

Match or mismatch: the influence of phenology on size-dependent life history and divergence in population structure

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Summary

1. In gape-limited predators, body size asymmetries determine the outcome of predator–prey interactions. Due to ontogenetic changes in body size, the intensity of intra- and interspecific interactions may change rapidly between the match situation of a predator–prey system and the mismatch situation in which competition, including competition with the prey, dominates.

2. Based on a physiologically structured population model using the European perch (*Perca fluviatilis*), analysis was performed on how prey density (bream, *Abramis brama*), initial size differences in the young-of-the-year (YOY) age cohort of the predator, and phenology (time-gap in hatching of predator and prey) influence the size structure of the predator cohort.

3. In relation to the seasonality of reproduction, the match situation of the predator–prey system occurred when perch hatched earlier than bream and when no gape-size limitations existed, leading to decreased size divergence in the predator age cohort. Decreased size divergence was also found when bream hatched much earlier than perch, preventing perch predation on bream occurring, which, in turn, increased the competitive interaction of the perch with bream for the common prey, zooplankton; i.e. the mismatch situation in which also the mean size of the age cohort of the predator decreased.

4. In between the total match and the mismatch, however, only the largest individuals of the perch age cohort were able to prey on the bream, while smaller conspecifics got trapped in competition with each other and with bream for zooplankton, leading to enlarged differences in growth that increased size divergence.

5. The modelling results were combined with 7 years of field data in a lake, where large differences in the length-frequency distribution of YOY perch were observed after their first summer. These field data corroborate that phenology and prey density per predator are important mechanisms in determining size differences within the YOY age cohort of the predator.

6. The results demonstrate that the switch between competitive interactions and a predator–prey relationship depended on phenology. This resulted in pronounced size differences in the YOY age cohort, which had far-reaching consequences for the entire predator population.

Key-words: hatching date, match–mismatch hypothesis, *Perca fluviatilis*, physiologically structured population model, predator–prey interactions, size variation, young-of-the-year

Introduction

Body size is one of the most important traits of an individual organism in many species. Introducing the size distribu-

tions of interacting species into models allows insights to be made into the structure and functioning of communities (De Roos, Persson & McCauley 2003). Body size determines to a large extent the type and strength of ecological interactions of the individual and influences key life-history processes like foraging, growth, physiology, behaviour, reproduction and mortality (Werner & Hall 1974; Peacor, Schiesari & Werner 2007). Due to ontogenetic changes in body size, which are most pronounced in early life stages,

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the intensity and nature of intra- and interspecific interactions may change rapidly.

Size-dependent interactions are often studied with respect to intra- and interspecific competition and predation (Persson & Greenberg 1990; Persson, De Roos & Byström 2007), including cannibalism as a special case of predation (Claessen, De Roos & Persson 2000; Persson *et al.* 2004; Byström 2006). At small sizes, the predator may compete with its prey, whereby the prey may limit the extent to which predatory individuals are recruited to larger predatory stages, inducing an interspecific competitive juvenile bottleneck in the predator (Olson, Mittelbach & Osenberg 1995). This was demonstrated in a whole-lake experimental study, in which the introduction of competing prey roach, *Rutilus rutilus*, into systems inhabited by the predator perch, *Perca fluviatilis*, led to a reduction in the shared zooplankton resource and thereby decreased individual growth and increased mortality in perch (Byström, Persson & Wahlström 1998; Persson *et al.* 1999).

The predicted outcome of such intra- and interspecific interactions becomes more complicated when the prey and predator have different initial growth rates while co-occurring and competing for similar food resources, or arriving in a shared habitat at different sizes. This was shown for divergent selection on prey growth of the spotted salamander (*Ambystoma maculatum*) larvae, for which the spatial and temporal dynamics of gape-limited predator distributions in temporary ponds created a heterogeneous and heretofore unexplored pattern of predation intensity (Urban 2007). Depending on environmental conditions, physiological constraints and behavioural responses, relative growth rates between prey and predator can result in varying periods of interaction, which switch between competition and predation (Wilbur 1988). While periods of competition have been shown to favour recruitment of the smaller species (Neill 1975), i.e. the prey species (Olson, Mittelbach & Osenberg 1995; Byström, Persson & Wahlström 1998), growth and recruitment of the predatory species are suggested to increase when there is a perfect match with their prey (Durant *et al.* 2005). These observations were formulated in the 'match-mismatch hypothesis' that states: if the most energetically expensive part of the breeding phenology of the higher level (i.e. the predator) occurs at the same time as the peak availability of the lower level (i.e. the prey), then recruitment will be high (Cushing 1990). If there is a mismatch between food requirement and food availability, then survival and thus recruitment of the predator will decrease. Using a novel time-series model explicitly quantifying both the timing and the abundance component for trophic relationships, Durant *et al.* (2005) recently showed that not only timing but additionally the abundance of food also affects recruitment differently in a marine (cod/zooplankton) and a marine-terrestrial (puffin/herring) ecosystem. In mammals, intermediate conditions between a perfect phenological match for the predator and his prey and a total mismatch may lead to intermediate offspring mortality (Soto, Trites & Arias-Schreiber 2004).

Intermediate levels between the match and the mismatch situation may not only result in intermediate mortality, but

may also add further variance when fitness parameters of the offspring are taken into account (e.g. in birds, Van Noordwijk, McCleery & Perrins 1995; Nager, Ruedger & Van Noordwijk 1997). Not only the amount of food but also the use of energetically different food resources was shown to affect growth and ontogenetic niche shifts (Post 2003), energy storage and over-winter survival (Borchering, Hermasch & Murawski 2007; Heermann *et al.* 2009). Even the early recruitment to the reproductive population has been shown to depend on the use of energetically rich food (Beeck *et al.* 2002). Thus, intermediate levels between the match and the mismatch situation are expected to affect a population multifariously.

Using the model organism perch in a match-mismatch situation between competition and predation on juvenile fish, the present study focused on the short-term effects of the size development of the young-of-the-year (YOY) predator cohort over the first growing season. YOY cyprinids in the littoral area are not only prey (Beeck *et al.* 2002) but also competitors on common food resources and were found to cause a bottleneck situation for the YOY perch (Persson & Greenberg 1990), which was assumed to also be the mismatch situation in our study. Such shifts between predation and competition relate to gape constraints. Size-dependent differences in competitive abilities between individuals contribute to the development of the size structure within the population (Persson 1988). To analyse the effects of a switch between match and mismatch, that is, between predation and competition of juvenile perch and bream (*Abramis brama*), a physiologically structured population model was used that is based on details given by Claessen, De Roos & Persson (2000), Claessen *et al.* (2002) and Persson *et al.* (1998; 2004). Such modelling results should give some cues on the effects of phenology on size-dependent life history in juvenile perch and how this may cause divergence in the population size structure. In a second step, the modelling results were then compared with the population structure of juvenile perch over 7 years in a lake. Data showed an increase in the width of the length-frequency distribution (LFD) over time, due to the establishment of piscivory of the largest individuals of the YOY age cohort (Beeck *et al.* 2002). Thus, to evaluate potential mechanisms that lead to different LFDs the study was focused on (i) the amount of piscivorous perch within the YOY age cohort, (ii) how long predation on bream is possible and (iii) how both is linked to the phenological occurrence of the predator and its prey.

Materials and methods

THE MODEL

The dynamics of the YOY perch age cohort were modelled by using a physiologically structured population model, a modelling approach that is designed (i) to handle continuously changing size-dependent processes and (ii) to describe the population dynamics explicitly in terms of individual processes, including foraging, consumption and growth (Claessen, De Roos & Persson 2000; Persson *et al.* 2004). An

important element of these models is that all assumptions pertain to the individual level, such that parameters can be estimated largely independently of the system under study (Persson *et al.* 2003). The environment consists of an unstructured population of zooplankton, as well as juvenile bream and perch.

The model was used to explore how the exploitation of alternative food resources (fish and the primary food resource, zooplankton) may influence the width of the LFD of the YOY perch cohort developing within the first 90 days after hatching under various conditions. The model design is largely based on the same assumptions and parameter values of Claessen, De Roos & Persson (2000), Claessen *et al.* (2002) and Persson *et al.* (1998, 2004) and simulates, besides the perch cohort, also the zooplankton concentration, as well as the numbers and growth of the YOY bream.

After hatching, perch live a certain period in the pelagic area before they shift to the littoral area, where they have the opportunity to use new food resources (mainly macrozoobenthos) besides the primary food, zooplankton (Byström & Garcia-Berthou 1999) and where they meet for the first time their potential prey, bream, which do not exhibit such a pelagic stage like perch. The model simulations began with the habitat shift of perch to the littoral area. Assuming an average pelagic period (hatching until habitat shift) of 28 days, perch shifted, with a mean total length (TL) of 32 mm, to the littoral area (this equals a mean growth rate of perch in the pelagic area of 0.92 ± 0.17 mm day⁻¹, W.R. Scharf, J.A. Groddeck & J. Borcherdig, unpublished data). Based on (i) our own observations and literature data on the size of bream at hatching (4.5 mm, Kucharczyk *et al.* 1997), (ii) the mean growth rate of bream larvae (0.3 mm day⁻¹, Beeck *et al.* 2002; P. Beeck & W.R. Scharf, unpublished data) and (iii) the time period between hatching of bream and the habitat shift of perch to the littoral area, it was next possible to calculate (i) initial bream size when perch shifted to the littoral area, and finally (ii) the difference in hatching time between perch and bream. Simulations were run for 64 days, which equals roughly 90 days after hatching. The model is described below using a variation on the scheme that Grimm *et al.* (2006) have recommended for describing individual-based models. Parameter values are defined in Table S1, Supporting information (Appendix S1, Supporting information), as well as their baseline values.

PURPOSE

Explore how the exploitation of alternative food resources (fish and the primary food resource, zooplankton) may influence the width of the LFD of the YOY perch cohort developing within the first 90 days after hatching under various conditions.

STATE VARIABLES AND SCALES

YOY perch

Young-of-the-year perch are simulated as individuals, i , each of which has an irreversible component to weight, $W_{P,i}(t)$, a reversible component, $Y_{P,i}(t)$, and a length, $L_{P,i}(t)$, that change over time. Reversible mass can be starved away when maintenance costs exceed energy intake, whereas irreversible mass cannot (Persson *et al.* 2004).

YOY bream

Young-of-the-year bream are grouped into size cohorts, j , which grow in physiological size, weight, $W_{B,j}(t)$ and length, $L_{B,j}(t)$, over time, and change in numbers per cohort, $N_{B,j}(t)$.

Zooplankton

Zooplanktons are described as a single state variable, $Z(t)$.

Spatial scale and resolution

The lake is treated as one compartment, with a size of 3×10^8 L.

Temporal scale and resolution

The temporal scale of a single growing season is assumed to be < 100 days. The time resolution of the simulation is 0.25 days; differential equations below are solved as difference equation using that time interval.

PROCESS OVERVIEW AND SCHEDULING

Dynamics of zooplankton

The zooplankton resources are not modelled. The biomass density of zooplankton has a carrying capacity. Both bream and perch feed on zooplankton. The dynamics of zooplankton are described under submodels in Appendix S1, Supporting information.

Dynamics of bream

Bream are assumed to be divided into 40 size cohorts. The feeding and individual growth in each cohort differs because of size differences. The bream feed on zooplankton and are fed on by perch. The dynamics of bream are described under submodels in Appendix S1, Supporting information.

Dynamics of perch

The perch have the option of feeding on zooplankton or, if the predator-prey size ratio permits, feeding on bream. The expected energetic gain is calculated for each individual perch in the population on a particular time step. The choice between feeding on zooplankton or bream is based on which choice will maximize growth. Details of perch dynamics are described in the submodels section (Appendix S1, Supporting information).

DESIGN CONCEPTS

'Design concepts' provide the important qualities of dynamics that the model emphasizes (Grimm *et al.* 2006).

Emergence

The size distributions of perch and bream emerge from the feeding of both on zooplankton and from the feeding of perch on bream. The dynamics of the size distributions are highly sensitive to initial conditions.

Stochasticity

The encounters of each perch with potential prey (bream) have a stochastic element. First, the number of bream in each size cohort is calculated. An individual perch of a certain size is assumed to be able to consume bream from any size cohort for which the length ratio of perch to bream is > 2.2 (Persson *et al.* 2004). Then, based on the number of bream per size class and the length ratio, a number of consumed bream is calculated stochastically for each time step. The

details are described under submodels (Appendix S1, Supporting information).

Initialization

At the start of a model run, the initial value of zooplankton biomass for the whole lake was assumed to be 1 000 000 g DW, which equals roughly 16 mg L⁻¹ biomass zooplankton (see below). Always the same initial number of perch was used (3000, mean size 32 mm TL, 0.38 g), which encounter a bream population which is assigned to 40 size classes. Intra-cohort size differences in perch were never >2.2 (Persson *et al.* 2004) within the simulation period of 90 days after hatching; thus, intra-cohort cannibalism was not assumed in the model. To simulate differences in hatching time between perch and bream, only the initial sizes of bream were varied according to the above outlined relationships (larval growth rates, size of perch at the time of the habitat shift). In the first series of simulations, the width of the initial perch LFD (always described by the difference between the 95% and 5% limits of the normal distribution, mean always 32 mm TL) ranged between 7 and 15 mm (based on our field observations in Lake Speldrop, see below). In this series, the initial prey density was kept constant at 520 bream per perch. In the second series of simulations, this initial density varied between 250 and 830 bream per perch (based on field data in pond experiments, L. Heermann & J. Borchering, unpublished data) while the width of the initial perch LFD was kept constant at 11.5 mm.

Input data

The input data are described in Appendix S1 and Table S1 in Supporting information.

Output

The model produces, as the main output, the size distributions of bream and perch every 4 days.

Submodels

The submodels describe the details of the dynamics of the interacting populations of perch, bream and zooplankton (see Appendix S1, Supporting information).

STUDY SITE

Lake Speldrop is a gravel pit lake situated in western Germany (location: 51°46'9"N, 6°22'6"E). It is about 7 ha in size and its maximum depth reaches 16 m. The steep, unreconstructed banks have slopes of about 20–45°; the banks are mainly covered with gravel, bricks and construction debris. Phanerophytes grow along almost the entire shoreline and submerged plants are almost absent. The adult fish community of Lake Speldrop is dominated by perch (over 50% in terms of biomass) and bream (about 30%); additional species are the predators pike (*Esox lucius*) and pikeperch (*Sander lucioperca*) as well as the cyprinids roach, tench (*Tinca tinca*) and carp (*Cyprinus carpio*); however, all these species occur only at low numbers (Beeck *et al.* 2002).

Lake Speldrop is highly eutrophic, with chlorophyll *a* concentrations of 10–50 µg L⁻¹ in the summer (Beeck *et al.* 2002). Except for some short periods during the phytoplankton peak in spring, secchi-depth during the summer was always in the range of 3–5 m (maximum 8 m). After short periods of high copepod abundance in April

(biomass up to 5 mg L⁻¹) daphnids regularly dominate the zooplankton community with peak biomasses of up to 15 mg L⁻¹ (Beeck *et al.* 2002, W.R. Scharf, J.A. Groddeck & J. Borchering, unpublished data).

FIELD SAMPLING

On average, perch spawn in Lake Speldrop around 30 April with only small seasonal variation (± 4.5 days SD). Bream spawn on average about 1 week later but with considerably greater variation (± 10.6 days SD). Perch shifted from the pelagic to the littoral area with a size of about 32 mm TL, and their duration of the pelagic period was shown to correlate with the available amount of zooplankton food in the pelagic area (W.R. Scharf, J.A. Groddeck & J. Borchering, unpublished data). The first occurrence of larval bream after hatching in the littoral area, as well as of juvenile perch directly after their habitat shift from the pelagic area, was monitored either with beach seining or by electrofishing with point abundance sampling by boat (Beeck *et al.* 2002).

Regularly from mid-June onwards until the end of the season, gill-nets were used to monitor the development of perch. Different types and numbers of sinking polyamide monofilament gillnets were used throughout the years (1999–2001: single mesh size gillnets, 25 m long, Beeck *et al.* 2002; 2004–2005: Nordic multi-mesh gillnets, Appelberg 2000; 2006–2007: small multi-mesh gillnets, Scharf *et al.* 2009). But at least the mesh sizes 6, 8, 10, 12 and 15 mm were applied at every sampling date to catch all sizes of perch > 40 mm TL. The nets were exposed during dusk, randomly distributed in the littoral area of Lake Speldrop. All fish were measured to the nearest 1 mm TL and, when available, the stomach contents of 20–40 YOY perch were analysed for each sampling date. Stomach content data were used in this study to describe the length of the period when YOY perch were feeding on fish in consecutive years.

DATA ANALYSIS

To describe the lower and upper margins (i.e. determine the breadth) of each LFD of YOY perch (regularly assumed as normal distribution), first the 5% and the 95% limits were calculated. These percentile data of each year were then fitted to a second degree polynomial, from which the hatching date (assuming a TL of about 6 mm, Thorpe 1977), as well as perch sizes 30 and 90 days after hatching were derived, independently of seasonal differences between the years. Calculated hatching data were supported by observations of newly hatched perch and bream in the lake.

Using an individual-based model of perch, the relative availability of prey fish for YOY perch was calculated. Based on the LFDs of both species, beginning with the date when perch arrive in the littoral area where they first contact bream, individual attack rates by YOY perch on the YOY bream were calculated according to their body length (Persson *et al.* 2004; Magnhagen & Borchering 2008). Further and also based on the data given by Persson *et al.* (2004), the percentage of the total YOY perch cohort that could potentially prey on bream was calculated.

Results

MODEL RESULTS OF THE LITTORAL PERIOD OF PERCH

The consumption of zooplankton by YOY perch and bream was modelled, as well as the predation of perch on bream, to

explore how the LFD of the YOY perch cohort develops within the first 90 days after hatching under various conditions. Regarding the predator–prey or competitive interactions between YOY perch and bream, the phenology of both species is of major importance. This determines to a large extent the sizes of individuals of both species at the time when perch shift to the littoral area where they first come in contact with their potential prey/competitor bream. Therefore, the hatching dates of both species were used as descriptive, primary variable in our simulations (recalculated from initial LFDs).

For the first series of simulations, the width of the perch's LFD varied between 7 and 15 mm (the borders of the empirical data), and was used as secondary initial variable. These perch met a bream population with a given LFD that varied depending on their date of hatching. The mean number of bream caught per perch per day varied from 0 to 5, depending on the difference in hatching dates of both species (Fig. 1a), clearly indicating a continuum from the competitive to the predatory situation between perch and bream. Accordingly, perch at the lower edge of the LFD (Fig. 1b) reached their largest sizes when they had hatched more than 10 days before bream. In contrast, perch at the upper edge of the LFD (Fig. 1c) grew better with smaller differences in hatching date (between -2 and 10 days, positive values indicate that perch hatched earlier than bream and vice versa) and stayed extremely small 90 days after hatching in the competitive situation, when bream had hatched more than 12 days earlier

than perch. The median perch length peaked when perch hatched about 4–6 days before bream (Fig. 1d). The skewness of the LFD describes the quantitative relationship of the small and large YOY perch within the age cohort, revealing the dominance of smaller perch when bream had hatched about 8 days before perch, and the dominance of the larger individuals when perch had hatched around 8–16 days before bream (Fig. 1e). Size differences > 40 mm in the LFD 90 days after hatching of perch were estimated for the situation when perch and bream hatching did not differ by more than a few days (Fig. 1f). In contrast, almost no differences were estimated when either perch had hatched much earlier than bream or vice versa.

In the first series of simulations the initial density of bream was kept constant at a mean value of about 520 individuals per perch. In the second series of simulations, this initial prey density was altered over a range from about 250 to 830 bream per perch, while keeping the width of the initial perch LFD constant at about 11.5 mm (mean difference of the empirical data). Again the difference between both hatching dates was used as the primary initial variable. As with the first series of simulations, the mean number of consumed bream increased per perch per day, depending on the difference in hatching of both species, but now further affected by prey density: higher initial densities of bream in relation to YOY perch allowed higher numbers of successful captures (Fig. 2a). Thus, the continuum from the competitive to the predatory situation between perch and bream of the first series of simulations

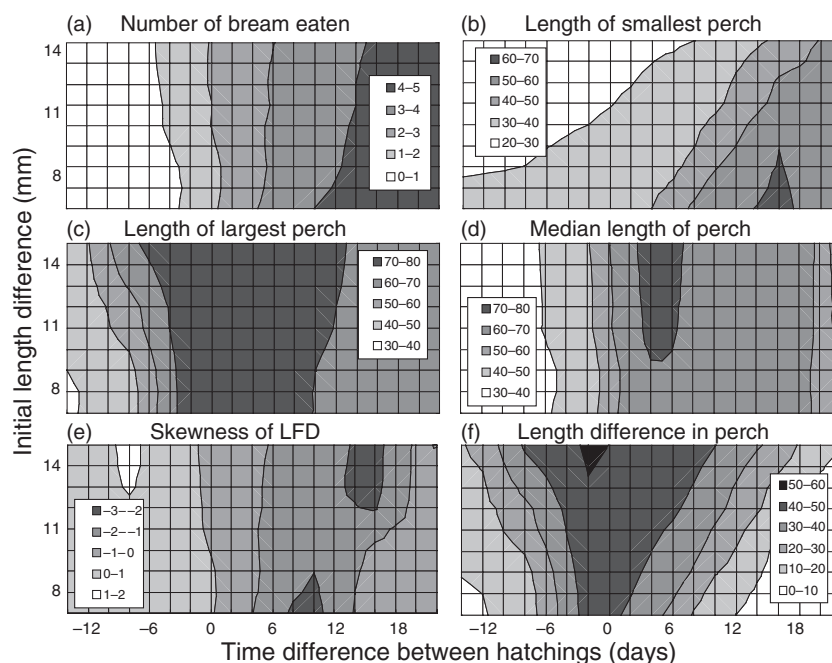


Fig. 1. Results of the population model of perch for the period from the perch habitat shift to the littoral area until 90 days after hatching depending on the time difference between the hatching of perch and bream (positive values indicate that perch hatched earlier than bream) and the initial length difference between the 5% and 95% limits (mm) of the perch shifting to the littoral area: (a) mean number of bream consumed by each perch per day, (b) lengths of the smallest perch (mm) described by the 5% limit of the length-frequency distribution, (c) lengths of the largest perch (mm) described by the 95% limit of the length-frequency distribution, (d) median length of perch (mm), (e) skewness of the length-frequency distribution (positive values indicate dominance of small sized perch in the population), and (f) length differences of perch (mm) described by the difference between the 95% and the 5% limits of the length-frequency distribution.

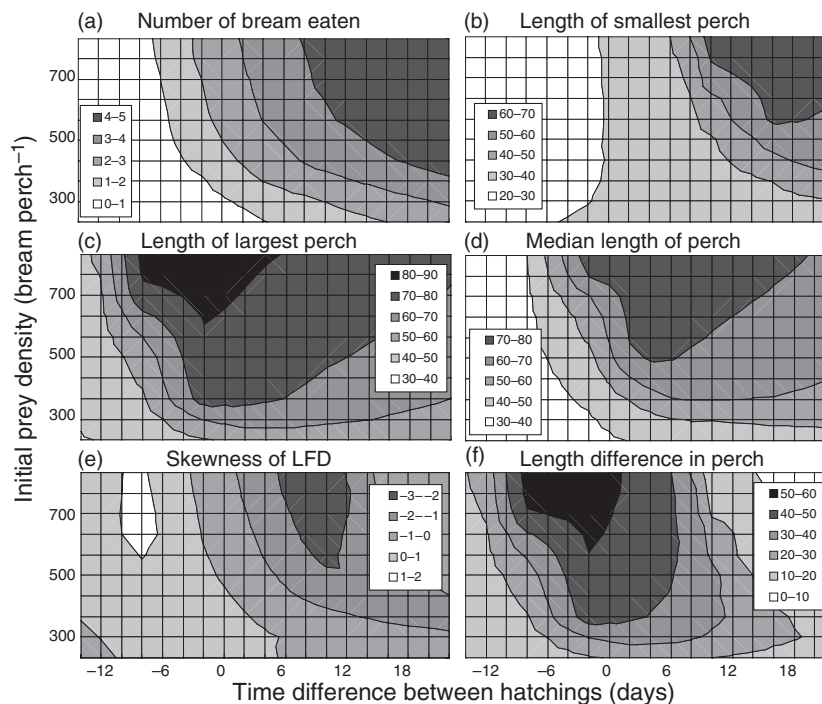


Fig. 2. Results of the population model of perch for the period from the perch habitat shift to the littoral area until 90 days after hatching depending on the time difference between the hatching of perch and bream (positive values indicate that perch hatched earlier than bream) and the initial prey density (bream per perch): (a) to (f) as in Fig. 1.

was further enhanced by increasing prey density. The modelling results of the small-sized and large-sized perch within the LFD, as well as the median length and the skewness, demonstrated also the pronounced effects of the difference in hatching in both species (Fig. 2b–e). Increasing initial densities of prey always led to increased size of perch, as well as increased proportions of the larger individuals within the modelled population.

There were almost no size differences within the YOY perch cohorts when perch hatched more than 15 days before bream and when initial prey density was >400 bream per perch (Fig. 2f). However, in the competitive situation when bream had hatched earlier than perch, also only small differences in size (<20 mm) between the upper and lower edge of the LFD were computed. The most pronounced size differences, above 50 mm occurred when bream hatched 0–8 days before perch and when initial prey density increased roughly above 600 bream per perch.

The dependencies of the perch sizes within a population 90 days after hatching on the mean number (averaged over all perch) of consumed bream is demonstrated in Fig. 3. When the initial LFD width, or length difference between the 5% and 95% limits of perch shifting to the littoral area, ranged between 7 and 15 mm (and a constant initial bream density of about 520 bream per perch), there was only little within-population variation for a given consumption rate (Fig. 3a). This small variation mainly depended on differences in the group of small-sized perch within the population. In contrast, large within-population variation for a given mean consumption rate was found, when the initial bream

density varied between 250 and 830 bream per perch (Fig. 3b). However, here this within-population variability for a given consumption rate depended mainly on differences of the large-sized perch within the population.

The small-sized perch only reached larger sizes when the mean consumption exceeded about 3.5 bream per perch per day. In contrast, large-sized perch reached larger sizes with an increasing consumption rate up to about one bream per perch per day and did not increase further in size with a further increase of the mean consumption rate (Fig. 3a). As a result, size differences between small-sized and large-sized perch exhibit a dome-shaped relationship, with the maximum (above 40 mm) at a mean consumption of about two bream per perch per day, and minimum values around 10 mm, when there was no predation on bream but only competition, or when perch preyed on more than four bream per day. When the initial bream density decreased, these trends were clearly damped, because the large-sized perch in the population could not profit further from scale of growth, while there was no within-population variation for a given consumption rate for the small-sized individuals (Fig. 3b).

THE LITTORAL PERIOD OF PERCH IN LAKE SPELDROP

The sizes of YOY perch in Lake Speldrop varied considerably among the years, and these differences are well described with the second degree polynomials for the 5% and 95% limits (Fig. 4, all $P < 0.001$). Years with large size differences between the upper and lower borders of the LFD at the end of the growing season in October (e.g. 2006: 64 mm size dif-

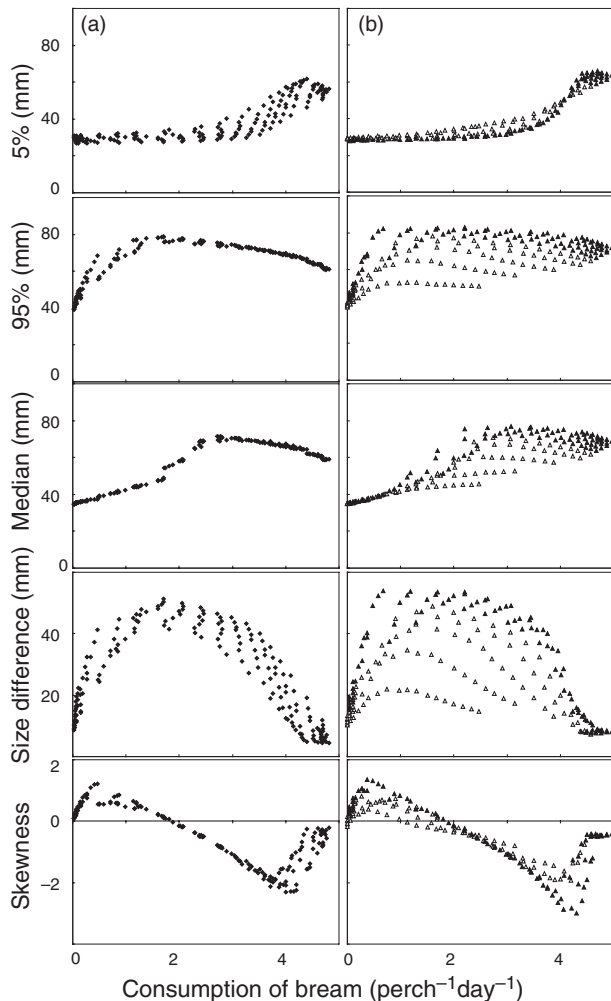


Fig. 3. Various output parameters of the simulations plotted on the mean number of bream preyed by each perch per day. On the left (a) the simulations of the first series are shown (see Fig. 1) in which initial bream density was constant at about 520 bream per perch, and the initial length difference between the 5% and 95% limits of perch shifting to the littoral area ranged between 7 and 15 mm (time gap between hatching of perch and bream ranging from –14 to 22 days). On the right (b) the simulations of the second series are shown (see Fig. 2) in which initial length difference between the 5% and 95% limits (mm) of perch shifting to the littoral area was constant at about 11.5 mm, and the bream density ranged between 250 and 830 bream per perch (time gap between hatching of perch and bream ranging from –14 to 22 days). The open symbols represent the values for the simulations with an initial bream density below 520 bream per perch and the black symbols those of higher initial bream density. Starting from the top, each plot shows the size of perch of the 5% limit, the size of perch of the 95% limit, the median size of perch, the length differences of perch described by the difference between the 95% and the 5% limits of the length-frequency distribution, and the skewness of the length-frequency distribution.

ference) contrast with those with a quite narrow LFD (e.g. 2005: 24 mm size difference). This size variation within the YOY age cohort was further mediated by large differences in the median size of all caught perch in October (e.g. 1999: 132 mm TL, 2005: 82 mm TL, Fig. 4).

The difference between the hatching date of perch and bream affected the width of the perch LFDs 30 days after

their hatching (Fig. 5a). When perch hatched much earlier than bream, the size difference was smaller (< 15 mm) compared to those years when bream hatched before perch (maximum 23 mm). This relationship, with a low level of significance 30 days after hatching of perch (i.e. for perch that had stayed most of their life in the pelagic area), became highly significant for perch 90 days after hatching (i.e. for perch that stayed in the littoral area for about 2 months, in addition to their pelagic period).

When perch hatched about 15 days before bream, all perch of the YOY age cohort were large enough to potentially prey on bream when they shifted from the pelagic to the littoral area (Fig. 5b). In contrast, less than 40% of the YOY age cohort of perch was large enough to potentially prey on bream in years when bream hatched before perch. This relationship coincides with a significant increase of the duration over which bream were found in the stomachs of YOY perch. When all perch of the YOY age cohort were able to prey on bream, the duration of the predation period was < 20 days, due to rapid overexploitation of the prey, while this period increased up to 50 days when only a small percentage of the age cohort were large enough to prey on bream (Fig. 6a). There was also a significant relationship between the duration of the period of perch predation on bream and the size difference 90 days after the hatching of perch (Fig. 6b). This relationship reveals that the longer a part of the YOY age cohort of perch was able to prey on bream the larger the size differences between the smallest and the largest perch of the age cohort were after about 2 months in the littoral area.

Discussion

The modelling results clearly demonstrate that the switch between competitive interactions and a predator–prey relationship depended on phenology, or more precisely on phenologically related sizes of both species when they met for the first time. When the whole age cohort of the predator was able to prey on the alternative and energetically profitable food resource prey fish, only small size differences between the upper and lower borders of the LFD of the predator were found. This match situation of the predator–prey system occurred when perch hatched earlier than bream and when the related size differences were so large that no gape-size limitations existed when predator and prey met in the littoral area. The same effect on the width of the LFD was found when bream hatched much earlier than perch, preventing predation from occurring, which, in turn, increased the competitive interaction of the predator with its prey; i.e. the mismatch situation that coincided with a lower mean size of the age cohort. In between the total match and the mismatch situations, however, only the largest individuals of the age cohort were able to prey on the alternative food resource, while the smaller siblings got trapped in competition with each other and with bream, leading to enlarged differences in growth that increased existing size differences within the LFD, above the two extreme scenarios, the match and the mismatch situation.

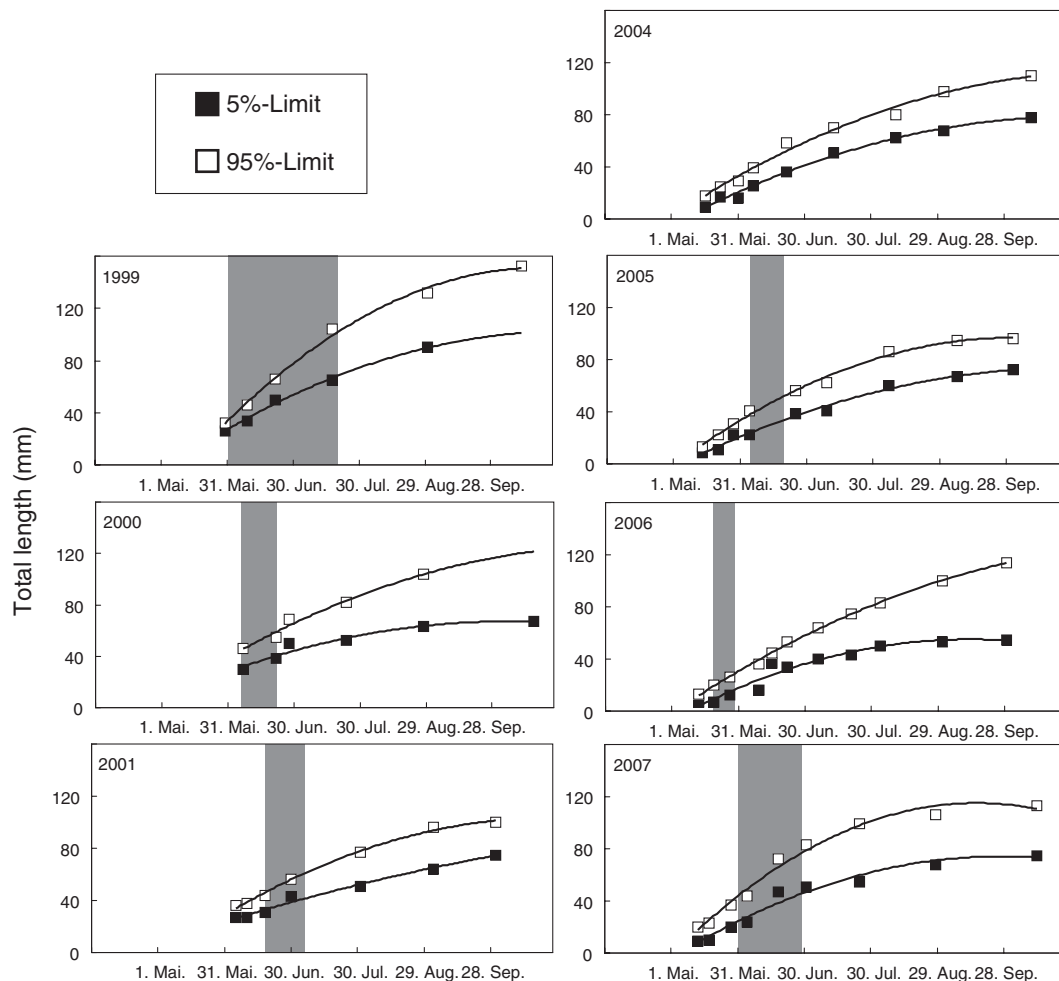


Fig. 4. Borders of length-frequency distributions of perch in Lake Speldrop in successive years (1999–2001, 2004–2007) described by the 5% (length of the smallest size class) and 95% limit (length of the largest size class). The shaded area shows the period when fish were found in the stomachs of perch.

The match–mismatch hypothesis was first proposed for marine systems and suggests that the inter-annual variability in fish recruitment is a function of the timing of the production of their food (Cushing 1990). However, not only survivorship may change in a match–mismatch continuum and thus affect successful recruitment to the reproductive population, but also, after a certain period, both the mean size and variation in sizes within an age cohort may change as well (Peacor, Bence & Pfister 2007). This was shown in tadpoles of wood frogs (*Rana sylvatica*), in which increasing competition resulted in increased size variation as a function of mean size (Peacor & Pfister 2006). For any new cohort of organisms, the variability among individuals in size either decreases over time, remains the same or increases (Pfister & Stevens 2002). Such changes in the initial size variation of individuals have been referred to as ‘growth compensation’, if the variation decreases or ‘growth depensation’ if the variation increases over time (Ricker 1958). Initial within-cohort size variation may depend on both inherent factors, such as genetic differences and maternal effects, and extrinsic factors related to the interaction between individual life histories and the environment (e.g. largemouth bass, *Micropterus salmo-*

ides, Post 2003). Differences in hatching time of perch in Lake Geneva depend on spawning time and depth, and most of the spawns were laid when water temperature exceeded 12 °C (Gillet & Dubois 2007). Temperature dependent variability between the years (e.g. in dependence to spawning depth and size of the females, Gillet & Dubois 2007) may add substantial variability in the initial size distribution. The result will be an extended hatching period, which is a common feature for many fish species (Post 2003) and is assumed as one of the most important basic factors that produces size variation within an age cohort (Huston & DeAngelis 1987). Development of size variation among individuals can have important implications for individual fitness as well as population level processes, such as recruitment success, population stability and population persistence (Huss, Persson & Byström 2007).

GROWTH COMPENSATION

Growth compensation, i.e. the decrease in size variability compared to the initial LFD (Ricker 1958), was predicted by our modelling results, particularly when all individuals of the

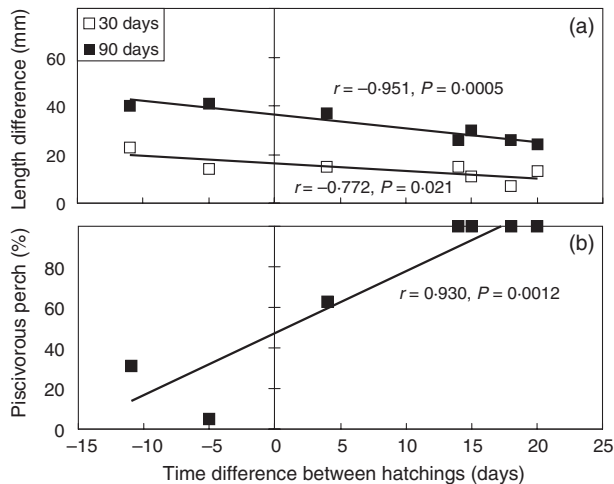


Fig. 5. (a) Length differences (mm) described by the difference between the 95% and the 5% limits of the length-frequency distribution 30 and 90 days after hatching and (b) the percentage of perch that can prey on bream (calculated amount of the total population) of perch in Lake Speldrop, as functions of the time difference between the hatching of perch and bream (positive values indicate that perch hatched earlier than bream).

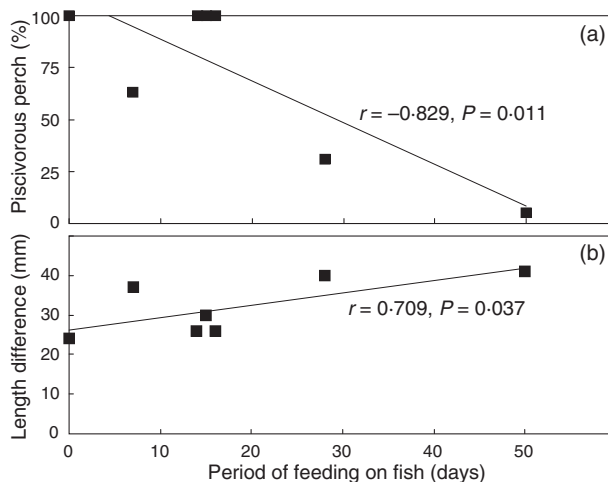


Fig. 6. (a) Percentage of perch that can prey on bream in Lake Speldrop (calculated amount of the total population) and (b) the length differences (mm) described by the difference between the 95% and the 5% limits of the length-frequency distribution 90 days after hatching of perch as functions of the length of the period when perch preyed on bream.

predator cohort were able to prey on the alternative food resource, that is, when perch hatched much earlier than bream (Fig. 1f). The related mechanism in the model is the availability of the alternative food resource: When the mean number of consumed bream per perch per day was > 4.3 , i.e. when all perch were able to prey on bream (cf. Fig. 6), then size differences at the end of the simulations were always lower than within the initial age cohort (Fig. 3a, also compare Fig. 1a,f). In Lake Speldrop, no growth compensation but only growth depensation was observed (linear relation-

ship in Fig. 5a). However, from the modelling results a dome-shaped relationship could be expected (cf. Fig. 1f and 2f). It is assumed that the results of Lake Speldrop are more likely caused by lower predator/prey ratios (for which no reliable data are available mainly because of differences in habitat use, activity and catch efficiency cf. Scharf *et al.* 2009) than on mechanistic differences to the model. This assumption is supported by the second series of simulations, in which the reduction of prey availability clearly diminished depensatory growth (Fig. 3b). In gape-limited animals such as fish the use of a higher variety of food resources may also affect the development of fast and slow growth-rate groups (e.g. perch feeding on macrozoobenthos Huss, Byström & Persson 2008), thus diminishing within-cohort competition through niche separation and increasing the possibility of increased individual energy accumulation of all individuals (Bolnick *et al.* 2003). However, in the case of overexploitation of bream, only zooplankton could be used as food resource in our model, while perch in Lake Speldrop may also feed on macrozoobenthos (Borcherding, Hermasch & Murawski 2007). Further, differences between the field study and the modelling approach are to be expected, because size divergence has been shown to be associated with the establishment of social hierarchies, which is believed to be a major cause of growth depensation (e.g. *Channa striatus*: Sampath & Pandian 1985; perch: Westerberg, Staffan & Magnhagen 2004; Huss, Byström & Persson 2008). Additionally, predation risk of the predator itself must be considered with respect to the habitat where the optimal food is available. For example, bluegill (*Lepomis macrochirus*) cannot access their preferred prey of zooplankton until they reach a large enough size that predators in the open water will not be a major threat (Werner *et al.* 1983). Obviously, such social and behavioural patterns are yet not implemented in the population modelling.

GROWTH DEPENSATION

In contrast to growth compensation, depensatory growth clearly became obvious in our field data, and the increase in size variability of the age cohort was significantly correlated to the length of the period in which bream were available as prey for the predator perch (Fig. 6b). This clearly coincides with the predictions from the model output that exhibited largest size differences within the age cohort, when the prey organisms were available only to a limited percentage of all individuals (i.e. decreasing number of preyed bream per perch per day, Fig. 3). Comparable results were found within a single group of perch larvae, in which smaller individuals grew substantially slower under high densities, whereas large individuals performed equally well independently of density, resulting in size variation among individuals within groups (Huss, Persson & Byström 2007). Large differences in size within an age cohort in southern flounder (*Paralichthys lethostigma*) depended on growth rate variation among juveniles, with an apparent bifurcation in the growth curve beginning at about 75–100 mm TL, which corresponded to the onset of

piscivory (Fitzhugh, Crowder & Monaghan 1996). Comparable growth differences within the YOY age cohort were also described for perch during their first weeks in the littoral area of Lake Speldrop, with rates that ranged between 0.6 mm day⁻¹ for planktivorous and 1.4 mm day⁻¹ for piscivorous individuals (Beeck *et al.* 2002).

SWITCH BETWEEN PREDATION AND COMPETITION

The interactions between prey and predator may shift between competition and predation, depending on how priority effects, environmental conditions, and behavioural responses alter their relative growth rates (Wilbur 1988; Persson, De Roos & Byström 2007; Urban 2007). In gape-limited predators, body size asymmetries often determine the outcome of predator–prey interactions, and predation on a focal prey species can be estimated by the relative size differences between predator and prey (Wilbur 1988; De Roos, Persson & McCauley 2003; Persson *et al.* 2004). When the predator and prey grow at different rates or shift at different sizes, the predicted outcome becomes more complicated (Urban 2007). Because perch in all years arrived with the same size in the littoral area, where they encountered their potential prey bream for the first time, the size of bream at that time largely determined the outcome of the predator–prey interaction. Because the observed body size asymmetries between perch and bream are related to differences in hatching time, phenology determines to a large extent the sizes of perch and bream, and, consequently the outcome of the predator–prey interaction. This is evident in the relationship between the time-gap in hatching of perch and bream and the percentage of piscivorous perch within the YOY age cohort (Fig. 5b). And of course, if more perch have the capability to prey on a fixed number of bream, the duration of bream availability will decrease. Thus, the time-gap in hatching of perch and bream also determined how long the profitable food resource bream was available to increase growth rates of the predator above average. When such increased growth rates exist only for a certain part of the predator's age cohort, initial size differences within this cohort are enlarged.

To understand and predict the dynamics of interacting predators and their prey, body size variation has been studied extensively (e.g. Huston & DeAngelis 1987; De Roos, Persson & McCauley 2003). However, most studies of trophic interactions omit a dynamic perspective that accounts for predator–prey ontogeny and phenology, which may be especially important in temporary habitats (Urban 2007). Also for permanent habitats like the marine environment or lakes, phenology is a necessary component of models that incorporate differences in ecology among life-history stages of single species (Werner & Gilliam 1984; Alford 1989; Durant *et al.* 2005). Keast (1985) noted that in temperate lakes, piscivorous species tend to spawn earlier in the year than do other fishes, thereby attaining sufficient size to enable consumption of the larvae of other fishes that had spawned later. Juvenile bluefish (*Pomatomus saltatrix*) grow with rates of 0.75–1 mm day⁻¹ feeding on plankton during the premigratory

oceanic phase in their life history and increasing their growth rate to 1.3–1.7 mm day⁻¹ in the estuary when preying on later-spawning fish species (Juanes, Buckel & Conover 1994). This is absolutely comparable to our match-situation when perch hatch much earlier than bream and all individuals are able to prey on bream, thereby profiting from the fact that a planktonic diet is inferior to a fish diet (and other energetically profitable organisms like Mysidacea, Keast 1985; Borchering, Hermasch & Murawski 2007). The growth advantage from feeding on bream can be estimated by exploring the second series of simulations, which reveals increasing median sizes 90 days after hatching with increasing initial prey density. With a constant initial prey density, however, two different processes shape the median sizes of the population in relation to the number of consumed bream. (i) Small size classes in the population profited only when the mean consumption rate exceeded 3.5 bream per perch per day, a situation, which was only observed when perch hatched at least 12 days before bream, enabling all individuals of the gape size limited predator perch to prey on its potential prey bream. (ii) In contrast, the larger size classes in the population increased their profit in relation to an early hatching of bream (6–12 days before perch). Here, more and more individuals were large enough to enter the gape-size mediated window of predation. This advantage over the small-sized individuals within the initial cohort of the predator diminished successively with further changes in the time-gap between hatching of predator and prey (from nearly equal hatching dates up to a much earlier hatching of perch compared to bream), because more and more of the small-sized individuals now also could prey on fish, thus increasing the competition on this profitable food resource.

Conclusions

Phenology, together with initial size differences in the predator cohort and the prey density per predator, are important variables for predicting the outcome of this predator–prey relationship and, consequently, for predicting the LFD of the predator. This was clearly reflected in the results of our modelling approach in which only these variables were initially changed within field related borders, while all other initial variables of the model were kept constant. The most important effects within the predator size cohorts pertain to the large-sized individuals that could escape the competitive bottleneck on the primary food resource (zooplankton) by feeding on the alternative food resource, fish, which includes even the reduction of the number of competitors on the primary food. When more and more of the smaller individuals enter the gape-size predetermined predation window, then competition with the smaller size-classes increases, but now the competition is for the alternative food resource, fish. However, if the large size-class within the YOY age cohort is able to use its growth advantages compared to their smaller conspecifics long enough, then size differences may become so large as to create a bimodal LFD (Beeck *et al.* 2002) and even intracohort cannibalism (Urbatzka *et al.* 2008). One

important aspect not considered in the predator–prey system of this study, is the size variability of the prey organisms and its implications for the development of size differences within the predator's age cohort (Huss, Byström & Persson 2008). This aspect will be a challenge for future studies.

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Supporting Information

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Appendix S1. Submodels within the physiologically structured population model.

Table S1. Parameter values of perch submodel.

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