

## Major contribution from littoral crustaceans to zooplankton species richness in lakes

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### *Abstract*

A study of pelagic and littoral species richness among microcrustaceans in 2,466 Norwegian lakes recorded 120 crustacean species: 77 cladocerans, 31 cyclopoids, and 12 calanoids, respectively. Very few species were strictly pelagic, and the pelagic crustacean zooplankton species were by far outnumbered by their littoral counterparts. More than two-thirds of the total crustacean species numbers in lakes were accounted for by species with a littoral preference. A considerable number of species occurred with low frequency, and the median total number of crustacean species in the lakes was only 14. A majority of littoral species also occurred commonly in pelagic samples, and vice versa. Some species are truly both littoral and pelagic, and nearly all species occurring in pelagic samples were also common in littoral samples. A high proportion of the common littoral species was only recorded occasionally in pelagic samples, and should thus be considered strictly littoral. There was no significant correlation between lake area and species richness for pelagic or littoral species. Our findings demonstrate the importance of including littoral species when assessing microcrustacean diversity in lakes, and we question the practice of considering species as either pelagic or littoral, because a majority of the recorded species was common in both habitats. It calls for a further discussion of the term “planktonic”, since most of the species are at least partly “semiplanktonic.”

Zooplankton species richness in lakes is, as for functional groups in other ecosystems, a key measure not only of the biological status, but also a link to ecosystem functioning, food web complexity, and ecosystem stability. Most studies on zooplankton diversity in lakes include species sampled by net-hauls in open waters, i.e., species assumed to be truly planktonic. Rather few studies include detailed studies of the littoral species, and comparative studies of pelagic and littoral species diversity are almost nonexistent. This is partly due to the higher complexity and frequently more demanding taxonomy of the littoral taxa, but also because there are no clear-cut boundaries separating the pelagic and littoral habitats.

The terms “crustacean zooplankton” as opposed to “littoral crustaceans” are commonly used by limnologists to describe species that are strictly living in open waters, or species associated with the surface of macrophytes/sediments,

respectively. There is, however, no sharp boundary between these two groups. According to Pennak (1966), true zooplankters are found not only in the pelagic but also among macrophytes. He emphasizes that “true” here refers to zooplankters that are swimming about in the water and are not associated with a plant substrate at the time of capture. In the macrophyte zone, however, there is undoubtedly a much larger number of niches available because of the spatial, nutritional, and food-web roles of the vegetation (Pennak 1957). The absence of strict categorical boundaries obviously has implications for diversity or species richness estimates of zooplankton in lakes, since these to a varying degree will include both pelagic and semilittoral species, depending on lake size, morphometry, and sampling method.

Some crustacean families like Chydoridae and Macrotrichidae tend to be primarily littoral (Flössner 2000). On the other hand, vertical movements of epiphytic and benthic microcrustacea have been observed in several studies (e.g., Whiteside 1974, Meyers 1984). Meyers (1984) suggested that many chydorid Cladocera are facultative planktivores that move upward at night to utilize phytoplankton. Low concentrations of edible phytoplankton may preclude vertical migration. Many epiphytic and benthic microcrustaceans also exhibit strong vertical movements with declining oxygen concentrations (Meyers 1980; Tinson and Laybourn-Parry 1985). In a study of horizontal migration,

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Lauridsen et al. (2001) found that *Bosmina* spp. and *Holopedium gibberum* were evenly distributed between the littoral and the pelagial in deep and shallow fishless lakes, but that their near-shore densities were lowest in the presence of fish. Macrophyte-related and benthic cladocerans concentrated either in the littoral or were evenly distributed between the littoral and the pelagic, irrespective of depth and the presence of fish. The boundary between littoral macrophyte beds and open waters may also be an important daytime refuge for potentially migrating pelagic cladocerans (Lauridsen and Buenk 1996). Such vertical and horizontal migrations render strict division between true zooplankton and littoral/benthic species difficult.

In this study we analyzed species number of microcrustaceans in a large data set covering a wide range of localities that have been sampled both for pelagic and littoral crustaceans or both habitats pooled, to test the importance of including littoral microcrustacean species when assessing diversity. On the basis of this we also discuss the validity of the terms "planktonic" and "littoral" crustaceans.

## Material and methods

This study is based on samples of microcrustaceans from 2,466 localities, covering the entire mainland of Norway (58°3' to 71°4'N) and spanning a wide range in terms of altitude, area, pH, and conductivity: 1.0–1,837 m above sea level (mean 434, median 307 m), 0.001–363 km<sup>2</sup> (mean 2.1, median 0.2 km<sup>2</sup>), 3.8–9.9 in pH (mean 6.2, median 6.5), and a conductivity from 0.41 to 200 mS m<sup>-1</sup> (mean 4.7, median 2.4 mS m<sup>-1</sup>). Total organic carbon (TOC) and total P was only recorded for a limited subset of localities, but confirmed the dilute and low-productivity nature of these pristine lakes with TOC ranging from 0.2 to 14.8 mg L<sup>-1</sup> (mean 3.1, median 2.1 mg L<sup>-1</sup>) and total P from 0.13 to 69 µg L<sup>-1</sup> (mean 17, median 8 µg L<sup>-1</sup>).

The data set includes lakes that are sampled only for pelagic zooplankton (575 lakes), only littoral samples (728 lakes), or both (1,163 lakes). In the last category pelagic and littoral samples were (unfortunately) pooled when they entered the database. There should be no a priori sampling bias with regard to these three categories of samples. The great majority of lakes (>90%) have been sampled only once or twice during summer or early autumn. Some lakes have been more intensively studied over 2 or more years. For these lakes, a single year was randomly picked as representative of that locality to avoid a bias in species richness for these lakes. For lakes sampled over several years, cumulative species number may be almost 50% higher than that of single samples (Arnott et al. 1998). However, many of the species contributing to the cumulative richness in our study were rare and perhaps transient visitors (for example occurring in single samples represented with a single individual over a 10-yr period).

For zooplankton sampling, a net haul (27.5–30-cm diameter, 90 µm net) was in most lakes taken from the deepest part from the bottom to the surface. This method ensures a high number of individuals and also an almost complete species list. The littoral species were sampled by

a net haul horizontally at low speed (about 25 m min<sup>-1</sup>) both outside and inside vegetation stands whenever possible in each lake. A smaller (10-cm diameter, 90 µm) net was used where vegetation was too dense to allow use of the regular net.

All crustaceans were identified to species; rotifers were not included in this survey. Cladoceran species were identified in accordance with Flössner (2000), whereas copepods were identified after Kiefer (1978). The taxonomic affinities remain vague for some of the cladoceran species. This holds especially for the *Daphnia* group, e.g., *Daphnia longispina*, where recent screening of genetic affinities by use of allozyme studies and mitochondrial or nuclear markers show that *D. rosea* and the melanistic alpine *D. umbra* should be separated from *D. longispina* s. str. (Schwenk et al. 2004; Hobæk 2005). Some species, notably *D. galeata*, commonly hybridize with other species (Schwenk et al. 2001; Hobæk et al. 2004), and there is no doubt that further genetic screening will reveal taxonomic revisions both for the daphnids as well as for other groups. However, these somewhat unclear taxonomic affinities for some species would not have major consequence for species richness per se in this large data set.

The pelagic and littoral samples were scored for presence or absence at the species level and each species was assigned to one of three categories: those present in pelagic samples only, those present in littoral samples only, and those present in both habitats. Great care was taken in rinsing the sampling gear between sampling in different localities. In spite of this, samples might become contaminated and 13 species that were abundant in the littoral samples while only recorded in a single pelagic sample (<0.2% of the samples, and then often in a typically dried condition) were omitted from combined pelagic–littoral category.

Data on relative abundance for species both in pelagic and littoral samples from the same localities were obtained from a subset of 80 lakes. Relative abundance for each species was assigned to three categories; <1%, 1–10%, and >10% of total number. The highest recorded abundance observed from a total of four samples (two from early summer and two from late summer) were used as input for each species. Patterns of distribution, relative abundance, and absence/presence were summarized by detrended correspondence analysis (DCA) (Hill 1979) using the program CANOCO (ter Braak and Smilauer 1998) with down-weighting of rare species. By using pelagic and littoral samples as input we expected the first axis to separate between the two main habitats. Since species that are far apart correspond to sites that are dissimilar in species composition, our aim was to visualize which species was associated with the two respective habitats on the basis of dominance score.

## Results

In total, 120 crustacean species were identified (77 cladocerans, 31 cyclopoids, and 12 calanoids) from the 2,466 localities included in this study. The highest number of species recorded within any given locality was 47 (1 yr, one to two visits), and the median number of species

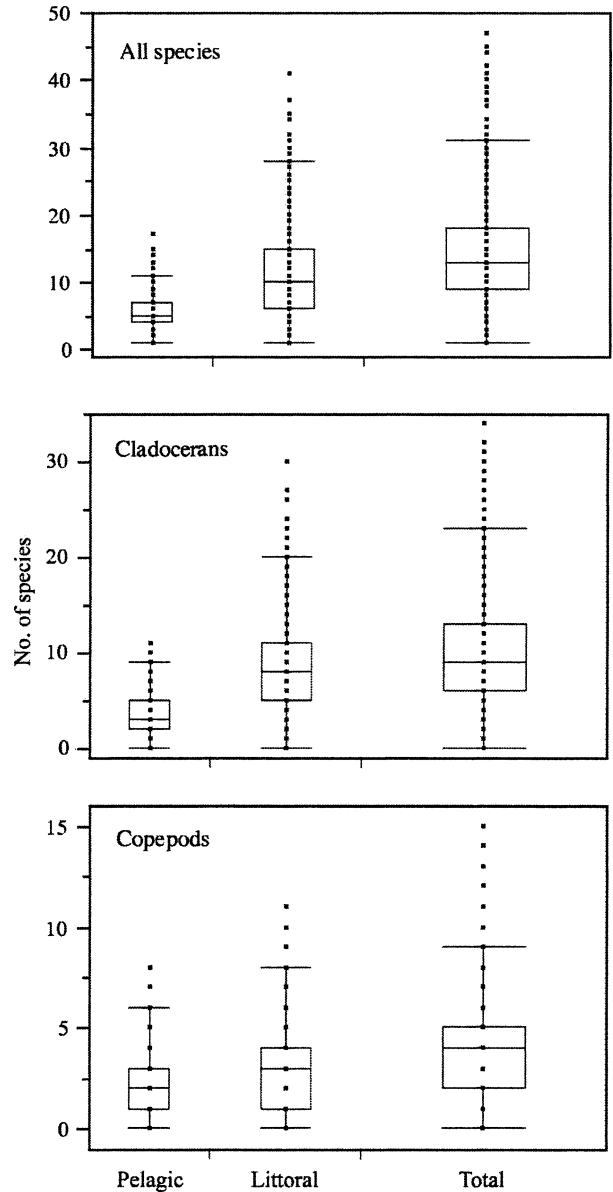
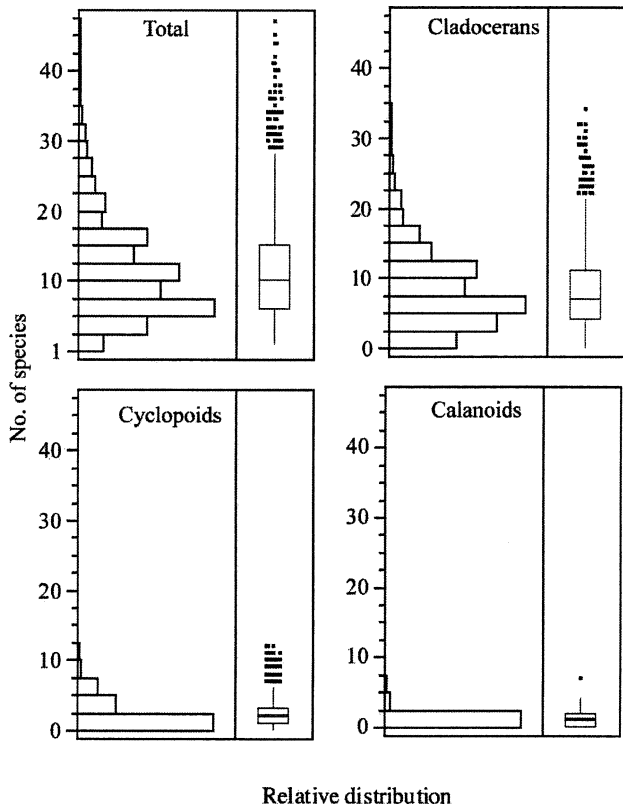


Fig. 1. Frequency distribution of species numbers of microcrustaceans and the major groups cladocera, cyclopoid copepods, and calanoid copepods. Extension of bars represent the relative fraction of sampled lakes with a certain number of species. Box plot in right panel displays medians as vertical line, extension of boxes represents 25th and 75th percentiles, and extension of lines are 10th and 90th percentiles. Observations outside 90th percentiles are represented as single dots. All categories include both pelagic and littoral samples from the 1,058 lakes where both habitats were sampled.

(pelagic plus littoral) was 14. On the basis of accumulated data, maximum number of species recorded within one lake was 69. A considerable number of species may be classified as rare, in the sense that they occurred in few localities. Cladocerans and copepods were, on average, constituting 70% and 30% of the species respectively (Fig. 1).

Species numbers were far higher in littoral than pelagic samples (Fig. 2). Median number of species occurring in pelagic samples (575 lakes) was 6 (maximum 17), whereas median number in littoral samples (728 lakes) was 11 (maximum 41). Corresponding numbers for cladocerans were 4 (maximum 11) for pelagic samples and 8 (maximum 30) for littoral samples. Copepods followed the same pattern with a median number of 2 (maximum 8) in pelagic versus 3 (maximum 11) in littoral samples (Fig. 2). The majority of copepods were cyclopoids. Calanoids were relatively rare, with a maximum species number of four per lake for both pelagic and littoral samples.

When assigning species to either the pelagic or the littoral group, both series of samples included a major fraction of rare species (Fig. 3). Among the species recorded in littoral samples, there was a wide variation in

Fig. 2. Box-and-whisker plot of total species numbers and numbers of cladocera and copepods from pelagic or littoral samples, or both pooled. Vertical line is median of all observations, line within boxes is median of the category, extension of boxes represents 25th and 75th percentiles, and extension of lines is 10th and 90th percentiles.

their relative frequency of occurrence. Mean frequency of occurrence was 11% only, and only five species occurred in more than 50% of the lakes. This was even more extreme for the pelagic samples, in spite of comparatively lower species richness. On the average, species recorded in the pelagic samples were present in 9% of the lakes, and only three species were found in more than 50% of the lakes. For the pelagic samples, many species were recorded infrequently.

When scoring each species for their relative occurrence in the pelagic versus the littoral samples, 23 species occurred with highest frequency in pelagic samples, whereas 86

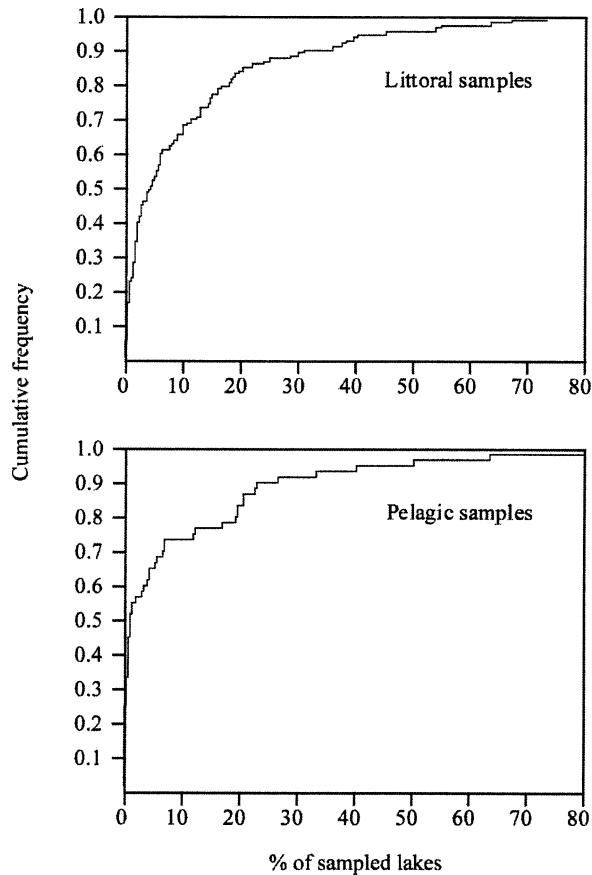


Fig. 3. Cumulative frequency of species recorded in all lakes.

species were most abundant in the littoral habitat. A large number of species that were common in littoral samples, and then often in high numbers, were more incidentally recorded in pelagic samples. For example, species like *Chydorus sphaericus* occurred in 67% of the littoral samples, while in no more than 3% of the pelagic samples. Also a very common littoral species like *Polyphemus pediculus* (present in 54% of the littoral samples) could be considered rare in relative terms in the pelagic samples (11% occurrence). Hence it is hard to arrive at any strict definitions on concepts such as “rare” since this also depends on their relative frequency of occurrence within lakes. However, species such as *C. sphaericus* and others that are very abundant in littoral samples and very rare in pelagic samples should be regarded as “pelagic visitors”.

Our data show that only two rare species could be considered strictly pelagic; the cyclopoid *Cyclops lacustris* and the large calanoid *Limnocalanus macrurus*. On the other hand, 59 species in total (41 cladocerans, 17 cyclopoids, and 1 calanoid) were assigned strictly littoral, whereas 48 species (30 cladocerans, 10 cyclopoids, and 8 calanoids) occurred regularly in both littoral and pelagic samples. This underlines the problems associated with estimating pelagic or planktonic species numbers.

Except for the two species mentioned above, the species occurring in pelagic samples were also recorded in littoral samples. When plotting the frequency of occurrence for all species that were recorded in both pelagic and littoral

samples (note that this will not comprise the full list of species, since many littoral species were not present in the pelagic samples), we observed a distinct branching pattern. One group of species was correlated, i.e., high frequency of occurrence in littoral habitats also means high occurrence in pelagic samples and thus no strong habitat preference, whereas the other group was always uncommon in the pelagic even while being widespread in the littoral samples (Fig. 4). The most frequently recorded species here was *Bosmina longispina*, which was also the most common species in the littoral samples. This species occurred in 89% of the pelagic samples. However, the majority of species was absent from most localities, in spite of having a wide geographic distribution. This is evident from the fact that in spite of a total of 120 species recorded, median richness was only 14. More than 50% of the species occurred in less than 5% of the samples, even though most of these species would not be considered rare on a national basis since they still often had a widespread spatial distribution.

Average size for the littoral lakes was somewhat less than that of the pelagic lakes. This could represent a bias if, as commonly reported, species number depends on lake area. However, our study does not reveal any correlation between lake area and species richness ( $p > 0.5$ , minimum least-square regression), neither for pelagic nor littoral samples (Fig. 5).

DCA ordination of relative abundance data from an 80-lakes subset confirmed that few species were assigned to the positive end of the first axis, representing the pelagic samples, while the great majority of species were found in the opposite (littoral) end (Fig. 6). As *B. longispina* was found in 78 of 80 lakes and was equally dominant in both habitats, we can assume that species having a higher score along axis 1 are more pelagic, whereas a more negative score indicates preferences for the littoral habitat. DCA

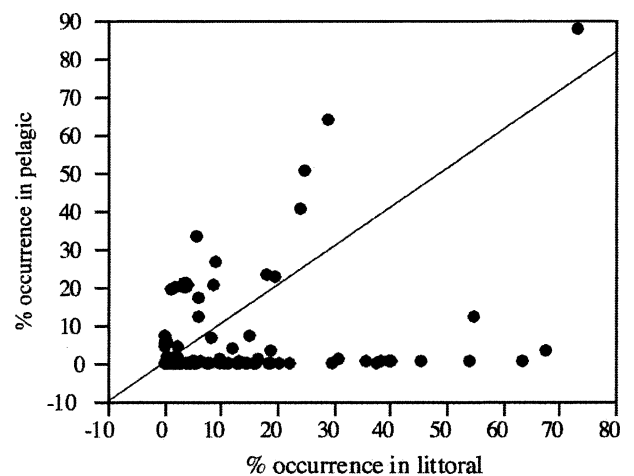


Fig. 4. Scatterplot showing the percentage occurrence of each species in pelagic samples versus littoral samples. The most abundant species, *Bosmina longispina*, occurred in 89% of the pelagic samples and 76% of the littoral. Only species occurring in more than 10% of the localities were included. Positive correlation indicates species that were equally common in pelagic and littoral habitats, whereas the uncorrelated cluster represents species uncommon in the pelagic samples.

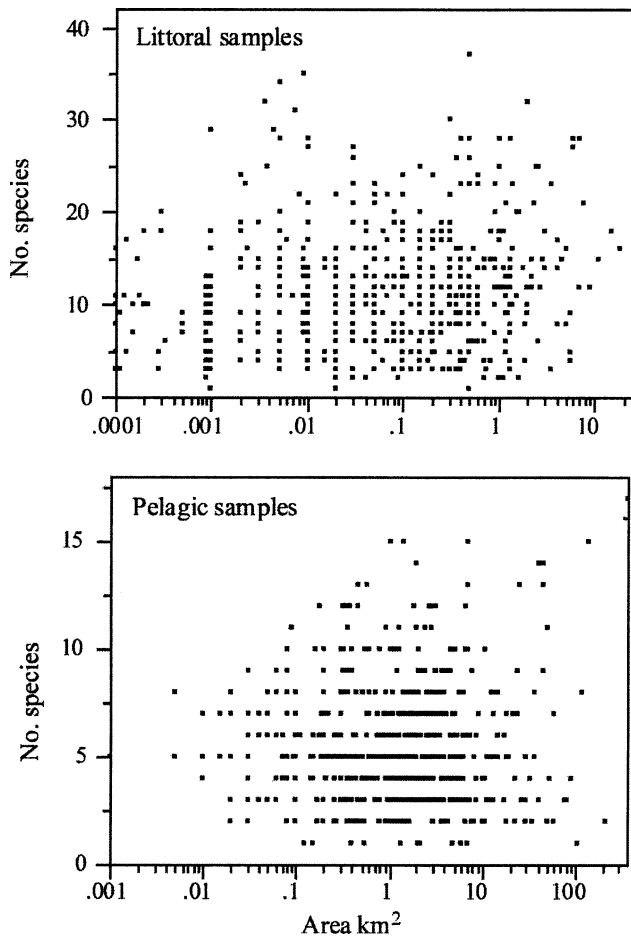


Fig. 5. Scatterplot of species number for littoral samples and pelagic samples. No significant correlation was found between species numbers and area.

ordination run on absence/presence (not shown) diverged slightly from Fig. 6. In the latter analysis a few of the numerically abundant species, i.e., *Cyclops scutifer* and *H. gibberum*, became less pelagic, i.e., their relative distance from *B. longispina*, along the first axis, decreased with 0.65 and 0.50 SD units, respectively. The calanoid copepod *Heterocope saliens* became more pelagic, and was separated from *B. longispina* by 0.67 SD units. A full list of species with their relative abundance in pelagic and littoral samples is provided in Web Appendix 1, [http://www.aslo.org/lo/toc/vol\\_51/issue\\_6/2600a1.pdf](http://www.aslo.org/lo/toc/vol_51/issue_6/2600a1.pdf).

## Discussion

The sampling for assigning littoral, pelagic, or total species richness was performed in separate localities. Owing to the very large sample size as well as geographical overlap in sampling sites, we believe that our conclusions are robust. The sum species numbers for pelagic and littoral samples correspond well with the total species numbers for the pooled samples. It is likely, however, that a more intensive sampling effort for each locality would have revealed more littoral species relative to pelagic species. This because the littoral is a more heterogeneous habitat

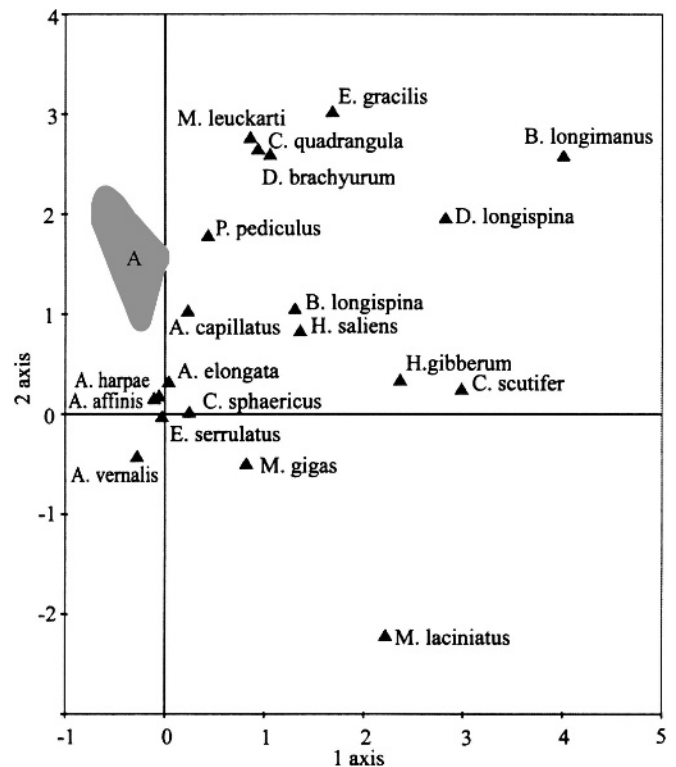


Fig. 6. DCA-ordination species plot based on parallel pelagic and littoral samples from a subset of 80 lakes. For clarity, only species that occurred in more than 10% of the localities ( $n = 40$ ) are included. Shaded area A includes *A. nana*, *E. lammelatus*, *A. excisa*, *S. crystallina*, *A. rustica*, *R. falcata*, *M. albidus*, *D. nanus*, *A. guttata*, *O. gracilis*, *A. curvirostris*, *S. mucronata*, *M. fuscus*, *A. robustus*, *G. testudinaria*, *C. piger*, *S. serricaudatus*, *P. truncatus*, *P. affinis*, and *A. intermedia*. Shaded area A represents a cluster of strictly littoral species. Full names of the respective species are shown in Web Appendix 1.

than the pelagic and therefore offers a higher number of potential niches but also more sampling constraints relative to the homogeneous pelagic.

One would also expect a higher occurrence of species that are typically considered littoral being represented in the pelagic of small and shallow lakes. While species number usually increases with the area of habitat (Browne 1981; Fryer 1985; Dodson et al. 2000), we found no correlation between lake area and species richness neither for pelagic nor littoral species. This accords with a previous study based on a different sample of Norwegian lakes (Hessen et al. 2006), where the absence of area–richness relation was accredited to the comparatively short time since the last glaciation, as well as a topography with mountain barriers that may constrain species dispersal. Consequently, many localities may be unsaturated with species (i.e., not in “equilibrium”). Local lake characteristics may also override any habitat–size effect (cf. Whittaker et al. 2001). The low mean number of species in the Norwegian lakes may also be explained by the high number of ultraoligotrophic localities, many situated in mountain areas.

There is no straightforward way of separating pelagic and littoral microcrustaceans, and the term zooplankton

commonly also includes littoral species. Wetzel (2001) stated that “littoral zooplankton communities are made up of a diverse assemblage of protozoans and other protists, rotifers, and microcrustaceans. Many of these animals are strongly associated with the sediments or macrophytes and are not truly planktonic, or are only intermittently planktonic”. Littoral microcrustacean communities have been assigned to three general groups in the littoral zone: the strictly plant-associated species, those free-swimming among the large plants, and the sessile species mainly living on or in littoral sediments (e.g., Pennak 1966; Whiteside et al. 1978; Fairchild 1981). Few of these strictly benthic or epiphytic microcrustacea enter the water column, even at night (Paterson 1993). On the other hand, truly planktonic species are common in areas within littoral zones devoid of vegetation but are rare within areas with dense macrophyte vegetation (Wetzel 2001). However, even predominantly pelagic species may utilize macrophyte boundaries as a refuge from fish predation (Lauridsen and Buenk 1996). Fryer (1985) suggested that members of littoral taxa like the chydorids may occur in planktonic samples by acting as opportunistic riders on filaments of blue-green algae (Fryer 1985). Our study confirms that there is no distinct boundary between most pelagic and littoral species. We believe that one reason for the high number of rare visitors in the pelagic samples was the generally high number of littoral species, of which some occasionally would be driven offshore by wind and waves.

Our study demonstrated that the microcrustaceans could be divided into three groups: a large group of strictly littoral/benthic species, another fairly large group that ranged freely among the pelagic and the littoral habitat, and a very few species that were strictly pelagic. The higher richness of littoral species clearly demonstrates that pelagic samples will only represent a modest fraction of total microcrustacean richness in lakes. The common presence of typically littoral species in pelagic samples creates a problem in the assessment of richness, since, if only a small fraction of the littoral species exploits the pelagic habitat, their presence would result in an overestimate of species richness in the pelagic zone. Since most studies on zooplankton richness in lakes are based on pelagic samples only, richness estimates are highly vulnerable to the input from littoral species. Not only will this contribution vary in space and time, but it could also differ with lake-specific properties such as the volume-to-surface ratio, the hypsographic profile, wind and mixing events, lake productivity, etc. This means that zooplankton species richness estimates based on strictly pelagic samples should be judged with some caution.

The dominance of littoral species reflects the higher niche diversity in littoral habitats compared with the homogenous pelagic habitat. Littoral cladocerans show highly diverse habitat preferences, including submerged macrophytes, sediments, sand and rock surfaces, as well as the water column (Pennak 1966; DiFonzo and Campbell 1988; Paterson 1993). Thus, the high richness of littoral species may reflect an adaptive radiation not only with regard to feeding preferences, but also for spatial niches. It may also reflect that the evolutionary origin of the several

species-rich microcrustacean taxa like the chydorids is littoral (cf., Fryer 1968). It should be noted that, because of the spatial diversity and potential constraints on adequate and representative sampling procedures in the littoral zone, it is more likely that the true number of species is underestimated in the littoral than in the pelagic habitat. Hence, our reported dominance of littoral species should be seen as minimum estimates.

Though many crustacean species occur in a large fraction of both pelagic and littoral samples, this does not necessarily imply that they are also numerically abundant. Species like *Holopedium gibberum* and *Cyclops scutifer* occurred in a large fraction of the localities, both in pelagic and littoral samples. Judged from their numerical abundance, however, their pelagic preference became clearer since they had high dominance score in pelagic samples while less so in the littoral samples. In contrast the large calanoid *Heterocope saliens*, which also occurred in a high fraction of both pelagic and littoral samples, was more typically littoral judged from the dominance score, i.e., when it occurred in littoral samples it often did so in large numbers. Dominance score had less effect in the littoral end of the first axis, since these species were so strongly associated with the littoral zone.

In conclusion, our study demonstrates not only that littoral or semilittoral species are major contributors to microcrustacean biodiversity in lakes, it also underlines the problems of separating between “true” pelagic zooplankton species and their littoral counterparts when assessing species richness on the basis of pelagic samples.

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