

Fishing-induced changes in predation pressure by perch (*Perca fluviatilis*) regulate littoral benthic macroinvertebrate biomass, density, and community structure

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Abstract We aimed to study whether the varying changes in predation pressure by perch (*Perca fluviatilis*) reflect the biomass, density, and community structure of the benthic macroinvertebrates. Prey preference is size-dependent, and overall predation pressure is density dependent, and thus the size structure of the *P. fluviatilis* population should affect the structure of the macroinvertebrate community, and the population density of *P. fluviatilis* should reflect the overall density of benthic macroinvertebrates. We sampled the littoral benthic community in a boreal lake that had been divided into two parts that were subjected to two different fishing procedures during 2007–2012 period and analyzed the macroinvertebrate diet of fish. The benthic macroinvertebrate community reflected the predation pressure. Total macroinvertebrate biomass increased during the study period in the lake division with a non-size-selective fishing procedure (NSF), i.e., all invertivorous perch size-classes targeted, but

decreased in the section with negatively size-selective fishing procedure (SSF), i.e., large invertivorous individuals ≥ 16 cm were not targeted. This difference was a result of the increase in large-sized species, such as Odonata, for the NSF procedure and decrease in the SSF procedure. In contrast to total biomass, total macroinvertebrate density did not show a response to predator size structure but rather total macroinvertebrate density decreased with increasing fish density. The study demonstrates the effect of predation pressure of *P. fluviatilis* on benthic communities, thus highlighting the keystone predator role of the species in boreal lakes and gives more insight on the multiple effects of fish predation on littoral benthic communities.

Keywords Benthic community · Selective fishing · Boreal lakes

Introduction

The effects of predators on the benthic community structure in aquatic ecosystems are highly complex, and the issue as to whether freshwater fish play an important role in regulating and shaping benthic macroinvertebrate assemblages is a timely topic (Pope and Hannelly 2013; Bonneau and Scarnecchia 2015). Many studies show a variety of effects of fish predation on benthic communities that range from strong negative effects on total biomass (Crowder and Cooper 1982) and density (Morin 1984; Mittelbach

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1988), to studies on the underlining variables (Gilinsky 1984; Diehl 1992; Brönmark 1994) or which show little or no effects (Thorpe and Bergey 1981; Hanson and Leggett 1986). The reason for this discrepancy among the results may partly be due to variety of methodological approaches. Predation pressure is an important aspect, as a single predatory species versus a number of different predators may result in different and complex intra- and interspecific interactions the net effect of which influence the overall predation pressure on the benthic community (Vance-Chalcraft and Soluk 2005; Nilsson et al. 2006). In addition to between-study variation in fish assemblages, fish density, initial invertebrate assemblages, and environmental conditions such as structural complexity and visibility may also determine how fish predation affects invertebrate communities (Pierce and Hinrichs 1997). Additionally, a very important issue that affects the outcome and interpretation of the results is the temporal and spatial scale of the study (Englund 2005). In addition to timescale, results may vary considerably between small-sized enclosures and ecosystem-scale studies depending on experimental methodology applied. High spatial and temporal variability in nature is more a rule than an exception, and it is not straightforward to extrapolate small-scale experimental studies into larger ecosystem scales (Petersen and Englund 2005). Therefore, more studies on ecosystem scales such as whole-lake manipulations are required to comprehend large-scale processes and to make adequate ecosystem management decisions (Schindler 1998).

High concentrations of dissolved organic compounds in boreal lakes affect the thickness of the productive layer since dissolved humic substances efficiently absorb light (Jones and Arvola 1984; Karlsson et al. 2009). As a result, humic lakes are often strongly stratified in terms of light availability and oxygen concentration, limiting the foraging possibilities of fish into narrow surface layers (Estlander et al. 2012, 2017). As deep benthic macroinvertebrate communities are usually unreachable for fish, the shallow oxygenated littoral zone provides the only suitable areas for benthic foraging (Rask et al. 1999). Due to limited light, macrophyte coverage is restricted and floating-leaved and emergent vegetation are dominant life forms (Estlander et al. 2009). Therefore, the littoral benthic macroinvertebrate community is usually restricted to a quite narrow surface

area (Estlander et al. 2012). Fish assemblages in boreal lakes are often species poor (Rask et al. 2000), and thus only few species are responsible for the predation pressure on the benthic community. In such structurally simple habitats with few fish species, the keystone predators may play a controlling role in regulating benthic macroinvertebrate communities (Nummi et al. 2012). Perch (*Perca fluviatilis*) has been reported to be a keystone predator on aquatic invertebrates in ecosystems with sparse vegetation and low interspecific competition (Power et al. 1996; Rask et al. 2001). *P. fluviatilis* undergoes ontogenetic diet shifts from feeding on zooplankton through a macroinvertebrate feeding phase to piscivory (Estlander et al. 2010). While feeding on benthic food, *P. fluviatilis* is known to prefer large invertebrates when these are available (Keast 1977; Nummi et al. 2012).

As relatively simple ecosystems, boreal lakes are suitable for ecosystem-scale experiments when attempting to comprehend the role of fish predation on benthic macroinvertebrates. We analyzed the effects of changing predation pressure that had been induced by non- and size-selective fishing of *P. fluviatilis* in an entire-lake experiment on the macroinvertebrate community of a small forest lake. We sampled the littoral benthic community yearly during the fishing manipulations of the 2007–2012 period and analyzed the macroinvertebrate diet of *P. fluviatilis*. We expected that the biomass, density and community structure of the benthic macroinvertebrates would reflect the predation pressure of the *P. fluviatilis* populations. Predation is considered the primary factor determining the size distribution of prey communities and prey preference is size-dependent (Blumenshine et al. 2000), therefore we hypothesized that a) the size structure of the *P. fluviatilis* population would affect the structure of the macroinvertebrate community. Additionally, predation pressure overall is density dependent (Leppä et al. 2003), and therefore we hypothesized that b) the density of the *P. fluviatilis* population would regulate the total macroinvertebrate density.

Materials and methods

Fish population treatments

The study was conducted in the Evo district (Southern Finland, 61°13'N, 25°12'E) in the meso-humic Lake

Iso Valkjärvi (3.8 ha) during 2007–2012. The lake had been divided into two parts by a double plastic wall (Rask et al. 1996), and both divisions were quite similar in their morphometry (surface area 1.6 and 2.2 ha; mean depth 2.8 and 3.8 m, respectively). The fish community in both sides consisted almost exclusively of *P. fluviatilis* and pike (*Esox lucius*) (Olin et al. 2010). The two halves of the lake underwent different fishing removal procedures of *P. fluviatilis* (targeted on the spawning stock > 7 cm) to study the effect of fishing on life-history traits of the population (Olin et al. 2017). The one side was fished non-selectively (non-selective fishing = NSF, all size-classes > 7 cm targeted), and the other side was treated negatively size selectively (size-selective fishing = SSF, large individuals, ≥ 16 cm not targeted). *P. fluviatilis* is the most important predator that feeds on the benthic macroinvertebrates in the lake, and the size limit was selected to correspond to the average size *P. fluviatilis* shifts from benthic food to piscivory (Estlander et al. 2010). The removal fishing was conducted every spring (May–June) in 2008–2011 (no fish removal occurred in 2007 and 2012) using wire-traps (12 × 12 mm mesh; 5 × 80 cm opening) and gillnets (mesh sizes in bar length 10–55 mm at NSF and 10–15 mm at SSF, net size 1.8 × 30 m), for more detailed methodology see Olin et al. (2017). Annual fish removal efforts were 10–235 wire-trap days and 47–186 gillnet days at NSF and 56–438 wire-trap days and 65–146 gillnet days at SSF, aiming to remove half of the biomass of the targeted length classes or total estimated population (Schnabel method; Seber 1982) every year. The cumulative removal catch during 2008–2011 interval was 70 (NSF) and 38 (SSF) kg ha⁻¹ year⁻¹ (Olin et al. 2017). The release of large individuals (≥ 16 cm) from the catch at SSF was successful because the numbers of yearly removed large individuals varied between only 3–70, i.e., 0.1–10% of total catch, whereas the numbers of removed large individuals from the NSF division ranged between 31 and 228 per year, i.e., 2–23% of the total catch. For more detailed methodology on fish removal and perch population estimates and responses, see Olin et al. (2017). The numbers of large perch decreased considerably in the NSF division but remained more stable in the SSF side of the lake (Olin et al. 2017) (Fig. 1). The manipulative fish removal effort from both experimental divisions caused an increase in recruitment and the density of

small-sized (< 12 cm) *P. fluviatilis* (Estlander et al. 2017; Olin et al. 2017) (Fig. 1). During the study period 2007–2012, the environmental parameters were quite similar, totals of chlorophyll *a* $7 \pm 2 \mu\text{g l}^{-1}$ and phosphorus $14 \pm 4 \mu\text{g l}^{-1}$ for both sides. Total nitrogen $560 \pm 50 \mu\text{g l}^{-1}$ and Secchi depth 2.9 ± 0.1 m were recorded for NSF, whereas $530 \pm 60 \mu\text{g l}^{-1}$ and 2.6 ± 0.2 m were recorded for the SSF side (no significant difference ($p < 0.5$), see also Estlander et al. 2017; Olin et al. 2017).

Macroinvertebrate sampling and analysis

Macroinvertebrate samples were taken by a tube sampler (diameter 86 mm) from three different sampling sites from the shallow littoral area (0.5–1 m depth, three replicates each) yearly (2007–2012) in late August to early September. The littoral area of the lake is very narrow and consists of sparse stands of floating-leaved *Nuphar lutea* (Estlander 2011), and the sampling sites were chosen evenly from around the narrow littoral belt with fixed yearly stations. The samples were sieved through a 0.5 mm mesh and frozen for later analysis. Samples were later picked, preserved in 80% ethanol and then analyzed under an Olympus SZ-ST stereo microscope. The macroinvertebrates were determined for the major taxonomic groups according to the method described by Wallace et al. (1990) and also Nilsson (1996, 1997). This coarse level of identification was selected to correspond to the same level that was possible in perch diet analyses. The wet weights of main taxa were determined by first soaking the animals in water for 10 min, drying them of excess water on paper and weighed with an accuracy of 1 mg (Grönroos 2009).

Diet analyses

P. fluviatilis for diet analyses (NSF; $n = 529$, SSF; $n = 491$) were sampled by Nordic multimesh gillnets according to the standard gillnetting procedure three times in July–August from 2005 to 2012 inclusive (CEN 2005, Olin et al. 2013). The total fishing effort was 6–8 nets and the soak time 12 h (overnight). The sampling procedure was stratified, random and included three depth strata (surface, < 3 m and 3–8 m) and randomly selected gillnet sites. Each fish was measured to the nearest millimeter (total length) and weighed to the

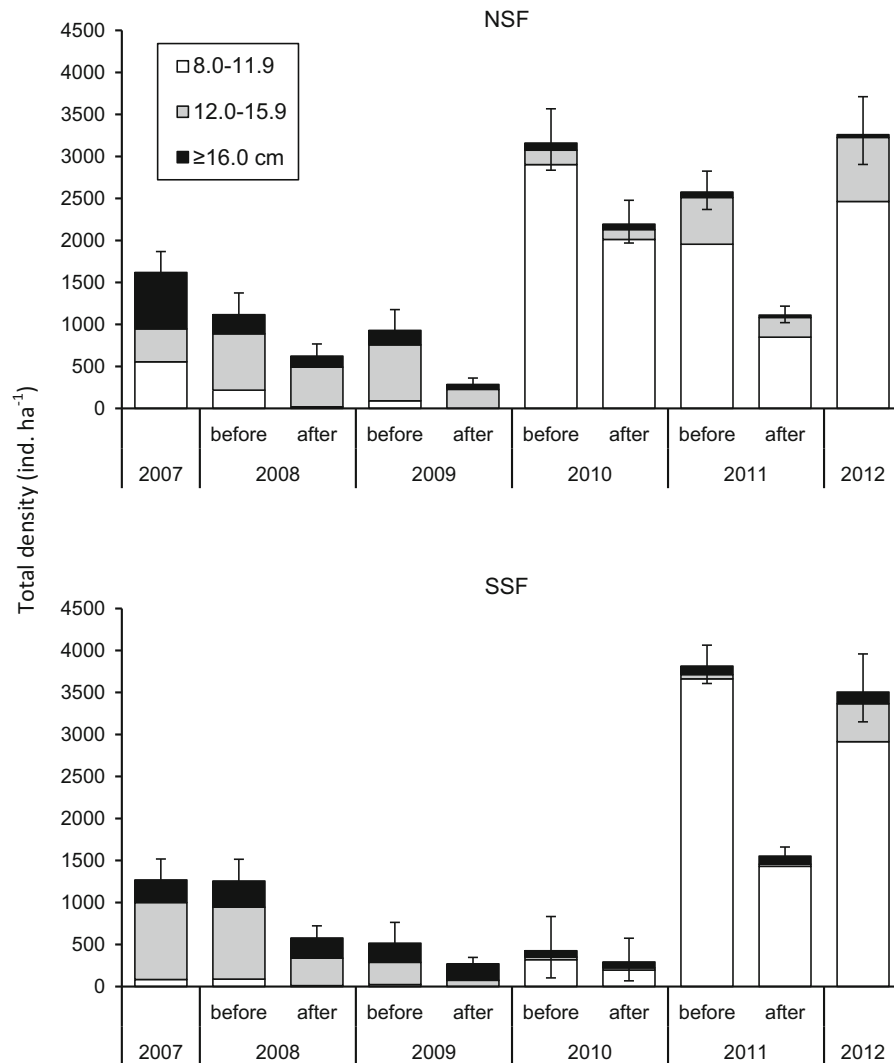


Fig. 1 Estimated annual total density (ind. ha⁻¹) of *P. fluviatilis* size-classes (< 12, 12–15.9, ≥ 16 cm) before and after the perch removal in spring 2007–2012 and both fishing procedures (NSF non-selective fishing, SSF size-selective fishing)

nearest gram. The stomach contents were analyzed for fullness (12 level scale) and volume proportions of different food items (Windell 1971). Different food items were pooled into three groups: zooplankton, macroinvertebrates and fish. Additionally, macroinvertebrates were categorized to the nearest identified taxon. The diet was split into three categories according to fish size, as the size-class < 12 cm is known mainly to consume zooplankton, 12–15.9 cm macroinvertebrates and at ≥ 16 cm to be piscivorous in Evo forest lakes (Estlander et al. 2010). The zooplankton diet of *P. fluviatilis* and fish removal responses in the zooplankton community are described in detail by Estlander et al. (2017).

Statistical analyses

To inspect the effects of fishing procedure and year on macroinvertebrate communities in general, a permutational multivariate anova (PERMANOVA; Anderson 2001) and a principal coordinate analysis (PCoA; Gower 1966) were performed. In PERMANOVA analysis of variance is performed for a community distance matrix and *p* values are based on a permutation test with pseudo-*F* ratios. Thus, PERMANOVA tests whether there are differences in the overall community structure. These multivariate methods were conducted using R (version 3.3.3; R Core Team 2017) and package

vegan (version 2.4.3.; Oksanen et al. 2017). Bray–Curtis dissimilarity measure was used in both methods, and PERMANOVA was run using 999 permutations. To study the community changes more in detail, i.e., which taxa were affected, also taxon-specific ANOVAs were performed. Thus, the effects of fishing procedure and year on the total density, total biomass, mean individual size, measured as mean weight and calculated as total biomass divided by total abundance, and taxon-specific density of benthic animals were analyzed by a two-way repeated-measures ANOVA (RM-ANOVA) that takes into account the temporal autocorrelation between sequential samples (SAS software). A $\ln(x + 1)$ transformation was applied to the data prior to analysis to ensure normality of residuals and homogeneity of variances. The differences between years, fishing procedures, and size-classes in *P. fluviatilis* diet were calculated by a multivariate analysis of variance (MANOVA, proc. GLM in the SAS software) including volume proportions of different food items. These food items were the following: zooplankton, macroinvertebrates and fish, or macroinvertebrate categories including: Chironomidae, *Asellus aquaticus*, Trichoptera, Megaloptera, Odonata, Ceratopogonidae, Ephemeroptera, and other macroinvertebrates as the dependent variables, and year (2005–2012), fishing procedure (NSF and SSF), and size-class (< 12, 12–15.9 and ≥ 16 cm) as independent variables including third order interactions (autocorrelation tested and found negligible). To equalize the variances, the diet data was arcsine-transformed before the analyses. Tukey's test with the Bonferroni correction was used for pairwise comparisons.

Results

Macroinvertebrate biomass, mean size, density, and community responses

The macroinvertebrate biomass increased for the NSF division (RM-ANOVA year \times fishing: $F_{5,18} = 17.64$, $p < 0.001$) toward the end of the study period 2007–2012 (RM-ANOVA year: $F_{5, 18} = 6.78$, $p < 0.001$) and remained relatively constant for the SSF procedure side (RM-ANOVA fishing: $F_{1, 18} = 29.81$, $p < 0.001$) with an increase in 2011 and decrease in 2012 (Table 1). The macroinvertebrate mean size increased at NSF (RM-ANOVA year \times

fishing: $F_{5, 18} = 6.78$, $p = 0.001$) toward the end of the study period (RM-ANOVA year: $F_{5, 18} = 13.11$, $p < 0.001$) and decreased at SSF (RM-ANOVA fishing: $F_{1,18} = 6.19$, $p = 0.023$). This size difference, which was reflected also on total biomass, was mainly due to the increase in the rather large-sized Odonata at NSF during 2011–2012 (Table 1). The total macroinvertebrate density first increased during 2007–2009, after which a steep decline occurred at both sections (RM-ANOVA year: $F_{5, 18} = 8.40$, $p = 0.003$) (Table 1). The effect of fishing alone or the interaction of year and fishing procedure were not significant (RM-ANOVA: $p > 0.05$).

PERMANOVA revealed that both year and fishing had significant main effects on macroinvertebrate community structure, and the effect of year was more significant and stronger than fishing (Table 2). No significant interaction was detected. Moreover, PCoA ordination (Fig. 2) showed that, in general, the differences in community composition were larger between the years than between the fishing treatments. Ordination also showed that for the SSF treatment years of 2007–2009 had a rather unchanging community composition, which then diverged in later years. There was more variation in the NSF treatment during the first years, but the years 2011–2012 differed from the earlier years. The community in both divisions was characterized by Arachnida, Chironomidae, Coleoptera, and Ephemeroptera in 2008–2009. Odonata especially increased in the NSF division in 2011 and 2012 in comparison with previous years.

The most numerous macroinvertebrate taxa in both sides of the lake were Chironomidae, Ephemeroptera, Trichoptera, Megaloptera, and Arachnida (Table 1), and the between-year density variations were significant among the most common taxa except for Trichoptera (Table 3). Chironomidae and Ephemeroptera densities in both sections of the lake increased during 2007–2009, thereafter they declined steeply (Table 1). Some taxa also showed a statistically significant response to fishing (Table 3), as the densities of *Asellus aquaticus* and *Bivalvia* were higher for the SSF treatment and the density of Ceratopogonidae at NSF (Table 1). Two taxa, Arachnida and Odonata, showed an interaction between year and fishing procedure (Table 3). Arachnida density was high for the SSF procedure until 2009 and vanished from samples after that year, whereas the Arachnida density in the NSF procedure side peaked

Table 1 Total yearly biomass (g m^{-2}), total density (ind. m^{-2}) mean size (mg ind^{-1}) and mean density (ind. m^{-2}) of main macroinvertebrate groups during the study period

		2007	2008	2009	2010	2011	2012
Total biomass	NSF	1.4 ± 0.2	4.0 ± 0.4	10.4 ± 1.3	5.7 ± 2.4	15.7 ± 8.9	24.2 ± 5.2
	SSF	2.2 ± 0.8	3.9 ± 0.4	4.4 ± 0.6	4.8 ± 0.9	12.3 ± 5.8	1.9 ± 0.9
Total density	NSF	2200 ± 750	4492 ± 1353	9898 ± 1096	2698 ± 2351	3136 ± 1778	1710 ± 807
	SSF	2257 ± 575	3117 ± 717	9210 ± 770	2028 ± 1240	2459 ± 1819	570 ± 124
Mean size	NSF	0.6 ± 0.2	0.8 ± 0.1	1.1 ± 0.2	3.1 ± 2.5	6.0 ± 3.5	15.8 ± 5.2
	SSF	1.0 ± 0.1	1.3 ± 0.2	0.4 ± 0.1	6.4 ± 2.7	3.5 ± 1.7	2.8 ± 2.4
Arachnida	NSF	0 ± 0	19 ± 33	172 ± 162	19 ± 33	0 ± 0	36 ± 62
	SSF	115 ± 57	77 ± 33	115 ± 81	96 ± 66	0 ± 0	0 ± 0
<i>Asellus aquaticus</i>	NSF	0 ± 0	0 ± 0	0 ± 0	57 ± 99	36 ± 62	0 ± 0
	SSF	19 ± 33	172 ± 152	0 ± 0	115 ± 57	36 ± 62	36 ± 62
Bivalvia	NSF	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	SSF	0 ± 0	19 ± 33	0 ± 0	0 ± 0	71 ± 62	0 ± 0
Ceratopogonidae	NSF	38 ± 33	19 ± 33	0 ± 0	19 ± 33	143 ± 62	0 ± 0
	SSF	19 ± 33	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Chironomidae	NSF	1358 ± 551	3960 ± 866	7001 ± 487	2048 ± 2167	1461 ± 1123	713 ± 589
	SSF	880 ± 133	1645 ± 316	2955 ± 365	880 ± 670	1568 ± 1536	356 ± 327
Coleoptera	NSF	0 ± 0	0 ± 0	29 ± 41	0 ± 0	0 ± 0	0 ± 0
	SSF	38 ± 66	19 ± 33	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Ephemeroptera	NSF	669 ± 133	555 ± 478	1951 ± 1217	96 ± 88	0 ± 0	0 ± 0
	SSF	976 ± 349	650 ± 271	5308 ± 933	249 ± 295	0 ± 0	0 ± 0
Megaloptera	NSF	19 ± 33	115 ± 57	57 ± 0	115 ± 57	0 ± 0	107 ± 107
	SSF	38 ± 33	38 ± 33	86 ± 41	172 ± 115	36 ± 62	36 ± 62
Odonata	NSF	0 ± 0	0 ± 0	0 ± 0	38 ± 33	392 ± 223	214 ± 107
	SSF	0 ± 0	38 ± 33	0 ± 0	0 ± 0	107 ± 107	0 ± 0
Trichoptera	NSF	115 ± 99	325 ± 166	689 ± 406	287 ± 152	1105 ± 810	642 ± 283
	SSF	172 ± 99	459 ± 199	746 ± 325	172 ± 57	606 ± 549	143 ± 247

Dotted line represents years before and after fish manipulations

Table 2 Results of PERMANOVA (permutational multivariate anova using distance matrices) with two factors fishing procedure and year. PERMANOVA was based on Bray–Curtis dissimilarity

Source of variation	<i>F</i>	Partial <i>R</i> ²	<i>df</i>	<i>P</i>
Year	5.11	0.46	5	0.001
Fishing	2.57	0.047	1	0.035
Fishing *year	0.97	0.088	5	0.487
Residuals	0.40		22	
Total			33	

Values significant at the 0.05 level are in bold

in 2009 but was very low before and after. Odonata was an abundant macroinvertebrate group in the NSF division from 2010 onward, whereas Odonata was found in the SSF side only in 2008 and 2011.

Diet of *P. fluviatilis*

The macroinvertebrate diet of *P. fluviatilis* categorized as zooplankton, macroinvertebrates, and fish showed an interaction between year, fishing procedure, and size-class (Fig. 3, Table 4). Zooplankton was the

2007–2012 and both fishing procedures (NSF non-selective fishing, SSF size-selective fishing) (\pm standard deviation)

preferred diet (volume percent composition > 60%) for size-class < 12 cm for both treatment sides, whereas a higher preference was detected for the NSF procedure for all size-classes (Fig. 3, Table 4). The macroinvertebrate diet was preferred by both larger size-classes 12–15.9 and 16 cm (> 60%) in both sides of the lake, although large *P. fluviatilis* (size-class \geq 16 cm) fed mainly on macroinvertebrates in the NSF side (> 80%). However, a considerable proportion (> 20%) of the diet in the SSF side consisted of juvenile *P. fluviatilis* (Fig. 3, Table 4).

When looking at the specific benthic taxa separately, diet differences were apparent. Chironomidae was a popular food source among all size-classes in both treatment sides but were predominantly preferred by the smallest size-class (Fig. 4, Table 5). Ceratopogonidae was sporadically found in the diets of all size-classes (Fig. 4) with some trend showing in the early years in the NSF side and in later years in the SSF side (Table 5). *A. aquaticus* was more abundant in the diets of *P. fluviatilis* in NSF especially for the larger-sized *P. fluviatilis* (12–15.9 and \geq 16 cm) (Fig. 4, Table 5). Ephemeroptera was consumed by all size-classes in both treatment sides

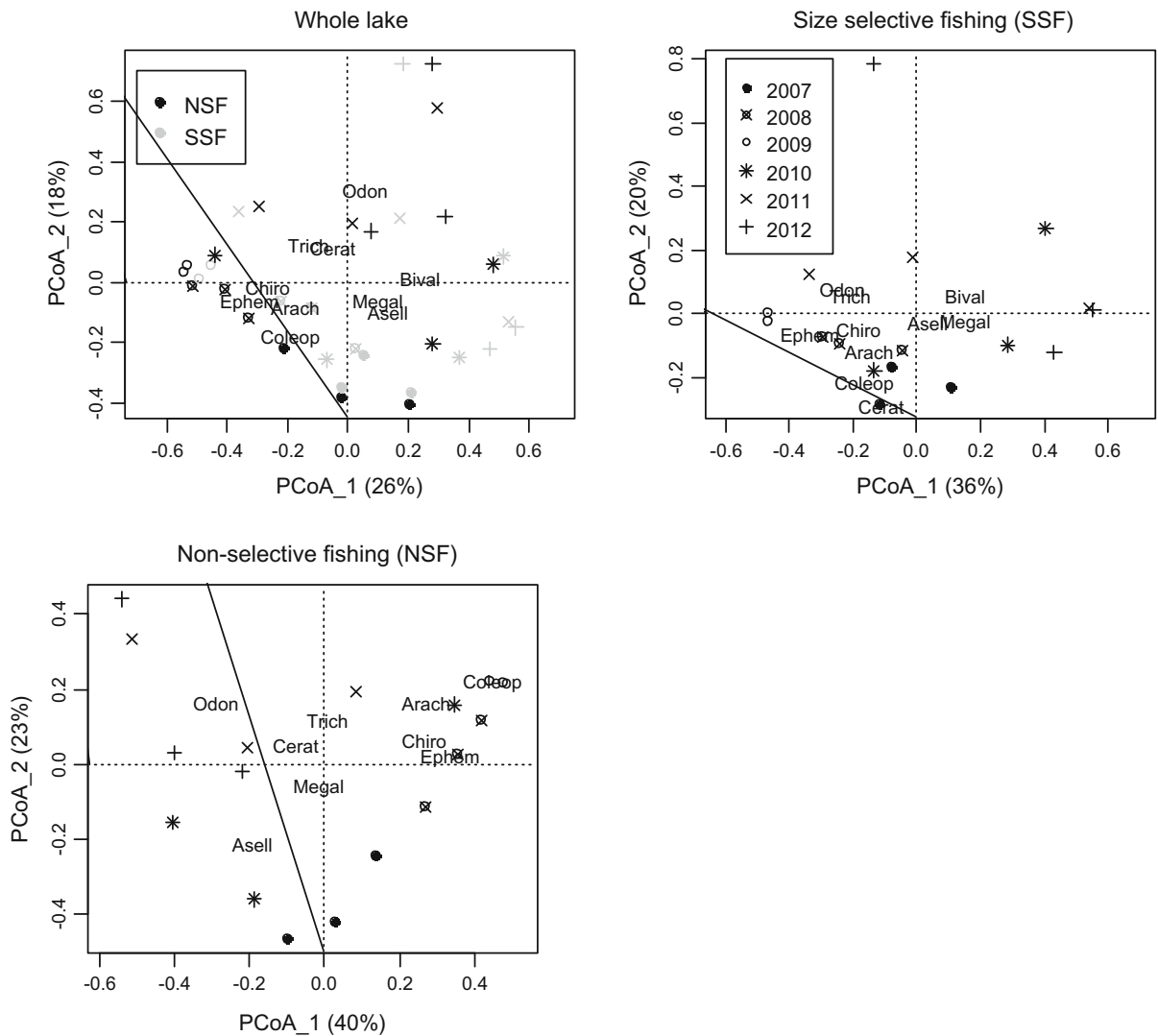


Fig. 2 First two axes of principal coordinate analysis for the whole lake and separately for the two different fishing treatments. The percent of variation explained by each axis is also shown. Species are plotted as weighted averages. Abbreviations for each taxon (Arach = Arachnida, Asell = *Asellus*

aquaticus, Bival = Bivalvia, Cerat = Ceratopogonidae, Chiron = Chironomidae, Coleo = Coleoptera, Ephem = Ephemeroptera, Megal = Megaloptera, Odon = Odonata, Trich = Trichoptera)

(Fig. 4, Table 5). Megaloptera was preferred by the larger-sized *P. fluviatilis* especially in the earlier years for the size-class 12–15.9 cm in the SSF and for the largest *P. fluviatilis* (≥ 16 cm) in the NSF side (Fig. 4, Table 5). Odonata was found in the diets of the larger size-classes (Fig. 4, Table 5), with interaction between fishing and the year, which indicated that the effect of fishing showed between-year variation (Table 5). Trichoptera was an abundant taxon consumed by the larger size-classes, in the NSF

side by *P. fluviatilis* ≥ 16 cm and in the SSF side by 12–15.9 cm with high between-year variation (Fig. 4, Table 5). The proportions of other taxa (Arachnida, Bivalvia) in the diets of *P. fluviatilis* displayed quite high variation (Table 5). In general, the proportion of chironomids for the size-class 12–15.9 cm decreased and larger-sized macroinvertebrate taxa such as *A. aquaticus*, Trichoptera, and Megaloptera for SSF increased, and Odonata for the NSF treatment increased (Fig. 4). For size-

Table 3 Two-way repeated-measures ANOVA (RM-ANOVA) of the effects of fishing procedure, year and the interaction of fishing procedure and year to the density of main taxa

	Source of variation	<i>F</i>	<i>df</i>	<i>P</i>
<i>ARACHNIDA</i>	Fishing	9.09	1,18	0.007
	Year	6.36	5,18	0.001
	Fishing * year	3.64	5,18	0.019
<i>ASELLUS</i>	Fishing	5.37	1,18	0.032
	Year	1.52	5,18	0.232
	Fishing * year	0.78	5,18	0.577
<i>BIVALVIA</i>	Fishing	5.23	1,18	0.035
	Year	2.54	5,18	0.232
	Fishing * year	2.54	5,18	0.577
<i>CERATOPOGONIDAE</i>	Fishing	9.52	1,18	0.006
	Year	2.52	5,18	0.067
	Fishing * year	2.05	5,18	0.119
<i>CHIRONOMIDAE</i>	Fishing	2.83	1,18	0.120
	Year	3.16	5,18	0.032
	Fishing * year	0.38	5,18	0.857
<i>COLEOPTERA</i>	Fishing	0.39	1,18	0.540
	Year	0.72	5,18	0.616
	Fishing * year	1.05	5,18	0.422
<i>EPHEMEROPTERA</i>	Fishing	0.48	1,18	0.496
	Year	30.39	5,18	< 0.001
	Fishing * year	0.05	5,18	0.998
<i>MEGALOPTERA</i>	Fishing	0.01	1,18	0.941
	Year	3.27	5,18	0.028
	Fishing * year	0.87	5,18	0.517
<i>ODONATA</i>	Fishing	10.36	1,18	0.005
	Year	10.96	5,18	< 0.001
	Fishing * year	7.60	5,18	< 0.001
<i>TRICHOPTERA</i>	Fishing	4.15	1,18	0.057
	Year	1.57	5,18	0.219
	Fishing * year	2.43	5,18	0.075

Values significant at the 0.05 level are in bold

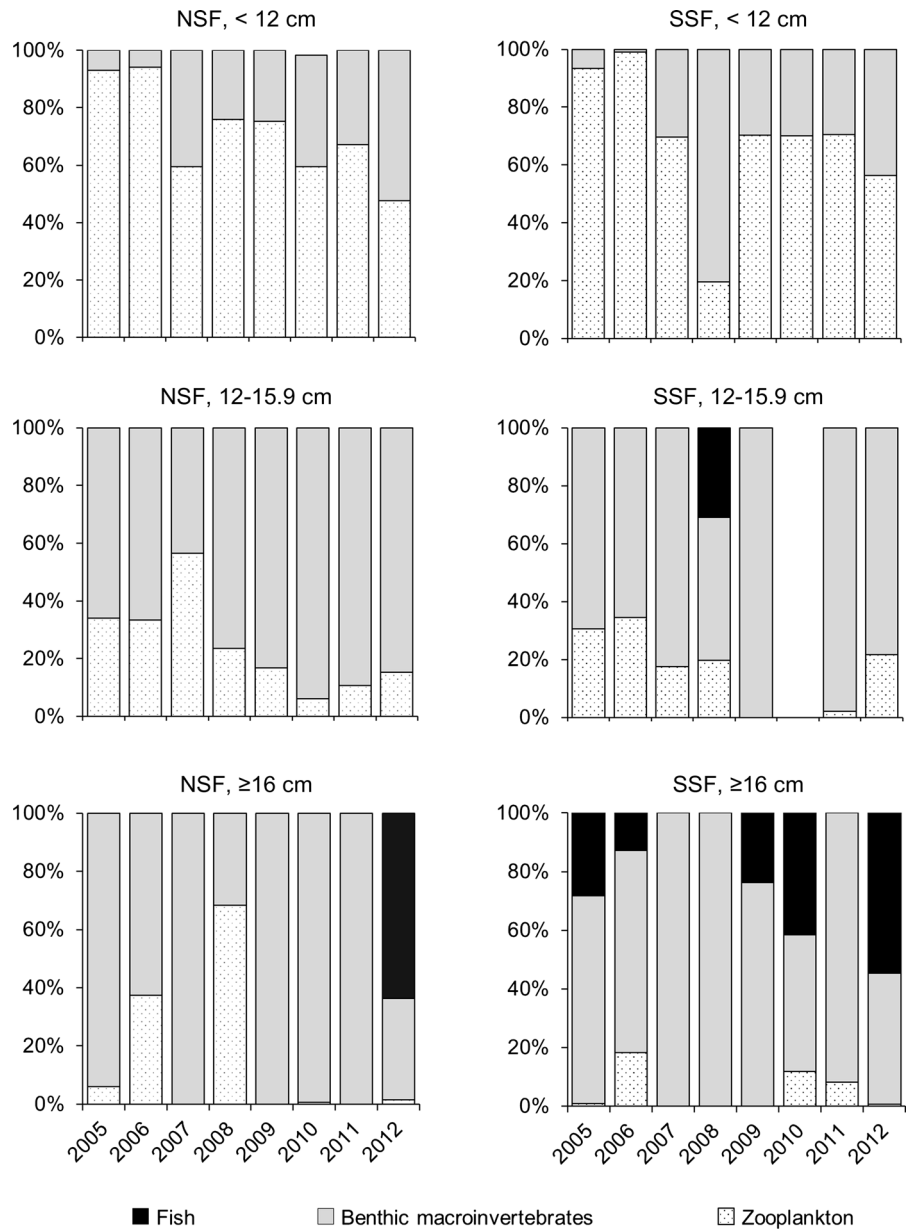
class ≥ 16 cm, the benthic macroinvertebrate diet of *P. fluviatilis* consisted mainly of larger taxa Trichoptera, *A. aquaticus* and Odonata in the NSF side, and Chironomidae in the SSF side (Fig. 4).

Discussion

As expected, the benthic macroinvertebrate community reflected the overall predation pressure by *P. fluviatilis*. The difference in size structure of the *P. fluviatilis* population within the two separate divisions of the lake affected the structure of the benthic community, as the macroinvertebrate biomass

increased for the NSF side and decreased for the SSF treatment side toward the end of the study period. These trends in biomass and mean size were mostly due to the increase in the large-sized macroinvertebrate taxa, specifically the Odonata for the NSF and decrease for the SSF. The selectivity in fishing affected the predator size structure which mirrored down to the size structure of prey. This compositional difference was consistent with our expectations and corroborated the findings of an earlier study (Blumenshine et al. 2000), as the density of large-sized taxa such as Odonata was suppressed at the SSF division where large *P. fluviatilis* individuals (> 16 cm) were released. Gilinsky (1984) reported the Odonata

Fig. 3 Percentage composition of food items zooplankton (white dotted), benthic macroinvertebrates (gray) and fish (black) in stomach content of three fish size-classes (< 12, 12–15.9, ≥ 16 cm) of *P. fluviatilis* during the study period 2007–2012 and both fishing procedures (NSF non-selective fishing, SSF size-selective fishing)



densities to be greater in the absence of predation, and Nummi et al. (2012) found large-sized macroinvertebrates such as odonates and dytiscids, to increase in the absence of *P. fluviatilis* predation. Although Trichoptera did not show any significant responses to fishing or from year to year, as it is preferred prey by larger perch (Estlander et al. 2010) and was widely consumed by the larger size-classes also in this study, the predation induced by large *P. fluviatilis* individuals can be expected to have influenced this large-sized and

heterogeneous macroinvertebrate group (Gilinsky 1984). High density and no clear response to predation pressure by fish may be explained by the complexity of this common and large group which has specialized taxa (predacious and nonpredatory species) living in the littoral area among debris (Gilinsky 1984). The density of *A. aquaticus* was constantly higher at SSF though *A. aquaticus* was especially consumed by the larger size-classes in both lake divisions. *A. aquaticus* is very common in the littoral zone of boreal lakes, and

Table 4 Multivariate ANOVA of diet categories (zooplankton, macroinvertebrate, fish) of perch between different size-classes (< 12, 12–15.9, \geq 16 cm) and fishing procedures (NSF non-selective fishing, SSF size-selective fishing) during the study period 2007–2012

	Source of variation	F	df	P	
Zooplankton	Fishing	10.81	1,1008	0.001	
	Year	10.59	7,1008	< 0.001	
	Size-class	97.60	2,1008	< 0.001	
	Fishing * year	2.13	7,1008	0.385	
	Fishing * size-class	0.07	2,1008	0.933	
	Year * size-class	4.20	14,1008	< 0.001	
	Fishing * year * size-class	1.95	14,1008	0.019	
	Macroinvertebrates	Fishing	0.43	1,1008	0.514
		Year	5.01	7,1008	< 0.001
		Size-class	51.90	2,1008	< 0.001
Fishing * year		1.42	7,1008	0.192	
Fishing * size-class		3.03	2,1008	0.049	
Year * size-class		1.69	14,1008	0.051	
Fishing * year * size-class		1.97	14,1008	0.017	
Fish	Fishing	4.28	1,1008	0.039	
	Year	1.49	7,1008	0.166	
	Size-class	6.39	2,1007	0.002	
	Fishing * year	1.57	7,1008	0.141	
	Fishing * size-class	1.73	2,1008	0.178	
	Year * size-class	1.84	14,1008	0.029	
	Fishing * year * size-class	1.99	14,1008	0.016	

Values significant at the 0.05 level are in bold

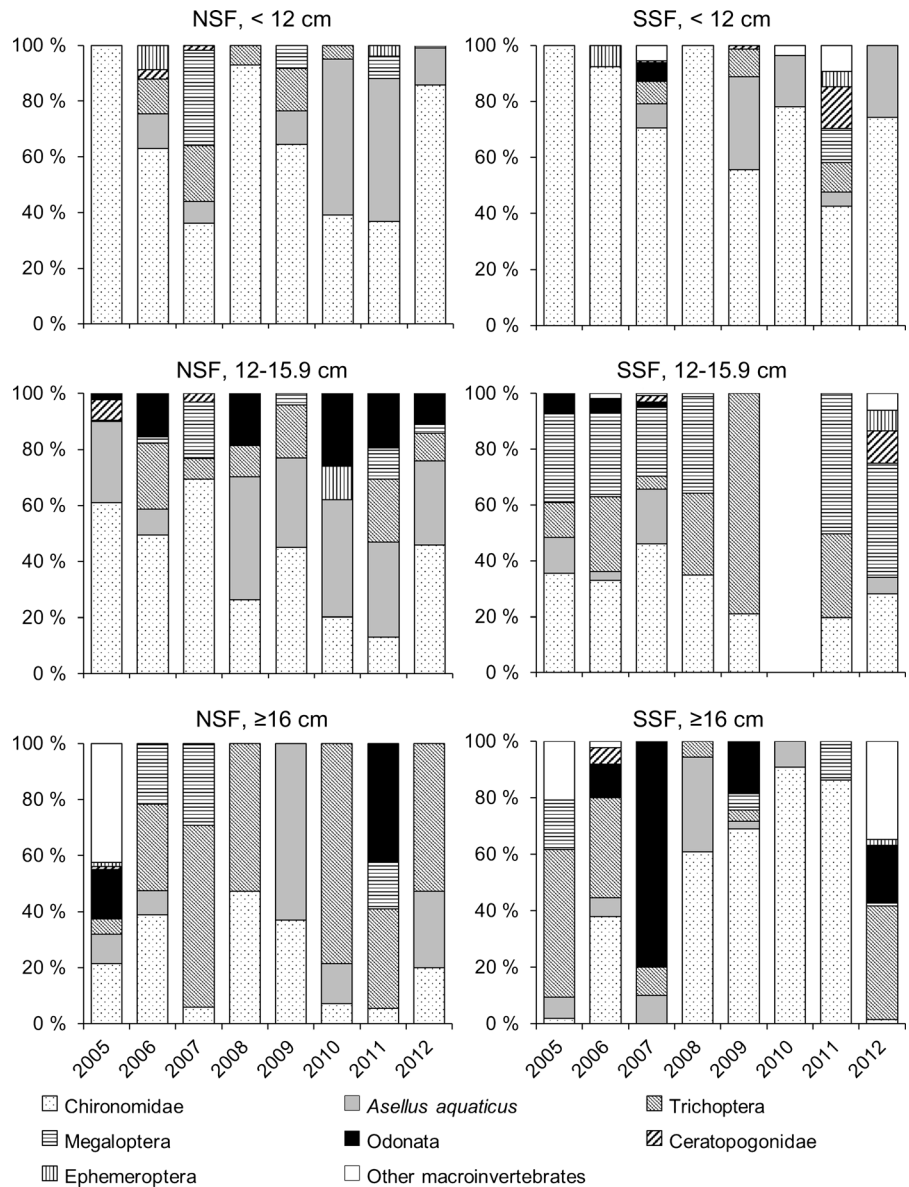
as a large-sized invertebrate it is preferred by *P. fluviatilis* (Rask and Hiisivuori 1985; Estlander et al. 2010). Therefore, the fluctuations in the *A. aquaticus* densities between the two fishing procedure divisions could be explained by the initial division-specific density differences and overall predation pressure (Rask et al. 2001).

The predator must maximize the energetic efficiency in terms of predator–prey body-size ratios, and thus predator size distribution often reflects down to the distribution of prey size (Rice et al. 1993). The phenomenon was also observed in our present study, as larger *P. fluviatilis* individuals targeted for larger prey items and the relatively sessile or slow-moving prey taxa that were suppressed. The results are also in agreement with those of studies on similar boreal lakes nearby which emphasizes the diet preference of *P. fluviatilis* on large prey individuals such as Odonata, Trichoptera and *A. aquaticus* (Rask 1986; Estlander et al. 2010). The results also suggest that size-selective fishing that affects the size structure of the fish population may have far-reaching effects on lake ecosystems, since large-sized macroinvertebrates are often predators that control their prey (Covich et al.

1999). When predator density increases and predators become food limited due to increasing intraspecific competition, the availability of energetically optimal large prey sizes decrease due to greater predation pressure (Pyke 1984). Therefore, the effect of fish predation on prey size distribution is not only dependent on predator size distribution but also on predator abundance *per se* (Blumenshine et al. 2000).

We found no clear response of total macroinvertebrate density to fishing procedure, mainly because the overall predation pressure has been reported not to be solely due to predator size but also partly due to density dependence (Leppä et al. 2003). We therefore hypothesized that the density of the benthic community would mirror that of the predator density. The macroinvertebrate densities of both divisions of the lake decreased notably after 2009 which was due to the changes in the predation pressure that resulted from the fishing conducted. Very strong *P. fluviatilis* year-classes emerged in both divisions after heavy fish biomass removal regardless of fishing procedure (Estlander et al. 2017; Olin et al. 2017) an event which created an increase in predation pressure. From 2010 onward, the density of small < 12 cm *P.*

Fig. 4 Macroinvertebrate diet of Chironomidae, *Asellus aquaticus*, Trichoptera, Megaloptera, Odonata, Ceratopogonidae, Ephemeroptera and other macroinvertebrates of three fish size-classes (< 12, 12–15.9, ≥ 16 cm) of *P. fluviatilis* during the study period 2007–2012 and both fishing procedures (NSF non-selective fishing, SSF size-selective fishing)



fluviatilis increased fivefold in both divisions, and a small increase was also detected in the middle size-class 12–15.9 cm (Estlander et al. 2017). An increase in the density of fish smaller than those depending on piscivory enhances predation pressure on the benthic community and increases intraspecific competition within and between *P. fluviatilis* year-classes associated with the depletion of benthic prey (Cobb and Watzin 1998). The fish density increase targeted the predation pressure especially for the most common taxa, such as Chironomidae and Ephemeroptera, both of which underwent steep density declines. These

rapid declines are in line with those reported by other studies, which found clear responses of chironomid densities to density-induced fish predation (Gilinsky 1984; Leppä et al. 2003; Tarvainen et al. 2008). The preferred macroinvertebrate diet of *P. fluviatilis* for both fishing procedures consisted mainly of Chironomidae that were particularly preferred by smaller fish (< 12 cm). Chironomids are one of the most important macroinvertebrate diet groups for benthic feeding fish in many lakes as they are often one of the most diverse and abundant groups from sediment-dwelling to macrophyte-associated species and therefore inhabit

Table 5 Multivariate ANOVA of perch diet categories as main macroinvertebrate groups between different size-classes (< 12, 12–15.9, \geq 16 cm) and fishing procedures (*NSF* non-selective fishing; *SSF* size-selective fishing) during the study period 2007–2012

	Source of variation	<i>F</i>	<i>df</i>	<i>P</i>
Asellus	Fishing	9.94	1,1008	0.002
	Year	1.39	7,1008	0.208
	Size-class	7.50	2,1008	< 0.001
	Fishing * year	1.51	7,1008	0.158
	Fishing * size-class	4.48	2,1008	0.012
	Year * size-class	1.01	14,1008	0.436
	Fishing * year * size-class	2.03	14,1008	0.014
Ceratopogonidae	Fishing	0.03	1,1008	0.869
	Year	1.44	7,1008	0.186
	Size-class	2.37	2,1008	0.094
	Fishing * year	2.49	7,1008	0.015
	Fishing * size-class	0.09	2,1008	0.918
	Year * size-class	1.60	14,1008	0.073
	Fishing * year * size-class	2.07	14,1008	0.011
Chironomidae	Fishing	1.23	1,1008	0.269
	Year	1.93	7,1008	0.061
	Size-class	0.64	2,1008	< 0.001
	Fishing * year	7.70	7,1008	< 0.001
	Fishing * size-class	1.71	2,1008	0.181
	Year * size-class	1.75	14,1008	0.041
	Fishing * year * size-class	0.83	14,1008	0.641
Ephemeroptera	Fishing	0.09	1,1008	0.767
	Year	0.41	7,1008	0.897
	Size-class	0.15	2,1008	0.860
	Fishing * year	1.00	7,1008	0.427
	Fishing * size-class	0.68	2,1008	0.507
	Year * size-class	0.64	14,1008	0.833
	Fishing * year * size-class	0.58	14,1008	0.879
Megaloptera	Fishing	0.46	1,1008	0.980
	Year	3.17	7,1008	0.003
	Size-class	8.19	2,1008	< 0.001
	Fishing * year	3.36	7,1008	0.002
	Fishing * size-class	5.86	2,1008	0.003
	Year * size-class	0.91	14,1008	0.550
	Fishing * year * size-class	1.24	14,1008	0.238
Odonata	Fishing	0.04	1,1008	0.835
	Year	0.75	7,1008	0.634
	Size-class	6.01	2,1008	0.003
	Fishing * year	2.30	7,1008	0.025
	Fishing * size-class	0.34	2,1008	0.715
	Year * size-class	1.05	14,1008	0.404
	Fishing * year * size-class	2.57	14,1008	0.001

Table 5 continued

	Source of variation	<i>F</i>	<i>df</i>	<i>P</i>
Trichoptera	Fishing	2.14	1,1008	0.144
	Year	1.45	7,1008	0.181
	Size-class	18.90	2,1008	< 0.001
	Fishing * year	4.17	7,1008	< 0.001
	Fishing * size-class	1.43	2,1008	0.239
	Year * size-class	2.91	14,1008	< 0.001
	Fishing * year * size-class	1.94	14,1008	0.019
Other taxa	Fishing	1.18	1,1008	0.277
	Year	3.14	7,1008	0.003
	Size-class	2.34	2,1008	0.097
	Fishing * year	0.64	7,1008	0.711
	Fishing * size-class	1.12	2,1008	0.327
	Year * size-class	5.27	14,1008	< 0.001
	Fishing * year * size-class	1.11	14,1008	0.343

Values significant at the 0.05 level are in bold

different niches (Gilinsky 1984; Estlander et al. 2010). Within the Chironomidae group, some taxa are predatory whereas others are nonpredatory, and thus density regulation may also occur within this group and in the absence of fish predation (Gilinsky 1984).

Ephemeroptera density also declined following the increased fish density in both fishing procedure divisions, which was a similar finding to that found for the decrease in chironomid densities. However, no clear change in the consumption of Ephemeroptera by *P. fluviatilis* was detected. Ephemeropterans are one of the most preferred food items for *P. fluviatilis* in nearby lakes (Estlander et al. 2010), and thus it can be presumed that the increasing predation pressure affected the overall density of that group. The taxa Megaloptera also displayed considerable yearly density fluctuation, and was consumed by larger size-classes when abundant. This is in line with that reported by Kornijów et al. (2016) who found a motile invertebrate *Sialis lutaria* from the order of Megaloptera to be significantly reduced by *P. fluviatilis*. Trichoptera was consumed by large size-classes in both divisions and was one of the most abundant groups together with Chironomidae and Ephemeroptera. Density variation of taxa such as Bivalvia, Ceratopogonidae, and Coleoptera could not be pinpointed to predation pressure solely due to their high initial lake-side-specific differences and yearly density fluctuations. The density of Arachnida showed

large yearly variation but similar to that found for *A. aquaticus* was more abundant for the SSF procedure in which the large perch individuals were spared. The density of the two taxa may be underestimated as the tube sampler used may underestimate the density of actively moving species (Rask and Hiisivuori 1985). The large-sized and less motile group Odonata displayed yearly fluctuation for the SSF procedure but showed a clear increasing density trend for the NSF procedure during the 2010–2012 interval. As stated, the density fluctuations may not be explained solely by predator density but rather by predator size structure, as Odonata was found in the diet of larger size-classes of *P. fluviatilis* and increased in the NSF side where the density of large perch was clearly decreased. However, yearly density fluctuation and distribution patchiness are also typical for the taxon (Gilinsky 1984).

Littoral benthic macroinvertebrate density and community structure display high natural spatial and temporal variation that relate to diverse spans of habitats (Hanson 1990; Strayer 1991). Fish select benthic prey on the basis of several prey characteristics such as: size, density, activity and exposure (Ware 1972; Ringler 1979). Our results are in line with those of other studies which suggest that intensive fishing of benthivorous fish can have pronounced effects on the macroinvertebrate community (Leppä et al. 2003), and predator size structure may affect the prey size

structure as big macroinvertebrate species are preferred by large fish individuals. Our results corroborate those reported by Hershey (1985) who showed that in addition to predator size-induced effects on prey body size, fish density may also have a greater effect on small but abundant chironomids than on larger taxa. In addition to size and density, the taxa most affected by fish predation are often the most active or exposed species (Stenson 1979; Kornijów et al. 2016), such as *A. aquaticus* and Odonata in our study (Rask 1986).

In whole-lake experiments, climatic factors and food web dynamics are principal sources of spatiotemporal variation in benthic communities (Schindler 1987). Moreover, the duration of ice-cover and yearly temperature fluctuations may strongly affect the structure of littoral benthic communities especially for the boreal lakes (Leppä et al. 2003). Additionally, longer experimental duration may allow for compensatory responses by the prey populations, such as intraguild competition and predation to emerge. Many large macroinvertebrates, such as odonates, are major predators on many other macroinvertebrate groups, such as trichopterans and chironomids (Gilinsky 1984; Diehl 1992). Moreover, many common invertebrate groups grow during their succession, and some groups, such as odonates, display a nymph phase lasting up to 3 years (Corbet 1980). All the afore-mentioned factors may confound the straightforward impact of the fish population and predation pressure changes. In addition to predation pressure by perch, pike is also present in this lake. Pike is known to consume macroinvertebrates and affect benthic community structure (Venturelli and Tonn 2005), but the structuring role of pike was not obvious in this present study, as the pike density increased in both divisions in concert with the density of small perch with no obvious difference between the two sides (Olin et al. 2017). Overall, pinpointing actual taxon-specific preference by *P. fluviatilis* to macroinvertebrate density and biomass changes is not straightforward due to seasonal variation of species-specific life cycles and spatiotemporal differences between macroinvertebrate sampling and snap-shot representation of fish diet.

In conclusion, our manipulative experiment on size-selective fishing demonstrated ecosystem effects cascading down from fish population structure changes to benthic communities. The study underlines the effect of predation pressure of *P. fluviatilis* on

benthic communities and highlights the keystone predator role of the species in relatively barren boreal lakes with limited opportunities for food supply and habitat segregation (Rask 1986). The study provides greater insight into the multiple effects of fish predation on littoral benthic communities, as though relatively clear fish size structure and density-dependent effects on the benthic community were detected, ecosystem effects can be highly variable and depend on the fluctuating population structure changes in targeted fish species or compensatory dynamics in prey communities. As the outcome of such manipulative ecosystem-scale experiments depends heavily on the initial benthic community structure and on the fish species used, to make broader generalizations on the effects of size-manipulative fishing on invertebrate communities requires further investigation using a larger array of fish species. Additionally, benthic habitats and communities are highly heterogeneous, thus accurate methods to discriminate between the functional prey availability to predators and the apparent prey availability and between the factors that affect the relationship between these two are needed to broaden our understanding of fish–macroinvertebrate interactions in littoral systems (Pierce and Hinrichs 1997).

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