Persistence of the predator feeding on juveniles may then crucially depend on the presence of the predator that feeds on adults (de Roos and Persson 2013). If juveniles and adults feed on different resources, predator facilitation may also be bidirectional, in that both predators need each other to persist (mutual predator facilitation). As an empirical example, Huss and Nilsson (2011) showed experimentally that an increase in the mortality of large stages of the herbivorous zooplankton *Holopedium* in a reproduction-controlled system facilitated the persistence of the juvenile-specialized predator *Bytotrephes*, and that this persistence depended on sustained, increased mortality of large *Holopedium*. Other possible empirical examples of emergent facilitation are discussed in de Roos and Persson (2013).

A third example of the effects of ontogenetic asymmetry in a consumer population concerns a situation in which juvenile and adult consumers feed on different resources (Fig. 2e, f). For such a system, Schreiber and Rudolf (2008) demonstrated the presence of alternative stable states characterized by either an adult-dominated or a juvenile-dominated consumer population. Thereby, gradual changes in resource productivities or mortalities can lead to abrupt regime shifts. Empirical support for dramatic changes in stage-specific growth performance in relation to changes in stage-specific resource abundance is present from sunfish systems (Osenberg et al. 1992). Importantly, even when juveniles and adults are *intrinsically* equal in energetics, ontogenetic asymmetry may develop due to *extrinsic* differences in resource productivities for the two stages. A predator feeding on juvenile consumers will be able to invade this system at a sufficiently large productivity of the juvenile consumer's resource. After predator establishment, juvenile biomass remains constant, with increased productivity of juvenile resource, whereas adult biomass increases, leading to an increase in adult/juvenile biomass ratio. A further increase in juvenile resource productivity will first lead to alternative stable states with predators either present or absent

and juvenile biomass at low density when predators are absent. At high juvenile resource productivity, only the equilibrium with low juvenile/high adult consumer emergent biomass remains and predators go extinct (Fig. 2e, f; predator exclusion). This pattern arises because an increase in resource productivity of the juvenile resource will lead to an increased biomass dominance of adults, whose fecundity thereby may decrease due to increased resource limitation in this stage, in turn leading to decreased juvenile biomass.

These examples (the first and third examples involving alternative stable states and the second example involving predator facilitation) represent only three of many possible feeding modules. Such feeding modules may include ontogenetic niche shifts in predator species, mixed interactions (intraguild predation), and interspecific competition in different ontogenetic niches. Still, in all these feeding modules there is a high propensity for the occurrence of alternative stable community states as a result of predator-induced shifts in consumer biomass distribution (de Roos and Persson 2013).

ONTOGENETIC ASYMMETRY AND POPULATION DYNAMICS

Generation/cohort cycles have been shown, in theory, to be a general outcome of size-dependent interactions and have been documented empirically in various taxa, including soil mites, *Plodia*, zooplankton, and fish (Townsend et al. 1990, Sait et al. 1994, McCauley et al. 1999, Sanderson et al. 1999, McCauley et al. 2008). Cohort cycles and predator-prey cycles also have been experimentally shown to form alternative attractors in the case of logistic resource growth (McCauley et al. 1999, 2008). Murdoch et al. (2002) quantitatively analyzed how common cohort cycles are compared to predator-prey cycles. They showed that generation/cohort cycles were as common as predator-prey cycles, based on data from the Global Population Dynamics Database (*available online*).⁴ Even more, >60% of all documented population cycles are cohort cycles or delayed feedback cycles, which is another type of stage-structure-induced cycle. Here we consider how and what type of generation cycles result from ontogenetic asymmetry.

To this end, we assume that the resource follows semi-chemostat dynamics (see Appendix) such that the standard predator-prey cycles from unstructured models (paradox of enrichment cycles) do not occur. Under ontogenetic symmetry, the dynamics consequently exhibits fixed-point dynamics (de Roos and Persson 2013). In contrast, ontogenetic asymmetry leads to the occurrence of two qualitatively different types of cycles, depending on whether juveniles or adults have greater energy efficiency (Figs. 3 and 4). When juveniles are more efficient, high-amplitude cycles occur that are shaped by a dominating, recruiting cohort. Their high

energy efficiency allows juveniles of this dominating cohort to depress the resource, leading to zero reproduction and increased starvation mortality among adults. The dominating cohort grows in body size over time and gives rise to a new dominating cohort upon maturation (Fig. 3a). Consequently, the cycle period is approximately equal to the time delay between birth and maturation, a characteristic of generation cycles (Murdoch et al. 2003). Because of the dominance by one juvenile cohort, these cycles are also called juvenile-driven cycles (de Roos and Persson 2013). The cycles differ qualitatively from predator-prey cycles in unstructured models, because juvenile and adult densities vary out of phase with each other. Detailed analyses furthermore show that the characteristics of juvenile-driven cycles closely resemble those of a reproduction-controlled system, including low fecundity and high mortality of adults combined with fast growth and low mortality of juveniles and a low average juvenile-adult biomass ratio, as is expected for a reproduction-controlled system.

Juvenile-driven cycles with one cohort dominating the population have been empirically documented in many fish populations (Townsend et al. 1990, Sanderson et al. 1999, Persson and de Roos 2006). An illustrative example of such a juvenile-driven cycle is the five-year cycle observed in a yellow perch (*Perca flavescens*) population in which a single year class totally dominated the population up to its maturation (Fig. 3b); see Sanderson et al. (1999). In this case, the competitive effect of the superior juveniles was reflected in a massive die-off of adults following the birth of the dominating year class.

Cycles also occur when adults have more efficient energetics, but fluctuations in numbers and size distribution are much smaller than in juvenile-driven cycles (Fig. 4a). These so-called adult-driven cycles have a periodicity that is slightly longer than the juvenile delay, due to the longer life span of adults in these cycles compared to juvenile-driven cycles. In the same way that juvenile-driven cycles have all the characteristics of a reproduction-controlled system, these adult-driven cycles have all the characteristics of a development-controlled system. Thus juvenile growth is slow and juvenile mortality is high, adult fecundity is high and adult mortality is low, and the juvenile/adult biomass ratio is high (de Roos and Persson 2013). Interestingly, there exists substantial experimental evidence that unicellular organisms such as bacteria, yeast, and phytoplankton can exhibit adult-driven cohort cycles (Massie et al. 2010). In particular, Massie et al. (2010) provided experimental evidence for the presence of adult-driven cycles in *Chlorella vulgaris* and other phytoplankton populations (Fig. 4b). Despite the relatively modest change in size (four times in volume) over the life cycle of *Chlorella*, a cohort cycle developed, resulting from synchronization of the cell cycle and the population cycle via a common nutrient pool (nitrogen).

⁴ <http://www3.imperial.ac.uk/cpb/databases/gpdd>

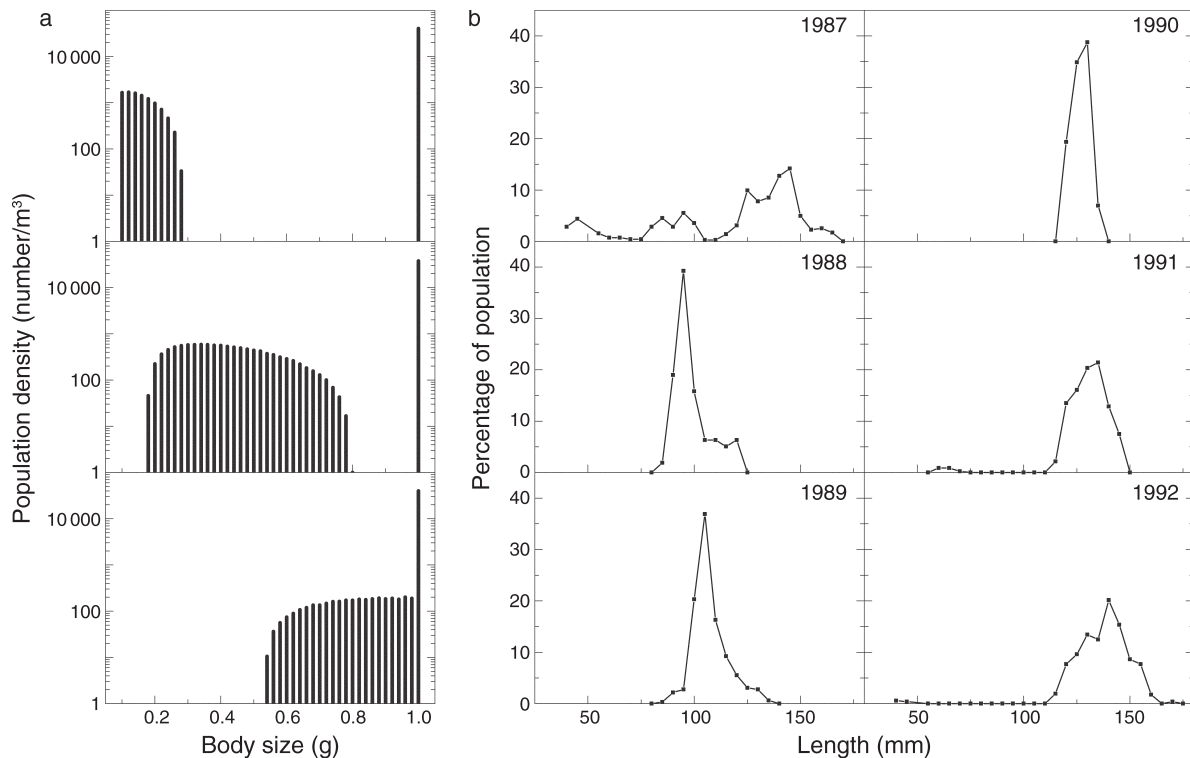


FIG. 3. (a) Model and (b) empirical examples of the effects of ontogenetic asymmetry with reproduction control on consumer–resource population dynamics. (a) Model predictions (see Appendix for model formulation) show the consumer size (biomass) distribution (population density on a log scale) at three different times (T) during the regular cycle that occurs when juveniles have a superior energy balance (ontogenetic asymmetry in net biomass production but not mortality, $q = 0.4$, $p = 1.0$; background mortality $\mu = 0.015 \text{ d}^{-1}$; other parameters are as in Fig. 1). (b) Changes in the length distribution of the yellow perch population in Chrystal Lake during 1987–1992 (data from Sanderson et al. [1999]). Note that the dominating cohort born in 1987 first appears in catches in 1988.

The interpretation of these cycles as adult-driven cycles is supported by the fact that progression through the cell cycle was retarded in the nitrogen-dependent, premitotic (“juvenile”) phase, during which individuals born at different times were stacked (Fig. 4b).

CONCLUSION AND PERSPECTIVES

We have postulated that ontogenetic asymmetry in energetics represents a fundamental property of most ecological systems, and that contemporary, unstructured population and community theory—corresponding to ontogenetic symmetry—only represents a limiting case of a more generic theory that includes ontogenetic symmetry and asymmetry. We have already considered that symmetry-breaking may result from characteristics intrinsic to the individual, such as differences between the size-scaling of ingestion and maintenance, as well as from extrinsic factors, e.g., different resource productivities for juvenile and adult consumers. We have focused on the effect of ontogenetic asymmetry in mass-specific net production due to variation in the maximum ingestion rate. The same type of ontogenetic asymmetry, however, also may result from differences in assimilation efficiency or maintenance rate. Two additional factors

that may affect patterns of biomass overcompensation and presence of cohort cycles are ontogenetic asymmetry in mortality and the ratio between the individual body size at birth and at maturation, because it characterizes the prominence of ontogenetic development in the life cycle of species. An extended analysis of these two factors shows that the birth size/maturation mass ratio only influences the domain of juvenile-driven cycles (these cycles disappear above a ratio of 0.24), and that the domain of ontogenetic symmetry is very limited (Appendix: Fig. A1); see de Roos et al. (2013). Thus, even organisms with a high birth/maturation size ratio, such as unicellular organisms, birds, and mammals, are generally expected to exhibit biomass overcompensation and adult-driven, but not juvenile-driven, cohort cycles.

The distinction between two different domains of ontogenetic asymmetry in energetics, with either development control or reproduction control, provides a novel conceptualization to handle the effects of both individual development and reproduction on population and community dynamics. At the community level, ontogenetic asymmetry in different trophic configurations will lead to alternative stable states through overcompensatory responses in biomass. At the popu-

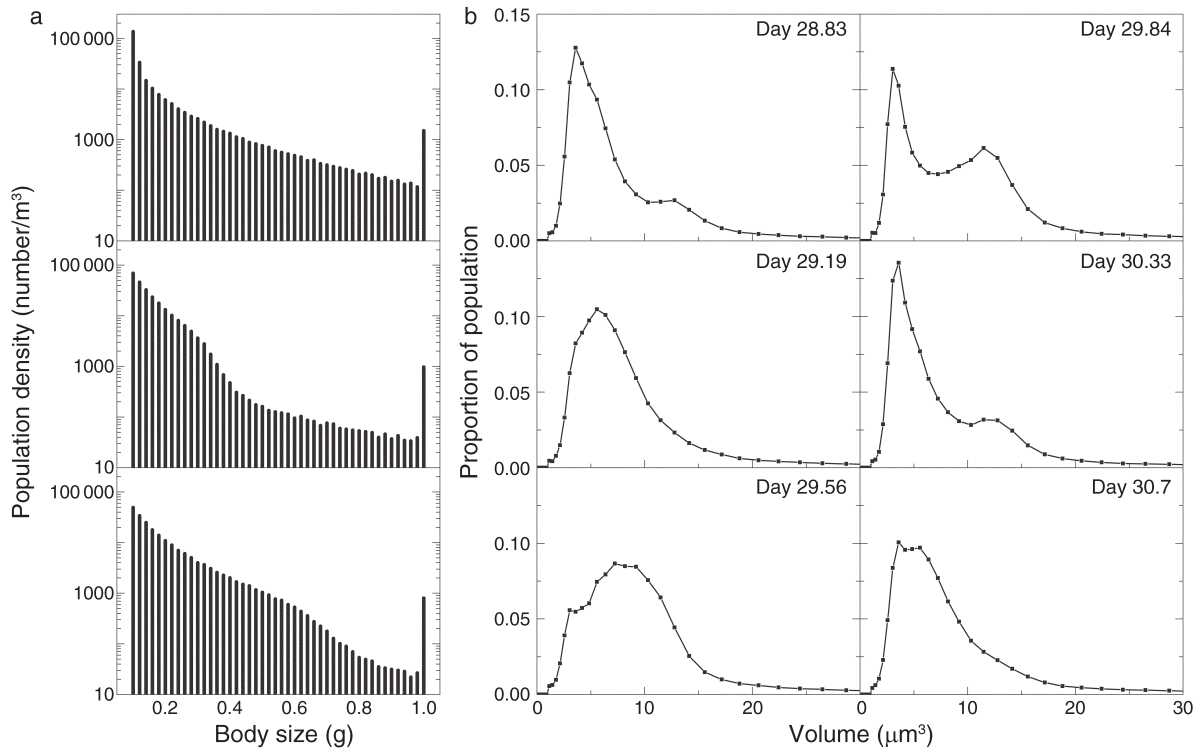


FIG. 4. (a) Model and (b) empirical examples of the effects of ontogenetic asymmetry with development control on consumer–resource population dynamics. (a) Model predictions (see Appendix for model formulation) show the consumer size (biomass) distribution (population density on a log scale) at three different times (T) during the regular cycle that occurs when adults have a superior energy balance (ontogenetic asymmetry in net biomass production but not mortality, $q = 1.6$, $p = 1.0$; background mortality $\mu = 0.015 \text{ d}^{-1}$; other parameters are as in Fig. 1). (b) Changes over time in the size (volume) distribution of an experimental *Chlorella* population under nitrogen limitation (data are from Massie et al. [2010]).

lation level, ontogenetic asymmetry will lead to cycles that differ qualitatively from the cycles predicted by unstructured population theory. Moreover, the presence of cohort cycles is intimately linked to the energetic performance of juveniles and adults per se, because the cycles also occur when juveniles and adults feed on different resources (no intercohort competition for resources) that have different productivities (de Roos and Persson 2013). Overall, our consideration of community structure and population dynamics thus shows that the concepts of ontogenetic symmetry and asymmetry form a productive conceptual framework on which to develop a population and community theory. Finally, the predator-induced biomass redistribution over prey stages also implies that consumer–resource interactions become indivisible units with behavior that can no longer be predicted from the constituting parts (the species), as in unstructured ecological theory. Thus, ontogenetic asymmetry in energetics is a strong driver of self-organization in ecological communities, with major ramifications for ecological theory in general.

Accounting for ontogenetic development in ecological theory superficially may be viewed like just adding one of the many complicating factors, in particular population size structure, that impinge on ecological dynamics

and hence lead to modifications of basic population dynamics. This view, however, is essentially incorrect. Just like reproduction and mortality, development is an elementary and immutable component of population dynamics that can never be excluded and whose impact can never be eliminated. Without development, mortality, and reproduction, there simply is no population dynamics. In contrast, other complicating factors such as spatial heterogeneity, temporal variation, or intra-specific genetic variability can be controlled for to the extent that their impact on ecological dynamics can be completely eliminated. Specifically, basic population dynamics unaffected by spatial heterogeneity and genetic variability has been measured as exemplified by the numerous experimental studies in homogeneously mixed chemostats or carried out with clonal or parthenogenetically reproducing organisms. Analogous experiments assessing dynamics in the absence of development are, however, biological impossibilities. Development is therefore on par with reproduction and mortality and is not a factor that only complicates basic population dynamics.

Although our theoretical understanding of the implications of ontogenetic asymmetry for ecological systems is rather recent, empirical evidence for the existence of

stage-specific overcompensation arising from ontogenetic asymmetry has already started to accumulate. Several major questions to be addressed here present themselves. First, is reproduction control indeed more prevalent than development control, as existing empirical evidence suggests, and is there a pattern among different taxa related to the basic size-scaling of intake vs. maintenance rates? Second, to what extent does ontogenetic asymmetry result from intrinsic properties of the individual compared to extrinsic size- or stage-specific resource productivities, and does the extent to which organisms are involved in nonexploitative interactions affect the form of asymmetry?

A most relevant and interesting question to address for the future is how ontogenetic asymmetry has evolved and is sustained. Does natural selection actually favor the evolution of ontogenetic asymmetry if only intrinsic factors are considered, or are extrinsic factors such as heterogeneity in resource productivities necessary? How does ontogenetic asymmetry link to the evolution in nature of so prevalent ontogenetic niche shifts in different organisms? Or more generally, what is the extent to which ontogenetic asymmetry in energetics has contributed to the evolution of complex life cycles, the complexity of life forms, and thereby the complexity of ecological communities?

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SUPPLEMENTAL MATERIAL

Appendix

Description of the fully size-structured model and parameter domains of ontogenetic asymmetry and ontogenetic symmetry ([Ecological Archives E094-135-A1](#)).