

# Movement of plankton through lake-stream systems

D. J. WALKS AND H. CYR

Department of Zoology, University of Toronto, Toronto, ON, Canada

## SUMMARY

1. River plankton are often assumed to come from upstream lakes, but the factors controlling the movement of plankton between lakes and rivers into outflow streams are unclear. We tested the possibility that the physical structure of the littoral zone near the lake outlet (depth, presence of macrophytes) and diurnal differences in plankton composition at the lake surface influence the movement of plankton from the lake into the stream and determine their persistence downstream.

2. Zooplankton and phytoplankton biomass, community composition and mean body size were compared between two deep lakes without macrophytes at the lake edge and two shallow lakes with macrophytes at the lake edge. Samples were collected day and night on three dates, in the lake centre, in the littoral zone adjacent to the lake outlet, at the outlet and at two sites downstream in Algonquin Park, Ontario, Canada.

3. The morphology of lake edges clearly affects the movement of lake zooplankton into outlet streams. Outlets draining deeper littoral zones had higher zooplankton biomass than shallow littoral outlets ( $P < 0.0001$ ), but these differences disappeared within 50 m downstream of the lake. There was no difference in mean zooplankton body size among lake outlets or between littoral and outlet samples. However, shallow littoral zones were dominated by cyclopoid copepods and deeper littoral zones were dominated by *Bosmina longirostris*. In contrast, phytoplankton biomass entering the outlet was similar to that found within the lake and did not vary with lake outlet morphology. These effects were consistent across several sampling weeks and were not affected by surface zooplankton biomass changes associated with diurnal vertical migration in the lake centre.

4. A comparison with published river zooplankton data suggests that zooplankton are rapidly eliminated from shallow outlet streams ( $\leq 1$  m deep) but persist in most deeper outlet rivers ( $\geq 2$  m deep). Because the depth of an outlet river determines downstream zooplankton community development, the contribution of lakes to river plankton communities may be influenced by the location of each lake within the drainage basin. These findings suggest that lake and outflow physical structure influences connection strength between spatially successive habitats.

*Keywords:* catchment morphology, lake outlets, lentic–lotic interface, macroinvertebrates, plankton

## Introduction

Whereas plankton and other suspended material in lake outflow water are thought to be high-quality food for river organisms (Elliot & Corlett, 1972; Malmqvist

& Bronmark, 1984; Richardson, 1984), it is not known what determines the degree to which lake plankton enters outlets, or what controls how far downstream the material and energy from a lake persist. In aquatic systems, where rivers typically exist as highly branched networks and often include lake and wetland inputs, we do not know how the presence of more or fewer lakes (connections), or how their connection strengths (the degree to which material

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Correspondence: D. J. Walks, 246 Albany Ave, Toronto, Ontario Canada M5R 3C8. E-mail: dwalks@sympatico.ca

and energy is transferable between them) might affect downstream processes. How a connection between different types of habitat functions to control material and energy flow through a landscape (Wiens, Crawford & Gosz, 1985), depends on the physical structure of the connection and how this structure scales with respect to different organisms (Puth & Wilson, 2001). The connection point between a lake and a river, where lake outflow becomes river inflow, represents a sudden alteration in physical habitat for organisms that generally dwell in the lake. Similar abrupt changes can occur along rivers through, for example, riffle-pool sequences, which cause organisms to experience habitat as patchy or heterogeneous. These changes along the river corridor also affect the downstream progression of material and energy (Statzner & Borchardt, 1994; Ward & Stanford, 1995). Questions of connection strength between different aquatic habitats and downstream persistence of populations along natural corridors are fundamental to enlarging our understanding of the river continuum to a landscape scale, incorporating lakes and wetlands into catchment networks (see e.g. Vannote *et al.*, 1980). Such a landscape context is crucial to understanding the origin of river plankton and what sustains them in their highly advective environment.

Two hypotheses, not mutually exclusive, explaining the origin and development of river plankton require that strong connections exist in catchment networks, both between lakes and rivers, and between river habitat units. One hypothesis states that river plankton communities develop within rivers, generally occurring in long rivers where organisms have enough time to grow and reproduce as they are moved downstream (Margalef, 1960; Pace *et al.*, 1992; de Ruyter van Steveninck *et al.*, 1992; Kohler, 1993; Basu & Pick, 1995, 1996). This hypothesis suggests that planktonic river habitat operates as a corridor where zooplankton density accumulates downstream through links between habitat patches. Thus, headwaters are expected to contain fewer plankton than downstream. As river plankton has been found in small headwaters, ideas are still emerging as to the mechanisms controlling their in-stream development (see Reckendorfer *et al.*, 1999; Reynolds, 2000; Walks, 2003) and downstream persistence (see Speirs & Gurney, 2001).

The other major hypothesis states that lake outlets are primary sources of river zooplankton (Brook &

Rzoska, 1954; Rzoska, Brook & Prowse, 1955; Talling & Rzoska, 1967; Winner, 1975; Shiel, Walker & Williams, 1982; Saunders & Lewis, 1988; Telesh, 1995; Kobayashi, 1997). The lake-outlet hypothesis assumes that plankton can move safely between the two different types of habitat. The circumstances under which river plankton has lake origins are still unclear. Conflicting evidence has found lake plankton abundance to either decrease downstream from the lake outlet (Chandler, 1937; Armitage & Capper, 1976; Sandlund, 1982; Jann & Burgi, 1988; Welker & Walz, 1998) or not decrease (Cushing, 1963; Basu, Kalff & Pinel-Alloul, 2000a), and few studies have actually compared outlet plankton to upstream lake plankton (but see Cushing, 1963; Jann & Burgi, 1988; Akopian, Garnier & Pourriot, 1999; Basu *et al.*, 2000a). Macrophytes (Chandler, 1937; Basu, Kalff & Pinel-Alloul, 2000b) and predation (Richardson & Mackay, 1991; Akopian *et al.*, 1999; Eriksson, 2001) have both been implicated in reducing plankton downstream from lake outlets. Examining the factors that affect plankton moving from lakes to rivers and their downstream persistence will help elucidate the mechanisms that can affect connection strengths within catchments.

The physical structure of the lake edge near the outlet, including depth and the presence of macrophytes, has the potential to alter the biomass and community composition of plankton entering the outlet. Macrophytes decrease the downstream movement of zooplankton in streams by reducing water velocity and increasing the heterogeneity of flow passing through the macrophyte bed (Chandler, 1937; Dodds & Biggs, 2002). Flow through a macrophyte bed would be more heterogeneous because friction associated with each plant's surface area will distribute slower velocities throughout the macrophyte bed (see Vogel, 1981; Knighton, 1998). This heterogeneity of currents might also allow for better avoidance of faster currents because many plankton can detect and respond to changes in current speed (Kaartvedt, 1993). At similar water velocities, larger cladocerans and copepods are better able to avoid being washed out than smaller crustaceans (nauplii, copepodites) and rotifers (Sandlund, 1982; Richardson, 1992). Along this gradient it is expected that phytoplankton is least able to avoid becoming entrained. Thus, the physical structure of the lake edge is expected to affect mean body size and taxonomic composition of plankton, in addition to biomass, entering the lake outlet.

Lake plankton entering an outlet move from one habitat type to another and thus physical habitat similarities between the outlet and the lake, as well as biotic factors such as predation, may play a role in determining its downstream persistence. Deep, slower moving outlets may function differently from a shallow rapid. Downstream survival or movement of lake zooplankton in rivers has been shown to decrease because of the presence of dense macrophyte beds within the river (Chandler, 1937; Hamilton *et al.*, 1990; Basu *et al.*, 2000b), physical damage or destruction within riffles and cascades (Ward, 1975), and by predation by benthic macroinvertebrates, such as passive filter feeders (e.g. Richardson & Mackay, 1991) and actively filtering mussels (Welker & Walz, 1998). Controls on the downstream development of river plankton communities, therefore, may be directly related to the physical habitat and morphology of the stream with respect to the availability of refugia from swift currents, rapids and from potential predators.

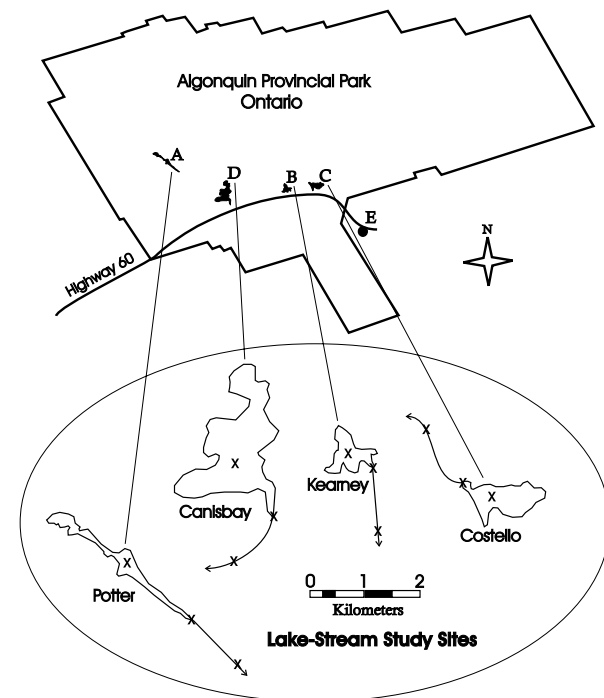
Changes in densities at the lake outlet could also vary throughout the day because of behaviours such as shoreline avoidance (Gliwicz & Rykowska, 1992; Wicklum, 1999) and diurnal vertical migration (e.g. Jann & Burgi, 1988). These behaviours could alter zooplankton composition and biomass within the surface waters of the lake edge, effects which may be conveyed downstream.

In this study, we compare diurnal plankton movement from lakes into outlets and downstream, between lakes with shallow (high structure) versus deep (low structure) littoral zones, in order to test: (i) whether the structure of the littoral zone (depth, macrophytes) is related to the biomass, size structure and taxonomic composition of plankton washed into the lake outflow; (ii) whether the taxonomic composition of zooplankton in the littoral zone influences the plankton composition that enters the outflow; (iii) the influence of diurnal patterns in zooplankton biomass on lake outlet biomass and downstream persistence; and (iv) whether the downstream movement and persistence of plankton differs between small and large outlet rivers. Small lake-outlet systems were selected in order to study non-dammed outlets within close proximity of each other to control for geological or other larger-scale effects; however, we compare our results to those from larger systems in the discussion.

## Methods

### Study sites

Four lake-stream systems located in Algonquin Provincial Park, Ontario, Canada were studied (Fig. 1). All systems had similar geophysical characteristics (calcareous sandstone or granite, MNR map 1979), outflow discharges ( $0.2\text{--}0.3\text{ m}^3\text{ s}^{-1}$ ), and riparian vegetation (mixed deciduous). Lakes were selected to have either a deep (3–3.5 m) or a shallow (1–1.2 m) littoral zone in the area adjacent to the outlet, as measured 50 m from the outlet (Table 1). Both shallow littoral zones had dense submergent and emergent macrophyte cover, whereas the deep littoral zones had open water right up to the outlets. All outflows had relatively similar velocity ( $10\text{--}16\text{ cm s}^{-1}$ ) and morphology (Table 1).



**Fig. 1** Lake-stream sampling locations in Ontario, Canada. Potter (A) and Kearney (B) lakes have deep littoral zones adjacent to the outlet ( $>3\text{ m}$ ), and Castello (C) and Canlsbay (D) lakes have shallow littoral zones ( $<1\text{ m}$ ). Gailaery lake (E) is dammed. Surface water sampling locations (X) for each lake are given showing lake centre, outlet and 1 km downstream. Because of map scale, the littoral zone site (50 m from outlet) and 50 m downstream from outlet are grouped with outlet sites. All lakes and outlet streams shown to scale.

Parameter	Potter	Kearney	Costello	Canisbay
Pelagic depth (m)	13.0	12.5	18.0	10.0
Littoral zone depth (m)	3.5	3.0	1.3	1.2
Outflow sill depth (m)	0.1	0.1	0.03	0.1
Sampling Dates				
Day, Night 1	July 23, 24	July 14, 20	July 13, 16	July 15, 21
Day, Night 2	July 29, 30	July 24, 25	July 27, 28	July 26, 27
Day, Night 3	August 6, 8	August 4, 1	August 7, 9	August 5, 2

**Table 1** Morphology and sampling schedule of four lake-outlets sampled in 1999. Littoral zone depth was measured 50 m from the outlet. Pelagic depth was measured in the centre of the lake. All depths were measured where samples were collected

### Sampling

Each site was sampled three times mid-day and three times mid-night in July and August 1999 (Table 1). Triplicate zooplankton and algal samples were collected from each lake at the centre, 50 m from the lake outflow (littoral zone), and at the outflow sill (Fig. 1). On the last daytime visit to each site, samples were also collected at 50 m and 1 km downstream from the outflow (Fig. 1).

Zooplankton was collected by filtering 40 L of water, pumped from just below the water surface using a bilge pump (rate =  $0.63 \text{ L s}^{-1}$ ) into a Wisconsin net (WildCo, Saginaw, MI, U.S.A.), mesh size  $65 \mu\text{m}$ , in order to keep sampling consistent between lake and stream sites (e.g. Pace, Findlay & Lints, 1991; Basu & Pick, 1996). Despite the fact that the shallower littoral zones had more macrophytes than the deeper ones, care was taken to sample well away from macrophytes in order to collect true planktonic organisms. In the stream, care was taken to ensure that the bottom was not disturbed during the pumping procedure in order to collect organisms in the water column only. Approximately one-third of a 3 g antacid tablet was added to each sample and allowed to dissolve until the zooplankters visibly slowed down (Haney & Hall, 1973; Prepas, 1978). The sample was then re-filtered and preserved with 95% ethanol. Algae were collected by pumping water into 1 L dark bottles, which were stored on ice. Triplicate algal samples were filtered the same day onto GF/F filters and frozen at  $-10 \text{ }^\circ\text{C}$ .

### Short-term temporal variability in zooplankton density at outlets

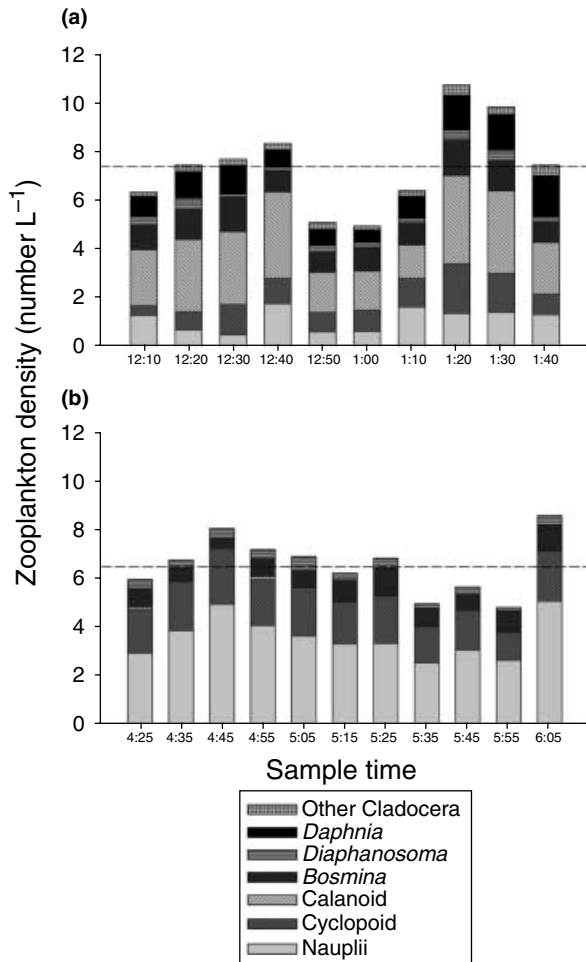
We determined the variability of zooplankton inputs at lake outlets over a 2-h window. This 2-h window was selected because at mean measured flow rates ( $13 \text{ cm s}^{-1}$ ) outlet water would take approximately 2 h

to reach the 1 km downstream sample site. For the purpose of collecting samples from downstream of the outlet, how exact to make the timing of the collections had to be known in order to be sampling a similar water mass as it moved downstream. Short-term variability in zooplankton density was measured in two lake outlets (Fig. 1). These lake outlets were selected in order to span a broad a range of flows; however, Gailaery, being artificially dammed, was not used for the other parts of this study. Costello was selected as a low-flow outlet and Gailaery as a higher-flow outlet (although flow not measured in Gailaery, all lake-outlets had lower flow than Gailaery on all sampling dates) in order to determine if variability in zooplankton density was affected by stream discharge. Single 40 L samples were collected every 10 min. and counted following procedures described below.

Zooplankton density and taxonomic composition entering lake outlets were fairly homogeneous between samples collected every 10 min. over the course of 1.5–2 h in the two lake-stream systems examined (Fig. 2). The coefficient of variation (CV) in mean crustacean zooplankton density for Gailaery lake was 0.08 and for Costello was 0.05. The coefficient of variation for each taxonomic group ranged from 0.07 to 1.0 in Gailaery outflow, and from 0.05 to 0.67 for Costello outflow. Large CVs ( $>0.1$ ) were found for taxa that were especially rare ( $<0.1 \text{ L}^{-1}$  individuals or absent in many samples). Short-term variability in zooplankton density among outlet samples within one lake was far less than differences observed between study lakes or between sampling locations within each lake (e.g. Fig. 5).

### Zooplankton

Zooplankton subsamples were counted using a dissecting microscope at  $40\times$  magnification until at least 100 organisms were counted of each taxon, except for rare taxa ( $<100$  per sample) which were enumerated



**Fig. 2** Short-term variability in zooplankton density and taxonomic composition in samples collected in the outflow of (a) Gailaery (mean =  $7.4 \mu\text{g L}^{-1}$ , CV = 0.08) and (b) Costello (mean =  $6.5 \mu\text{g L}^{-1}$ , CV = 0.06) lakes. Mean total zooplankton densities for each lake outflow are shown with dashed lines.

by counting the entire sample. Copepod zooplankton were identified as either calanoid, cyclopoid, or nauplii. Cladoceran zooplankton were identified to genus (Pennak, 1989; Thorp & Covich, 1991). In order to determine mean body size, 30 organisms of each taxon per sample, or all of rare taxa, were measured using an image analysis system calibrated against a stage micrometer. Zooplankton dry-weight biomass was calculated using length-mass equations (Dumont, Van de Velde & Dumont, 1975; Bottrell *et al.*, 1976).

### Phytoplankton

Phytoplankton biomass was measured as chlorophyll *a* concentration. Pigment extraction was carried out

within 4 months of sample collection. Filters were ground with warm 90% ethanol and allowed to extract overnight at room temperature in the dark (Marker *et al.*, 1980). Pigment extraction after heat shock is more efficient than cold extraction (Nusch, 1980). Samples were centrifuged at 5500 rpm (3400g) for 15 min or until the absorbance at 750 nm was  $<0.1$  (a measure of turbidity). Absorbances at 665 nm were measured on a Spectronic 1001+ spectrophotometer ( $\pm 2$  nm wavelength accuracy) using a 10 cm cuvette. Chlorophyll *a* measurements were corrected for phaeopigments by adding a few drops of 2 N HCl and reading changes in absorbance after 2 min. Chlorophyll *a* and phaeopigment concentrations were calculated using the equations of Lorenzen (1967).

### Statistical analysis

We compared outflow zooplankton biomass ( $\mu\text{g L}^{-1}$ ), mean body size ( $\mu\text{g}$  dry weight) and outlet chlorophyll *a* concentration ( $\mu\text{g L}^{-1}$ ) from the two deep littoral zone lakes with no macrophytes (DEEP) and the two shallow littoral zone lakes with macrophytes (SHALLOW), at night and in the day using a two-way ANOVA (Statgraphics Plus v2.0, 1996; Manugistics, Rockville, MD, U.S.A.), with replicate and date as repeated measures. All analyses were performed on  $\log_{10}$  transformed data to equalize variances. Alpha values were corrected for multiple tests using the Bonferroni correction ( $\alpha/\text{no. tests}$ ) (Zar, 1984).

Zooplankton community composition was compared between DEEP and SHALLOW littoral zones using discriminant function analysis (type III sum of squares) on taxon percent biomass data (Sokal & Rohlf, 1981, p. 685) that had been transformed (square root [ $\text{ArcSin}(x)$ ]) to standardize for community composition rather than differences in biomass between samples. This same test was used to compare zooplankton community composition in DEEP littoral versus DEEP outlet samples to determine if specific taxa entered the outlet more frequently than others. The littoral and outlet community composition of SHALLOW lake-outlets could not be compared because of the low numbers of organisms entering SHALLOW outlets.

Downstream changes in plankton biomass and mean body size were tested using one-way ANOVA. Because the entire lake-stream system was only sampled on the final visit, the first two visits to each site were excluded from this analysis.

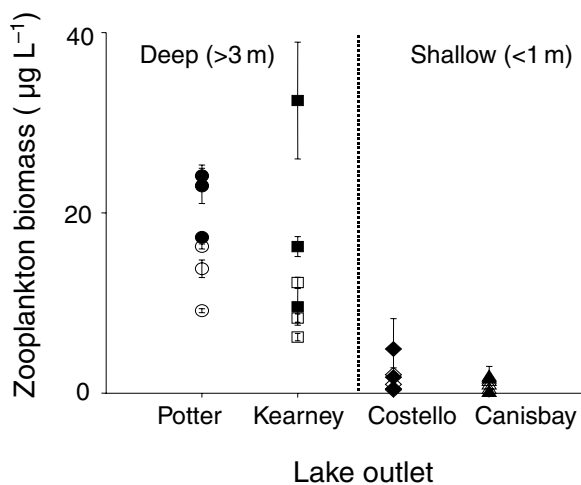
## Results

### Zooplankton

Outlets draining deep, open littoral zones contained higher zooplankton biomass (ZB,  $\mu\text{g}$  dry weight  $\text{L}^{-1}$ ) than outlets flowing from shallow littoral zones with macrophytes (Table 2,  $P < 0.0001$ ; Fig. 3). All of the major taxa (Cyclopoid, copepod nauplii, *Bosmina longirostris* (O.F. Mueller), *Diaphanosoma*, *Daphnia*) showed the same pattern ( $P < 0.0001$ ). A repeated measures ANOVA showed that both replicates ( $P = 0.63$ ) and dates ( $P = 0.44$ ) were not significantly different, thus they were used as replicates in all analysis. Four samples of a total of 72 outlet samples were not able to be used in the analysis. The difference

**Table 2** Comparison of zooplankton biomass in the outlets of lakes with shallow and deep littoral zones, at night and during the day. Depth coded as either shallow or deep, time coded as day or night

Source	Sum of Squares	d.f.	Mean square	F-ratio	P-value
Depth	30.0	1	30.0	141.0	<0.0001
Time	0.3	1	0.3	1.6	0.2
Interaction	0.2	1	0.2	0.8	0.4
Residual	13.6	64	0.2		
Total	44.1	67			



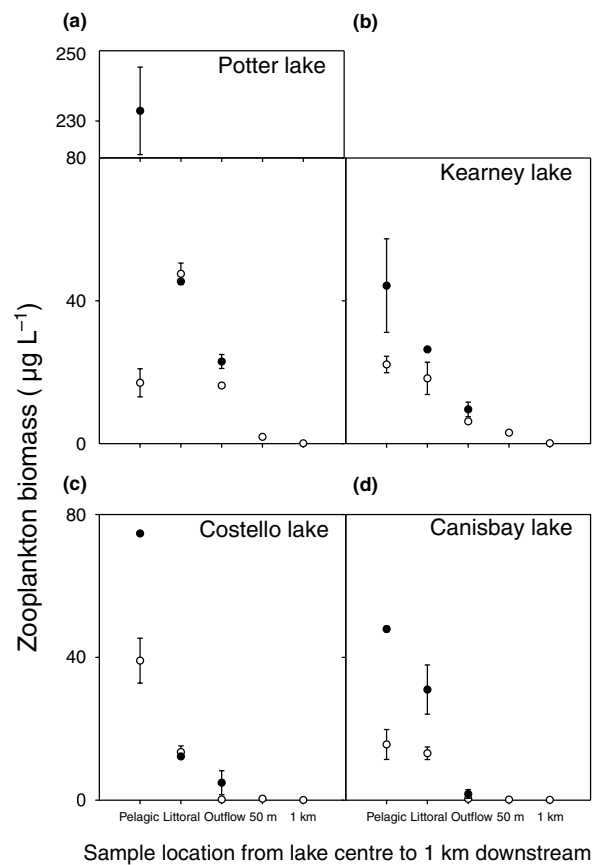
**Fig. 3** Zooplankton biomass at lake outlets in day (open symbols) and night (closed symbols) samples. Potter and Kearney lakes have deep littoral zones without macrophytes and Costello and Canisbay lakes have shallow littoral zones with dense macrophytes. Error bars are standard errors of three replicates.

between shallow and deep outlets was consistent during the day and at night (Table 2).

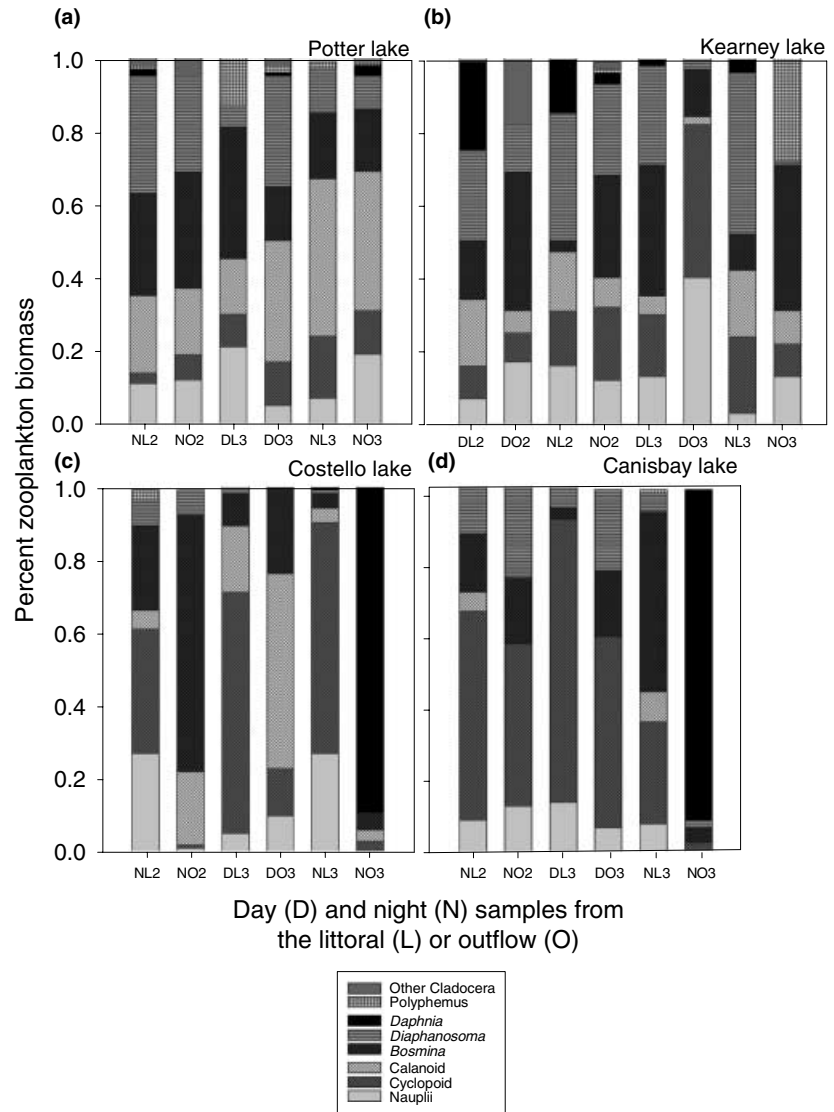
In both SHALLOW and DEEP systems, zooplankton was virtually eliminated within 50 m downstream (Fig. 4). At 50 m and again at 1 km downstream there was no difference in zooplankton biomass between streams draining from deep or shallow littoral zones (one-way ANOVA, d.f. = 11,  $P = 0.05$ ,  $P = 0.30$ , respectively; Fig. 4).

We found no significant difference between day and night zooplankton biomass at lake outlets (two-way ANOVA, d.f. = 67,  $P = 0.35$ ; Fig. 4) or within littoral zones (one-way ANOVA, d.f. = 35,  $P = 0.32$ ; Fig. 4), despite clearly higher night-time biomass in the pelagic area of lakes (one-way ANOVA, d.f. = 24,  $P = 0.006$ ; Fig. 4).

The community composition of zooplankton differed between deep and open, versus shallow and



**Fig. 4** Day (open circles) and night (closed circles) mean zooplankton biomass from lake-outlet transects (from lake centre through to 1 km downstream of outlet). Error bars are standard errors of three replicates. Potter Lake had one extreme value, which is shown by breaking and elongating the y-axis.



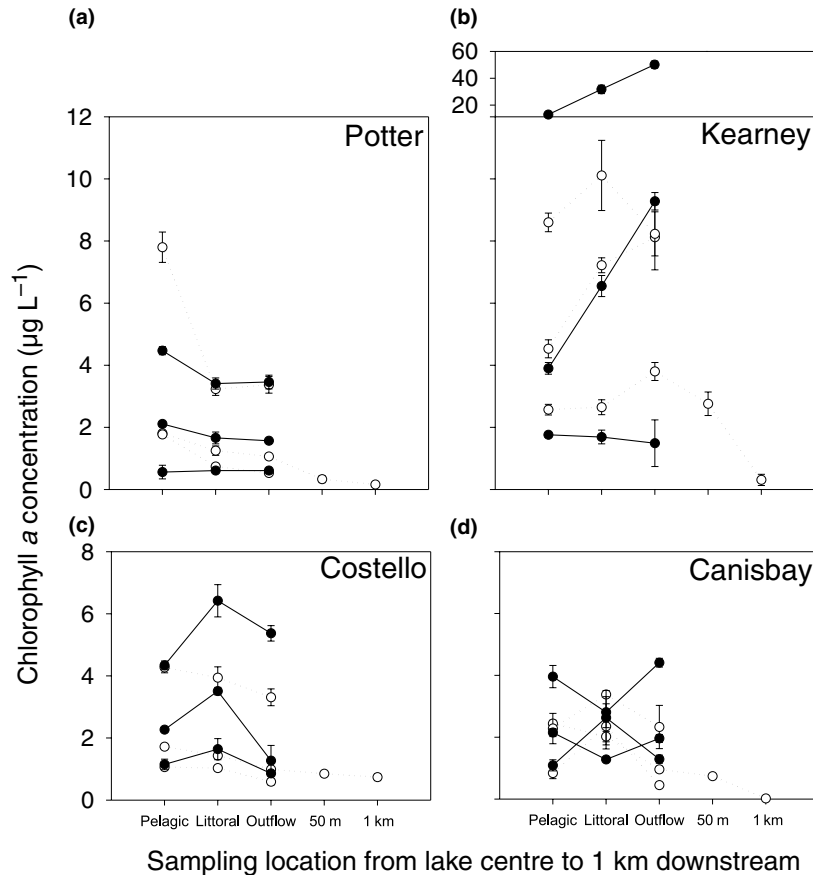
**Fig. 5** Taxonomic composition of littoral (L) and outflow (O) sites by proportion of total biomass for day (D) and night (N) samples in all four lakes. Data from three sampling dates are given for Potter, Costello and Canisbay lakes and four dates for Kearney lake (see Table 1 for dates). Note that very few organisms were collected from the outlets of Costello and Canisbay Lakes (see Fig. 3).

macrophyte-rich littoral zones (discriminant function analysis: overall  $P = 0.0001$ ,  $r^2 = 0.85$ ; Fig. 5). Deep littoral zones had higher relative percent biomass of *Bosmina* ( $P = 0.04$ ) and shallow littoral zones contained more cyclopoid copepods ( $P = 0.002$ ). *Daphnia*, *Diaphanosoma*, *Polyphemus*, *Leptodora*, *Holopedium*, nauplii and calanoid copepods made up a similar percentage of the total biomass between the two systems (Fig. 5). Copepod nauplii made up approximately the same percentage of DEEP and SHALLOW littoral zone zooplankton biomass (11–14%; Fig. 5).

The community composition of zooplankton entering outlets from deep littoral zones did not differ from that seen within the adjacent littoral zone (discrimi-

nant function analysis: overall  $P = 0.21$ ,  $r^2 = 0.05\%$ ; Fig. 5). There were not enough organisms found at the SHALLOW outlets to compare community composition between shallow littoral zones and their outlets.

Mean body weight ( $\mu\text{g}$  dry weight) of zooplankton organisms (including nauplii) did not differ between DEEP and SHALLOW littoral zones (d.f. = 35,  $P = 0.16$ ). This result was consistent in day and night sampling, and was not affected by the removal of copepod nauplii from the calculation of mean weight. Mean zooplankton body size, with or without nauplii, did not change systematically from the littoral zone to 1 km downstream in either the DEEP lakes ( $P > 0.05$ ) or the SHALLOW lakes ( $P > 0.05$ ).



**Fig. 6** Mean phytoplankton biomass in day (open circles) and night (closed circles) for all sampling locations, dates and lakes. Error bars are standard errors of three replicates. Note break in scale on *y*-axis for Kearney Lake.

### Phytoplankton

Phytoplankton biomass was generally low at all sites ( $<10\mu\text{g L}^{-1}$ ) and did not differ between SHALLOW and DEEP lake-stream outlets in the day or night (two-way ANOVA, d.f. = 71,  $P = 0.14$ ; Fig. 6). Phytoplankton biomass was significantly lower 1 km downstream of the outlet than in the outlet, but was not significantly lower at 50 m (Fishers LSD contrast, d.f. = 11,  $P < 0.0001$ ; Fig. 6). Phytoplankton in Kearney lake varied the most dramatically, with a large increase in phytoplankton biomass on the second nighttime sampling occasion on 24 July (Fig. 6).

### Discussion

#### *The movement of zooplankton and phytoplankton from lakes into outlets*

The connection strength between a lake and outlet stream is highly dependent on the physical structure of the adjacent littoral zone. Outlets flowing from

shallow, high-structure littoral zones contained almost no zooplankton, whereas those flowing from deep, open littoral zones had much higher zooplankton biomass. This effect was seen on each of the six visits to each lake and was not affected by differences in zooplankton biomass within the littoral zone of the lake, or by large changes in zooplankton biomass in surface pelagic waters that could have been associated with diurnal vertical migration. Winds can affect plankton distribution within lakes (Hart, 1978) but are not likely to be the cause for the observed effect because the littoral zone biomass was not higher in the two deep as compared with the two shallow littoral zone lakes. These results are consistent with findings that in-stream macrophyte beds cause downstream decreases in plankton densities (Chandler, 1937; Brook & Woodward, 1956; Beach, 1960), and with results from the large lake-outflows in the St Lawrence River where relatively little lake plankton production was exported into the river through macrophyte beds (Basu *et al.*, 2000b).

Interestingly, the pattern of less zooplankton wash-out from shallow littoral zones than from deep littoral zones is not replicated in the phytoplankton data. Macrophytes add structure and increase the heterogeneity of currents near the outlets. Because zooplankton can detect currents and modify their swimming behaviour accordingly (Richardson, 1992; Kaartvedt, 1993), macrophyte beds in shallow littoral zones may decrease washout of zooplankton into outlet streams by increasing small-scale flow refugia around individual plants. The fact that there was no difference in chlorophyll *a* among the four outlets studied, but all zooplankton taxa, including copepod nauplii, were able to avoid entering the outlets draining shallow, macrophyte-rich littoral zones, may be related to differences in behaviour between zooplankton and phytoplankton in detecting and responding to currents. The potential for macrophyte beds to reduce downstream movement of zooplankton was also noted by Chandler (1937), who called it 'straining' by macrophytes. Basu *et al.* (2000a) reported that very little zooplankton and phytoplankton produced in Lake Ontario was found downstream of the macrophyte beds at the outlet to the St Lawrence River. However, because these decreases were measured 90 km downstream of the outlet, in-stream effects of filter-feeders were also implicated in the decrease.

The fact that the shallow littoral zones were dominated by cyclopoid copepods may have influenced some of the difference in zooplankton biomass observed in outlets adjacent to shallow versus deep littoral zones. Cyclopoid copepods were found to better avoid washout (Richardson, 1992) than cladocerans; so in shallow littoral zones it is possible that cyclopoid copepods are avoiding the outlet. In terms of percent relative biomass, fewer cyclopoids entered the outlet than were present in the adjacent littoral zone of both the shallow lake systems, but so few organisms were found within the outlets of the shallow systems that no conclusion can be drawn about the potential of cyclopoids to avoid these outflows. However, all zooplankton taxa in the deeper littoral zones were found to enter the outlet equally, including cyclopoid copepods, thus in these systems they were not better at avoiding washout than cladocerans.

Lake edge structure and the presence of macrophytes clearly can affect the export of lake plankton into outflow streams as demonstrated both in this study and for Lake Ontario's outlet (Basu *et al.*, 2000b). These

findings suggest that lake-river connection strength is controlled by physical structure and the associated differences in current flows within the littoral zone adjacent to the lake outlet, and that this physical structure can be affected by biotic processes such as the growth of macrophytes. Macrophytes appear to alter downstream movement of motile plankton far more than non-motile organisms and other matter. For example, there was no change in bacteria or flagellate abundance and no change in dissolved organic carbon or total phosphorous downstream of Lake Ontario, although chlorophyll *a* and zooplankton decreased (Basu *et al.*, 2000a). Therefore, differences in lake outlet physical structure because of macrophyte beds do not affect all components of the food web equally.

Lake outlets have often been shown to be important sources of high-quality food for benthic organisms in outlet rivers (Elliot & Corlett, 1972; Bronmark & Malmqvist, 1984; Malmqvist & Bronmark, 1984; Richardson, 1984; Richardson & Mackay, 1991). If the export of high-quality food to lake outlet streams is controlled by macrophytes and not by the depth of the littoral zone then seasonal differences in this spatial food subsidy to outlet streams would also be expected.

Our results suggest that benthic organisms in outlet streams flowing from deeper, low-structure, littoral zones may receive a larger subsidy of high-quality food (plankton) than is exported to outlet streams from shallow, high-structure, littoral zones (see e.g. Polis, Anderson & Holt, 1997). Therefore, streams may differ in their secondary productivity (growth of macroinvertebrates, fish, etc.) depending on upstream physical structure and the type and frequency of connections existing within the catchment.

#### *Persistence of zooplankton and phytoplankton downstream from lakes*

While littoral zone characteristics play an important role in determining the input of lake zooplankton into outlet streams, they did not influence the downstream persistence of plankton in these small streams. In all lake-streams examined, zooplankton biomass was virtually eliminated by 1 km downstream, although a higher biomass of zooplankton 'founded' outlet stream communities flowing from deep, low-structure littoral zones. Chlorophyll *a* also decreased downstream from the lake outlet, although not as rapidly as zooplankton biomass. The observed decrease in

zooplankton within the first 50 m after the outlet is likely because of filter feeding by high densities of hydropsychid and philopotamid caddisfly (Trichoptera), *Simulium* (Diptera), and *Rheotanytarsus* (Chironomidae, Diptera) larvae observed at these sites (filter feeder density up to 1900 individuals m<sup>2</sup>, mean = 900 individuals m<sup>2</sup>, Walks, 2003). Predation by filter feeding macroinvertebrates has often been implicated in downstream decreases of lake plankton in rivers (Sheldon & Oswood, 1977; Oswood, 1979; Malmqvist & Bronmark, 1984; Richardson, 1984; Wotton, 1984; Richardson & Mackay, 1991; Carter, Taylor & Tudorancea, 1995). These macroinvertebrates can filter particles ranging from <0.1–350 µm (*Simulium*) to 53–432 µm (*Hydropsyche*) (Wotton, 1994). As benthic filter feeders are present throughout these outlet streams (D. J. Walks & H. Cyr, personal observation), they are probably also implicated in the continued decrease in zooplankton biomass from 50 m to 1 km downstream of the lake.

Some of this decrease in zooplankton density and biomass downstream of lakes could also be due to dilution of the initial concentration entering the outlet by the addition of water to the river through tributaries or groundwater. In the four study systems there

were no tributaries entering any of the streams within the study area and discharge did not visibly increase although small groundwater inputs are possible. However, it is unlikely that sufficient water inputs were present within the first 50 m from the lake outlet to account for the dramatic decreases in zooplankton as observed.

Studies of larger river systems have reported the persistence of lake assemblages much further downstream than found in this study (e.g. Brook & Rzoska, 1954; Rzoska *et al.*, 1955; Cushing, 1963; Talling & Rzoska, 1967; Shiel *et al.*, 1982; Saunders & Lewis, 1988; Kobayashi, 1997; Welker & Walz, 1998; Basu *et al.*, 2000a) suggesting that downstream persistence of lake plankton may be related to river size. Published lake-outlet zooplankton data that measured zooplankton densities (no. L<sup>-1</sup>) in a lake outlet and at downstream sites (Table 3) were used to test the effect of river size on downstream persistence of zooplankton. In all instances where multiple samples were reported, the sampling time closest to 31 July was selected because it was the median date of collection for this study. Only crustacean data were used, except in two studies where rotifers were included in the zooplankton densities reported (Table 3). Outlet

**Table 3** Lake-outlet characteristics, methodological details and source of data sets to compare changes in downstream zooplankton densities in rivers worldwide. Data sources are: 1. Armitage & Capper (1976); 2. Basu *et al.* (2000a); 3. Chandler (1937); 4. Cushing (1963); 5. Jann & Burgi (1988); 6. Sandlund (1982); 7. Welker & Walz (1998); 8. This study

Lake	River	Country	No. of sampling sites	Transect length (km)	Sample date (closest to 31 July)	Mean discharge (m <sup>3</sup> s <sup>-1</sup> )	Outlet depth (m)	Symbol in Fig. 7	Source
Canisbay	Canisbay	Canada	3	1.0	5 August 1999	0.01	0.1	▽	8
Costello	Costello	Canada	3	1.0	7 August 1999	0.1	0.1	●	8
Cow Green Reservoir*	Tees	U.K.	6	6.5	6 August 1973	1.1	1.0	▲	1
Douglas	Maple	U.S.	5	2.6	28 October 1932	0.1	0.2	◇	3
Egg	Montreal	Canada	3	10.0	1 August 1960	0.9	2.5	▼	4
Griffenensee	Glatt	Switzerland	2	0.06	28 July 1986	2.4	0.5	○	5
Kearney	Kearney	Canada	3	1.0	4 August 1999	0.02	0.0	○	8
Lancaster	Bessey	U.S.	5	2.6	11 August 1933	0.4	1.0	◆	3
Neuendorfer See <sup>†,‡</sup>	Krumme	Germany	11	21.1	18 July 1994	8.2	2.0	▽	7
Ontario	St Lawrence	Canada	9	175.0	July to August 1997	8850.0	12.5	■	2
Oppheimsvatn <sup>†,‡</sup>	Strandaelva	Norway	6	3.4	17 June 1974	2.3	0.3	▼	6
Partridge Crop	Montreal	Canada	3	7.0	1 August 1960	0.9	8.0	●	4
Portage & Base Line	Huron	U.S.	4	8.1	12 August 1932	7.2	1.0	△	1, 3
Potter	Potter	Canada	3	1.0	6 August 1999	0.1	0.1	◇	8
Sikachu	Montreal	Canada	3	5.0	1 August 1960	0.9	2.0	○	4

\*Outlet dammed.

<sup>†</sup>River discharge was estimated from width × depth × velocity.

<sup>‡</sup>Zooplankton density includes rotifers.

depth was not given for the St Lawrence River, but was estimated from bathymetric maps.

Downstream changes in zooplankton density from each lake outlet were separately fitted to a semi-log linear regression (best fit to data; Statgraphics Plus v2.0, 1996) in order to determine the slope of the downstream change, where  $\log$  zooplankton density ( $Z$ ) =  $\beta_0 + \beta_1$  (distance downstream). Multiple linear regression was then carried out on the slope of the downstream change ( $S$ , Table 3) against discharge ( $Q$ ) and outlet sill depth ( $D$ ), with the model:  $S = \beta_0 + \beta_1 Q + \beta_2 D$ . This model tests for the effects of both discharge and outlet depth on changes in downstream zooplankton density. Downstream changes in  $\log$  zooplankton density ranged from  $-11.78$  to  $+0.29 \log(\text{individuals}) \text{ km}^{-1}$  (Fig. 7).

Zooplankton density decreases faster in shallow outlet streams ( $\leq 1$  m in depth; Fig. 7a), than in deeper outlets ( $\geq 2$  m; Fig. 7b; Kruskal–Wallis com-

parison of median rates of change in zooplankton densities,  $n = 15$ ,  $P = 0.005$ ). Outlet discharge ( $\text{m}^3 \text{ s}^{-1}$ ) did not affect the rate of change downstream ( $n = 15$ ,  $P = 0.65$ ) in zooplankton density. Some effect of dilution of the initial concentration of lake zooplankton entering the outlet might have played a role in decreasing downstream density. However, large zooplankton density decreases have clearly happened within the first 5 km in the shallow streams, but not within 5 km in the deeper rivers (Fig. 7). Although we were unable to test the effect of dilution, it is unlikely that the shallower streams all have more substantial water inputs from tributaries or groundwater than the deeper rivers. Shallow river depths ( $\leq 1$  m) appear to limit the development and downstream persistence of in-stream zooplankton communities.

In contrast, zooplankton densities in deeper outlet rivers ( $\geq 2$  m) did not decrease with distance, with one

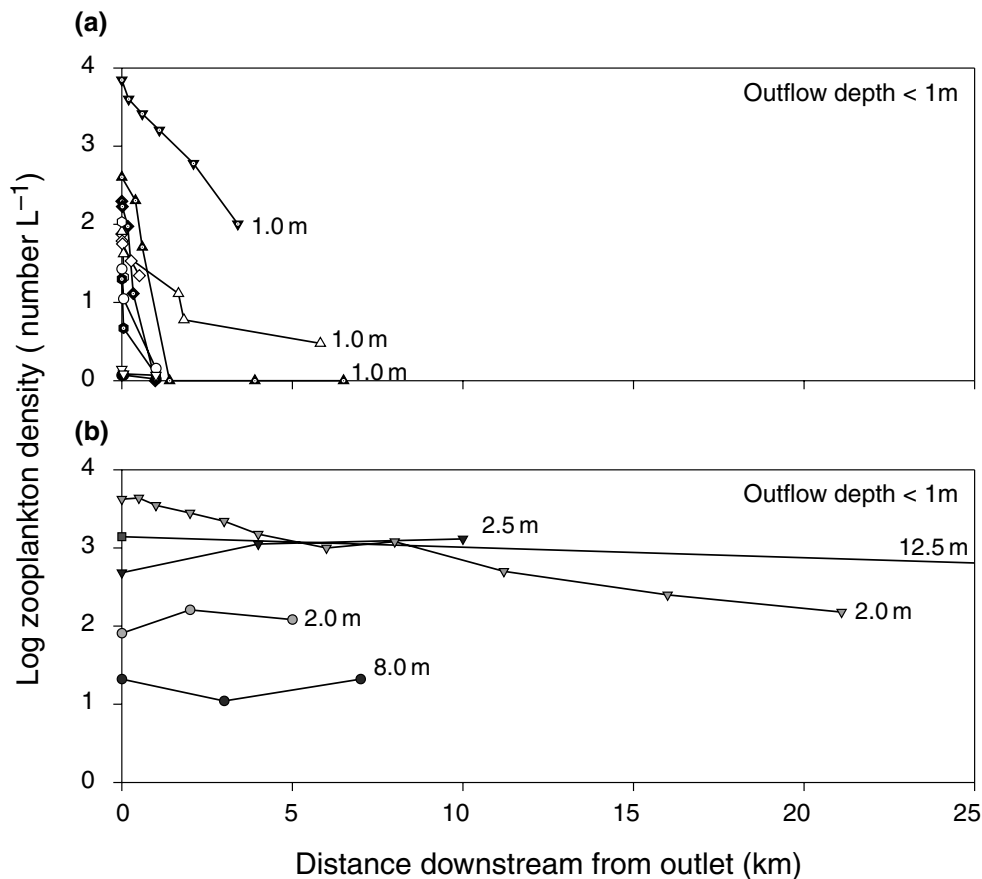


Fig. 7 Changes in zooplankton density downstream from lake outlets (0 km) in rivers worldwide. Rivers with (a) shallow ( $\leq 1$  m) and (b) deep ( $\geq 1$  m) lake outlet sills are compared. Data sources and sampling details are listed in Table 3.

exception (inverted triangles, Fig. 7b). Zooplankton density decreased downstream from the Neuendorfer See (depth = 2 m; discharge =  $8 \text{ m}^3 \text{ s}^{-1}$ ), amounting to 90% lost over 21 km (Welker & Walz, 1998). This rapid decrease was attributed to large populations of *Dreissena polymorpha* (Pallas) and of unionid mussels ( $925 \text{ individuals m}^{-2}$ ), which have been shown to filter particles up to  $750 \mu\text{m}$  in diameter (Ten Winkel & Davids, 1982). Mussels filter feed by actively moving water, and thus can exist in rivers or lakes (Nalepa & Schloesser, 1993). In contrast, trichopteran and dipteran larvae rely on current flow to bring food particles to their filter apparatus (Merritt & Cummins, 1984). Thus, active benthic filter feeders can also be important in reducing zooplankton in deeper, large rivers, but the downstream development and persistence of plankton is more likely in these systems than in shallow streams.

Persistence of lake plankton in rivers may be strongly limited by predation. Predation on plankton could be controlled by the effective contact between the river benthos and the water column; where, in shallow rivers, the water column and therefore suspended plankton, has a higher rate of contact with the stream bottom and benthic filterers than that in deeper rivers. However, active filtration of plankton by zebra mussels (see Bunt, MacIsaac & Sprules, 1993) may increase the rate of contact between organisms in the water column and benthic filter feeders.

Although lakes with deep open littoral zones can contribute large densities of zooplankton to small streams, lake zooplankton almost completely vanishes by 1 km downstream from the outlet. Thus, when assessing the importance of upstream lakes on downstream river zooplankton communities, the connection strength between a lake and its outflow appears to depend more on the morphology of the stream than on the amount of plankton entering the outlet. The inclusion of lakes and floodplain water bodies within river basins may be important locally in supporting productive benthic river communities; however, they may not be important contributors to the founding of plankton populations in rivers. The influence of upstream lakes in founding river plankton communities depends on the strength of connections both between the lake and the river, and between the river water column community and the benthic community.

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