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Vertical distribution of benthic community responses to fish predators, and effects on algae and suspended material

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Abstract

The vertical positioning of benthic invertebrates should be a trade-off between the risky, but productive, sediment surface and the safer, but physiologically harsher, conditions deeper down in the sediment. This is because the foraging efficiency of benthic fish decreases with sediment depth, whereas the sediment surface is generally better oxygenated and has a higher resource quality than lower layers. We studied how two benthic fish predators, bream (*Abramis brama*) and ruffe (*Gymnocephalus cernuus*), affected the community composition and vertical distribution of benthos, and their indirect effects on algae and suspended material, in field enclosures. Whereas bream had significant effects on the density, composition and distribution of the benthos, ruffe had no such effects. The total benthos biomass in bream treatments was an-order of magnitude lower in the upper sediment layer (0–1 cm) and three times lower in the middle layer (1–3 cm) than in the controls, whereas there were no significant effects in the deepest layer (3–10 cm). Bivalves persisted in the deepest layer although their density was reduced in shallow sediment, whereas gastropods faced the risk of local extinction in the presence of bream. As indirect effects, small-bodied cladocerans, phytoplankton, periphyton and both organic and inorganic suspended material were higher in the bream treatments. We conclude that the impact of bream diminished substantially with increasing sediment depth, enabling invertebrates to survive in the sediment and to persist in the presence of bream. However, there were no indications of any group adjusting their vertical position behaviourally as a response to predation threat.

Introduction

The interplay between the spatial environment and species interactions has received the attention of ecologists for decades (Levin 1992). Habitat heterogeneity has been shown to have a stabilizing impact on community structure and on population dynamics (Fryxell and Lundberg 1988) by promoting coexistence (Holt 1984) and preventing overexploitation and unstable dynamics (Jansen 1995; Scheffer and Boer 1995; Abrams and Walters 1996). In aquatic environments, strong interactions often observed between species are, indeed, derived from homogeneous pelagic communities (Brooks and Dodson 1965; Kerfoot and Sih 1987), whereas it has been much harder to detect strong interactions in environments that contain physical structures, such as the littoral zone (Hanson and Legget 1986; Persson and Greenberg 1990; Diehl 1992) or on soft bottoms (Wilson 1991; Thrush 1999).

The inconsistency in the results from benthic communities has inspired a more detailed analysis of the interactions between fish and benthic macroinvertebrates. For example, foraging plasticity allows fish to switch from benthivory to zooplanktivory (Lammens et al. 1985; Persson and Hansson 1999; Persson and Brönmark 2002) or fish (Schindler et al. 1997). Furthermore, omnivory is common in benthic communities, which may cause compensatory responses of prey along density gradients of top predators, for example, when a top predator feeds on both prey and intermediate predators (Diehl 1995). Moreover, Blumenshine et al. (2000) argued that the strength of fish effects was more correlated with fish consumption rates than traditional, static measures such as fish biomass. Altogether, these studies have revealed that strong interactions are, indeed, possible in benthic communities, but the effects are often more complex than in pelagic communities in which they are more straight forward.

The physical properties of the environment may cause inconsistent results if the spatial distribution of predator effects is asymmetric. Hence, the strength of an interaction depends on where you look for it, generally being weak in habitats providing shelter from predators and strong in open habitats (Savino and Stein 1982; Gilinsky 1984; Winfield 1986; Diehl 1992; Diehl and Eklöv 1995). Spatial heterogeneity is commonly incorporated into predator–prey models by dividing the environment into different habitats, and describing predator and prey performance with a habitat-specific set of parameters (Scheffer and Boer 1995; Fryxell and Lundberg 1998). Although this approach is simple and appealing, in reality it may be difficult to separate distinct types of habitats that represent different search efficiencies of the predator. For example, the vertical structure of the environment at the sediment-water interface only shifts gradually from one type to another. Hence, if a predator is searching along such a gradient, prey availability may change independent of prey density (Lammens et al. 1986; Haddon et al. 1987; Duncan and Szelistowski 1998; Gawlik 2002; Persson and Brönmark 2002).

In this paper, we study how benthivorous fishes affect the vertical distribution and community composition of invertebrates in the sediment. At the sediment-water interface biological, chemical and physical conditions change gradually within the spatial scale of foraging predators (Ritchie 1998; Thrush 1999). Laboratory studies have shown that predation risk for prey on the sediment surface may be much higher than for prey inhabiting the sediment only a few centimetres deeper (Lammens et al. 1986; Persson and Brönmark 2002). In contrast, the environment for invertebrates becomes harsher with increasing sediment depth due to lower oxygen concentration and poorer resource quality (Heinis and Crommentuijn 1992). Despite this, invertebrates in sediments are typically sampled with techniques that embrace the whole gradient within a single sample (Thrush 1991; Lee 1996). Moreover, there are no freshwater studies on the vertical pattern in the response of the benthic community to fish predators (but see Kornijów 1997, for an example of a generalist predator). We refined sampling resolution by separating different vertical strata, which represent regions of different vulnerability to predators (Bund and Groenendijk 1994). At this finer, vertical resolution we could infer, with greater precision and predictability than previously, how the abundance and distribution of different invertebrate groups responded to the presence of fish predators.

The predators in our study were two benthivorous fishes common in Europe, bream (*Abramis brema*) and ruffe (*Gymnocephalus cernuus*). Bream has a mouth that is adapted to penetrating deep into the sediment, and it forages by taking mouthful of sediment (Lammens et al. 1986; Persson and Brönmark 2002). Conversely, ruffe actively search only close to the sediment surface and attacks only the animals detected (Bergman 1990). Hence, observations of foraging behaviour suggest that bream and ruffe may have fundamentally different effects on the benthos. We hypothesized that the effects of benthic fish predators in general would diminish with increasing sediment depth, but that effects of bream would be detected deeper in the sediment than effects of ruffe. This would in turn have implications for community composition, such that prey that live deep in the sediment would be able to coexist with benthivorous fish, especially with ruffe, whereas prey associated with the sediment surface would risk local extinction, especially if both ruffe and bream are present.

Material and methods

We performed a field experiment using the presence or absence of ruffe (*Gymnocephalus cernuus*) and bream (*Abramis brama*) as treatment factors in a factorial design. The four treatments (fishless control, ruffe, bream, and ruffe + bream) were replicated four times and were assigned randomly to sixteen enclosures (3 × 4 m) that were built in May 2000 in a shallow pond (30 × 80 m, depth 0.8 m) close to Vomb in the south of Sweden. The bottom of the pond consisted of sand covered with a ~10 cm deep mud layer. At the start of the experiment, there were no macrophytes in the enclosures and only a few plants of *Potamogeton pectinatus* developed during the experiment. The enclosures were made of plastic walls inserted 20 cm into the sediment and supported by wooden frames. Each enclosure had a "window" (20 × 20 cm) of 2 mm mesh to allow equalization of water levels. Between 1 June and 15 June, the enclosures were stocked with ruffe caught in Heljasjön (a lake connected to the pond by a short ditch) using gill nets that were checked every hour. On each stocking occasion, all ruffe enclosures received the same amount of fish. During the stocking phase, enclosures were carefully checked on alternate days and any dead fish were replaced. The first stocking of ruffe (1 June) was largely unsuccessful due to extremely high temperature and was followed by a second one on the 7th of June when great care was taken to minimise damage to fish. Between 7th and 15th June, minor complementary stockings were performed, replacing less than 10% of the fish from the second stocking.

Bream occur naturally in the pond, but due to difficulties in catching them there, all bream were caught in Snogeholmssjön by angling. All bream were stocked on 15 June. Ruffe and ruffe + bream enclosures were stocked with 11–12 ruffe individuals (total mass 60 ± 5 g), and bream and ruffe + bream enclosures with one bream (725 ± 95 g). In addition, about 30 perch *Perca fluviatilis* larvae from the pond were stocked in each enclosure to further increase the likelihood that both ruffe and bream would feed on the benthos.

The biomass relationship between ruffe and bream is close to the relationship found in gill net surveys of south Swedish lakes (ruffe mass:bream mass = 0.10, $n = 23$, A. Persson unpublished data), and the fish densities are within the range found in shallow, eutrophic lakes (Persson et al. 1991; Persson 1997), although they are in the upper end of this range. Bream are planktivorous up to a total length of 10-30 cm (Lammens et al. 1986; Persson and Hansson 1999). Since the purpose was to get a mechanistic understanding of the vertical distribution of benthic fish effects on invertebrates, we chose bream of ca. 40 cm length to ensure that they were feeding on benthos. Because this resulted in a high mass, the size of bream effects may be overestimated and care should be taken for quantitative extrapolations to natural conditions. However, to obtain a mechanistic understanding of the vertical distribution of the effects, which is the focus here, the design is appropriate.

The experiment was terminated on 15th August, i.e., two months after the start, and remaining fish were recaptured by electrofishing. All bream survived and individual biomass increased by 25 ± 48 g (mean ±1 SD) during the experiment. No individual lost more than 25 g biomass (or 4%), which is within the measurement error for the scale used. The total biomass of ruffe in each enclosure decreased by 21 ± 16 g due to the unexplained loss of 50% of the individuals in both ruffe treatments (possibly due to unsuccessful recapture). Final total mass of perch at the end of the experiment was 14 ± 16 g, with an average individual mass of 0.62 ± 0.41 g.

Benthic invertebrates were sampled at both the beginning and at the end of the experiment using a transparent Plexiglas tube (∅45 mm) to collect intact cores of sediment. Five such cores were collected in each enclosure, and immediately sliced in the field to separate three vertical strata; 0–1, 1–3 and 3–10 cm sediment depth (Bund and Groenendijk 1994), which were then preserved in 70% alcohol for analysis later. The samples were stained with Rose Bengal and sieved through a 0.3 mm net. Invertebrates were identified, counted and measured to the nearest 0.1 mm. Lengths were transformed to dry mass using regressions obtained from earlier studies in the same system (A. Persson unpublished data). Invertebrates were divided into seven categories to distinguish between animals that differ with respect to availability to benthivores; (1) predators, (2) Diptera, (3) ephemeropterans, (4) gastropods, (5) bivalves, (6) cladocerans and (7) copepods. Predators were represented in the samples by *Sialis lutaria* (max. 20 mm), *Herpobdella* (max. 50 mm) and coleopteran larvae of the family *Ilybius*, which are all aggressive searching predators. Diptera were mainly represented by the subfamily Chironominae (ca. 1 cm long): red chironomid larvae (mainly collectors). However, the category also included the subfamilies Orthocladinae (grazers or collectors) and Tanypodinae (mainly predators), as well as biting midges Ceratopoginidae (mostly predators). Ephemeropterans were represented in the sediment by *Caenis* (max. 6 mm), which feeds on detritus at the sediment surface, *Lymnaea peregra* (max. 20 mm), a snail, common in most eutrophic waters was the dominant species among gastropods; they scrape epiphytic algae. Bivalves were dominated by *Pisidium sp.* (max. 10 mm), which is a mussel that lives at or just below the sediment surface and filters detritus and planktonic material. The recorded cladocerans (*Pleuroxus, Alona* and *Ilyocryptos*; max. 5 mm) and copepods (*Cyclops* sp.; max. 2 mm) have several species, which feed on small detritus particles and planktonic organisms within and at the sediment surface. Hence, the categories differed with respect to their spatial preferences, feeding behaviour and size.

Our primary interest was in treatment effects on benthic invertebrates, but we also sampled water at the beginning and at the end of the experiment to elucidate indirect treatment effects on algae, representing a food resource for grazing invertebrates, and suspended material, representing a measure of sediment disturbance by resuspension. Water was sampled with a plastic tube (∅70 mm) that integrates water from the surface to the bottom. Phytoplankton was filtered on a GF/C filter and frozen for later extraction in ethanol for chlorophyll determination (Jespersen and Christoffersen 1987). Plastic strips (1.5 × 80 cm) were placed in each enclosure at the beginning of the experiment. At the end of experiment, periphyton were brushed of the strips and suspended in water. A subsample was filtered on GF/C filters and treated in the same way as phytoplankton samples. The concentration of organic and inorganic matter in the water was analysed by filtering water on to preweighed and precombusted GF/C filters. The filters were weighed after drying for 24 h at 60 °C, then ashed for 4 h at 550 °C and weighed again. Organic matter was defined as the mass loss after ashing, and inorganic matter was defined as the mass remaining on ashing.

Statistical analyses were performed on mean values from each enclosure using data from both the start and the end of the experiment. Biomass data were $\log(x)$ or $\log(x+1)$ transformed before analysis to normalise distributions and stabilise variances. First, we used multivariate analysis of variance (MANOVA), with all invertebrate groups as dependent variables, to test for overall treatment effects on invertebrate biomass at the end of the experiment. In the MANOVA we used the total biomass of benthic invertebrates in all layers. To interpret the MANOVA, we applied univariate ANOVAs to test for treatment effects on each invertebrate group separately, and on the total biomass of all layers. Because the study was focused on the vertical distribution of treatment effects, we continued the analysis by using a repeated measure ANOVA design, with biomass in each layer as a repeated measure. However, the top or bottom layers were excluded from the analysis in the cases of predators and gastropods, respectively, due to zero abundance in these layers. Invertebrate density was expressed on a volumetric basis, which facilitates comparing different sediment layers. Because there were no significant treatment effects on invertebrates at the start of the experiment, either when applying MANOVA with all invertebrate groups as dependent variables ($p > 0.2$) or when applying univariate ANOVAs on each invertebrate group separately ($p > 0.05$), the differences at the end of the experiment between enclosures assigned to different treatments were assumed to reflect the effects of the introduced fish.

Due to the variable final biomass of perch, we also tested if perch affected the biomass of invertebrates using linear regression between invertebrate biomass and final perch mass. We found no significant effects on any invertebrate group ($p > 0.05$). Finally, we used a MANOVA, with phytoplankton and periphyton biomass, particulate organic matter and particulate inorganic matter as dependent variables, followed by univariate ANOVAs on each response variable to test for treatment effects on algae and suspended particulate matter.

Results

Invertebrate biomass

Bream had significant effects on density of benthic invertebrates (MANOVA, $F_{7,6} = 32.5, p < 0.001$, Figure 1), whereas ruffe exhibited no such effects. Bream also affected the composition of the benthos: at the end of the experiment, biomass of both mussels and gastropods was significantly larger and dominated the invertebrate community in enclosures without bream (Table 1, Figure 2). In contrast, the biomass of cladocerans was significantly higher and their densities dominated the invertebrate community in bream enclosures (Table 1, Figure 2). Ephemeropterans and predators both made up significant parts of the community in some enclosures. Ephemeropterans did not respond to the treatments, whereas there was a significant negative effect of bream on predatory invertebrates (Table 1). Diptera and copepods were abundant but, due to their small body size, they contributed significantly to the total biomass only if the other groups were reduced. No overall treatment effects were observed for any of these two groups (Table 1). However, Diptera biomass was lower at the end of the experiment compared with starting conditions due mainly to a decrease in both average length (from 3.8 to 2.2 mm) and abundance (from 10000 to 6000 ind. m^{-2}) of chironomids.

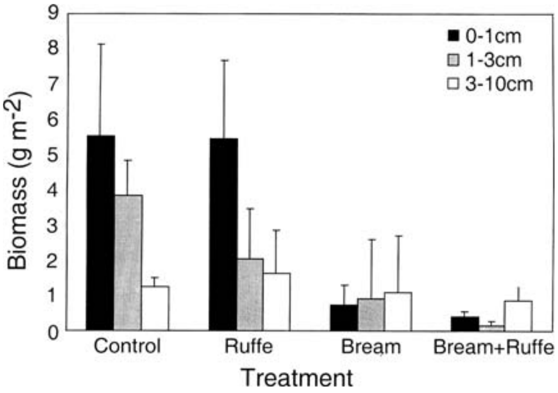

Figure 1. Total biomass (gm^{-2}, mean ± 1 SE, $n = 4$) of invertebrates at the end of the experiment in different sediment layers in control (C), ruffe (R), bream (B) and ruffe + bream (R + B) enclosures.

Vertical distribution

Invertebrate biomass was significantly different in different layers irrespective of invertebrate group and treatment (Table 2). In general, invertebrate biomass was higher at the sediment surface, especially in treatments without bream (Figure 1). Compared with the control and ruffe alone treatments, total biomass of invertebrates in bream treatments was an order of magnitude lower in the top sediment layer and three times lower in the middle layer, but no treatment effects were observed in the bottom layer (Figure 1). Invertebrate predators were almost absent in the top layer but dominated the benthic community in the deepest sediment layer. There was a significant negative effect of bream on predators, mostly due to a negative effect in the middle layer (Figure 2, Table 2). The biomass of ephemeropterans decreased with sediment depths, but there were no treatment effects (Table 2).

The biomass of Diptera, bivalves and gastropods decreased with increasing sediment depth. There was a significant layer × bream effect on bivalves and gastropods (Table 2) due to a strong negative bream effect in the upper two layers but not in the lowest layer (Figure 2). However, the responses of bivalves and gastropods to the presence of bream differed somewhat. Bivalves, apparently, escaped predation in the deepest layer, whereas gastropods did not and were not found in some samples from bream enclosures (Figure 2). The presence of bream had an overall positive effect on crustaceans. Cladoceran biomass was significantly higher in bream treatments, and there was a significant layer × bream interaction due to the particular strong positive bream effect close to the sediment surface (Table 2, Figure 2). Copepods were more evenly distributed than cladocerans. Overall, copepod biomass was greater in bream treatments, but there was a significant layer × bream interaction effect due to the lower biomass in the middle layer compared with the control and ruffe treatments (Table. 2, Figure 2).

The MANOVA showed a significant bream effect on algae and particulate matter (Table 3).

Table 1. F-statistics from ANOVA for the effects of ruffe, bream and their interaction on total biomass of meio- and macroinvertebrates.

	df	Predators	Gastropods	Ephemeropterans	Diptera	Bivalves	Cladocerans	Copepods
Ruffe	1	0.538	2.01	0.001	0.089	0.033	0.085	0.283
Bream	1	4.72*	93.8***	0.065	0.960	50.8***	42.9***	0.374
Ruffe × bream	1	0.855	1.07	0.688	0.013	0.835	0.036	0.840
Error	12							

$^*p \leq 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

Enclosures with bream were more turbid due to a significantly greater resuspension of particulate organic and inorganic matter and, to a lesser extent, due to a tendency towards higher phytoplankton biomass in bream treatments compared with the control and the ruffe treatment (Table 3, Figure 3). Moreover, periphyton biomass was twice as high in bream treatments (Table 3),

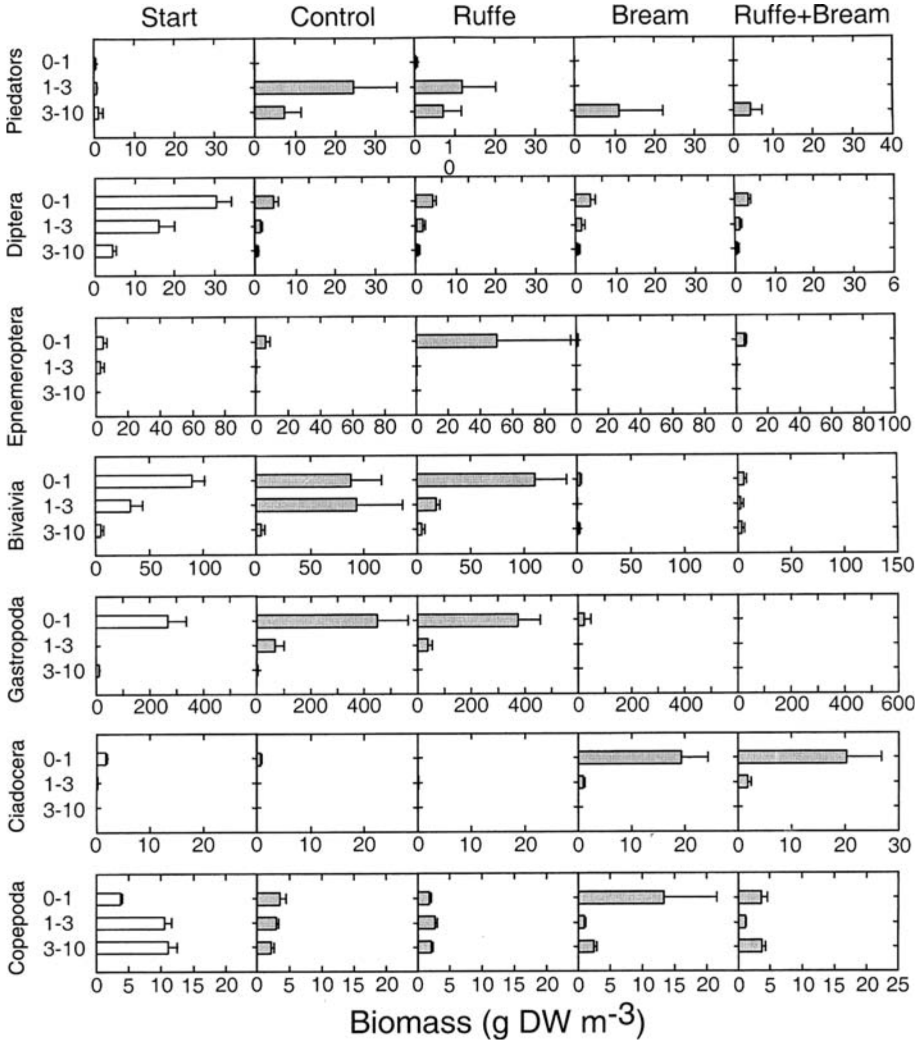

Figure 2. Biomass (gm^{-2}, mean ± 1 SE, $n = 4$) of benthos groups at the start (open bars) and at the end of the experiment (filled bars) in control (C), ruffe (R), bream (B) and ruffe + bream (R + B) enclosures. Data are given for each sediment layer separately (y-axis).

Table 2. *F*-statistics from repeated measures ANOVAs with sediment layer as repeated measure, for the effects of ruffe, bream and their interaction on meio- and macroinvertebrates. In the cases of predators and gastropods, the top or the bottom layer, respectively, were excluded from the analysis due to zero abundance.

	df	Predators	Gastropods	Ephemeropterans	Diptera	Bivalves	Cladocerans	Copepods
Ruffe	1	0.182	2.89	0.001	0.269	0.0344	0.00887	0.780
Bream	1	4.73*	74.3***	0.065	0.292	44.1***	38.5***	0.190
Ruffe × bream	1	0.313	2.89	0.69	0.110	1.95	0.0149	0.0526
Error	12							
Layer	2	0.133	34.3***	50.5***	148***	21.1***	82.1***	5.75**
Layer × ruffe	2	0.319	0.001	0.229	0.462	0.470	0.645	3.02
Layer × bream	2	3.32	34.3***	0.126	1.57	18.8***	37.3***	8.74**
Layer × ruffe × bream	2	0.167	0.001	0.747	0.187	1.86	0.205	0.610
Error	24							

*$p \leq 0.05$, **$p < 0.01$, ***$p < 0.001$.

compared with the control and the ruffe treatments (Figure 3).

Discussion

The distribution of animals is affected by interactions with other animals and with the environment (Wellborn et al. 1996). In our study we found evidence for such interactions. Some groups, e.g., (Diptera), clearly avoided the harsher conditions deep in the sediment, presumably due to oxygen concentrations, other groups (predators and bivalves) could coexist with bream by surviving in the deep parts of the sediment, and others seemed indifferent with respect to vertical position. When present, the depth-specific response was due to the foraging behaviour of bream and not to anti-predator behaviour of the benthos. The results suggest that predation from bream affects large and immobile prey negatively, releasing small prey from resource competition. The strong treatment effects on molluscan prey would have been detected without vertical resolution of the benthos data. The interpretation was greatly improved by the vertical resolution of effects, and some more subtle effects that emerged would not have been detected otherwise.

The ruffe did not significantly affect the biomass or the distribution of benthic invertebrates. This could be due to either low ruffe densities or low foraging efficiency, or a combination of both. Our

Table 3. (a) MANOVA and (b) ANOVAs for the effects of ruffe and bream on the biomass of phytoplankton and periphyton, and on particulate organic and inorganic matter.

	Source	df	Wilks'λ	SS	*F*	*p*
(a)	Ruffe	4,9	0.685		1.04	0.44
	Bream	4,9	0.0891		33.0	< 0.001
	Ruffe × bream	4,9	0.649		1.22	0.37
(b) Phytoplankton	Ruffe	1		0.15	0.62	0.44
	Bream	1		0.96	4.0	0.069
	Ruffe × bream	1		0.013	0.052	0.82
	Error	12		2.87		
Periphyton	Ruffe	1		0.013	0.10	0.75
	Bream	1		1.84	14.9	0.002
	Ruffe × bream	1		0.18	1.49	0.26
	Error	12		1.48		
Organic matter	Ruffe	1		0.37	3.78	0.076
	Bream	1		3.05	31.5	< 0.001
	Ruffe × bream	1		0.0066	0.068	0.79
	Error	12		1.16		
Inorganic matter	Ruffe	1		0.055	0.19	0.67
	Bream	1		35.7	120	< 0.001
	Ruffe × bream	1		0.84	2.83	0.12
	Error	12		3.56		

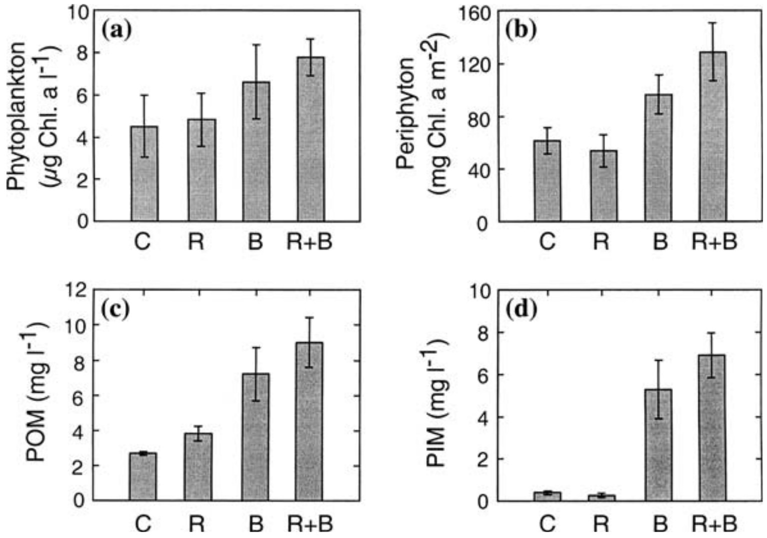

Figure 3. Biomass (mean ± 1 SE, $n = 4$) of (a) phytoplankton and (b) periphyton measured as chlorophyll a concentration, and particulate (c) organic and (d) inorganic suspended matter at the end of the experiment in control (C), ruffe (R), bream (B) and ruffe + bream (R + B) enclosures.

aim was to mimic natural conditions, ruffe generally occurs at lower biomass but higher abundance than bream. We used a density within the natural range, and similar to the densities used by earlier workers in adjacent ponds (Bergman 1990; Bergman and Greenberg 1994). In line with our results, Bergman and Greenberg (1994) found weak ruffe effects on macroinvertebrates, although ruffe occasionally affected *Sialis*, trichopterans and ephemeropterans. Moreover, the high ruffe mortality in our study does not allow any clear conclusions from ruffe treatments. Therefore, we restrict our further discussion to the effects of bream.

As predicted, bream has a strong impact on benthic macroinvertebrates, and this effect diminish with sediment depth. The effect on molluscan prey is particularly strong, and this supports previous studies using cyprinid fish predators (Brönmark 1994; Beklioglu and Moss 1998) and crabs (Haddon et al. 1987). Gastropods decreased in abundance with sediment depth in the absence of bream and were almost extinct in the presence of bream. *Lymnaea peregra*, which dominated gastropod species in our experiment, has been shown to have a weak morphological defence (Rundle and Brönmark 2001). Their morphological defence is clearly inefficient against a predator with a high crushing power, such as the large individuals of bream in our study. The abundance of *L. peregra* at greater depths was negligible in the presence of bream, suggesting that this gastropod do not respond vertically to avoid predation. Behavioural responses to predation are fairly common among gastropods in both limnetic and marine environments (Appleton and Palmer 1988; Yamada et al. 1998; Rochette and Dill 2000; Rundle and Brönmark 2001), although there are large variations between species (Rundle and Brönmark 2001). In theory, individuals can choose the level of predation exposure by adjusting vertical position. Differences in predatory regimes will reflect a difference in vertical distribution between treatments, although we did not specifically design our experiment to separate consumptive and trait-mediated effects. However, there were no indications of behavioural responses to predation in gastropods (or any invertebrate groups). This supports the observations of Rundle and Brönmark (2001), that these snails (*L. peregra*) weakly respond to predation. express a weak behavioural response to predation.

That bream reduced the abundance of bivalves and predators generally supports earlier studies in the presence of benthivorous fish (Persson and Greenberg 1990; Diehl 1992; Bergman and Greenberg 1994; Brönmark 1994). However, with vertical resolution of benthos distribution, we can show that bivalves and invertebrate predators escape predation deep in the sediment so as to maintain a viable population even at a high density of benthivorous fish. Thus, the effect on bivalves and invertebrate predators differs from, e.g. gastropods, which risk local extinction at similar levels of predation. Hence, with appropriate vertical resolution of predation effects we detected a potentially important mechanistic relationship that otherwise would have remained unknown.

Other ways to prevent being detected are inconspicuous coloration (camouflage) and small size. Some earlier studies with benthivorous fish have shown negative effects on chironomids (Gilinsky 1984; Tátrai et al. 1994; Kornijów 1997). We were, therefore, surprised that Diptera larvae in our experiment were unaffected by the presence of bream, although their biomass and average individual size decreased during the course of the experiment. However, since this pattern is observed irrespective of treatment, it is probably driven by replacements of generations rather than predation. The dipterans were so small (mean length 2–4 mm), that the bream most likely experienced a low encounter rate and/or low capture efficiency. This supports the observations of Tátrai et al. (1994) in their pond experiments where bream only reduced the abundance of large chironomids, leaving the small ones unaffected. Another explanation to the absence of bream effects on Diptera is positive, indirect effects: our study bream tended to reduce the biomass of predators, thereby releasing Diptera from invertebrate predation. Such a mechanism will compensate for any losses due to bream predation. Indeed, Diptera biomass shows the opposite pattern compared with invertebrate predators (Figure 2). Similar direct and indirect effects of top predators have been on record for other top predators (Diehl 1992), and in salt-march communities (Kneib and Stiven 1982; Kneib 1988). Thus, the absence of bream effects on Diptera appears to be due to both weak direct effects and compensatory indirect effects.

A commonly observed phenomenon in aquatic systems is the replacement of species, or succession, as the structuring force for community composition alters between competition and predation (Sommer et al. 1986; Fretwell 1987). One underlying mechanism is the demand of multiple, but incompatible, traits that in practice renders organism suitable only for specific conditions. Our study provides an example of this: bream has an indirect positive effect on cladocerans, and in particular *Pleuroxus*, which are small (<1 mm) and probably difficult to handle by the bream (Lammens 1985; Hoogenboezem et al. 1991). There are several possible explanations for the increase in cladocerans in bream treatments. Gastropods and cladocerans were negatively correlated in the upper two sediment layers (Spearman correlation, $n=16$, $R=-0.80$, in both layers), indicating that the increase in cladocerans was a result of release from resource competition with gastropods. Both gastropods and *Pleuroxus* are grazers and the highest resource quality is probably found at the sediment surface where periphytic production occurs. The biomass of periphytic algae increases if bream removes gastropods due to predation. The increase in grazing cladocerans appears insufficient to compensate for the removal of gastropods, suggesting less efficient resource utilization in cladocerans compared with gastropods. It is also possible that the cladoceran increase is caused by release from predation from invertebrate predators, or that cladocerans benefit from the physical disturbance of the sediment caused by bream. However, the experimental design does not allow any determination of the actual mechanisms to explain the observed patterns.

The bream appears to have indirect or cascading effects on lower trophic levels: it increases turbidity by resuspension of organic and inorganic material, leading to lower primary production due to lower light availability as known from other studies on lake biomanipulation (Meijer et al. 1990; Breukelaar et al. 1994; Zambrano et al. 2001). Despite lower light availability, periphytic algal biomass in our study was higher in the presence of bream than in other treatments. Hence, the removal of the dominant grazer, gastropods, had indirect positive effects on periphytic algae outweighing the negative effects of lower light availability (Brönmark 1994).

By deriving information of prey density at a scale relevant to the predator, we were able to detect patterns that otherwise would have remained unknown. For all animal groups except ephemeropterans and dipterans, bream has significant effects. Even though such impacts may be detected without vertical separation of different layers, the spatial distribution of effects provides valuable information evaluating the probability of coexistence between predators and their prey. Moreover, because burrowing benthic invertebrates influence the three-dimensional structure of the sediment and the extent of sediment-water interfaces, the spatial resolution may affect our ability to explain the link between community organization and sediment function (Palmer et al. 2000).

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