Size-selective predation and predator-induced life-history shifts alter the outcome of competition between planktonic grazers

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Summary

1. We studied the effect of size-selective predation on the outcome of competition between two differently sized prey species in a homogenous environment.
2. Using a physiologically structured population model, we calculated equilibrium food concentrations for a range of predation scenarios defined by varying maximum predation intensity and size-selectivity, the latter being characterized by the neutral selection length (NSL), where negative selection of small prey size-classes turns into positive selection of larger prey. We parameterized the model according to the well-studied example of fish predation on two differently sized cladoceran species, *Daphnia pulicaria* and *Daphnia galeata*.
3. Although the larger *D. pulicaria* was principally the better competitor for food, competitive superiority shifted to the smaller *D. galeata* under certain predation scenarios. The lowest predation intensity needed to induce a shift from *D. pulicaria* to *D. galeata* was found at NSL values in between the sizes at maturity of both species.
4. Analysing the per capita mortality rates as a result of the underlying parameters of the mortality model, NSL and maximum predation intensity, revealed that the tolerable mortality rate of daphnids decreased as NSL increases towards values close to the size at maturity. This effect was most pronounced in *D. pulicaria*, thus explaining a higher vulnerability of the larger species to size-selective predation.
5. A reduction of the size at maturity in the smaller species (*D. galeata*) as a phenotypic response to the presence of fish resulted not only in an increased capability to withstand predation, but also in competitive dominance shifts over the larger *D. pulicaria* at lower predation intensities and a much wider range of NSL as a trait-mediated indirect effect.
6. Overall, our results demonstrate that shifts in dominance of differently sized herbivores under size-selective predation regimes may be facilitated by the demonstrated alteration in competitive capacities and thus might not be exclusively caused by direct predation effects.

Key-words: *Daphnia*, fish predation, induced defence, phenotypic plasticity, physiologically structured model, size selection, size at maturity, threshold food concentration, trait-mediated indirect effect

Introduction

Considering the multitude of factors affecting competition and predation, it is not surprising that their interaction 'appears to present a confusing picture' (Chase *et al.* 2002).

These authors conclude that a close connection between theory and empirical work is essential for a deeper understanding of this interaction, which is already (partly) established with respect to predation effects on competitive exclusion or coexistence. The simplest case is represented by unselective mortality that alters competitive dominance of two species exploiting a common food resource (depicted in

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fig. 1 in Chase *et al.* 2002). The crucial factor determining competitive dominance is the threshold food concentration (at the population level) indicating the minimal resource availability just high enough to allow population losses to be compensated by reproduction (Lampert 1977; Gliwicz & Lampert 1990). This threshold thus corresponds to the 'resource requirement at equilibrium' (R^* ; Tilman 1982): The species with the lowest threshold food concentration (at a given mortality level) will be the superior competitor and ultimately exclude species with a higher threshold food concentration. The R^* concept is experimentally well supported for planktonic systems (Wilson, Spijkerman & Huisman 2007).

The impact of predation on competition is, however, difficult to test experimentally with organisms not suitable for chemostats (as used in Rothhaupt 1988) and thus model approaches seem more feasible for this analysis. When adding one common predator of two consumers (exploiting one resource), the setting resembles the 'diamond food web module' extensively studied earlier, albeit considering unstructured consumer populations only (e.g. Holt, Grover & Tilman 1994; Grover 1997). In an earlier study, we modified an established physiologically structured model based on dynamic energy budgets (De Roos, Diekmann & Metz 1992; De Roos 1997) to analyse the outcome of competition between size structured *Daphnia* populations under varying predation intensity (Hülsmann, Rinke & Mooij 2005). Concentrating on the upper triangle of the diamond food web module, we could ignore the equations describing *Daphnia* feeding rate and autonomous algal dynamics compared with the original model. Based on seven easily interpretable parameters per species (Table 1), the model was able to reproduce threshold food concentrations, which were established in an experimental study of competitive interactions between two differently sized *Daphnia* species, *D. pulicaria* and *D. galeata* (Kreutzer & Lampert 1999). This allowed the prediction of the relative difference in predation rates necessary to cause a shift in dominance of the competitively superior

large bodied species (*D. pulicaria*) to the small bodied species (*D. galeata*).

A potential major shortcoming of the model was, however, that only the per capita mortalities of both species (thus assuming equal mortalities of all size classes of a given species) were varied and the respective existence boundaries for a range of food concentrations were determined. As a first approximation, this might be acceptable because positive size selective predation, as generally assumed for planktivorous fish (Brooks & Dodson 1965), will in general lead to higher per capita mortality rates of the larger species, confirmed also for the two *Daphnia* species considered here (Mills, Forney & Wagner 1987; Luecke, Rudstam & Allen 1992). Still, in reality, prey selection of fish is considered to depend primarily on size, not on species (Gliwicz, Jawinski & Pawlowicz 2004). If predator related mortality is not equally distributed among size classes of a species, this will (i) modify the overall predation effect on the population via effects on demography and (ii) may change competitive interactions due to the size dependency of filtering rates, reproduction, etc.

As somatic growth rate (usually described by a von Bertalanffy growth function, De Roos, Diekmann & Metz 1992; Rinke & Vijverberg 2005) strongly declines after reaching maturity, predation risk, when assuming a positively size selective feeding pattern of planktivorous fish, will steeply increase during the late juvenile instars of *Daphnia*, but more gradually between successive adult instars. When translated into selectivity indices, such a predation regime results in negative selection of small prey, a switch to positive selection at a certain prey size and continuously positive selection from this size onwards (Köpke *et al.* 1988). Moreover, prey selection of fish is mainly determined by visibility, which does not only depend on size, but also depends on pigmentation (Tollrian & Heibl 2004) or on the occurrence of pigmented resting eggs (Mellors 1975) or subitaneous eggs in the brood pouch (S. Hülsmann, M. Janßen, A. Wagner & W.M. Mooij, unpublished data). These considerations suggest that there

Table 1. Model parameters and derived parameters of the physiologically structured population model for *Daphnia pulicaria* and *Daphnia galeata*

Parameter (unit)	Description	<i>D. pulicaria</i>	<i>D. galeata</i> (standard)	<i>D. galeata</i> (induced)
Model parameters				
f_m (eggs)	Maximum clutch size	60	30	30
D (days)	Egg development time	2.75	2.75	2.75
l_b (mm)	Length at birth	0.65	0.55	0.37
l_j (mm)	Length at maturity	1.7	1.35	0.90
l_m (mm)	Maximum length	3.5	2.7	1.8
a_j (days)	Minimum age at maturity	5.5	5.5	5.5
a_m (days)	Maximum lifespan	70	70	70
F_h (mg C L ⁻¹)	Half saturation food concentration	0.042	0.054	0.054
Derived parameters				
F_c (mg C L ⁻¹)	Lower critical food level	0.040*	0.054*	0.054
b_m (day ⁻¹)	Maximum birth rate	0.485	0.407	0.407

Two parameterizations are given for *D. galeata*: a standard parameterization for the non induced morph and an induced parameterization with reduced values of l_b , l_j and l_m accounting for the phenotypic plasticity in this species.

*Species specific values in accordance with empirical results (Kreutzer & Lampert 1999).

should be a neutral selection length (NSL) of prey body length from which size onwards positive size selection occurs in planktivorous fish, which are usually visually oriented feeders of single prey items.

Vulnerability to a size selective predation regime strongly depends on size at maturity (SAM) of the prey. SAM is, however, not a fixed trait, but shows high phenotypic plasticity, which may be induced by predator released chemical cues (kairomones). As one model organism for this phenomenon (Tollrian & Dodson 1999), *Daphnia* was shown to respond to predators showing positive size selection, such as fish, by reducing SAM (Macháček 1991). If *Daphnia* species manage to reduce SAM below NSL of planktivorous fish, one can assume that this will enable them to coexist with their predators. A considerable reduction of SAM is, for example, known for *D. galeata* (Hülsmann & Wagner 2007), whereas the larger *D. pulicaria* does not display such phenotypic plasticity of life history traits (Bernot *et al.* 2006; Vijverberg, Doksaeter & Van Donk 2006), but instead seems to rely on behavioural responses to the presence of fish if possible (Leibold & Tessier 1991; Flik & Vijverberg 2003).

Here, we study the outcome of competition of two differently sized *Daphnia* species under various size selective predation regimes and in response to phenotypic plasticity of life history traits in one of the species. In particular, we want to establish the selectivity regime (as determined by NSL) at which the intensity of fish predation needed for a shift to the smaller species is minimal. Finally, we study the effect of predator induced phenotypic life history shifts on the existence boundaries and the outcome of competition between both species paying special attention to empirical evidence available.

Materials and methods

MODEL PARAMETERIZATION

We used a physiologically structured population model (Hülsmann, Rinke & Mooij 2005), which was modified from De Roos, Diekmann & Metz (1992) and De Roos (1997). Somatic growth rate of *Daphnia* g (mm day⁻¹), as a function of body length l and food F is described by a von Bertalanffy's growth function (parameter values and explanations are given in Table 1), with the growth rate constant from the original equation being substituted by empirically measurable parameters (Hülsmann, Rinke & Mooij 2005):

$$\frac{dl}{dt} = g(F, l) = \frac{\ln\left(\frac{l_m - l_b}{l_m - l_j}\right)}{a_j} \left(l_m \frac{F}{F_h + F} - l \right). \quad 1$$

This equation can be solved analytically giving body length $l(a, F)$ (mm) as a function of age a and food F :

$$l(a, F) = l_m \frac{F}{F_h + F} - \left(l_m \frac{F}{F_h + F} - l_b \right) \left(\frac{l_m - l_b}{l_m - l_j} \right)^{-\frac{a}{a_j}}. \quad 2$$

Also the reproductive rate constant from the original reproduction term was replaced, resulting in *Daphnia* reproductive rate m (eggs day⁻¹) as a function of food F and body length l :

$$m(F, l) = \frac{f_m}{D_m^2} \frac{F}{F_h + F} l^2 \quad \text{if } l > l_j, \text{ otherwise } m = 0. \quad 3$$

The lower critical food level F_c (mg C L⁻¹) at which the *Daphnia* population can just maintain itself (without mortality) is calculated by assuming that it allows a maximum body length equal to SAM (setting $l_j = l_m$), which leads to:

$$F_c = \frac{F_h l_j}{l_m - l_j}. \quad 4$$

According to the parameterization for the two *Daphnia* species considered (Table 1), F_c is lower for the larger *D. pulicaria* than for *D. galeata*, making *D. pulicaria* the superior competitor for food.

In order to account for phenotypic plasticity of life history traits, we provide an alternative parameterization for the smaller species, *D. galeata*. Representing a strong reaction of this life history shift, for SAM, a value of 0.9 mm was applied for the induced morph of *D. galeata*, accounting to a reduction by one third (compare Hülsmann & Wagner 2007). As we assumed size relations to be constant (Boersma, Van Tongeren & Mooij 1996; Hülsmann & Weiler 2000), we reduced the size of neonates and maximum body size accordingly, resulting in values of 0.37 and 1.8 mm, respectively, fully compatible with empirical findings. In the presence of fish, the relationship between *Daphnia* size and egg number is shifted to smaller sizes (Macháček 1991; Hülsmann *et al.* 2004), which means that at a given size individuals have more, but smaller eggs. Due to the reduction of maximum size we assumed, however, that maximum clutch size remained unchanged (but is achieved at a smaller maximum length). Reduced SAM in response to fish kairomones is due to reduced length increments per juvenile instar. Additionally, a certain proportion of induced animals mature already in the fourth instar instead in the fifth instar (Macháček 1991). Only in the latter case, age at maturity is affected. Here, we assumed that only length increments per juvenile instar are reduced and consequently, kept minimum age at maturity constant in the induced morph compared with the standard morph. Generally, we did not account for clonal diversity in life history traits (De Meester & Weider 1999), but assumed a strong shift in life history patterns of *D. galeata*, resulting in a population being uniformly composed of only small individuals (see Hülsmann & Weiler 2000).

By reducing these three size parameters equally, but keeping the model and the other parameters constant, the critical minimum food concentrations over the range of predation rates *D. galeata* can with stand remain unaffected by the realized life history strategy. This means the induced and the not induced morph of *D. galeata* have the same existence boundaries (allowing coexistence of both morphs) when mortality is non selective. This implies not only that, in the model, there are no apparent physiological costs associated with the induced defence, but also that only under conditions of size selective predation the induced morph of *D. galeata* will have an advantage over the non induced morph.

SIZE-SELECTIVE PREDATION REGIMES

Selectivity for different size classes of zooplankton was modelled using a sigmoid mortality function according to earlier approaches (Taylor & Gabriel 1992) and in line with empirical data (Kopke *et al.* 1988). Thus, mortality rate of *Daphnia* d was calculated as a function

of body size $l(a)$ at age a and food concentration F (Rinke, Hulsman & Mooij 2008):

$$d(l(a, F)) = \mu_b + (1 + \tanh(2(l(a) - l_{NSL}))) \frac{\mu_i}{2} \quad 5$$

This mortality function includes three parameters (Fig. 1): background mortality μ_b , neutral selection length l_{NSL} and maximum predation intensity μ_i (assigned $d_{background}$, L_{mid} and $d_{deflection}$, respectively, in the original publication). In our analyses, we assigned a constant value of 0.05 day^{-1} to μ_b , whereas μ_i and l_{NSL} were varied over a wide range. Note that the maximum possible predation rate is $\mu_b + \mu_i$ and that the maximum predation intensity (μ_i) is only incurred by the largest size classes of prey (Fig. 1). We interpret μ_i to be directly proportional to the abundance of planktivorous fish, which may fluctuate dramatically between years (Rudstam, Lathrop & Carpenter 1993). On a seasonal time scale, variation in μ_i can be related to young of the year (YOY) fish densities which, due to pulsed reproduction and subsequent decline of the new cohort, vary enormously (Mooij 1996). We considered l_{NSL} to represent the selectivity in the predators feeding behaviour. It describes the prey body length at which the selectivity of the predator is neutral, i.e. prey individuals with a body length below l_{NSL} are negatively selected by the predator whereas individuals larger than l_{NSL} are positively selected (Fig. 1). In the natural environment, dramatic changes in l_{NSL} occur during growth of YOY fishes, which progressively feed on larger prey as they grow during their first season (Mehner *et al.* 1998; Hulsman *et al.*, unpublished data). In addition, NSL can be assumed to vary in dependence of the availability of different food items (Gliwicz, Jawinski & Pawlowicz 2004).

MODEL ANALYSES

The core of our analysis consists of the Euler–Lotka equation for calculating the intrinsic rate of increase (r) from demographic data:

$$1 = \int_0^{a_m} m(a) S(a) e^{-ra} da \quad 6$$

Fig. 1. Mortality function of the model. A slight background mortality was applied independent of size (dotted line). Maximum predation intensity (μ_i) is represented by the total amplitude of the curve. Size selection was modelled by varying the neutral selection length (NSL).

In our application, the maternity function $m(a)$, describing the reproductive rate as a function of age a , can be directly calculated by eqn 3. Age dependent survival $S(a)$ in a size selective predation regime as given by eqn 5 can be calculated under the assumption of equilibrium conditions by integrating size dependent mortality rates d over age a :

$$S(a) = e^{\int_0^a -d(l(a', F)) da'} \quad 7$$

Note that in this setting the somatic growth, i.e. $l(a, F)$, of the individuals depends on the food concentration F in the habitat as given by eqn 2.

Solving eqn 6 for r as outlined above, i.e. by inserting eqns 2, 3, 5 and 7 into eqn 6, gives the population rate of increase r of a *Daphnia* population in the ecological setting given by food concentration and predation regime. Accordingly, if we assume r to be zero, the exponential term in eqn 6 becomes one and results in:

$$1 = \int_0^{a_m} m(F, l(a)) e^{\int_0^a -d(l(a', F)) da'} da \quad 8$$

with a' denoting age within the integral term in the exponent. This formula can be used to calculate the existence boundaries of both species with respect to (i) the critical minimum food concentration under a defined predation regime (l_{NSL} and μ_i), (ii) the maximum tolerable predation intensity at a given food concentration and NSL, or (iii) the minimum tolerable NSL at a given food concentration and predation intensity. In addition, for a given combination of NSL, predation intensity and the corresponding equilibrium food concentration, we calculated an effective per capita mortality rate (day^{-1}) by computing a weighted average of size dependent mortality, weighted by the relative abundance within each size class.

Results

We calculated for a range of predation scenarios (given by μ_i and NSL) the equilibrium food density at which the population of each species can just maintain itself. Setting NSL to 1.4 mm and scanning the equilibrium food concentration for a range of predation intensities, we find that predation intensity can shift a replacement of *D. pulicaria* by *D. galeata* through food competition. At low predation intensities, *D. pulicaria* is superior but at high intensities *D. galeata* is superior (Fig. 2a). In Fig. 2b–d, the same was carried out for a range of NSLs at fixed maximum predation intensities of 0.3, 0.5 and 0.6 day^{-1} representing low, intermediate and high predation, respectively. These analyses show that at low values of μ_i , *D. pulicaria* has the lowest equilibrium food density and hence is the superior competitor irrespective of NSL. At high maximum predation intensities, the balance has shifted towards *D. galeata*, although *D. pulicaria* can still win at very high values of NSL. At intermediate predation pressures, *D. galeata* is superior at intermediate values of NSL (close to l_j of *D. galeata*, but below l_j of *D. pulicaria*), with a shift towards dominance of *D. pulicaria* at either very low (unselective predation) or very high ($> l_j$ of *D. pulicaria*)

Fig. 2. Equilibrium food conditions of *Daphnia pulicaria* (solid line) and *Daphnia galeata* (dotted line) under varying size selective predation regimes. In panel (a), neutral selection length (NSL) was set to 1.4 mm and the equilibrium food concentrations were scanned for a range of maximum predation intensities (μ). In panels (b–d), the same was carried out for a range of NSLs with μ being fixed at 0.3, 0.5 and 0.6, representing low, intermediate and high predation rates, respectively.

values of NSL. Except in Fig. 2b, the equilibrium food conditions of both species cross, meaning that under a wide range of predation scenarios a shift in either NSL or μ_i may change the outcome of competition.

To further illustrate this, we plotted equilibrium food concentrations under a range of predation regimes defined by μ_i and NSL. Performed at very high food densities, this analysis shows that *D. pulicaria* can withstand slightly higher maximum predation intensities (not to be mixed up with per capita mortality rates) compared with *D. galeata* at low values of NSL (Fig. 3). When NSL is about 1 mm the lines cross: both species can equally withstand predation intensity. At higher NSL values, *D. galeata* rapidly gains an advantage over *D. pulicaria* in coping with intense predation.

We repeated the analysis shown in Fig. 3 for a range of food conditions, resulting in domains of dominance of either species (Fig. 4a). On the left hand side of the graph, predation becomes virtually unselective (NSL is so small that daph-

Fig. 3. Existence boundaries of *Daphnia pulicaria* (solid line) and *Daphnia galeata* (dotted line), given by the equilibrium food conditions for both species under a range of NSL and maximum predation intensity (μ) and at unlimited food supply.

nids of all sizes are equally eaten). If predation intensity is additionally strong, this will lead to extinction of both *Daphnia* species (predation exceeding maximum birth rates). The grey area (marked with *Dg*) represents predation regimes where *D. galeata* is the superior competitor and *D. pulicaria* is unable to persist. The thick line separating the *Dg* area from the *Dp* area defines those predation scenarios where both species have the same equilibrium food concentration. Only along this line (unstable) coexistence is predicted. The line that separates the extinction from the *Dp* area coincides with the lower part of the solid line in Fig. 3. The border between the extinction and the *Dg* area coincides with the upper part of the dotted line in Fig. 3. Hence, the intersection of the line separating the extinction from the *Dp* and *Dg* areas, with the line separating the *Dp* from the *Dg* area coincides with the intersection of the solid and the dotted line in Fig. 3. The other points on the line that separates the *Dp* from the *Dg* area where obtained by redoing the analysis leading to Fig. 3, but now for a decreasing range of food levels. The specific shape of the resulting line reflects the results shown in Fig. 2c where the existence boundaries of both species at intermediate predation intensity have two crossings. This analysis also resulted in isolines of equilibrium food density for *D. pulicaria* in the *Dp* area and for *D. galeata* in the *Dg* area. Finally, we added an additional isoline of equilibrium food densities of *D. pulicaria* representing the critical food concentration of *D. galeata* at zero mortality (dashed line). Below this food level, *D. galeata* cannot exist, irrespective of the predation regime and this line therefore functions as an asymptote for the *Dg* area.

In order to account for fish induced life history shifts in *D. galeata*, we repeated the analysis presented in Fig. 4a, by using the parameterization for the induced morph (parameters given in Table 1). In this analysis (Fig. 4b), the existence boundary and equilibrium food isolines for *D. pulicaria*, including the one for the critical food concentration of *D. galeata*, remain unchanged. The existence boundary of *D. galeata* and its equilibrium food isolines change dramatically, however, resulting in a much larger area where *D. galeata* can exist and out competes *D. pulicaria* (*Dg* area).

Fig. 4. Equilibrium food concentrations of *Daphnia pulicaria* and *Daphnia galeata* under various predation regimes defined by neutral selection length (NSL) and μ . The grey areas (marked *Dg*) represent predation regimes where *D. galeata* is the superior competitor and *D. pulicaria* is unable to persist. The thick line delimiting these areas at higher NSL values defines those predation scenarios where both species have the same equilibrium food concentration. Inside the grey area, isolines of equilibrium food concentrations are given for *D. galeata*. Outside the grey area, the food isolines for *D. pulicaria* (marked *Dp*) are given. The dashed line marks the critical food concentration of *D. galeata* at zero mortality. (a) *Daphnia pulicaria* and non induced morph of *D. galeata*; (b) *D. pulicaria* and induced morph of *D. galeata*.

The existence boundary of *D. galeata* shifts to the left because its smaller size now allows for a more intense predation at a given NSL, resulting in a much smaller extinction area compared with Fig. 4A. The line separating the *Dg* area from *Dp* shifts to below, because at a given predation regime, *D. galeata* can now survive at a lower equilibrium food density. For that reason, the shift from *D. pulicaria* to *D. galeata* at a given NSL occurs at lower predation intensity. For the same reason, the *Dg* area for the induced morph more quickly approaches the asymptote set by the equilibrium food isoline of *D. pulicaria* at the critical food concentration of *D. galeata* (dashed line). The life history shift of *D. galeata* thus not only enlarges its capability to withstand size selective predation (i.e. pushing its existence boundary towards more intense predation), but also increases its competitive capacities against the larger *D. pulicaria* in the habitat.

When changing the parameters of the mortality function, NSL and maximum predation intensity, how will the resulting per capita mortality rate vary? Plotting this relationship results in isolines of per capita mortality rates (Fig. 5), which are similar, but not identical to the food isolines discussed above (Fig. 4). This analysis revealed that the maximum tolerable per capita mortality rate of *D. pulicaria* is virtually equal to the maximum tolerable predation intensity if NSL is low (unselective predation). Increasing values of NSL result in higher tolerable maximum predation intensities, but in decreasing values of tolerable per capita mortality rates (with increasing NSL, the existence boundary intersects the lines with equal per capita mortality rate in a decreasing order). If we approach this relation from another perspective, this means that the population may still persist when facing a certain per capita mortality rate (e.g. 0.3 day^{-1}) as long as predation is unselective (NSL low). If predation turns size selective (NSL increasing), the same per capita mortality rate (now

concentrated on large individuals) will drive the population to extinction. At NSL values beyond SAM, the per capita mortality rates gradually decline more or less parallel to the axis of the maximum predation intensity. Repeating this analysis for the default and the induced morph of *D. galeata* shows principally the same pattern. However, the extinction area within the chosen parameter space becomes smaller and the disparity between tolerable maximum predation intensity and per capita mortality with increasing NSL is less pronounced. Both effects are particularly marked in the induced morph of *D. galeata*.

Discussion

We consider our approach to be a major step towards more realistic models of the combined impacts of competition and predation in natural systems, extending the common bottom up approach based on Tilman's R^* concept typically considering only unselective per capita mortality rates. Focussing on existence boundaries under various predation regimes and the impact of phenotypic plasticity in SAM, the first striking result of the analysis presented in this study is the finding that size selective predation, in our case, represented by the parameter NSL affects competitive capacities of differently sized zooplankton grazers. Whereas at non selective predation the larger of the two competing species, *D. pulicaria*, always has a lower threshold food level to withstand unselective predation compared with the smaller species *D. galeata* (as shown in Hülsmann, Rinke & Mooij 2005; Fig. 3), size selection radically changes the picture. Only when predation intensity is very low, *D. pulicaria* retains its competitive superiority regardless the size selection (NSL) of the predator. At intermediate predation intensity, the outcome of the competition depends on NSL, *D. galeata* being superior at

Fig. 5. Per capita mortality rates resulting from various predation regimes defined by neutral selection length (NSL) and μ given separately for *Daphnia pulicaria*, *Daphnia galeata* and the induced morph of *D. galeata*. The existence boundary separating the extinction area intersects the lines with equal per capita mortality rate in a decreasing order.

intermediate NSL values. If predation is intense, *D. galeata* will virtually always be superior, except at very high NSL values of predation.

A further major outcome of our analysis is the theoretical underpinning of the fact that size selective predation may cause a shift in the size structure of zooplankton communities at much lower predation rates than at non selective predation. This is illustrated by the biplot (Fig. 4) showing equilibrium food concentrations of differently sized prey species as a function of NSL and predation intensity. Minimum values of predation intensity are

needed to shift the balance to the smaller species when size selection turns positive at a prey size in between the given sizes at maturity of prey species ($SAM\ D. galeata < NSL < SAM\ D. pulicaria$). At the far right side of Fig. 4, when predation is only directed towards very large size classes of *Daphnia*, predation intensity needed to cause a switch in species dominance increases steeply. This steep increase is due to the fact that the larger NSL, the fewer size classes of *Daphnia* are affected. On the left hand side of the graph, predation turns virtually unselective. In this region, the increase of predation intensity leading to a switch in competitive superiorities of species is less steep and soon leads to extinction of daphnids altogether.

The analysis of per capita mortality rates (resulting from the applied predation scenarios) revealed that size selective predation will lead to decreasing maximum tolerable per capita mortality rates. This effect was most pronounced in the larger of the two competitors, confirming its high vulnerability to a size selective predation regime, and markedly reduced in the induced morph of the smaller competitor. These findings illustrate one of the major problems inherent in per capita mortality rates obtained from field samples (as difference in birth rate and rate of population change): by ignoring the underlying (most likely) size selective mortality pattern they not necessarily tell much about the threat of predation actually faced by the population, nor are they comparable through time or between habitats. When searching for drivers of population dynamics in the field, more laborious approaches to estimate mortality rates (e.g. Hülsmann & Weiler 2000) or coupling of field and model studies (Mooij *et al.* 2003; Mooij *et al.* 2010) are necessary.

With respect to the rich body of theoretical studies on the effects of predation on competition (e.g. Chase *et al.* 2002), it emerges that the simplistic view that predation will generally promote coexistence of prey species is not justified. Even in the case of keystone predation (Leibold 1996), which should be applicable to the studied system, coexistence is only predicted for a limited range of environmental conditions. In the specific case of *D. pulicaria* competing with *D. galeata* studied here, dominance of either species, mediated by fish predation, is typically very strong when they may not segregate by habitat as observed in deep stratifying lakes (Leibold & Tessier 1991; Flik & Vijverberg 2003). When both species are forced to dwell together, usually one species clearly dominates whereas the other has densities close to zero, alternations occurring either inter annually (Lake Mendota, Luecke, Rudstam & Allen 1992 and Oneida Lake, Cáceres 1998) or seasonally (Glen Elder Reservoir, Bernot *et al.* 2006). Even if one of the competitors indeed happens to go extinct during the course of the season, recolonization is ensured due to the regular production and storage in long lasting egg banks of diapausing eggs (Hairston 1996). These resting eggs, the production of which may even be induced by fish infochemicals (Slusarczyk 1995), are thus a major factor promoting long term coexistence.

In each of the above mentioned cases, predation by fish was suggested to induce the shift in dominance from

D. pulicaria to *D. galeata*. For the main planktivorous fish in Lake Mendota and Oneida Lake, yellow perch, size selective feeding was confirmed (Luecke, Rudstam & Allen 1992), suggesting an NSL between 1.0 and 1.5 mm, i.e. very likely in the highly sensitive range of NSL where relatively low predation intensities are needed to shift competitive dominance in favour of *D. galeata*. Similar values of NSL may be deduced from feeding patterns observed in European perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) (Köpke *et al.* 1988; Hülsmann & Mehner 1997; Vasek, Kubecka & Seda 2003), which confirms the importance of predation in structuring herbivorous zooplankton communities and implies that reducing SAM below NSL may represent an effective strategy to cope with predation.

In cases where invertebrate predation prevails (e.g. by *Chaoborus* larvae, being gape limited), competitive dominance in our studied system would, in contrast, be shifted (further) to the larger species, *D. pulicaria*. Assuming again no phenotypic response in this species, but an increase in SAM of the smaller *D. galeata* (see Rinke, Hülsmann & Mooij 2008; online Appendix), which does not alter its threshold food levels, predation only on small size classes would accelerate its competitive exclusion by *D. pulicaria*. In natural systems with strong invertebrate predation, the dominance of large *Daphnia* species (often *D. pulex*, similar size as *D. pulicaria*) is additionally facilitated by morphological defences in their juvenile instars (Sell 2000).

In extreme (and rare) habitats free of fish, *D. pulicaria* may indeed represent the only pelagic herbivore obviously resulting from competitive exclusion (Gliwicz, Slusarczyk & Slusarczyk 2001). Although pure exploitative competition (not mediated by predation) in fact can drive species to extinction, this may not hold true for predation due to density dependence of the predation rate (Gliwicz & Wrzosek 2008). The model employed by Gliwicz & Wrzosek (2008), based on a detailed description of size and density dependent mortality, predicts a low density anti predation refuge. This mechanism allows for the coexistence of differently sized *Daphnia* species, with each species being kept at a density level at which it becomes included in the predators diet (with densities differing by orders of magnitude). Interestingly, the predicted dominance of small bodied species in that model results from predation alone. It was assumed that 'as the prey density levels resulting from fish predation are so much lower than those in predation free habitats, the effects of resource competition ... could be considered negligible' (Gliwicz & Wrzosek 2008). While ignoring competition, their model is therefore unable to predict the dominance of large bodied species when predation is absent or low. This, in contrast, constitutes the conceptual basis of our approach, in line with empirical evidence (Gliwicz 1990; Kreutzer & Lampert 1999). In conclusion, whereas we neglect density dependent foraging behaviour of the predator, Gliwicz & Wrzosek (2008) neglect resource competition among prey species. At high predation levels, the principal result of both model approaches is similar: small *Daphnia* species will dominate.

However, while Gliwicz & Wrzosek (2008) attribute this exclusively to the predation impact, our results imply that predation and competition interact and may change competitive superiorities of the species. Furthermore, our results suggest a strong impact of phenotypic plasticity (see below). The next step in this line of research would therefore be to include density dependence of predation into our model.

Our analysis, being based on the classical theory of exploitative competition ultimately predicts competitive exclusion of the inferior species (having a higher threshold food level) in dependence of the predation regime. This prediction only holds, according to theory, if the competitors indeed exploit one common food resource of constant quality, which is unlikely to be the case under field conditions. Still, concerning the two *Daphnia* species considered here, there is no evidence that they might exploit different food resources according to their filtering apparatus (Geller & Müller 1981). And despite seasonal variability in food quality, particulate organic carbon (used as food currency in our model) seems to predict both somatic growth and reproduction of *Daphnia* reasonably well (Müller Navarra & Lampert 1996). We therefore consider it justified, as a first approximation, to consider only one resource of constant quality. For future studies, dynamic energy budget models considering stoichiometric relations (Müller *et al.* 2001; Kooijman, Andersen & Kooij 2004) should be adapted to study stoichiometrically explicit competition between grazers not only for unstructured (Hall 2004), but also for structured populations. Considering also size selective predation, such models, in conjunction with experimental approaches (Hall *et al.* 2004), may further sharpen our understanding of the relative role of various factors shaping trophic interactions. Likewise, it remains to be seen if and how stage specific differences in resource use (not yet documented in *Daphnia*), by determining whether a single consumer population is limited by reproduction or maturation (De Roos *et al.* 2007) will affect the outcome of competition between species under size selective predation regimes.

Our results clearly show that the existence boundaries of the induced morph of *D. galeata* are shifted such as to allow for persistence under a wider range of predation regimes (compare Fig. 4A and B). Although this was an expected outcome, our analysis also points to dramatic effects on the competition with *D. pulicaria*. To our knowledge, this is the first time that the interaction between phenotypic plasticity of life history traits and (size selective) predation on competition has been studied and such an effect has been described. Our study thus adds a new aspect to the rich body of literature on trait mediated indirect interactions (Werner & Peacor 2003), which up to now almost exclusively dealt with behavioural and to some extent with morphological traits (Werner & Peacor 2003). Specifically, behavioural and morphological responses to the presence of predators were shown to modify or even reverse the outcome of competition between prey species (Persson 1991).

Here, we show that life history shifts may have similarly strong effects on competition. We suggest this notion to hold true even if the positive effects of life history shifts on competitive capacities of *D. galeata* might be overestimated to a certain extent, as in our model structure and parameterization there are no costs associated with the induced defence. By applying a modified version of the size structured *Daphnia* model to empirical data of life history shifts (from De Meester & Weider 1999), we confirmed, however, that allocating more energy into reproduction (as underlying physiological mechanism of reducing SAM) is not necessarily associated with energetic costs (Rinke, Hülsmann & Mooij 2008). For the current analysis, comparing two species clearly differing in size and also with respect to defence strategies, we even argue that including energetic costs of fish induced life history shifts would not qualitatively change the outcome of our analysis.

Linking phenotypic plasticity of life history shifts to energy allocation would also allow to study possible trade offs between responses to predators and food limitation (Hülsmann *et al.* 2004). In the current version of the model, we assume that minimum age at maturity is fixed and that SAM is variable only in the smaller species as an induced defence. In fact both traits (also) depend on food conditions in *Daphnia*, but differ in their variability. Age at maturity depends on juvenile instar duration, which is only a function of temperature at intermediate and high food levels. At low food, this trait may increase, as an individual may need more instars to accumulate sufficient energy to produce a clutch (McCauley, Murdoch & Nisbet 1990). SAM, on the other hand, increases with increasing food levels even though age at maturity remains constant because the length increment per instar increases. However, SAM may also increase at low food levels if additional instars are needed to produce a clutch (McCauley, Murdoch & Nisbet 1990). Mechanistically linking these traits to energy allocation both in response to food conditions and kairomones is not possible yet due to the lack of data. Once feasible, this would not only allow to disentangle the effects of different predatory processes (induction, selection, thinning) on the phenotypic response (Relyea 2002), but also on competition and the extent of trait mediated indirect effects.

In conclusion, our results clearly demonstrate that positive size selection of predators can lead to shifts in species dominance at relatively low predation intensity if the size of prey at which the predator starts to select them is in a critical range, i.e. close to the SAM of the prey. Phenotypic plasticity in this life history trait (reducing SAM below the critical size for positive selection) therefore increases persistence to predation but additionally may increase competitive strength as a trait mediated indirect effect.

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