Size- and food-dependent growth drives patterns of competitive dominance along productivity gradients

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Abstract. Patterns of coexistence among competing species exhibiting size- and food-dependent growth remain largely unexplored. Here we studied mechanisms behind coexistence and shifts in competitive dominance in a size-structured fish guild, representing sprat and herring stocks in the Baltic Sea, using a physiologically structured model of competing populations. The influence of degree of resource overlap and the possibility of undergoing ontogenetic diet shifts were studied as functions of zooplankton and zoobenthos productivity. By imposing different size-dependent mortalities, we could study the outcome of competition under contrasting environmental regimes representing poor and favorable growth conditions. We found that the identity of the dominant species shifted between low and high productivity. Adding a herring-exclusive benthos resource only provided a competitive advantage over sprat when size-dependent mortality was high enough to allow for rapid growth in the zooplankton niche. Hence, the importance of a bottom-up effect of varying productivity was dependent on a strong top-down effect. Although herring could depress shared resources to lower levels than could sprat and also could access an exclusive resource, the smaller size at maturation of sprat allowed it to coexist with herring and, in some cases, exclude it. Our model system, characterized by interactions among size cohorts, allowed for consumer coexistence even at full resource overlap at intermediate productivities when size-dependent mortality was low. Observed shifts in community patterns were crucially dependent on the explicit consideration of size- and food-dependent growth. Accordingly, we argue that accounting for food-dependent growth and size-dependent interactions is necessary to better predict changes in community structure and dynamics following changes in major ecosystem drivers such as resource productivity and mortality, which are fundamental for our ability to manage exploitation of living resources in, e.g., fisheries.

Key words: coexistence; community structure; competition; diet shifts; food-dependent growth; herring; productivity; size-dependent mortality; size structure; sprat.

Introduction

Competitive interactions fundamentally depend on body size, as body size scaling of foraging capacity strongly influences competitive ability (Persson et al. 1998). In many animal taxa, such as fish and amphibians, intake rate of individuals, and in many cases also diet, changes as they grow in body size (Werner and Gilliam 1984). Such ontogenetic diet shifts may change the type and strength of competitive interactions with implications for overall community dynamics (Rudolf and Lafferty 2011). Competition theory has long relied on Lotka-Volterra type models, ignoring variation in body size (Gause 1934). The main body of theory dealing with competition for shared resources largely suffers from the same lack of biological realism (Tilman

1982). Intraspecific variation in body size and size-dependent patterns of resource use throughout ontogeny have only recently been considered in studies of the implications of interspecific competition for community structure (Schellekens et al. 2010), while earlier studies on the implications of ontogenetic niche shifts have focused on cases when competition only occurs within life stages (i.e., by habitat or resource segregation; Loreau and Ebenhoh 1994, McCann 1998, Moll and Brown 2008). For species exhibiting ontogenetic niche shifts, changing resources over ontogeny may be a way of escaping interspecific competition. For species without this option, an alternative life-history strategy may be to mature at a small size, hence allowing for a fast turnover rate (short generation time) also when feeding on a single shared resource. Interestingly, species that feed on the same resource throughout life often compete with species that shift resources over ontogeny. For example, many small pelagic fish species typically compete for zooplankton resources and have short life spans, but in several cases also include species that

PLATE 1.   Gillnet herring fishery in the Baltic Sea. Photo credit: Sara Königson.

undergo diet shifts (Garrison and Link 2000, Casini et al. 2006).

A major theme in ecology is how mortality and productivity influence the outcome of competitive interactions and hence community structure (Tilman 1982, Chesson 2000). Despite many theoretical studies showing a complex relationship between mortality and species coexistence (reviewed in Chase et al. 2002), the commonly held view is still that mortality promotes coexistence because it reduces the intensity of interspecific competition as consumer density is reduced (Gurevitch et al. 2000). The main prediction of resource competition theory is that the competitive ability of species for a shared resource is determined by its ability to reduce the density of the resource (Tilman 1982). Hence, independent of resource productivity, in equilibrium there cannot be more consumers than there are limiting resources. Adding intraspecific differences in resource use may however change this view (Schellekens et al. 2010). For predator–prey systems, the relative importance of competition and mortality in determining community patterns has been extensively explored. These studies show that mortality only has a major effect on community structure at high productivity whereas the influence of competition dominates at low productivity (Holt et al. 1994, Bohannan and Lenski 2000), but also that there may be an interaction between mortality and productivity effects relating to a trade-off between abilities to depress resources and to withstand predation (Holt et al. 1994). For pure competition systems, however, little is known about the importance of a mortality–productivity interaction for community structure.

Here we aim to advance our mechanistic understanding of factors governing the structure and stability of food webs with coexisting consumers exhibiting food-dependent growth by studying an example of competing zooplanktivorous fish. Competitive communities of small pelagic fish species occur in all the world's oceans, and include examples like anchovy–sardines (*Sardinops sagax–Eugraulis ringens*) outside Chile and Peru and herring–sprat (*Clupea harengus–Sprattus sprattus*) in the North Sea and Baltic Sea (Alheit and Niquen 2004, Casini et al. 2006; see Plate 1). These fish species are commercially important and often key players in marine food webs, as predators on zooplankton and as prey for top predators. We used a sprat–herring system as a basis for developing a model within the framework of physiologically structured population models (Metz and Diekmann 1986, de Roos and Persson 2001), which explicitly takes food-dependent growth and intraspecific variation in body size into account. We used this model to address a number of potentially important mechanisms to explain shifts in community structure (species composition and size distributions) in competition systems of small pelagic fish. The food web configuration used and the explicit incorporation of size-dependent feedbacks allowed us to study a number of novel mechanisms determining the outcome of competitive interactions (cf. Schellekens et al. 2010). The effects of resource overlap, the possibility of undergoing an ontogenetic diet shift and thereby gaining access to an exclusive resource, and the competitive advantage of early maturation on community structure were studied as functions of resource productivity. We show that the extent to which inclusion of an additional resource into
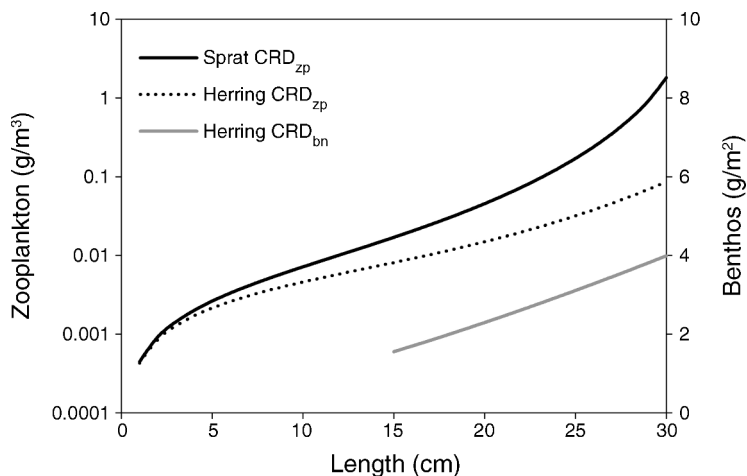
Fig. 1. The size dependency of the critical resource density (CRD) of sprat feeding on zooplankton and herring feeding on zooplankton (zp) or on benthos (bn).

the diet at larger body sizes provides a competitive advantage depends on sufficiently high resource productivity in the first niche. The inferior species in terms of its ability to depress shared resources could, as a result of its smaller size at maturation, under certain circumstances coexist with and sometimes even exclude the species that could best depress shared resources and furthermore had access to an exclusive resource. By studying the influence of size-selective mortality (targeting small individuals) on competitive outcomes we provide results that show a strong dependency on mortality level and life-history type (the possibility of undergoing a diet shift) for productivity effects. We thereby demonstrate an interaction between top-down and bottom-up effects on community structure previously not accounted for in structured competition models.

MODEL DESCRIPTION

The model studied here is a physiologically structured population model and describes the interaction between sprat and herring and their respective resources. It is based on an approach specifically designed to handle implications of size-dependent individual performance for population and community dynamics (Metz and Diekmann 1986, de Roos and Persson 2001). Using this approach we can separate the individual-level (i) and population-level (p) states: the i state represents the state of the individual in terms of physiological traits such as body size, and the p state is a frequency distribution over all i states. Hence, all assumptions pertain to the individual level and results on the population level emerge from the individual-level processes. An environmental state (e state) is also recognized, which in our model corresponds to ambient densities of three unstructured resources: two zooplankton and one zoobenthos resource (hereafter referred to as benthos). The individual-level model formulation (details in

Appendix A), is a mathematical description of how individual performance (growth, survival, and reproduction) depends on the physiological characteristics of the individual (reversible and irreversible mass) and the state of the environment (resource densities).

We explicitly considered exploitative competition by means of shared resources. Both sprat and herring can feed on zooplankton throughout ontogeny. In addition, herring start to include benthos in their diet when reaching a body length of 15 cm after which they gradually increase their time feeding on benthos and reduce time feeding on zooplankton as they grow in size (see Appendix A: Fig. A1; Fig. 1). The parameter R is introduced as a measure of resource overlap (only zooplankton considered) between sprat and herring and is hence a proxy for the strength of interspecific competition. $R = 0$ implies no overlap in resource use and herring and sprat feed exclusively on their respective zooplankton resource, $R = 0.5$ represents full overlap such that both species feed on all zooplankton. Note that figures represent R as percentage niche overlap.

We assume that in the absence of predation by fish, zooplankton and benthos grow with a constant productivity independent of resource density (Appendix A: Table A3). The resources are assumed to consist of homogenously mixed populations, distributed in the whole sea volume (zooplankton) or over the whole bottom surface (benthos). Hence, resource densities are expressed as biomass per unit volume (zooplankton) and biomass per bottom surface (benthos), and consumer populations in number of individuals per unit volume. The volume-to-bottom ratio was set at 50, which corresponds to assuming an average depth of 50 m.

THE POPULATION STATE AND MODEL ANALYSIS

We model the dynamics only during the growing season (250 days), assuming that the remainder of the year is a period of stasis. Reproduction occurs during a
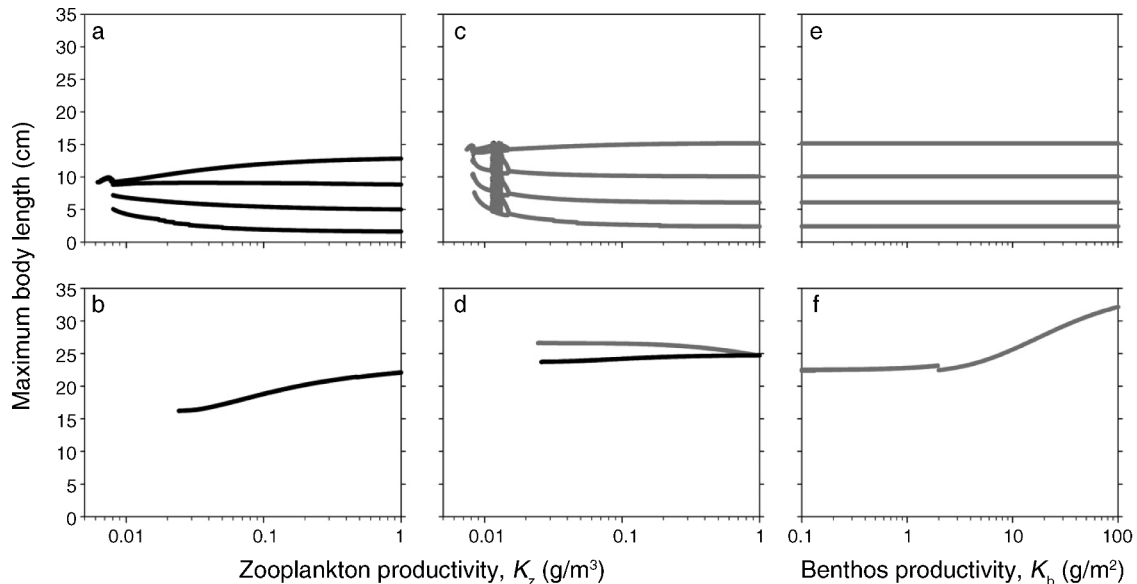
FIG. 2. Variation in (a, b) sprat and (c, d) herring maximum body length as a function of zooplankton productivity (K_z), and (e, f) herring body length as a function of benthos productivity (K_b) for low (size-dependent mortality constant, $\mu_s = 0.01$, top panels) and high ($\mu_s = 0.13$, bottom panels) size-dependent mortality ($K_z = 0.5$ is assumed). Panels (c) and (d) include both a scenario where herring only feed on zooplankton [black symbols, not visible in panel (c) as they coincide with gray symbols in this case] and a scenario where benthos feeding also is assumed [gray symbols, $K_b = 10$]. For every value of K_b and K_z, the model was run for 400 years. The figure shows the population state at the end of each year in the run. Hence, populations exhibiting a 4-year regular cycle (as for low μ_s) show up as four points at the same productivity value, whereas populations with fixed-point dynamics, where the population state is identical every year (as for high μ_s), show up as only one point.

spawning period at the start of the growing season. For computational purposes we lump individuals born within three-day periods into separate cohorts of individuals. Individuals within a cohort are assumed to be identical at birth (in terms of irreversible, x_n and reversible mass, y_n; Appendix A: Table A3). Furthermore, as individuals within cohorts experience the same environmental conditions, they all follow the same growth and survival trajectories throughout life. Sprat and herring populations are thus represented as a finite number of discrete cohorts of individuals and our model is a combination of a continuous system in terms of consumer growth and survival, as well as of production and consumption of resources, and a discrete system in terms of reproduction. Following reproductive events and/or extinction of cohorts, the number of cohorts changes. The dynamics of these cohorts are described by sets of ordinary differential equations (ODEs; Appendix A: Table A3), which were numerically integrated using the escalator boxcar train method (de Roos et al. 1992).

To study effects of resource productivities on population dynamics and individual growth patterns, we investigated the asymptotic dynamics of the model by means of bifurcation analysis using long numerical integrations, in which we systematically varied one of the parameters of interest in small steps. For every value of the bifurcation parameter, system dynamics were integrated over a period of 400 years, after which the integration continued with a slightly increased (or

decreased) parameter value. Assessment of long-term dynamics pertains only to the last 50 years of each integration period to discard any transient dynamics that result from the small parameter change. The results of these analyses are summarized in bifurcation diagrams (Fig. 2), which represent, for the given parameter value, the state of the populations and resource densities at the start of the growing season. To assess regions of different sprat–herring community states we identified the extinction and invasion boundaries. To locate extinction boundaries we used bifurcation analysis and subsequently monitored the persistence of the populations that were initially present. When the number of individuals dropped below 1×10^{-9} individuals/m^3, a population was considered extinct. Invasion boundaries were determined starting with a situation in which the invading population was not present. If the invading population experienced positive population growth the invasion was considered successful (see Appendix A for details on invasion calculations). Note that since the invading species invades at small numbers it is assumed not to affect resource densities, which prevents any feedback from the invader on the resident. By repeating these procedures we could construct the boundaries between different community states (i.e., coexistence, herring-only, and sprat-only states) as a function of resource overlap and productivity, for two different values of the size-dependent mortality constant (μ_s; Appendix A: Table A1, Eq. A.21; Fig. 3). We also
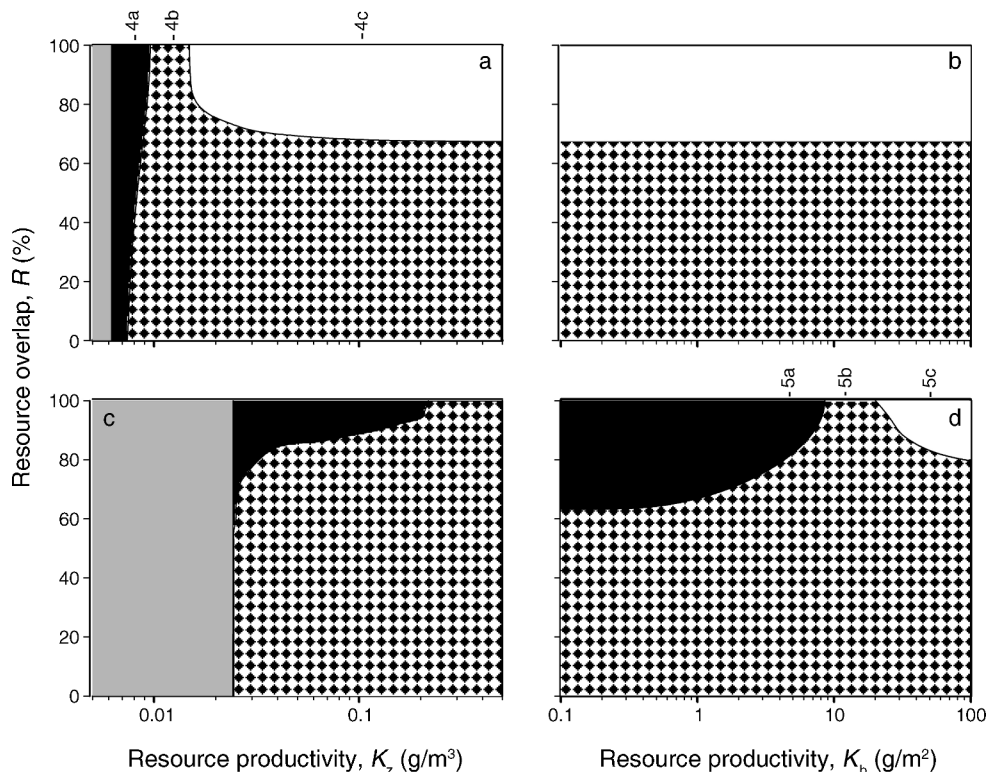
FIG. 3. Regions with possible community states occurring in the sprat–herring model at different values of zooplankton resource overlap and (a, c) zooplankton and (b, d) benthos productivity for a low (a, b; $\mu_s = 0.01$) and high (c, d; $\mu_s = 0.13$) size-dependent mortality constant. For the left-hand panels, $K_b = 10$ is assumed, and for the right-hand panels, $K_z = 0.5$ is assumed, all other parameter values being equal. The light gray region shows the resource-only equilibrium; the black region shows sprat-only equilibrium; the white region shows herring-only equilibrium; and the black and white region shows stable coexistence. For references to figures showing the corresponding time-series dynamics, see text above panels (a) and (d).

constructed the boundaries between community states as a function of zooplankton and benthos productivity (Appendix B: Fig. B1). Mortality values were chosen such that sprat and herring in one scenario would exhibit cohort cycles and in the other fixed-point dynamics. We further made sure that the dynamic behavior would be qualitatively the same for sprat and herring for the same value of μ_s (i.e., same cycle period). For all scenarios investigated, extinction and invasion thresholds coincided, which is why we hereafter do not differentiate between these types of boundaries. To identify the biological mechanisms responsible for changes in community structure we studied time series of consumer and resource dynamics in different community states (Figs. 4 and 5). Note that for scenarios with competitive exclusion, transient dynamics (i.e., population dynamics prior to exclusion of one of the consumers) are shown.

CRITICAL RESOURCE DEMANDS

In the study of competitive interactions, information on the ability of individuals to depress shared resources is a key factor. This can be expressed in terms of the critical resource density (CRD) of individuals, which is the resource density at which intake rate equals maintenance requirements, i.e., at which individuals neither grow nor reproduce. Since CRD scales with body size (relating to the size-scaling of intake and maintenance), it determines size-dependent competitive ability (Persson et al. 1998) and sets an upper limit to the maximum size that an individual can reach (equal to the size at which the CRD equals the carrying capacity of the resources). Given our parameterization of maximum intake rate and maintenance (see Appendix A), CRD is a monotonically increasing function with size for sprat and herring (Fig. 1), implying that small individuals can sustain themselves on lower resource densities than large individuals, and therefore are competitively superior to larger individuals. Furthermore, our parameterization leads to the result that herring can be sustained on lower resource densities than sprat throughout ontogeny. For an alternative scenario that relaxes the assumption of herring being competitively superior for all body sizes, see Appendix A.

RESULTS

Population dynamics and growth patterns

The dynamics and growth patterns of sprat and herring were heavily dependent on the level of size-
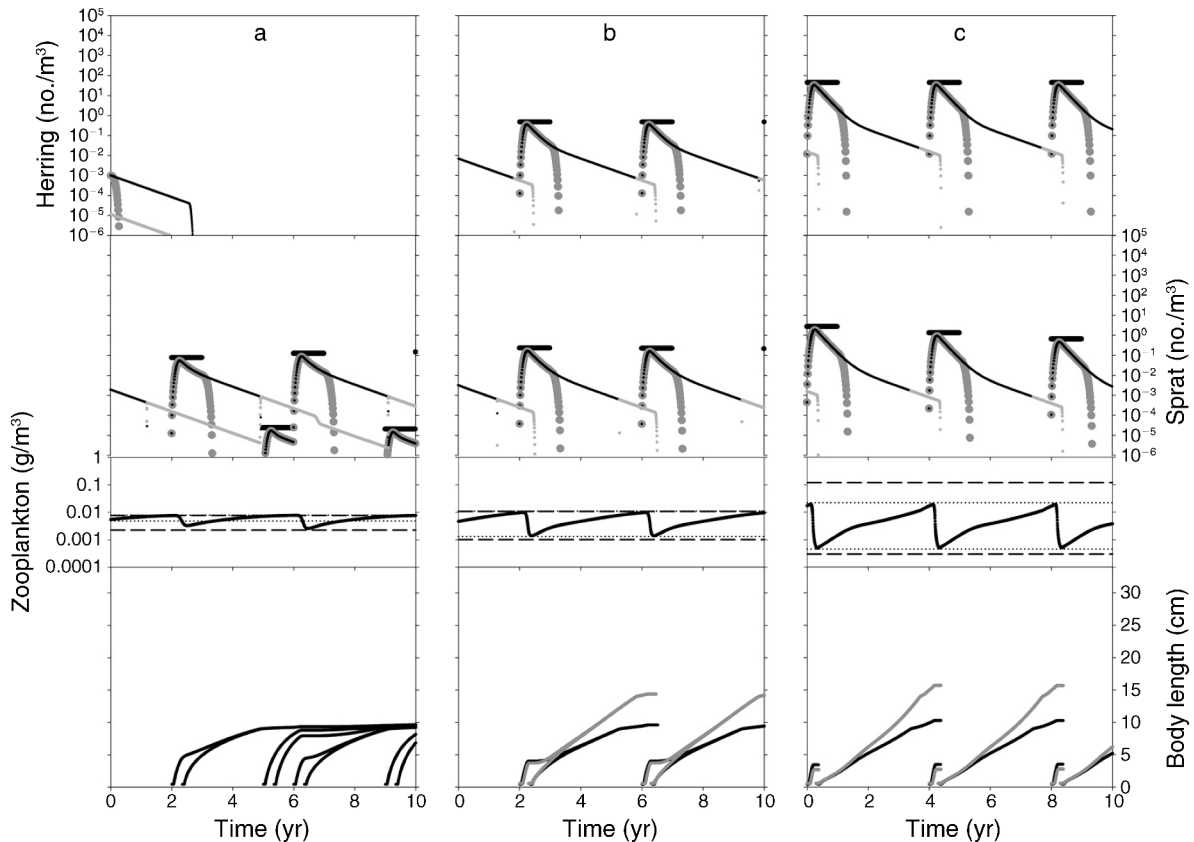
FIG. 4.   Model dynamics for (a) low ($K_z = 0.008$), (b) intermediate ($K_z = 0.012$), and (c) high ($K_z = 0.5$) zooplankton productivity for a given benthos productivity ($K_b = 10$) and size-dependent mortality ($\mu_s = 0.01$). Total zooplankton resource overlap between herring and sprat is assumed. The top panel in each column shows herring eggs (heavy black dots), young-of-the year (heavy dark-gray dots), juveniles (thin black dots), and adults (thin light-gray dots). The second panel in each column is the same, but for sprat. The third panel in each column shows zooplankton biomass. For comparison, the minimum and maximum zooplankton biomasses in systems with only herring (dotted line) or sprat (dashed line) are shown. The bottom panel in each column shows growth curves of the first and last herring (gray) and sprat (black) cohort (i.e., first and last spawn group, see Appendix A: Fig. A2) born each year (if any). Note that, for the highest productivity [panel (c)], the graphs show transient dynamics as sprat is eventually going extinct. At intermediate productivity [panel (b)], there is stable coexistence.

dependent mortality (Fig. 2). Increased mortality on small individuals resulted in stabilized population dynamics. At low size-dependent mortality, both sprat and herring experienced cohort cycles in which a cohort of juvenile individuals dominate the population until they reach maturity (in this case at 4 years of age), after which they produce the next dominant cohort (see Fig. 4). In the high-mortality scenario, individuals matured within their first year of life leading to fixed-point dynamics, where the population state is identical at the beginning of each year (see Fig. 5). This relates to faster growth rates because of the higher mortality on small cohorts and relaxed resource competition (i.e., a thinning effect), causing a younger age at maturation. Eventually, when mortality increases even further, populations go extinct.

At low mortality, sprat and herring only reached sizes just above their maturation size thresholds, irrespective of resource productivities (Fig. 2: top panel and Fig. 4). At high mortality and relaxed resource competition both

species reached larger sizes (Fig. 2: bottom panel). Although there was a positive relationship between zooplankton productivity and sprat maximum size there was no such relationship for herring. At low productivity sprat could not reach large body sizes because of their relatively high CRD (Fig. 1). Herring was instead already at low productivity limited by population feedbacks depressing the zooplankton resource. Hence, as productivity increased, sprat, but not herring, could respond in body size. When herring also fed on benthos, its maximum size even decreased slightly as zooplankton productivity increased (Fig. 2d, gray symbols). This results from reduced availability of benthos at high zooplankton productivity (results not shown), a consequence of an increased herring density (caused by the high zooplankton productivity) that depressed the benthic resource to low levels. The effect of benthos productivity on herring growth patterns was highly dependent on the level of size-dependent mortality. This relates to the threshold size for first benthos feeding at
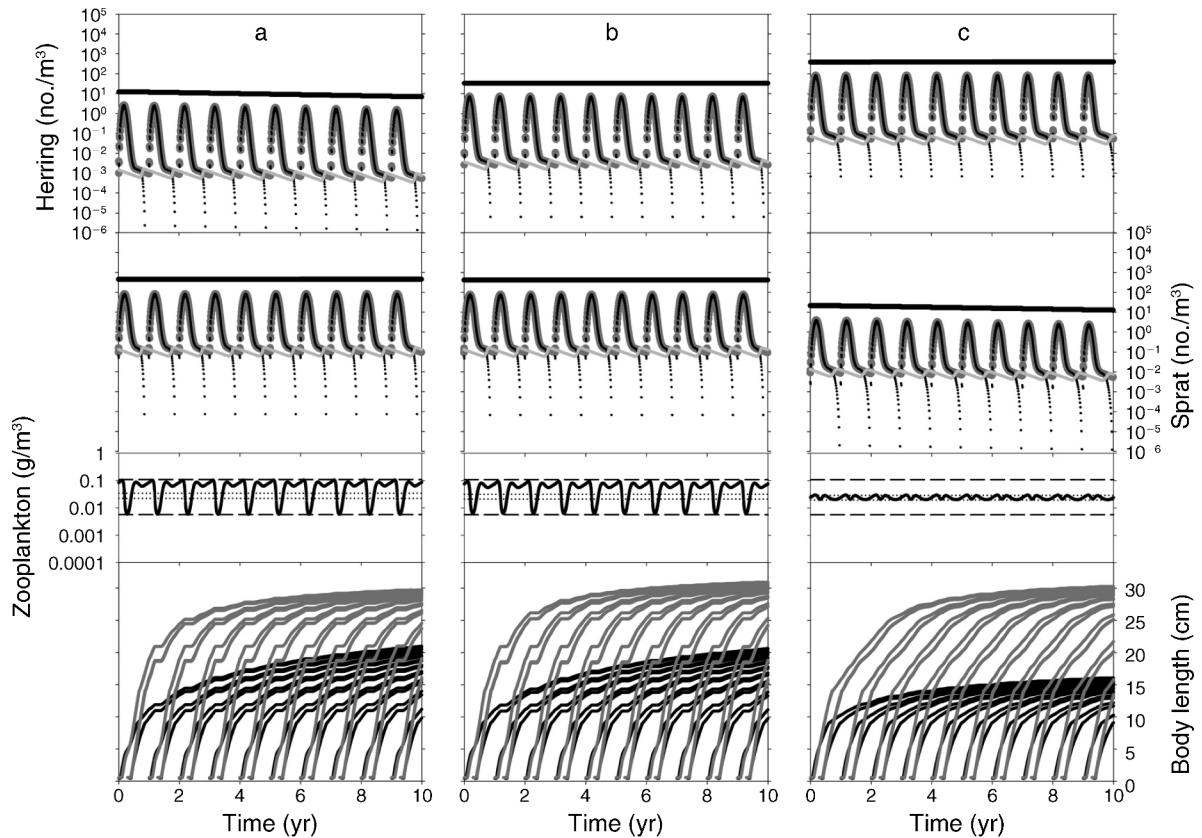
FIG. 5. Model dynamics for (a) low ($K_b = 5$), (b) intermediate ($K_b = 10$), and (c) high ($K_b = 50$) benthos productivity for a given zooplankton productivity ($K_z = 0.5$) and size-dependent mortality constant ($\mu_s = 0.13$). Total zooplankton resource overlap between herring and sprat is assumed. Note that, at low productivity [panel (a)], herring is approaching extinction and, at high productivity [panel (c)], sprat is approaching extinction. For these two productivities, the graphs show the transient dynamics toward extinction of herring and sprat, respectively. At intermediate productivity [panel (b)], there is stable coexistence. Symbols are as in Fig. 4.

15 cm. Only at high mortality and relaxed intraspecific competition for the zooplankton resource (compare zooplankton densities in Fig. 4c and 5b, representing scenarios with identical parameter values except for the size-dependent mortality constant) did herring experience fast enough growth rates to reach sizes where they could benefit energetically from feeding on benthos.

Community structure

The outcome of competition between sprat and herring for shared resources was dependent on both resource productivity and size-dependent mortality (Fig. 3). At low levels of resource overlap, stable coexistence was always possible, provided productivity was high enough to allow both species to persist. At high levels of resource overlap, several different community states were observed. As sprat can persist at a lower productivity than herring because of its smaller size at maturation, sprat-only systems always prevailed at low productivity levels (Fig. 3 and 4a). Also, at productivity values slightly above that at which herring can reach maturity in the absence of interspecific competition, herring was excluded at high levels of resource overlap.

This is because sprat can mature at a younger age than herring, leading to newborn sprat cohorts outcompeting the larger, older, herring individuals (Fig. 4a). Nevertheless, given high enough productivity of the shared zooplankton resource for herring to mature within the same season as sprat, a herring-only system resulted at low size-dependent mortality (Figs. 3a, b, 4c), as predicted based on the species' relative CRDs (Fig. 1). This was also apparent from the fact that, in this case, herring determined the resource level (Fig. 4c: compare resource levels in the one-species systems to that in the two-species system). Accordingly, only at intermediate productivities was stable coexistence possible in the low-mortality scenario (Fig. 3a and Appendix B: Fig. B1). Given a combination of low size-dependent mortality and high productivity (i.e., Fig. 4c) the first individuals (i.e., first cohort; see Appendix A: Fig. A2) to hatch suffered from mortality as the season proceeded, relating to a drastic drop in resource level as their smaller and more-abundant siblings hatched and started exogenous feeding. However, this seems only to have minor effects on overall population dynamics. The competitive advantage of herring over sprat was

weakened at high size-dependent mortality (Figs. 3a, c, 5a).

Whereas zooplankton productivity may influence community structure irrespective of the level of mortality (although the community structure for a given zooplankton productivity may differ depending on mortality level; Fig. 3a and c), the influence of benthos productivity depends strongly on size-dependent mortality (Fig. 3b and d). As discussed above, benthos only matters energetically for herring if they can grow large in their first niche, when feeding on zooplankton. At low levels of mortality, resource competition is intense due to the lack of a thinning effect. Herring therefore only reached small sizes (Fig. 2e) and the role of benthos for community structure can in such cases be ignored (Fig. 3b). On the other hand, at high mortality and consequently relaxed competition, herring could grow large enough when feeding on zooplankton for energy gained from benthos feeding to matter for community structure (Fig. 3d and 5c). The combination of high mortality and high benthos productivity allowed herring to outcompete sprat by depressing the shared zooplankton resource to low levels, meeting their maintenance requirements by feeding on the herring-exclusive benthos resource (Figs. 3d and 5c). Note that, although the minimum zooplankton density observed in sprat-only dynamics is lower than with herring (Fig. 5), the zooplankton densities were, on average, much lower when herring was present at high benthos productivity. This is also evident when comparing sprat growth trajectories at low and high benthos productivity (Fig. 5, bottom row). As a consequence of their exclusive resource, large herring individuals did not suffer when newborn sprat and herring cohorts entered, which they did at lower benthos productivity (cf. Fig. 5c to Fig. 5a and b). In contrast, at low benthos productivities, a high mortality level favored sprat over herring (Figs. 3d and 5a). This occurred despite herring reaching much larger sizes than sprat (cf. Fig. 2b and f). Somewhat counterintuitively, in this case, it is actually the fast growth of herring over early ontogeny that caused them to suffer from competition with sprat. As the zooplankton resource drops following the emergence of newborn cohorts, old (>1 year) herring individuals with large body sizes suffered as they need high resource densities to sustain themselves, which they cannot compensate for by extracting enough energy from feeding on benthos due to its low productivity (compare Fig. 5a zooplankton densities and body sizes to Fig. 1 zooplankton densities needed for maintenance for corresponding body sizes of sprat and herring >1 year old). Accordingly, sprat determines the resource level when mortality is high but benthos productivity is low (Fig. 5a).

DISCUSSION

We have presented several results that contrast with predictions made based on classical competition theory: (1) We were able to show that coexistence is possible at full resource overlap in a system of consumers exhibiting cyclic dynamics, emerging as a result of interactions between different size cohorts. (2) Despite the superior ability of one species to depress shared resources for any given body size, shifts in competitive dominance along productivity gradients occurred as the other species could compensate by a smaller size at maturation. (3) An exclusive resource did not grant competitive dominance, but its effect was dependent on mortality level. These results and their mechanistic basis were only possible to obtain by explicitly taking population size-structure, size-dependent foraging capacities, and food-dependent growth into account.

Life-history variation and productivity

Intuitively, herring has a two-fold competitive advantage over sprat; it has a more efficient prey consumption and a wider diet base. Consequently, all else equal, we would predict that exploitation of shared zooplankton resources would lead to competitive exclusion of sprat. However, advantageous life-history traits of an inferior competitor, such as high reproduction ability, may mitigate competitive exclusion (Levine and Rees 2002). In the sprat–herring model, stable coexistence was accomplished by a compensatory balance between the smaller size at maturation of sprat and the capacity of herring to tolerate lower food levels. The likelihood of stable coexistence decreased as the intensity of interspecific competition increased. This is in line with predictions based on Lotka-Voltera type models in that coexistence is favored when interspecific competition is weak relative to intraspecific competition (Gause 1934). In all situations where competitive exclusion occurred, the dominant species controlled the resource and was thus regulated by intraspecific competition, whereas the inferior species, facing a resource environment set by the other species, experienced more intense interspecific competition. Still, for certain parameter combinations, stable coexistence was possible even at full resource overlap, also without exclusive resources (see Appendix B: Fig. B1). This contrasts with classical theory on competition for resources stating that coexistence between two consumers feeding on one resource is not possible (Tilman 1982). This framework has later been modified to allow for several consumers to persist on a limiting number of resources. For example, similar to our study, which accounts for a combination of continuous and discrete time processes, it has been shown in both continuous as well as in discrete-time models that internally generated oscillations may allow for coexistence on a single resource (Armstrong and McGehee 1980, Adler 1990, Abrams and Holt 2002). Implications of oscillatory dynamics caused by interactions among size cohorts have, however, so far been ignored in the context of consumer coexistence. Similarly, implications of ontogenetic diet shifts for competition systems have been long disregarded. Loreau and Ebenhoh (1994) and Moll and Brown (2008) analyzed the consequences of competition within and between stages for coexistence of competing species, while Schellekens et al. (2010) analyzed the consequences of

intraspecific variation in body size and size-dependent patterns of resource use for the coexistence of energetically equivalent competitors that exploit two shared resources. Our study is hence the first to analyze the interplay between size-dependent life history changes and interspecific trait variation, such as diet shifts and size at maturation, and its effects on competitive community structure.

The extent to which resource overlap prevented stable coexistence was strongly dependent on resource productivity. Generally, a high productivity favored herring and low productivity favored sprat. At low productivity, sprat cope better due to their smaller size at maturation allowing them to reproduce before herring. However, as productivity increased, a smaller size at maturation was no longer an advantage, leading to herring dominance due to their superior capacity to depress shared resources. This productivity–competitive-dominance relationship (i.e., a shift from sprat-only via stable coexistence to herring-only systems) was obvious for both resource types, although the influence of benthos productivity manifested itself only at high mortality. Similar shifts in species composition over productivity are predicted for intra-guild predation systems, shifting from prey-only to predator-only communities as productivity increases (e.g., Mylius et al. 2001). However, for pure competition systems, there is a lack of general predictions concerning shifts in competitive dominance over productivity as a function of consumer life-history type. Here we showed that shifts in species dominance over productivity gradients can occur also in pure competition systems, when size-structure and food-dependent growth is accounted for.

Size-dependent mortality and ontogenetic diet shifts

While the presence of ontogenetic diet shifts has been long recognized (Werner and Gilliam 1984), their implications for competitive interactions and community structure have been largely ignored. Still, the importance of niche differentiation among species for coexistence has been central in ecological competition theory (Levin 1970, Tilman 1982, Chesson 2000), although the niche concept has commonly been based on species means. Recently it was shown that to understand implications of interspecific competition also intraspecific trait variation may be important, in some cases leading to completely different predictions on patterns of coexistence than when the niche concept is based on species means (Schellekens et al. 2010). Similarly, studies on intraguild predation have shown that taking intraspecific trait variation and size-specific competition into account may generate different outcomes than when ignoring size/ stage structure (Mylius et al. 2001, Rudolf 2007). Nevertheless, the consequences of intraspecific size variation and ontogenetic diet shifts for interspecific competitive interactions have hitherto not been explored in the framework of fully size-structured population models, which allow for a more explicit consideration of

individual level processes. Also, in contrast to the model studied by Schellekens et al. (2010), which only considered scenarios with shared resources, we considered implications of size-dependent life-history traits and resource overlap for competitive outcomes using a food web configuration including an exclusive resource.

Similar to what has been shown previously, using comparable size-structured population models (van Kooten et al. 2007), increased mortality on small individuals resulted in stabilized population dynamics, relaxed competition for food, and accelerated individual growth rates. Mortality also determined the influence of productivity, especially that of the exclusive resource. Depending on the combination of mortality and productivity of the herring-exclusive benthos resource, a herring-only, a sprat-only, or sprat–herring community state resulted. The influence of size-dependent mortality on the extent to which an exclusive resource provided a competitive advantage is due to the feedback between population density, food availability, and individual growth rates. In the high-mortality scenario, juvenile density was heavily reduced, leading to higher resource availability and accelerated growth of surviving individuals. Herring could therefore reach large enough sizes for them to later benefit energetically from feeding on benthos. However, similar to many piscivorous fish species facing intense competition as juveniles when competing for invertebrate prey (Mittelbach and Persson 1998), the zooplankton niche may constitute an ontogenetic bottleneck for herring at low mortality as they cannot successfully exploit benthos when competition for zooplankton is too strong. These outcomes are only possible if intraspecifc size-structure and food-dependent growth are taken into account. In an unstructured population model, the effects of size thresholds for diet shifts disappear and should hence always grant the species with an exclusive resource a competitive advantage. Taking size structure into account, but not food-dependent growth, would also not result in a mortality effect, as individual growth rates in the zooplankton niche would not respond to thinning. However, once intraspecific size structure, a threshold size for first benthos feeding, and food-dependent growth are accounted for, the advantage of an exclusive resource is not granted but depends on mortality level.

The sprat–herring system

Large-scale eutrophication and depletion of top predators has led to dramatic changes in the Baltic Sea ecosystem (Österblom et al. 2007). Following the collapse of the cod (*Gadus morhua*) stock in the early 1980s, there was a dramatic increase in sprat but a drop in herring biomass (ICES 2010). Hence, we have shifted from a state with high abundances of cod and herring but low sprat population biomass to the complete opposite. In light of this and other recent predator collapses, resulting in dominance of zooplanktivorous fish, it is increasingly important that we understand how

food webs lacking top predators are governed (Llope et al. 2011). For Baltic Sea sprat and herring, there is increasing evidence that both intra- and interspecific competition for shared resources is a key to understand what governs population and community dynamics (Casini et al. 2010, Lindegren et al. 2011). Accordingly, concurrent with the increase in overall clupeid biomass, the body size and condition of both sprat and herring have declined (Casini et al. 2010). Using a modeling approach in which a detailed representation of individual-level processes, such as foraging, and an explicit consideration of the ecological changes that individuals go through over ontogeny (i.e., diet shifts) are embedded, allowed us to explicitly study how resource competition within and between species determines community structure in a sprat–herring model system. It was shown that to correctly predict the outcome of resource competition, individual-level responses mediated via resource densities may be crucial.

In the Bothnian Sea in the northern Baltic Sea, there is a historically low biomass of top predators and the pelagic fish community is consequently naturally dominated by sprat and herring (ICES 2010), in this respect conforming well to our model system. Using a statistical age-structured approach, Lindegren et al. (2011) provided results supporting the view that herring dynamics in the Bothnian Sea is determined by a combination of top-down and bottom-up forces. Here we showed, using a mechanistic mathematical model, that the influence of bottom-up (productivity) and top-down (mortality) forces on community dynamics in the sprat–herring system are not independent of each other. Our results suggest that, for a bottom-up effect to occur, top-down control may have to be strong. One cannot, for example, by default assume that high benthos productivity favors herring over sprat. Herring only gained a competitive advantage by exploitation of a benthic resource when mortality and hence zooplankton density was high. We could also show that a large body size does not need to be a competitive advantage (see Fig. 5a). Again, to understand this phenomenon, the interaction between productivity and mortality was crucial. In a situation where benthos productivity is low but mortality high and hence growth conditions favorable, herring may outgrow its first niche without the possibility to enter a second niche that can provide enough energy to cover the high maintenance costs associated with a large body size, leading to the ability of emerging cohorts of sprat to exclude herring by depressing the zooplankton resource.

Although both the importance of body size for ecological interactions and the relationship between food availability and individual growth has been long recognized within the field of fish biology (Brett 1979), these factors are rarely taken into account in fish population models. In light of our results, we argue that, to better be able to predict changes in community structure in exploited communities of competing fish, the roles of food-dependent growth and size-dependent

interactions are crucial. Likewise, the advantages of an individual and size-based approach hold for studies of all ecological communities with species exhibiting complex life cycles.

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Supplemental Material

Appendix A

Details on functions, parameters, and analyses (*Ecological Archives* E093-075-A1).

Appendix B

Community states as functions of zooplankton and zoobenthos productivity (*Ecological Archives* E093-075-A2).