Variation in spatial and temporal gradients in zooplankton spring development: the effect of climatic factors

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SUMMARY

1. We examined the temporal and spatial heterogeneity of zooplankton in lake surface waters during the spring of 3 years in Lake Washington, U.S.A., a large lake with a high production of sockeye salmon fry.
2. We show large within-season and among-year variation in the horizontal distribution of temperature, chlorophyll *a* concentration, and zooplankton in the lake. The main pattern, a delay in zooplankton population increase from the north- to the south-end of the lake, recurred in each year and was persistent within each spring.
3. The delay is primarily caused by the development of a temperature gradient during spring warming, as cold mountain water enters the south end of the lake, while warm water enters the north end via a river draining a nearby lake. Climate factors, such as air temperature and precipitation during winter and spring, appear to influence the extent of the delay of zooplankton increase.
4. If the climate continues to warm, the temporal disconnection in zooplankton development between lake areas immediately influenced by cold river inflow and areas that are influenced by spring warming may increase in magnitude. Thus, the different areas of the lake may not contribute equally to fish production.

Keywords: climate effects, *Daphnia*, spatial gradient, temporal gradient, zooplankton

Introduction

Zooplankton communities are dynamic systems in which the species composition changes with time. During the spring in temperate lakes, the temporal development and succession of zooplankton species has been explained by many factors, including temperature, food, competition and predation (according to the PEG model Sommer *et al.*, 1986). Spatial heterogeneity of zooplankton has also been shown

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to be an ecologically important feature of freshwater ecosystems (Pinel-Alloul *et al.*, 1999 and references therein). Zooplankton spatial development, like the temporal development, is the result of many physical and chemical processes interacting with several biological processes at a range of spatial scales, as described by the 'multiple driving force hypothesis' (for a review, see Pinel-Alloul, 1995). As water temperature is thought to be one of the most important factors influencing zooplankton abundances during spring and summer in large lakes (Patalas & Salki, 1992; Stockwell & Sprules, 1995; Pinel-Alloul *et al.*, 1999) climatic factors such as an increase in winter/ spring air temperature will affect the timing of zooplankton spring development (Gerten & Adrian,

2000; Winder & Schindler, 2004). Recent evidence suggests a trend towards warmer winters and spring in many areas, including the north-western United States (Lettenmaier *et al.*, 1999).

While some studies have examined the temporal and spatial patterns of zooplankton at the whole-lake scale over one or several seasons of 1 year (Patalas, 1969; Patalas & Salki, 1992; Stockwell & Sprules, 1995; Fernandez-Rosado & Lucena, 2001), to the best of our knowledge there are no studies showing both within-season and among-year variation in horizontal distribution of zooplankton during its spring development, and how these variations are influenced by abiotic factors [but see Thackeray *et al.* (2004) for a comparison of summer data from 2 years]. In a 3-year study we examined the temporal and spatial heterogeneity of zooplankton in the surface waters of Lake Washington, WA, U.S.A., from February to June. A north–south temperature gradient is likely to occur in this lake as the south, but not the north, end of Lake Washington receives a large inflow of cold water from the mountains during spring. Our aim was to document spatial variation in zooplankton abundance across the extent of the lake during late winter and spring, together with biotic and abiotic factors (temperature, chlorophyll *a* concentration, river discharge and fish abundance). By repeated sampling during the spring of 3 years, we aimed to assess if large-scale patterns of zooplankton population development during spring persisted from year to year, and whether they were influenced by climatic factors.

Fish biomass is considered to be too low to drive zooplankton dynamics in Lake Washington (Beauchamp *et al.*, 2004). Food supply, however, is vitally important for growth and survival of fish (Chick & Van Den Avyle, 1999; Romare, 2000), and is itself determined by the spatial and temporal overlap with zooplankton. Large numbers of sockeye salmon fry [*Oncorhynchus nerka* (Walbaum)] enter the south and north ends of Lake Washington in early spring. For these immigrating fry it is important that the preferred zooplankton prey is present where they enter the lake. Juvenile sockeye salmon in Lake Washington strongly prefer *Daphnia* over other zooplankton, switching uniformly and almost completely to *Daphnia* when the latter reaches a relatively low threshold density of $0.4 \, L^{-1}$ (J.M. Scheuerell, University of Washington, unpublished manuscript). Long-term data (1972–99) from the central sampling station

(Madison Park) and fry trap data (1992–99) from Lake Washington's major tributary infer that sockeye fry must have experienced increasingly prolonged periods of development before *Daphnia* became the primary food source (S. Hampton, University of Idaho, unpublished manuscript). This seems to have been caused by a trend towards later achievement of the threshold density for *Daphnia* during the 1990s (S. Hampton, unpublished manuscript). Studying the inter- and intra-annual variation in spatial patterns of zooplankton spring development will show if this apparent temporal predator-prey mismatch is the same all over the lake and consistent among years.

We hypothesise that climatic factors during late winter and spring, here air temperature and precipitation, influence the large-scale patterns of zooplankton, and especially *Daphnia*, in Lake Washington. We also hypothesise that the time of increase of the *Daphnia* population is influenced by their over-winter abundance. Finally, we hypothesise that, if water temperature is one of the main driving forces of zooplankton heterogeneity, zooplankton development will differ between the north and the south end of Lake Washington.

Methods

Lake and site description

Lake Washington (47°37′N 122°16′W) is a large, urban lake located at the eastern edge of Seattle, Washington, U.S.A. The lake is a popular recreational area, and its fisheries are of significant recreational, economic and cultural importance. This glacial lake is 32.2 km long, averages 2.5 km in width, and has a maximum depth of 66 m. Thermal stratification generally persists from April until October (Winder & Schindler, 2004). The major tributaries of Lake Washington are the Cedar River in the south, and the smaller Sammamish River in the north. The Lake Washington zooplankton is dominated by the cyclopoid copepod *Cyclops bicuspidatus thomasi* (Forbes), the calanoid copepod *Leptodiaptomus ashlandi* (Marsh) and the cladocerans *Daphnia pulicaria* (Forbes), *Daphnia thorata* (Forbes) and *Daphnia galeata* (Birge) (hereafter referred to collectively as *Daphnia*). The abundances of the different zooplankton taxa are generally highest in the surface water (0–10 m), and no vertical migration has been observed (Lake Washington data set). The

primary zooplanktivores in the lake are juvenile sockeye salmon (*O. nerka*), other juvenile salmonids [*O. clarki* (Richardson), *O. mykiss* (Walbaum), *O. tschawytscha* (Walbaum), *O. kisutch* (Walbaum)], long-fin smelt [*Spirinchus thaleichthys* (Ayres)], threespine stickleback [*Gasterosteus aculeatus* (Linnaeus)], juvenile yellow perch [*Perca flavescens* (Mitchill)], and the freshwater shrimp *Neomysis mercedis* (Holmes). Sockeye salmon fry enter Lake Washington in late February to April each year, most from the Cedar River but some also from the Sammamish River. During this study 18–52 million sockeye fry per year entered the lake from the Cedar River, and 1–3 million sockeye fry entered from the Sammamish River (D. Seiler, Washington Department of Fisheries and Wildlife, personal communication).

Sampling and analysis

Daytime zooplankton samples were collected bi-weekly between February and June in the years 1998, 1999 and 2001. In 1998 and 1999 samples were collected on ten dates beginning in early/mid-February, and in 2001 on nine dates beginning in late February. The whole sampling period will hereafter be called 'the spring period'. Sampling sites were located in the limnetic zone in the middle, north end, and south end of Lake Washington (Fig. 1). Over the spring period in 1998 and 1999 four stations were sampled: Arrowhead Point (AHP), Madison Park (MP), Bailey Peninsula (BP), and south end (SE), but in 2001 we only sampled three stations, omitting BP. The water depth is 30 m at AHP and SE, and 60 m at BP and MP. Zooplankton sampling and processing were done according to the methods of Edmondson & Litt (1982) and are part of the long-term study of Lake Washington plankton that began in 1949. The zooplankton was sampled during the day by taking one oblique tow from 10 m to the surface at each station using a closing Clarke-Bumpus sampler (Clarke & Bumpus, 1950) equipped with a 130 μm mesh net and flow meter. During sampling the boat circled the sampling area for 2–3 min until about 400 L was sampled. Samples were preserved in either 95% ethanol or 10% formalin. For counting, at least two subsamples each with a minimum of 100 individuals of the most abundant species were counted. The entire sample was then counted for rare species. Counts were extrapolated to abundance per litre. At each
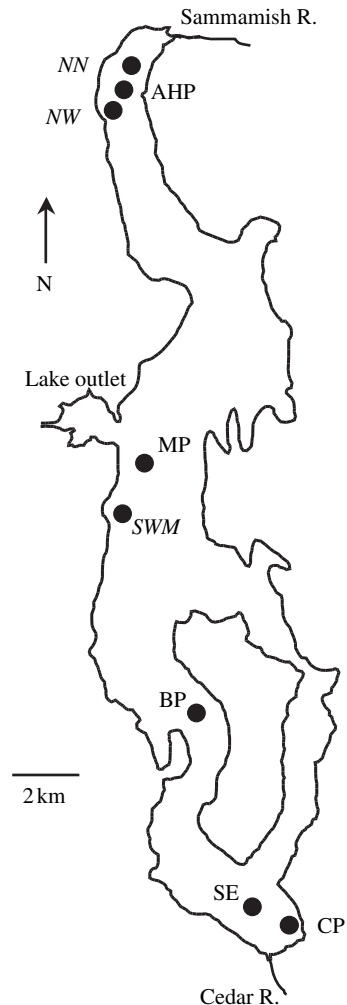
Fig. 1 Map of Lake Washington showing the following sampling stations Arrowhead Point (AHP), Madison Park (MP), Bailey Peninsula (BP), Coulon Park (CP), and south end (SE). Stations AHP, MP and SE were sampled all 3 years 1998, 1999 and 2001, but BP was not sampled in 2001. The CP near shore station provided additional data on *Daphnia* 1998 and 1999. Additional stations visited during the simultaneous fish–zooplankton sampling (NNE, NWN, SWMP) are shown in italics.

station water was collected as a surface dip for chlorophyll *a* analysis, and temperature was measured at each metre from just below the surface and down to 10 m using a Kahl digital thermometer. Chlorophyll *a* concentration was analysed by acetone extraction using an adapted Strickland and Parsons Scientific Committee on Oceanic Research (SCOR) method for sea water analysis (Strickland & Parsons, 1965; SCOR Unesco, 1966).

We measured the three-dimensional locations of fish once each year (3 April 1998, 20 March 1999, 26

March 2001, coinciding with zooplankton samplings) using a BioSonics DT6000 split-beam echosounder operating at 200 kHz with an elliptical transducer consisting of −3 dB beam angles of 6.7 and 13.5 degrees (BioSonics Inc., Seattle, WA, U.S.A.); the narrow beam was parallel to the direction of travel. We used a 0.4 ms pulse at a rate of 4 s^{-1} with the lower threshold set at −70 dB. Using the BioSonics Visual Acquisition 4.0 software, all incoming signals were digitised at the transducer and then stored on a computer hard drive for later analysis. The transducer was attached to a tow-sled immediately under the water surface and towed alongside the boat at a speed of 10 km h^{-1} as the survey followed 16 predetermined transects across the lake over a total distance of 51.5 km. Acoustic transects were selected non-randomly in an effort to provide adequate survey coverage without biasing any particular depth contours, embayments, docks, houses, etc. All hydroacoustic surveys occurred between 19:00 and 02:00 hours. Fish density and the depth and size of individual echoes were obtained using the BioSonics DT Analyser 4.0 software, but we only analysed depths >1 m because of near-field effects of the acoustic beam. For these analyses we combined all small fish together (targets less than −46 dB, which correspond to sockeye salmon lengths <100 mm, Burczynski & Johnson, 1986). All subsequent analyses refer only to these small fishes. The density of small fishes was obtained by multiplying the total fish density by the proportion of all target strength values within this class (fish less than −46 dB). During early spring the primary small, pelagic zooplanktivores in the lake are juvenile sockeye salmon, longfin smelt and, to a lesser extent, threespine stickleback (Beauchamp *et al.*, 2004).

Statistical methods

Spearman rank-order correlation with associated bootstrapped confidence intervals was used to examine the spatial correlation of each zooplankton species with water temperature and chlorophyll, respectively. Data were correlated across stations for each sampling date and year. As multiple comparisons were performed we also tested whether the proportion of significant correlations within a species and covariate was greater than that expected by chance (i.e. 5%), and found all tests to be significant. To test the

relation (over stations) between the day of increase of *Daphnia* and winter abundance for the years 1998 and 1999, linear regression analysis was used.

The spatial correlation (Spearman rank-order) between total *Daphnia* abundance and fish number was calculated for one date per year. In our study we are aware that fish and zooplankton were not sampled over exactly the same scale, which would be preferred (Swartzman *et al.*, 1999; Masson *et al.*, 2001), as fish were sampled continuously while the zooplankton was point sampled. By correlating zooplankton data with fish data (from 1 to 10 m depth) from the transects (varying from 1 to 4 km in length) closest to the zooplankton stations sampled at the same date (NNE, NWN, AHP, MP, SWMP, BP, SE, CN; see Fig. 1), however, we believe that a good indication of the effect of fish predation on zooplankton distribution was obtained. To compare how much plankton biomass is available to fish shoals in different areas, a proximity-based approach may be preferred over a perfect spatial overlap, (see Swartzman *et al.*, 1999), an approach that would also have required sampling at the same scale. In this study, however, we argue that the sampling stations AHP and SE may represent the regions which sockeye salmon fry enter first. Thus, to test if the overall abundance (over the spring season) of *Daphnia* was lower in the south end of the lake (SE), a one-way paired *t*-test was used on log-transformed data to compare the mean between AHP-SE and MP-SE, respectively. The *t*-test was chosen as we did not use the same time periods in the comparison between AHP-SE as between MP-SE and, thus, could not use ANOVA.

Results

The three sampling years were rather extreme climatically (Table 1). The winter of 1997–98 was warm and spring water temperature was very high (Winder & Schindler, 2004), while the winter of 1998–99 was extremely wet and spring water temperature very low (Winder & Schindler, 2004). Finally, the winter 2000–01 had one of the driest 'wet' seasons in a century. On any individual date, water temperature and chlorophyll *a* concentration were generally lower in the south end than in the north end of Lake Washington (Fig. 2). Temperature in the middle area of Lake Washington was close to that at the north end, while chlorophyll *a* concentration showed a more variable

Table 1 Total winter precipitation (November to February, mm) and mean winter air temperature (November to February, °C) from 1990 to 2002. The mean values for the November to February periods from 1931 to 2004 (precipitation) and 1949 to 2004 (temperature) are also given.

Year	(mm)	°C
1990–91	1003	5.8
1991–92	840	7.5
1992–93	558	5
1993–94	524	5.6
1994–95	826	6.7
1995–96	962	6.4
1996–97	951	5.2
1997–98	**694**	**6.9**
1998–99	**1347**	**6.0**
1999–2000	1040	6.4
2000–01	**451**	**5.2**
2001–02	1088	5.9
Mean	**828**	**5.6**

Data are from the Western Regional Climate Center for Snoqualmie Falls (precipitation), and Seattle (temperature), Washington.
Values shown in bold are the sampling periods of this study.

pattern. There were substantial north-south temperature differences in the surface water of Lake Washington, for each sampling date and year, which were associated with the Cedar River discharge (see Fig. 3 which also indicates the stratification dates). The whole lake became stratified at about the same time each year, but the stratification was weaker in the south end during the first weeks of the stratification period of 1999 and 2001.

There was substantial variation in north to south spring-time development in zooplankton abundance during 1998, 1999 and 2001 in Lake Washington (Fig. 4a–d). Nearly all populations developed earlier in the northern sections of the lake in each year. The general pattern of temporal succession observed in the lake was an early increase in *Leptodiaptomus* followed by first *Cyclops* and then *Daphnia*. Also present in low numbers during spring all years was the large calanoid copepod *Epischura nevadensis* (Lillj.) and, in 2001 the cladoceran *Bosmina longirostris* (Müller) was
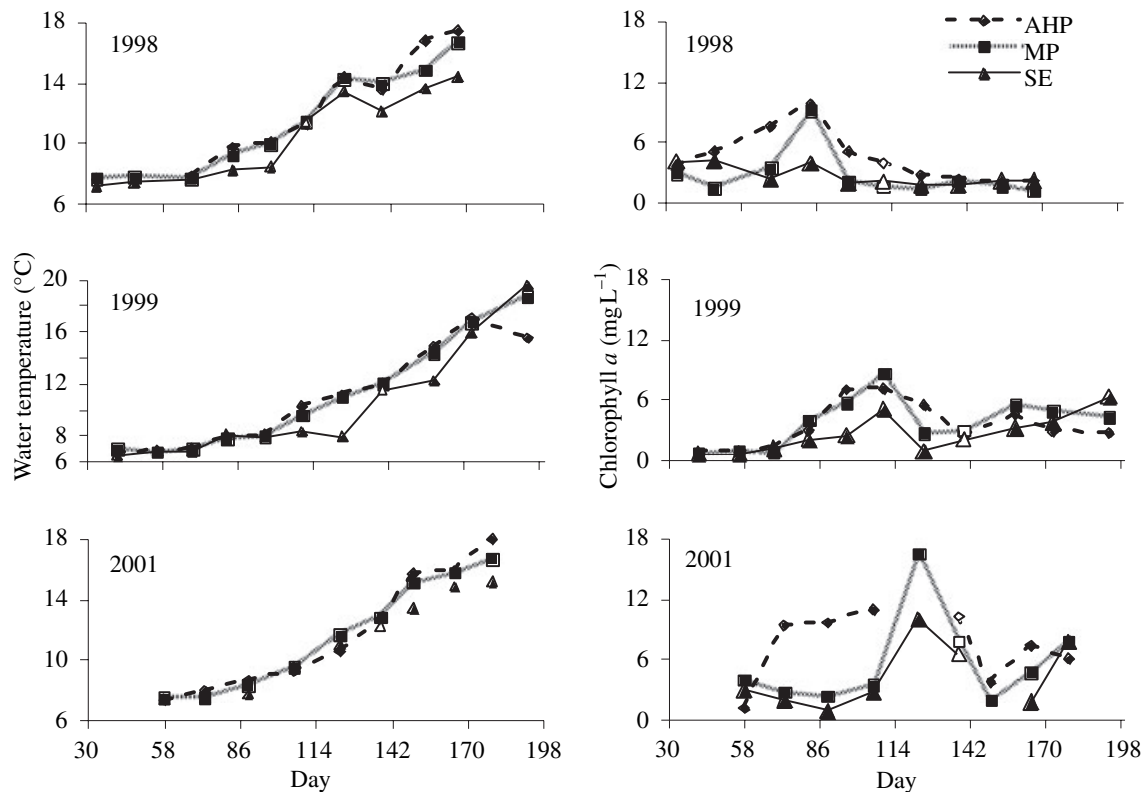

Fig. 2 The development in water temperature (left) and chlorophyll *a* concentration (right) during spring of 1998, 1999, and 2001 in Lake Washington. Values are shown for three sampling stations AHP (filled diamond), MP (filled square) and SE (filled triangle). Also indicated is the time of thermal stratification for each year (open signs).

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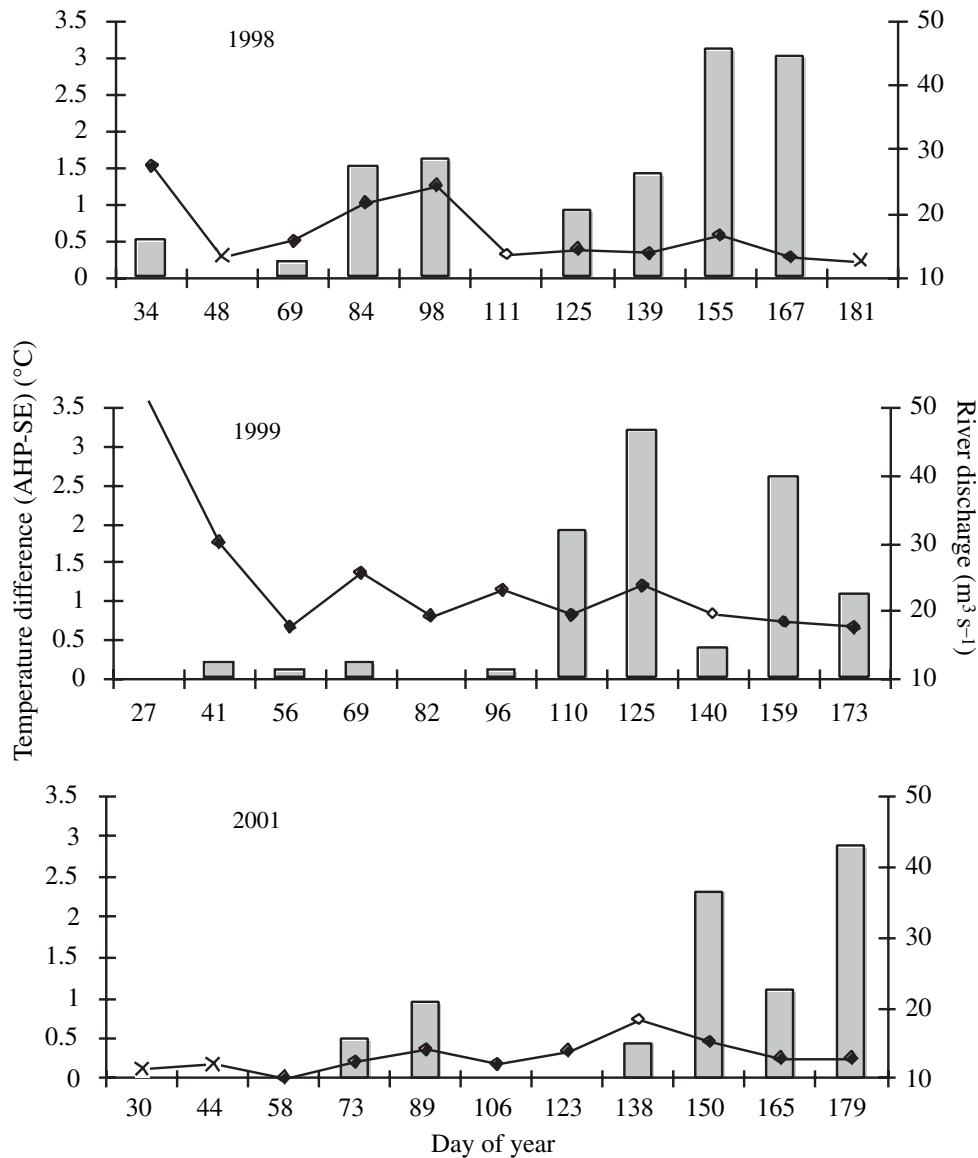
Fig. 3 The difference in surface water temperature (°C) between station AHP and SE (bars) in Lake Washington together with the Cedar River discharge ($m^3 s^{-1}$, filled diamonds) the years 1998, 1999, 2001. Dates when only river discharge values (and not temperature) are available are marked with a cross. Also indicated is the time of thermal stratification for each year (empty diamonds).

abundant. Numerically dominant genera at the time of peak total zooplankton abundance (average across stations) were, in 1998, *Cyclops* (60%) *Daphnia* (20%) and *Leptodiaptomus* (14%), in 1999, *Leptodiaptomus* (70%) and *Cyclops* (30%) and, in 2001, *Cyclops* (70%). The timing of spring-time development in zooplankton abundance varied from north to south in Lake Washington during all three sampling years (Fig. 4a–d). All zooplankton species started to increase in abundance later in the south than in the north end of the lake, leading to time lags in the 'day

of first increase' varying from 3 to 9 weeks (Table 2). We defined 'day of increase' as the date when zooplankton, having varied around lower winter abundances, reached a species-specific threshold abundance (*Leptodiaptomus* and *Cyclops* >10 L^{-1}, *Epischura* >0.1 L^{-1}, *Daphnia* >0.4 L^{-1}) and then continued to a first spring peak. These species-specific thresholds were chosen based on 40 years of zooplankton data collected at the MP station in Lake Washington. A north–south gradient was evident for the timing of spring increase of *Cyclops* and *Daphnia*
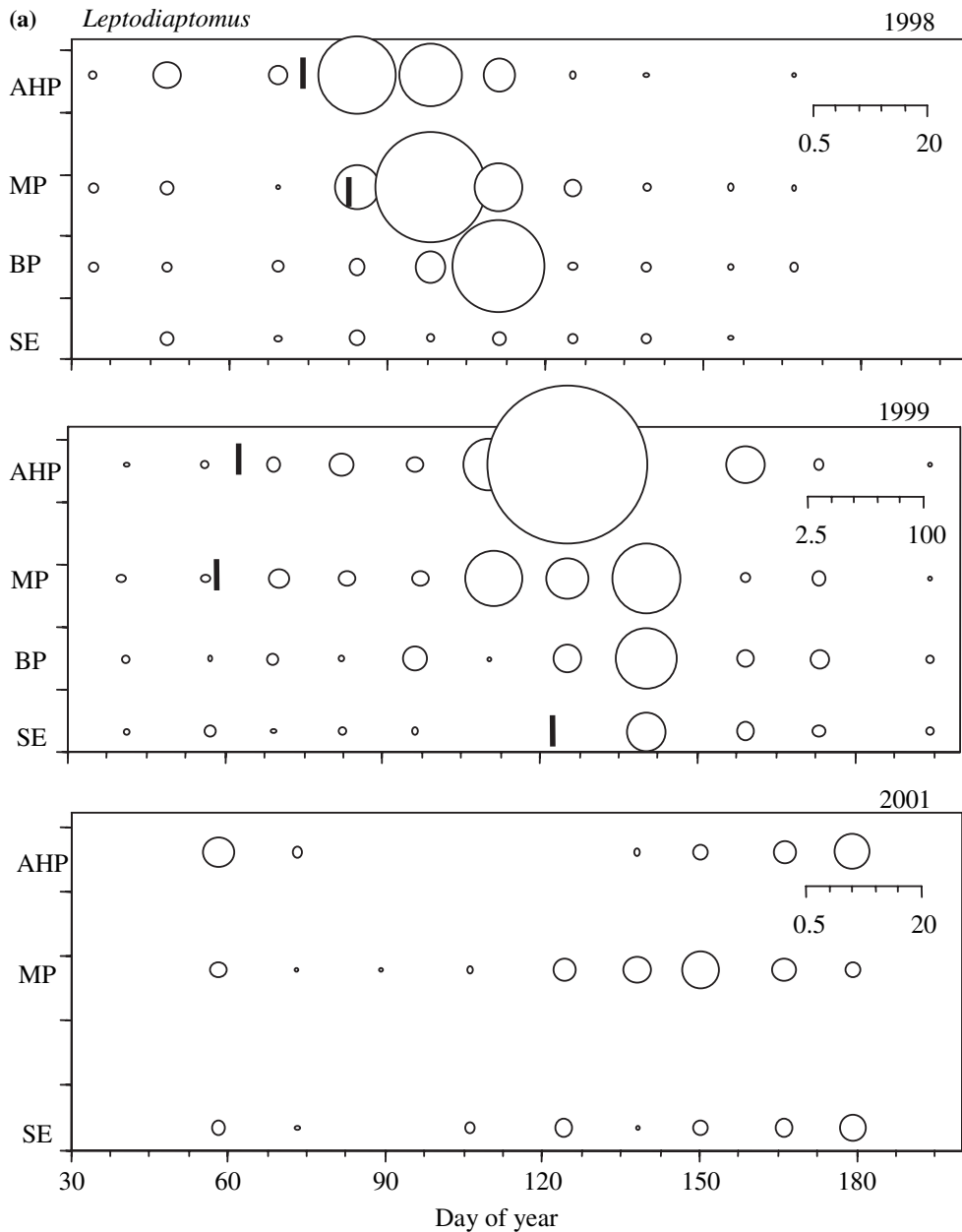
Fig. 4 Spring development in zooplankton density (L^{-1}) and their north-south distribution in Lake Washington for 1998, 1999, and 2001. Shown are (a) *Leptodiaptomus*, (b) *Epischura*, (c) *Cyclops* and (d) *Daphnia*. Observe that the lowest abundance shown varies among graphs, and that low *Daphnia* densities (L^{-1}) have been indicated on the graphs to show the early spring development. A vertical bar marks the 'day of increase', when zooplankton increased above a species-specific threshold. See Methods section for details.

(Fig. 4c,d). The timing of the *Daphnia* spring increase (the day when *Daphnia* abundance exceeded 0.4 L^{-1}) was positively related to winter abundance (mean January to February abundance) 1998 and 1999 (regression: $P < 0.001$, $R^2 = 0.95$, $n = 9$; Fig. 5). In 2001 sampling started too late in the season to get a good estimate of winter abundance.

The timing of first peak abundance also differed among the sampling stations, with lags varying from 2 to 7 weeks (Table 2). This difference in peak timing occurred in all 3 years and for all species, except for *Leptodiaptomus* and *Cyclops* in 2001 (Table 2). The size of the peak abundance was two to four times lower in the south than in the north
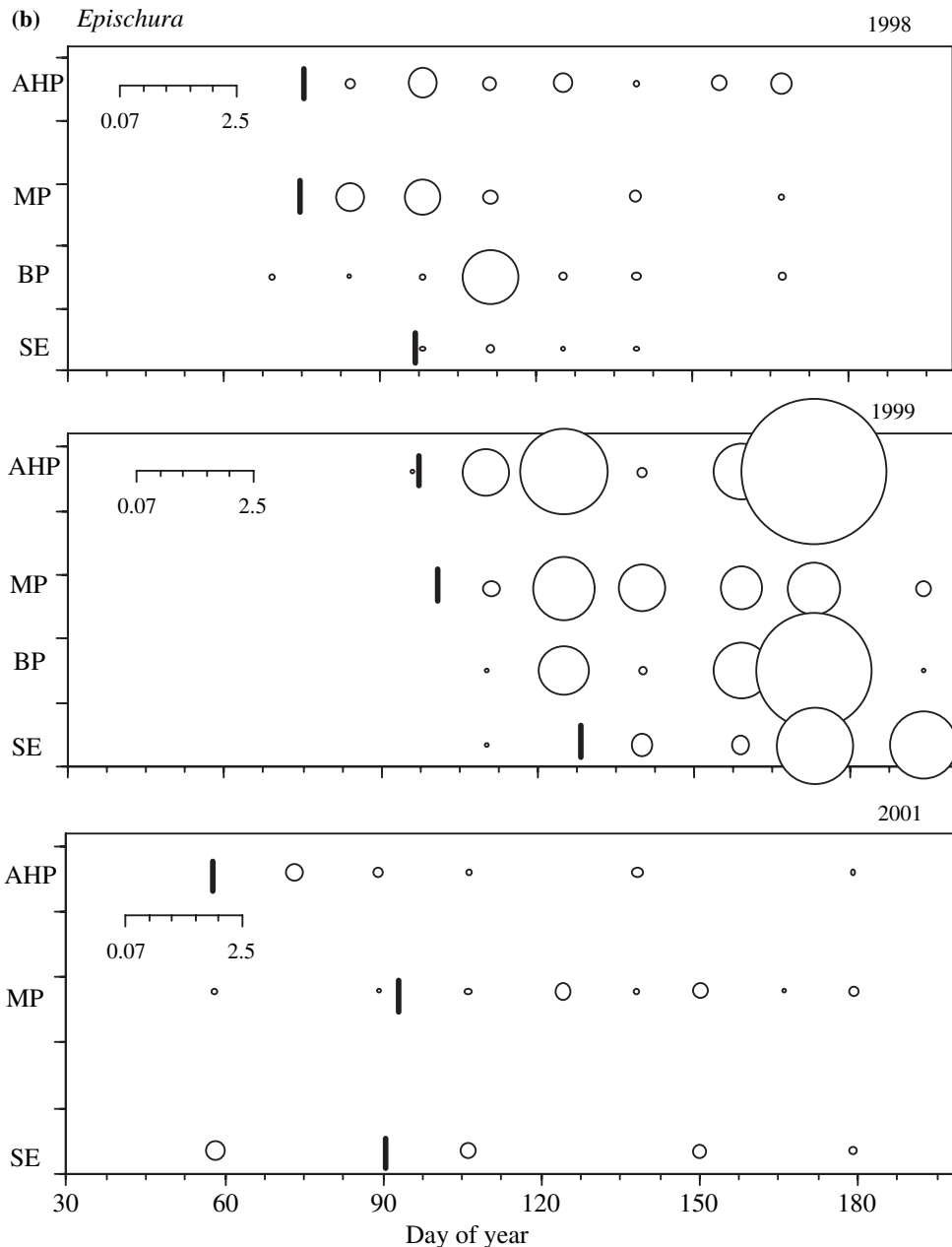
Fig. 4 (*Continued*)

end of the lake for *Leptodiaptomus* and *Epischura* in 1998 and 1999 and for *Cyclops* in 1999 and 2001 (Fig. 4a–c). Although there was no obvious spatial difference in the size of peak abundance for *Daphnia*, the overall abundance (seen over at least the period March and April) was lower in the south end than in the north and middle area of the lake in 1998 and 1999, and lower than in the middle area 2001 (Table 3).

The coefficients from the correlations performed over stations for each date and year are shown in Fig. 6. As the statistical power of the tests was limited (low number of stations), few correlations were significant. However, seen over the whole spring season, the abundance of *Epischura* seemed to be positively related to temperature in all years, while *Daphnia* abundance was positively related to temperature in 1999. *Leptodiaptomus* and *Cyclops* were
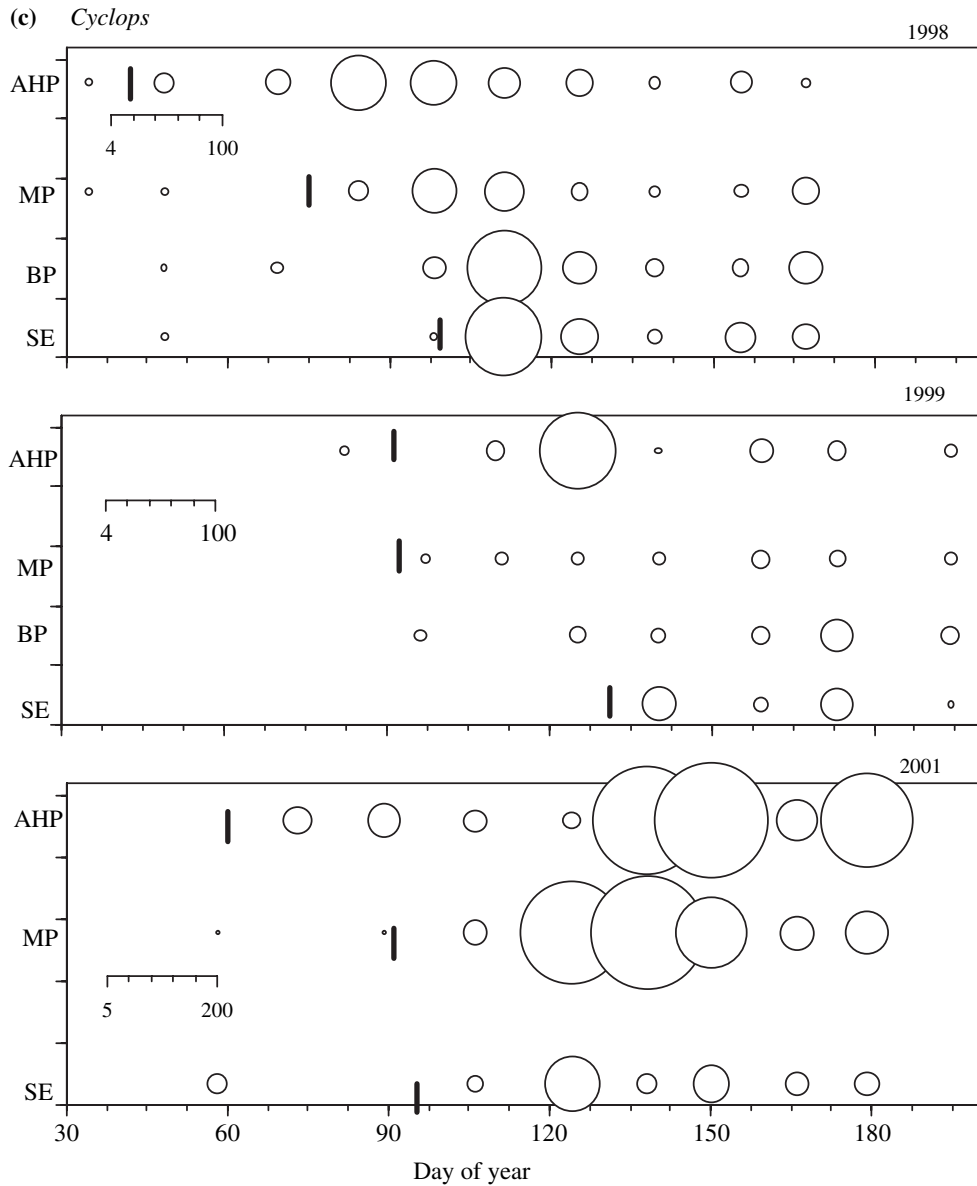
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positively related to temperature in early 1998 and late 2001 (Fig. 6). *Daphnia* and *Leptodiaptomus* were positively related to chlorophyll *a* concentration in 1999, and *Cyclops* in 2001 (Fig. 6). The highest planktivore fish abundance in the surface water was recorded in the north end of the lake in all years, abundances being highest in 2001 at stations AHP, MP and SE (Table 4). The correlations between fish abundance and total zooplankton and with *Daphnia* tended to be positive in the early spring of all years, but were only significant in 1998 (Table 4).

Discussion

In this study we found recurrent and persistent north–south gradients in both abiotic and biotic factors during spring in a large temperate lake. The spring patterns involved both the timing and the extent of surface water warming and chlorophyll *a* and zooplankton development.

The most obvious recurrent pattern was a delay in zooplankton succession along a north–south gradient in Lake Washington (Fig. 4a–d). This pattern was
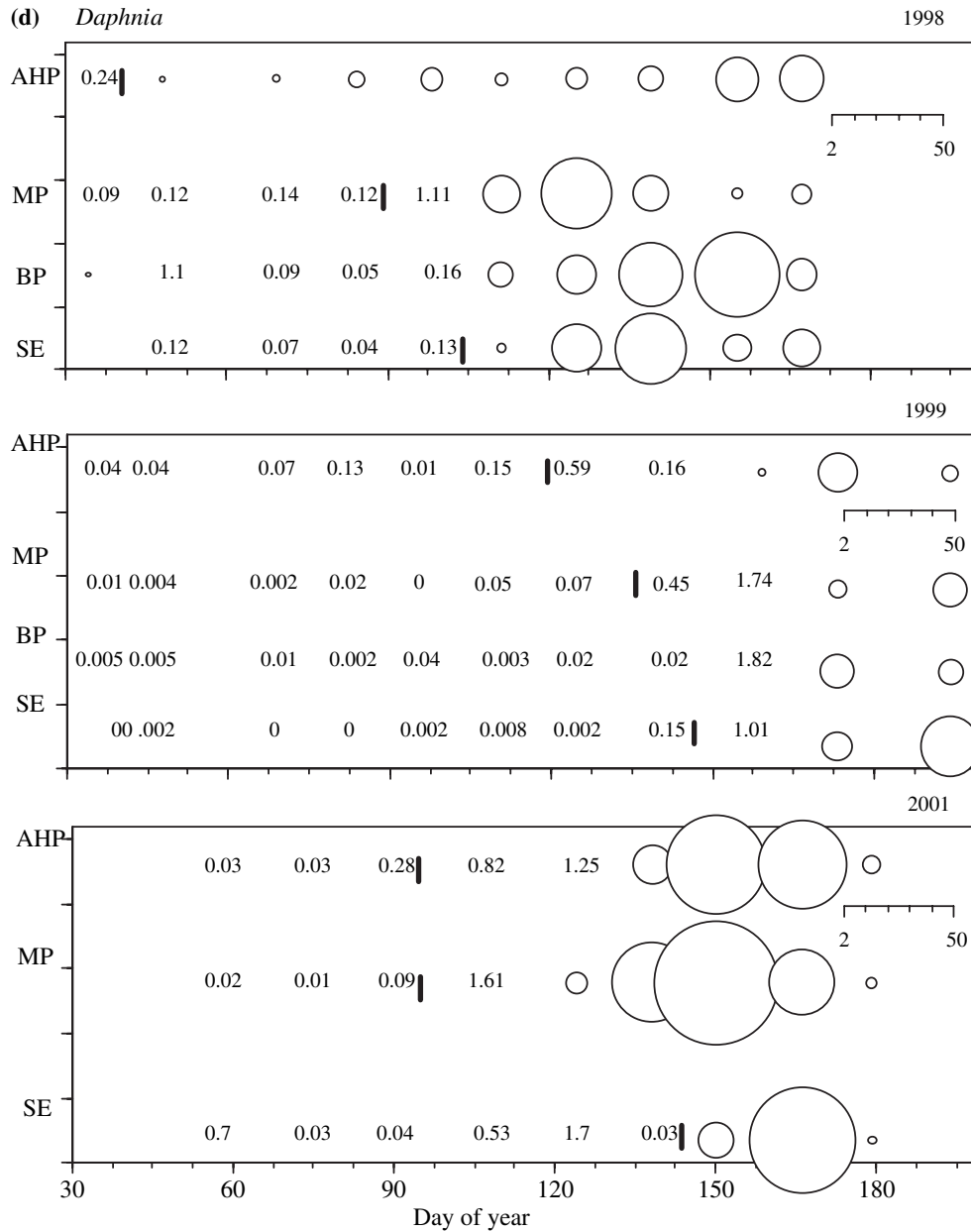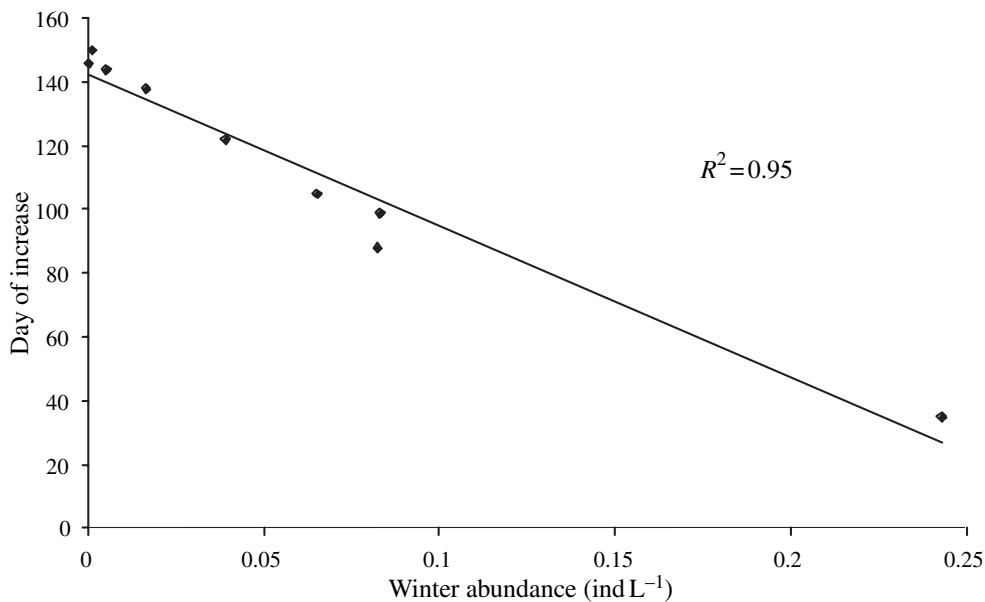
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observed primarily as a delay in the onset of the spring increase, but also as a delay of peak abundance in the south-end compared with the north-end of the lake. Similar patterns of delayed successions have also been observed in Lake Winnipeg (Patalas & Salki, 1992), primarily caused by a gradient in temperature. In Lake Washington a temperature gradient develops in early spring when the high inflow of cold water from the Cedar River, draining mountainous areas, delays the warming of surface water in the south end

of the lake. At the north end the water of the smaller Sammamish River, draining Lake Sammamish, is already of lake temperature when entering Lake Washington. During the spring temperature increase, before the lake is thermally stratified, high differences in temperature between the north and the south end of the lake coincide with periods of high flow. During the short period of weak stratification, before a stable thermocline is established, thermal differences are small, while after the thermocline is established

Table 2 The delay (in weeks) in the dates of increase and peak abundance between the north end (AHP) and the south end (SE), and between the central (MP) and the south end of Lake Washington for the sampling years 1998, 1999 and 2001. We defined 'day of increase' as the date when zooplankton remained above a species-specific threshold (*Leptodiaptomus* and *Cyclops* >10 L^{-1}, *Epischura* >0.1 L^{-1}, *Dapnia* >0.4 L^{-1}). *Leptodiaptomus* did not increase in numbers at any station in 2001, or at SE in 1998.

Response variable	Year	*Leptodiaptomus*	Epischura	Cyclops	Daphnia
The north end (AHP) and south end (SE)					
Day of increase	1998	–	3	9	9
	1999	9	4.5	4	3.5
	2001	–	5	5	6.5
Day of peak abundance	1998	–	2	4	6
	1999	2	7	2	3
	2001	–	–	−4	2
The central (MP) and the south end					
Day of increase	1998	–	4	3	2
	1999	10	4	4	1
	2001	–	0	1	6
Day of peak abundance	1998	–	2	2	2
	1999	0	7	−2	0
	2001	–	–	−2	2

Fig. 5 The relationship between the timing of *Daphnia* spring increase (the day when *Daphnia* abundance was higher than 0.4 individuals L^{-1}) and *Daphnia* winter abundance (mean January to February abundance) in 1998 and 1999 in Lake Washington. Observe that data from a fifth station, Coulon Park (CP), are included in this regression. Data on winter abundance was missing from BP in 1998.

Table 3 Results of a one-way paired *t*-test testing if *Daphnia* numbers (L^{-1}) are lower at the south end (SE) of Lake Washington than in the north end (AHP) or the middle area (MP) during the whole, or part of, the spring period 1998, 1999 and 2001

	SE < AHP				SE < MP			
Year	*n*	*t*-value	*P*-value	Time period	*n*	*t*-value	*P*-value	Time period
1998	7	2.26	<0.05	February to May 6th	10	0.19	ns	Whole period
1999	10	2.63	<0.05	Whole period	9	1.99	<0.05	Whole period
2001	9	1.37	ns	Whole period	6	2.16	<0.05	March to May 6th
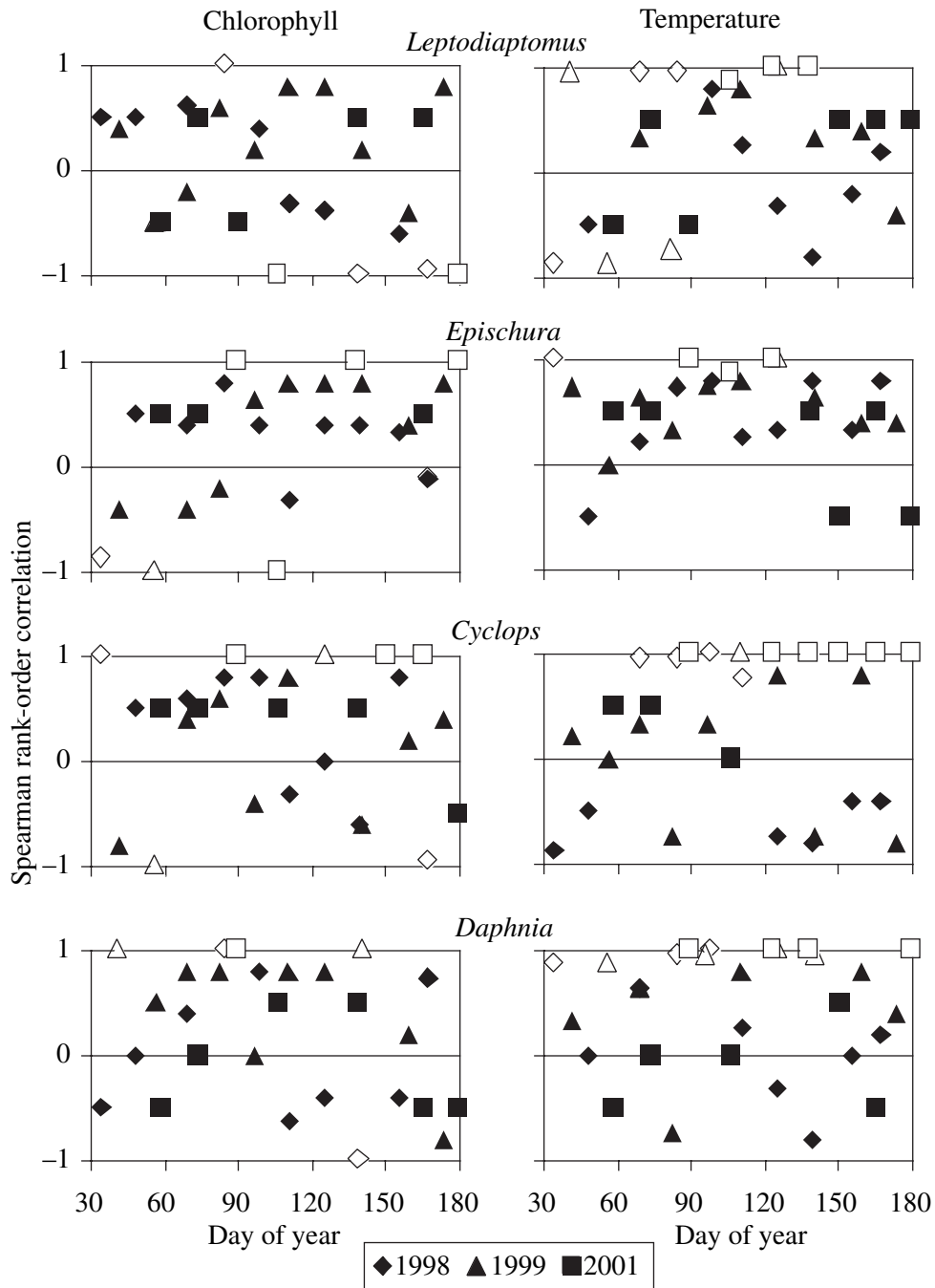
Fig. 6 The distribution of Spearman rank-order correlation coefficients for each sampling date in 1998 (diamond), 1999 (triangle) and 2001 (square) in Lake Washington. Open symbols indicate significant correlations. Associated bootstrapped confidence intervals for significant correlations <1 and $n = 4$ (r: ±0.87, ±0.95) are: ±0.77–±1 and ±0.82–±1. Shown are the coefficients from chlorophyll a–zooplankton (left) and temperature–zooplankton (right) correlations. Included are the zooplankton species: *Leptodiaptomus*, *Epischura*, *Cyclops*, and *Daphnia*.

thermal differences occur once again. River inflow has been observed to shape temperature and zooplankton gradients in other large lakes (Patalas; 1969; Pinel-

Alloul *et al.*, 1999). Because of lower temperature, zooplankton as well as phytoplankton production is probably lowered in the south end of the lake. The

Table 4 Density of *Daphnia* (L^{-1}), total zooplankton (L^{-1}) and fish (1000^{-1} m^{-3}) at one yearly sampling occasion (late March or early April) along a north-south gradient of stations in Lake Washington in 1998, 1999 and 2001. Station names shown in bold are the ones included in the whole spring sampling of zooplankton. At the bottom are shown the Spearman rank-order correlation (*r*) between zooplankton and fish and associated bootstrapped confidence intervals. Significant relationships are in bold type.

Year/station	Fish (1000^{-1} m^{-3})	Daphnia (L^{-1})	Total zooplankton (L^{-1})
1998			
NNE	21.2	10.9	40.8
NWN	3.1	59.2	108.3
AHP	2.4	10.1	62.5
MP	1.7	1.1	61.1
BP	0.8	0.2	26.2
SE	0.6	0.1	9.0
CN	0.8	0.1	7.1
1999			
AHP	15.3	0.1	28.7
MP	2.7	0.02	17.5
SWMP	7.9	0.002	6.5
BP	5.5	0.002	6.7
SE	0.3	0	8.3
CN	3.1	0.002	5.9
2001			
AHP	86.0	0.3	60.1
MP	16.0	0.1	6.5
SE	17.0	0	1.7

	Fish × Daphnia		Fish × total zooplankton	
Correlations/year	*r*-value	CI	*r*-value	CI
1998	**0.90**	0.41 to 1	**0.72**	0.059 to 1
1999	0.58	−0.89 to 1	0.086	−0.94 to 0.94
2001	0.5	−1 to 1	0.5	−1 to 1

combination of higher temperature and higher chlorophyll *a* concentrations may partly explain why zooplankton abundance (copepod peak abundance and *Daphnia* overall abundance) was often greater at the north than the south of Lake Washington.

Besides being dependent on environmental requirements such as temperature and food, zooplankton succession also depends on predation and interspecific competition (Sommer *et al.*, 1986). Fish biomass is generally too low to drive zooplankton dynamics in Lake Washington (Beauchamp *et al.*, 2004), and in this study we found no evidence that fish predation shaped the distribution of zooplankton in the lake. Instead the distribution of small planktivores in the surface waters of Lake Washington followed the same

north–south gradient as zooplankton at the time of the sampling, although most sockeye fry enter south of the lake. This distribution probably does not reflect a rapid migration of sockeye fry from the south end all the way to the north end of the lake, but may instead indicate a greater use of the plankton rich surface waters in the north. Trawling data showing the vertical distribution of fish in different areas of Lake Washington indicate that the proportion of fish near the surface (at 7 m depth) is much higher in the north than in the south area of the lake (Beauchamp *et al.*, 2004). Wind induced currents are another factor that may be involved in shaping zooplankton spatial patterns, either indirectly by shaping temperature gradients (Pinel-Alloul *et al.*, 1999; Thackeray *et al.*, 2004) or directly by transporting zooplankton (Patalas, 1969; George & Winfield, 2000). In Lake Washington the prevailing wind direction during spring is from the south, and strong southerly winds may reinforce the north–south temperature gradient. The pattern of changing wind directions during the spring of each year did, however, not map on to changing thermal or zooplankton distribution patterns (data from Department of Atmospheric Sciences, University of Washington, http://www.atmos.washington.edu/data).

Our study indicates that yearly differences in air temperature and precipitation affect the spatial and temporal patterns of zooplankton development. In a year with a very warm winter and spring (1998), zooplankton increased much earlier in the north end than in the south end of the lake, and the time-lags were longer than in the cold year 1999. It is reasonable to expect more spatial disconnection between the south and the north end of Lake Washington in warm years, as the inflowing water of the Cedar River will be less affected by high air temperatures than the waters of the north end of the lake and, thus, the temperature difference will be higher. Although the long-term trend in the timing of *Daphnia* peak abundance in the central area of Lake Washington does not seem to be affected by increasing spring water temperature (Winder & Schindler, 2004), the timing of the spring onset of *Daphnia* in Lake Washington has been shown to be affected by a combination of water temperature, chlorophyll *a* concentration, and the over-winter population (S. Hampton, University of Idaho, unpublished manuscript). In our study the winter abundance of *Daphnia* also explained a large part of the variation (76%) in the timing of *Daphnia* increase along the

north–south gradient, suggesting the possible importance of weather conditions during the preceding winter. The effect of precipitation could be seen when comparing the very dry 2001 with the other sampling years. In a year with low river discharge all through winter and spring, there was no temperature difference between the north and the south end in early spring and a north–south gradient in zooplankton abundance did not evolve in the same way in 2001 as in 1998 and 1999. Spring water temperatures (March to June) in Lake Washington has shown significant warming trends during the last 40 years (Winder & Schindler, 2004), and in the future we may expect warmer winters and springs in the Pacific Northwest (Lettenmaier *et al.*, 1999). We may also expect less precipitation as snow and more as rain, causing slightly increased runoff magnitudes, and a snowmelt pattern that is shifted earlier in the year (Lettenmaier *et al.*, 1999). Both higher temperature and greater river discharge will lead to an increasing spatial disconnection in zooplankton spring development, which means that the temporal mismatch between salmon fry and their preferred prey, *Daphnia*, will differ among areas within the lake. Thus, the difference in food availability for sockeye fry entering in the south and in the north end of Lake Washington may increase in the future.

While other studies have shown that horizontal spatial patterns of abiotic and biotic factors occur in large North American lakes (Patalas, 1969; Patalas & Salki, 1992; Stockwell & Sprules, 1995), this is the first study to show that spring time gradients in temperature and zooplankton abundance recur among years, and that the extent of these gradients is influenced by climate change. If the climate continues to warm, the temporal disconnection in zooplankton development between lake areas immediately influenced by cold river inflow and areas that are influenced by spring warming may increase in magnitude in the future. Thus, the different areas of the lake may not contribute equally to fish production.

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