



Diel variation in horizontal distribution of *Daphnia* and *Ceriodaphnia* in oligotrophic and mesotrophic lakes with contrasting fish densities

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Abstract

Recent studies document diel horizontal migration by large zooplankton in eutrophic shallow lakes. Risk of predation from planktivorous fishes could induce such behaviour. We studied diel horizontal distribution of cladocerans in 31 mainly shallow oligotrophic and mesotrophic New Zealand (NZ) and North American (NA) temperate lakes. In terms of weight, fish catch per net (CPUE_w) in multiple mesh-sized gill nets was similar in the two sets of lakes, while CPUE by number (CPUE_n) was overall higher in the NA lakes. Unlike previous results from eutrophic, temperate lakes, we found no significant diel variations in density in the pelagic and littoral zones, suggesting no diel horizontal migration of zooplankton. In the NZ lakes, *Daphnia* and *Ceriodaphnia* were evenly distributed between the littoral zone and the pelagial, while in the NA lakes *Daphnia* were more abundant in the pelagial and *Ceriodaphnia* in the littoral zone. In the oligotrophic fishless NZ lakes, large *Daphnia carinata* dominated, whereas the smaller *Ceriodaphnia dubia* dominated in lakes with high CPUE's. In both the NZ and the NA lakes, *Daphnia* showed no clear correlation to fish CPUE_n. However, in the NA lakes, *Daphnia* occurred at fish CPUE_n values at which they were eliminated in the NZ lakes, which may be related to differences in water transparency, reflecting a higher chlorophyll *a* and humic content in the NA lakes.

Introduction

Zooplankton, especially cladocerans such as *Daphnia* and *Ceriodaphnia*, play an important role in shallow lakes as they reduce algal abundance via filtration and constitute an important food source to both planktivorous fish and omnivorous and piscivorous fish fry (Wetzel, 1983). Large-bodied zooplankton, such as *Daphnia* spp., are extremely vulnerable to predation by fish (Brooks & Dodson, 1965). High densities of planktivorous fish imply a significant reduction in the abundance of large-sized zooplankton species which may contribute to the shift from a clearwater to a turbid state (Scheffer et al., 1993). To avoid predators, large-bodied zooplankton seek refuge during the day when they are particularly vulnerable to visually foraging predators. In deep stratified lakes, zooplankton seek daytime refuge in the cold darker waters of the metalimnion-hypolimnion (Gliwicz, 1986; Dini &

Carpenter, 1988; Lampert, 1993). In shallow lakes with less severe gradients in light and temperature, vertical migration cannot be exploited to the same extent as in deep lakes. Instead, daytime aggregation of pelagic zooplankton in structured areas may occur (Kairesalo, 1980; Timms & Moss, 1984; Lauridsen & Buenk, 1996; Stansfield et al., 1997). Such areas with high structural complexity, e.g. macrophytes within a littoral zone, may serve as refuge for zooplankton against their predators (Timms & Moss, 1984; Lauridsen & Lodge, 1996).

Daytime aggregation in or near macrophytes, diel horizontal migration (DHM), was initially suggested by Timms & Moss (1984). Today several studies confirm the existence of DHM (Davies, 1985; DeStasio, 1993). In Denmark, this phenomenon is documented by studies in eutrophic lakes (Lauridsen & Buenk, 1996; Lauridsen et al., 1996; Jeppesen et al., 1997a). However, these eutrophic lakes have high densities of

planktivorous fish and, consequently, a high predation pressure on zooplankton. Recent studies show a more even horizontal distribution during the day in oligo- and mesotrophic systems than in eutrophic lakes (Visman et al., 1994; Smiley & Tessier, 1998), but little is known about night-time distribution and DHM.

In deep lakes, diel vertical migration (DVM) is reduced when fish are removed (Dini & Carpenter, 1988; DeStasio, 1993). Thus, assuming the advantage of DVM and DHM is the same, i.e. avoidance of predators, we predict that DHM in shallow lakes increases with increasing abundance of zooplanktivorous fish. Therefore, we studied the horizontal distribution and DHM of daphnids and ceriodaphnids in oligo-mesotrophic shallow lakes with contrasting fish densities. The two genera were selected because they are key grazers in the pelagial (daphnids) and macrophyte-covered areas (ceriodaphnids) (Dodson & Hanazato, 1995; Perrow et al., in press) in both sets of lakes. The two sets of lakes differed in that the NZ lakes were dominated by few large fish, while the NA lakes were dominated by large numbers of smaller fish. In addition, the NA lakes were less clear than the NZ lakes.

Study areas

We surveyed 16 New Zealand (NZ) and 15 North American (NA) temperate lakes. The NZ lakes were situated on the South Island in the Canterbury and the Otago region, and the NA lakes in the Ottawa National Forest, in the upper peninsula of Michigan. With a few New Zealand exceptions, we focused on shallow (unstratified) oligo- mesotrophic lakes with a size range of 0.2–615 ha (Table 1).

Materials and methods

The lake sampling was conducted in late summer, January/February in New Zealand and August in the NA lakes, when fish predation was expected to be at the seasonal maximum (Jeppesen et al., 1997b). We sampled fish by conducting overnight catches using multiple mesh-sized gill nets. Each net was 42 m long and 1.5 m deep and consisted of 14 different mesh sizes ranging from 6.25 mm to 75 mm, randomly distributed in 3 m sections. We suspended the nets at mid-depth. In the NZ lakes, 6 nets were set in 10 of the 16 lakes and only 2–5 nets in six lakes because

of their smaller size. Half of the nets were set in the littoral, 20–30 m from the shore and parallel to it, and the rest were set mid-lake. In the NA lakes, only 3 nets were used, and they were all suspended mid-lake. For each section in each net, we weighed and measured a representative sample of at least 10 of each species; in addition, all fish were counted per section and the total catch per net was weighed.

In five NA lakes containing game fish according to the Michigan Department of Natural Resources (MDNR) (Perch, Harding, Bobcat, Holly and Crystal Lakes), regulations prevented us from using gill nets. Instead, we used fyke nets (1.6 m wide, 1 m deep, 20 mm mesh with a 15–20 m long lead) in Perch Lake and Harding Lake and obtained fyke net data from MDNR on Bobcat, Holly and Crystal Lake.

We sampled zooplankton at 3 and 5 (NA and NZ lakes, respectively) stations in both the littoral zone and the pelagial (defined as the central parts of the lakes irrespective of whether macrophytes were present or not). Daytime sampling took place between noon and 4 p.m. and night-time sampling between 11 p.m. and 2 a.m. The littoral samples were taken at 20% of maximum depth or maximum 1 m depth with a transparent tube sampler (1.5 m long, diameter 75 mm). When submerged macrophytes occurred, we collected water near the plant bed edge. In the pelagial, we took depth-integrated samples (2–5 samples depending on depth) using a Patalas sampler. From each of the 6–10 stations, a sample consisted of 3–5 pooled subsamples to account for patchiness. Of this pooled sample we filtered a 6–15 l sub-sample on a 20 or 50 μ m filter (NZ and NA lakes, respectively) which was then fixed with Lugol's solution. Zooplankton were counted and keyed to genus/species at 40–100 \times magnification.

We visually estimated macrophyte coverage (percentage of bottom covered by macrophytes) using a water glass. If this was not possible (a few pelagial stations in deeper lakes), macrophytes were registered as being present or absent after sampling with a plant rake.

From the pelagial mid-station, we collected water for total phosphorus (0.25 l unfiltered) and chlorophyll *a* (1 l). Lake water total phosphorus (TP) was determined as molybdate reactive phosphorus (Murphy & Riley, 1962) following persulphate digestion (Koroleff, 1970). In NZ, chlorophyll *a* was filtered on GF/C filters and determined spectrophotometrically after ethanol extraction (Jespersen & Christoffersen, 1987). In

Table 1. Morphometric data, total phosphorus and chlorophyll *a*, and littoral (Litt) and pelagic (Pel) macrophyte coverage at the sampled stations in the 16 New Zealand (NZ) and 15 North American (NA) lakes. If macrophytes could not be estimated visually, they were registered as present (+) or absent (–). Lakes are in order of increasing CPUEs by numbers

Lake name	Max. depth at pel. sampling stations (m)	Area (ha)	Total-P ($\mu\text{g P l}^{-1}$)	Chl <i>a</i> ($\mu\text{g l}^{-1}$)	Litt. macrophyte coverage (%)	Pel. macrophyte coverage (%)
<i>NZ lakes</i>						
Kelland Pond	4.0	4	16.5	1.4	0	20
Swan Lagoon	2.3	25	42	4.2	10	+
All Day Bay	0.7	10	603	5.6	80	100
Grey Duck Pond	1.9	3	41	1.7	68	+
Howden	3.0	30	14.8	1.2	82	+
Sarah	7.1	20	6.3	1.6	100	+
Henrietta	2.5	4	12.8	5.5	20	100
Evelyn	3.0	15	7.5	1.8	100	100
Middleton	4.5	20	10.4	5.8	0	+
Horseshoe	1.6	3	15.9	2.5	94	5
Red Lagoon	1.2	15	15.0	4.0	58	18
Butchers Dam	9.0	20	52		100	–
Emma	1.6	155	15.4	1.6	82	70
Roundabout	2.5	13	63	8.4	92	100
Waihola	1.9	615	60	7.7	0	+
Tomahawk L. 2	1.1	10	85	10.1	0	0
<i>NA lakes</i>						
Brown	3.5	25.5	12	11.5	67	–
Bobcat	3	30	17	14	97	–
Holly	3.5	15	16	10.2	77	–
Crystal	2.7	6	8	8.1	90	37
Harding	3.75	18	15	53	57	–
Foxpaw	5.5	5	12	2.7	100	–
Perch	1.5	33	5	4.7	63	–
Ridge	2.5	5	5	9.4	33	–
Mullahy	2	0.5	4	4.1	52	+
Heart	1.1	80	8.6	12.3	83	–
Orchid	3	9	24	13.1	100	+
Trout Pond	0.75	0.2	17	23.8	50	24
Houser	1.5	16	23	7.1	100	–
Sucker	2	190	18	22.7	90	+
Lower Holmes	0.9	24	11.4	6.3	100	100

NA, chlorophyll *a* was filtered on GF/C filters and determined using fluorometry after methanol extraction.

Results

The lakes studied were generally shallow with a maximum depth ranging from 0.7 m to 9 m and covered a fish gradient of 6–309# net⁻¹ (CPUE_n – catch per

unit effort by number) in the NA lakes and of 0–140# net⁻¹ in the NZ lakes. TP ranged from 4 to 603 $\mu\text{g P l}^{-1}$ (median=16 $\mu\text{g P l}^{-1}$) in the NZ lakes and 4–24 $\mu\text{g P l}^{-1}$ (median 12 $\mu\text{g P l}^{-1}$) in the NA lakes (Table 1). In the NZ lakes, chlorophyll *a* ranged from 1.2 to 10.1 $\mu\text{g l}^{-1}$ (median=4.0 $\mu\text{g l}^{-1}$), while chlorophyll *a* was significantly higher (*t*-test, $p=0.002$) in the NA lakes, ranging between 2.7 and 23.8 $\mu\text{g l}^{-1}$ (median=9.4 $\mu\text{g l}^{-1}$).

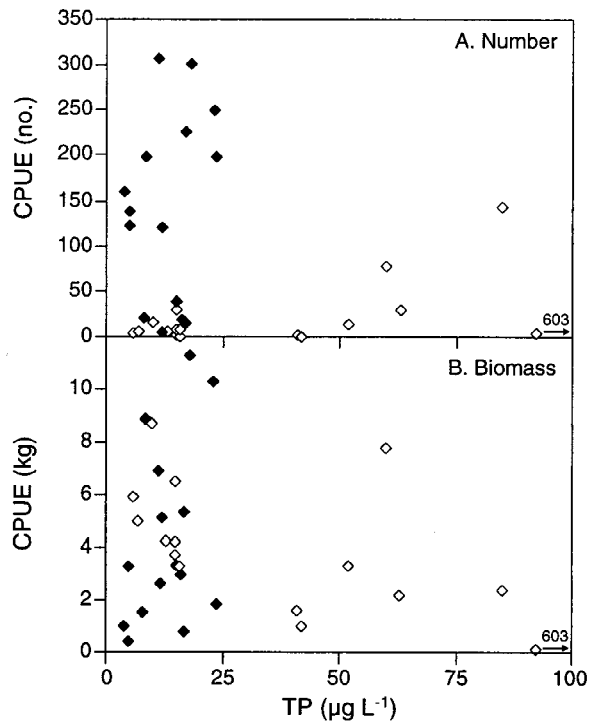


Figure 1. Fish CPUE by numbers (top) and by biomass (bottom) vs. total phosphorus (TP) for the New Zealand (\diamond) and North American (\blacklozenge) lakes.

Macrophytes

In the NZ lakes, macrophytes occurred in the littoral and pelagic zones of 12 and 14 of the 16 lakes, respectively. In the littoral zone, macrophyte coverage ranged from 20 to 100% and from 5 to 100% in the pelagic zone. In the NA lakes, macrophytes occurred in the littoral zones of all lakes and coverage ranged from 50 to 100%. In the pelagic, however, we found only macrophytes in 6 of the 15 lakes, with coverage ranging from 24 to 100%.

Fish

The fish composition in both the NZ and NA lakes ranged widely. In the NZ lakes, we found 9 species (Table 2). Brown trout (*Salmo trutta*), or in a few lakes rainbow trout (*Oncorhynchus mykiss*), occurred in all eleven lakes with fish. Brown trout were most abundant, ranging between 0.2 and 7.3# net⁻¹. Perch (*Perca fluviatilis*) were found in 5 lakes and were abundant in all the 5 lakes; 12–72# net⁻¹. Native species consisted of common bully (*Gobiomorphus cotidianus*), upland bully (*Phylypnodon breviceps*) and koara (*Galaxias brevipinnis*), between 0.1 and 70# net⁻¹. Total CPUE

in the NZ lakes ranged from 0 to 140# net⁻¹ (Figure 1) (median CPUE=6). By weight, brown trout and perch dominated the catches. CPUE_w ranged from 0 to 8.5 kg net⁻¹. There was no significant difference in fish CPUE between the littoral and the pelagic zones (paired *t*-test, *p*=0.51).

In the NA lakes, we found 17 fish species (Table 2), with common shiner (*Notropis cornutus*) as the most commonly occurring species (0.5–77# net⁻¹ in 12 lakes). The species found in highest densities included shiners, dace, bullheads and yellow perch (Table 2). Total CPUE_n in the NA lakes ranged from 6 in Brown Lake to 309# net⁻¹ in Lower Holmes (median CPUE_n=139) and by weight from 0.4 in Ridge Lake to 11.3 kg net⁻¹ in Sucker Lake (Figure 1). Fyke net data for the five game fish lakes ranged from 15 in Bobcat Lake to 123# net⁻¹ in Perch Lake and by weight from 1.5 kg net⁻¹ in Crystal Lake to 5.3 kg net⁻¹ in Bobcat Lake.

In order to compare fyke net data with gill net data, we used both measures in Brown Lake (game fish lake), Heart Lake (no game fish) and Orchid Lake (no game fish). However, we did not find any relationship between the catches by the two methods. For the three lakes, gill net data were 6, 198 and 199 (# net⁻¹), respectively, and fyke net data 78, 69 and 330, respectively. We found that fyke net data from the game fish lakes (Holly, Crystal, Bobcat and Harding) were a factor 2–10 lower than the corresponding data from the other lakes (Brown, Heart and Orchid Lakes). We therefore assume that fish density was low in these game fish lakes.

Zooplankton

In the NZ lakes, we found only one species of *Daphnia* (*Daphnia carinata*) and one species of *Ceriodaphnia* (*Ceriodaphnia dubia*). *D. carinata* occurred in 5 lakes (Figure 2) of which 4 had few or no fish. The fifth lake was Tomahawk Lagoon – the one with highest CPUE_n. In the five lakes, littoral daytime density of *Daphnia* ranged between 2 and 7# l⁻¹. At night, the density increased up to three-fold, albeit there was no statistical difference between day and night-time densities (*t*-test, *p* > 0.05). In the pelagic, both night-time and daytime densities in the five lakes ranged between 1 and 35# l⁻¹, and we did not find any significant diel differences. In Swan Lagoon and Grey Duck Lagoon, significantly more daphnids were found in the pelagic than in the littoral zone during day (*t*-test, *p*=0.0023 and *p* < 0.0001). However, in the other three

Table 2. Fish species caught in 16 New Zealand (NZ) and 15 North American (NA) lakes. Catch net⁻¹ and no. of lakes in which the species was caught

Name	Latin name	No. net ⁻¹ (range)	No. of lakes
<i>NZ-lakes</i>			
Brown trout	<i>Salmo trutta</i>	0.2–7.3	11
Common bully	<i>Gobiomorphus cotidianus</i>	>	
Upland bully	<i>Phylypnodon breviceps</i>	0.1–70	9
Rainbow trout	<i>Oncorhynchus mykiss</i>	0.3–16	5
Perch	<i>Perca fluviatilis</i>	12–72	5
Koaro	<i>Galaxias brevipinnis</i>	0.8–3.5	2
Smelt	<i>Retropinna retropinna</i>	0–1	1
Black flounder	<i>Rhombosolea retioria</i>	0–6	1
Yellow eyed mullet	<i>Aldrichetta fosteri</i>	0–2	1
<i>NA-lakes</i>			
Common shiner	<i>Notropis cornutus</i>	0.5–77	12
Black bullhead	<i>Ictalurus melas</i>	0.2–117	9
Yellow perch	<i>Perca flavescens</i>	2–153	9
Golden shiner	<i>Notemigonus crysoleucas</i>	0.3–93	8
Pumpkinseed	<i>Lepomis gibbosus</i>	0.3–15	8
Blackline dace	<i>Notropis heterolepis</i>	0.5–69	7
Common white sucker	<i>Catostomus commersoni</i>	0.5–16	7
Mudminnow	<i>Umbra limi</i>	0.5–88	6
Northern pike	<i>Esox lucius</i>	0.3–3	6
Redbelly dace	<i>Phoxinus eos</i>	5–94	5
Black crappie	<i>Pomoxis nigromaculatus</i>	1–14	4
Bluegill	<i>Lepomis macrochirus</i>	1–18	4
Finescale dace	<i>Phoxinus neogaeus</i>	10–72	4
Largemouth bass	<i>Micropterus salmoides</i>	0.5–4	4
Brassy minnow	<i>Hybognathus hankinsoni</i>	0.5–4	3
Fivespined stickleback	<i>Culaea inconstans</i>	1.5–017	3
Walleye	<i>Stizostedion vitreum</i>	0.3	1
Rock bass	<i>Ambloplites rupestris</i>	1–2.8	2

lakes with daphnids we found no statistically significant difference between the littoral and pelagic zones. Based on data from all lakes, there was no difference in *Daphnia* density between the pelagial and the littoral zone either during day or at night (paired *t*-test, $p=0.11$ and $p=0.07$). Neither in the littoral zone nor in the pelagial were any day/night differences found (Figure 2).

C. dubia occurred in 11 NZ lakes. In the littoral, *C. dubia* daytime density ranged between 3 and 160# l⁻¹ and 5 and 50 at night (Figure 2). Only in Lake Evelyn did we see a significant reduction in density in the littoral zone from day to night ($p=0.015$) and thus evidence for DHM. In the pelagial, the density ranged between 3 and 150# l⁻¹. No significant

differences between day and night were found, excepting Lake Middleton where night-time densities were higher ($p=0.011$). Lake Henrietta was the only lake with significantly higher densities (day as well as night) in the pelagial than in the littoral zone ($p=0.021$ and $p=0.0022$, respectively). In the other lakes, no statistically significant difference in distribution between zones occurred either during night or day (Figure 2). On the full data set, we found no difference in *Ceriodaphnia* density between the pelagial and the littoral zone during day (paired *t*-test, $p=0.76$), but at night more *Ceriodaphnia* were found in the pelagial (paired *t*-test, $p=0.05$).

In the NA lakes, we found seven species of *Daphnia* (*D. mendotae*, *D. retrocurva*, *D. parvula*, *D.*

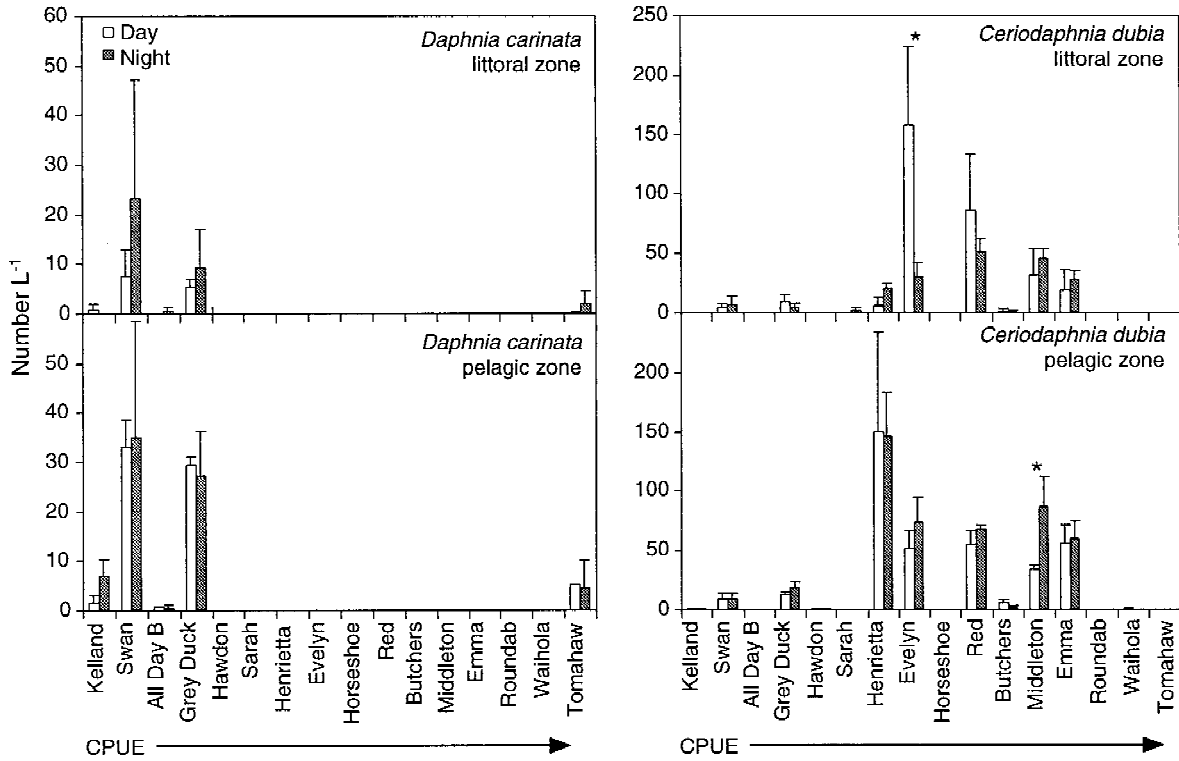


Figure 2. Day (open column) and night (dark column) densities ± 1 SD in New Zealand lakes of *Daphnia carinata* (left panel) and *Ceriodaphnia dubia* (right panel) in both littoral (top figure) and pelagic (bottom figure) zones. The lakes are sorted according to increasing CPUE by number. *indicates significant statistical difference at $p < 0.05$.

pulicaria, *D. laevis*, *D. dubia* and *D. dentifera*), which were pooled for analysis, and two species of *Ceriodaphnia* (*C. pulchella* and *C. sp.*) that were also pooled. *Daphnia* occurred in 8 lakes with density in the littoral zone ranging between <1 and $6 \# \text{ l}^{-1}$. In the pelagial, density ranged from <1 to $41 \# \text{ l}^{-1}$ (Figure 3). Except for the pelagic stations in Brown Lake ($p=0.014$) and Heart Lake ($p=0.0083$), no significant differences between day and night densities emerged; in these two lakes, more *Daphnia* occurred at night. Based on data from all lakes, density of *Daphnia* was significantly higher in the pelagial than in the littoral zone both during day and at night (paired t -test, $p=0.014$ and $p=0.011$, respectively), whereas no significant difference was found between day and night.

We found *Ceriodaphnia* in 14 of the 15 lakes. The density ranged, however, from <1 to $30 \# \text{ l}^{-1}$ in the littoral zone during day and up to $44 \# \text{ l}^{-1}$ at night. In the pelagial, daytime density ranged from <1 to $14 \# \text{ l}^{-1}$ and at night up to $47 \# \text{ l}^{-1}$ (Figure 3). In 12 of the 14 lakes, we found no difference in density between

day and night, for either the littoral or the pelagic zone. However, in Trout Pond and Houser Lake there were significantly higher densities during day than at night at the littoral stations (t -test, $p=0.0013$ and 0.004 , respectively). Data from all lakes showed a significantly higher density of *Ceriodaphnia* in the littoral zone than in the pelagial during day ($p=0.047$, paired t -test), but not at night, whereas there was no overall difference in densities between day and night either in the littoral or the pelagic zones (Figure 3).

In order to test if daphnids and ceriodaphnids in the littoral zone or the pelagial correlated with fish CPUE_n , we performed regression analysis on log-transformed data. For the NZ lakes, we found a significant negative correlation between *Daphnia* and CPUE_n in the littoral zone during day (Table 3). In the pelagial at night, there was a tendency to a negative correlation (Table 3). For *Ceriodaphnia* there was no significant correlation. Because of difficulties in comparing gill net and fyke net data, we restricted our analysis to only gill net data in the NA lakes (10 lakes). We found a weak, but not significant, negat-

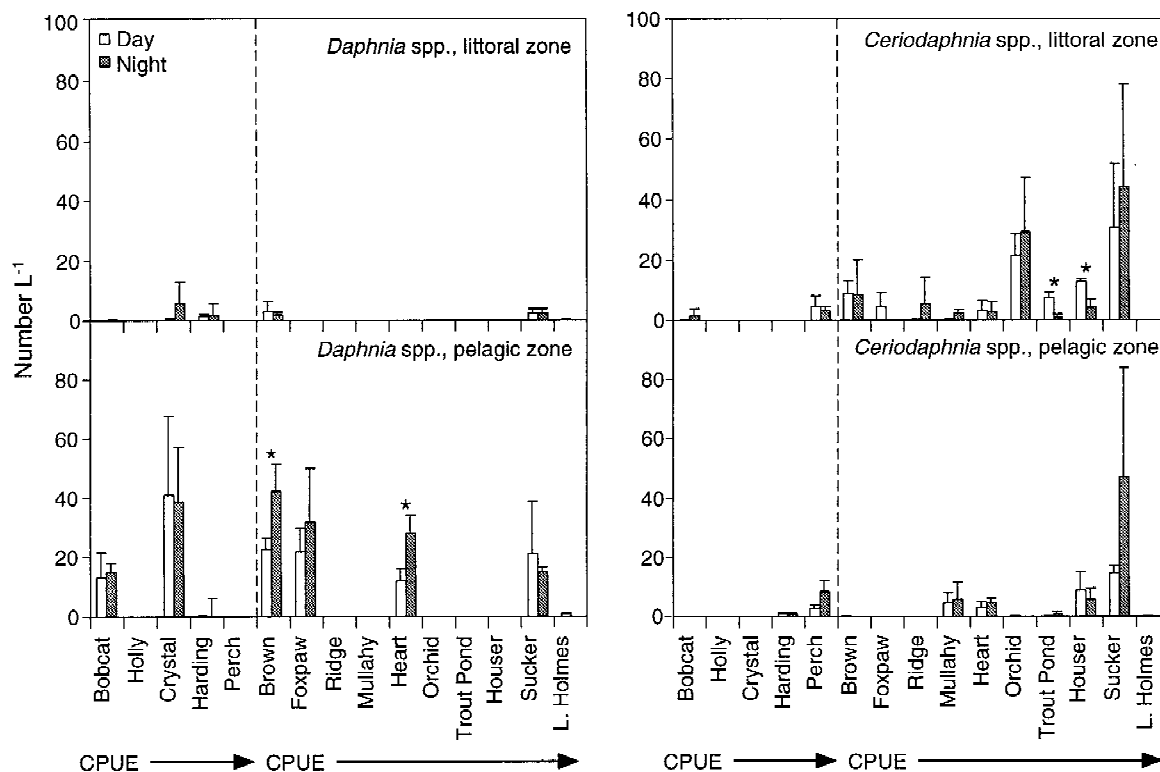


Figure 3. Day (open column) and night (dark column) densities ± 1 SD in North American lakes of *Daphnia* spp. (left panel) and *Ceriodaphnia* spp. (right panel) in both littoral (top figure) and pelagic (bottom figure) zones. The lakes are sorted according to increasing CPUE by number. Lakes at the right and left side of the vertical dashed line are lakes where fyke nets and gill nets, respectively, were used. * indicates significant statistical difference at $p < 0.05$.

Table 3. Relationships between *Daphnia* (daph) density in terms of numbers l^{-1} by day and night in the littoral (litt) and pelagic (pel) versus catch per unit effort of all fish in multiple mesh-sized gill nets in terms of numbers net^{-1} (CPUE). $N=16$ in NZ lakes, $n=10$ in NA-lakes

	Intercept		P	r^2
<i>NZ-lakes</i>				
$\log_{10} (daph+1)_{litt}$	0.69 ± 0.21	$-0.46 \pm 0.19 \log_{10} (CPUE+1)$	0.03	0.29
<i>NZ-lakes night</i>				
$\log_{10} (daph+1)_{pel}$	1.01 ± 0.37	$-0.55 \pm 0.33 \log_{10} (CPUE+1)$	0.12	0.16
<i>NA-lakes day</i>				
$\log_{10} (daph+1)_{litt}$	1.18 ± 0.48	$-0.46 \pm 0.21 \log_{10} (CPUE+1)$	0.062	0.34
<i>NA-lakes night</i>				
$\log_{10} (daph+1)_{litt}$	0.99 ± 0.48	$-0.39 \pm 0.22 \log_{10} (CPUE+1)$	0.112	0.26
$\log_{10} (daph+1)_{pel}$	2.93 ± 1.38	$-0.99 \pm 0.62 \log_{10} (CPUE+1)$	0.15	0.24

ive correlation between *Daphnia* and $CPUE_n$ for the littoral zone during day and for the littoral and pelagic zone at night (Table 3). There was no correlation

between *Ceriodaphnia* and $CPUE_n$. We did multiple regressions including also littoral macrophytes, but the contribution from macrophytes was not significant in

either the NZ or the NA lakes ($p > 0.25$ and $p > 0.2$, respectively).

Discussion

Great differences in fish CPUE by numbers existed between NZ and NA lakes despite similar total phosphorus levels. Fish CPUE_n in NA lakes was generally higher than in NZ lakes. Also, when compared with Danish lakes of similar nutrient concentrations, NA lakes showed much higher fish CPUE's. To find corresponding fish densities in Danish lakes, a TP level of 100–200 $\mu\text{g P l}^{-1}$ is required (Jeppesen et al., 1997a). The reason for the major differences in CPUE_n in the lakes reflects that the fish community in the NA lakes included a number of small species, large predatory fish occurred only in few of the investigated NA lakes. These few lakes were characterized by relatively low total fish CPUE_n's. In contrast, the fish in the NZ lakes were dominated by the large species: brown trout, rainbow trout and perch. Hence, there were no differences in CPUE by weight between NZ and NA lakes (Figure 1).

Distribution of zooplankton in NZ and NA lakes did not exhibit diel variation despite a large fish CPUE_n gradient. In the NZ lakes, we found both *D. carinata* and *C. dubia* evenly distributed between the littoral and the pelagial, and daphnids mostly confined to lakes with no or very few fish. Daphnids only rarely occurred at fish CPUE_n > 2# net⁻¹, while ceriodaphnids were found at intermediate fish CPUE's, consistent with the hypothesis that fish are size-selective in their choice of prey (Brooks & Dodson, 1965). Moreover, no clear relations between daphnids or ceriodaphnids *versus* fish CPUE existed for the NZ lakes. Nevertheless, in Jeppesen et al. (submitted) evidence is given for an impact of fish combined with nutrients on zooplankton in these NZ lakes. However, as we observed no general differences between day and night in daphnid and ceriodaphnid densities in the littoral or the pelagic zones, there is no evidence for diel horizontal migration (DHM).

In the NA lakes, data showed a very weak negative correlation between daphnids and CPUE_n. However, contrary to our expectations, we did not find DHM even in the lakes with high CPUE_n's. In addition, daphnids showed 'shore avoidance' (Hutchinson, 1967) by aggregating in the pelagial both during day and night. This is in contrast to what is found in Danish shallow, eutrophic lakes with high fish CPUE (Laurid-

sen & Buenk, 1996; Lauridsen et al., 1996; Jeppesen et al., 1997a) where large cladocerans concentrate in or near dense macrophyte beds during day and migrate to the pelagial at night. In contrast to daphnids, ceriodaphnids were found in higher densities in the littoral zone than in the pelagial during day, consistent with the expectation that *Ceriodaphnia* is a littoral-related species. However, at night *Ceriodaphnia* were found evenly distributed between the littoral zone and the pelagial, indicating that they were not highly restricted to the macrophyte-dominated nearshore area.

Potentially, several mechanisms may be responsible for the observation of 'shore avoidance' of *Daphnia* in the NA lakes at the generally high CPUE and the high macrophyte coverage in the littoral zone. Firstly, macrophyte chemicals repel daphnids (Hasler & Jones, 1949; Pennak, 1973; Lauridsen & Lodge, 1996), an effect that may, however, be counteracted by a high abundance of fish outside the plant beds (Lauridsen & Lodge, 1996). It is, however, unlikely that the repellent effect is greater than in the Danish lakes where DHM occurs. Secondly, macrophytes serve as habitat for invertebrate predators (Paterson, 1994; Kornijow & Kairesalo, 1994; Arner et al., 1998) that constitute a predation risk to large-bodied zooplankton, and this may induce aggregation of daphnids in open water. Invertebrate predators were sampled in the NA lakes as part of an ongoing comparison of invertebrate predator densities in North American and Danish lakes. Preliminary results show higher densities in the NA lakes compared to Danish lakes (R. Burks, unpubl. data). Thirdly, several of the fish species caught in the NA lakes are not strictly zooplanktivorous, but also prey on macroinvertebrates, phytoplankton, filamentous algae and higher plants (Becker, 1983). For instance bluegill, pumpkinseed and yellow perch forage in the littoral and macrophyte-covered areas (Dewey et al., 1997; Weaver et al., 1997) and also planktivorous species, such as dace, often reside in vegetated areas (Weaver et al., 1997; Gauthier & Boisclair, 1997). Consequently, the fish are not restricted to open water, but are found in macrophyte-covered areas as well. Here they constitute a predation risk to large-sized zooplankton and this may lead to 'shore avoidance' (Boikova, 1986). Fourthly, young-of-the-year (YOY) fish may be concentrated in macrophyte-covered areas either on a seasonal (Whiteside, 1988; Hall & Rudstam, 1999) or a diel basis (Gauthier & Boisclair, 1997). Any of these mechanisms or combinations thereof could be responsible for the distributions of *Daphnia* and *Ceri-*

odaphnia that we found. However, we are currently unable to evaluate these hypotheses.

When compared with the NA lakes, the lack of shore avoidance among *Daphnia* in NZ lakes is striking. However, a major difference between the two sets of lakes is the substantially higher number of fish species in the NA lakes of which several are littoral foragers that may induce shore avoidance. In the NZ lakes, the fish were evenly distributed among the two habitats, which may explain the more even distribution of *Daphnia* observed in NZ lakes. Another major difference between the two sets of lakes is water clarity. The NA lakes had higher chlorophyll *a* (Table 1) and many were also coloured by humic substances (range of 3–22 mg l⁻¹ DOC, unpubl. data), while most of the NZ lakes were clear with Secchi depths reaching the lake bottom. In accordance with experiences from northern Swedish lakes (Nilsson & Pejler, 1973), differences in transparency may help explain both why daphnids occurred at higher fish densities in the oligotrophic/mesotrophic NA lakes and why they were abundant in the open water in those lakes. In addition, daphnids in the NA lakes were transparent where daphnids in the NZ highland lakes were highly pigmented, which also enhances the predation risk in these clear water lakes (Sægrov et al., 1996).

Our results, which showed either no diel migration of *Daphnia* and *Ceriodaphnia* between the littoral and the pelagial or 'shore avoidance' by *Daphnia* (but never pelagial avoidance) in a number of oligo- and mesotrophic lakes, are in accordance with other observations from NA shallow lakes (Smiley & Tessier, 1998). They contrast, however, observations from eutrophic lakes in Northern Europe, which show major daytime aggregation in the littoral zone. The results are in accordance with a tentative model developed by Jeppesen et al. (1998), who argued that submerged macrophytes may be a less efficient refuge in the littoral zone in oligo- and mesotrophic lakes because the macrophyte beds in these lakes are often less dense compared to eutrophic lakes. Although in several of the investigated lakes, macrophyte coverage was high, macrophyte density in the water column (PVI, according to Canfield et al., 1984) was not particularly high because the macrophyte communities typically consisted of small species such as characeans, *Najas* and *Potamogeton pusillus*, with few taller macrophytes growing in-between. Density seems to be a critical factor for the efficiency of the beds as a zooplankton refuge (Jeppesen et al., 1997a; Stansfield et al., 1997). In addition, the proportion of piscivores is higher in

mesotrophic lakes than in eutrophic lakes, which may enhance migration of young planktivorous fish into the vegetation, thereby increasing the predation on hiding zooplankton (Jeppesen et al., 1998).

The results of this study showed no DHM in shallow oligo-mesotrophic lakes, which contrasts with results from shallow eutrophic lakes. We encourage further studies of this issue to elucidate, in particular, how the role of invertebrate predators, the importance of plant bed density and composition, and the effects of the interactions among macrophytes, planktivorous and piscivorous fish change along a nutrient gradient.

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