

## Foraging capacities and effects of competitive release on ontogenetic diet shift in bream, *Abramis brama*

Anders Persson and Christer Brönmark

Persson, A. and Brönmark, C. 2002. Foraging capacities and effects of competitive release on ontogenetic diet shift in bream, *Abramis brama*. – Oikos 97: 271–281.

Bream (*Abramis brama*) undergo ontogenetic diet shift from zooplankton to benthic macroinvertebrates, but the switching size may be highly variable. To unravel under what conditions bream are pelagic versus benthic foragers, we experimentally determined size-dependent foraging capacities on three prey types from the planktivory and benthivory niche: zooplankton, visible and buried macroinvertebrates. From these data we derived predictions of size-dependent diet preferences from estimates of prey value and competitive ability, and tested these predictions on diet data from the field. Planktivorous foraging capacity described a hump-shaped relationship with bream length that peaked for small bream of 67 mm total length. Benthivory capacity increased with increasing bream size, irrespective if benthic prey were visible on the sediment surface or buried in the sediment. From the experimental data and relationships of metabolic demand we calculated minimum resource requirement for maintenance (MRR) for each of the prey categories used in experiments. MRR increased with bream size for both zooplankton and visible chironomids, but decreased with bream size for buried chironomids, suggesting that intermediate sized bream (120–300 mm) may be competitively sandwiched between small and large bream that are more competitive planktivores and benthivores, respectively. Prey value estimates and competitive abilities qualitatively predicted diet shift in a bream population being released from competition. Competitive release did not change the diet of the largest size-class feeding on an optimal diet of benthic invertebrates both before and after competitive release. However, profound diet shifts towards benthic macroinvertebrates were recorded for intermediate size-classes that fed on a suboptimal diet prior to competitive release. Thus, laboratory estimates of size-dependent foraging capacity of bream in planktivorous and benthivorous feeding niches provided useful information on size-specific competitive ability, and successfully predicted diet preference in the field.

A. Persson, Christer Brönmark, Dept of Ecology, Limnology, Ecology Building, Lund Univ., S-223 62 Lund, Sweden ([anders.persson@limnol.lu.se](mailto:anders.persson@limnol.lu.se)).

Individuals of size-structured populations typically feed on progressively larger prey over ontogeny (Peters 1983, Werner and Gilliam 1984, Persson 1988, Stein et al. 1988, Persson et al. 1998), because fundamental individual characteristics, such as energy requirements and foraging capacity, scales with individual size (Mittelbach 1981, Lundberg and Persson 1993). However, availability of differently sized prey may be highly discontinuous in nature (Werner and Gilliam 1984, van Densen et al. 1996), ultimately leading to dramatic diet

and habitat shifts of the predator. Discontinuous prey availability may also enhance intra- and interspecific competition by forcing different size-classes and species to overlap in diet (Hamrin and Persson 1986) and preventing transitions between feeding stages (Persson and Greenberg 1990a). Population dynamics will therefore depend heavily on individual success in transferring between feeding stages.

The process leading to progressively larger prey items in the diet of larger predators is size-selective predation

Accepted 31 January 2002

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ISSN 0030-1299

(e.g. Brooks and Dodson 1965). Selection occurs when the distribution of prey items in the diet of predators differs from the distribution of prey in the environment. The diet of a predator, being the outcome of this selection, is the combined result of predator ability and prey density. Foraging models assume that natural selection has favoured consumers that select among the variety of food objects to optimize fitness, traditionally using energy gain as a measure of fitness (reviewed in Stephen and Krebs 1986). Although the traditional energy-maximizing theory has been questioned frequently (Pierce and Ollason 1987, Stearns and Schmid-Hempel 1987, Nonacs 1993, Ward 1993), it has proven a successful model applicable to field situations (Persson 1990, Sih 1993). Especially, energy-maximizing models have been effective when laboratory estimates of foraging capacity are combined with field experiments to predict the effects of competitive interactions on habitat shift (Werner and Hall 1979, Werner et al. 1981, 1983b) and diet choice (Werner and Mittelbach 1981, Werner et al. 1983a, Persson and Greenberg 1990b).

A fundamental prediction from optimal foraging theory is that a predator should always select the highest ranked prey item, whereas lower ranked food items should be selected only when the encounter rate with higher ranked food items is below a critical level. Thus, the ranking of prey items is mainly a function of prey-specific energy content per unit handling time, termed the prey value. Even if many different predators rank a particular prey high, that item may not necessarily be found in the diet of all these predators. This is because different predators may encounter prey at different rates depending on their search capacity for that particular prey item.

Here we apply the energy-maximizing premises to unravel mechanisms behind ontogenetic diet shift in bream (*Abramis brama*). Bream is a common fish in Eurasian temperate lakes and rivers that may dominate the fish community in highly eutrophic systems and profoundly affect community dynamics (Meijer et al. 1990, Persson 1997, Bergman et al. 1999). Bream typically undergo ontogenetic diet and habitat shifts from feeding on zooplankton in pelagic habitats to feeding on benthic invertebrates buried in the sediment. It is important to unravel under what conditions bream are pelagic versus benthic foragers because these two feeding strategies will have different community consequences. In a previous study it has been shown that the size where the diet switch occur may be highly variable and possibly dependent on competitive interactions (Persson and Hansson 1999). This study aims at providing a mechanistic explanation for the observed variation in switching size, and is structured in the following way. First, we calculate the profitability for pelagic and benthic resources using *Daphnia* and chironomid larvae as model prey from the pelagic and benthic habitat,

respectively. We then use laboratory estimates of foraging capacity and calculations of minimum resource requirements to evaluate competitive ability of different size-classes of bream on different prey types. Thus, we are able to evaluate the probability that a certain size-class should shift diet if competition is reduced. These predictions are tested on field data from a bream population subjected to competitive release.

## Material and methods

### The foraging model

When determining individual foraging capacity, we assumed that capture rate was dependent on (i) the density of prey according to a Holling type II functional response, and (ii) on the length ( $l$ ) of the predator. The size specific capture rate ( $c(l, N)$ ) as a function of prey density is given by:

$$c(l, N) = \frac{a(l)N}{1 + a(l)h(l)N} \quad (1)$$

where  $a(l)$  is attack rate,  $h(l)$  is the instantaneous handling time, and  $N$  is the prey density. The attack rate has repeatedly been shown to describe a hump-shaped relationship with predator size (Werner 1994, Byström and García-Berthóu 1999, Hjelm 2000, Wahlström et al. 2000). Following Persson et al. (1998), the attack rate is a function of body length ( $l$ ) according to:

$$a(l) = A \left( \frac{l}{l_0} \exp \left( 1 - \frac{l}{l_0} \right) \right)^\alpha \quad (2)$$

where  $\alpha$  is the rate of initial increase with body size, and  $l_0$  is the body length at which the maximum attack rate,  $A$ , is achieved. Size-specific attack rates were determined for bream foraging on zooplankton prey (*Daphnia*), and on visible and buried benthic prey (chironomidae larvae belonging to *Chironomus* sp. and *Polypedilum* sp., respectively). In the cases of benthic prey, the maximum attack rate was obtained for the largest fish used. Therefore, an exponential function was fitted to size-specific attack rates instead of eq. (2). Further, because prey saturation was not obtained for buried benthic prey, attack rates were estimated by fitting the data to a type I functional response, i.e. by assuming capture rate to be a linear function of prey density. Thus, the handling times for benthic prey were derived from experiments with visible prey. Non-linear technique was used to fit observed feeding rates to the Holling type II functional response, and to fit the estimated size-specific attack rates to the size-dependent attack rate function (eq. (2)).

## Minimum resource requirement (MRR)

As a measure of competitive ability, we calculated the size-dependent MRR for maintenance for each prey type. MRR was defined as the prey density  $N$ , when net mass intake equals metabolic demand. The net mass intake was calculated for each prey type by multiplying eq. (1) with a conversion efficiency (including specific dynamic action) of 0.61 (Persson et al. 1998). In the laboratory experiments we derived short-term handling times based on manipulation of prey. In calculations of long-term consumption rates, the relevant handling time includes digestion time. To our knowledge, estimates of digestion rate are not available for bream. We therefore used published relationships for the closely related roach, *Rutilus rutilus* (Lessmark 1983). Following Claessen et al. (2000), handling time is:

$$h(w) = \beta w^\chi$$

where  $\beta$  and  $\chi$  are given the values 5 and  $-0.8$ , respectively (Hjelm 2000). As with handling time, parameterization of metabolic demand is based on published data on roach, and was calculated as a function of predator mass (Persson et al. 1998, Claessen et al. 2000, Hjelm 2000) according to:

$$m(w) = \delta w^\varepsilon$$

where the constants  $\delta$  and  $\varepsilon$  are given the values 0.033 and 0.77, respectively. To convert fish mass to length, we used the relationship  $l = 55.8w^{0.299}$  (A. Persson unpubl.).

## Laboratory experiments

Experiments were performed in aerated tanks at a constant temperature of 18°C. Bream were collected from Lake Krankesjön by electro-fishing and trap nets. Pilot experiments showed that small fish had a low foraging activity when kept alone. Therefore, all experiments were performed with groups of three fishes, except for fish longer than 300 mm that were kept alone. Fish were introduced to tanks and fed on the same prey as used in the experiments at least one week before the experiment started. All experiments were performed with fish that were starved for 24 h, and each fish was used only once for each prey density.

Planktivory experiments were performed in 60 l tanks and benthivory experiments in 200 or 600 l tanks (using bream < 200 and > 200 mm, respectively). As zooplankton prey we used *Daphnia* sp. that were netted from cultures and sieved through two nets with mesh diagonals 1.37 and 0.64 mm to determine upper and lower size limit, respectively. The average size of individuals in the sieved samples was  $0.93 \pm 0.16$  mm

(mean  $\pm 1$  SD,  $n = 30$ ). From sieved samples, *Daphnia* sp. was counted individually to obtain a certain prey density.

Before each experiment, aeration was shut off and a known number of zooplankton individuals were mixed into the water of a test tank containing bream. At the onset of feeding, one individual was selected as test fish and the time it took for that fish to ingest five prey was recorded. If feeding was not initiated within 10 minutes, the experiment was discarded. At low prey densities (0.125–0.5 ind.  $l^{-1}$ ), the time spent to ingest only three prey was recorded to minimize errors related to prey depletion. Replicated ( $n = 4$ ) experiments on seven different size-classes of bream (10, 20, 30, 40, 55, 70 and 120 mm) foraging at six to seven densities of *Daphnia* sp. (0.25–16 ind.  $l^{-1}$ ) were performed.

It has been shown earlier (Lammens et al. 1986) that the foraging efficiency of bream when feeding on sediment-dwelling macroinvertebrates is significantly affected by both the vertical distribution of the prey and the grain size of the sediment substratum. Therefore, all experiments on benthivory were standardized using a 3 cm thick layer of sand (grain size: 0.3 mm). We used *Polypedilum* sp. and *Chironomus* sp. (length, 10 mm) as prey. *Polypedilum* sp. is common in lakes and is frequently found at high densities in sandy sediments. Their thick cuticle allow them to burrow into harder substrates compared to *Chironomus* sp., which are generally found in softer sediments with higher organic content. The chironomidae larvae were introduced to a tray with sediment at least two hours prior to the experiments. *Polypedilum* sp. generally disappeared from the sediment surface within a few minutes, whereas *Chironomus* sp. remained at the sediment surface. Thus, the *Chironomus* sp. and the *Polypedilum* sp. experiments differ with respect to prey vulnerability, *Chironomus* sp. being visible and *Polypedilum* sp. being buried up to 3 cm deep in the sediment.

Benthivory experiments were performed with six different size-classes of bream foraging at a minimum of three different densities of either *Chironomus* sp. or *Polypedilum* sp. (100–1600  $m^{-2}$ ). The foraging rate was zero for the two smallest size-classes of bream in *Polypedilum* experiments. Therefore, experiments with *Chironomus* were performed with somewhat larger bream (90, 110, 200, 250, 290, 310, and 350 mm, compared to 50, 70, 100, 150, 220 and 330 mm with *Polypedilum*).

Experiments were initiated by placing a tray ( $0.3 \times 0.35$  m) containing sediment and prey in tanks with bream. Initial experiments showed a very low feeding efficiency of small fish. Therefore, the fish were allowed to feed for up to 30 minutes depending on fish size and prey density used. After termination of each experiment, the sediment was sieved and the number of remaining prey recorded. Experimental duration was adjusted such that prey depletion never was more than

30% of initial density. Capture rate (number of prey consumed per unit time) was determined as individual averages.

### Prey value and field predictions

Two parameters were derived from the laboratory experiments, handling time (excluding digestion time) and attack rate, for each prey type and bream size-class combination. Prey values were calculated by dividing the dry weight values (as equivalent to energy) of the prey with the handling times. It was then possible to determine the optimal prey type, pelagic or benthic, (i.e. having the highest prey value) for each size-class of bream. This predicted prey choice was then compared to actual diet data from two different years in Lake Finjasjön, representing high and low fish population density, respectively. According to optimal foraging theory, a diet consisting of mainly the highest ranked prey would indicate that the encounter rate with that prey type was above a critical value. Reducing competition should consequently not affect diet composition. On the other hand, a diet consisting of lower ranked prey types indicate that the encounter rate with high ranked prey was below a critical value. In such a case, reducing competition would presumably allow a larger fraction of high ranked prey in the diet. Our analysis was structured in the following way. First, we used prey value estimates to determine if the diet consisted of the most profitable prey or not at high bream density. We expected that reducing competition would alter the diet composition for only those size-classes including a large fraction of the low-ranked prey type. We then used our calculations of prey-specific MRR to rank the probability that a certain size-class would shift diet. Consequently, we assigned the highest probability rank of diet shift to the size-class with the lowest value of MRR. Our predictions were then tested on diet choice of the Lake Finjasjön bream population after the fish community was significantly reduced in size by biomanipulation (Persson and Hansson 1999).

### Field sampling

Field sampling was carried out in Lake Finjasjön (area 11 km<sup>2</sup>; mean depth 3.5 m), a eutrophic lake situated in southern Sweden. The methods used to sample fish and zooplankton are described in Persson and Hansson (1999) and Hansson et al. (1998), where data on fish and zooplankton densities and fish diets are also presented. Therefore, the methods will only be briefly described here.

Fish were sampled at five different depths by trawling (duplicate tows at 2, 3, 4, 6, and 8 m; Persson and Hansson 1999) in Aug./Sept. 1992–1995 to determine

the relative abundance and fish community composition. Bream were measured and sorted into different size-classes; < 80 mm, 80–120 mm, 120–150 mm, 200–300 mm, and > 300 mm, corresponding to 0+, 1+, 2–3+, 4–5+ and ≥ 6+ old fish.

Diet composition in bream was determined on six occasions in 1992 and five occasions in 1995 from fish caught in survey gill nets placed overnight at 2 m and 5 m depths. When possible, at least 5 (1992) or 10 (1995) individuals from each date and size-class were analyzed for diet composition. The diet was determined by identifying, counting and measuring the length of the different food items. All fish within a size-class were then pooled and the dry mass of each prey item determined using length-mass relationships (Bottrell et al. 1976, A. Persson unpubl. data).

## Results

### Foraging capacity

The zooplanktivory experiments showed that bream of 10 mm length were unable to ingest the prey, although attempts were made. The behavioural observations during the experiments showed that this was probably due to a combination of gape-size limitation of the bream and successful escape behaviour of *Daphnia*. With increasing bream size, foraging rate increased and the attack rate peaked at 0.73 l s<sup>-1</sup> for bream of 67 mm length (Fig. 1a). Handling times decreased with bream size from 4.4 s prey<sup>-1</sup> for 20 mm bream to 0.3 s prey<sup>-1</sup> for 120 mm bream (Fig. 1b), resulting in maximum consumption rate increasing with bream size.

In experiments with visible benthic prey (*Chironomus* sp.), bream < 100 mm made attempts to forage on the chironomidae larvae, but generally only parts of prey were actually consumed. Size-specific attack rates were therefore only calculated for bream ≥ 100 mm. With increasing size of fish, estimated attack rates increased (Fig. 2a), whereas handling time decreased. The highest size-specific attack rates were recorded for the largest fish size in both the *Chironomus* sp. and the *Polypedilum* sp. experiments.

Size-specific attack rates were significantly affected by prey availability, as attack rate was more than a magnitude higher in the *Chironomus* than in the *Polypedilum* experiments. Bream used vision when foraging on visible prey, whereas in experiments with non-visible prey, sampling rate was independent of prey density, indicating random searching for prey (data not shown). No successful attacks on non-visible prey were recorded for bream smaller than 100 mm, and for 100 mm bream successful attacks were only detected at the highest prey density used (1600 m<sup>-2</sup>). Large bream could penetrate deeper into the sediment compared to small bream, resulting in size-specific attack rate increasing with increasing fish size (Fig. 2b).

### Minimum resource requirement

The minimum resource requirement (MRR) was highly dependent on bream size (Fig. 3). However, the size-dependent patterns were very different when the three prey types were compared. MRR of zooplankton increased exponentially (Fig. 3a), whereas the MRR of chironomids was dependent on their visibility. The MRR of visible chironomids first increased exponentially for bream < 100 mm, to thereafter increase linearly for larger fish (Fig. 3b). For buried chironomids, however, it decreased exponentially (Fig. 3c). When comparing the MRR for a 200 mm bream foraging on chironomids, it was about 500 times higher for buried compared to visible prey. Comparing the MRR with zooplankton and chironomid densities from natural habitats suggests that bream longer than 250 mm should be unable to survive on zooplankton, whereas bream smaller than 100 mm should be unable to survive on buried chironomids.

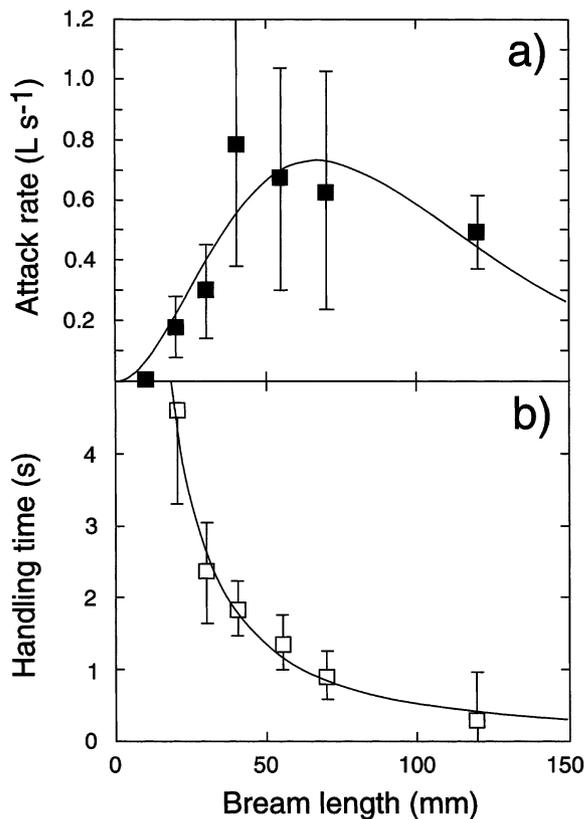


Fig. 1. Estimated ( $\pm 1$  SE) attack rates (a) and handling times (b) for bream foraging on *Daphnia* in laboratory tank experiments. Size-dependent attack rates are fitted to eq. (2) (see Material and methods) ( $R^2 = 0.83$ ), and the function fitted to the handling time data is  $y = \exp(5.52 - 1.34 \cdot \log(x))$ ,  $R^2 = 0.99$ .

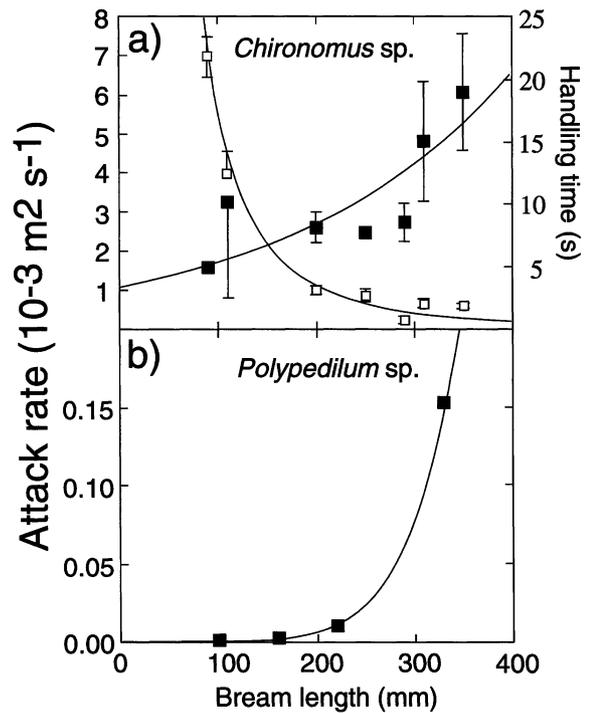


Fig. 2. Estimated ( $\pm 1$  SE) attack rates (closed symbols) and handling times (open symbols) on (a) visible chironomids (*Chironomus* sp.), and (b) attack rates on buried chironomids (*Polypedilum* sp.). Vertical bars are 1 SE. Functions fitted to the attack rate data are: (a)  $y = \exp(-6.83 + 0.0045x)$ ,  $R^2 = 0.59$ ; (b)  $y = \exp(-47.6 + 6.69 \log(x))$ ,  $R^2 = 1$ . Handling time function is  $y = \exp(13.2 - 2.27 \log(x))$ ,  $R^2 = 0.99$ .

### Changes in fish community composition

In 1992, the total fish biomass (wet weight) in L. Finjasjön was 300 t (95% C.I., 215–495; Persson 1997), corresponding to 273 kg ha<sup>-1</sup>. The fish community was dominated by bream and roach (*Rutilus rutilus*), constituting 51 and 27% of the total biomass, respectively (Fig. 5). Between Oct. 1992 and June 1994, a fish reduction program was carried out that removed 400 t. The biomanipulation was efficient in removing bream, which had a biomass in 1995 < 10% of that in 1992. Despite a considerable fish removal, total fish biomass in 1995 was only reduced by 50% compared to 1992. An increased recruitment of perch as a response to reduced competition caused a change in species composition from cyprinid (79% in 1992) to percid dominance (55% in 1995). Perch constituted only 4% of total fish biomass in 1992, but dominated fish biomass in 1995 (39% of total biomass). Piscivore biomass was not affected significantly, but due to the reduction in biomass of planktivores and benthivores, the fraction of the fish community being piscivorous was doubled in 1995 compared to 1992. Although total fish biomass was reduced by the fish removal, fish abundance (i.e. number of fish caught) was slightly higher (140%) in

1995 compared to 1992 due to a reduction in mean fish weight from 39 to 13 g wet weight.

### Predicted and observed diet

Prey value increased with increasing bream size for both *Daphnia* and visible chironomids (linear regression,  $p < 0.001$ ), but was higher for the latter (Fig. 4) when equally sized bream were compared. This suggests that visible chironomids were always more profitable than *Daphnia*. The prey value for visible chironomids was not determined for bream 50 and 70 mm because chironomids were only partially consumed. Extrapolating linear models of bream size and prey value suggests that optimal prey type switches from *Daphnia* to visible chironomids, at a bream length of 71 mm (Fig. 4), suggesting similar profitability of both prey types for the smallest size-class.

According to diet data from Lake Finjasjön 1992, only the largest ( $> 300$  mm) size-class was feeding on

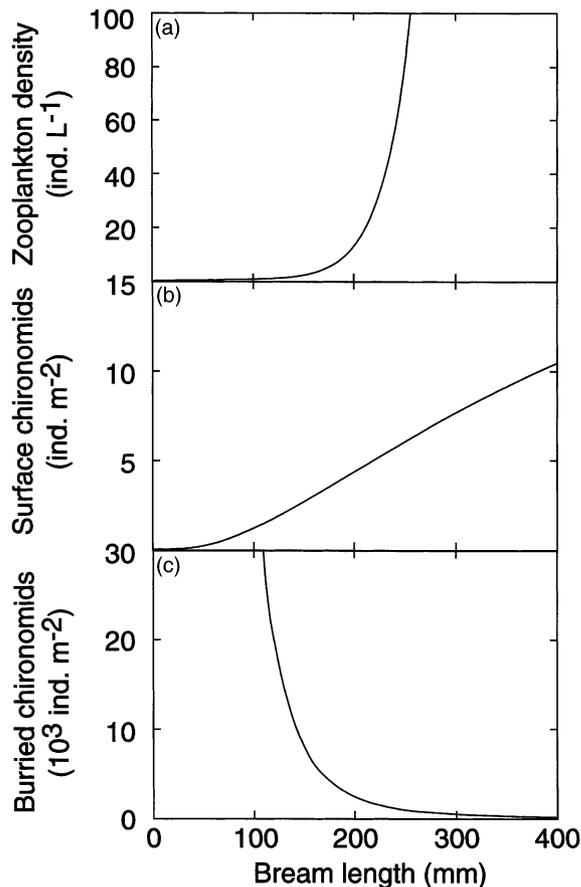


Fig. 3. Size-dependent minimum resource requirements (i.e. prey density when consumption rate  $\times$  conversion efficiency - metabolic rate = 0) of bream for three different prey types: (a) *Daphnia*, (b) visible chironomids, and (c) buried chironomids.

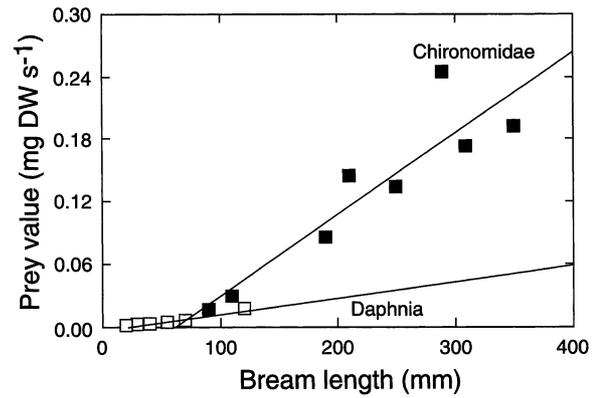


Fig. 4. Estimated prey values of pelagic (*Daphnia*) and benthic (*Chironomidae*) prey as a function of bream size. Prey value increased with increasing predator size, but was higher for benthic prey for predator sizes  $\geq 71$  mm. The data were fitted to linear models with slopes being 0.00016 and 0.0078 mg DW  $s^{-1}$   $mm^{-1}$ , and intercepts being 0.034 and 0.048 mg DW  $s^{-1}$  for *Daphnia* ( $R^2 = 0.93$ ) and *Chironomidae* ( $R^2 = 0.83$ ), respectively.

the most profitable prey (Fig. 6). The smallest size-class only fed on pelagic zooplankton, but a large part of the diet was composed of the large sized *Leptodora kindtii*, suggesting a profitable diet. For intermediate size-classes (80–300 mm), a disproportionate large part of the diet originated from small pelagic or benthic crustaceans, compared to the prediction. Consequently, it was predicted that these intermediate size-classes would be more likely to alter their diet when released from competition than the largest size-class. Estimates of minimum resource requirements showed that small bream were more competitive than large bream on zooplankton and, to a lesser extent, on visible chironomids. Conversely, large bream had a much higher competitive ability on buried chironomids compared to their smaller conspecifics. Consequently, we predicted that the probability of diet shift towards benthic prey following competitive release should be highest for the 200–300 mm size-class, followed by the 120–200 mm size-class, and the 80–120 mm size-class (Table 1).

The diet of bream in 1995, after the competitive release, largely followed the predictions (Fig. 6). Large bream ( $> 300$  mm) remained, as predicted, on a diet composed exclusively of chironomidae larvae Fig. 5. For smaller size-classes, the diet changed markedly between 1992 and 1995, from dominance of pelagic to benthic prey (Fig. 6). In 1995, benthic cladocerans were important prey for bream up to 200 mm and the fraction of chironomidae larvae in the diet increased with bream size, from 10% for bream  $< 80$  mm to 100% for bream  $> 200$  mm. This was completely in agreement with the predictions that the 200–300 mm size-class should be the most likely to alter its diet towards chironomidae larvae (Table 1). In 1995, pelagic prey were only important in the diet of the smallest

Table 1. Observed and predicted diet after competitive release in bream. Probability ranks are derived from size-dependent minimum resource requirement when feeding on pelagic and visible benthic prey.

Size-class	Observed diet	Predicted optimal diet	Probability rank of diet change	Observed diet after competitive release
<80	Z	Z/B	0	Z/B
80–120	Z	B	1	Z/B
120–200	Z/B	B	2	Z/B
200–300	Z(B)	B	3	B
>300	B	B	0	B

bream (<80 mm), the size-class for which the most profitable prey could not be determined (Fig. 5).

There was no relationship between mean cladoceran size in the diet and bream size, nor any significant difference between years although mean cladoceran size generally was slightly higher in 1995 compared to 1992 (ANOVA,  $p > 0.2$ ; Fig. 7). Chironomid size in the diet was positively related to bream size in both years (ANOVA,  $F = 18$ ,  $p < 0.001$ ); chironomids fed by the largest bream size were three times as long as those found in the diet of smaller size-classes (Fig. 7). However, there was no significant difference between years (ANOVA,  $p > 0.2$ ) with respect to chironomid size in the diet.

## Discussion

### Foraging capacity and competitive ability

Predator size affected foraging capacity, in terms of attack rates, both in the zooplanktivore and benthivore niche. The attack rate of bream feeding on zooplankton described a hump-shaped relationship with bream size, whereas the attack rate increased exponentially for bream feeding on chironomidae larvae. The parameter estimates are characteristics of foraging ability, useful for comparisons between species. The parameter values of planktivorous bream illustrate this. Both optimum size and maximum attack rate were lower in comparison with the planktivore specialist roach *Rutilus rutilus* (Hjelm 2000), but higher than the piscivore specialist pikeperch *Stizostedion lucioperca* (Persson and Brönmark unpubl.). In comparison with the ontogenetic generalist perch *Perca fluviatilis* (Wahlström et al. 2000), optimum size of planktivorous bream was slightly lower whereas maximum attack rate was almost twice as high. Hence, specialisation on one prey type seem to be on the expense of competitive ability in other feeding niches. The comparison with roach is particularly interesting because both roach and bream tend to dominate fish communities of highly productive lakes where the zooplankton resource is heavily exploited (Persson et al. 1991, Mooij et al. 1996). Based solely on foraging capacity derived from the experiments, bream should be competitively inferior com-

pared to roach in the planktivore niche. Maximum attack rate when feeding on zooplankton peaked at a size (67 mm) that is normally reached within one year in Lake Finjasjön, suggesting a narrow window of planktivory. However, bream has been shown to adopt a filter-feeding mode in situations when only small prey are available (Lammens 1985, Hoogenboezem et al. 1990, 1991). This feeding mode is passive in the sense that visual encounters are not necessary, and with the advantage that several prey can be captured and handled simultaneously. We did not observe filter-feeding in our experiments, and therefore the attack rate and handling time estimates are for particulate feeding bream. However, we acknowledge that the filter-feeding mode may sustain bream of intermediate size-classes in the absence of more profitable prey such as chirono-

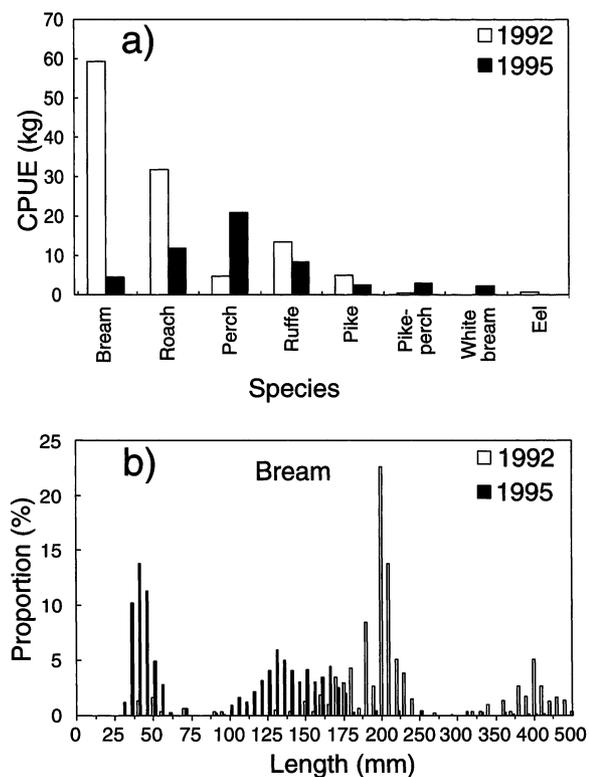


Fig. 5. (a) Fish community composition and (b) bream length frequency distribution before (1992) and after (1995) biomanipulation.

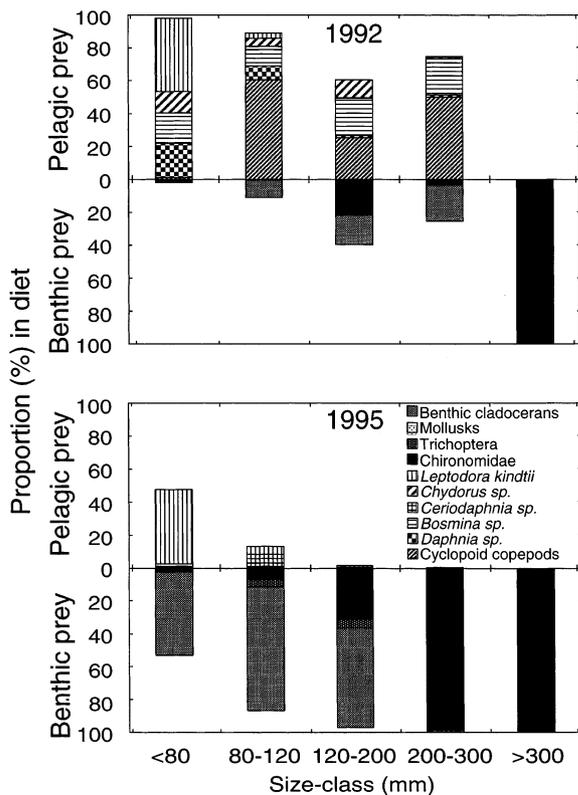


Fig. 6. Diets (% of biomass) of bream before (1992) and after (1995) biomanipulation. Diets are expressed as dry-mass based average proportions during summer. Proportions above zero line are pelagic prey and those below benthic prey.

mids and large zooplankton. It is also notable that filter-feeding increase the profitability of zooplankton if handling time per prey item is lowered compared to particulate feeding.

The attack rate for benthivorous feeding bream increased exponentially with bream size and showed no indications to level off at larger sizes. This is in agreement with previous studies showing that large bream penetrate deeper, and take more voluminous samples of sediment than small bream (Braband 1984, Lammens et al. 1986). One obvious explanation to the absence of a hump-shaped attack rate relationship for benthivorous bream is that the attack rate peak at larger sizes than used in our experiments. Bream may reach a large size (800 mm), and individuals of approximately 400 mm TL were common in Lake Finjasjön in 1992. It may therefore be possible, although not necessary, that a peak in attack rate could have been identified if larger bream had been used in the experiments.

A striking result was the large difference in attack rate between bream foraging on visual and buried benthic prey. Lammens et al. (1986) showed that the vertical position of prey in the sediment strongly influence foraging efficiency, which makes quantitative extrapolations of laboratory results to field conditions

hazardous. Still, the predator size-dependence of the attack rate showed the same general pattern independent of prey position, suggesting that qualitative comparisons are possible between treatments in a standardized experimental set-up. We conclude that foraging capacity increased with bream size and that this pattern was accentuated when prey were buried in the sediment.

The predicted minimum resource requirement of different prey types could be used to compare the competitive ability of different size-classes. Our calculations suggests that small bream are superior competitors on zooplankton and visible macroinvertebrates, whereas large bream are superior competitors on buried macroinvertebrates. This leaves intermediate sized bream sandwiched in between, being more competitive than large bream on zooplankton and to a lesser extent on visible macroinvertebrates, but less competitive than small bream on zooplankton and less competitive than large bream on buried macroinvertebrates.

The strong depth- and substrate-dependence of benthivorous feeding efficiency (Lammens et al. 1986) makes comparisons between different studies difficult. Still, Persson (1987) reported on the feeding of juvenile perch on chironomids buried in gravel, i.e. in an experimental setting resembling ours. The attack rates of 1 + and 2 + perch were of the same magnitude as our data on intermediate sized bream foraging on *Polypedilum*.

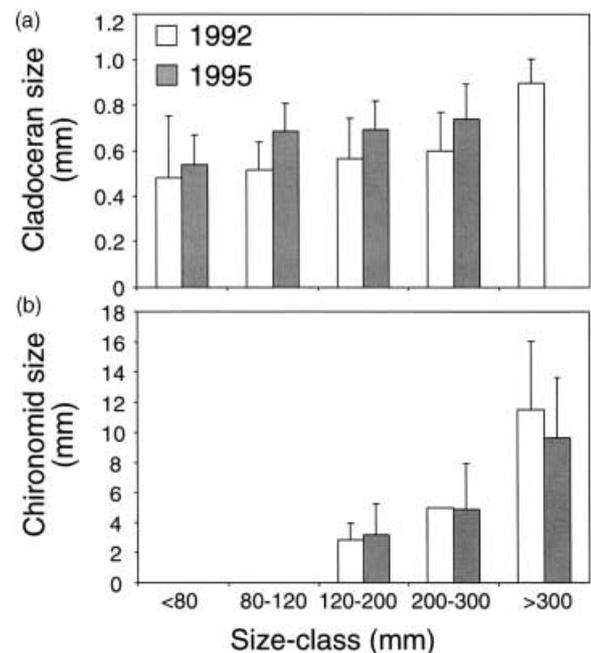


Fig. 7. Prey size (+ 1 SE) in diet of bream in Lake Finjasjön before (open bars) and after (filled bars) biomanipulation. Prey size is given as mean (a) cladoceran and (b) chironomids length. We did not compute standard errors between individual for bream < 120 mm due to low sample size of measurable chironomids.

This supports previous studies showing that juvenile perch and intermediate sized bream are equivalent competitors on buried macroinvertebrates in open habitats (Diehl 1988). The fact that larger perch generally become piscivorous, whereas larger bream become benthivorous suggests that perch foraging capacity on buried prey does not increase with fish size at the same rate as bream. A possible explanation to this is the ability of large bream to penetrate deeper into the sediment compared to other species (Lammens et al. 1986). However, this prediction still remains to be tested.

Our data suggest that intermediate sized bream may suffer from strong intra- and interspecific competition, especially if visible macroinvertebrates are not available as would be the case if the bream population is large and dominated by large individuals. However, intermediate sized bream has two advantages not treated in our study. First, a filter-feeding strategy of intermediate sized bream may be an advantage over roach and small bream, which both have higher particulate foraging capacities on zooplankton. Secondly, the larger size of intermediate sized bream renders lower vulnerability to predation in comparison with small bream and roach and, further, a deeper body shape reduce vulnerability of bream in comparison to roach of similar length (Nilsson and Brönmark 2000). Indeed, Mooij et al. (1996) showed that recruitment of adult bream could be highly variable between years depending on the growth rate in the planktivore niche. Hence, the rate by which bream grow through the window of predation susceptibility is a strong determinant of planktivore survival and, ultimately, population dynamics.

### Diet in the field

The classical tests of optimal foraging theory predict foraging behaviour in natural environments from estimates of habitat profitability and encounter rates. We have used a somewhat simplified approach since the lack of data on resource densities prevented a quantitative estimation of habitat profitability. Still, prey value estimates and estimates of minimum resource requirement (MRR) derived from laboratory studies qualitatively predicted diet shifts in the field. Accordingly, the results from the field study showed a considerable increase in the use of benthic resources by intermediate size-classes, whereas the largest size-class remained on a benthic diet after the biomanipulation.

The more or less complete shift to benthic resources by intermediate size-classes was only partly a result of a higher inclusion of large benthic invertebrates such as chironomids in the diet. The remaining part was due to a higher proportion of benthic cladocerans, mainly *Alona*, which were in the same size-range as the pelagic cladocerans found in the diet 1992. Despite the fact that

both zooplankton biomass and the fraction of *Daphnia* increased, benthic cladocerans replaced zooplankton in the diet. This suggests that the profitability of benthic cladocerans was higher and the encounter rate high enough to exclude zooplankton from the diet when resource competition was relaxed. Unfortunately, the sampling program was not designed to appropriately quantify benthic cladocerans and no attack rate estimates are available. However, it is questionable if profitability was higher for benthic than pelagic cladocerans given their similar size. Below we will therefore treat the possibility that the diet shift was a result of a habitat shift.

Within the context of optimal foraging theory, diet shifts may be explained by food and/or habitat preferences. Each of these possibilities depends on the scale for which a particular problem is applied. The traditional way is to view this as a sequence of decisions, where a forager first select habitat and then select food items within that habitat. This infers that there exist costs, such as learning and travelling, related to habitat switching (Hughes 1979, Werner et al. 1981). It is possible that the benthic habitat, including both benthic cladocerans and insect larvae, became more profitable than the pelagic habitat after the biomanipulation. Thus, while searching for the most profitable prey, chironomids, benthic cladocerans were encountered and included in the diet as a complement. If so, benthic cladocerans constituted a large part of the diet in intermediate sized bream, only if encounter rate with chironomids was enough for bream to go benthic, but below a threshold value. Laboratory estimates of attack rates on chironomids increased with increasing bream size, suggesting that this threshold decreased with bream size. This explains why 200–300 mm bream completely and 80–200 mm bream only partly shifted to chironomids when released from competition.

The competitive interaction was assumed to be density-dependent such that competitive release would occur if planktivorous and benthivorous fish were reduced in abundance. At first, it may seem fair to assume interdependence between resource availability and predator density. A high predator density generally exposes a prey population to higher mortality rate, and results in prey being less available, than do a low predator density. However, it may be hazardous to view predator and prey pairs in isolation from the surrounding environment because the structure and the function of the environment may be dependent on the predator-prey interaction, and not only the other way around. The available evidence for interdependence between resource availability and predator density is that the availability of the zooplankton resource certainly increased as expected after biomanipulation (Hansson et al. 1998), despite that small zooplanktivorous fish increased (Persson and Hansson 1999). Total biomass of zooplankton increased and the proportion

*Daphnia* increased from 35 to 65% of the total zooplankton community. However, due to lack of data on benthic resources, it was not possible to evaluate if the biomanipulation caused a general increase in resource density.

We therefore have to consider that a change in diet may be related to a number of different factors besides resource availability, such as changes in habitat availability, altered behaviour related to predation risk or interference competition. All these factors may have been affected by the biomanipulation in Lake Finjasjön, which clearly altered the function of the ecosystem. Phytoplankton biomass decreased, possibly due to both increased grazing and decreased nutrient availability (Persson 1997, Hansson et al. 1998), and blue-green algae that previously dominated the phytoplankton community almost disappeared. As a consequence, the summer average in secchi depth increased dramatically from about 0.5 m to 1.5 m. This increase was accompanied by colonization of submerged macrophytes, that caused the littoral zone to expand from being essentially absent to cover about 25% of the lake area (Strand 1999). This point to two possible outcomes related to bream foraging behaviour. First, an increase in size of littoral habitats may directly cause a shift in the diet towards more benthic-related prey. Second, an increase in transparency may increase predation risk from piscivorous fish and alter the behaviour, such that more time is spent in vegetation habitats. This may indirectly, and independent of resource availability, cause a change in the diet towards benthic prey in. Previous studies have shown that habitat shift may occur as an effect of altered risk of predation (Lima and Dill 1990, Brabrand and Faafeng 1993). Werner et al. (1983a) showed that when predation risk was increased, forage fish spent more time in refuges such as vegetation stands, and that this change in behaviour was reflected in the diet. The combined effects of increased predation risk and increased availability of refuge habitats may cause small bream that are susceptible to predation to hide in the littoral zone. However, bream is a poor predator in structurally complex habitats (Diehl 1988), especially compared to perch, which were abundant in Lake Finjasjön 1995. Although the available data on habitat use in bream is sparse, there is no indication of a change in the spatial distribution of bream between 1992 and 1995 (A. Persson unpubl.). In fact, the fraction of bream caught at 2 m depth, i.e. potentially vegetated areas, were even lower in 1995 compared to 1992 (2 and 12% of total bream numbers, respectively) irrespective of bream size, indicating that bream preferred open water. Hence, it seem more likely that the observed diet shifts were related to shifts from pelagic to profundal feeding, which in shallow lakes as Finjasjön involves a small adjustment in vertical position, rather than increased use of littoral habitats. In intermediate sized bream this may have been caused by increased availability of prey on the sediment surface.

In conclusion, estimates of size-dependent foraging capacity in planktivorous and benthivorous feeding bream were used to provide information on size-specific competitive ability. These estimates suggest that intermediately sized bream should experience low competitive ability in comparison to other size-classes, because small and large bream showed better performances on zooplankton and invertebrates buried in the sediment, respectively. Foraging capacities qualitatively predicted diet shifts in a the field. Size-classes feeding on an optimal diet before competitive release did not change diet, whereas profound diet shifts were recorded for size-classes showing a suboptimal diet prior to competitive release. In our view, this point convincingly to the advantage of linking a mechanistic understanding derived under simplified conditions, with patterns obtained from the complexity of a natural community.

*Acknowledgements* – We are thankful to Jan Johansson and Henrik Linge for their help in the laboratory, and Anders Eklöv, Marie Eriksson, Niklas Nilsson and Pia Romare for assistance in the field. The city of Hässleholm kindly helped in solving logistic problems. Two anonymous referees provided valuable comments on a previous version of this paper. This study was supported by grants from the European Union and the Swedish Council for Forestry and Agriculture

## References

- Bergman, E., Hansson, L.-A., Persson, A. et al. 1999. Synthesis of theoretical and empirical experiences from nutrient and cyprinid reductions in Lake Ringsjön. – *Hydrobiologia* 404: 131–144.
- Bottrell, H. H., Duncan, A., Gliwicz, Z. M. et al. 1976. A review of some problems in zooplankton production studies. – *Norw. J. Zool.* 24: 419–456.
- Brabrand, Å. 1984. Microhabitat segregation between bream (*Abramis brama* L.) and white bream (*Blicca bjoerkna* L.) in a mesotrophic lake, SE Norway. – *Pol. Arch. Hydrobiol.* 31: 99–108.
- Brabrand, Å. and Faafeng, B. 1993. Habitat shift in roach (*Rutilus rutilus*) induced by pikeperch (*Stizostedion lucioperca*) introduction: predation risk versus pelagic behaviour. – *Oecologia* 95: 38–46.
- Brooks, J. L. and Dodson, S. I. 1965. Predation, body size, and composition of plankton. – *Science* 150: 28–35.
- Byström, P. and García-Berthou, E. 1999. Density dependent growth and stage-specific competitive interactions in young fish. – *Oikos* 86: 217–232.
- Claessen, D., De Roos, A. M. and Persson, L. 2000. Dwarfs and giants – cannibalism and competition in size-structured populations. – *Am. Nat.* 155: 219–237.
- Diehl, S. 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. – *Oikos* 53: 207–214.
- Hamrin, S. F. and Persson, L. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. – *Oikos* 47: 223–232.
- Hansson, L.-A., Annadotter, H., Bergman, E. et al. 1998. Biomanipulation as an application of food-chain theory: constraints, synthesis, and recommendations for temperate lakes. – *Ecosystems* 1: 558–574.
- Hjelm, J. 2000. Size-dependent performance and ontogenetic niche shifts. – Ph.D. thesis. Umeå Univ., Sweden.

- Hoogenboezem, W., Sibbing, F. A., Osse, J. W. M. et al. 1990. X-ray measurements of gill-arch movements in filterfeeding bream (*Abramis brama* (Cyprinidae)). – *J. Fish Biol.* 36: 47–58.
- Hoogenboezem, W., van den Boogart, J. G. M., Sibbing, F. A. et al. 1991. A new model of particle retention and branchial sieve adjustment in filter-feeding bream (*Abramis brama*, Cyprinidae). – *Can. J. Fish. Aquat. Sci.* 48: 7–18.
- Hughes, R. N. 1979. Optimal diets under the energy maximisation premise: the effects of recognition time and learning. – *Am. Nat.* 113: 209–221.
- Lammens, E. H. R. R. 1985. Resource partitioning and niche shifts of bream (*Abramis brama*) and eel (*Anguilla anguilla*) mediated by predation of smelt (*Osmerus eperlanus*) on *Daphnia hyalina*. – *Can. J. Fish. Aquat. Sci.* 42: 1342–1351.
- Lammens, E. H. R. R., Geursen, J. and McGillivray, J. 1986. Diet shifts, feeding efficiency and coexistence of bream (*Abramis brama*), roach (*Rutilus rutilus*) and white bream (*Blicca björkna*) in hypertrophic lakes. – *Proc. V Congr. Eur. Ichthyolog. Stockholm.*
- Lessmark, O. 1983. Competition between perch and roach in south Swedish lakes. – Ph.D. thesis, Lund Univ.
- Lima, S. L. and Dill, L. M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. – *Can. J. Zool.* 68: 619–640.
- Lundberg, S. and Persson, L. 1993. Optimal body size and resource density. – *J. Theor. Biol.* 164: 163–180.
- Meijer, M.-L., de Haan, M. W., Breukelaar, A. W. and Buiteveld, H. 1990. Is reduction of the benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? – *Hydrobiologia* 200/201: 303–315.
- Mittelbach, G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. – *Ecology* 62: 1370–1386.
- Mooij, W. M., van Densen, W. L. T. and Lammens, E. H. R. R. 1996. Formation of year-class strength in the bream population in the shallow eutrophic Lake Tjeukemeer. – *J. Fish Biol.* 48: 30–39.
- Nilsson, P. A. and Brönmark, C. 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. – *Oikos* 88: 539–546.
- Nonacs, P. 1993. Is satisficing an alternative to optimal foraging theory? – *Oikos* 67: 371–375.
- Persson, L. 1987. The effects of resource availability and distribution on size class interactions in perch, *Perca fluviatilis*. – *Oikos* 48: 148–160.
- Persson, L. 1988. Asymmetries in predatory and competitive interactions in fish populations. – In: Ebenman, B. and Persson, L. (eds), *Size-structured populations: ecology and evolution*. Springer, pp. 203–218.
- Persson, L. 1990. Predicting ontogenetic niche shifts in the field: What can be gained by foraging theory? – In: Hughes, R. N. (ed.), *Behavioural mechanisms of food selection*. Springer, pp. 303–321.
- Persson, A. 1997. Phosphorus release by fish in relation to external and internal load in a eutrophic lake. – *Limnol. Oceanogr.* 42: 577–583.
- Persson, L. and Greenberg, L. A. 1990a. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)-roach (*Rutilus rutilus*) interaction. – *Ecology* 71: 44–56.
- Persson, L. and Greenberg, L. A. 1990b. Optimal foraging and habitat shift in perch (*Perca fluviatilis*) in a resource gradient. – *Ecology* 71: 1699–1713.
- Persson, A. and Hansson, L. -A. 1999. Diet shift following competitive release. – *Can. J. Fish. Aquat. Sci.* 56: 70–78.
- Persson, L., Diehl, S., Johansson, L. et al. 1991. Shifts in fish communities along the productivity gradient in temperate lakes – patterns and the importance of size-structured interactions. – *J. Fish Biol.* 38: 281–293.
- Persson, L., Leonardsson, K., de Roos, A. M. et al. 1998. Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. – *Theor. Pop. Biol.* 54: 270–293.
- Peters, R. H. 1983. *The ecological implications of body size*. – Cambridge Univ. Press.
- Pierce, G. J. and Ollason, J. G. 1987. Eight reasons why optimal foraging theory is a complete waste of time. – *Oikos* 49: 111–118.
- Sih, A. 1993. Effects of ecological interactions on forager diets: competition, predation risk, parasitism and prey behaviour. – In: Hughes, R. N. (ed.), *Diet selection. An interdisciplinary approach to foraging behaviour*. Blackwell Scientific Publications.
- Stearns, S. C. and Schmid-Hempel, P. 1987. Evolutionary insights should not be wasted. – *Oikos* 49: 118–125.
- Stein, R. A., Threlkeld, S. T., Sandgren, C. D. et al. 1988. Size-structured interactions in lake communities. – In: Carpenter, S. R. (ed.), *Complex interactions in lake communities*. Springer.
- Stephen, D. and Krebs, J. R. 1986. *Foraging theory*. – Princeton Univ. Press.
- Strand, J. A. 1999. Submerged macrophytes in shallow eutrophic lakes – regulating factors and ecosystem effects. – Ph.D. thesis. Lund Univ., Sweden.
- van Densen, W. L. T., Ligtoet, W. and Roozen, R. W. M. 1996. Intra-cohort variation in the individual size of juvenile pikeperch, *Stizostedion lucioperca*, and perch, *Perca fluviatilis*, in relation to the size spectrum of their food items. – *Ann. Zool. Fenn.* 33: 495–506.
- Wahlström, E., Persson, L., Diehl, S. and Byström, P. 2000. Size-dependent foraging efficiency, cannibalism and zooplankton community structure. – *Oecologia* 123: 138–148.
- Ward, D. 1993. Foraging theory like all other fields of science, needs multiple working hypotheses. – *Oikos* 67: 376–378.
- Werner, E. E. 1994. Ontogenetic scaling of competitive relations: size-dependent effects and responses in two anuran larvae. – *Ecology* 75: 197–231.
- Werner, E. E. and Gilliam, J. F. 1984. The ontogenetic niche and species interactions in size-structured populations. – *Ann. Rev. Ecol. Syst.* 15: 393–425.
- Werner, E. E. and Hall, D. J. 1979. Foraging efficiency and habitat switching in competing sunfishes. – *Ecology* 60: 256–264.
- Werner, E. E. and Mittelbach, G. G. 1981. Field tests of diet choice and habitat switching. – *Am. Zool.* 21: 813–829.
- Werner, E. E., Mittelbach, G. G. and Hall, D. J. 1981. The role of foraging profitability in habitat use by the bluegill sunfish. – *Ecology* 62: 116–125.
- Werner, E. E., Gilliam, J. F., Hall, D. J. and Mittelbach, G. G. 1983a. An experimental test of the effects of predation risk on habitat use in fish. – *Ecology* 64: 1540–1548.
- Werner, E. E., Mittelbach, G. G., Hall, D. J. and Gilliam, J. F. 1983b. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. – *Ecology* 64: 1525–1539.