



## Long-term changes in benthic Cladocera populations in Lake Myvatn, Iceland

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### Abstract

Benthic Cladocera were monitored at five sites in Lake Myvatn, Iceland, over a decade (1990–1999), as part of a programme documenting the population fluctuations of animals at different trophic levels in the lake. The species composition remained relatively stable over the first seven years, but in 1997 the population of *Eurycercus lamellatus* was greatly reduced at all sites. The following year saw a mass occurrence of *Alona rectangula* and *Alonella nana* that were previously abundant only locally and rare at most sites. *Alona affinis*, *A. quadrangularis*, *Acroperus harpae* and *Chydorus sphaericus* were not affected. In 1999 the Cladocera assemblages returned to the pre-1997 situation. The shift was from large-bodied epibenthic and planktonic species (*Eurycercus*, *Daphnia*) to small infaunal (*Alona rectangula*) and ubiquitous (*Alonella nana*) species. Medium sized (*Alona*, *Acroperus*) and some small cladocerans (*Chydorus*) were not affected. The course of events was reminiscent of a trophic cascade caused by a change in size-selective predation pressure. If so, the impact of a predatory fish population (three-spined stickleback, *Gasterosteus aculeatus*) depended on whether cyclic chironomid populations were in a high or a low phase. The change in the Cladocera coincided with profound changes in the sediment characteristics associated with low chironomid abundance. We suggest that the relative competitive ability of the Cladocera species is reversed when the sediment has become homogeneous and nutrient-poor after overexploitation by the dominant, tube building and detritivorous chironomid *Tanytarsus gracilentus*.

### Introduction

Cladocera form an important component in most lake ecosystems and have been studied extensively. The main focus has been on the planktonic genera, especially *Daphnia*, which ranks among the best studied freshwater zooplankton. The life history and population dynamics of planktonic Cladocera have been described in detail (e.g., Lynch 1980a; Grover et al. 2000), and long-term studies have shown how the populations respond to factors like nutrient loading and the predatory environment (e.g., Jeppesen et al. 1998). The planktonic Cladocera can themselves induce changes in the lake ecosystem: as their populations vary, so does the grazing pressure on small phytoplankton with resulting changes in water trans-

parency (e.g., Christoffersen et al. 1993). Although the causal pathways are not always clear, manipulation of planktonic Cladocera through suppressed fish predation has become a potential tool for lake management (“biomanipulation”) (Gulati et al. 1990; Jeppesen et al. 1996).

In contrast to the planktonic Cladocera, the benthic families (mainly Chydoridae and Macrothricidae), have received far less attention as an ecosystem component. Yet they are very abundant and comprise a suite of species that occupy various littoral and profundal habitats. The seasonal dynamics of benthic Cladocera is quite well documented but their long-term year-to-year population variation has rarely been studied. Benthic Cladocera have been shown to modify their environment (van de Bund and Davids

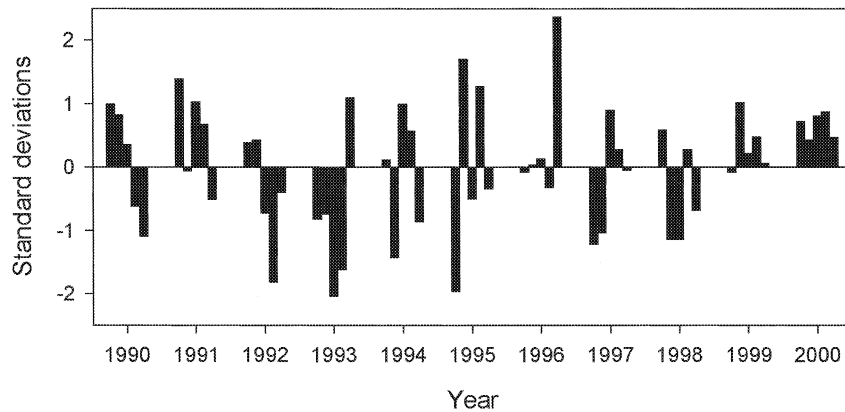


Figure 1. Air temperature at Lake Myvatn during May to September in 1990–2000 shown as standard deviations from the average of monthly averages. Each bar indicates one month.

1993) and a few species form important links in lake food webs.

In Lake Myvatn, Iceland, which is renowned for its abundance of wildlife, a large proportion of the secondary production is channelled through the zoobenthos where chironomids play a major role and Cladocera are prominent (Jónasson 1979). The largest Cladocera species there, *Eurycercus lamellatus* (Müller), serves as food for certain duck species (Gardarsson 1979; Gardarsson and Einarsson 2002) and the Arctic charr *Salvelinus alpinus* (L.), the main commercial fish in the lake. Analyses of duck and fish stomach contents over a number of years indicate large year-to-year variation in the abundance of *E. lamellatus*, and similar evidence exists for long-term variation also in the smaller species like *Chydorus sphaericus* (Müller) (Gardarsson 1979, 1988).

Changes in bird and fish populations in the lake (Gardarsson and Einarsson 2004) have stimulated monitoring of their food resources. Monitoring of the chironomid populations started in 1977 (Gardarsson et al. 1995, 2004), three-spined sticklebacks (*Gasterosteus aculeatus* L.) in 1989 (Gíslason et al. 1998), and since 1990 density of benthic Cladocera has been monitored with activity traps (Örnólfssdóttir & Einarsson 2004). Monitoring at Lake Myvatn has already yielded much insight into the long term food web dynamics of the lake, notably its oscillatory behaviour, interaction between chironomids and their sediment resources (e.g., Einarsson et al. 2002) and the response of breeding duck populations to year-to-year variation in chironomid abundance (e.g., Gardarsson and Einarsson 2004).

The aim of this study was to explore the long-term variation in the abundance of benthic Cladocera. We expect this will enable us to track food web oscillations in the lake. During the first few years of the study, benthic Cladocera were quite stable, both in terms of abundance and species composition, but in 1997 a dramatic, temporal shift occurred that coincided with profound changes in other components, especially chironomids and sediment structure. The shift can be seen as a lake-wide change in the size structure of the benthic community. This paper describes the shift and discusses its causes in relation to two alternative but not mutually exclusive hypotheses, those of predation pressure and resource characteristics.

#### Study area

Lake Myvatn (65°35' N, 17°00' W, altitude 277 m a.s.l.) in northern Iceland is a shallow spring-fed lake. It is 37 km<sup>2</sup> in area and divided into two main basins. The South Basin is the larger of the two; it is mostly between 2 and 3.2 m deep and receives most of its water from cold-water springs along its east shore. The South Basin also receives water from the North Basin which in turn is fed by both cold and thermal springs (up to 30 °C). The temperature of the springwater influences the lake temperature within about 2 km from the springs but the temperature of the main lake follows that of the air (Ólafsson 1979). The temperature is usually above 8 °C in summer (May–September) with a maximum of about 18 °C. The North Basin is 1–2 m deep except for a part, 2–6 m deep, where the sediment has been dredged. The main macrophyte species are *Myriophyllum* spp. and *Potamogeton filiformis* Pers. in the shallow parts, *Ranunculus trichophyllus*

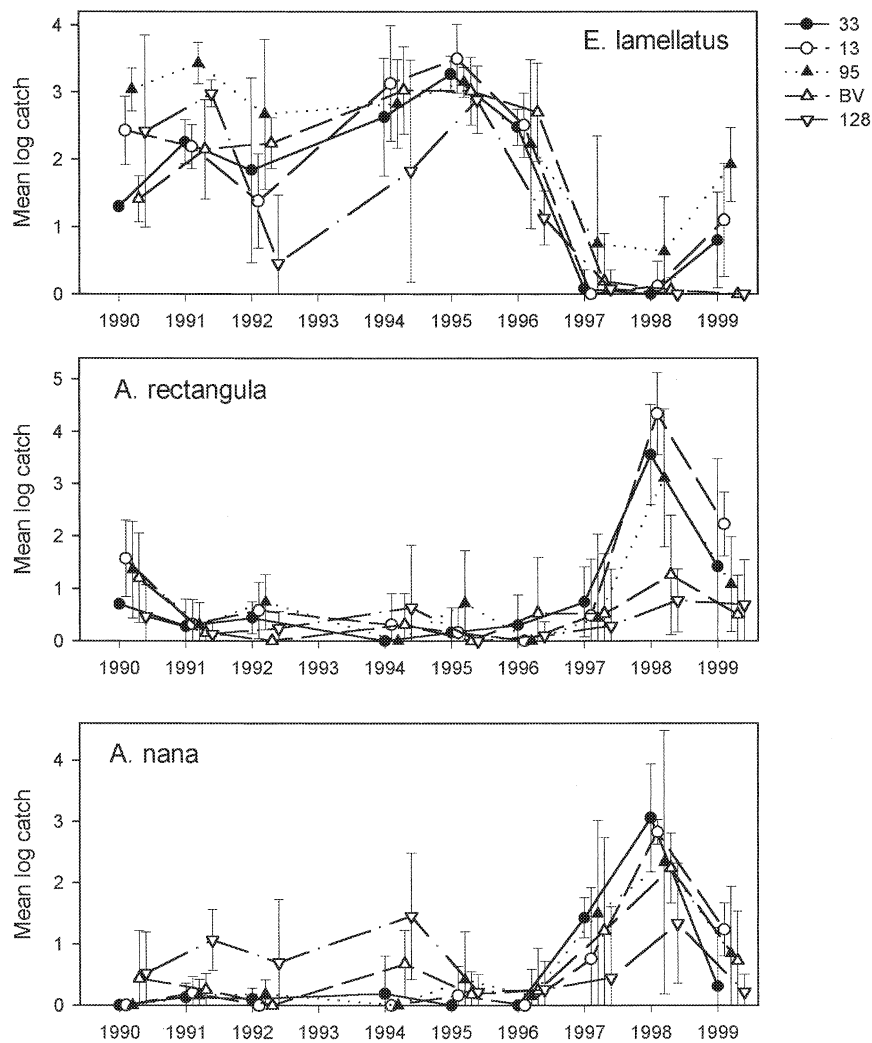


Figure 2. Trap catches of Cladocera, Copepoda and Chironomidae 1990–1999, excluding 1993, when the samples were not preserved due to a defect fixative. Shown is the mean catch (with 95% confidence limits) in July and August for each station and year. Note the log scale. Stations no. 13, 33 and 95 were well spaced out in the South Basin, station 128 was in the undredged part of the North Basin (no. 128) and station BV in the cold spring area at the SE corner of the lake.

Chaix in the cold spring areas and filamentous green algae (Cladophorales) cover large areas in the South Basin. The zoobenthos, dominated by chironomid midges, has been described by Lindegaard & Jónasson (1979). The dominant species is *Tanytarsus gracilentus* (Holmgren) whose density fluctuates greatly in a regular manner along with several other chironomid species (Gardarsson et al. 2004). The benthic cladocerans were studied by Adalsteinsson (1979) and Örnólfssdóttir and Einarsson (2004) and a palaeolimnological record of the Cladocera was presented by Einarsson and Hafliðason (1988; see also Einarsson et al. 2004). The main predators on the Myvatn Clado-

cera are three-spined stickleback, Arctic charr diving ducks, *Hydra* sp. and predaceous oligochaetes (*Chaetogaster* spp.) and chironomids (mainly *Procladius islandicus* (Goetghebuer)) (cf. Einarsson et al. 2004).

### Methods

The Cladocera were collected by an activity trap containing a set of 10 jars mounted with inverted funnels, based on a prototype introduced by Whiteside and Williams (1975). A modified type of their “pattern sampler” was used in Lake Myvatn and was described

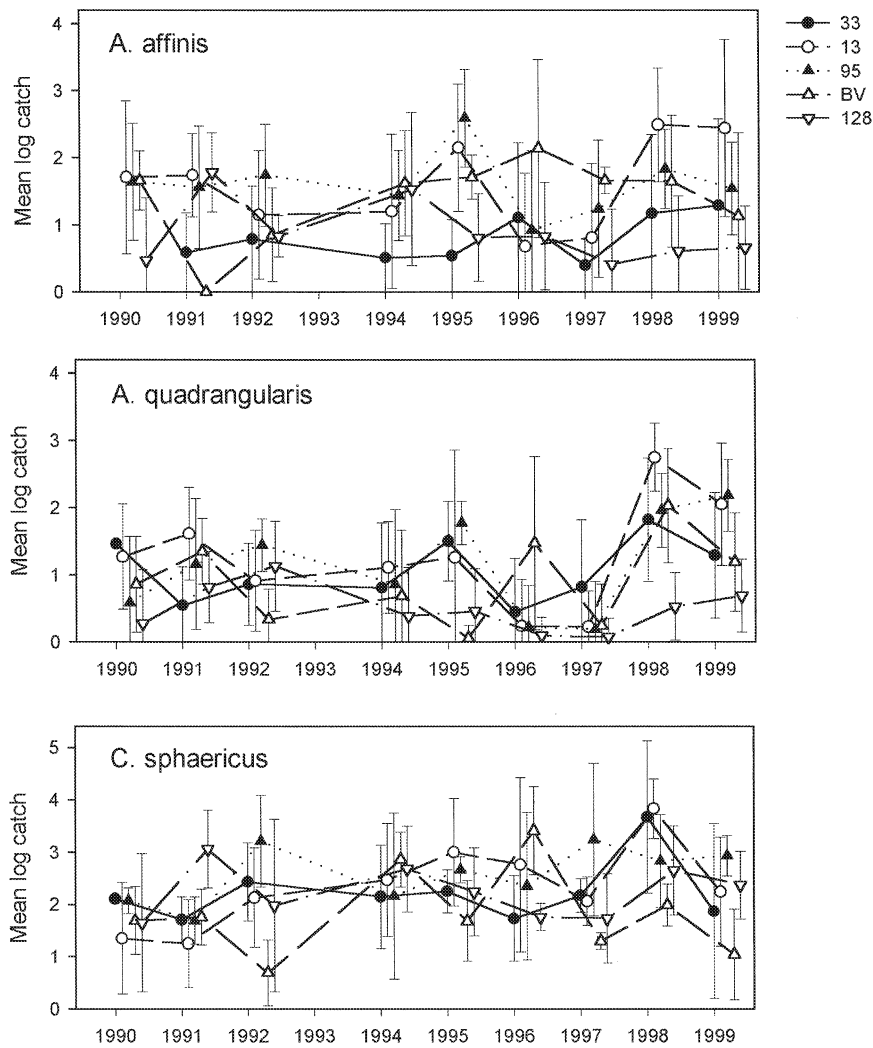


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by Örnólfssdóttir and Einarsson (2004). The basic unit of the Myvatn Cladocera trap is a plastic jar with a funnel mounted on the lid. A battery of 10 jars is mounted on a frame and suspended upside down on legs above the sediment surface and retrieved 24 h later. Benthic and planktonic Cladocera venture through the funnel and get trapped in the jar. Copepods and chironomid larvae (mainly Orthocladinae) are also caught. The total area of funnel openings in the trap was 442 cm<sup>2</sup>, but the sampling area is somewhat larger because the funnel openings were placed 3 cm above the sediment surface. Hence, the trap did not yield a direct density estimate, but the catches of *E. lamellatus* have been calibrated against density estimates obtained by conventional benthic sampling (Örnólfssdóttir and

Einarsson 2004). We assume that the trap catches for other species also reflect variation in density although this has not been tested. When the trap was retrieved the jars were removed from the frame, closed with a lid and taken to the laboratory on the lake shore where the animals were fixed in lugol. The contents of all 10 jars from a frame were examined individually during the first two years of monitoring but in later years the contents of the jars were lumped together on retrieval. Large samples were subsampled before counting the Cladocera; usually the subsample contained at least 200 individuals belonging to Cladocera. The sample or subsample was placed on a gridded Petri dish and the Cladocera were identified and counted under a dissecting microscope (30–50× magnification). The samples

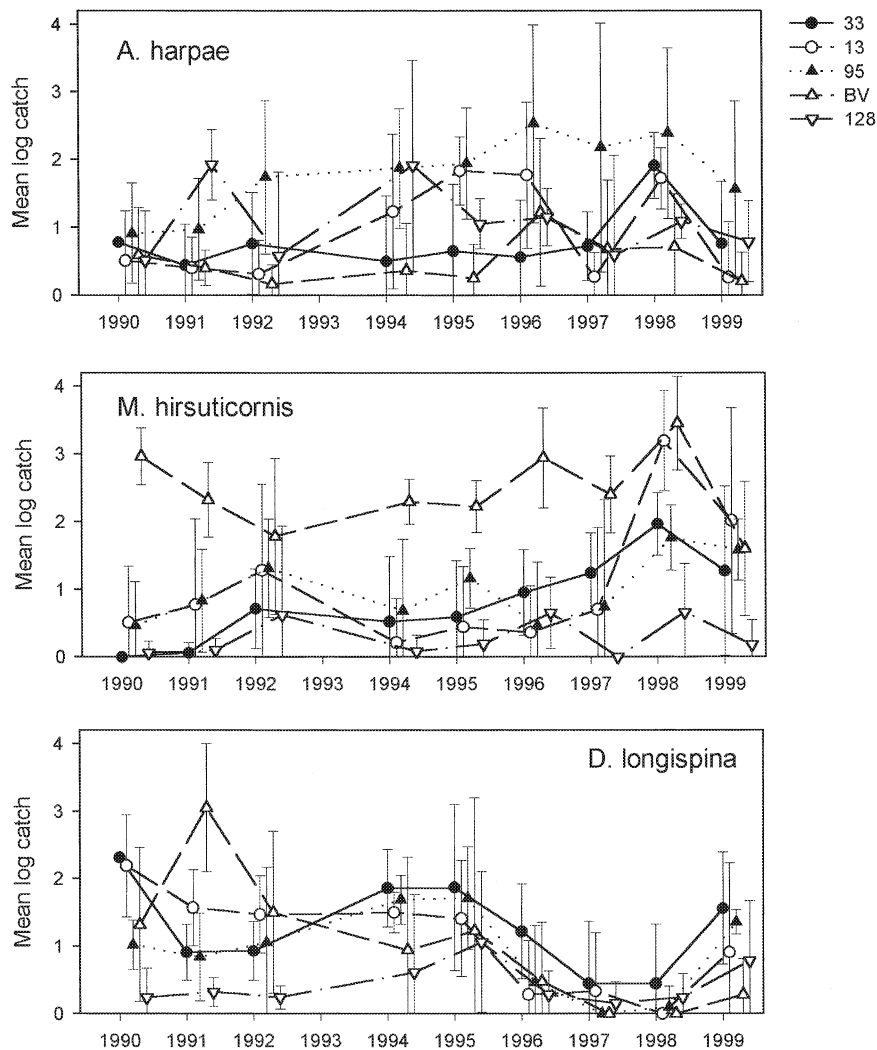


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from 1993 were not preserved because of a faulty fixative, but an examination of chydorid exuviae in the jars revealed that *E. lamellatus* was abundant that year.

The monitoring was carried out at five locations in the lake. Three stations (Nos. 13, 33 and 95) represented the South Basin, one station (No. 128) represented the undredged part of the North Basin and one (BV) was in the cold spring area at the SE corner of the lake. One trap (a frame with 10 jars) was operated on each location for 24 h at about 10-days intervals in summer. A 6-l zooplankton sample was collected at the same time from the whole water column and filtered through a 63- $\mu\text{m}$  sieve and fixed in lugol.

Meteorological data for the Reykjahlid weather station were obtained from the Icelandic Meteorolo-

gical Institute (Figure 1). Data on the abundance of three-spined stickleback (*G. aculeatus*) was obtained from five minnow traps deployed at eight stations around the lake at two times of the year, late June and August/September (Gíslason et al. 1988). Correlation analyses were performed between Cladocera indices and certain environmental variables (temperature, wind velocity and abundance of three-spined stickleback and the chironomid *T. gracilentus*). An index of Cladocera abundance was calculated using the mean log catches of a particular species in July and August, averaged over the three South Basin stations. The stickleback index used is log catch per station (four stations in the South Basin) in June and August/September separately and a combined index: log

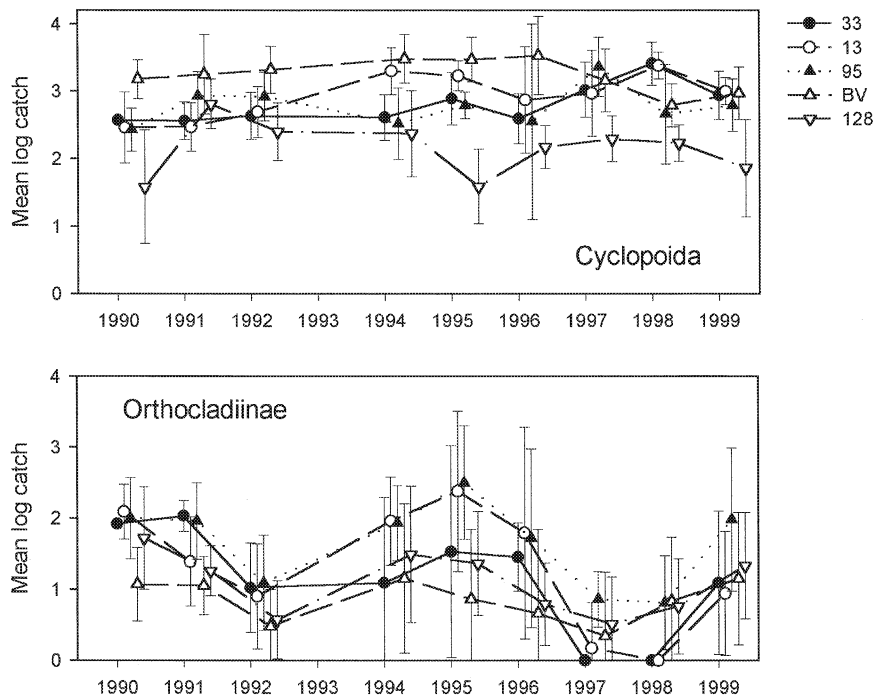


Figure 2. Continued.

total catch of the year per station in the South Basin. The *T. gracilentus* index is the log geometric mean of the total annual catches of two flytraps, one on each side of the South Basin (see Gardarsson et al. 2004).

## Results

In the period 1990–1996, the Cladocera assemblages in Lake Myvatn were fairly stable despite seasonal variation (see Örnólfssdóttir and Einarsson 2004). In this period *Eurycercus lamellatus* was usually the most abundant species in the traps, followed by *Chydorus sphaericus*. Other benthic species, in order of abundance in the traps, were *Alona affinis* (Leydig), *Alona quadrangularis* (Müller), *Acroperus harpae* (Baird), *Macrothrix hirsuticornis* Norman & Brady, *A. rectangularis* Sars and *Alonella nana* (Baird). *Graptoleberis testudinaria* (Fischer) was present but infrequent. Cyclopoid Copepoda and *Daphnia longispina* (Müller) were abundant in the traps. In the cold spring area *M. hirsuticornis* dominated the Cladocera community (Örnólfssdóttir and Einarsson 2004) (Figure 2).

In 1997 a complete shift occurred at all the sampling stations. *E. lamellatus*, and *D. longispina* almost disappeared while *C. sphaericus*, *M. hirsuticornis*, *A. affinis*, *A. quadrangularis* and the cope-

pods seemed unaffected (Figure 2). Late that year, *A. rectangularis* and *A. nana* increased and reached phenomenal numbers ( $10^3$ – $10^5$  per trap) the year after, whereas *E. lamellatus* seemed almost absent from the lake in 1998. In 1999 the Cladocera assemblages approached the pre-1997 situation.

The population of three-spined stickleback fluctuated widely (Figure 3). High densities were observed in 1991–1992 and 1995–1998. Extreme low density was observed in 1993. The population of the chironomid *T. gracilentus* fluctuated from a low in 1990 to a peak in 1992 and then showed a gradual decline to a low in 1997–1998 when it started to rise again (Figure 3). Transparency which varied much during the study period (Figure 3) was mainly determined by algal blooms in July and August. The Secchi-disc depth was rather high (SD = 3–4 m) in 1990, 1991, 1993 and 1995, but low in 1992 and in 1997–1999 and lowest (< 1m) in 1997.

The Cladocera trap time series for the South Basin were compared with weather variables and the population indices of three-spined stickleback and *T. gracilentus*. No relationship was found with wind (monthly mean values and monthly mean max values). Air temperature (monthly means), which correlates well with the summer water temperature in the lake (Ólaf-

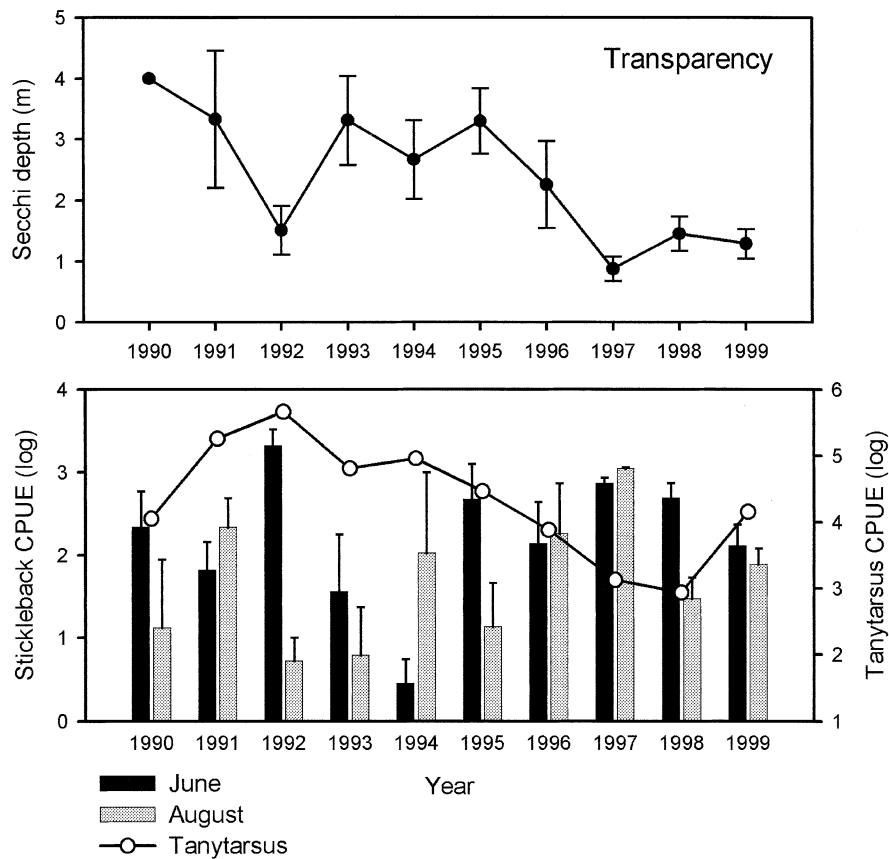


Figure 3. Transparency (upper panel) and population indices (as catch per unit effort – CPUE) of three-spined stickleback (*Gasterosteus aculeatus*) and the chironomid *Tanytarsus gracilentus* (lower panel) in the South Basin of Lake Myvatn in the period 1990–1999. Transparency (in the South Basin) is indicated by mean Secchi depth  $\pm$  95% confidence limits in July and August. The stickleback index is mean (and 95% upper confidence limit) log catch per station and the *Tanytarsus* index is the log geometric mean of 2 flytraps.

son 1979), did not correlate with Cladocera numbers except a negative correlation of *C. sphaericus* with July mean temperature ( $r = -0.772$ ,  $p < 0.05$ , d.f. 7). No correlation was found with the indices of abundance of three-spined sticklebacks, the main potential predator. *E. lamellatus* correlated positively ( $r = 0.699$ ;  $p < 0.05$ ) and *A. nana* negatively ( $r = -0.727$ ;  $p < 0.05$ ) with the chironomid *T. gracilentus* population, a major influencing factor on the physical structure of the sediment surface (Gardarsson and Snorrason 1993; Ólafsson and Paterson 2004). Correlation coefficients of the annual catches could be grouped into three clusters (Figure 4). The first cluster contained *E. lamellatus*, the Orthoclaadiinae and *D. longispina*. The second cluster had *A. affinis* and *A. quadrangularis* and the third cluster contained all the other species.

## Discussion

Two major observations emerge from this study: first, large and rapid lake-wide shifts in species composition take place on a decadal scale; and second, the change involves a shift in the size distribution of species. Large planktonic (*Daphnia*) and epibenthic (*Eurycerus*, orthoclaadiin chironomids) species were temporarily replaced by small infaunal or ubiquitous species (*A. rectangula*, *A. nana*, cf. Adalsteinsson, 1979; Flößner, 1972) while medium sized benthic species remained unaffected (Table 1).

Regression analyses of the annual catches of Cladocera against environmental variables such as temperature and wind (resuspension of sediment) did not reveal any interesting relationships; there was a general lack of correlation (with the exception of that between *C. sphaericus* and mean July temperature).

Table 1. Maximum body size of the Cladocera species occurring in the study and the changes in their abundance in the year 1997 (+ increase; – decrease; 0 no change). Maximum body sizes are from Alonso (1996).

Species	Maximum size (mm)	Shift
<i>Alonella nana</i>	0.26	+
<i>Alona rectangularis</i>	0.43	+
<i>Chydorus sphaericus</i>	0.50	0
<i>Alona quadrangularis</i>	0.80	0
<i>Acroperus harpae</i>	0.85	0
<i>Alona affinis</i>	1.00	0
<i>Macrothrix hirsuticornis</i>	1.30	0
<i>Daphnia longispina</i>	2.30	–
<i>Eurycerus lamellatus</i>	3.30	–

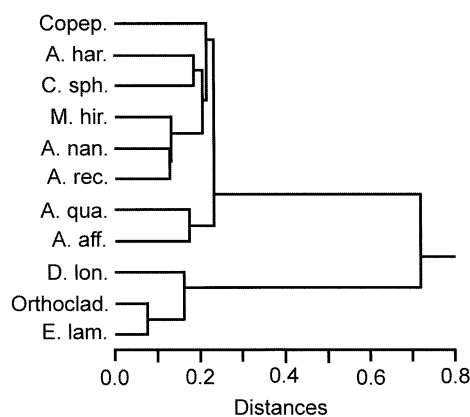


Figure 4. A single-linkage dendrogram showing how closely the time series of Cladocera trap catches were correlated among species, using Pearson's  $r$  as a measure of similarity.

Furthermore, 1997, the year of faunal change, was not anomalous in terms of temperature (Figure 1).

Many pelagic Cladocera seem vulnerable to cyanobacterial blooms and this response is directly size-dependent (e.g., Gliwicz 1990). The shift in the Lake Myvatn Cladocera occurred at the lowest water transparency recorded over the study period (Figure 3). The shift occurred lakewide, also in the clear spring-water at station BV which is unaffected by cyanobacterial blooms. This seems to rule out Cyanobacteria as a causal factor.

Size-selective predation and size-specific reproductive rates are two main factors that determine the size distribution of animals in a community (Goulden et al. 1978). Valuable insight is provided by studies of planktonic Cladocera. The "size-efficiency hypothesis" advanced by Brooks and Dodson (1965)

implies a direct relationship between body size and competitive strength in herbivorous species. In environments with no vertebrate predators, larger species dominate and exclude smaller species by competition. However, when predation by vertebrate planktivores is intense, the larger species are more vulnerable than the smaller species which then tend to dominate (see, e.g., Hrbacek 1962; Brooks and Dodson 1965; Brett and Goldman 1997). The shift in the size structure of Lake Myvatn Cladocera was in line with this scenario. It coincided with a high density of small fish (three-spined stickleback) and low chironomid density (Figure 3). One problem with this interpretation is that in 1992 although the fish density was also high (Figure 3), the size distribution of the Cladocera did not change. Another problem is that the Cladocera did not show any significant correlation with population density of the three-spined stickleback. Both problems are suggestive rather than conclusive: in 1992 fish density was high in early summer and low in late summer, whereas in 1997 fish density was high all summer (Figure 3). Also, there is no reason to expect a linear relationship between predation pressure and the size distribution of Cladocera.

An important difference between 1997 and 1992 is that in 1992 chironomids were abundant, whereas 1997 had very low chironomid densities (Figure 3; see also Gardarsson et al. 2004). Perhaps fish predation is only effective when chironomids are decreasing and food resources are becoming scarce.

All three groups (*Daphnia*, *Eurycerus*, orthocladid Chironomidae) that declined in 1997, are relatively large planktonic or epibenthic feeders of detritus and microalgae (Einarsson et al. 2004). The shift in species composition coincided with extremely low abundance of the dominant chironomid *T. gracilentus* after a period of great abundance. This change is part of long-term cycles of the *T. gracilentus* population (Gardarsson et al. 2004). The density of *T. gracilentus* correlated positively with *E. lamellatus* and negatively with *A. nana*. Analyses of predator populations (three-spine stickleback and tanypodine chironomids) and changes in the body size of *T. gracilentus* associated with the cycles indicate that the cycles are driven by consumer-resource interactions, i.e., *T. gracilentus* as a consumer interacting with its detrital food resources (Einarsson et al. 2002). The interaction is of two types: (1) digestion of the sediment; and (2) its modification by forming a dense, coherent mat of tubes and silk strands, peppered with fecal pellets. However, the relative importance of the two is unknown.

Reduced nutritive quality of the detritus is suggested by a delayed negative correlation between body size and population density of *T. gracilentus* observed by Einarsson et al. (2002). The changes in physical structure are described by Gardarsson & Snorrason (1993) and Ólafsson and Paterson (2004). When the density of *T. gracilentus* was at a low level (as in 1996–1997) the sediment surface was fine-grained, loose and watery, in sharp contrast to the firm mat of larval tubes observed in the preceding and following years. It seems plausible that the shift in the size-distribution of detritus-feeding invertebrates was caused by the change in the structure and quality of detritus, resulting from the feeding and tube forming activities of *Tanytarsus*. At this point, the mechanism is unknown but important variables of the sediment probably include firmness, particle size and nutrient value (see, e.g., Wilson 1991). Romanovsky and Feniova (1985) proposed a hypothesis, backed up by simulations and laboratory experiments with Cladocera, which implies that when the food situation is poor and stable, small species outcompete the juvenile stages of the larger species, and thus become dominant. The species with the lowest food level threshold for reproduction will be the best competitors under these food conditions (see also Lampert and Schober 1980; Lynch 1980b; Bengtsson 1987; Milbrink and Bengtsson 1991). It is still unknown to what extent the size efficiency and food density thresholds observed or postulated in the pelagic species apply to the littoral chydorids. Experiments conducted by de Eyto and Irvine (2001) suggest that chydorid Cladocera species differ in their ability to utilize the available food resources (see also Fryer 1968). If a shift in the size structure of the Cladocera community continues to follow the food web cycles in Lake Myvatn in the future (preliminary analyses suggest that it does), further research should focus on the possible reversal of competitive ability (Connell 1983) of the large- and small-sized detritus-feeders following the decline in *T. gracilentus*.

In conclusion, the lakewide temporal shift in the size distribution of the benthic community shows certain features that would suggest size-selective predation. The two main obstacles to this hypothesis are that high vertebrate predator densities at other times do not cause such effects and there is no correlation between the Cladocera and the abundance of three-spined stickleback. The shift in the size distribution of the benthic community coincided with profound changes in sediment characteristics resulting from density fluctuations in the resource-limited,

tube-building and dominant *Tanytarsus gracilentus*. The hypothesis of Romanovsky and Feniova (1985) that different levels of food supply may reverse the competitive strength of small- and large-bodied Cladocera offers a plausible explanation of the observed changes in the cladocerans in Lake Myvatn. By over-exploiting the detrital resource, *Tanytarsus* not only causes its own demise but also alters the exploitative competition between small-bodied cladocerans and juveniles of large-bodied detritivores (*Eurycerus*, *Daphnia*, Orthoclaadiinae), leading to the suppression of the latter.

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### References

- Adalsteinsson H. 1979. Seasonal variation and habitat distribution of benthic Crustacea in Lake Myvatn in 1973. *Oikos* 32: 195–201.
- Alonso M. 1996. Crustacea, Branchiopoda. *Fauna Iberica*, Vol. 7. Ramos M.A. (ed.). Museo Nacional de Ciencias Naturales. CSIC. Madrid.
- Bengtsson J. 1987. Competitive dominance among Cladocera: Are single-factor explanations enough? An examination of the experimental evidence. *Hydrobiologia* 145: 245–257.
- Brett M.T. and Goldman C.R. 1997. Consumer *versus* resource control in freshwater pelagic food webs. *Science* 275: 384–386.
- Brooks J.L. and Dodson S.I. 1965. Predation, body size and composition of plankton. *Science* 150: 28–35.
- Christoffersen K., Riemann B., Klynsner A. and Søndergaard M. 1993. Potential role of fish predation and natural populations of zooplankton in structuring a plankton community in eutrophic lake water. *Limnol Oceanogr* 38: 561–573.
- Connell J.H. 1983. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *Am. Natural.* 122: 661–696.
- de Eyto E. and Irvine K. 2001. The response of three chydorid species to temperature, pH and food. *Hydrobiologia* 459: 165–172.
- Einarsson Á. and Haffidason H. 1988. Predictive paleolimnology: Effects of sediment dredging in Lake Myvatn, Iceland. *Verh internat Verein Limnol* 23: 860–869.
- Einarsson Á., Gardarsson A., Gíslason G.M. and Ives A.R. 2002. Consumer-resource interactions and cyclic population dynamics of *Tanytarsus gracilentus* (Diptera: Chironomidae). *J. Anim. Ecol.* 71: 832–845.

- Einarsson Á., Stefánsdóttir G., Jóhannesson H., Ólafsson J.S., Gíslason G.M., Wakana I., Gudbergsson G. and Gardarsson A. 2004. The ecology of Lake Myvatn and the river Laxá: variation in space and time. *Aquat. Ecol.* 38: 317–348 (this issue).
- Flößner D. 1972. *Krebstiere, Crustacea. Kiemen- und Blattfüßer, Branchiopoda Fischläuse, Branchiura. Die Tierwelt Deutschlands* 60. Gustav Fischer Verlag, Jena.
- Fryer G. 1968. Evolution and adaptive radiation in the Chydoridae (Crustacea: Cladocera): A study in comparative functional morphology and ecology. *Phil Trans R Soc (B)* 254: 221–385.
- Gardarsson A. 1979. Waterfowl populations of Lake Myvatn and recent changes in numbers and food habits. *Oikos* 32: 250–270.
- Gardarsson A. 1988. Population changes in Lake Myvatn and their probable causes. *Tímarit Háskóla Íslands* 1: 55–66 (in Icelandic).
- Gardarsson A. and Einarsson A. 2002. The food relations of the waterbirds of Lake Myvatn, Iceland. *Verh internat Verein Limnol* 28: 1–10.
- Gardarsson A. and Einarsson A. 2004. Resource limitation of diving ducks at Myvatn: food limits production. *Aquat. Ecol.* 38: 285–295 (this issue).
- Gardarsson A. and Snorrason S.S. (1993) Sediment characteristics and density of benthos in Lake Mývatn, Iceland. *Verh internat Verein Limnol* 25: 452–457.
- Gardarsson A., Ólafsson J.S., Hrafnisdóttir T., Gíslason G.M. and Einarsson A. 1995. Monitoring chironomid numbers at Myvatn, Iceland: The first sixteen years. In: Cranston P. (ed.), *Chironomids: From Genes to Ecosystems*. CSIRO Publications, East Melbourne, pp. 141–154.
- Gardarsson A., Einarsson A., Gíslason G.M., Hrafnisdóttir T., Ingvason H.R., Jonsson E. and Ólafsson J.S. 2004. Population fluctuations of chironomid and simuliid Diptera at Myvatn in 1977–1996. *Aquat. Ecol.* 38: 209–217 (this issue).
- Gíslason G.M., Gudmundsson A. and Einarsson A. 1998. Population densities of the three-spined stickleback (*Gasterosteus aculeatus* L.) in a shallow lake. *Verh internat Verein Limnol* 26: 2244–2250.
- Gliwicz, Z.M. 1990. *Daphnia* growth at different concentrations of blue-green filaments. *Archiv. Hydrobiol.* 120: 51–65.
- Goulden C.E., Hornig L. and Wilson C. 1978. Why do large zooplankton species dominate? *Verh internat Verein Limnol* 20: 2457–2460.
- Grover J.P., McKee D., Young S., Godfray H.C.J. and Turchin P. 2000. Periodic dynamics in *Daphnia* populations: Biological interactions and external forcing. *Ecology* 81: 2781–2798.
- Gulati R.D., Lammens E.H.H.R., Meijer M.-L. and van Donk E. 1990. Biomaniipulation, tool for water management. *Hydrobiologia* 200/201: 1–628.
- Hrbacek J. 1962. Species composition and the amount of zooplankton in relation to fish stock. *Rozpravy Csekoslovenske Akademie Ved, Rada Matem Prir Ved* 72 (10): 1–114.
- Jeppesen E., Søndergaard M., Jensen J.P., Mortensen E. and Sortkjær O. 1996. Fish-induced changes in zooplankton grazing on phytoplankton and bacterioplankton: A long-term study in shallow hypertrophic Lake Søbygaard. *J Plankton Res* 18: 1605–1625.
- Jeppesen E., Søndergaard M., Jensen J.P., Mortensen E., Hansen A.-M. and Jørgensen T. 1998. Cascading trophic interactions from fish to bacteria and nutrients after reduced sewage loading: An 18-year study of a shallow hypertrophic lake. *Ecosystems* 1: 250–267.
- Jónasson P.M. (ed.) 1979. *Ecology of Eutrophic, Subarctic Lake Myvatn and the River Laxá*. *Oikos* 32: 1–308.
- Lampert W. and Schober U. 1980. The importance of ‘threshold’ food concentrations. In: Kerfoot W.C. (ed.), *Evolution and Ecology of Zooplankton Communities*, Hanover (N.H.) London, The University Press of New England, pp. 264–267.
- Lindegaard C. and Jónasson P.M. 1979. Abundance, population dynamics and production of zoobenthos in Lake Myvatn, Iceland. *Oikos* 32: 202–227.
- Lynch M. 1980a. The evolution of cladoceran life histories. *Quart Rev Biol* 55: 23–42.
- Lynch M. 1980b. Predation, enrichment, and the evolution of cladoceran life histories: a theoretical approach. In: Kerfoot W.C. (ed.), *Evolution and Ecology of Zooplankton Communities*. The University Press of New England, Hanover (N.H.), London, pp. 367–376.
- Milbrink G. and Bengtsson J. 1991. The impact of size-selective predation on competition between 2 *Daphnia*-species. *J Animal Ecol* 60: 1009–1028.
- Ólafsson J. 1979. Physical characteristics of Lake Myvatn and River Laxá. *Oikos* 32: 38–66.
- Ólafsson J.S. and Paterson D.M. 2004. Alteration of biogenic structure and physical properties by tube building chironomid larvae in cohesive sediments. *Aquat. Ecol.* 38: 219–229 (this issue).
- Örnólfsson E.B. and Einarsson A. 2004. Spatial and temporal variation of benthic Cladocera (Crustacea) studied with traps in Lake Myvatn, Iceland. *Aquat. Ecol.* 38: 239–251 (this issue).
- Romanovsky Y.E. and Feniova I.Y. 1985. Competition among Cladocera: Effect of different levels of food supply. *Oikos* 44: 243–252.
- van de Bund W. and Davids C. 1993. Complex relations between freshwater macro- and meiobenthos: Interactions between *Chironomus riparius* and *Chydorus piger*. *Freshw. Biol.* 29: 1–6.
- Whiteside M.C. and Williams J.B. 1975. A new sampling technique for aquatic ecologists. *Verh internat Verein Limnol* 19: 1534–1539.
- Wilson W.H. 1991. Competition and predation in marine soft-sediment communities. *Ann Rev Ecol Syst* 21: 221–241.