

Diet shift in fish following competitive release

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Abstract: We determined the diet preference of roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), and bream (*Abramis brama*) before and after a fish removal program in Lake Finjasjön, Sweden. The biomass of roach and bream was reduced to 33 and 10%, respectively, after the program. The predominate diet change following this major reduction in fish biomass was an increased use of benthic organisms by most size-classes of roach. Also, bream shifted to benthos at an earlier ontogenetic stage. These diet shifts were most probably attributed to the drastic reduction in biomass of the benthivorous bream, resulting in underexploited benthic invertebrates. In order to test if alterations in diet choice were reflected in the composition of stable isotopes of consumer tissue, we determined the temporal changes in the $^{15}\text{N}/^{14}\text{N}$ ratio (δN) of potential fish prey as well as in fish tissue. No temporal trends were found for δN of fish, possibly due to the high temporal variability in δN of zooplankton. However, minimum and maximum δN values of major food organisms (chironomids and zooplankton) were generally reflected in the δN of both small roach and perch one sampling occasion later (3 months) and in piscivorous perch (exclusively feeding on small fish) two sampling occasions later. Hence, the stable isotope composition could be followed through food links, providing that the consumer mainly fed on one specific food item. However, several other predictions regarding connections between diet and stable isotope composition were not corroborated. We conclude that stable isotope analysis of consumer tissue cannot replace traditional methods of diet determination, but might well provide complementary data.

Résumé : Nous avons déterminé les préférences alimentaires du gardon commun (*Rutilus rutilus*), de la perche commune (*Perca fluviatilis*) et de la brème d'eau douce (*Abramis brama*) avant et après la mise en oeuvre d'un programme de retrait du poisson dans le lac Finjasjön, en Suède. La biomasse du gardon et de la brème a été réduite de 33 et de 10% respectivement après l'application du programme. Le principal changement alimentaire observé après cette réduction majeure de la biomasse de poisson a été une utilisation accrue des organismes benthiques par la plupart des classes de taille du gardon. La brème s'est aussi tournée vers le benthos plus tôt dans son développement. Ces changements alimentaires étaient le plus probablement attribuables à la réduction très marquée de la biomasse de la brème, un poisson benthivore, ce qui a entraîné une sous-exploitation des invertébrés benthiques. Pour vérifier si les modifications des choix alimentaires se reflétaient dans la composition en isotopes stables dans les tissus des consommateurs, nous avons déterminé les changements temporels du rapport $^{15}\text{N}/^{14}\text{N}$ (δN) dans les proies potentielles des poissons de même que dans les tissus des poissons. Nous n'avons observé aucune tendance temporelle de δN dans le poisson, peut-être à cause de la forte variabilité temporelle de δN dans le zooplancton. Cependant, les valeurs minimales et maximales de δN dans les principales proies (chironomides et zooplancton) étaient généralement reflétées dans le δN des petits gardons et des petites perches lors d'un échantillonnage ultérieur (3 mois plus tard) et de la perche piscivore (qui se nourrit exclusivement de petits poissons) lors de deux échantillonnages ultérieurs. Ainsi, la composition en isotopes stables peut être suivie à travers les liens alimentaires, pourvu que le consommateur se nourrisse principalement d'une seule espèce de proie. Cependant, plusieurs autres prévisions concernant les liens entre le régime alimentaire et la composition en isotopes stables n'ont pas été corroborées. Nous concluons que l'analyse des isotopes stables dans les tissus des consommateurs ne peut pas remplacer les méthodes classiques de détermination du régime alimentaire, mais qu'elle peut très bien fournir des données complémentaires.

[Traduit par la Rédaction]

Introduction

Human-induced alteration of consumer communities, or biomanipulation (Shapiro et al. 1975; Shapiro and Wright 1984), has been suggested as a method for managing eutrophicated lake ecosystems that suffer from severe algal

blooms. The effects of manipulation of consumer communities are expected to cascade down to lower trophic levels (Hairton et al. 1960; Carpenter et al. 1985) and ultimately to the producer level. Usually, increased grazing on algae is believed to be achieved by alterations in the fish community, either by removing zooplanktivorous fish or by increasing predation on zooplanktivorous fish by piscivorous fish. In theory, this view is appealing, but field studies have shown a variety of unexpected results. When changing the biomass proportions of food web components, a number of processes, apart from predation, may be affected in an unpredictable way. Nutrient cycling may be altered due to changes in species composition (Wright and Shapiro 1984; Sterner 1990; Carpenter et al. 1992; Schindler et al. 1993, 1996). Light conditions may improve due to decreases in

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both phytoplankton (Van Donk et al. 1990) and benthivorous fish biomass (Meijer et al. 1990; Brönmark and Weisner 1992). Such “side-effects” will in turn affect phytoplankton biomass by altering the growth conditions and the competitive relationships within the producer community, such as the relationship between submerged macrophytes, periphyton, and phytoplankton.

Several processes within the fish community could potentially compensate for a selective removal of fish. Growth and recruitment rates generally increase after a biomanipulation and partly compensate for the removal of fish. Moreover, diet of the remaining fish community may be altered, obscuring the anticipated effects of a biomanipulation effort. A deeper understanding of such community-level responses is needed if biomanipulation is to become a reliable management tool in the future. Such knowledge will also increase predictability and provide information about where, when, and how a biomanipulation is best performed.

Fish diet is generally determined by examination of gut content (Elliott and Persson 1978). However, the gut content only reflects the last hours of feeding, and single estimates may not give an accurate picture of the diet on a seasonal scale. It would therefore be useful to have access to a method that estimates feeding over a longer time period. A possible complementary tool in estimating diet on longer time scales is the determination of naturally occurring stable isotopes in fish tissue. The stable isotope ^{15}N is excreted in lower amounts than the more abundant ^{14}N , so that organisms become enriched in ^{15}N compared with their food (Peterson and Fry 1987). In this way, the $^{15}\text{N}/^{14}\text{N}$ ratio (δN) of a predator's tissue will be a result of the δN of its food items. Under ideal conditions, the δN increases with 4–5‰ for each additional trophic level due to isotopic fractionation (Peterson and Fry 1987). In simple food chains, where the predator feeds mainly on one food item, stable isotope analysis may give a clear signal. However, fish often feed on different trophic levels by eating benthic invertebrates as well as zooplankton and small fish. Furthermore, fish may also shift their diet during ontogenesis, feeding on zooplankton as young, then shifting to mainly benthic invertebrates, and finally becoming exclusively piscivorous.

In the present study, the applicability of stable isotope analysis of fish tissue for the determination of fish diet is evaluated. Moreover, we examine the structure and resource utilization of a fish community before and after a selective mass removal directed towards the two most abundant species, roach (*Rutilus rutilus*) and bream (*Abramis brama*). We have compared the gut content measured over an extended period of time and the stable isotope (δN) composition of the two species roach and perch (*Perca fluviatilis*), which dominated the fish community after the fish removal. The extensive literature concerning the competitive interaction between roach and perch (Lessmark 1983; Persson 1983c, 1986, 1987; Diehl 1988; Persson and Greenberg 1990) covers mainly two niche dimensions: resource availability and habitat complexity. Roach is considered more of a generalist, feeding on both animals and plants (Lessmark 1983; Persson 1983c), whereas perch is a strict carnivore, potentially undergoing ontogenetic shifts in diet from zooplanktivorous, via benthivorous, to piscivorous stages (Persson 1983a). Roach is a superior zooplankton predator compared

with perch because it is capable of capturing smaller prey, resulting in roach being unaffected by perch abundance (Persson 1987). Perch is a superior benthivore and is less affected by habitat complexity compared with roach (Persson 1987; Diehl 1988), but the benthivorous stage of perch is often the bottleneck for the recruitment to the piscivorous stage due to intraspecific competition for benthic resources (Persson and Greenberg 1990). The diet of bream resembles that of roach, with the exception that bream is a more distinct benthivore at a large size (>30 cm in length) and is able to penetrate the sediment to a greater depth than roach (Lammens 1985). Therefore, a reduction of roach and bream biomass could potentially release perch from interspecific competition at both planktivorous and benthivorous stages. Such a competitive release is hypothesized to be reflected in the abundance and diet of the fish.

Materials and methods

Lake description

The study was carried out in Lake Finjasjön (area 11 km², maximum depth 12 m, mean depth 3.5 m), a eutrophic lake situated in southern Sweden (62°27'31"N, 13°69'20"E). In the 1970s, the external load of phosphorus reached its maximum (2 g P·m⁻²·year⁻¹) but was lowered in the 1980s to 0.5 g P·m⁻²·year⁻¹. Despite this reduction, the lake continued to suffer from heavy blooms of mainly *Microcystis* sp. and *Aphanizomenon* sp. due to the internal loading of phosphorus. In 1992, the total fish biomass (wet weight) was calculated to be 300 t (95% CI 215–495; Persson 1997), corresponding to 273 kg·ha⁻¹. Between October 1992 and June 1994, a fish reduction program was carried out with the aim to reduce the densities of the roach and bream populations, which dominated the fish community (79% by biomass). The fish reduction was performed by trawling, and 400 t of mainly roach, bream, and small (<150 mm) perch was removed. Piscivorous fish accidentally caught in the trawl were immediately released back to the lake.

Density

Fish were sampled by pair-trawling (Bergman et al. 1999) in August–September 1992–1995 to determine the relative abundance and fish community composition. The trawl used was a modified herring trawl (length 30 m, arm length 5 m, 264 meshes along the opening and 5-mm mesh size in the codend), which was towed along the bottom by two boats. Each year, the trawl was towed twice at a speed of 1 m·s⁻¹ for 5–10 min at each of the depths 2, 3, 4, 6, and 8 m. Individuals were separated by species and individual lengths were determined. In addition, at least 200 individuals were both measured and weighted separately to obtain length–mass relationships. These relationships were then used to calculate the biomass of each size-class (see below) separately.

Diet

On six occasions in 1992 (April, May, June, July, August, and October) and five occasions in 1995 (May, June, July, August, and October), the stomachs of perch and the intestines of roach and bream were collected from fish caught in survey gill nets placed overnight at 2 and 5 m depths. Fish were sorted in five different size-classes corresponding to age 0+, 1+, 2–3+, 4–5+, and >6+ (roach and perch: <80, 80–120, 120–150, 150–180, and >180 mm; bream: <80, 80–120, 120–150, 200–300, and >300 mm). When possible, at least five (1992) or 10 (1995) individuals from each date and size-class were analyzed. However, the mass removal affected bream abundance especially, resulting in bream being only rarely caught. Consequently, the diet of bream in 1995 could only be determined adequately in August, when sampling was per-

formed by trawling as well as with gill nets. Stomachs and intestines were preserved in the field with 70% alcohol for later analysis in laboratory.

Using a microscope, the diet was determined by identifying, counting, and measuring the length of the different food items. For abundant prey, a maximum of 10 individuals of each prey item were measured for each fish. All fish within a size-class were then pooled. The dry mass of each prey item was determined using length–mass relationships (Bottrell et al. 1975; Persson and Greenberg 1990). Food items were then sorted into four categories: planktonic grazers (*Daphnia* sp., *Bosmina* sp., *Chydorus* sp.), planktonic predators (*Leptodora kindtii* and cyclopoid copepods), benthic crustaceans (*Alona* sp. and *Ostracoda*), and benthic insects (mainly Chironomidae, Micronecta, and Tricoptera). The biomass of each prey category found in one average individual fish for each sampling date was calculated for each species and size-class of fish. Then, all sampling dates were pooled and the fraction (percent) of a certain prey category was calculated to achieve a seasonal average diet for each species and size-class. Mean prey dry weight was calculated by dividing the total biomass of prey by the total number of prey found in all fish of a certain size-class. Since prey biomass was obtained by using average prey size measures, no error statistics was performed when calculating mean prey weight.

To obtain functional groups, the fish community was divided into benthivores, planktivores, and piscivores by multiplying the relative abundance (catch per unit effort, CPUE) of each size-class and the fraction of benthic, planktonic, and fish items, respectively, in the diet. These calculations include unpublished data on abundances of other, less abundant species than those of primary concern in this paper (i.e., northern pike (*Esox lucius*), zander (*Stizostedion lucioperca*), and ruffe (*Gymnocephalus cernuus*). All northern pike and zander caught were larger than 200 mm and considered piscivorous whereas the functional position of ruffe was calculated using the same method, based on diet data and relative abundance, as mentioned above.

Stable isotopes

Samples of fish, benthic invertebrates, phytoplankton, zooplankton, and sediment were collected in February, May, July, August, and November 1994 and in April, July, September, and October 1995 for determination of stable isotopes. Sediment and benthic invertebrates were sampled with an Ekman dredge. Sediment was sieved through a 0.5-mm sieve and benthic invertebrates were then picked out by hand. To collect different size-classes of zooplankton, a bucket with a 300- μ m net followed by a 45- μ m net was dragged behind a boat at about 1 m depth. Phytoplankton samples (<45 μ m) were retrieved on a preburned (560°C) GF/C (Whatman) filter after sieving through a 45- μ m net. Roach and perch were sampled by trawling and then separated into three size-classes: <80, 120–150, and >180 mm. Muscle samples (between the head and the dorsal fin) of 5–10 fish from each species and size-class were pooled for each sampling occasion.

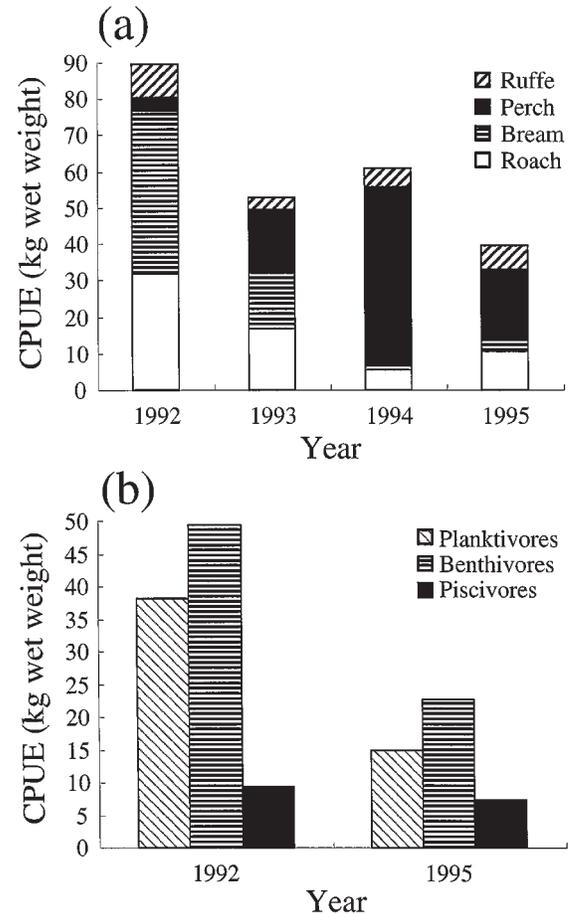
All samples were frozen and dried (65°C for at least 48 h). Sediment, benthic invertebrates, zooplankton, and fish were then ground to a particle size of <0.2 mm. After combustion (1800°C), analysis for stable isotopes was done with a Carlo Erba element analyzer (E 1108 CHNS-O) connected to a mass spectrometer (Optima). IAEA-N1 and IAEA-N2 were used as standards for ^{15}N .

Results

Fish abundance

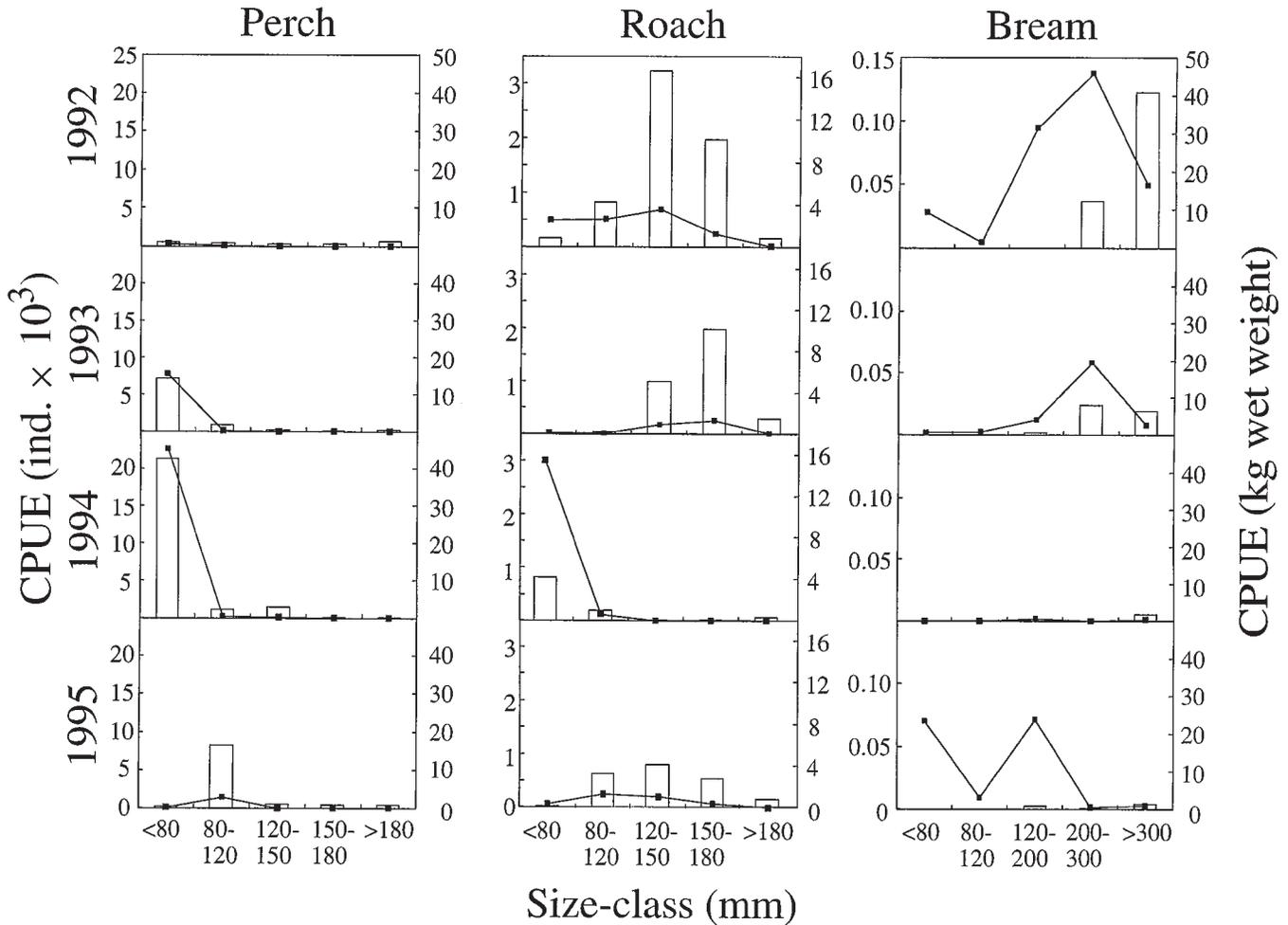
In 1992, the fish community was dominated by roach and bream, constituting 33 and 46% of the total biomass, respec-

Fig. 1. CPUE of different (a) species and (b) functional groups in Lake Finjasjön, 1992–1995. Sampling was performed by trawling in August at five different depths (2, 3, 4, 6, and 8 m). CPUE of functional groups was calculated using diet and abundance data (see Materials and methods). In 1992 the total fish community was estimated to be 300 t (95% CI 215–495; Persson 1997). A fish reduction program was carried out between October 1992 and June 1994, removing 400 t of mainly bream and roach.



tively. The fishing program reduced the roach biomass in 1995 to 33% of the density in 1992 (Fig. 1a). The fish reduction was even more efficient in removing bream, which in 1995 had a biomass <10% of that in 1992 (Fig. 1a). Despite the fish removal (400 t), total fish biomass in 1995 was only reduced by 50% compared with 1992 (Fig. 1a). An increased recruitment of perch in both 1993 and, especially, 1994 caused a change in species composition from cyprinid (79% in 1992) to percid dominance (59% in 1995). Perch constituted only 4% of total fish biomass in 1992, but totally dominated fish biomass in 1994 (78% of total biomass) and was still the most dominant species in 1995 (44% of total biomass) (Fig. 1a). A fivefold increase in perch biomass, in combination with the reduced cyprinid densities, caused this change in fish community species composition. In 1993 and 1994, the catch of perch young-of-the-year (YOY) was 20 and 60 times the numbers in 1992, respectively. In 1995, however, the number of perch YOY was below that in 1992 and the perch population was dominated by the strong year-

Fig. 2. CPUE of different size-classes of perch, roach, and bream in Lake Finjasjön, 1992–1995. Bar graphs denote biomass (kg wet weight) and line graphs represent abundance (thousands of individuals). Sampling was performed by trawling in August at five different depths (2, 3, 4, 6, and 8 m). A fish reduction program was carried out between October 1992 and June 1994.



class of 1994 (Fig. 2). Large year-classes of other species were rare, but in 1994, roach showed a YOY year-class 100 times larger in number compared with 1992. However, this year-class suffered from high mortality during the subsequent year, and the 1+ class in 1995 was not notably larger than normal. Piscivore biomass was not affected significantly, although a reduction was observed in 1993–1994. However, due to the reduction in biomass of planktivores, the fraction of the fish community being piscivorous was doubled in 1995 compared with 1992 (Fig 1b).

Although total fish biomass was reduced by the fish removal, fish abundance increased by an order of magnitude (11×) and average fish weight decreased from 39 to 2.3 g between 1992 and 1994. In 1995, fish abundance was only slightly higher (140%) compared with 1992, but mean fish weight was still one third (13 g) of the mean in 1992.

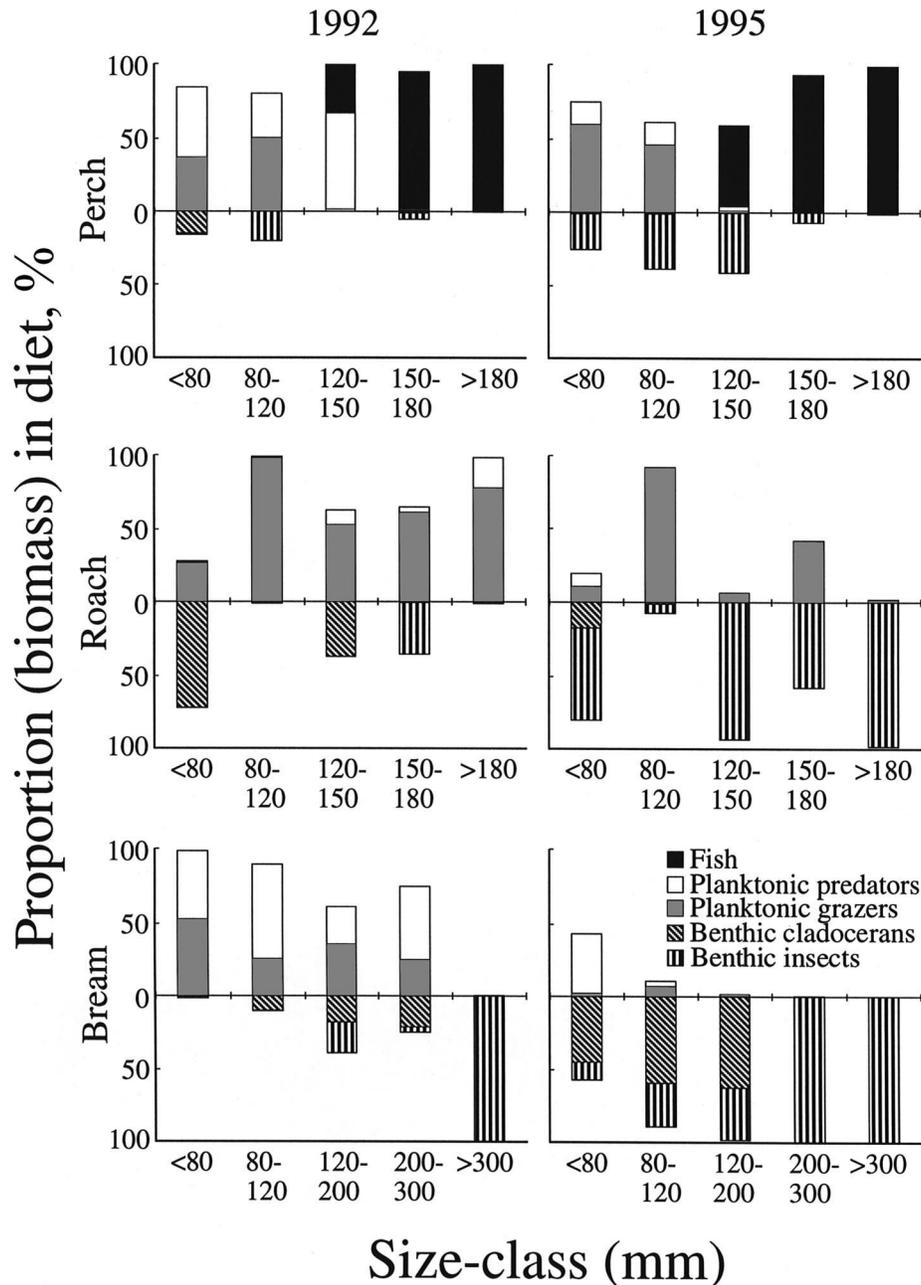
Fish diet

The overall tendency in diet choice was a utilization of benthic resources at earlier life stages, possibly as a result of the reduction in specialized benthivores (bream) by the fish reduction program. Although bream biomass was reduced drastically, the relationship between biomass of benthivores

and planktivores remained unchanged (Fig. 1b) as a result of dietary change in the other species (i.e., perch, roach, and ruffe).

In 1992, perch with lengths up to 150 mm fed mostly on pelagic prey whereas fish became an important food item for medium-sized individuals (>120 mm) (Fig. 3). Benthic prey were not important in the diet for any size-class of perch in 1992, but in 1995 constituted about 30% (mainly chironomids) of the diet for perch up to a size of 150 mm (Fig. 3). Perch larger than 150 mm fed almost exclusively on fish in both years (Fig. 3). All size-classes of roach fed almost exclusively on planktonic grazers in 1992, with the exception of the smallest size-class (<80 mm), for which benthic crustaceans dominated. The diet of the smallest size-classes (<80 and 80–120 mm) did not differ between years with respect to habitat origin (pelagic or benthic) (Fig. 3). For the 80–120 mm size-class, planktonic grazers dominated the diet in both years. The <80 mm size-class fed on about 25% pelagic prey and 75% benthic prey in both years. The most striking exception was that benthic insects, prey items not detected in the diet of this size-class in 1992, were an important part of the diet in 1995. For larger roach (>120 mm), there was an exceptional change in resource utilization between 1992

Fig. 3. Diet of different size-classes of perch, roach, and bream in Lake Finjasjön, 1992–1995. Prey categories above the zero lines are pelagic prey and those below are benthic prey. Diets are based on stomach contents of fishes pooled from six (1992) or five (1995) sampling occasions between April and October.



and 1995. In 1992 the pelagic component (mainly planktonic grazers) dominated the diet whereas benthic food items (mainly chironomids) were important resources for all of these size-classes of roach in 1995 (Fig. 3). This trend was most notable for the largest size-class of roach (>180 mm), which fed exclusively on pelagic prey in 1992 and exclusively on benthic prey in 1995 (Fig. 3). The change in diet resulted in mean weight of roach prey being significantly higher in 1995 compared with 1992 (paired *t*-test, $p = 0.02$).

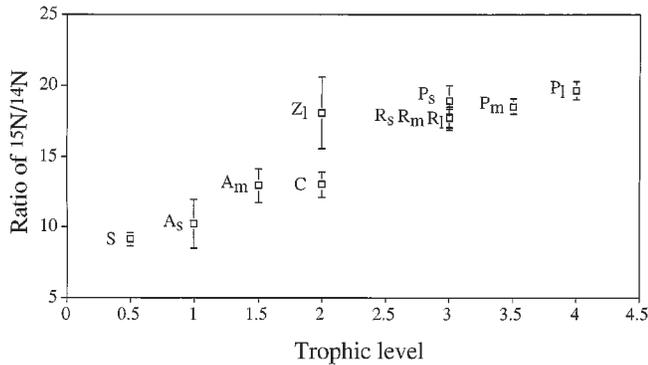
Large bream (>300 mm) fed exclusively on chironomids in both 1992 and 1995. For smaller size-classes, the diet changed markedly between 1992 and 1995 from dominance of pelagic to benthic prey. In 1995, pelagic prey signifi-

cantly contributed to the diet of only the smallest size-class (<80 mm). Benthic cladocerans, detected only in low abundance in 1992, were important prey for bream with lengths of up to 200 mm in 1995. The fraction of benthic insects in the diet increased with bream size in 1995 from 10% for bream <80 mm to 100% for bream >200 mm.

Stable isotopes

The temporal differences in δN during the period of investigation (February 1994 to October 1995) were small with respect to sediment, algae, benthic invertebrates, and fish whereas δN for zooplankton (>300 μm) varied considerably (Fig. 4). No significant temporal patterns were found for δN

Fig. 4. Mean $^{15}\text{N}/^{14}\text{N}$ ratio (δN) for sediment (S), phytoplankton (A_s and A_m , $<45\ \mu\text{m}$), and fish food items, including zooplankton (Z_1 , $>300\ \mu\text{m}$) and benthic invertebrates (C, chironomids). δN values are also given for three size-classes of roach (R) and perch (P): small (s, $<80\ \text{mm}$), medium (m, $120\text{--}150\ \text{mm}$), and large (l, $>180\ \text{mm}$). Bars show the temporal variation (range) in δN during the investigation period (February 1994 to October 1995).

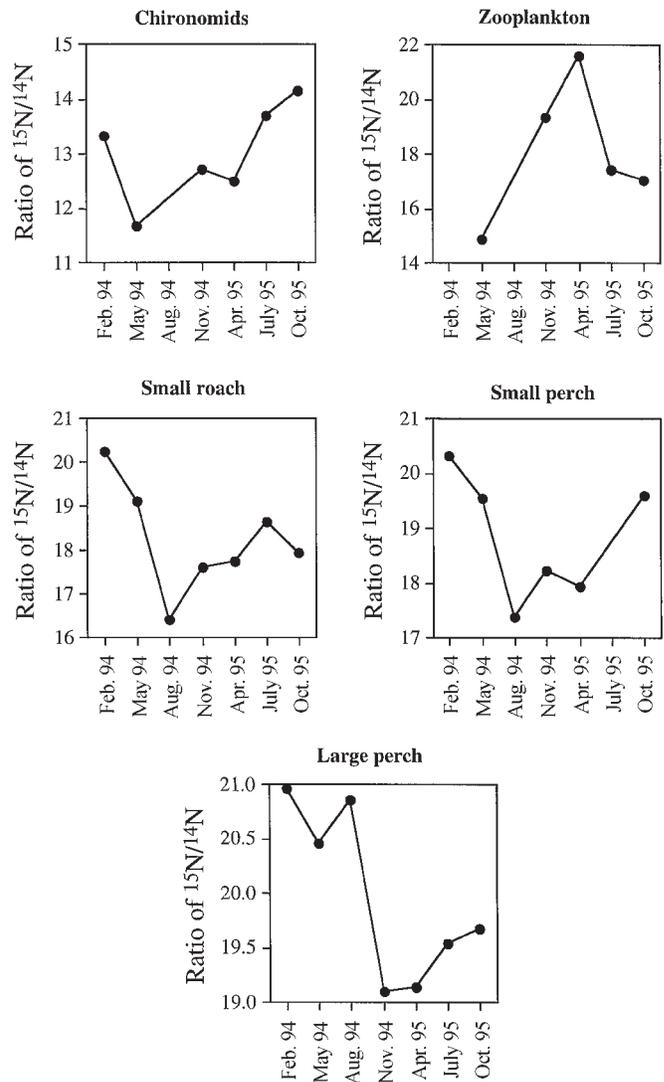


(linear regression: $p > 0.05$). There were differences in δN values among size-classes of perch (ANOVA: $F = 4.72$, $p = 0.03$). However, Fisher's PLSD contrast revealed differences in δN only between medium and large sizes and small and large sizes of perch ($p = 0.01$) (Fig. 4). With respect to roach, there was no difference in δN between different-sized fishes (ANOVA: $p > 0.5$).

The δN of surface sediment was 9.11 ± 0.45 (mean \pm 1 SD) whereas planktonic algae ($<45\ \mu\text{m}$) had a somewhat higher δN (10.22 ± 1.74) (Fig. 4). Zooplankton larger than $300\ \mu\text{m}$ had δN values of 18.05 ± 2.53 whereas benthic invertebrates (chironomids) had lower δN values (13.01 ± 0.90), indicating feeding on particles at the sediment surface (Fig. 4). The next trophic level, feeding on zooplankton and benthic invertebrates, had δN values of 18.94 ± 1.09 (small perch), 18.20 ± 1.15 (small roach), and 17.75 ± 0.95 (medium-sized roach), respectively. In addition to invertebrates, medium-sized perch also fed on small fish and may thereby be placed in a trophic level between 3 and 4 ($\delta\text{N} = 18.73 \pm 0.60$) (Fig. 4). Large, exclusively piscivorous perch showed the highest δN values of all organisms investigated (19.92 ± 0.74). The δN of chironomids showed a minimum in May 1994 and then increased throughout the sampling period (Fig. 5). Zooplankton also had minimum δN in May, but showed a maximum in April 1995. The fish feeding on these prey, small roach and perch, had minimum δN in August 1994 and then showed increasing trends except for roach in October 1995. Piscivorous perch showed high δN values from February to August 1994, but low values during winter (November 1994 to April 1995). Thereafter, δN increased (Fig. 5).

The correlations between δN values of food organisms and consumers were low when correlating the same sampling occasions, but high ($r = 0.67\text{--}0.88$) when correlating the consumer δN with the food organism δN of the previous sampling date ($t = +3$ months) (Fig. 6). Unfortunately, one sampling of small perch (July 1995) and one of zooplankton were missing due to too low sample size for analysis of sta-

Fig. 5. Temporal variation in δN of chironomids and zooplankton ($>300\ \mu\text{m}$), small perch and roach ($<80\ \text{mm}$), and piscivorous perch ($>180\ \text{mm}$) in Lake Finjasjön between February 1994 and October 1995. The figure shows that minima and maxima in food organisms can generally be detected in consumer tissue within 3 months (one sampling occasion).



ble isotopes (February 1994). Therefore, it was not possible to perform the correlations for zooplankton and small perch.

Discussion

When manipulating a planktivorous fish community, strong effects on closely positioned trophic levels are expected. However, many large-scale fish removals have failed to show any significant effects on zooplankton biomass (reviewed in DeMelo et al. 1992). A possible explanation is the large capacity within a fish community to compensate for a removal and rapidly (within a few years) turn back to its previous state. In the short term, a selective mass removal of planktivorous fish may have no, or even negative, effects on the zooplankton community. The per capita consumption of remaining fish is likely to increase when competition is low-

ered. This may result in a higher per capita reproductive rate because more energy could be invested in gonad development, which in turn often results in a high number of young planktivorous fish in subsequent years (Jeppesen et al. 1990; Bergman et al. 1999). Small individuals generally have a higher mass-specific consumption rate and select for smaller prey than large fish (Lessmark 1983). Therefore, predation pressure on grazers may actually increase after biomanipulation, obstructing improvements in water quality (Romare and Bergman 1999). Hence, despite a removal of 80% of the original fish community in Lake Finjasjön, successful reproduction of perch resulted in biomass only being reduced by 50%. The high recruitment of perch caused fish abundance to increase and mean fish size to decrease. Although the fish community structure changed considerably with respect to species composition and size structure, the biomass relationship between planktivores and benthivores remained constant.

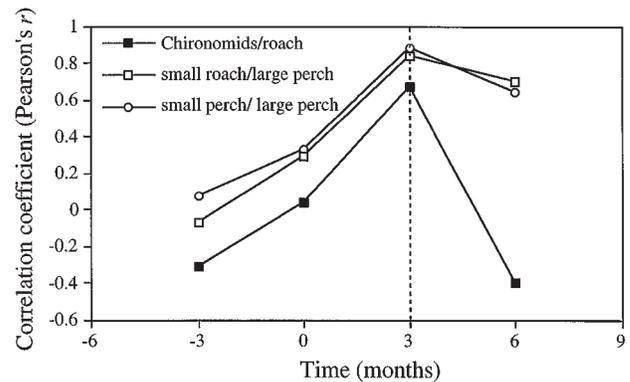
Another possible scenario is that the resource utilization changes among other species that have not been removed. Many fishes are omnivorous or undergo ontogenetic diet shifts leading to changes in resource utilization, which may obscure the anticipated effects of biomanipulation.

Perch abundance in Lake Finjasjön increased due to high recruitment following the fish removal (Fig. 1). Consequently, the fish community changed from a dominance by cyprinids (roach and bream) to a dominance by percids (perch and ruffe). This finding supports the hypothesis that competitive release should increase perch abundance (Persson et al. 1991). Zooplankton biomass and species composition remained unchanged during the period of investigation (Annadotter et al. 1998). The overall tendency was an increasing use of benthic resources by fish. This tendency was observed for all species, but the change in resource utilization was most pronounced for large, nonpiscivorous fish (>120 mm) whereas the diet of small roach (<120 mm) did not differ between 1992 and 1995 (Fig. 3).

With respect to diet, there is a notable difference between the results obtained for Lake Finjasjön and for a fish reduction experiment performed in Lake Sövdeborgssjön (Persson et al. 1993). In Lake Sövdeborgssjön, roach biomass was reduced by more than 20%, which resulted in an increased use of pelagic resources (zooplankton) by perch and roach, opposite to that of Lake Finjasjön. A notable difference between the lakes is that bream is not present in Lake Sövdeborgssjön. Both roach and perch were utilizing the benthic resource in Lake Sövdeborgssjön before the removal of roach whereas bream was the sole exploiter of benthos in Lake Finjasjön. Moreover, roach fed on sediment in the former lake, which is a resource considered to be of low nutritive value compared with a carnivorous diet (Lessmark 1983; Persson 1983b). Sediment was not found in the intestines of roach in Lake Finjasjön. This indicates the likelihood of higher inter- and intra-specific competition within the fish community of Lake Sövdeborgssjön compared with Lake Finjasjön. Thus, the resource utilization in Lake Sövdeborgssjön after roach removal corresponded to the resource utilization in Lake Finjasjön before the fish removal.

Diet of fish may be an indicator of habitat use (Werner et al. 1983), which in turn may be affected by the abundance of competitors and predators. The two smallest size-classes of

Fig. 6. Cross correlations of tissue δN of consumers and their dominant prey. Analysis of gut content showed that chironomids were the dominant food organism for small perch and that small roach and perch dominated the diet of large perch. Correlation coefficients are calculated for δN of food organisms at $t = 0$ and δN of the consumer at $t = -3$, $t = 0$, $t = 3$, and $t = 6$ months, showing highest correlation between δN of food at $t = 0$ and consumer one sampling occasion later ($t = 3$ months).



roach showed notable differences in diet. Roach <80 mm had a large fraction of benthic resources in the diet whereas the 80–120 mm size-class of roach fed almost exclusively on pelagic prey. The difference in diet of <80 and 80–120 mm roach may indicate a habitat segregation of competing size-classes towards a preference for the open water with increasing size. Furthermore, the habitat use of juvenile roach has been shown to be highly dependent on mortality risk (Brabrand and Faafeng 1993). In Lake Finjasjön, piscivorous fish biomass did not differ between 1992 and 1995, but the proportion of piscivorous fish of the total fish community in 1995 was two times the proportion in 1992. Moreover, Secchi depth increased significantly during the investigation period from a summer average of <1 to >2 m (Annadotter et al. 1998). The latter factor is likely to increase the per capita encounter rate between prey and piscivorous fish. When mortality risk is high, small roach may be confined to refuge habitats (Brabrand and Faafeng 1993), which may limit the recruitment of roach. Perch <80 mm, on the contrary, had a higher proportion of pelagic prey in the diet, indicating that they were exploiting resources in the pelagic areas. By exploiting the whole lake, juvenile perch may benefit more when released from competition than roach. This may be one explanation for the higher recruitment rate of perch compared with roach, despite the higher adult biomass of the latter.

The most striking changes in resource utilization were recorded for bream smaller than 300 mm, larger size-classes of roach, and the 120–150 mm size-class of perch. The general tendency for all these groups was the increasing use of benthic resources, especially benthic insects. In particular, large roach (>180 mm) changed their diet from entirely pelagic to entirely benthic prey. There may be several reasons for this, but we will consider two of the most important. First, large individuals may have been forced to change their diet due to the increased abundance of smaller individuals. Small individuals are generally more efficient consumers of smaller prey (zooplankton) whereas larger individuals have a

broader prey-size window, allowing the capture of larger prey as well. Thus, both inter- and intra-specific competition may have forced large individuals to feed on benthic instead of pelagic prey. A second possible explanation may be that resource availability changed. The fish reduction program was particularly efficient in removing large bream, which feed exclusively on chironomids. Large bream are efficient foragers on benthic resources (Lammens 1985), potentially removing this resource from roach and perch. It is therefore likely that chironomids became more available for other species when large bream were removed. The overall tendency towards increased use of benthic resources indicates that this is a likely explanation. Unfortunately, we do not possess data on the benthic community to support this hypothesis.

One of the aims of this study was to assess if analysis of stable isotopes of consumer tissue could be used as a method to determine diet. One of the strengths of stable isotope analysis is that it measures the actual assimilation integrated over the time scale of tissue turnover in the organism (Kling et al. 1992) whereas gut analyses only reflect the last hours of consumption.

It has been repeatedly demonstrated (Kling et al. 1992; Zohary et al. 1994) that the stable isotope composition of consumers may mirror their resource utilization. Here, large perch were exclusively piscivorous and had, accordingly, significantly higher δN values than roach or other size-classes of perch (Fig. 4). Between size-classes of roach and between smaller size-classes of perch, the diet was too similar to be visible in the stable isotope content. Hence, only the most pronounced differences in diet were detected in consumer tissue whereas several differences predicted from actual determinations of diet choice were not substantiated. For example, the results from the gut content analysis suggest that the δN would decrease with time during the study period for those fish groups showing the largest difference in diet between 1992 and 1995. Despite this, there were no significant time effects on δN of fish tissue. The stable isotope analysis did not necessarily fail at detecting a real difference; the gut analyses only tell us the relative proportion of different prey items consumed at different times, not the actual consumption of a certain prey item. The consumption rate, in turn, may change markedly during a season depending on food availability and temperature. We conclude that, although the use of stable isotopes for determination of diet choice is appealing, it is not an alternative but rather a complement to traditional methods.

To use stable isotope analysis as a tool for diet determination, it is important to assess how fast consumers at different trophic levels respond to temporal changes in stable isotope composition. In this study, temporal variation, expressed as maxima and minima, in the stable isotope composition of prey organisms was detectable in consumer tissue within 3 months, providing that the food item constituted a major food source of the consumer. Our sampling intervals were about 3 months (except during winter), allowing for a relatively finely tuned test of how fast the stable isotope composition in the food is implemented in the consumer tissue. A plausible prediction is that minima and maxima in food stable isotope composition should be mirrored by those of the consumer the next sampling occasion 3 months later. According to the diet analysis in 1995, the most important food

items for small roach (<80 mm) were chironomid larvae and zooplankton, constituting 60 and 20% of the diet, respectively (Fig. 3). Hence, the minimum in δN of chironomids in May 1994 was expected to generate a minimum in stable isotope composition of small roach the next sampling occasion (August); this was the case (Fig. 5). Similarly, the increasing trend in δN of chironomids should lead to an increasing trend in δN of small roach from August 1994 to October 1995. This was also the case, except for the October sampling, which may be reflecting that small roaches were also eating zooplankton, which showed a considerable decrease in δN between April and July 1995 (Fig. 5).

With respect to small perch (<80 mm), zooplankton constituted 78% and chironomids 22% of the diet (Fig. 3). The δN of zooplankton showed a minimum in May 1994 and a maximum in April 1995, which were reflected in minimum and maximum δN values of small perch in August 1994 and October 1995, respectively (Fig. 5). Large perch (>180 mm) were exclusively piscivorous and the low δN in November 1994 and April 1995 mirrored the minima in δN of small roach and perch in August (Fig. 5). Hence, a minimum in δN of chironomids and zooplankton in May was detectable in small fish in August and in piscivorous fish in November (Fig. 5). There was a high correlation between the δN of the food and the consumer examined 3 months later whereas there were no, or lower, correlations between food and consumer δN caught at other times (Fig. 6). This might be an indication of the time scale for the turnover rate of nitrogen in fish tissue.

We conclude that a mass removal of planktivorous and benthivorous fish in Lake Finjasjön resulted in a dietary change in the remaining species to increased utilization of benthic resources. Thus, although the fish community structure changed considerably with respect to species composition and size structure, the biomass relationship between planktivores and benthivores remained constant. The influence of processes such as mass recruitment of young fish and alterations in diet following fish removal has to be better understood if biomanipulation is to become a method for the restoration of lakes. Currently, the unpredictability of biomanipulation as a management tool make investments hazardous and may cause a societal resistance to the development of biological solutions to environmental problems (Strong 1997).

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