

Project KESKALA: Studies on Ecologically Sustainable Fishing

Zooplankton rhapsody: Unexpected response in community following increased fish predation

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The impact of increased fish density on the crustacean zooplankton was studied in a small, forest lake. Interestingly and contrary to our hypothesis, increased fish density resulted in an increase in biomass of large-sized cladocerans, but a decrease in biomass of smaller and dominant cladoceran species. Thus, the effect of increased planktivory of fish was likely tempered by compensatory dynamics of zooplankton, wherein abundance of some species increased to compensate for population decreases by other species. This change in the relative species composition of zooplankton was seen as the increased diversity in crustacean zooplankton community. We conclude that instead of simple “top-down” or “bottom-up” regulation of zooplankton, the diverse array of connections among species is more likely to cause community dynamic fluctuations in zooplankton. Moreover, behavioural changes e.g. habitat change of fish may also have a pronounced effect on the response of zooplankton community on fishing.

Introduction

It is widely accepted that fishery exploitation can play an important role in structuring aquatic food webs (Kitchell *et al.* 2000, Harvey *et al.* 2003). Fishing directly affects the density, and community and population structures of fish, thus affecting predation of fish on zooplankton that has been cited as one of the most important factors influencing zooplankton community structure (Brooks and Dodson 1965). For example, Skoglund *et al.* (2013) showed that planktivorous fish generally prey upon large-bodied zooplankton comprising more efficient grazers on phytoplankton than the small-bodied zoo-

plankton (Brooks and Dodson 1965). Therefore, planktivorous fish can indirectly control primary production (Shapiro and Wright 1984, Carpenter *et al.* 1985, Hulot *et al.* 2014). However, food webs are complex and a large number of organisms interact directly and indirectly with each other (Polis and Holt 1992). For example, fish may exhibit ontogenetic niche shifts to or from planktivory (Werner and Gilliam 1984, Persson and Greenberg 1990) providing additional variability in predation pressure on zooplankton. Further, the role of competitive interactions among zooplankton in structuring zooplankton communities is also complex and still poorly understood (Pantel *et al.* 2015, Ryabov *et al.* 2015).

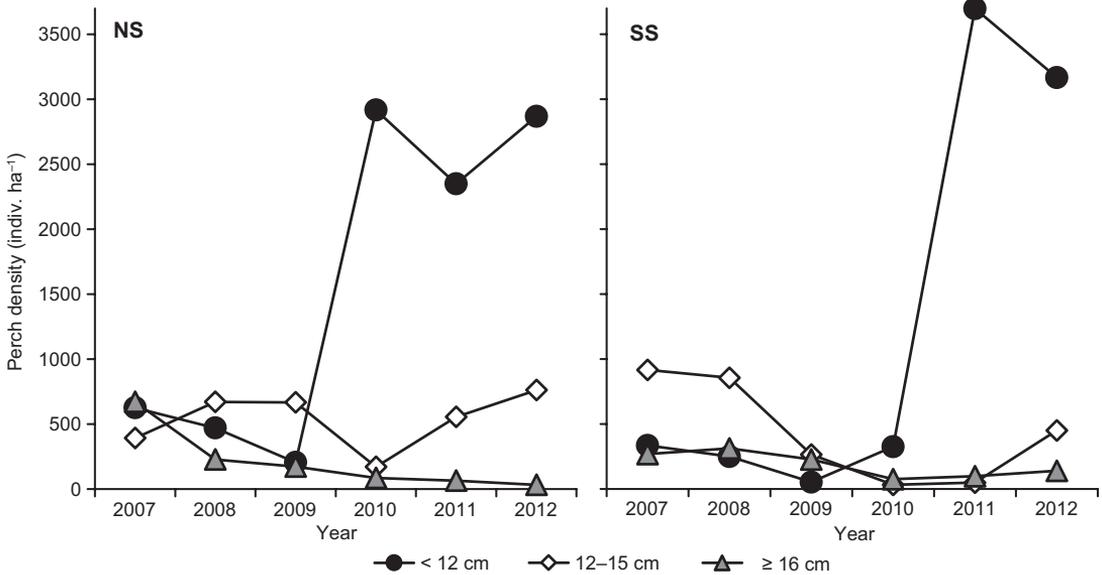


Fig. 1. Estimated annual total densities per length groups of perch in the lake compartments NS and SS.

When considering the importance of fish as top-down regulators in food webs, small oligotrophic forest lakes of boreal regions provide good opportunities to study the interactions between species, because those ecosystems are often relatively simple (Rask 1983) and the predatory control of zooplankton is usually pronounced (McQueen *et al.* 1986, 1989). The European perch (*Perca fluviatilis*) is often the dominant or only fish species in small, oligotrophic boreal lakes (Rask *et al.* 2000). Although adult perch is considered a predatory fish species, juveniles feed on zooplankton and as they grow, switch to larger food items, such as benthic macroinvertebrates and finally turn to piscivory (Allen 1935, Estlander *et al.* 2010).

Here, we studied an artificially-divided oligotrophic lake where perch is the only planktivorous fish species. One perch population was exposed to negatively size-selective fishing (SS = large individuals were released) and the other one to non-selective fishing (NS = all length classes were targeted). Both fishing procedures changed perch population structure towards smaller size (Fig. 1) and higher density (Olin *et al.* 2017). Earlier studies have shown (Estlander 2011, Estlander *et al.* 2012) that in the study lake small perch (< 12 cm) feed mainly on crustacean zooplankton, and they switch to

feeding on benthic macroinvertebrates at the length of 14–15 cm. Therefore, we expected that the increasing density of small perch (< 12 cm) would increase the predation pressure on crustacean zooplankton. Consequently, we hypothesized that the biomass of crustacean zooplankton would decrease along with increasing density of planktivorous perch and the small-sized species become more dominant in the zooplankton community due to the increasing size-selective planktivory (Skoglund *et al.* 2013, Hulot *et al.* 2014). We also expected the crustacean zooplankton species diversity to change, since changes in predation intensity are known to increase or decrease the diversity, depending on the degree of the predation pressure (Menge and Sutherland 1976, Huston 1979, Hixon 1986). Finally, we also assumed that the changes in zooplankton community (decreased biomass and average body size) would be reflected in phytoplankton.

Material and methods

Study lake and fishery treatments

The study was conducted in a small, oligotrophic, forest lake, Iso Valkjärvi (3.8 ha), in southern

Finland (61°13'N, 25°12'N), during 2007–2012. For experimental purposes, the lake was divided into two compartments by a plastic wall in 1991 (Rask *et al.* 1996). The compartments “NS” and “SS” were quite similar in morphometry (surface areas 1.6 and 2.2 ha and mean depths 2.8 and 3.8 m, respectively) and the trophic status (total phosphorus content $14 \pm 4 \mu\text{g l}^{-1}$ in both compartments; total nitrogen content 560 ± 50 and $530 \pm 60 \mu\text{g l}^{-1}$ in NS and SS compartments, respectively; chlorophyll *a* $7 \pm 2 \mu\text{g l}^{-1}$ in both compartments). The Secchi depths were 2.9 ± 0.1 and 2.6 ± 0.2 m in the NS and SS compartments, respectively. The surface water temperature during growing seasons 2007–2012 was slightly higher in the NS compartment (17.2 ± 0.5 °C) than in the SS compartment (16.9 ± 0.7 °C), but showed no significant variation among the years (Olin *et al.* 2017). In both compartments, fish community consisted of perch and the northern pike (*Esox lucius*).

Manipulative fishing procedure targeted perch and was conducted during 2008–2011 in both compartments of the lake. In non-selective fishing (NS), conducted in the NS compartment, all size classes of perch were targeted, whereas in size-selective fishing (SS), conducted in the SS compartment, large individuals (≥ 16 cm) were released from traps. For a detailed description of the fishing procedures, see Olin *et al.* (2017). The manipulative fishing procedure caused a strong increase in the density of the small (< 12 cm) perch in 2010 (NS compartment) and in 2011 (SS compartment), after which the small-sized perch density remained high in both compartments (Fig. 1). Since we were interested in fish predation pressure on zooplankton, for statistical analyses < 12 cm perch densities were considered treatments and divided into two density classes: “high” > 2000 indiv. ha⁻¹ (years 2010–2012 and 2011–2012 in NS and SS compartments, respectively) and “low” < 700 indiv. ha⁻¹ (years 2007–2009 and 2007–2010 in NS and SS compartments, respectively) (Fig. 1).

Zooplankton sampling

To examine the effects of the fish manipulation on the crustacean zooplankton community,

zooplankton samples were taken yearly (2007–2012) from both compartments in June, July, August and September from the pelagic zone at the deepest part of lake (5.5–7 m) and from the littoral zone (depth 2 m). Zooplankton samples were taken with the 50- μm -mesh plankton net (25 cm opening), towed vertically through the water column from the bottom to the surface (NS compartment, pelagic: 0–5.5 m; littoral 0–2 m; SS compartment, pelagic: 0–7 m; littoral 0–2 m) at approx. 0.5 m s⁻¹. From the pelagic and littoral zones, three parallel plankton net hauls were taken and preserved with formaldehyde. In the laboratory, crustacean zooplankton were enumerated and carapace length measured under an inverted microscope, identified to the species level, and carbon biomass were calculated from measured sizes using species-specific length-carbon regressions (Vasama and Kankaala 1990, Luokkanen 1995). On each sampling date, samples for water quality parameters were also taken (e.g. Secchi depth, vertical profiles of temperature and dissolved oxygen, total phosphorus, total nitrogen, chlorophyll *a*), but as those results have already been published elsewhere (Horpila *et al.* 2010, Estlander 2011, Estlander *et al.* 2012), they are considered here as initial information. The annual crustacean zooplankton species diversity was calculated using the Shannon-Weaver diversity index (H'): ($H' = -\sum p_i \ln p_i$), where p_i is the proportion of a species in the sample (Shannon and Weaver 1949).

Fish diet

To estimate the predation pressure of perch on the crustacean zooplankton, the diet data of perch were collected annually (2007–2012) from the Nordic gillnet samples. The stomach contents of perch ($n = 529$ and $n = 491$ for NS and SS compartments, respectively) were analysed for fullness and volume proportions of different food items (Windell 1971), and consumed zooplankton taxa were classified to the species level. The selectivity index of Ivlev (1961) was used as a measure of selectivity (E) for various zooplankton taxa in rations: $E = (r_i - p_i)(r_i + p_i) - 1$, where r_i is the percentage of the food item in the ration, and p_i is the percentage of the

food item in the environment. Food availability in the environment was calculated from samples taken on the same dates the fishes were sampled. The selectivity index values of E range from -1 (complete avoidance) to $+1$ (exclusive selection).

Statistical analyses

The littoral and pelagic zooplankton were pooled for further analyses, since no significant differences in crustacean zooplankton length or biomass within the lake compartments were found between the pelagial and littoral sampling locations (ANOVA for repeated measurements: NS: $F_{2,5} = 2.49$, $p = 0.177$; and SS: $F_{2,5} = 0.36$, $p = 0.716$). In this analysis, we had compartment (NS or SS) and site (littoral and pelagial) as fixed explanatory variables, month (June–September) as replicate, and year (2007–2012) as a repeated variable. We analysed the within- and between-compartment annual variation in the crustacean biomass, density and carapace length with ANOVA. To test whether fish density and lake compartment were significant sources of variation in zooplankton biomass, density or average carapace length, two-way ANOVA was performed on each zooplankton variable with fish density (two levels) and lake compartment (two levels) as treatment factors.

The differences in Shannon-Weaver indices between high and low fish densities (NS and SS pooled) were tested with the independent samples t -test. The relationship between the diversity index vs. fish density and other environmental variables (total phosphorus, chlorophyll a and temperature) were studied with Spearman's rank-order correlation. Before the analyses, all the data were checked for normality and $\ln(x + 1)$ -transformed if necessary.

The proportional volumetric dietary data for individual fish (< 12 cm) from each sampling year were allocated into annual groups. Mean diet composition was calculated for each of these groups. For zooplankton dietary analysis, only stomach with zooplankton contents $\geq 50\%$ were considered. The number of individuals of each group selected for the analysis varied between 44 and 125 individuals. The fishery manage-

ment effect (high and low fish densities) on the proportion of littoral cladoceran species (*Sida crystallina*, *Polyphemus pediculus*, *Eurycercus* sp., *Chydorus* sp., *Alona* sp.) in the diets of perch (arcsine-square-root-transformed data) were studied using ANOVA. For between-management comparisons, a logistic regression model was used to analyse the proportion of perch utilizing zooplankton as a function of perch length (L) following Tolonen et al. (1999):

$$y = \exp(\alpha + \beta L + \gamma M + \delta LM) \times [1 + \exp(\alpha + \beta L + \gamma M + \delta LM)]^{-1},$$

where y is the occurrence of zooplankton in a single fish recorded as 0 (does not occur) or 1 (does occur), L is the perch length, M is the fish density class (high and low), α is constant, and β , γ , δ are parameters. This model was used to test whether consumption of zooplankton was dependent on perch length, and if there was an interaction with perch length and different fishery management. The Hosmer-Lemeshow test for logistic regression suggested that the fit of the data to the model was good (NS compartment: $p = 0.45$; SS compartment: $p = 0.12$).

Results

Zooplankton biomass

The annual average crustacean zooplankton biomass varied from 9 to 39 $\mu\text{g C l}^{-1}$ (NS compartment) and 8 to 38 $\mu\text{g C l}^{-1}$ (SS compartment) (Table 1), but no significant variation among the years or between compartments in zooplankton biomass (ANOVA: $F_{5,15} = 0.18$, $p > 0.05$) were observed (Table 1). The cladoceran length showed no significant variation (ANOVA: $F_{5,15} = 4.99$, $p > 0.05$) in either lake compartment along with increasing fish density (Table 1). Lake compartment or variation in fish density showed no significant effect on biomass of total crustacean zooplankton (two-way ANOVA: $F_{4,43} = 0.53$, $p > 0.05$), cladocerans ($F_{4,43} = 0.84$, $p > 0.05$) or copepods ($F_{4,41} = 0.26$, $p > 0.05$). However, when cladoceran taxa were examined in more detail, the biomass of *Holopedium* sp., *Daphnia* sp. and littoral cladoceran species was significantly higher

and the biomass of *Ceriodaphnia* sp. lower in high-fish-density years in both lake compartments (Table 2 and Fig. 2). The biomass of *Bosmina* sp. increased when the fish density was high, but only in the SS compartment of the lake (Fig. 2). The interaction between lake compartment (SS and NS) and fish density was significant in the biomass variation of *Bosmina* sp. (Table 2): the response of bosminids to increased fish density

was highly positive in the SS compartment but no response was observed in the NS compartment (Table 2 and Fig 2).

Species diversity

During the study period (2007–2012), a total of 7 copepod species and 13 cladoceran spe-

Table 1. The mean annual crustacean biomass and cladoceran length with standard deviations (SD) in the studied lake compartments.

Lake compartment	Fish density	Year	Crustacean biomass (\pm SD) ($\mu\text{g C l}^{-1}$)	Cladoceran length (\pm SD) (μm)
NS	Low	2007	11 (\pm 2)	504 (\pm 21)
		2008	39 (\pm 41)	438 (\pm 38)
		2009	15 (\pm 12)	417 (\pm 33)
	High	2010	19 (\pm 19)	463 (\pm 23)
		2011	9 (\pm 6)	415 (\pm 39)
		2012	19 (\pm 15)	500 (\pm 51)
SS	Low	2007	8 (\pm 5)	485 (\pm 48)
		2008	17 (\pm 13)	441 (\pm 28)
		2009	38 (\pm 47)	346 (\pm 35)
	High	2010	21 (\pm 19)	531 (\pm 14)
		2011	6 (\pm 5)	437 (\pm 35)
		2012	25 (\pm 33)	529 (\pm 65)

Table 2. Results of two-way ANOVA: Species biomass = fish density (two levels) \times lake compartment (two levels) and year (2007–2012) as a covariate; *p* values indicating significant differences are set in boldface.

Source of variance	Species	SS	MS	df	<i>F</i>	<i>p</i>
Fish density	Cladocera	0.42	0.42	1,32	0.85	0.363
	Copepoda	2.31	2.31	1,32	1.30	0.262
	<i>Ceriodaphnia</i>	8.33	8.33	1,32	8.34	0.007
	<i>Daphnia</i>	19.32	19.32	1,32	13.15	0.001
	<i>Bosmina</i>	3.10	3.10	1,32	3.34	0.077
	<i>Holopedium</i>	31.00	31.00	1,32	37.49	< 0.001
	Littoral species	12.00	12.00	1,32	6.42	0.016
Lake compartment	Cladocera	1.32	1.32	1,32	2.66	0.113
	Copepoda	1.09	1.09	1,32	0.61	0.440
	<i>Ceriodaphnia</i>	2.78	2.78	1,32	2.79	0.105
	<i>Daphnia</i>	0.03	0.03	1,32	0.02	0.889
	<i>Bosmina</i>	0.37	0.37	1,32	0.40	0.533
	<i>Holopedium</i>	0.96	0.96	1,32	1.16	0.299
	Littoral species	0.76	0.76	1,32	0.41	0.529
Fish density \times lake compartment	Cladocera	0.66	0.66	1,32	1.33	0.257
	Copepoda	1.25	1.25	1,32	0.70	0.408
	<i>Ceriodaphnia</i>	0.07	0.07	1,32	0.07	0.787
	<i>Daphnia</i>	0.15	0.15	1,32	0.10	0.755
	<i>Bosmina</i>	4.08	4.08	1,32	4.41	0.044
	<i>Holopedium</i>	1.16	1.16	1,32	1.40	0.256
	Littoral species	1.18	1.18	1,32	0.63	0.432

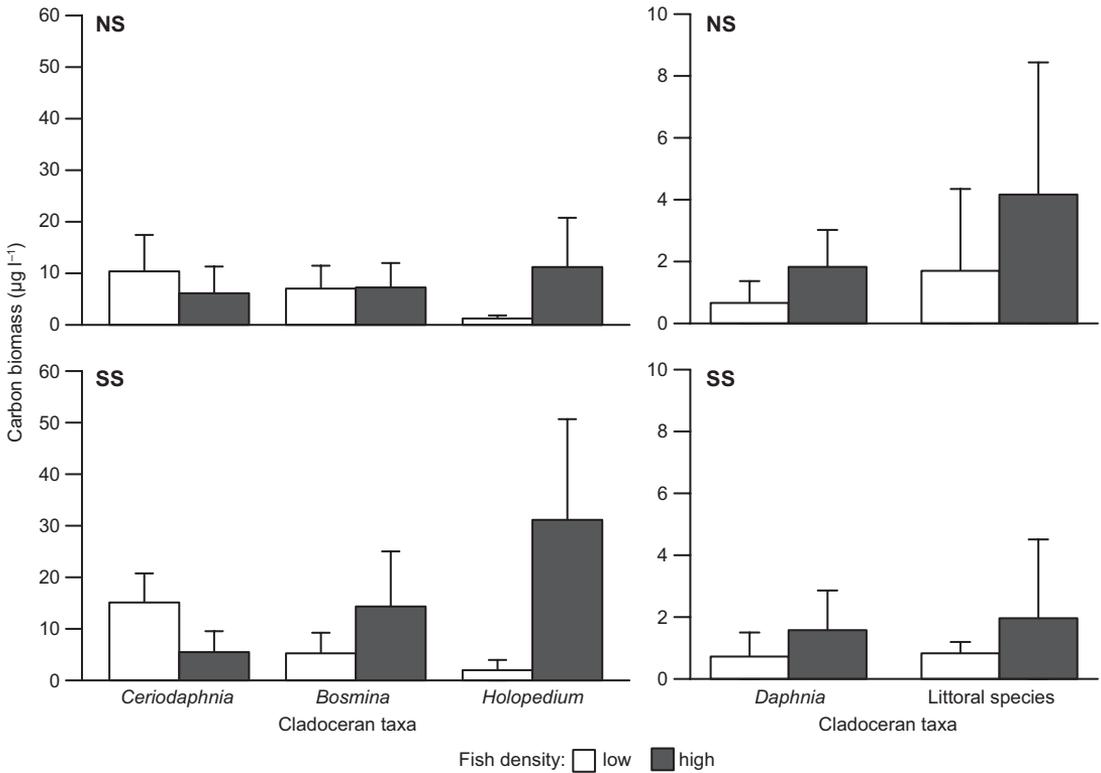


Fig. 2. The annual carbon biomass (+ 95%CI) of cladoceran taxa in the lake compartments NS and SS.

cies were observed in both compartments of the lake. In the years 2007–2009, the amount of detected species was 12–15 (NS compartment) and 14–17 (SS compartment), while in 2010–2012 the species richness increased to 18–20 species in both compartments of the lake. Among cladocerans, the most dominant species was *Ceriodaphnia pulchella*, especially in the NS compartment (Fig. 2), where *Ceriodaphnia* sp. contributed 60%–80% to the cladoceran biomass. Other abundant taxa were *Bosmina* sp., *Daphnia* sp. and *Holopedium gibberum*. Among copepods, the most abundant species were *Mesocyclops leuckarti*, *M. viridis*, *Heterocope borealis* and *Eudiaptomus gracilis*, but none of those dominated. Interestingly, the relative species composition of cladocerans changed and overall, the crustacean zooplankton species diversity increased (Fig. 3) in both compartments of the lake after the fish density increased (NS and SS pooled: t -test $t_{10} = -2.583$, $p = 0.027$). Crustacean zooplankton diversity index (H') showed significant and strongly positive correlation (Spear-

man's $r = 0.746$, $p < 0.001$) with fish density. No significant relationships between the diversity index (H') and total phosphorus, chlorophyll a and temperature were found.

Perch diet

A logistic regression analysis showed that the probability of perch to feed on zooplankton was dependent on perch length (Table 3 and Fig. 4) and that small-sized perch (< 12 cm) fed mainly on zooplankton (Nagelkerke's $R^2 = 0.42$ and 0.48 in NS and SS compartment, respectively). Overall, the prediction success of the regression model was 76% in the NS compartment (70.2% for zooplankton not in diet and 80.2% for zooplankton in diet) and 77% in the SS compartment (66.2% for zooplankton not in diet and 86.2% for zooplankton in diet). Since the density of the small-sized perch increased five-fold in 2010 (NS compartment) and 2011 (SS compartment) (Fig. 1), it can be assumed that the preda-

tion pressure on the zooplankton community increased markedly during those years. In the NS compartment of the lake the, a shift from planktivory to other food resources occurred at a smaller size after the fishery measures were applied than before (Table 3 and Fig. 4), but no similar change occurred in the SS compartment of the lake. The diet analyses also showed that the diet of small-sized (< 12 cm) perch consisted mainly of zooplankton (~70%), of which > 90% were cladocerans. In 2007–2010, perch fed mainly on *Ceriodaphnia* sp., littoral species and *Bosmina* sp., and later its diet became more variable (Fig. 5). Especially *Holopedium gibberum* appeared in the perch diet in 2010 and at the same time the share of littoral cladocerans decreased significantly (ANOVAR: $F_{1,9} = 5.50, p = 0.040$). Overall, during the entire study period perch favoured large-sized cladocerans *Eurycercus* sp. and *Sida crystallina* (littoral species) and *Holopedium gibberum* ($E = 0.8$). Ivlev's index of diet selectivity showed weak

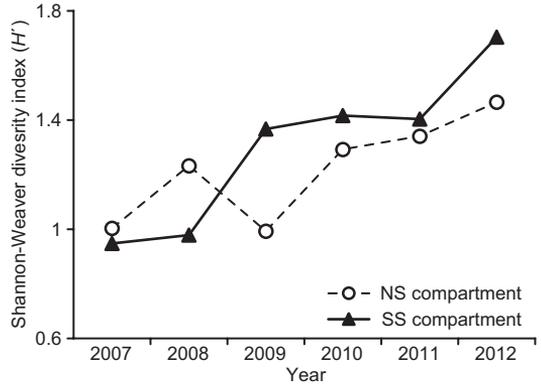


Fig. 3. The Shannon-Weaver diversity indices of the crustacean zooplankton in the NS and SS compartments of the lake.

positive selectivity also for *Daphnia* sp. (0.3) in the SS compartment and *Bosmina* sp. (0.2) in both compartments, but negative or no selectivity (values ~0) for other zooplankton species in both compartments during the study period.

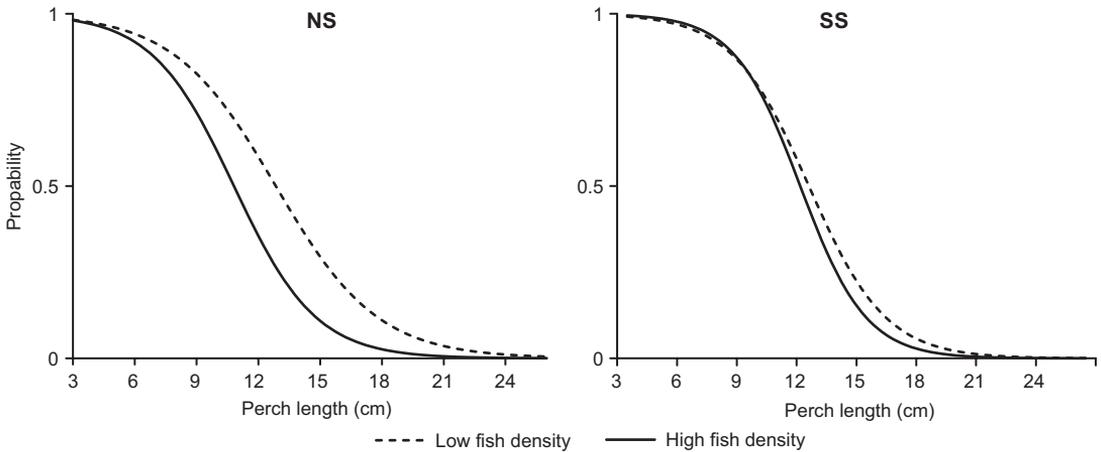


Fig. 4. Probability of ingestion of zooplankton depending on perch length estimated with logistic regression for low and high fish densities in the lake compartments NS and SS.

Table 3. Results from the logistic regressions, (probability of ingestion of zooplankton against perch length in high and low fish density = management). Nagelkerke's $R^2 = 0.42$ in NS and 0.48 in SS compartment.

Compartment	Parameter	Estimate	SE	Wald's χ^2 -test	p
NS	β (length)	-0.454	0.035	166.11	< 0.001
	γ (management)	0.975	0.225	18.74	< 0.001
	α (constant)	4.808	0.374	165.12	< 0.001
SS	β (length)	-0.545	0.046	143.09	< 0.001
	γ (management)	0.420	0.229	3.38	0.066
	α (constant)	6.190	0.493	157.63	< 0.001

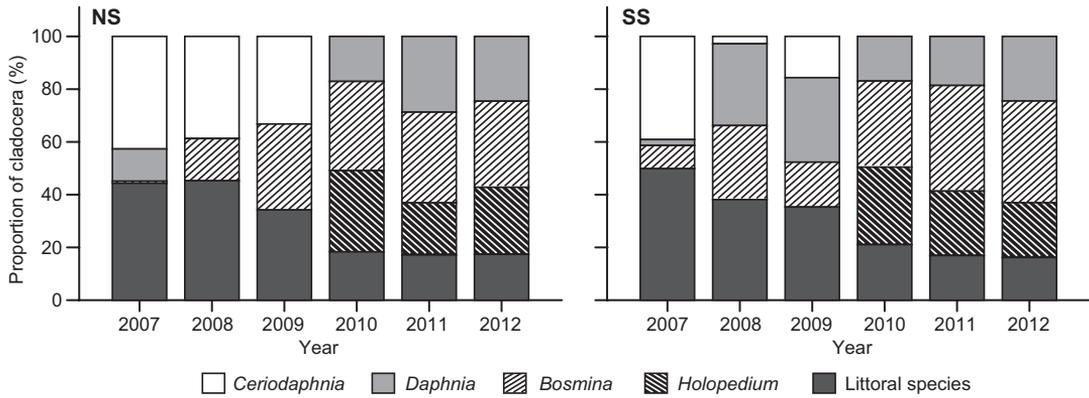


Fig. 5. Annual abundance of various cladoceran taxa in small-sized (< 12 cm) perch diet in the NS and SS compartments of the lake.

Discussion

Contrary as expected, zooplankton biomass or mean length did not differ between high and low fish densities. The enhanced planktivory decreased the biomass of the most dominant species, while it increased the biomass of other species. Interestingly, and unexpectedly, large-sized cladoceran species became relatively more abundant when fish density increased and therefore no notable effect on overall crustacean zooplankton biomass was detected. The increased proportion of the larger-sized species (*Holopedium* sp. and daphnids) was also detected in fish diets, thus corroborating the generally accepted idea (Skoglund *et al.* 2013, Hulot *et al.* 2014) that planktivorous fish favour larger prey items. Since smaller species, especially *Ceriodaphnia* sp., decreased with increasing fish density, we suggest that interspecific competition among cladocerans was an important factor affecting the species composition of the zooplankton, even though competition is thought to play a minor or insignificant role in structuring the zooplankton community (Dodson 1992). However, Neill (1975) and Lynch (1977) have shown that *Ceriodaphnia* sp. can exclude *Daphnia* sp. when resources are limited. Our study lake is rather oligotrophic and nutritional overlaps between crustacean zooplankton are likely to occur (Gliwicz and Prejs 1977). Moreover, Paine (1966, 1971) suggested that predation on dominant competitors can induce relatively high species diversity by preventing the dominant competi-

tors from controlling the major resource (food or space). Here, *Ceriodaphnia* was clearly the most dominant genus among cladocerans, thus it is possible that increased predation reduced the competition for resources among crustacean zooplankton overall, and especially between *Ceriodaphnia* and daphnids. In addition, the relationship between fish predation and cladoceran community was probably obscured because of the presence of invertebrate predators such as chaoborids that can act even as main predators on zooplankton in the absence of fish (Rask *et al.* 1996). For example, according to Riessen *et al.* (1988) *Ceriodaphnia* is greatly preferred by chaoborids over daphnids. However, no change in *Chaoborus* density or predatory zooplankton species during the study period was observed in the studied lake (authors' own data).

The effects of perturbation in ecosystems can be mitigated by compensatory dynamics of zooplankton, wherein abundance of some species increased to compensate for other species' population decrease (Tilman 1996, Havens and Carlson 1998, Fischer *et al.* 2001). Here, this was seen as the increased diversity in crustacean zooplankton community. It is stated that intermediate predation pressure likely increases prey species diversity, while very strong predation leads to the opposite (Menge and Sutherland 1976, Dyer and Letourneau 2003). Even though the fish predation pressure multiplied as a result of the applied fishing measures, the strength of increased fish predation was not sufficient to decrease the zooplankton diversity or affect fluctuations in zoo-

plankton biomass. However, the predation pressure was sufficiently strong, to increase diversity among zooplankton (Maguire 1971, Addicott 1974). In addition to predation, also lake area, its productivity and chemical properties are known to explain the species richness of crustacean zooplankton (Hessen *et al.* 1995). Since fish density was the only variable that changed significantly during the study period, we suggest that increased predation pressure was the major factor affecting the zooplankton species richness and diversity in the study lake. There are, however, other factors (not studied here) influencing separately or simultaneously zooplankton communities, such as intraguild predation and variation in phytoplankton communities, which cannot be entirely ruled out.

Our results are in line with Hessen *et al.* (1995), who studied non-cyprinid fish communities and showed that the biomass of cladocerans, calanoids, or daphnids is poorly correlated with fish predation. Hessen *et al.* (1995) suggested that at low lake productivity, water quality parameters and species physiological adaptations appear as the main determinants for the success of herbivorous zooplankton. Even though the zooplankton biomass or average body size showed no significant response to increased density of small-sized perch, the predation pressure on zooplankton likely increased. This was also seen as an earlier diet shift of perch in the NS compartment of the lake. According to Persson and Greenberg (1990), perch shift earlier and at smaller size to feeding on macroinvertebrates, if the competition for planktonic food is high. In the SS compartment however, no such change was observed. This may be due to the difference between the lake compartments in the densities of 12–15 cm perch (Fig. 1), which also feed on zooplankton (Estlander *et al.* 2010) and therefore, the competition for planktonic food was higher in the NS compartment. The diet analyses also suggest, that before the fish density dramatically increased, small-sized perch favoured littoral areas when consuming zooplankton. After the increase in fish density, a greater proportion of perch diet consisted of pelagic cladocerans, thus the increased competition for the zooplankton resources probably drove perch to feed in wider areas. This was also reflected in the littoral cla-

doceran biomass, which clearly increased when the fish density multiplied. In addition, the overall biomass increase of *Bosmina* sp. in the SS compartment of the lake was mainly due to the biomass increase in the littoral samples (Fig. 2), thus supporting the notion, that perch extended their feeding area beyond the littoral.

In conclusion, our manipulative experiment of size selective fishing in a relatively simple food web system suggested that the biomass or body size of crustacean zooplankton does not fluctuate severely under notable increase in fish predation. We argue that instead of simple “top-down” or “bottom-up” regulation of zooplankton, the diverse array of connections among species and fluctuations in environment are more likely to explain changes in zooplankton community dynamics. Moreover, variation in the timing of ontogenetic diet shift and behavioural changes such as habitat change, complicate the assessment of fish predation pressure on the zooplankton community.

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