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Seasonal Changes in Vertical Distribution of Zooplankton in an Oligotrophic, Subarctic Lake (Lake Takvatn, Norway)

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With 7 Figures

Key words: Zooplankton, habitat choice, vertical distribution, population dynamics, competition, predation, coexistence, oligotrophic lake

Abstract

Zooplankton vertical distribution was studied in Lake Takvatn (69°07' N) by discrete sampling of the water column during the open water season. Attention was focused on predation risk and competition to understand when, where and to what degree a given species should aggregate along the water column. Temperature profiles and phytoplankton abundance and composition were recorded to assess degree of heterogeneity and food availability in the pelagic zone. Vertical segregation was evident during thermal stratification. Rotifers partitioned the water column, with species less susceptible to predation (e.g. *Conochilus unicornis*) in the epilimnion, where they overlapped with the predators *Asplanchna priodonta* and *Polyphemus pediculus*, and species more vulnerable to these predators (e.g. *Keratella cochlearis*) in the hypolimnion. Cladocerans remained in the epilimnion, in a year when predation by fish was limited. The copepodites of *Eudiaptomus graciloides* and *Cyclops scutifer* maintained different depths staying respectively near surface and in the meta-hypolimnion. A broader distribution with increasing density was evident among rotifers and *C. scutifer* nauplii. Density-dependent habitat selection behaviour is considered as a mechanism explaining the observed distribution of predators and competing prey and promoting species coexistence.

Introduction

Species may differ in their ability to exploit various habitats, with distinct phenotypes promoting differences in habitat ranking or tolerance of suboptimal habitats (ROSENZWEIG 1995). The resulting differences in habitat selection produce spatial segregation, a condition that favours coexistence of competing species. In zooplankton, competitors may coexist by selecting different depth-habitats (DEMOTT 1989; LEIBOLD 1991; NOGRADY et al. 1993), which vary in food availability and risk of predation. Vulnerabilities to competitors and predators will affect habitat choice and influence the character of vertical distribution.

In metazooplankton, greater body-size is generally associated with a superior competitive ability for food (ROTHHAUPT 1990), a trend that at low food concentrations is seemingly reversed in some taxa (STEMBERGER & GILBERT 1985; DEMOTT 1989). These size-related asymmetries in competitive ability affect the habitat use of competitors. The presence of predators may modify asymmetry in competition, neutralizing it or reversing it (MILLER & KERFOOT 1987). Planktivores may force a prey species to a sub-optimal habitat allowing an inferior competitor to occupy the optimal habitat. The effect of predators on prey distribution is predictable, and depends on the susceptibility to predation of different prey species. Species that are vulnerable to a predator after encounter should avoid contact with this, which can be obtained by minimizing spatial overlap. Like for competition, vulnerabilities of zooplankters to predation have a strong size-dependent component (GLIWICZ & PIJANOWSKA 1989) due to predator's optimal foraging decisions, and sensory and handling constraints.

Large and conspicuous zooplankters are the most susceptible to fish predation (LAZZARO 1987; O'BRIEN 1987). Fish planktivores are visual predators, and small and unconspicuous prey escape their perceptual powers. Moreover, sensory acuity of fish decreases with depth as a result of decreased light intensity, producing a refuge for susceptible prey in the deeper layers of lakes. This hypolimnetic refuge has set the stage for the evolution of anti-predatory behaviour consisting in an active search of dark, deep waters during the day (GLIWICZ 1986; LAMPERT 1993). Small zooplankters escape fish predation by exploiting a size-refuge, but are exposed to predation by invertebrates (ZARET 1980; GLIWICZ & PIJANOWSKA 1989), often represented by larger zooplankters. Small planktonic prey will tend to avoid spatial overlap with invertebrate predators, particularly when lacking effective

means of predator evasion (STEMBERGER & GILBERT 1987; WILLIAMSON 1993).

The effect on depth-habitat selection of tolerance of suboptimal habitats and asymmetries in competitive ability on one side, and of predation risk on the other, allows to make predictions about vertical distributions. However, in order to make accurate predictions of habitat use, the active movements directed by habitat choice must be considered together with the passive movements due to physical factors (KRAMER et al. 1997), such as water movements. Seasonal variation in abiotic and biotic conditions will determine changes in patterns of distribution along the water column. In periods of full circulation, active choice of specific depth habitats will be opposed by passive transport. During summer stratification, increased zooplankton density and reduced edible phytoplankton production reduces the food available to herbivores, intensifying interspecific competition and favouring the development of marked spatial segregation. The intensity and character of zooplanktivory will also change as a consequence of changes in predator abundance and phenology of habitat- and diet-choice.

In the present study I consider the changes in patterns of zooplankton vertical distribution that occurred in the subarctic Lake Takvatn during the ice-free season of 1994. During the periods of full circulation I expected to find a high degree of dispersion along the water column. During thermal stratification I expected to find low spatial overlap among herbivorous species and stages at dates characterized by low food availability, avoidance of regions with high densities of invertebrate predators by small zooplankters (*i.e.* rotifers, small cladocerans and nauplii of copepods) in a degree proportional to their susceptibility to those predators, and a deeper distribution of the large species and late ontogenetic stages of crustaceans, which are the most exposed to fish predation. Further, I relate the observed patterns of habitat use to rotifers population dynamics and copepods development in the same year.

Methods

The study site

Takvatn is a dimictic lake situated in the North of Norway (69°07' N) at 214 m a.s.l., with a maximum depth of 80 m and a surface area of 15 km². The lake is surrounded by a birch wood (*Betula pubescens*). The shoreline is mainly rocky or gravelly with no emergent vegetation. There is a belt of submerged vegetation dominated by *Nitella* sp. between about 5 and 15 m of depth. The water of the lake is cold and reached a maximum epilimnetic temperature of 13.5 °C by the end of July 1994. In 1994, the ice broke around June 10, and in the middle of June there was full circulation with a temperature of 2.5 °C. Vernal circulation protracted until the beginning of July. The period of thermal stratification was short, starting the second week of July and ending the first week of September (Fig. 1). During stratification, the metalimnion ranged between 9 and 15 m of
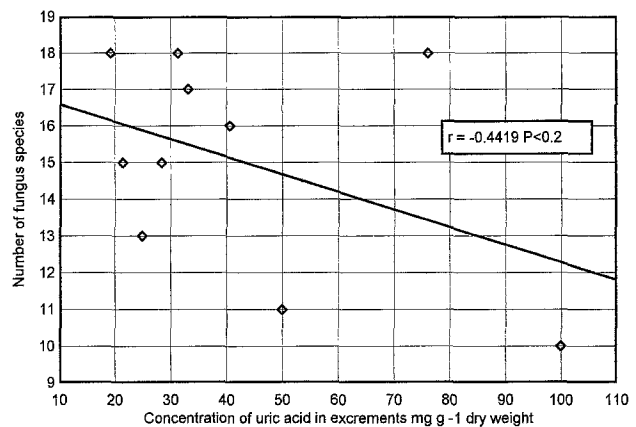

Fig. 1. Seasonal changes in temperature (°C) along the water column of the lake.

depth. The autumn circulation is usually long because of heavy winds, and the lake normally freezes in November.

The water of the lake is nutrient poor (total phosphorus < 6 µg l⁻¹) and neutral to slightly alkaline (pH ranges between 6.9 and 7.4). Throughout the ice-free season the lake is well oxygenated with minimum epilimnetic and hypolimnetic oxygen concentrations of respectively 10.40 mg l⁻¹ and 11.10 mg l⁻¹. During summer stratification an orthograde oxygen profile develops along the column and oxygen saturation remains above 90%. Further details on physicochemical characteristics of the lake are found in KILDEMO (1982) and WALSENG & HALVORSEN (1993).

The long-term changes of crustacean plankton in the lake are discussed by DAHL-HANSEN (1995), zooplankton seasonal dynamics in 1994 are presented in PRIMICERIO & KLEMETSEN (1999). The main vertebrate planktivore in the pelagic zone is Arctic charr, *Salvelinus alpinus* (L.). The predatory impact of this salmonid is moderate when compared to more specialized fish planktivores such as coregonids but nevertheless sufficient to affect the abundance of *Daphnia galeata* SARS (LANGELAND 1978) and the body-size distribution of *Bosmina longispina* LEYDIG, the smallest of the cladocerans dominating Takvatn zooplankton (DAHL-HANSEN 1995). Threespine stickleback (*Gasterosteus aculeatus* L.) is the other vertebrate planktivore in the lake, but it was not observed in the pelagic zone in 1994. It remained in the littoral zone together with brown trout (*Salmo trutta* L.). Details on basin morphometry, climatic conditions, vegetation and fauna of the lake are given by KLEMETSEN et al. (1989).

Plankton sampling and analysis

Phytoplankton was sampled on 13 dates throughout the ice-free season of 1994. The samples were collected with a 2 l Ruttner bottle and integrated over the water column by sampling at 1, 3, 5, 7, 9, 12 and 15 m of depth. The samples were fixed with one percent Lugol solution, and analysed using an inverted microscope. The counts were carried out on 50 ml subsamples using an algal sedimentation chamber. The biovolume of each species was calculated from linear dimensions fitted to formulae for the corresponding geometrical shape (WETZEL & LIKENS 1991).

To record vertical distribution, zooplankton was collected by discrete sampling at 1, 5, 9, 15, 20, 25 and 30 m of depth, except for August 9 when the last two depths were not sampled. The fine scale was used to emphasize patterns of distribution largely due to biotic processes (PINEL-ALLOUL 1995). Sampling started on June 21, under spring circulation, and ended the second week of September, under autumn circulation. The short period of summer stratification encompassed six sampling dates, with the lake being only weakly stratified on the second sampling date (July 11). The samples were collected at a fixed station during the day, starting at about 11 a.m., using a 30 l Schindler-Patalas trap equipped with a mesh size of 50 μm to ensure inclusion of rotifers, cladocerans and copepods. Rotifer dynamics and copepod development during the ice-free season of 1994 were monitored by weekly sampling at the above fixed station via vertical hauls (mesh size, 50 μm) drawn from 30 m of depth. Neutralized formaldehyde was added to the samples to obtain a 4% solution. For analysis, zooplankton samples were placed on a counting glass (Hydrobios) with 1.5 mm spacings. All counts were performed on a microscope with 100× magnification.

Results

Phytoplankton

The mean phytoplankton biovolume for the whole season was 42.7 mm³ m⁻³, characterizing the lake as markedly oligotrophic. The seasonal maximum of phytoplankton biovolume (107 mm³ m⁻³), was recorded on July 11 when the lake started to stratify, it was followed by a second peak of similar magnitude on July 30 (Fig. 2). Thereafter, the biovolume declined rapidly and reached nearly a sevenfold reduction early in September. Overall, the phytoplankton displayed an unimodal pattern of seasonal development.

The Bacillariophyceae dominated the phytoplankton throughout the growing season and had a taxonomic composition typical of cold, oligotrophic lakes (REYNOLDS 1996).
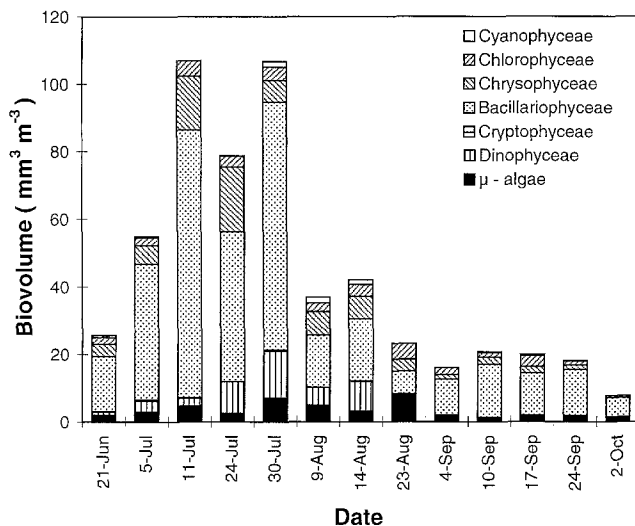

Fig. 2. Seasonal changes in phytoplankton biovolume (μ-algae indicate indeterminate forms with cell diameter of 2–4 μm).

The main species within the group were *Cyclotella kützingiana*, largely responsible for the first peak in phytoplankton abundance, and *Cyclotella comensis*, the dominant diatom in occasion of the second peak in the end of July. The species *Asterionella formosa* and *Stephanodiscus medius* were the other diatoms mainly responsible for the seasonal dynamics of the group, but their presence was restricted to the period preceding and immediately following the beginning of thermal stratification. The other main groups of phytoplankton were Chrysophyceae and Dinophyceae. The former group was represented mainly by chrysomonads and the latter by *Ceratium hirundinella* and *Gymnodinium helveticum*.

Zooplankton abundance and vertical distribution

In 1994, the dominant microconsumers were the nauplii of *Cyclops scutifer* SARS and *Eudiaptomus graciloides* (LILLJE-BORG), and the rotifers *Keratella cochlearis* (GOSSE), *Conochilus unicornis* ROUSSELET, *Polyarthra* sp. and *Kellicottia longispina* (KELLICOTT). Among the macroconsumers, *Bosmina longispina* reached the highest densities, *Holopedium gibberum* ZADDACH was present with low numbers and *Daphnia galeata* was rare. Planktonic predators, feeding on smaller zooplankters, were represented by the rotifer *Asplanchna priodonta* GOSSE, the cladoceran *Polyphemus pediculus* (L.) and by late developmental stages of the cyclopoid *C. scutifer*.

Before the development of thermal stratification, rotifers had low densities in Lake Takvatn. About two weeks after the beginning of the ice-free season, on June 21, the most abundant species were *Keratella cochlearis* and *Kellicottia longispina*, both evenly distributed down to 30 m of depth (Fig. 3). On July 10, *K. cochlearis* and *K. longispina* displayed some degree of aggregation in the upper section of the water column, reaching maximum density at 5 m of depth, while *Filinia terminalis* (PLATE) occupied deeper waters. When a marked thermal stratification developed in the lake in late July, *Conochilus unicornis* and *Polyarthra* sp. increased in abundance and occupied the upper portion of the epilimnion together with *A. priodonta*, while *K. cochlearis* and *K. longispina* clustered at 9 m of depth (Fig. 3). On August 9, with a further increase in abundance and in concomitance with the decline in phytoplankton density, *C. unicornis* expanded its distribution in the epilimnion as did *A. priodonta*; *K. cochlearis* and *K. longispina* moved deeper, displaying a density peak at 15 m of depth together with *Polyarthra* sp., which stretched ulteriorly its distribution from the epilimnion. At the end of August the above pattern was maintained, with the exception of *Polyarthra* sp. spreading down to 30 m. Throughout the period of thermal stratification *Synchaeta* sp., *F. terminalis* and *Keratella hiemalis* (CARLIN) kept mainly in the colder hypolimnion (Fig. 3). On September 10, following the disruption of the thermocline, the patterns of vertical distribution among filterfeeding rotifers
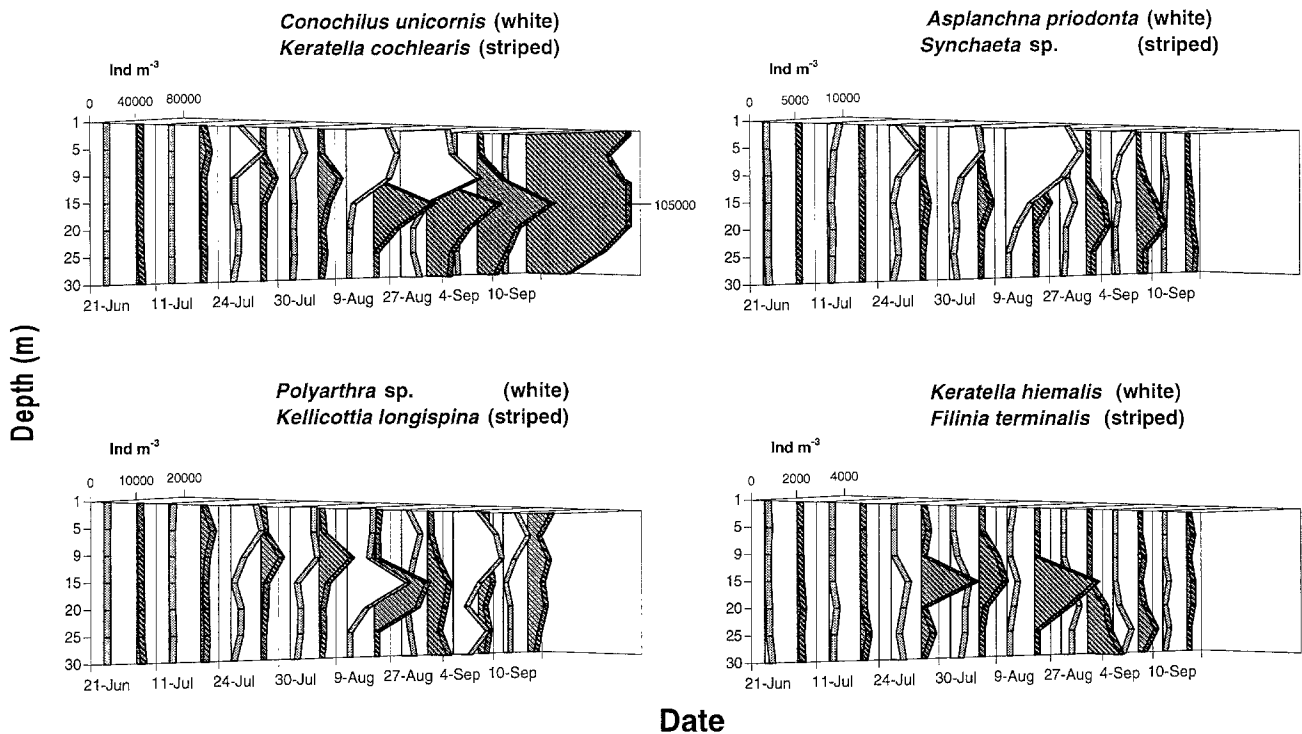
Fig. 3. Changes in vertical distribution of rotifers during in the ice-free season. Note differences in scale.

changed dramatically. *Keratella cochlearis*, *K. longispina* and *Polyarthra* sp. were found along the entire water column, but had higher densities in the upper section.

The dominant cladocerans *Bosmina longispina* and *Holopedium gibberum* were mainly restricted to the epilimnion, while *Daphnia galeata* had a somewhat deeper distribution (Fig. 4). The predator *Polyphemus pediculus* was found in the epilimnion in August, and increased its density towards the end of that month (max 500 ind m⁻³ near surface on August 27). At the beginning of the autumn circulation, on September 10, the highest densities of *D. galeata* were recorded in the epilimnion, but individuals were found down to 25 m. On the same sampling date, the number of *B. longispina* and *H. gibberum* reached a seasonal minimum.

During spring and autumn circulation, the naupliar stages of copepods were distributed along the entire water column (Fig. 5). On July 10, the nauplii of *Eudiaptomus graciloides* had higher densities close to the surface. Towards the end of thermal stratification, on September 4, *Cyclops scutifer* nauplii increased in density and kept in the upper part of the

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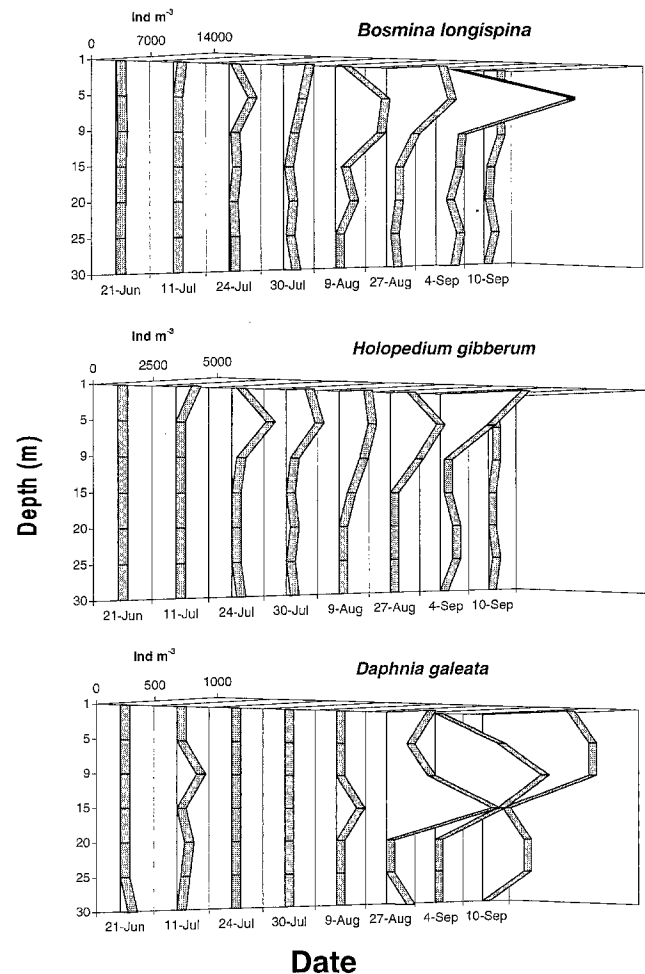
Fig. 4. Vertical distribution of filter-feeding cladocerans in the ice-free season. Note differences in scale.

water column, with the highest abundance registered at 5 and 9 m of depth. The copepodites of *E. graciloides* and *C. scutifer* occupied different depths during thermal stratification, with *E. graciloides* keeping closer to surface, between 1 and 9 m, and *C. scutifer* staying mainly between 9 and 20 m (Fig. 5). The adults varied greatly their vertical distribution throughout the season (Fig. 5), and in *E. graciloides* they had a deeper distribution relative to conspecific copepodites during stratification.

Discussion

The zooplankton of Lake Takvatn had a high degree of dispersion along the water column during spring and autumn circulation. This was particularly evident in poorly motile taxa, such as the rotifers *K. cochlearis* and *K. longispina*, and developmental stages, such as the nauplii of copepods. These zooplankters were found at all sampled depths and displayed a relatively homogeneous distribution along the water column, in accordance with the expectations. It can however not be excluded that the patterns observed during circulation arise by active habitat choice. Indeed, the increased environmental homogeneity due to circulation would reduce the advantage of selecting a specific depth-habitat, leading to predictions similar to those based on passive transport. The passive transport hypothesis is simply the most conservative. In contrast with the period of circulation, a high degree of aggregation characterized the vertical distribution of most members of the zooplankton community during summer stratification.

Rotifer species are known to partition the water column extensively (MIRACLE 1977; NOGRADY et al. 1993). In Takvatn, the dominant primary consumers *K. cochlearis* and *C. unicornis* developed a clear pattern of vertical segregation as their densities increased throughout summer. *Keratella cochlearis* is adapted to low food concentrations (WALZ 1997), and this explains how it could persist in deeper waters while *C. unicornis* was restricted to the epilimnion. The other rotifer in the epilimnion was *Polyarthra* sp. which feeds on larger food particles of up to 45 μm (BOGDAN & GILBERT 1982, 1987), partitioning food rather than habitat for coexistence with other herbivorous species. The raptorial feeders *A. priodonta* and *Synchaeta* also prefer larger particles when feeding on algae. *Asplanchna priodonta*, however, can rely on a carnivorous diet of other rotifers (DUMONT 1977) and thereby avoid competition by herbivores altogether.

Intense competition should have occurred in the lake between *K. longispina* and *K. cochlearis* due to their high de-
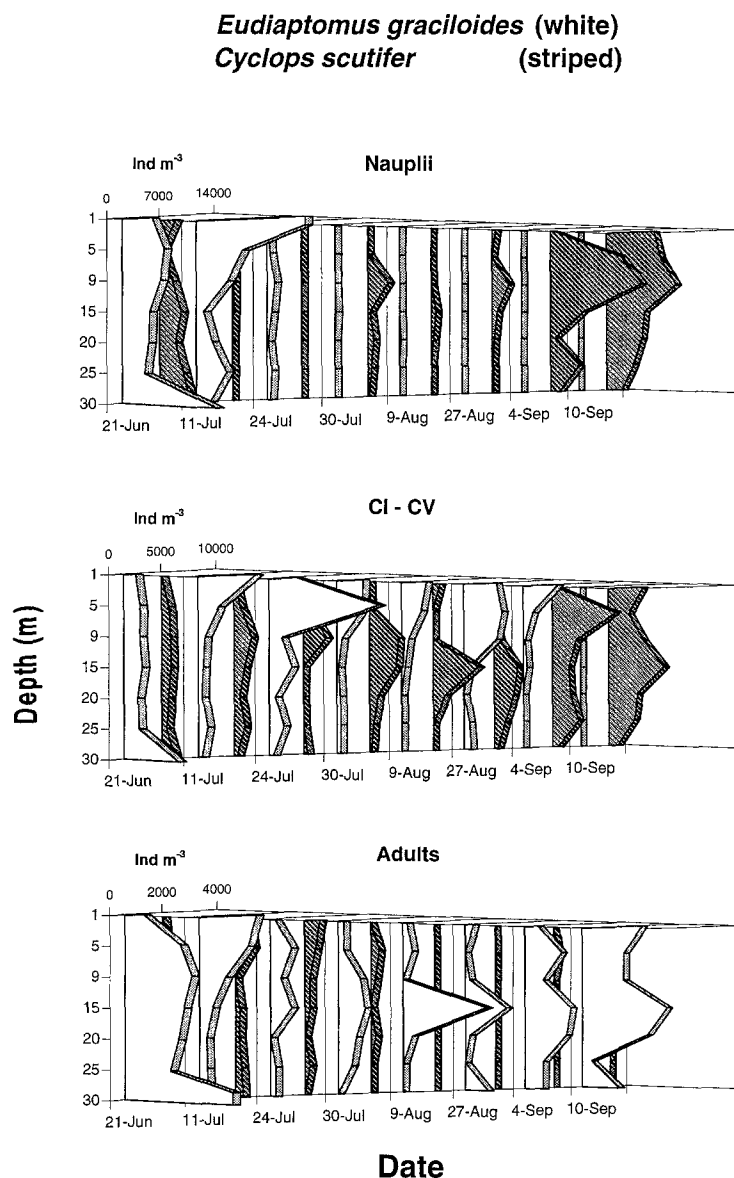
Eudiaptomus graciloides (white)
Cyclops scutifer (striped)

Fig. 5. Seasonal changes in vertical distribution of the two pelagic copepods. Developmental stages are displayed separately so as to emphasize ontogenetic differences in depth-habitat use. Note differences in scale.

gree of spatial overlap, combined with their overlap in diet (POURRIOT 1977). Such intense interspecific competition is expected to result in the exclusion of one of the species. In this regard, it is interesting to note that the density of *K. longispina* declined for the whole month of August (PRIMICERIO & KLEMETSEN 1999), while overlapping with *K. cochlearis* in the meta-hypolimnion. The latter species, more tolerant of food scarcity, slightly declined in the end of August only, to increase again in September (Fig. 6).

As the density of *K. cochlearis* increased, and phytoplankton biovolume decreased, its population expanded to new depth-habitats, displaying a broader vertical distribution. The same change in distribution could be observed for
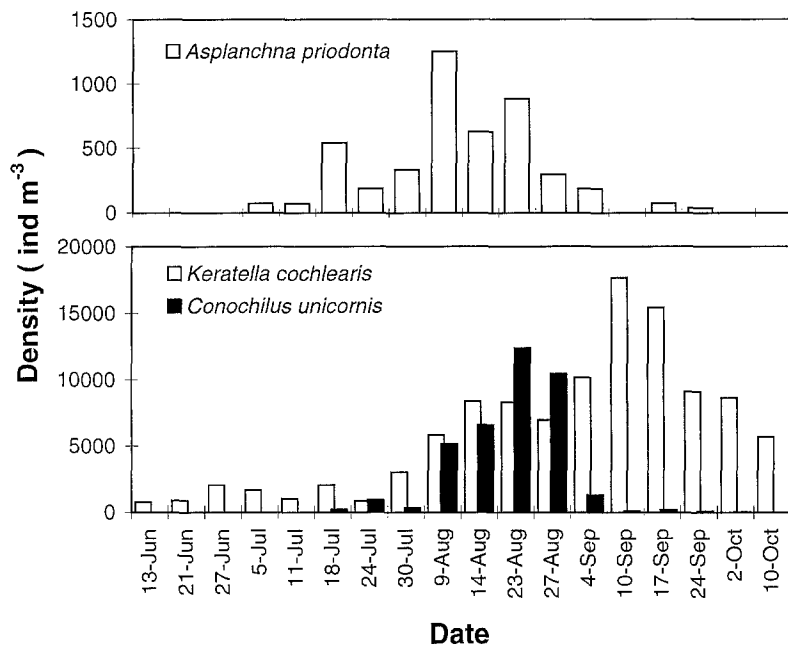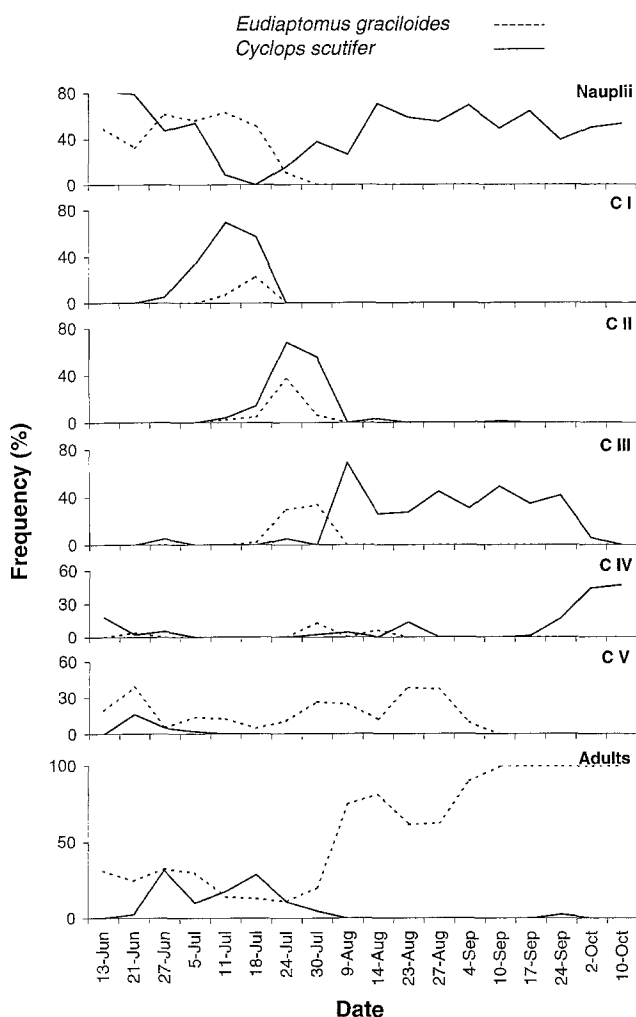
Fig. 6. Seasonal dynamics of three rotifer species, the dominant *Keratella cochlearis* and *Conochilus unicornis* and their predator *Asplanchna priodonta*. Note the August stagnation in *K. cochlearis* density when the species stayed in the colder, unproductive hypolimnion. Top and bottom panel differ in scale.

the population of *C. unicornis* in the epilimnion, and for less abundant species such as *A. priodonta* and *K. longispina*. This pattern is consistent with the expectations of the ideal free distribution (FRETWELL & LUCAS 1970; MILINSKY & PARKER 1991), and is symptomatic of the deterioration of depth-habitat profitabilities with crowding.

The cladocerans in the pelagic zone of LakeTakvatn had an epilimnetic distribution. Their populations grew late in the season and undoubtedly contributed to erode the food resources available in the epilimnion in August and early September. The dominant, filter-feeding herbivores would experience poor food conditions and reduced temperature if they moved to deeper waters. The carnivore *P. pediculus* resorts heavily upon visual stimuli (BUTORINA 1986), and this forces it close to the surface, into well illuminated regions of the water column.

An epilimnetic distribution of nauplii may favour the copepods by exposing them to higher temperatures that accelerate growth. The early ontogenetic stages of copepods, particularly cyclopoids, are most susceptible to starvation (SANTER & VAN DEN BOSCH 1994; SOTO & HURLBERT 1991) and have been identified as population bottlenecks because of their high mortalities. Growing quickly out of a vulnerable life stage is clearly an advantage and in Takvatn, where the low temperature and poor food conditions pose strong limitations on growth rates, it may be the main factor affecting

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Fig. 7. Stage frequency distribution of copepods in the ice-free season. *Cyclops scutifer* has a two years life cycle, overwintering first as nauplius and then as copepodite IV. Note faster development of *Eudiaptomus graciloides* relative to *C. scutifer* and stagnation in growth of copepodite III in the cyclopoid.

depth-habitat choice of nauplii. Towards the end of the period of stratification only the nauplii of *C. scutifer* were present. When these reached maximum density, the first week of September, they expanded their distribution. This trend, already discussed for the rotifers, suggests an increased intraspecific competition.

The copepodites segregated in space, with *E. graciloides* in the epilimnion and *C. scutifer* in the metalimnion and hypolimnion. The early copepodite stages of the two species are herbivorous (PEJLER 1983; HAMBURGER & BOËTIUS 1987), and an overlap in diet should stimulate depth-habitat segregation. The warmer waters to which *E.graciloides* was exposed favoured a relatively rapid development and the calanoid reached the adult stage by the end of thermal stratification. At that time *C. scutifer*, which experienced colder waters, had only reached the stage of copepodite III (Fig. 7).

As KERFOOT & KIRK (1993) suggest, life in the hypolimnion of oligotrophic lakes may be possible for copepods due to the joint effect of their efficiency in food selection and of low temperature reducing metabolic rates. An hypolimnetic distribution may thereby favour adults of *E. graciloides*, which no longer require an environment supporting rapid growth, by reducing metabolic demands and competition for food. Similarly, the copepodite stages of *C. scutifer* may survive periods of food shortage experienced in summer by staying below the metalimnion, without the need of diapausing in the bottom sediments (HALVORSEN & ELGMORK 1976).

The reduction of spatial overlap with predators is a form of behavioural defence used by susceptible rotifer prey (STEMBERGER & GILBERT 1987; WILLIAMSON 1993). In Takvatn, the deeper distribution of *K. cochlearis* relative to *C. unicornis* or *Polyarthra sp.* is probably due to its greater vulnerabilty to *A. priodonta* (GILBERT 1980a). A greater resistance to predation of *C. unicornis* is due to the protection offered by the colony in which they live (GILBERT 1980b; EDMONDSON & LITT 1987), a protection also effective against *P. pediculus* (MATVEEVA 1989), the other invertebrate predator in the epilimnion. *Polyarthra* can evade predator attacks by rapidly swimming away with the help of its fins (GILBERT 1980b).

Kellicottia longispina, Synchaeta and *K. hiemalis* are all susceptible to invertebrate predators (DUMONT 1977; MATVEEVA 1989) and displayed little overlap with these in Takvatn. Loricae of the latter species, in some cases with loricae of *K. cochlearis*, were observed in the body cavity of *A. priodonta* (end of August, 15 m of depth) providing direct indication of exposure to predation. The low spatial overlap between vulnerable rotifers and their invertebrate predators is consistent with the expectations and reproduces a pattern documented in earlier works (MAKAREWICZ & LIKENS 1975; WILLIAMSON 1993). These patterns support the predictions of the predation risk model (WILLIAMSON et al. 1989), which revolve around the assumption of a cost of anti-predator defences.

Late stages of *C. scutifer* may switch to a carnivorous diet, including rotifers and nauplii (MOORE 1978). This predator should not represent a serious risk for loricate species as *K. cochlearis* or *K. longispina* due to the protective nature of their thick integument (STEMBERGER & GILBERT 1987), but may threaten soft-body forms such as *Synchaeta* (WALZ 1997). *Synchaeta* sp. grew in abundance only after the density of *C. scutifer* adults had declined in July. Nauplii can evade invertebrate predators by rheotactic escape response, the form of defence used also by *Polyarthra* (WILLIAMSON & VANDERPLOEG 1988). But the spatial overlap with adults in the upper epilimnion of Takvatn early in July and, for *C. scutifer* nauplii, towards the end of the period of stratification, may still imply a loss due to predation.

The visual-predator avoidance hypothesis predicts that, during the day, the largest and most conspicuous individuals should stay deeper in the water column, being the most exposed to fish predators (LAMPERT 1993). This expectation is supported by both experimental and field studies (LOOSE 1993; GLIWICZ 1994), marking the importance of the hypolimnetic refuge for coexistence of susceptible cladoceran prey with fish (TESSIER & WELSER 1991). The epilimnetic distribution of *P. pediculus*, a large species highly conspicuous due to its huge eye, may seem at odds with the above hypothesis. But *P. pediculus* moves into the open waters of lakes in swarms, which constitute a protection against predators (BUTORINA 1986; TURNER & PITCHER 1986). Also, census data of the Arctic charr population in 1994 showed a low density of this predator in the pelagic zone of the lake (PRIMICERIO & KLEMETSEN 1999). Among the herbivore cladocerans found, the most exposed to fish predation is *Daphnia* (DAHL-HANSEN et al. 1994), followed by *H. gibberum* and lastly by *B. longispina* (HE et al. 1994). While *B. longispina* and *H. gibberum* remained in the upper epilimnion of Takvatn, the few *D. galeata* found during summer stratification aggregated in deeper waters, in accordance with the expectations. *Bosmina* is also a prey of *P. pediculus*, but its swarming behaviour may represent an effective defence against this invertebrate predator (KLEMETSEN 1970), in addition to protect against fish (JAKOBSEN & JOHNSEN 1988).

Copepods are more efficient than cladocerans at evading predators due to their ability to perform jumps when attacked (O'BRIEN 1987). Therefore they may not need to rely so heavily on spatial avoidance. Albeit adults of *E. graciloides* did aggregate below the metalimnion in August, they were found in the epilimnion both in July and September. An earlier study by KILDEMO (1982), done when fish planktivory in the lake was intense, also registered epilimnetic distributions of adult copepods.

The separate treatment of the biotic factors that influence habitat-selection is not a simple task because these factors act in concert. In Lake Takvatn, the concurrent operation of predation and competition is exemplified by the vertical distribution of the dominant rotifers *K. cochlearis* and *C. unicornis* in presence of *A. priodonta*, their shared predator. The

depth-habitat segregation displayed by *Keratella* and *Conochilus* during stratification may be best explained as the combined effect of predator avoidance and interspecific competition. Predator avoidance forces the more susceptible prey *Keratella* away from the productive, warmer epilimnion, where *Asplanchna* aggregates, whereas interspecific competition prevents *Conochilus* from expanding into the deeper, less productive habitats and *Keratella* from invading the epilimnion as the respective densities increase. This suggests that depth-habitat segregation between *Keratella* and *Conochilus* will be maintained as long as the predator *Asplanchna* aggregates in the epilimnion. In the absence of *Asplanchna*, *K. cochlearis* should stay near the surface like *C. unicornis*, as observed by LAXHUBER (1987).

The epilimnetic distribution of *Asplanchna* may seem counterintuitive because its most susceptible prey aggregates in deeper waters. An earlier interpretation of the near surface distribution of *A. priodonta*, observed in many lakes (e.g. ELLIOTT 1977; HOFMANN 1987; WALZ et al. 1987; MIKSCHI 1989; OEHMS & SEITZ 1992), is based on its limited tolerance of low oxygen concentrations experienced in deeper waters (WALZ 1997). In rotifers, tolerance ranges of physico-chemical variables are often inferred from distributions observed in the field and are therefore questionable, particularly if used to explain those distributions. But even accepting the lower threshold concentrations proposed in the literature (e.g. 9 mg O_2 l^{-1}, MIKSCHI 1989) the above explanation does not apply in Takvatn where the hypolimnion is well oxygenated during summer stratification (>11 mg O_2 l^{-1} down to 30 m). Neither will apply a sensory constraint hypothesis as proposed for fish and *P. pediculus*, because *Asplanchna* is not a visual predator (NOGRADY et al. 1993).

So what keeps *Asplanchna* in the epilimnion? The answer can be found in the predictions of evolutionary game theory (MAYNARD SMITH 1982) applied to habitat-selection behaviour of a predator and its prey. When the prey is free to move between habitats of different profitability, the predator is expected to choose the habitat most profitable for its prey (VAN BAALEN & SABELIS 1993; HUGIE & DILL 1994; reviewed and expanded by SIH 1998); in the present case the nutritionally and thermally favourable epilimnion (LAMPERT 1993). As stressed by HUGIE & DILL (1994), earlier models of zooplankton habitat selection in presence of a predator did not highlight this point because they either failed to meet the requirements to reach stability (IWASA 1982) or assumed, but did not model, the habitat choice of the predator (GABRIEL & THOMAS 1988).

Summarizing the above explanation of habitat choice by *Keratella* and *Conochilus* in presence of *Asplanchna*, in a heterogeneous environment with a predator that is free to move between habitats, two competitors with similar habitat preferences but different tolerance of sub-optimal habitats and susceptibility to predation may be expected to segregate if the species more tolerant of low food availability is also the most susceptible to predation; given the expected aggre-

gation of the predator in the habitat most profitable to its prey. A trade-off between tolerance of low food availability, experienced in the nutritionally poor habitat refuge, and investment in escape or fight to evade predators sets the stage for habitat segregation of competing prey (BROWN 1998). This suggestion, inspired by vertical distributions observed in this and previous works, is derived from game theoretic models of habitat selection in heterogeneous environments that treat, respectively, habitat selection by predator and prey (SIH 1998) and habitat selection by competitors with shared preferences in presence of a predator that uses the habitat most profitable for its prey (BROWN 1998). The model is valuable in that it is self-contained accounting for the behaviour of predator and competing prey. The above ideas about habitat selection behaviour have relevance for community dynamics, due to the stabilizing effect of increased aggregation and decreased overlap between interacting species (HANSKI 1988), and emphasize the importance of adaptive behaviour as a source of local mechanisms promoting species coexistence.

While in temperate lakes zooplankton seasonal dynamics is characterized by temporal segregation, with successional patterns often pulsed by end and onset of diapause, at the high latitudes of Lake Takvatn time partitioning is not as relevant. The short productive season resulting from the particular combination of photoperiod and duration of ice-cover, and the low temperature, force a strong degree of temporal overlap on interacting species. Habitat-selection behaviour becomes critical for persistence and is affected by susceptibility to predators and tolerance of poor food conditions, producing patterns of distribution that appear to be a balance between the aggregative pressure of interspecific competition and predation and the dispersive pressure of intraspecific competition. The implications of habitat-selection behaviour for the demography and community organization of zooplankton are easier to determine at these high latitudes because of a reduced importance of vertical migration (BUCHANAN & HANEY 1980; KILDEMO 1982), and are thereby liable to study in the field.

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