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Spatial and temporal variation of benthic Cladocera (Crustacea) studied with activity traps in Lake Myvatn, Iceland

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Abstract

Benthic Cladocera were studied with a modified type of an activity trap in Lake Myvatn in 1990–1992. After feasibility experiments, the operation time and the distance of the traps from the benthic substrate were adjusted in order to minimize the effects of diurnal variation and the trapping of planktonic organisms. The trap catches of *Eurycercus lamellatus* were positively correlated with their abundance at the bottom as estimated by grab sampling ($r = 0.910$, $P < 0.001$). The usefulness of the activity trap was demonstrated by: (1) a lake-wide survey of the benthic Cladocera; (2) a study of the seasonal variation in the size distribution, abundance and sex ratio of *E. lamellatus*; and (3) a study of the seasonal succession of *Chydorus sphaericus* and *Alona affinis*. The variation of benthic Cladocera among 21 trap sites distributed on a 1–2-km scale across the lake exceeded the within-site variation. The sampling sites could be divided into five main groups based on cluster analysis. *Eurycercus lamellatus* was the most common species in the mat of filamentous green algae (Cladophorales). *Alonella nana* dominated the area of spring water inflow in the north basin and *Macrothrix hirsuticornis* the area of spring water inflow in the southeastern part of the lake. In other parts of the lake either *Chydorus sphaericus* or *Alona quadrangularis* tended to dominate. The size distribution and sex ratio of *E. lamellatus* was followed at two sites through one summer. In early summer most individuals were females less than 1.45 mm long. Around mid-summer they had grown to 0.69–3.1 mm. By the end of August the size distribution had become bimodal, with a large number of small males and a smaller number of much larger females. The seasonal succession in the abundance of *E. lamellatus*, *A. affinis* and *C. sphaericus* was followed at four sites over two seasons. With some exceptions the abundance of a species followed a similar seasonal trajectory on the different stations in any one year. There was, however, a marked difference between the two years (1991 and 1992), probably related to different temperatures.

Introduction

The need for monitoring of aquatic biota is steadily growing, not only because of an increased human pressure on the aquatic environment but also because long-term data sets are needed for effective modelling of the dynamics of aquatic ecosystems. Traditionally, monitoring of freshwater lakes has been based on sampling the pelagic zone (e.g., Lund 1964), which is relatively easy and yields clean and homogeneous samples. The heterogeneous nature of the benthic substrate creates problems, one of them is the large amount of fine-grained, often flocculated sediment that must be processed before a useful sample of benthic organisms can be obtained. The conventional solution to this problem is to employ stationary activity traps (e.g., Hanson et al. 2000; Hyvonen and Nummi 2000).

Lake Myvatn is a shallow eutrophic lake in northern Iceland, renown for scenic volcanic landscape and a wealth of waterfowl (Jónasson 1979). Secondary production of the lake goes mainly through a benthic pathway and is dominated by chironomids but chydorid Cladocera are also abundant. The largest Cladocera, *Eurycercus lamellatus* (Müller), is a preferred

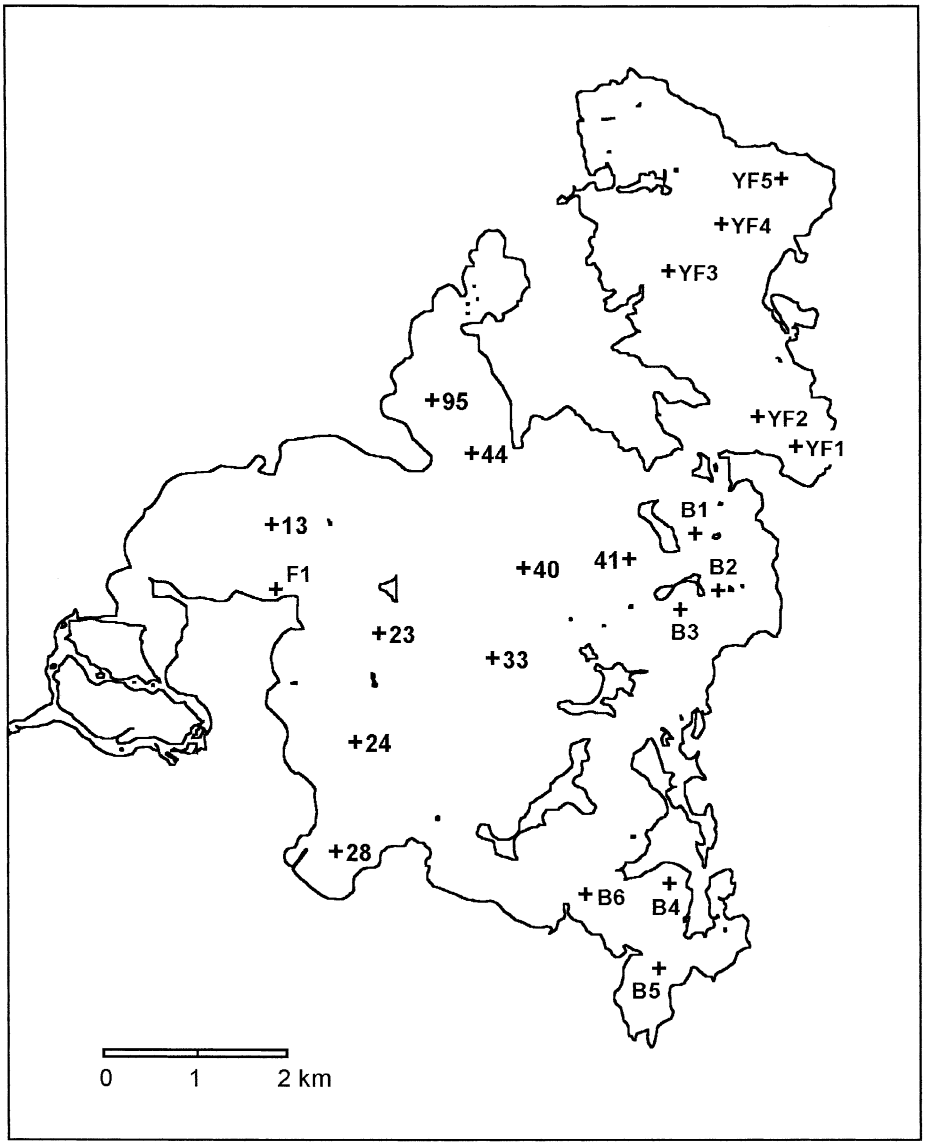

Figure 1. Sampling stations in Lake Myvatn in July 1990.

food species for fish and some ducks (Gardarsson and Einarsson 2002). Studies in Lake Myvatn indicate considerable variation in the benthic Cladocera community on both spatial (Adalsteinsson 1979) and temporal scales (decades) (Gardarsson 1979; Einarsson and Örnólfsdóttir 2004) and there were indications that the year-to-year variation in the chydorids was synchronized with large scale oscillations in the chironomid populations of the lake (cf. Gardarsson et al. 2004). These observations called for a cost-efficient method for the monitoring of the benthic Cladocera in order to promote understanding of the long-term dynamics of the food web.

In 1990–1992 the benthic Cladocera of Lake Myvatn were studied using specially designed activity traps. The design is based on the principle of the "pattern sampler" developed by Whiteside and Williams (1975) that takes advantage of the movements of the cladocerans up from the benthic substrate and uses inverted funnels to trap the animals in glass or plastic jars. The trap has the advantage that large numbers of benthic Cladocera can be collected without having to process large amounts of sediment.

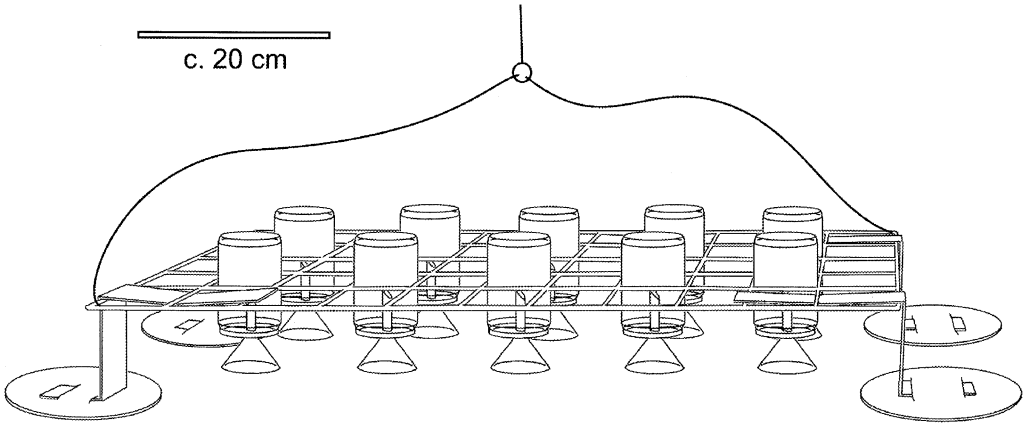

Figure 2. The Lake Myvatn Cladocera trap. For the sake of clarity the outermost frame is shown as a single unit, but in reality the grid is sandwiched between two identical frames, which gives extra stability. Length of frame is 78 cm.

In this paper we present tests of the usefulness of the Myvatn Cladocera trap. The initial feasibility tests included: (1) comparison of trap catches and conventional grab samples for one species (*E. lamellatus*); (2) comparison of trap catches of several species during day and night; and (3) estimates of the effect of trap height over the sediment surface. After the initial tests the trap was employed for exploring the spatio-temporal variation in the benthic Cladocera: (1) surveying the benthic cladocerans of Lake Myvatn; (2) following the phenology of the most abundant species; (3) focusing in more detail on the sesonal variation in the size distribution and sex ratio of *E. lamellatus*. This study forms the starting point of a monitoring programme of the benthic Cladocera of Lake Myvatn that has continued to the present day (Einarsson and Örnólfsdóttir 2004).

Study area

Lake Myvatn (65°35′ N, 17°00′ W, altitude 277 m a.s.l.) is 37 km^2 and divided into two main basins (Figure 1). The larger southern basin is up to 4 m deep and is mostly fed by cold-water springs (ca. 5 °C) along its eastern shore. The northern basin is 1–2 m deep except for a part where sediment dredging has been taking place and is now 2–6 m deep. It is fed by both thermal and cold springs (up to 30 °C). The lake temperature follows that of the air (Ólafsson 1979a) and is usually above 8 °C in the ice-free period (May–September) with a maximum of about 18 °C. Theoretical retention time of the lake water is about one month. The pH in the inflowing springwater ranges from 8.3 to 9.2 (Ólafsson 1979b). Macrophytes vary with location. In the north basin the main macrophytes include *Myriophyllum* spp. and *Potamogeton filiformis* Pers.; *Ranunculus trichophyllus* Chaix dominates in the cold spring areas in the south. Filamentous green algae *Aegagropila linnaei* Kütz. and *Cladophora glomerata* (L.) Kütz. form a loose mat that covers extensive areas in the south basin. A considerable part of the soft lake bottom has no macrophytes. Chironomid midges are very abundant (Lindegaard and Jónasson 1979) but Cladocera are also prominent. Seasonal and spatial variation in the benthic cladocerans of Lake Myvatn was formerly studied by Adalsteinsson (1979) and a palaeolimnological record was presented by Einarsson and Haflidason (1988).

Methods

The principle of using inverted funnels to catch benthic Cladocera was introduced by Whiteside and Williams (1975). We used a modified sampler based on the same principle. Our device makes use of commercially available material which is easy to assemble into a sampling unit, but samples a less well defined area than the pattern sampler of Whiteside and Williams (1975). The trap is easily deployed as the frame creates little turbulence when lowered through the water column from a boat. The basic unit of the Myvatn Cladocera trap consisted of a plastic jar with a funnel mounted on the lid. The jar was suspended upside down, 3 cm above the sediment surface. Benthic and other Cladocera ventured through the funnel and got trapped in the jar. A metal frame (44 × 78 cm) with grid squares held a set of 10 jars in place (Figure 2). Four detachable legs made of 5 cm wide and 2-mm thin aluminium strips were fixed to the frame raising it 14 cm above the lake bottom. Each leg had a 21-cm diameter plastic lid from a bucket fixed to its lower end to prevent sinking in the sediment. The jars (11×7 cm, 300 ml each) were made of flexible clear plastic and could be squeezed into the grid squares of the frame. The funnels were made of soft semitransparent plastic. They were 13 cm long, 7.5 cm wide (inner diameter) at the wider end and 8 mm (inner diameter) at the narrower end. The total area of all ten funnel openings was 442 cm^2, but the sampling area was somewhat larger because the funnel openings were placed above the sediment surface. The jars were filled with filtered lake water (63 μm mesh) and the trap was lowered horizontally by a string from the boat to the lake bottom. Microcrustaceans only entered the trap by their own swimming motion. When the trap was collected, the jars were removed from the frame, closed with a lid and taken to the laboratory where the organisms were fixed in lugol. The catch contained in each jar was kept separate. The contents of each jar were identified and counted on a prelined Petri dish under a dissecting microscope (30–50 × magnification). Large samples were subsampled before counting.

A number of mud samples were obtained parallel to the trap sites in order to relate trap catches of *E. lamellatus* to its abundance at the bottom. In 1990 one Ekman-Birge grab sample (234 cm^2) was taken at the end of July on 4 trap sites. On August 19, two grab samples were taken per site, at two sites, and one grab sample was obtained at one site, for a total of nine samples. In 1991, four grab samples were collected on one sampling site during 11 trap operations in the period July 29 to September 21. One grab sample was collected at four sites August 9, 1991. Each sediment sample was filtered through a 0.5-mm mesh and fixed with 4% formaldehyde. This coarse mesh size was used to allow comparison with earlier attempts to monitor the abundance of *E. lamellatus*. These attempts focused on the larger size classes, which are a valuable food source for ducks (Gardarsson 1979). The sieve contents were spread on a white tray and separated by hand under a magnifying glass. When more than one grab sample was taken per site per sampling occasion, the average numbers of *E. lamellatus* were used for analyses.

Experiments were conducted to test the effect of the height of the funnel openings above the sediment surface on trap catch efficiency. Two heights were compared, 5 cm and 3 cm. Two traps, one with each height, were placed side by side and retrieved twelve hours later. Each jar constituted a sample. The first experiment was made at night on July 6, 1990. Two more experiments were conducted at another sampling location during the day and night July 6–7, 1990.

Experiments to compare the catch during day and night were made July 17–18, 1990. On the bottom, 6 traps were placed and left for 12 h between 08.00 and 20.00 hours. These were replaced by 6 traps for the next 12 h, care being taken not to place the new traps on the previous sampling areas. Each trap (10 jars pooled) constituted a sample. All the above mentioned experiments were carried out in the south basin of Lake Myvatn in which the bottom is soft sediment overlain by a 1–3-cm-thick layer of filamentous green algae (Cladophorales).

During the period 20–29 July, 1990 Cladocera traps were placed at 21 stations in the lake (Figure 1). Of these, 5 stations were in the North Basin, 16 in the South Basin, 6 of which were located in its eastern part (sometimes considered a separate East Basin). Per site, 1 trap was used for 24 h; each jar constituted a sample. The Kruskal–Wallis one-way analysis of variance by ranks (program SigmaStat from Jandel Scientific) was used to compare the median trap catches among the stations. On basis of this survey we selected five sites for continued monitoring (cf. Einarsson and Örnólfsdóttir 2003).

In 1990, the Cladocera were monitored in the period 29 July–25 September, all together seven sampling dates (not shown in this paper). In 1991, monitoring studies were carried out 12 times in the period 8 June–21 September and in 1992, 18 times on 2 sites and 11 times on 3 sites in the period 16 June–25 August (15 October on 2 sites). The water temperature (Figure 3) was monitored at the outlet (see Ólafsson 1999).

On two sites (33 and 95 in Figure 1) the sex ratio and body size of *E. lamellatus* was studied. In samples with fewer than 100 individuals, all the animals were measured. Larger samples were subsampled by placing 3 plastic rings on top of the sample in the Petri dish; 100 individuals from within the rings were measured. The length was measured with a grated ocular in a dissecting microscope from the anterior tip of the head-shield to the posterior margin of the carapace. If possible, 300 individuals from each sample were sexed. Flößner (1972) was consulted for the identification of the sexes. Detrended correspondence analyses

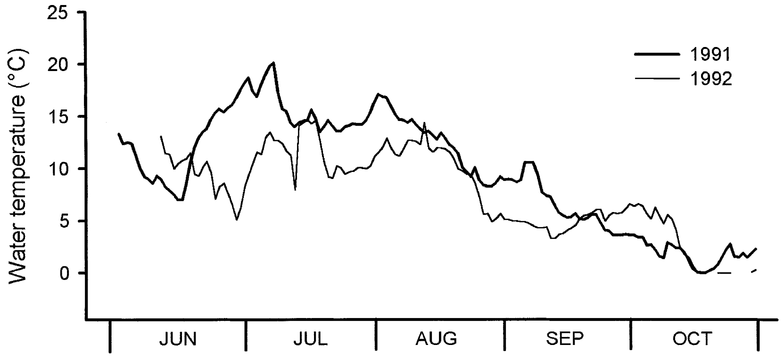

Figure 3. Water temperature at the outlet of Lake Myvatn in 1991 and 1992.

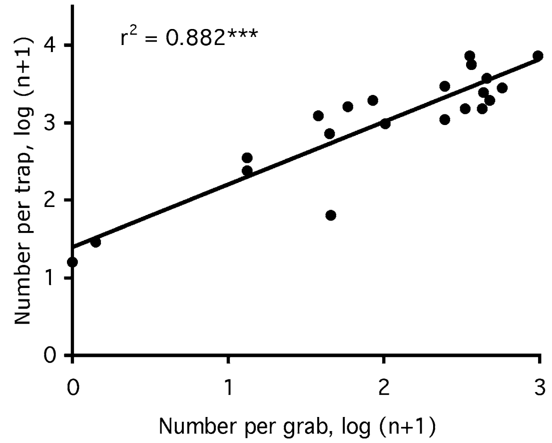

Figure 4. Trap catches of *Eurycercus lamellatus versus* abundance estimates based on grab sampling at the bottom. The linear relationship is $\log(y+1)=1.39 + 0.81 \log(x+1)$.

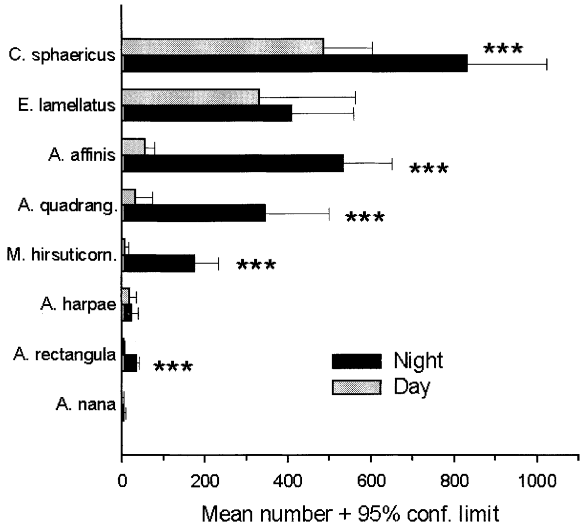

Figure 5. Trap catches (mean numbers per trap and 95% confidence limits) of Cladocera in Lake Myvatn during the day and night. Statistical significance is indicated with asterisks (*t*-tests): *: $P<0.05$; **: $P<0.01$, ***: $P<0.001$.

(DCA) were carried out with the CANOCO (v. 4.02) program (ter Braak and Simlauer 1997).

Results

Tests of traps

The most abundant benthic species caught in the traps were *E. lamellatus*, *Chydorus sphaericus* (Müller), *Alona affinis* (Leydig), *A. quadrangularis* (Müller), *A. rectangula* Sars, *Acroperus harpae* (Baird) and *Macrothrix hirsuticornis* Norman and Brady. *Alonella nana* (Baird), *Graptoleberis testudinaria* (Fischer) and *Simocephalus vetulus* (Müller) occurred less often. *Daphnia longispina* was commonly trapped. Only three individuals of *Bosmina* sp. were found. A number of chironomid larvae were caught, most of which belonged to the subfamily Orthocladiinae. Copepoda were also commonly caught. Snails (*Lymnaea peregra* (Müller)), Ostracoda, three-spined sticklebacks (*Gasterosteus aculeatus* L.), *Hydra* sp., Hirudinea and *Chaetogaster* sp. (Oligochaeta) were less frequent. A large number of Rotifera entered the traps.

Trap catches of E. *lamellatus* were significantly correlated with density estimates based on grab samples (Figure 4) ($r = 0.910$, $P < 0.001$, d.f. 20). A comparison was made between 12-h catches during the day and night. All the species except *E. lamellatus* and *A. harpae* were caught in significantly greater numbers during the night (Figure 5) (*t*-tests, $n = 6$ traps, $P < 0.001$ in all cases). The test was not performed on *A. nana* because too few individuals were caught.

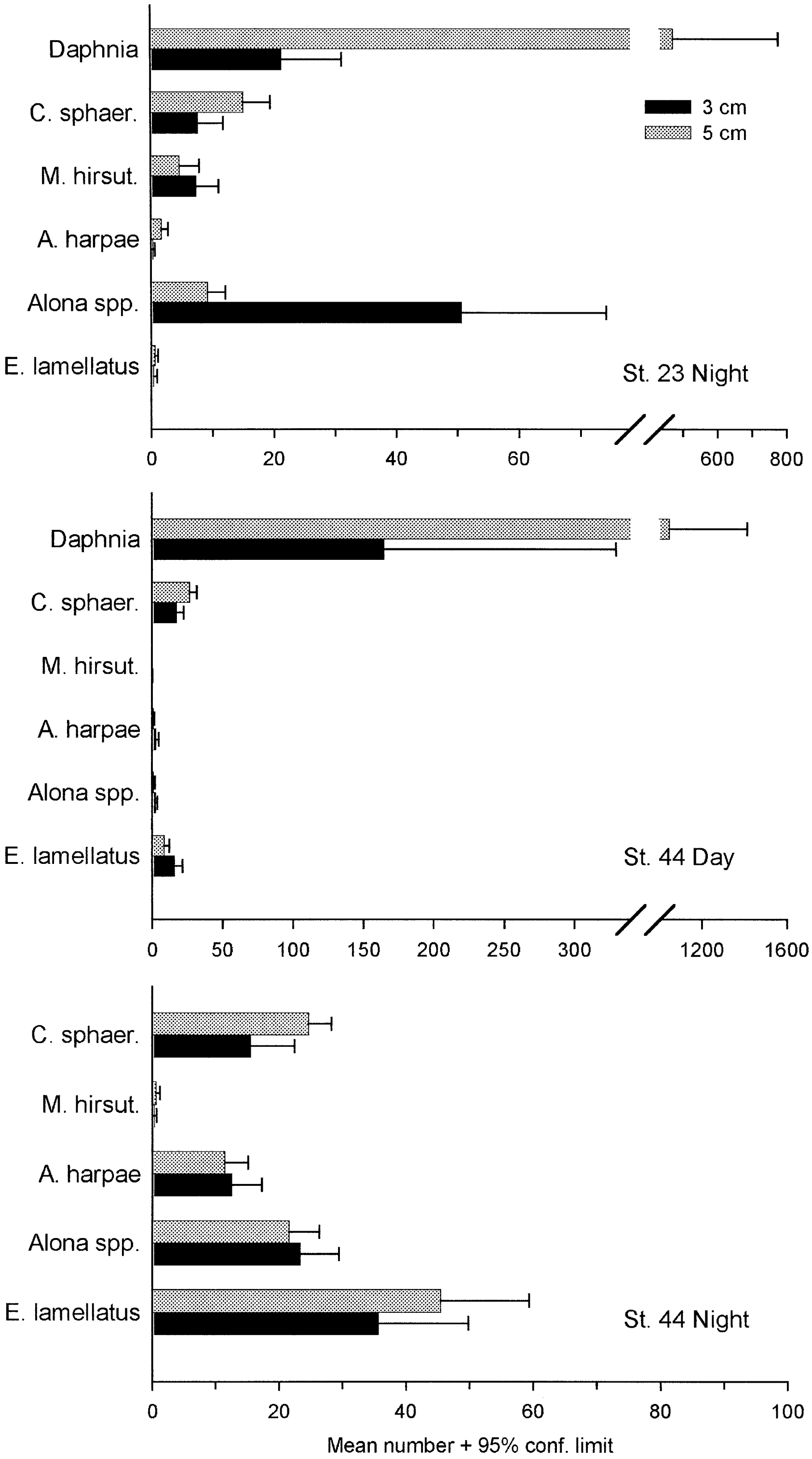

Figure 6. Trap catches (mean numbers per jar and 95% confidence limits) in which the funnels were placed 3 cm above the sediment compared with traps in which the funnels were placed 5 cm above the sediment.

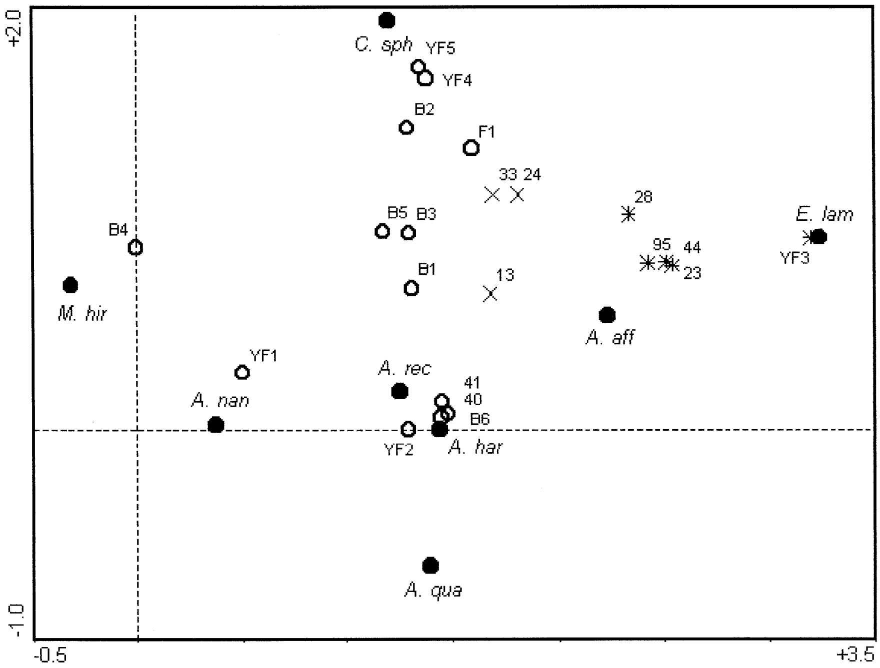

Figure 7. A detrended correspondence analysis plot of sampling stations and Cladocera species in Lake Myvatn in late July 1990. Abbreviations as in Table 1. Stars: sampling sites with a mat of filamentous green algae; crosses: sites with a thin layer of filamentous green algae; open circles: other sites; filled circles: Cladocera species.

The effect of the funnel height on trapping efficiency was variable. The most pronounced effect was that *D. longispina* entered the traps in far greater numbers when the funnel openings were 5 cm above the sediment rather than at 3 cm (Figure 6) (*t*-tests, $n = 10$ jars, $P < 0.01$ at night and $P < 0.001$ during day). Significantly more *Alona* spp. entered the trap at night at the lower position (3 cm) at one site (*t*-test, $n = 10$ jars, $P < 0.001$) but no significant difference was observed at another station at night. Too few *Alona* spp. (34) entered the trap during the day to allow a statistical comparison. Significantly more *C. sphaericus* entered the higher traps in all 3 experiments (*t*-test, $n = 10$ jars, $P < 0.05$ in one experiment at night and $P < 0.01$ in 2 experiments during day and night). *E. lamellatus* was caught in significantly ($P < 0.05$) higher numbers by the lower traps in one of the experiments but no significant difference was found in the other two (Figure 6).

The Cladocera survey

The results from the lakewide survey indicated a pronounced spatial variation (Figure 7, Table 1). A Kruskal-Wallis analysis indicated that the differences in median values of all species among the 21 sampling sites were greater than expected by chance (H-values: 126.2–165.1, d.f. 20, $P < 0.001$ for all species). A single linkage cluster analysis based on correlation coefficients (Pearson's r) defined five main groups, each one characterized by a dominant species (Table 1). (1) *E. lamellatus* was characteristic for the algal mat (Stations YF3 (= St. 128), 23, 28, 44 and 95). (2) *C. sphaericus* dominated various bare bottom habitats, including nearshore gravel bottom (station F1), soft diatomeous gyttja (stations B1–3) and the mined area (stations YF4–5) which has a high deposition rate and is characterized by loose and watery gyttja (Gardarsson and Snorrason 1993). In this cluster, 3 stations (13, 24 and 33) also had a high percentage of *A. affinis* (which was dominating at one of them, station 13). (3) *M. hirsuticornis* characterized the cold water spring area in the southeast corner of the lake (stations B4–5). (4) *A. nana* dominated at one station (YF1), in the cold water spring area in the southeast corner of the North Basin. (5) *A. quadrangularis* was the dominating species at St. YF2 in the south part of the north basin, St. 40 and 41 in the NE part of the south basin and B6 in the spring area in the southeast part of the lake. *A. rectangula* was nowhere dominating. It tended to co-occur with *A. quadrangularis* and was only common at stations B1–3 and stations 41

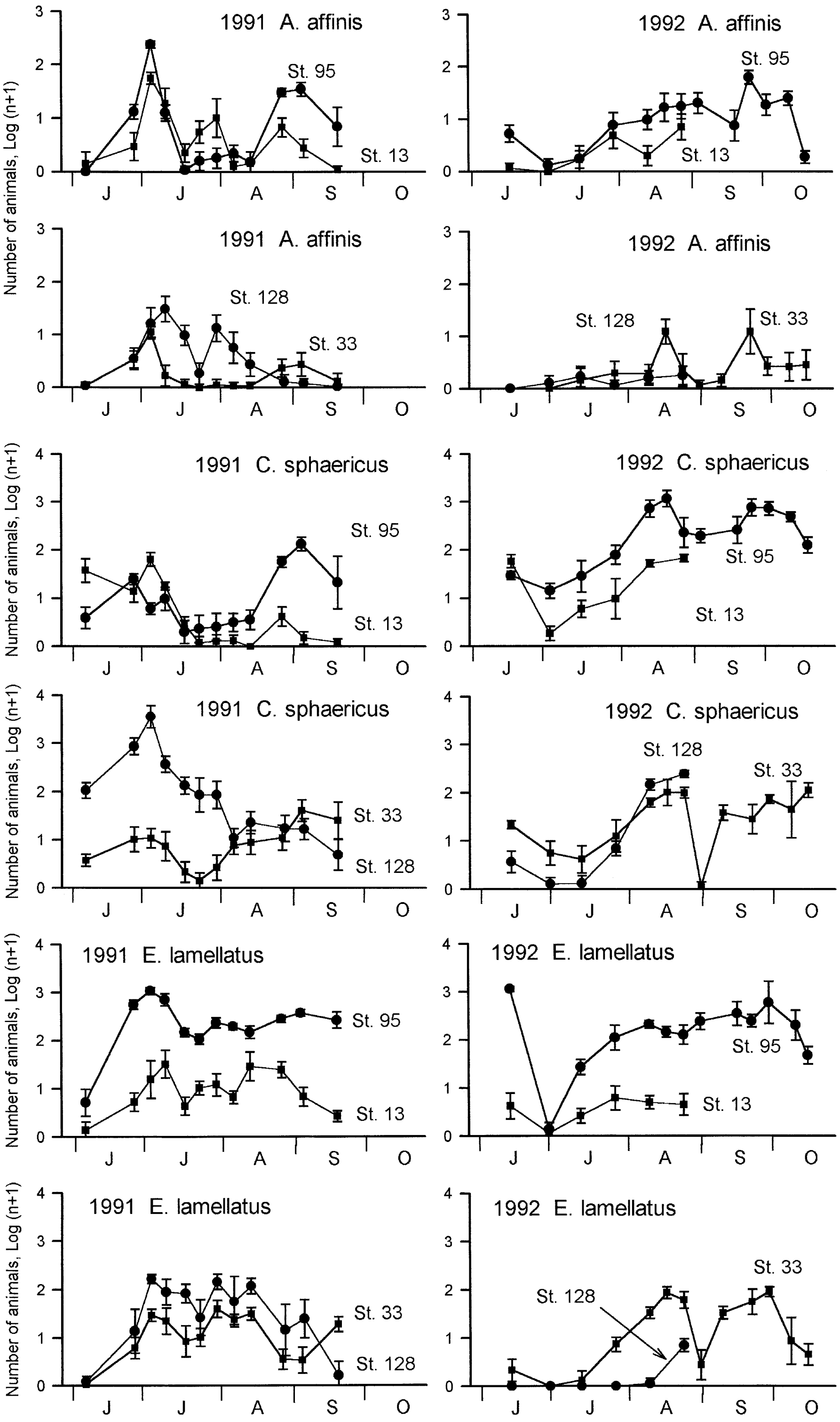

Figure 8. Variation in the abundance (numbers per jar) of *Alona affinis*, *Chydorus sphaericus* and *Eurycercus lamellatus* at four sites during two summers in Lake Myvatn. Bars indicate 95% confidence limits. Note the log scale and that station 128 is approximately the same as YF3 in Figure 1.

Table 1. Species composition (%) of benthic Cladocera at 21 trap stations in Lake Myvatn at the end of July 1990. Percentages of dominant or subdominant (>30%) species in bold type. The species are *Eurycercus lamellatus* (E. lam.), *Alona affinis* (A. aff.), *Alona quadrangularis* (A. qua.), *Alona rectangula* (A. rec.), *Acroperus harpae* (A. har.), *Chydorus sphaericus* (C. sph.), *Alonella nana* (A. nan.) and *Macrothrix hirsuticornis* (M. hir.). Clusters are defined by a single-linkage cluster analysis using Pearson's r as a measure of similarity. For location of the stations see Figure 1.

Cluster	Station	E. lam.	A. aff.	A. qua.	A. rec.	A. har.	C. sph.	A. nan.	M. hir.	n
1	B4	1.4	0.1	0.1	0.0	1.6	15.1	0.0	**81.7**	3342
	B5	24.8	4.5	0.6	0.0	8.3	21.7	0.0	**40.1**	157
2	YF3	**98.1**	0.3	0.3	0.0	0.2	0.8	0.3	0.0	7692
	44	**55.5**	22.3	5.8	1.4	1.8	9.3	0.2	3.7	1577
	23	**52.0**	24.9	5.1	0.9	6.8	10.0	0.0	0.2	1255
	95	**45.7**	24.4	4.4	9.4	0.4	14.7	0.0	1.0	1621
	28	**46.4**	17.2	4.7	0.2	3.7	27.3	0.2	0.2	407
3a	B3	0.3	9.4	2.7	**39.6**	1.6	**42.6**	3.5	0.3	371
3b	B1	0.7	12.4	20.5	19.1	2.1	**35.7**	8.1	1.4	283
3c	B2	0.0	10.6	3.8	9.6	1.0	**71.2**	3.4	0.3	292
	YF4	4.6	9.5	2.6	0.0	0.1	**81.9**	0.4	0.8	2229
	YF5	4.4	5.4	2.5	0.5	0.0	**86.0**	1.2	0.0	845
	F1	11.3	20.2	1.1	3.7	3.5	**56.5**	0.1	3.6	2232
3d	33	7.3	**31.0**	10.0	0.0	2.3	**49.4**	0.0	0.0	261
	24	10.3	**37.2**	3.3	0.6	4.6	**43.9**	0.0	0.0	478
3e	13	5.0	**35.2**	16.5	14.0	2.0	**24.8**	0.0	2.5	2241
4	41	0.4	15.0	**52.8**	8.9	2.0	19.1	0.8	0.8	246
	40	0.3	15.6	**56.7**	9.3	0.2	17.6	0.0	0.3	591
	YF2	0.1	18.2	**44.2**	5.2	8.0	6.7	9.6	8.1	2385
	B6	9.1	13.9	**40.6**	1.6	7.7	7.1	18.1	1.9	678
5	YF1	0.0	1.4	0.4	1.6	2.4	11.2	**78.4**	4.6	761

and 13. A detrended correspondence analysis (DCA, Figure 7) showed similar clustering with the stations pulled apart towards the five dominating species mentioned above. The cold-water species/stations and the algal mat species/stations defined the lower and upper extremes along axis 1, respectively. The lower extreme of axis 2 had a dense cluster of four stations characterized by *A. quadrangularis*. All four stations are located in a transition zone between spring-water areas and the main lake. The upper extreme of axis 2 is defined by the two stations in the dredged part of the lake.

Phenology of three species

Three species were followed throughout the summer in two successive years, *E. lamellatus*, *A. affinis* and *C. sphaericus*. With some exceptions the overall abundance of a species followed a similar seasonal pattern on the different stations in any one year (Figure 8). In 1991 *A. affinis* rose to peak abundance at the end of June then fell to a low in mid-July to mid-August. A second peak occurred in August–September. The timing of the peaks was different in the North Basin (station 128 in Figure 8): there was a distinct peak at the end of July. In 1992 there was no early summer peak.

The pattern in *C. sphaericus* in 1991 was similar to that of *A. affinis*. There was an early summer peak at the end of June and a midsummer low in late July–early August, and finally an autumn peak in August–September. The north basin station only showed the early summer peak and then declined steadily for the rest of the summer. Similar to the observed pattern in *A. affinis* in 1992 there was no early summer peak but the population rose to a maximum in mid-August. There was a low in *C. sphaericus* in late August–early September and then a late autumn rise in late September (Figure 8).

In 1991 *E. lamellatus* rose to maximum abundance in the beginning of July and stayed at a high level throughout the summer. There was a slight midsum-

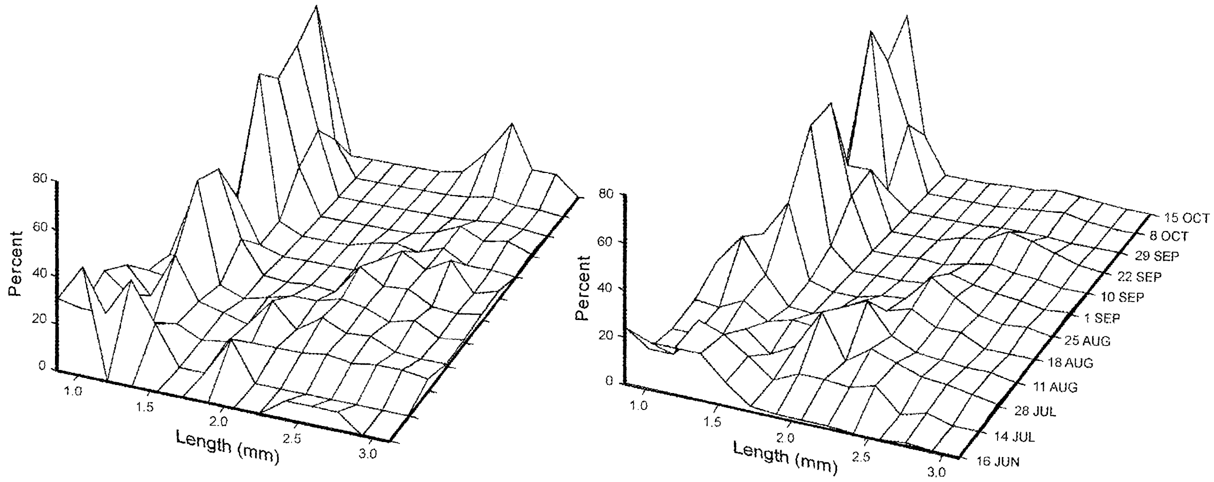

Figure 9. Seasonal variation in the size-distribution of *Eurycercus lamellatus* trapped at two sampling sites in 1992 (station 33 left; station 95 right).

mer low in late July–early August at two sites, but the other two did not show any such trend. In 1992 *E. lamellatus* rose slowly to peak abundance in August and stayed abundant till October. The exceptions to this is a large peak occurring at station 95 at the first sampling date, in the middle of June, and at station 33, where there was a sudden temporary drop at the end of August (Figure 8).

The water temperatures in 1991 were considerably higher than in the following year (Figure 3). In 1991 the temperature rose rapidly in late June to a peak of 20 °C in early July. Water temperature in July and early August stayed around 15 °C when a late summer decline set in. In contrast, the 1992 temperature declined from 13 °C to 5 °C in June and then rose to a maximum of 15 °C in mid-July. Late July–early August temperatures ranged between 10 and 13 °C.

Size distribution of E. lamellatus

The size distribution (Figure 9) of *E. lamellatus* at station 95 was unimodal in the beginning of sampling in the middle of June, mostly between 1 and 1.5 mm. The distribution soon became bimodal, the smaller size-class stayed much the same length while the larger size-class grew in length throughout the summer and had reached about 2.5 mm by the end of September. The development at the other station (33) was almost identical, except that the population was bimodal already in the middle of June.

Before late August the majority of the small individuals (< 1.45 mm) at both stations were females, whereas in late August and thereafter, with one exception, the great majority of the small individuals were males (Figure 10).

Discussion

The activity traps

A large number of active sampling devices for benthic invertebrates exist, most of them being either grabs or corers with a scooping or penetrating action (e.g., Hopkins 1964; Sly 1969). Some of these have become standard equipment in limnological investigation, yielding quite accurate estimates of the density of soft bottom biota. Various active sampling devices have been designed for other types of bottom substrate (e.g., New 1998). Most of the active samplers collect the substrate as well as the organisms being studied and much effort is needed to separate the two components. Passive sampling devices (traps) have the advantage of giving clean samples, because these devices are based on the movements of the animals themselves instead of the scooping action of grabs and similar equipment. Another advantage is that the traps are less dependent on substrate type, i.e., they can easily be deployed on sand, gravel or plant substrate. Additionally, the traps leave the bottom intact. Furthermore the traps integrate diurnal behaviour, which may bias samples collected instantly by active devices. Traps have the disadvantage that an extra effort must be spent to calibrate their catch against more realistic abundance estimates, and these calibrations are

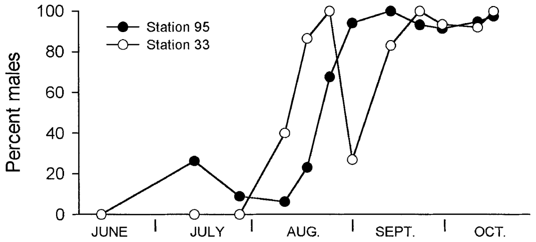

Figure 10. Seasonal variation in the proportion of males in trap catches of small (< 1.45 mm long) *Eurycercus lamellatus* at two sampling stations in Lake Myvatn in 1992.

needed for each species and lake. For monitoring studies this may not be a disadvantage, because the goal is to obtain an index of relative abundance that can be compared over time. In this study we calibrated the trap catches of *E. lamellatus* against grab samples from the sediment. We assume that the other species also show a positive relationship between abundance and trap catches, although such relationships may not be linear. Until the necessary calibrations have been made the results should be viewed with some caution, focusing on the general patterns of spatial and seasonal variation rather than exact numbers.

The main drawback of the traps is that they have to be picked up on another occasion, preferably within 24 h, to minimize mortality and decomposition of the trapped organisms. However, having a clean sample will outweigh the disadvantages. The Myvatn trap described in this paper does not sample a well defined area, because the funnels are placed above the sediment surface and the organisms are free to move under the trap. This is necessary in order not to disturb the algal mat. This is in contrast to the 'pattern sampler' developed by Whiteside and Williams (1975) which has the funnel openings touching the substrate.

The advantage of the Cladocera traps is greatest when dealing with minute taxa (e.g., *Chydorus, Alonella, Acroperus* and *Alona rectangula*) or juveniles of larger species which are very numerous and difficult to separate from the sediment. The Myvatn trap has now been used for a number of years to monitor the foodweb of Lake Myvatn and has proved very useful (Einarsson and Örnólfsdóttir 2004). The lower position (3 cm) of the funnels has been used in order to avoid the immense numbers of *Daphnia* entering at 5 cm height. In addition, because of the higher numbers of almost all the cladoceran species caught during the night and because daylength varies over the summer, we have standardized the operation time at 24 h, deploying the traps around noon.

Spatiotemporal variation

Lake Myvatn exhibits large lake-wide variation in various factors like temperature, water chemistry, predation and bottom substrate, including macrophyte cover (Einarsson et al. 2004). The Cladocera survey indicates considerable spatial variation on the lake-scale. Adalsteinsson (1979) observed some variation also that he attributed to different limnological conditions of the two lake basins. Our study suggests that some of the lake-wide variation is related to the inflow of spring-water: the area close to the cold springs stands out with its dominance of *M. hirsuticornis*, and *A. nana* was typical for the spring water area of the north basin. The mat of filamentous green algae (Cladophorales) in the south basin had a characteristic community dominated by *E. lamellatus*, also described by Gardarsson and Snorrason (1993). Our sampling scheme did not provide information about the Cladocera communities of other macrophyte species. Vegetation cover at a micro-scale and habitat type at the lake scale have turned out to be important factors for distinguishing chydorid assemblages in a lake in Ontario, Canada (Tremel et al. 2000).

In 1992 the Cladocera increased more slowly than in the year before and there was no peak in numbers in early July. This was probably related to the much lower water temperature in 1992 (Figure 3); in late June that year two snowstorms occurred in succession. An association of cooler water temperature and a delay in Cladocera increase has also been suggested for crustacean populations in Lake Biel, Switzerland (Vuille 1991).

The midsummer (late July) decline in *C. sphaericus* and *A. affinis* in 1991 cannot be explained without further work on the life history of the species. A midsummer decline has been observed in chydorid populations both in Myvatn and in other lakes (Goulden 1971; Keen 1973; Whiteside et al. 1978; Adalsteinsson 1979; Vuille 1991). The subsequent rise observed in our study in the autumn was not observed by Adalsteinsson (1979) in his study of Lake Myvatn. A pattern similar to that of 1991 was observed in Jack Lake (Nova Scotia, Canada) by Paterson (1994). According to Paterson (1994) qualitative examination of cladoceran birth rates suggested that seasonal abundance was most affected by changes in population loss rates. Predation has been suggested in earlier studies (Whiteside et al. 1978). However, examination of predator-prey relationships in Jack Lake, failed to provide evidence that invertebrate predators were responsible for population declines (Paterson 1994). Manipulations of densities of the most important predators in this fishless lake provided no evidence of strong predator effects on the microcrustacean community structure and seasonal changes in the densities of these predators were not negatively correlated with microcrustacean abundance (Paterson 1994). A relationship with food conditions, e.g., breakdown of detritus or periphyton, seems the most plausible explanation (e.g., Vuille 1991 and Fairchild *et al.* 1989).

The size distribution and sex ratio of *E. lamellatus* (Figures 9 and 10) indicate that the production of females takes place primarily in early summer, presumably by parthenogenic reproduction of individuals hatching from ephippia in the early spring. Young females could be found in late summer but the distinctly bimodal size distribution after mid-August indicates that they did not grow to maturity. According to the analysis of Frey (1973) the sizes of the seven instars overlap, and the sixth instar (large pre-reproductive females) seemed missing from Lake Myvatn after mid-August. The females produced in spring continued growing in size throughout the summer and in late August started to produce males which are small, not growing larger than 1.4 mm. In late summer, therefore, the lake contains a large number of males, a small number of young females not reaching maturity, and finally a number of large reproductive females.

This study is largely exploratory in nature but provides evidence for large spatial and seasonal variation in the benthic Cladocera assemblages in Lake Myvatn. Some of the ecological factors involved seem clear, such as the inflow of spring-water and the habitat provided by filamentous green algae. The stage is set for more detailed analyses of the environmental factors moulding the benthic cladoceran communities of the lake and a useful tool for their monitoring has been provided.

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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.

Einarsson A., 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).

Einarsson A. and Haflidason H. 1988. Predictive paleolimnology: Effects of sediment dredging in Lake Mývatn, Iceland. Verh. internat Verein. Limnol. 23: 860–869.

Einarsson A. and Örnólfsdóttir E.B. 2004. Long-term changes in benthic Cladocera populations in Lake Myvatn, Iceland. Aquat. Ecol. 38: 253–262 (this issue).

Fairchild G.W., Campbell J.M. and Lowe R.L. 1989. Numerical response of chydorids (Cladocera) and chironomids (Diptera) to nutrient-enhanced periphyton growth. Arch Hydrobiol 114: 369–382.

Flößner D. 1972. Krebstiere, Crustacea. Kiemen- und Blattfüßer, Branchiopoda Fischläuse, Branchiura. Die Tierwelt Deutschlands 60. Gustav Fischer Verlag, Jena.

Frey D.G. 1973. Comparative morphology and biology of three species of *Eurycercus* (Chydoridae, Cladocera) with a description of *Eurycercus macrocanthus* sp.nov. Int Revue ges Hydrobiol 58: 221–267.

Gardarsson A. 1979. Waterfowl populations of Lake Myvatn and recent changes in numbers and food habits. Oikos 32: 250–270.

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 Snorrason S.S. 1993. Sediment characteristics and density of benthos in Lake Mývatn, Iceland. Verh internat Verein Limnol 25: 452–457.

Gardarsson A., Einarsson Á., Gíslason G.M., Hrafnsdottir Th., 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).

Goulden C. 1971. Environmental control of the abundance and distribution of the Chydoridae: Cladocera. Limnol. Oceanogr. 16: 320–331.

Hanson M.A., Roy C.C., Euliss N.H., Zimmer K.D., Riggs M.R. and Butler M.G. 2000. A surface-associated activity trap for capturing water-surface, and aquatic invertebrates in wetlands. Wetlands 20: 205–212.

Hopkins T.L. 1964. A survey of marine bottom samplers. In: Sears M (ed.), Progress in Oceanography, Vol. II. Pergamon-MacMillan, New York, pp. 213–256.

Hyvonen T. and Nummi P. 2000. Activity traps and the corer: Complementary methods for sampling aquatic invertebrates. Hydrobiologia 432: 121–125.

Jónasson P.M. (ed.) 1979. Ecology of Eutrophic Subarctic Lake Myvatn. Oikos 32: 1–308.

Keen R. 1973. A probabilistic approach to the dynamics of natural populations of the Chydoridae (Cladocera, Crustacea). Ecology 54: 524–534.

Lindegaard C. and Jónasson P.M. 1979. Abundance, population dynamics and production of zoobenthos in Lake Myvatn, Iceland. Oikos 32: 202–227.

Lund J.W.G. 1964. Primary production and periodicity of phytoplankton. Verh internat Verein Limnol 15: 37–56.

New T.R. 1998. Invertebrate Surveys for Conservation. Oxford University Press.

Ólafsson J. 1979a. Physical characteristics of Lake Myvatn and River Laxá. Oikos 32: 38–66.

Ólafsson J. 1979b. The chemistry of Lake Myvatn and River Laxá. Oikos 32: 82–112.

Ólafsson J. 1999. Connections between oceanic conditions off N-Iceland, Lake Mývatn temperature, regional wind direction variability and the North Atlantic Oscillation. Rit Fiskideildar (Reykjavik) 16: 41–57.

Paterson M.J. 1994. Invertebrate predation and the seasonal dynamics of microcrustacea in the littoral zone of a fishless lake. Arch Hydrobiol (Suppl) 99: 1–36.

Sly P.G. 1969. Bottom Sediment Sampling. Proc. 12th Conf. Great Lakes Res., Ann Arbor, 883–898.

ter Braak C.J.F. and Simlauer P. 1997. CANOCO – Version 4.02. Unpublished computer program. Centre for Biometry. Wageningen, The Netherlands.

Tremel B., Frey S.E., Yan N.D., Somers K.M. and Pawson T.W. 2000. Habitat specificity of littoral Chydoridae (Crustacea, Branchiopoda, Anomopoda) in Plastic Lake, Ontario, Canada. Hydrobiologia 432: 195–205.

Vuille B. Th. 1991. Abundance, standing crop and production of microcrustacean populations (Cladocera, Copepoda) in the littoral zone of Lake Biel, Switzerland. Arch Hydrobiol 123: 165–185.

Whiteside M.C. and Williams J.B. 1975. A new sampling technique for aquatic ecologists. Verh internat Verein Limnol 19: 1534–1539.

Whiteside M.C., Williams J.B. and White C.P. 1978. Seasonal abundance and pattern of chydorid Cladocera in mud and vegetative habitats. Ecology 59: 1177–1188.