Effects of invading vendace (<u>Coregonus albula</u> L.) on species composition and body size in two zooplankton communities of the Pasvik River System, northern Norway.

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Abstract

Species composition and body-size distribution were studied in the crustacean zooplankton communities of two limnologically similar lake localities situated 50 km apart in the Pasvik River System, northern Norway. A recent invasion and successive downstream expansion of vendace (<u>Coregonus albula</u>), a specialized zooplanktivorous fish, allowed comparisons between sites with different predation pressures. Vendace had established a high population density and was the dominant fish species in the pelagic of the upper locality, but had just invaded the lower locality with a small number of individuals. Whitefish (<u>Coregonus lavaretus</u>), a closely related but less specialized zooplanktivore species, dominated the native fish community of both lakes.

The zooplankton community of the upper locality was in June and August dominated by <u>Bosmina longirostris</u>, the smallest zooplankton species represented in the watercourse, and in September by <u>Daphnia cristata</u>. The lower locality was dominated by the larger <u>Holopedium gibberum</u> and <u>Eudiaptomus graciloides</u> in

June, by <u>D</u>. <u>cristata</u> in August, and by <u>D. cristata</u> and <u>B. longirostris</u> in September. The mean body size of the three most abundant cladoceran species was significantly smaller in the upper locality, compared to the lower locality. It was concluded that the invasion and establishment of a dense vendace population in the upper locality had increased the predation pressure in the pelagic, resulting in a reduction of body size and a shift towards smaller species in the zooplankton community.

Keywords: Fish invasion, zooplankton predation, prey selection, community structure.

Introduction

Two main controlling mecanisms may influence the structure and dynamics of zooplankton communities: The physical and chemical environment, by providing a certain level of available nutrients, limit the production (Wetzel, 1983), while predation from fish and invertebrates may modify both species composition and size structure (Hall *et al.*, 1976; Gliwicz and Pijanowska, 1989). Increased predation pressure from fish generally leads to a reduction or elimination of large zooplankton species and to a reduced body size (Hrbácek *et al.*, 1961, Hrbácek, 1962; Brooks and Dodson, 1965; Nilsson and Pejler, 1973; Threlkeld, 1979; Lazzaro, 1987). Studies of predation effects on zooplankton communities are usually based on comparisons between water bodies in which a fish predator is present or absent (e.g. Brooks and Dodson, 1965; Hall *et al.,* 1976). Such studies can be done when a predator invades a new area, or arranged experimentally by

introducing a predator to ponds or natural systems (Vooren, 1972; Nilsson, 1978). Invasions and artificial introductions of exotic fish species can be viewed as experimental disturbances that may increase the understanding of community structuring (Simberloff 1981; Pimm, 1989; Ross, 1991). However, the negative effects that frequently follow fish introductions (Herbold and Moyle, 1986), have been met by international agreements aimed to reduce the outspread of exotic species (WRI/IUCN/UNEP, 1992). Thus, when new introductions accidentally occur, a strong effort should be made to extract as much knowledge as possible from the event (Evans *et al.,* 1987).

The present study is related to a recent invasion of vendace (<u>Coregonus albula</u> L.), a highly specialized zooplanktivore fish species (Ekstrøm, 1975; Hamrin, 1983; Viljanen, 1983; Kankaala *et al.*, 1990), into the Pasvik River System in northern Norway. The natural distribution of vendace does not include northern Fennoscandia, but in the 1960's, the species was translocated and introduced into tributaries of Lake Inari, northern Finland (Mutenia and Salonen, 1992). In Lake Inari, vendace reached a high population density in the second half of the 1980's (Mutenia and Ahonen, 1990), and from there it has migrated downstream into the Pasvik River System, where it was registered for the first time in 1989. The pelagic fish communities in the Pasvik River System were originally dominated by whitefish (<u>Coregonus lavaretus</u> L.), a species closely related to vendace, but less efficient as a zooplanktivore (Svärdson, 1976). As vendace invaded the upper part of the watercourse, it replaced whitefish as the dominant fish species in the pelagic zone (Amundsen <u>et al.,</u> 1993). The gradual downstream expansion of vendace in the Pasvik River System, opened the possibility to study the consequences of a large scale "natural experiment",

comparing zooplankton communities of lake localities with and without vendace. Accordingly, two lake localities were investigated in 1993: one in the upper part of the watercourse where vendace had reached a high population density; the other in the lower part of the watercourse, where a low abundance of vendace was registered for the first time that year. We assumed that the invasion and establishment of a dense vendace population would increase the predation pressure on zooplankton, and we hypotesized that the increased predation pressure would change the zooplankton community towards smaller species and individuals.

Study area and fish communities

The Pasvik River System belongs to three countries. It originates from Lake Inari (1102 km^2) in Finland, runs into Russia and then defines the borderline between Norway and Russia for about 120 km (Figure 1). The Norwegian-Russian part of the river system has a total area of 142 km^2, a catchment area of 18.404 km^2 and a mean annual waterflow of about 175 m^3 s^{-1}. There are altogether seven water impoundments in the watercourse. Most rapids and waterfalls have disappeared, and today, the river system consists primarily of lakes and reservoirs. The water level fluctuations are small, usually less than 80 cm. The ice-free season in the lakes and reservoirs lasts from late May, beginning of June, to the end of October, early November. The lakes and reservoirs in the watercourse are oligotrophic with some humic impacts, the Secchi-depth ranging from 2.1 to 5.5 m (table 1). The geology in the region is dominated by bedrock, mainly containing gneiss, and a birch- and pinewood landscape with stretches of boggy

land surrounds the watercourse. Annual mean air temperature is low (-3 ºC), and minimum and maximum monthly mean temperatures are -13.5 ºC and +14.0 ºC, respectively. The precipitation in the area is low, with an annual mean of 358 mm.

Two different lake localities situated about 50 km apart in the watercourse, were investigated: Ruskebukta in the upper part, and Skrukkebukta in the lower (figure 1). Both basins are located beside the main path of the Pasvik River System, and have negligible water flow. Ruskebukta (69º 13' N, 29º 14' E; 52 m a.s.l.) has an area of 5.3 km^2, and a maximum depth of 15 m. Skrukkebukta (69º 33' N, 30º 7' E; 21 m a.s.l.) has an area of 6.6 km^2, and a maximum depth of 19 m. The water chemistry of the two lakes is similar (table 2).

Altogether, 15 species of fish have been recorded in the Pasvik River System. The most commonly occurring native species are whitefish (Coregonus lavaretus sensu lato), perch (Perca fluviatilis), pike (Esox lucius), burbot (Lota lota) and brown trout (Salmo trutta). The whitefish consists of two different morphs, differentiated by the morphology and number of gill rakers, here referred to as densely and sparsely rakered whitefish. The densely rakered whitefish has numerous long and narrowly spaced gill rakers (mean number 33.0, s.d.=2.82, n=423), whereas the sparsely rakered form has fewer, shorter and more widely spaced rakers (mean number 23.1, s.d.=3.65, n=213). Gill raker counts on vendace showed a mean number of 41.3 (s.d.=3.37, n=65). According to Reshetnikov (1980), the two whitefish forms may be referred to as Coregonus lavaretus lavaretus (densely rakered whitefish) and C. lavaretus pidschian

(sparsely rakered), whereas Svärdson (1957, 1979) described these forms as two different species; Coregonus lavaretus and C. nasus, respectively. The densely rakered whitefish usually occupies the pelagic zone, feeding predominantly on zooplankton, whereas the sparsely rakered form mainly feeds on zoobenthos in littoral and profundal habitats (Amundsen, 1988). Prior to the invasion of vendace, whitefish was the dominant fish species both in the pelagic, profundal and littoral habitats of the lakes and reservoirs in the Pasvik River System. In the pelagic zone, the densely rakered whitefish, hereafter referred to as whitefish, constituted, on average, more than 95% of the total catches (Amundsen et al., 1993). The mean catch per unit effort in the pelagic (sum of vendace and whitefish) through the season in 1993 was similar in the upper and lower locality, respectively 33 and 30 fish per 100 m^2 per 12 hours.

Methods

Sampling activity was performed in the upper and lower locality in June, August and September 1993. Fish were sampled using pelagic gillnets with mesh sizes of 8, 10, 12.5, 15, 18.5, 22, 26 and 35 mm (knot to knot). Stomach samples were taken from vendace and whitefish, and conserved in 96 % ethanol. Zooplankton was sampled with a 30 l Schindler-box using a mesh size of 65 μm, and fixed with Lugol solution. Two parallel samples were taken at 1, 3, 5, 7, 9 and 12 m of depth.

In the laboratory, all crustacean species from the zooplankton samples and stomach samples of vendace and whitefish were identified and counted. Five cladoceran species, Bosmina longirostris Müller, Bosmina longispina Leydig,

Daphnia cristata Sars, Holopedium gibberum Zaddach and Leptodora kindtii
Focke, and four copepods, Cyclops scutifer Sars, Eudiaptomus graciloides
Liljeborg, Heterocope appendiculata Sars and Megacyclops gigas Claus were
found. Body lengths (from the top of the head to base of caudal spine) of
eggbearing females and immature, both from plankton and stomach samples,
were measured for the three most abundant cladoceran species. A binocular with
50x magnification was used for counting and measuring. Differentiation between
the two species of Bosmina was impossible in most stomachs, and a combined
selection estimate of Bosmina spp. therefore replaced separate estimates for each
species. Selection indices were calculated for both fish species, considering the
six most important crustacean taxa using Manlys index (α) (Manly et al., 1972):

$$\alpha_i = (r_i / j_i) / \Sigma_{i=1}(r_i / j_i), \quad i = 1,2,...,n$$

which can be modified to range from -1 to +1, with positive selection above and
negative selection below zero (Chesson, 1983):

$$\alpha N_i = n\alpha_i - 1 / (n-2)\alpha_i + 1, \quad i = 1,2,...,n$$

where αN_i = selection on species i, r_i = proportion of species i from the diet of
the fish, j_i = proportion of species i from the environment, and n = the number of
species. When $\alpha N_i = 0$ the selection is random, but it is reasonable also to
include low values of αN_i to the random category. αN_i between +/-0.3 was thus
considered as random selection.

Results

Zooplankton species composition

Upper locality (high vendace density)   *Bosmina longirostris* was the dominant species in June and especially in August, when it contributed 80% of the total number in the community (figure 2). *Daphnia cristata* increased throughout the season and became dominant in September (52%). *Bosmina longispina* and the copepod species *Eudiaptomus graciloides* and *Cyclops scutifer* were present throughout the season with highest proportions in June (11 and 24%, respectively). The invertebrate predator *Leptodora kindtii* had the highest densities in June and August, whereas *Holopedium gibberum, Megacyclops gigas* and *Heterocope appendiculata* were found in small numbers throughout the season.

Lower locality (low vendace density)   *Eudiaptomus graciloides* (39%) and *H. gibberum* (30%) made up the major portion of the zooplankton community in June, while *B. longispina* was less frequent and *B. longirostris* relatively rare (figure 2). In August, *D. cristata* was the dominant species (64%), followed by the copepods and *B. longirostris*. In September, *B. longirostris* (42%) and *D. cristata* (38%) dominated, whereas the copepods and *B. longispina* were less frequent. *Leptodora kindtii, M. gigas* and *H. appendiculata* were found at all seasons, but made negligible contributions to the total number of individuals.

Zooplankton species selection by vendace and whitefish

Strong variation in zooplankton selection was found throughout the season, and there were clear differences between the two localities for both fish species

(figure 3). However, within the same locality the two fish species showed nearly identical pattern of selection for the six zooplankton species studied. Copepods were mainly positively selected, while D. cristata, H. gibberum and L. kindtii were mainly negatively selected. Bosmina spp. was randomly to positively selected except for the upper locality in August, when B. longirostris reached a very high density in the environment.

Zooplankton body size in the environment

The ranges in mean body size for eggbearing females throughout the season and for both localities, were 0.63 to 0.81 mm for D. cristata, 0.44 to 0.49 mm for B. longispina, and 0.30 to 0.38 mm for B. longirostris (figure 4). All significant differences in mean body size between the two localities were due to smaller individuals in the upper locality. Daphnia cristata was smaller in the upper compared to the lower locality in August and September (t-test; $p<0.001$), while B. longispina and B. longirostris were smaller in August (t-test; $p<0.01$ and $p<0.001$, respectively). Within the upper locality, both D. cristata and B. longirostris were significantly smaller in August than in June and September (t-test; $p<0.001$), whereas within the lower locality, there was a significant increase in mean body size of eggbearing B. longispina from June to August (t-test; $p<0.01$).

Zooplankton body-size selection by vendace and whitefish

Size selection of plankton by the two fish species was similar within the same locality (figure 5; table 3). Both vendace and whitefish selected a narrow range of the largest zooplankters, always in the size span of the eggbearing females (figure

5). Within the two localities, only one comparison (out of 15) showed significant difference in size selection between the fish species: Vendace had eaten smaller B. longirostris than whitefish in September in the upper locality (t-test; $p<0.05$). However, differences between the localities were clear, with the eaten sizes of each zooplankton species always being smaller in the upper locality (t-test; 11 out of 15 comparisons significant at $p<0.001$ level; table 3), reflecting the differences in the environment (cf. figure 4).

The minimum size of zooplankton individuals (B. longirostris) found in the stomachs of vendace and whitefish was 0.26 mm and 0.28 mm, respectively.

Zooplankton contribution in the fish diets

In the upper locality, where vendace was abundant, whitefish fed predominantly on bottom animals and surface insects. Zooplankton made up just about 20 % of the whitefish diet throughout the season (figure 6). In comparison, the average vendace diet consisted of about 70 % zooplankton.

In the lower locality whitefish had a small percentage of surface insects in its diet while zooplankton contributed to more than 95 %. Vendace fed exclusively on zooplankton (figure 6).

Discussion

In the upper locality, Ruskebukta, where the specialized zooplanktivore vendace dominated in the pelagic, the zooplankton community was dominated by B. longirostris, the smallest cladoceran species in the system. In contrast, larger species were more abundant in the lower locality. This may illustrate that large

zooplankton species in general are competetively superior to smaller species (Hall *et al.*, 1976), but that size-selective predation from fish can reduce and even overrule the effect of competition (Zaret, 1980; Gliwicz and Pijanowska, 1989).

The three most abundant zooplankton species were smaller in the upper locality than in the lower, differences being highly significant in August and partly in September. Predation of zooplankton is positively correlated with temperature, and strong predation from fish in summer often leads to reduced body size of individual zooplankters (Gliwicz and Pijanowska, 1989). The significant size-reduction of B. longirostris and D. cristata in the upper locality in August, support this hypothesis. In contrast to zooplanktivore fish, the invertebrate predator L. kindtii normally feeds selectively on smaller sized zooplankton (Manca and Comoli, 1995), causing an increase in mean body size of the prey population. In June and August, L. kindtii had a relatively high density in the upper locality. Nevertheless, the body size of B. longirostris and D. cristata decreased, strongly indicating that fish predation was the major component structuring the zooplankton community. Accordingly, the significant increase in size for B. longispina in the lower locality in summer, support the assumption that the predation impact was weaker there than in the upper locality. Further, both vendace and whitefish had eaten significantly smaller zooplankton individuals in the upper locality than in the lower. This reflects and even seems to caricature the size-differences found between the zooplankton communities of the two environments. The caricature can be explained by the size preferences of the fish: Both vendace and whitefish had selected a narrow size class of the largest zooplankton individuals available (figure 5).

Vendace is discribed as a highly specialized zooplankton predator that is competetively superior to whitefish (Svärdson, 1976). The higher zooplanktivore efficiency of vendace, as compared to whitefish, is supported by a higher number of gill rakers in the vendace from the Pasvik River system (mean 41.3 vs. 33.0). Further, the small zooplankton contribution to the whitefish diet in the upper locality, where the vendace population density was high, indicates an interactive segregation caused by competition between the closely related species. Vendace, as an invading food competitor, seems to force the inferior whitefish out of its original food niche. It may also be argued that even though the total density of fish in the pelagic was similar between the two localities, a more profound effect of predation on zooplankton was found in the upper locality, supporting the hypothesis that vendace have a higher zooplanktivore efficiency. On the other hand, the observed size and species-selection of vendace and whitefish offers only weak support for this hypothesis: Vendace had only eaten significantly smaller individuals of B. longirostris than whitefish in September, and the minimum zooplankton size found in the stomachs were just slightly smaller in vendace. The similar size and species-selection indicate that the two fish species have the same prey optima. Zooplankton predators tend to select the largest prey available (Lazarro, 1987; Hambright and Hall, 1992), and studies of size and species selection may, thus, have limited abilities to detect differences in capture capabilities of different fish species. The clear differences in zooplankton feeding behaviour between the two localities for both vendace and whitefish emphasize the influence of prey availability on zooplankton selection by fish. It may also illustrate methodological problems in comparing food preferences between different localities or environments.

Different community structure models seem to agree that the effect of a predator is followed by a cascading effect on the lower levels in the food web (Shapiro, 1980; Carpenter *et al.,* 1985, McQueen *et al.,* 1989). According to McQueens "bottom-up/top-down" model (McQueen and Post, 1986), these effects are increasingly damped along a trophic gradient: A higher nutrient level gives more resistance to a cascading effect from a predator, than a lower nutrient level does. This indicates that trophic cascades have a stronger potential in oligotrophic systems. Introductions or invasions of planktivorous fish are, thus, likely to cause more pronounced effects on zooplankon and primary production in northern areas. The observed Secchi-depth differences between the upper and lower locality in the Pasvik River System, may be explained as a trophic cascade effect of the vendace invasion history and the much higher population density of vendace in the upper locality. In future years, the lower part of the Pasvik River System may be expected to have an increased phytoplankton biomass (and consequent decrease in Secchi-depth), caused by the expansion of vendace.

In conclusion, the study demonstrated large differences in both species and size structure of the zooplankton communities between the upper and lower locality. Smaller species and individuals dominated in the upper locality, and the differences can be explained by stronger predation pressure after invasion of vendace. Even a short time after the invasion, vendace seems to possess a central role as the dominant zooplankton predator in the upper part of the Pasvik River System, presumably with strong cascading effects on the lower trophic levels.

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Fig. 1. Map of The Pasvik River System. Arrows show the upper (Ruskebukta) and lower locality (Skrukkebukta).

Fig. 2. Relative species composition (from numbers) of zooplankton through the season in the upper and lower locality. Cladoceran species are sorted on size, smallest species on top. All copepodite stages are included in the copepods.

Fig. 3. Selection of zooplankton for vendace and whitefish through the season in the upper and lower locality.

Fig. 4. Body lengths for *D. cristata* (top), *B. longispina* (middle) and *B. longirostris* (bottom) through the season in the upper (open symbols) and lower locality (filled symbols). Mean values with 95% confidence intervals are given for females with eggs. Size-differences between the localities are not significant (**NS**) or significant (****= p<0.01; ***=p<0.001**; t-test).

Fig. 5. Relative size-distribution of immature (open bars) and mature (filled bars) individuals of a) *B. longirostris*, b) *B. longispina* and c) *D. cristata* in the two localities through the season. Mean size with 95% confidence intervals of eaten zooplankton individuals are given for vendace (○) and whitefish (◈). Arrows indicates minimum- (◁) and maximum-size (▷) of each zooplankton species found in the stomachs.

Fig. 6. Relative contribution of bottom animals (open bars), zooplankton (filled bars) and surface insects (hatched bars) in the fish diets. In the upper locality, whitefish: n=60 stomachs; vendace: n=65, lower locality, whitefish: n=60 stomachs; vendace: n=17,

Tab. 1. Secchi-depth (in meters) for the two localities through the season.

Tab. 2. Limnological data from the two localities in 1991 (from Langeland 1993).

Tab. 3. Differences in size-selection between vendace and whitefish, and between eaten individuals from the two localities. The following tests were made for mean lengths of *B. longirostris, B. longispina* og *D. cristata*: (t-test; not significant = NS, *=p<0.05, ***=p<0.001): [1] vendace vs. whitefish in the upper locality, [2] vendace vs. whitefish in the lower locality, [3] vendace in upper vs. vendace in the lower locality, and [4] whitefish in upper vs. whitefish in the lower locality.

Table 1.

	June	August	September
Upper locality	2.1	2.3	2.9
Lower locality	3.5	4.7	5.5

Table 2.

	Date	Turb.	Cond. $\mu S\ cm^{-1}$	pH	Alk. $\mu ekv\ l^{-1}$	Ca $mg\ l^{-1}$	Na $mg\ l^{-1}$	Cl $mg\ l^{-1}$	NO3-N $\mu g\ l^{-1}$
Upper locality	30/6-91	2.10	32.6	6.83	177	2.21	1.71	1.75	3
Upper locality	8/9-91	4.60	33.5	6.43	167	2.44	1.77	1.66	6
Lower locality	1/7-91	1.40	43.1	6.97	199	2.87	2.07	1.74	12
Lower locality	8/9-91	0.85	41.4	6.93	200	3.35	1.94	1.76	8

Table 3.

	B. longirostris			*B. longispina*			*D. cristata*		
	June	Aug.	Sept.	June	Aug.	Sept.	June	Aug.	Sept.
Upper loc. [1]	NS	NS	*	NS	NS	NS	NS	NS	NS
Lower loc. [2]	-	NS	NS	-	NS	NS	-	NS	NS
Vendace [3]	NS	***	*	***	*	***	NS	***	***
Whitefish [4]	-	***	***	-	***	***	-	***	***

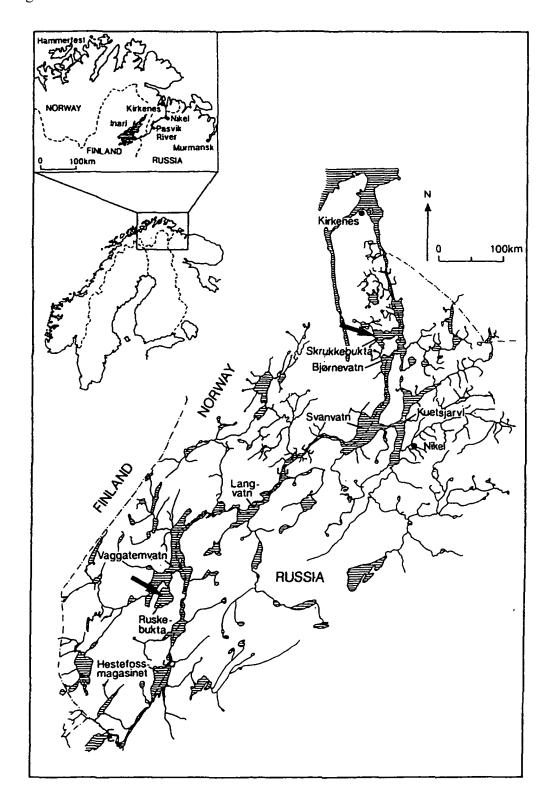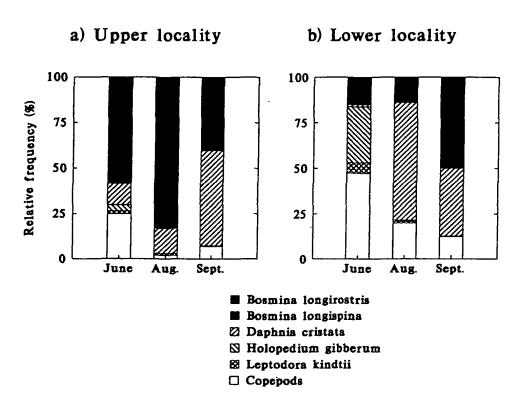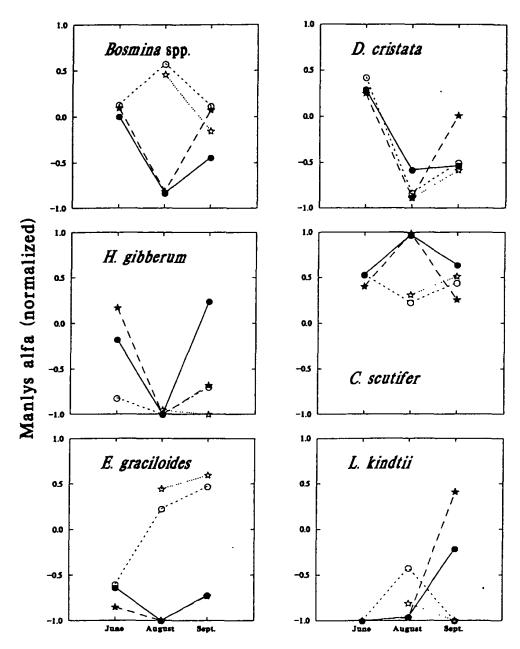|	June	August	September
Daphnia cristata	NS	***	***
Bosmina longispina	NS	**	NS
Bosmina longirostris	NS	***	NS

Figure 1.

Figure 2.

a) Upper locality   b) Lower locality

■ Bosmina longirostris
■ Bosmina longispina
▨ Daphnia cristata
◪ Holopedium gibberum
▨ Leptodora kindtii
☐ Copepods

25

Figure 3.

★ Vendace upper locality
● Whitefish upper locality
☆ Vendace lower locality
○ Whitefish lower locality

26

Figure 4.
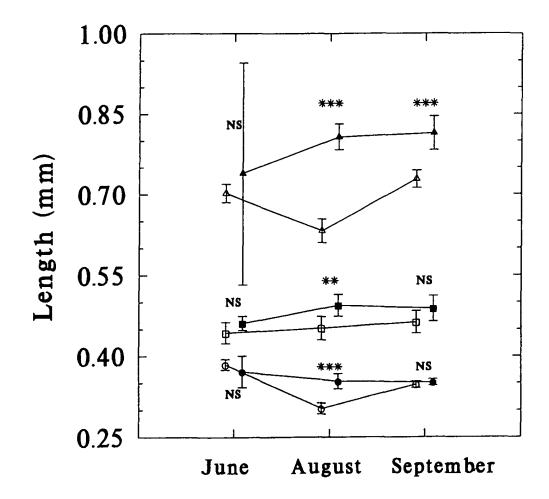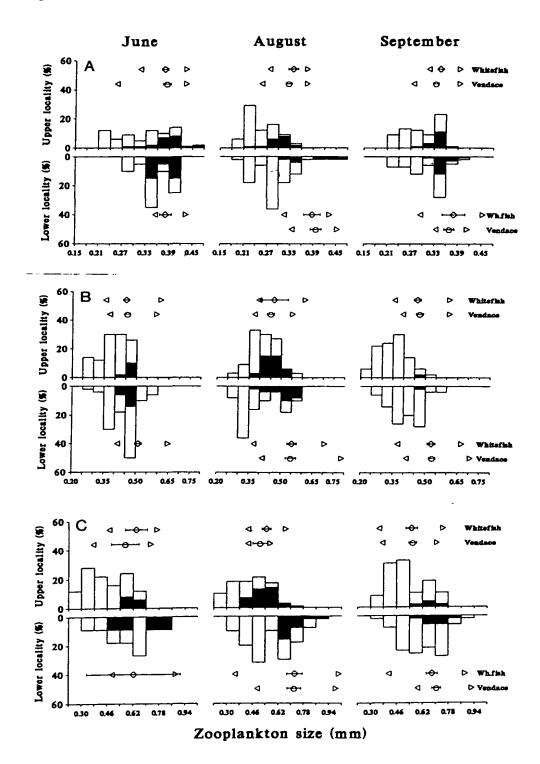
Figure 5.

Zooplankton size (mm)

28

Figure 6.

Whitefish   Vendace