

Seasonal and diel patchiness of a *Daphnia* population: An acoustic analysis

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Abstract

Detailed information about the location and extent of zooplankton patches is fundamental to understand how abiotic and biotic forces interact to structure the spatial distribution of zooplankton. We mapped zooplankton patchiness in a Minnesota lake during spring, summer, and autumn with high-frequency (192-kHz) single-beam sonar. Conventional plankton samples of aggregations detected acoustically revealed that *Daphnia pulicaria* (mean body length 1.6 mm, mean target strength -120 dB) scattered most ($\sim 63\%$) of the sound. Other taxa were smaller ($< \frac{1}{2}$ the length of *D. pulicaria*) and were usually less abundant and therefore scattered much less sound than *D. pulicaria*. Our acoustic estimates of *Daphnia* concentrations illustrate extreme patchiness, with concentrations varying by as much as four orders of magnitude over vertical distances of less than 1 m. Seasonal patterns of patchiness were related to predation by rainbow trout and to abiotic factors associated with stratification. *Daphnia* concentrations were highest from June to October in a deep-water “refuge zone” where oxygen concentrations were between 3 and 5 mg L⁻¹. These oxygen levels are suitable for *Daphnia* but are lower than those required by rainbow trout. Heterogeneity in *Daphnia* concentration along the lake’s long axis was highest in May and June, when the population resided primarily in the oxic hypolimnion during the daytime. From July to October, as oxygen concentrations declined in the hypolimnion, the population became more metalimnetic and more uniformly distributed in the horizontal dimension. A diel study of the population in October indicated that the patchiness of population also changed dramatically between day and night. During the day the population aggregated densely in a thin layer (~ 2 m thick) in the thermocline. After sunset the population dispersed into the epilimnion, where concentrations were $\sim 100,000$ m⁻³ less than they were during the day in the thermocline.

Patchy spatial distributions and the low resolution of conventional sampling methods have impeded analyses of zooplankton populations. Zooplankton concentrations have been shown to vary by a factor of 1,000 within distances of meters horizontally or vertically, and the sampling resolution of conventional plankton nets and hoses is usually too coarse to identify the spatial limits of aggregations precisely (Coyle 2000). Variation in population density estimates due to sampling often cannot be distinguished from real changes of population density, and the effects of biological processes are difficult to distinguish from those of advective transport (Megard et al. 1997). Acoustic and optical plankton samplers developed during recent decades are major advances. They have very high sampling rates and spatial resolution, comparable to modern instruments (e.g., CTD profilers) used to measure environmental variables. Large numbers of plank-

ton samples can be obtained rapidly from large geographic areas. The new technology dramatically improves the ability to locate and describe aggregations and to identify how aggregations are related to physical variables (e.g., Ross et al. 1996; Megard et al. 1997; Zhou et al. 2001).

High-frequency sonar (~ 200 kHz) can detect sound-scatterers in the size range of lake zooplankton. While sonar by itself cannot discern the biological identities of sound-scatterers in aggregations, it can be used in conjunction with plankton nets to identify scatterers and to gain other information that neither method can provide alone. A large number of acoustic samples can be acquired and displayed rapidly to delineate aggregations at high precision with respect to depth and geographic coordinates. Surveys along transects, therefore, can detect and record major features of spatial distribution that are invisible with conventional sampling. Because sonar data can be displayed instantaneously, they also can identify sites and depth increments for more intensive sampling with plankton nets and other devices. Zooplankton investigations are no longer constrained by limits imposed by conventional “blind sampling” with nets at localities and depths selected arbitrarily.

Sonar may be used as a tool to assess the relative importance of abiotic versus biotic drivers of zooplankton patchiness (Zhou 1994; Pinel-Alloul 1995; Folt and Burns 1999). Abiotic factors that influence the spatial distribution of zooplankton include water movements (e.g., upwelling, Megard et al. 1997; Langmuir circulation, George and Edwards 1973) and thermal stratification (Pinel-Alloul et al. 1988; Pinel-Alloul and Pont 1991). Biological forces/activities that cause zooplankton to be distributed patchily include diel vertical migration (Young and Watt 1996), predation avoidance

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(Pijankowska and Kowalczewski 1997), searching for food (Tiselius 1992), and locating mates (Strickler 1998).

Patchiness is ecologically significant because it influences the interactions among individuals and populations. For example, extremely dense patches of zooplankton exert intense grazing pressure on phytoplankton in localized areas (Hembre 2002), and competition for food among individuals in a densely aggregated population will be stronger than in a population that is more evenly distributed. Also, interactions between predators (e.g., fish) and their zooplankton prey will be greatly affected by the ability of the fish to locate patchily distributed zooplankton aggregations.

Here we use single-beam, high-frequency sonar to investigate the properties of a population of a *Daphnia pulicaria*, a planktonic cladoceran (in the *D. pulex* group) that congregates below the mixed layer of a Minnesota lake (Long Lake) in the daytime during summer stratification. With a body length up to 3 mm, *D. pulicaria* is larger than most other zooplankton. The properties of *D. pulicaria* populations are of special interest because they and other large-bodied cladocerans play a central role in lacustrine food webs.

Large-bodied *Daphnia* feed efficiently on phytoplankton and can cause a "clear-water phase" in many lakes during late spring and early summer (e.g., Lampert et al. 1986; Luecke et al. 1990; Wright and Shapiro 1990; Hembre 2002). They are also important for fisheries management because they are often the preferred prey for size-selective planktivorous fish. The dominant planktivore in Long Lake is rainbow trout (*Oncorhynchus mykiss*), which is stocked annually by the Minnesota Department of Natural Resources (MDNR). Rainbow trout require cold water (<21°C), and abundant oxygen (>5 mg L⁻¹; Wang et al. 1996), which largely restricts them to foraging in the metalimnion during summer stratification. Because *D. pulicaria* migrate below the mixed layer during the daytime, there is substantial overlap in their habitat space with trout. Because of their spatial proximity, *D. pulicaria* comprise most of the trout diet during the summer (Hembre 2002), as they do in other lakes stocked with rainbow trout (e.g., Bevelhimer and Adams 1993; Geist et al. 1993; Wang et al. 1996).

Previous studies (Hembre 1996; Ross et al. 1996) of *D. pulicaria* in Long Lake used acoustic methods qualitatively to locate aggregations for sampling and to provide information about the overall spatial distribution of the population. To date, few acoustic studies have analyzed freshwater zooplankton populations quantitatively (exceptions: Rudstam et al. 1992; Melnik et al. 1993; Megard et al. 1997; Gal et al. 1999), and none have analyzed the target strength of *Daphnia*.

The research presented here (1) shows the spatial variation in backscattered sound over a season, (2) determines the relative contributions by *D. pulicaria* and smaller zooplankton to the total strength of backscattered sound as well as the target strength *D. pulicaria*, and (3) identifies how abiotic and biotic factors interact to shape the spatial distribution of the population.

Methods

Study site—Long Lake is a dimictic, oligo- to mesotrophic lake located in northwestern Minnesota (latitude 47°17'N, longitude 95°17'W). The lake has a single basin, is 2.4 km long, and has a surface area of 66.5 ha and a volume of 7.63 × 10⁶ m³. The basin is symmetrical, relatively deep (maximum depth = 24 m, mean depth = 13 m), and has a small littoral zone (~15% of lake surface area) (Schmid 1965). Its depth and simple morphometry make it ideal for acoustic analysis, and because interactions in the pelagic zone dominate the ecology of the lake, an understanding of the spatial distribution and abundance of *Daphnia* is especially relevant.

Fisheries management—Long Lake has been stocked with rainbow trout by the MDNR since 1961. Rainbow trout require streams with current-washed gravel to spawn. Such streams are not available to the trout in Long Lake, so trout abundance is not affected by reproduction. Instead, their abundance depends on the number stocked, natural mortality, and fishing mortality. Acoustic estimates of trout abundance indicate that fewer than 10% of the stocked trout remain in the lake after 12 months (Hembre 2002). In 1998, the MDNR switched from autumn to spring stocking of trout in Long Lake. So, on the first sampling date in 1998 (22 April), the lake had not been stocked with trout for 17 months (since November of 1996), and the acoustic estimate of trout density was very low (2.4 ha⁻¹). On 23 April 1998, 14,500 yearling rainbow trout were stocked (density = 218 ha⁻¹). Thereafter, the density of trout decreased linearly from 191 ha⁻¹ on 25 May to 30 ha⁻¹ on 24 October (Hembre 2002); representing 80 to 12 times the density of trout present on 22 April.

Instrument design and capabilities—We used a sonar system described earlier (Megard et al. 1997) to sample zooplankton in Long Lake at high resolution. The system consists of a Lowrance X-16 high-frequency (192-kHz) single-beam echosounder and a Loran-C navigation receiver connected to a portable computer. A narrow-beam transducer (4° half angle), directed vertically and suspended from the bow of the boat ~½ m below the lake surface emitted 100 μs acoustic pulses (often called "pings") at a rate of approximately one pulse per second. An analog-digital converter in the computer digitizes voltage variation due to sound back-scattered by zooplankton, fish, and other particles in 2,000 50-μs increments (bins), which correspond to depth increments of ~4 cm (28 acoustic samples m⁻¹). Backscattered sound from a near-field "dead zone" less than 1.2 m from the transducer is ignored.

The software calculates the strength of backscattered sound from the digitized signal strength in terms of volume scattering strength, using the sonar equations (Urick 1983) to compensate for transmission losses due to beam-spreading as sound travels from the transducer to scatterers and returns to the transducer. Volume scattering strengths, calculated with reference to a standard tungsten-carbide sphere (Foote and MacLennan 1984), are displayed in the format of an echogram on the computer monitor and saved on the hard

disk of the computer. Depths to be sampled with nets or other devices can be selected efficiently with respect to the locations of sound-scatterers, because echograms are displayed instantaneously.

Volume backscattering strength, expressed in terms of decibels, is

$$S_v = 10 \log s_v \quad (1)$$

where s_v , the volume backscattering coefficient, is the strength of backscattered sound at a distance of 1 m from an ensonified water volume. The volume backscattering coefficient depends on the concentration of animals N (m^{-3}) and their backscattering cross section, σ_{bs} ,

$$\sigma_{\text{bs}} = s_v/N \quad (2)$$

The backscattering cross section depends on the size of an acoustic target and often is expressed logarithmically in decibels as the target strength,

$$\text{TS} = 10 \log \sigma_{\text{bs}} \quad (3)$$

The size of scatterers can be calculated in terms of their equivalent spherical radius from backscattering cross section and wave number $k = 2\pi/\lambda = 838 \text{ m}^{-1}$ with

$$a = \{\sigma_{\text{bs}}/[k^4 \alpha^2]^{-1}\}^{1/6} \quad (4)$$

where $\alpha = 0.056$ is an acoustic contrast coefficient that depends on the relative density (g) and relative speed of sound (h) in a sound-scatterer (table 1 in Stanton 1989).

Field operations—To obtain information about the distribution and abundance of zooplankton across the whole lake on each sampling date, acoustic data were collected while traveling slowly ($\sim 5 \text{ km h}^{-1}$) along a transect of the lake's longest axis.

Conventional plankton samples and environmental data were obtained nearly simultaneously while the boat was anchored at a central sampling station where the lake is deepest (22–24 m). Zooplankton were collected with vertical tows of a closing Wisconsin-style plankton net (27 cm diameter, 130 μm mesh size) in depth increments that were identified by inspection of sound-scattering layers displayed on the computer (Fig. 1). To minimize the variance within samples, short tows (usually 2–3 m) were taken from depths with similar backscattering intensity within 15 min of recording acoustic data. Samples collected with nets were preserved in the field with a chilled sucrose–formalin solution (Prepas 1978) and refrigerated until they were analyzed. Temperature and dissolved oxygen concentration were measured at 1-m intervals with a YSI model-58 dissolved oxygen meter.

Laboratory methods—For each sample, the number of animals in five 5-ml subsamples were counted in six categories: large *D. pulicaria* ($>1.3 \text{ mm}$ in length), small *D. pulicaria* ($<1.3 \text{ mm}$ in length), calanoid copepods, cyclopoid copepods, nauplii, *Diaphanosoma*, and *Bosmina*. The 1.3-mm threshold for dividing *D. pulicaria* into 'large' and 'small' categories was chosen because it was the smallest size of a reproductive individual (Hembre 2002). Body lengths of 15–25 individuals of each taxon were measured

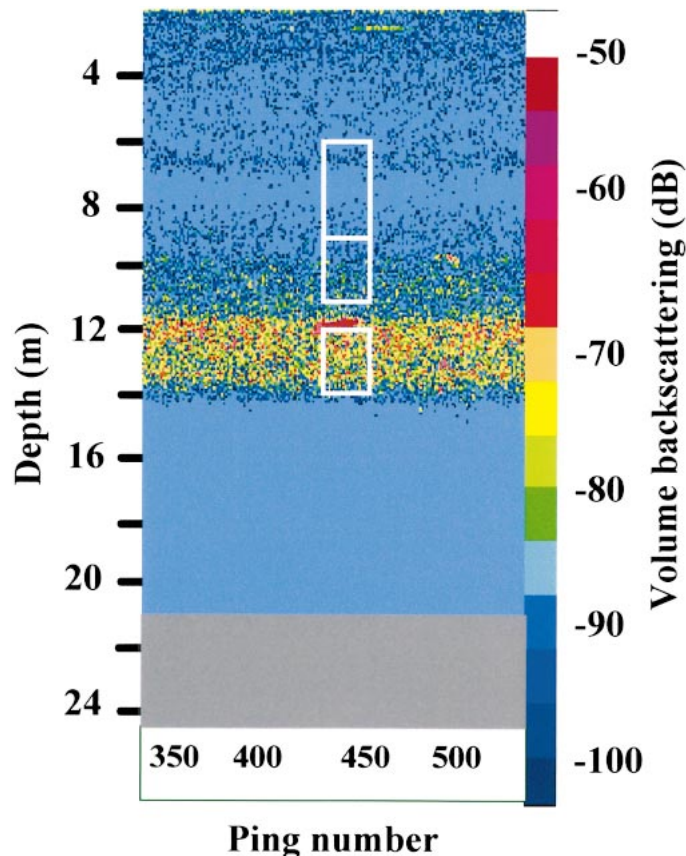


Fig. 1. Layers of sound scatterers detected while anchored at a sampling station (19 August 1999). Colors on echogram correspond to strength of backscattered sound (decibels, dB). Blue indicates weak backscattering, and orange–red indicates strong backscattering, as indicated by decibel values on the color scale. To calibrate the sonar information, sound scattered from depth increments (indicated by white rectangles) was compared with zooplankton densities calculated from plankton net samples.

to the nearest 0.05 mm. Biomass was calculated from body length with regression equations (Malley et al. 1989).

A subset of the samples ($n = 32$) was analyzed for displacement volume (Postel et al. 2000). Displacement volume is a measure of zooplankton biovolume, independent of acoustic estimates. To determine displacement volume, the sample volume was measured in a 25-ml graduated cylinder. The sample was then filtered through a glass-fiber filter with gentle vacuum pressure ($\sim 250 \text{ mm Hg}$). The displacement volume is the difference between the initial sample volume and the filtrate volume.

Calibration of acoustic data—Target strengths of large *Daphnia* (Eq. 3) were computed with data from 13 dates between 11 October 1996 and 16 May 2000 (Table 1) when acoustic data were collected just prior ($<15 \text{ min}$) to net sampling. Mean volume backscattering strength (MVBS) in depth increments sampled with plankton nets was calculated from volume backscattering strengths from 50 consecutive acoustic pulses at a vertical resolution of 10 acoustic samples

Table 1. Mean volume backscattering (MVBS), target strengths (TS), concentrations (10^3 animals m^{-3}), and mean body lengths of zooplankton in depth increments that were sampled with both sonar and a plankton net. Body lengths were not measured (nm) for samples from 1996–97.

Date	Z (m)	MVBS (dB)	TS (dB)	Concentration (10^3 animals m^{-3})					Mean body length (mm)						
				Ldp	Sdp	Cal	Cyc	Nau	Bos	Dia	Dp	Cal	Cyc	Nau	Bos
11 Oct 1996	20–15	-96.6	-122	0.35	0.35	4.61	14.7	1.12	1.53	—	nm	nm	nm	nm	nm
11 Oct 1996	13–11	-80.6	-116	3.38	0.00	3.21	23.3	22.2	1.82	—	nm	nm	nm	nm	nm
11 Oct 1996	10–7	-92.7	-117	0.26	0.26	18.9	4.98	1.40	6.89	—	nm	nm	nm	nm	nm
11 Oct 1996	22–0	-91.4	-120	0.69	0.08	9.11	7.76	0.57	2.67	—	nm	nm	nm	nm	nm
7 Aug 1997	13–10	-81.8	-118	4.21	2.07	11.0	19.6	1.94	—	0.47	nm	nm	nm	nm	nm
7 Aug 1997†	11–8	-76.0	-115	7.77	3.83	5.85	23.5	1.40	—	0.09	nm	nm	nm	nm	nm
7 Aug 1997†	8–5	-79.2	-117	5.79	1.45	23.7	25.6	0.84	—	8.12	nm	nm	nm	nm	nm
21 Sep 1997†	12.5–11	-86.4	-125	7.30	4.10	3.58	24.9	2.49	—	—	nm	nm	nm	nm	nm
21 Sep 1997†	10–8	-85.7	-119	2.18	0.09	3.40	7.24	1.05	0.35	—	nm	nm	nm	nm	nm
21 Sep 1997†	7–2	-73.0	-112	8.40	0.35	10.5	2.27	0.38	0.97	0.22	nm	nm	nm	nm	nm
22 Apr 1998	23–19	-97.4	-121	0.24	0.57	0.29	9.25	0.47	—	—	1.30	1.05	0.83	0.20	—
22 Apr 1998	15–11	-99.8	-123	0.23	1.28	2.16	29.6	3.34	—	—	1.37	1.05	0.54	0.20	—
22 Apr 1998	11–7	-95.9	-121	0.30	0.94	1.24	2.16	0.95	—	—	1.30	1.02	0.53	0.20	—
22 Apr 1998	7–3	-81.7	-112	1.18	3.74	2.17	75.8	8.13	—	—	1.30	1.08	0.56	0.21	—
25 May 1998	22–18	-71.9	-108	3.60	0.54	0.58	5.86	1.36	—	—	2.30	0.86	0.74	0.20	—
25 May 1998	18–14	-72.2	-110	5.60	2.06	1.88	6.81	1.73	—	—	2.07	1.04	0.61	0.20	—
25 May 1998	13–11	-69.2	-110	11.2	6.02	4.40	9.84	2.62	—	—	1.79	1.02	0.58	0.20	—
25 May 1998	11–9	-71.3	-115	23.4	7.39	5.65	7.12	4.40	—	—	1.67	0.73	0.52	0.20	—
25 May 1998	9–5	-76.7	-108	1.49	19.8	13.9	9.01	4.03	—	—	1.59	0.84	0.52	0.20	—
25 May 1998	22–0	-73.1	-110	4.97	0.74	3.97	2.79	0.19	—	—	1.78	0.85	0.61	0.20	—
25 Jul 1998	19–16	-76.8	-118	14.4	1.60	1.02	26.6	0.15	—	—	1.94	0.88	0.78	0.20	—
25 Jul 1998	15–13	-80.9	-117	3.88	4.75	5.24	21.6	1.31	0.13	—	1.49	0.83	0.59	0.18	0.30
25 Jul 1998	13–10	-84.6	-113	0.68	6.11	30.2	20.8	1.07	0.39	0.10	1.12	0.82	0.54	0.18	0.30
25 Jul 1998	22–0	-86.3	-121	3.05	2.04	5.50	1.17	0.38	0.17	0.02	1.64	0.77	0.71	0.20	0.33
22 Aug 1998	16–14	-83.9	-124	10.1	3.65	1.47	21.8	2.30	—	—	1.70	0.85	0.60	0.19	—
22 Aug 1998	13–11	-82.5	-116	2.34	1.26	13.7	11.1	1.09	0.11	1.64	1.61	0.93	0.53	0.19	0.35
22 Aug 1998	4–2	-97.2	-117	0.10	0.25	1.51	0.76	2.85	—	0.29	1.41	0.57	0.63	0.2	0.52
24 Oct 1998	16–13	-86.5	-121	2.77	3.12	0.78	68.6	0.16	0.16	—	1.75	1.08	0.88	0.19	0.30
24 Oct 1998	22–0	-108.1	-135	0.48	0.21	4.15	16.6	0.37	0.29	—	1.70	1.20	0.90	0.20	0.40
24 Apr 1999	18–16	-77.3	-118	10.9	0.95	0.42	5.97	1.57	—	—	2.11	0.73	0.67	0.19	—
24 Apr 1999	12–9	-108.7	-132	0.19	0.57	6.86	17.6	4.48	—	—	1.13	0.86	0.45	0.19	—
31 May 1999	22–19	-85.0	-120	3.10	2.07	1.40	10.7	0.18	—	—	1.54	0.68	0.63	0.20	—
31 May 1999	19–16	-84.3	-119	3.18	0.80	5.08	8.41	0.29	—	—	1.68	0.87	0.62	0.19	—
31 May 1999	15–12	-94.2	-127	2.00	4.27	22.8	8.80	2.61	—	—	1.31	0.76	0.58	0.20	—
31 May 1999	12–9	-93.3	-123	0.87	3.46	10.6	7.51	3.10	—	—	1.10	0.88	0.46	0.18	—
31 May 1999	8–4	-94.5	-122	0.54	2.18	15.1	3.01	2.03	—	—	1.02	0.77	0.49	0.15	—
31 May 1999	22–0	-90.3	-126	3.30	2.60	24.2	9.85	1.60	—	0.07	1.51	0.73	0.51	0.20	1.10
10 Jul 1999	18–17	-77.5	-125	51.3	8.36	5.24	46.1	0.70	—	—	1.86	0.79	0.64	0.20	—
10 Jul 1999	16–13	-84.2	-126	16.1	7.59	7.21	9.19	0.23	—	—	1.68	0.86	0.61	0.25	—
19 Aug 1999	14–12	-79.3	-126	41.9	7.98	1.05	25.1	0.70	0.35	0.35	1.54	0.70	0.72	0.18	0.33
19 Aug 1999	11–9	-95.2	-131	3.36	13.4	3.32	12.7	2.27	1.05	0.35	1.14	0.68	0.63	0.16	0.28
19 Aug 1999	9–6	-110.2	-133	0.20	0.74	5.93	6.05	1.86	2.09	4.42	1.14	1.01	0.44	0.17	0.33

Table 1. Continued.

Date	Z (m)	MVBS (dB)	TS (dB)	Concentration (10^3 animals m^{-3})						Mean body length (mm)					
				Ldp	Sdp	Cal	Cyc	Nau	Bos	Dia	Dp	Cal	Cyc	Nau	Bos
16 May 2000	20–18	-73.5	-114	10.1	2.52	0.11	25.5	0.73	—	1.80	0.82	0.68	0.18	—	—
16 May 2000	18–16	-73.9	-116	14.6	0.61	1.92	6.12	0.93	0.04	1.90	0.70	0.61	0.18	—	—
16 May 2000	16–14	-72.9	-115	17.6	4.40	1.36	28.2	3.25	—	1.85	0.85	0.58	0.21	—	—
16 May 2000	14–12	-81.7	-124	16.6	5.26	3.35	27.6	1.26	—	1.67	0.77	0.52	0.18	—	—
16 May 2000	12–10	-81.2	-120	8.00	1.53	2.62	12.4	3.35	—	1.76	0.92	0.48	0.21	—	—
16 May 2000	10–8	-86.6	-128	13.4	10.6	18.0	30.1	8.69	—	1.50	0.76	0.50	0.23	—	—
16 May 2000	8–6	-113.3	-139	0.33	1.24	37.5	16.4	8.38	—	1.01	0.79	0.52	0.22	—	—
Mean		-85.6	-120	7.12	3.26	7.51	16.7	2.42	0.39	1.57	0.86	0.60	0.19	0.36	0.81

* Z, net sampling intervals; MVBS, mean volume backscattering strength; TS, target strength of large *Daphnia*; Ldp, large *Daphnia* (>1.3 mm); Sdp, small *Daphnia* (<1.3 mm); Cal, calanoid copepods; Cyc, cyclopoid copepods; Nau, copepod nauplii; Bos, *Bosmina*; Dia, *Diaphanosoma*.

† Samples collected at night, a Dp, mean length of all *Daphnia pulex*.

per meter. Saturating signals from large targets (presumably fish) were omitted.

Patchiness analysis—The exponent b in an equation ($s^2 = am^b$) that relates the variance (s^2) to the mean (m) concentrations of *Daphnia* equivalents was used as an index of *Daphnia* patchiness along the lake's longest axis (i.e., horizontal heterogeneity) on each date. Values of b increase as aggregation increases (Taylor 1961; Downing 1991; Pinel-Alloul 1995). Means and variances of acoustic backscattering were computed from 50 evenly spaced acoustic pulses at 0.1-m increments in depths that contained *Daphnia*.

To evaluate vertical patchiness, mean daytime acoustic concentrations of *Daphnia* in three "habitat zones" were compared on four dates in 1998: 27 June, 25 July, 22 August, and 24 October. We defined the habitat zones (i.e., trout zone, refuge zone, hypoxic zone) on the basis of oxygen concentration. Depths below the epilimnion where oxygen concentrations exceed 5 mg L^{-1} are considered the "trout zone" because they are suitable for rainbow trout (Wang et al. 1996) and represent depths where trout and *Daphnia* potentially overlap. Depths with oxygen concentrations between 3 and 5 mg L^{-1} are defined as the "refuge zone," because oxygen levels are lower than the threshold for trout but greater than the threshold concentration at which *Daphnia* become physiologically stressed. Kring and O'Brien (1976) showed that *D. pulex* (a closely related species) had significantly higher filtering rates and elevated hemoglobin production at oxygen concentrations below 3 mg L^{-1} . Depths with oxygen concentrations between 1 and 3 mg L^{-1} are defined as the "hypoxic zone." Studies have shown that 1 mg L^{-1} is typically the lower limit for survival of *Daphnia* (Weider and Lampert 1985; Wright and Shapiro 1990). These analyses were not done for 22 April and 25 May 1998 because oxygen concentrations exceeded 5 mg L^{-1} at all depths.

Results

Spatial variation of backscattered sound—Backscattered sound varied by many orders of magnitude, typically between -100 and -50 dB, during daylight over a distance of nearly 2.5 km along the longest (east–west) axis of the lake during spring, summer, and autumn (Fig. 2). The spatial distribution of the sound-scatterers changed substantially during this time. Sound-scatterers were aggregated in a surface layer (depths <7 m) in April, and in a deeper layer within and below the thermocline during summer and autumn. Large-scale water movements affected the locations, sizes, and shapes of the layers. Upwelling of deep water diluted the surface scattering layer at the east end of the lake in April. Internal stationary waves (seiches) tilted the deep scattering layer in July and August. Smaller-scale transport processes produced several kinds of curved echotraces. Traveling internal waves produced sinuous echotraces at the tops and bottoms of scattering layers, and eddies produced longer curved echotraces within and between the layers.

Identity of sound-scatterers—Attributes of the layers indicate that the sound-scatterers were zooplankton, as con-

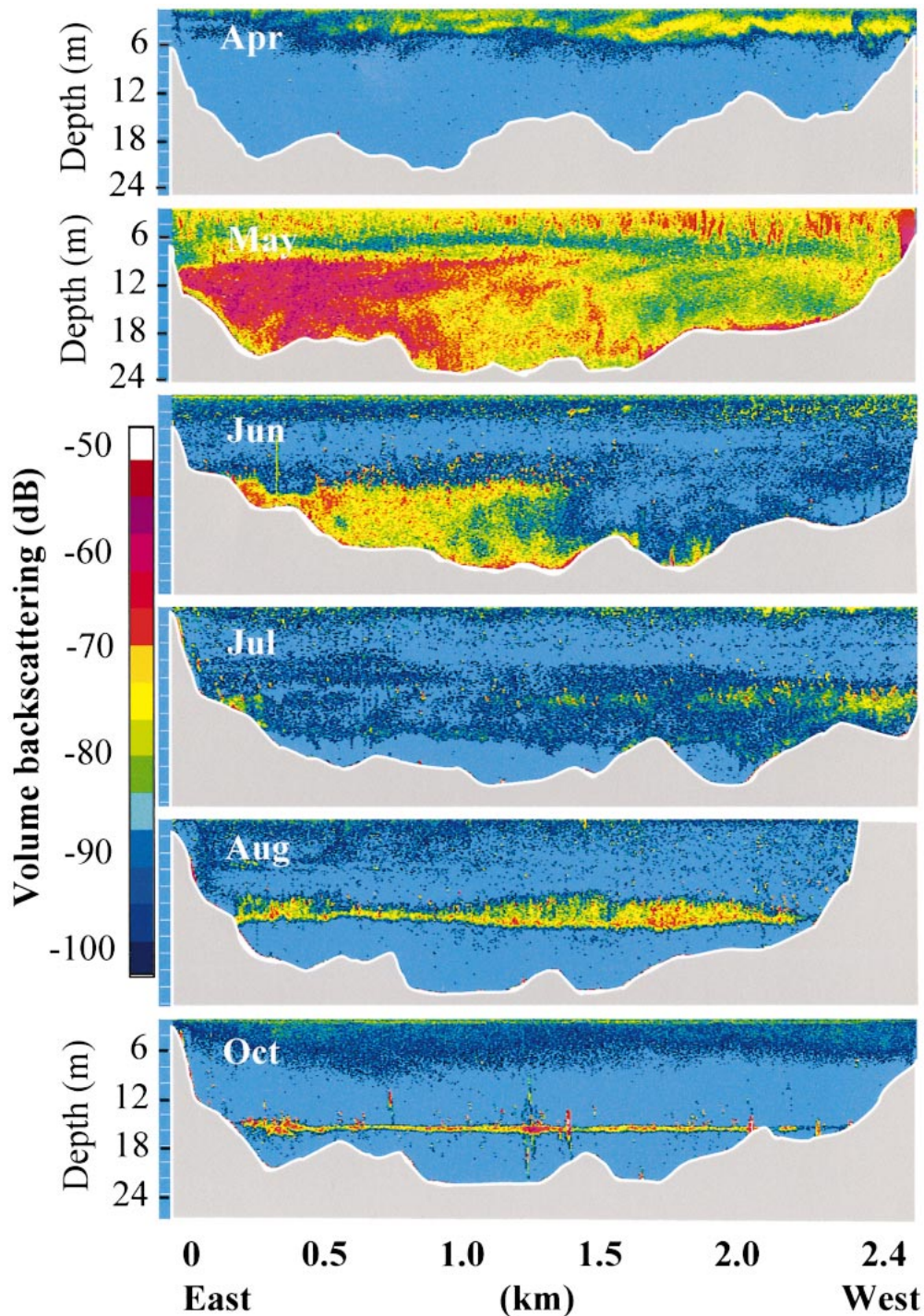


Fig. 2. Seasonal variation of backscattered sound along the long axis (2.4 km) of the lake during spring, summer, and autumn 1998. Gray area indicates lake bottom.

firmed by precise sampling with plankton nets of depth increments identified with sonar (Fig. 1). Most of the backscattered sound in 49 depth increments sampled with plankton nets during 4 yr was attributable to large (body length >1.3 mm) *Daphnia* (Fig. 3, top left; Table 1) with a mean target strength (TS) of -120 dB.

All planktonic crustaceans in this lake are “Rayleigh scat-

terers” of 192 kHz sound, with body lengths (0.2–3 mm) that are shorter than the wavelength (7.5 mm) at this frequency. Rayleigh scattering is proportional to the sixth power of size (Clay and Medwin 1977; Holiday and Pieper 1980, 1995; Stanton 1989). Since *D. pulicaria*, with mean body length ~ 1.6 mm, is about twice as large as the next-largest zooplankters in this lake (Table 1), scattering by individual

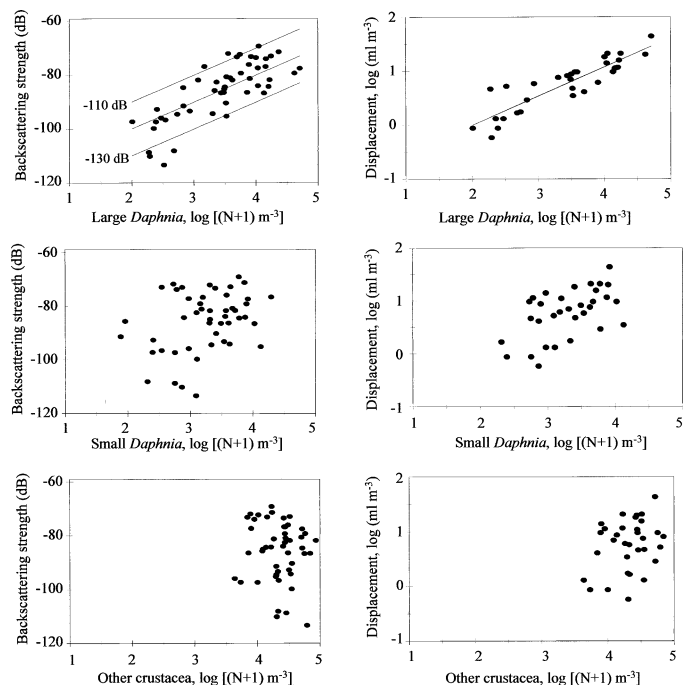


Fig. 3. Dependence of mean volume backscattering strength (left) and displacement volume of zooplankton (right) on concentration of large *Daphnia*, small *Daphnia*, and other planktonic crustaceans. Volume backscattering strength and displacement volume depend most strongly on the concentration of large *Daphnia* (Table 2).

Daphnia is about $2^6 = 64$ times larger than that of individuals of the second-largest taxon.

MVBS was independent of the concentration of smaller *Daphnia* and other planktonic crustaceans (Fig. 3, left). In a multiple linear regression of MVBS versus log zooplankton concentrations, large *Daphnia* was the only predictor variable that was significant ($P < 0.0001$, $r^2 = 0.67$, Table 2). A backward stepwise regression revealed that no other coefficients were significant. A simple linear regression of MVBS on the log concentration of large *Daphnia* also was significant ($P < 0.0001$) and explained nearly as much of the variance (63%) in MVBS as the multiple regression (Table 3).

Displacement volume, an independent measure of zooplankton biovolume (Postel et al. 2000), also covaried with the concentration of large *Daphnia*, but not with concentrations of smaller crustaceans (Fig. 3, right). This is consistent with the dependence of acoustic backscattering on large *Daphnia*, because volume backscattering strength is a function of the total acoustic cross sections (and therefore volumes) of scatterers ininsonified water volumes (Eq. 4).

Much of the variance of MVBS not attributable to *Daphnia* concentration is due to variation of the size and target strength of individuals. The mean target strength (-120 dB) corresponds to an equivalent spherical radius (ESR) of 0.28 mm (Eq. 4), which is about 20% of the mean body length of *Daphnia* (1.6 mm), computed independently from measurements of individuals with an optical micrometer (Table 1). Most of the data in the scattergram (Fig. 3, top left) fall within boundaries predicted for animals with target strengths between -110 and -130 dB. The ESR of animals with these target strengths is 0.19 mm and 0.40 mm, respectively. Equivalent spherical volumes of animals with the minimum, mean, and maximum target strengths are 0.03 , 0.09 , and 0.27 mm³, respectively. Thus, a doubling of ESR corresponds to a 10-fold change of volume and is a partial indication of why acoustic backscattering is sensitive to small changes of ESR. Other zooplankton scattered relatively little sound in this lake because they were smaller or less abundant than *Daphnia*. For example, the mean body length of calanoid copepods was typically <1.0 mm, and that of cyclopoids was usually <0.7 (Table 1), so their target strengths are considerably less than -130 dB.

MVBS was also regressed against the biomass of all the zooplankton taxa ($\log_{10}(x+1)$ transformed). Fewer samples ($n = 39$) were included in this analysis because the body lengths of animals in the samples from 1996 to 1997 were not determined. This regression was also highly significant and explained a higher percentage of the variance ($P < 0.0001$, $r^2 = 0.79$, Table 4) than did the regression on zooplankton concentration (Table 2). In this analysis, *Daphnia* were not separated into 'large' and 'small' categories. As in the multiple regression of MVBS versus zooplankton concentration, none of the coefficients other than *Daphnia* became significant in a backward stepwise regression. The sim-

Table 2. Multiple linear regression of mean volume backscattering strength (dB) versus $10 \log_{10}$ concentration (no. m^{-3}) of zooplankton taxa. The regression is significant ($p < 0.0001$) and the R^2 is 0.67.

Predictor variable	Coefficient	Std. error	Student's T	<i>p</i> -value	
Constant	-104.1	13.19	-7.89	<0.0001	
Large <i>Daphnia</i>	1.343	0.164	8.17	<0.0001	
Small <i>Daphnia</i>	-0.110	0.176	-0.63	0.533	
Calanoid	-0.217	0.202	-1.08	0.389	
Cyclopoid	-0.445	0.262	-1.70	0.097	
Nauplii	0.061	0.225	0.27	0.787	
<i>Diaphanasoma</i>	-0.018	0.090	-0.20	0.842	
<i>Bosmina</i>	-0.027	0.091	-0.30	0.765	
Source	df	SS	MS	<i>F</i>	<i>p</i> -value
Regression	7	3842	548.8	11.97	<0.0001
Residual	41	1880	45.85		
Total	48	5722			

Table 3. Simple linear regression of mean volume backscattering strength (dB) versus 10 Log_{10} concentration (no. m^{-3}) of large *Daphnia*. The regression is significant ($p < 0.0001$) and the R^2 is 0.63.

Predictor variable	Coefficient	Std. error	Student's T	p -value	
Constant	-128.8	4.966	-25.93	<0.0001	
Large <i>Daphnia</i>	1.254	0.142	8.86	<0.0001	
Source	df	SS	MS	F	p -value
Regression	1	3578	3578	78.44	<0.0001
Residual	47	2144	45.61		
Total	48	5722			

ple regression of MVBS on *Daphnia* biomass was significant and explains a larger proportion of the variance of MVBS ($P < 0.0001$, $r^2 = 0.73$, Table 5) than does *Daphnia* abundance alone, because total biomass depends on both abundance and body size.

Net tows from the entire water column indicated that *Daphnia* comprised most (60–90%) of the total zooplankton biomass during spring and summer but only 20% in October (Fig. 4), when *Daphnia* were compressed into a very thin deep layer and calanoid copepods were relatively abundant in shallower water.

Spatial heterogeneity of Daphnia—Because sound-scattering by other zooplankton was negligible (Table 2, Fig. 3), most measurements of backscattered sound in Long Lake can be expressed in terms of equivalent concentrations of large *Daphnia*. For this, we define a “*Daphnia* equivalent” as a unit of sound-scattering equal to the mean backscattering cross section and mean target strength (–120 dB) of large *Daphnia*.

To aid in the biological interpretation of the sound-scattering layers in Fig. 2, we examined the concentrations of *Daphnia* equivalents at several depths along the longest axis of the lake in May and October (Fig. 5). In May, the level of backscattered sound measured in the deep scattering layer (9 and 12 m) was approximately –60 dB for a distance of about 800 m from the eastern end of the lake (Fig. 5, top left, left scale), and this level decreased to about –75 dB at the western end. These backscattering levels are equivalent to concentrations that range between 10^6 and 10^4 equivalents m^{-3} (Fig. 5, left panels, right scale). Concentrations in a

shallower depth increment (6 m), where backscattering was much lower (~ -80 dB) at the time of the May sampling, corresponded to only $\sim 10^4$ equivalents m^{-3} .

In October, volume backscattering strength in the thin deep scattering layer (16 m) corresponded to concentrations between 10^4 and 10^6 *Daphnia* equivalents m^{-3} (Fig. 5, right panels). The typical concentration was only 10^2 equivalents m^{-3} in water only 0.8 m above the scattering layer. These estimates of concentration in terms of *Daphnia* equivalents are probably close approximations, since the target strengths of most *Daphnia* are -120 ± 10 dB (Fig. 3).

Seasonal changes in horizontal and vertical patchiness—Data from the long-axis acoustic transects (Fig. 2) reveal seasonal changes in the daytime spatial distribution of *Daphnia*. On 22 April (Fig. 2, top), the day before 14,500 rainbow trout were stocked to the lake, the population was aggregated in surface waters (<7 m). Temperatures at depths shallower than 7 m were slightly warmer (6–8°C) than in deeper water, where temperatures were between 4°C and 6°C (Fig. 6). After trout were stocked and thermal stratification intensified, the *Daphnia* population resided below the mixed layer during daytime to the deepest extent possible given oxygen constraints ($\sim < 1.0$ mg L^{-1} , Fig. 6). On 25 May and 27 June, when oxygen levels were high in the hypolimnion, the population was largely distributed below the thermocline, and the horizontal heterogeneity of the population's spatial distribution was high (Fig. 7). On 25 July, anoxia in the deep hypolimnion (below 20 m) excluded *Daphnia*, and the population was distributed in the upper hypolimnion (14–20 m) and the lower metalimnion (10–14 m). On 22 August, the

Table 4. Multiple linear regression of mean volume backscattering strength (dB) versus $\text{Log}_{10}(x + 1)$ biomass ($\mu\text{g m}^{-3}$) of zooplankton taxa. The regression is significant ($p < 0.0001$) and the R^2 is 0.79.

Predictor variable	Coefficient	Std. error	Student's T	p -value	
Constant	-124.9	13.16	-9.49	<0.0000	
<i>Daphnia</i>	14.11	1.494	9.44	<0.0000	
Calanoid	-2.692	1.838	-1.46	0.153	
Cyclopoid	-4.463	2.254	-1.98	0.056	
Nauplii	-1.166	2.244	-0.52	0.607	
<i>Diaphanosoma</i>	-0.548	1.091	-0.50	0.619	
<i>Bosmina</i>	-0.978	1.703	-0.57	0.570	
Source	df	SS	MS	F	p -value
Regression	6	4084	680.7	19.89	<0.0001
Residual	32	1095	34.2		
Total	38	5179			

Table 5. Simple linear regression of mean volume backscattering strength (dB) versus $10 \log_{10}(x + 1)$ biomass ($\mu\text{g m}^{-3}$) of *Daphnia*. The regression is significant ($p < 0.0001$) and the R^2 is 0.73.

Predictor variable	Coefficient	Std. error	Student's T	p -value
Constant	-155.5	7.07	-22.0	<0.0001
<i>Daphnia</i>	14.0	1.41	9.93	<0.0001
Source	df	SS	MS	F
Regression	1	3766	3766	98.6
Residual	37	1413	38.2	
Total	38	5179		

population was almost entirely aggregated in the metalimnion (11–14 m). Only the upper hypolimnion (14–15.5 m) contained enough oxygen for *Daphnia*. On 24 October, the hypolimnion was devoid of oxygen, and the population was compressed into the metalimnion (15–16.5 m). From July to October, as the population became increasingly restricted to the metalimnion, horizontal spatial heterogeneity decreased (Fig. 7).

On all dates on which the lake contained a *Daphnia* refuge (i.e., depths with oxygen concentrations between 3 and 5 mg L⁻¹), *Daphnia* were significantly more abundant in the refuge than in the other habitat zones (Fig. 8). On 27 June, concentrations were significantly higher ($t = 4.62$, $df = 152$, $P < 0.0001$) in the refuge (depths below 17 m) than in the trout zone (5–17 m). On 25 July, concentrations in the refuge (15–17.5 m) were significantly higher ($F_{2,129} = 12.32$, $p < 0.0001$) than in the trout zone (6–15 m) or the hypoxic zone (17.5–20 m). On 22 August, concentrations in the refuge (13.5–15 m) also significantly exceeded ($F_{2,206} = 298.7$, $P < 0.0001$) those in the trout zone (8.5–13.5 m) and the hypoxic zone (15–16 m). By 24 October, the daytime habitat for *Daphnia* was compressed to a depth interval of just 2 m (15–17 m) in the thermocline. Again, concentrations in the refuge (16–16.5 m) were significantly higher ($F_{2,53} = 12.32$,

$P = 0.0001$) than in the trout (15–16 m) or hypoxic (16.5–17 m) zones.

Diel changes of spatial distribution—As a result of diel vertical migration, the spatial distribution of the sound-scatterers at night was very different than it was during the day, as illustrated by backscattered sound recorded on 24 October before, during, and after upward migration (Fig. 9A). The daphnid sound-scatterers, congregated in the thin metalimnetic lens at the interface between oxic and anoxic water before sunset (Fig. 9B,C), began to migrate vertically within minutes after sunset. Within an hour, they had dispersed throughout the surface mixed layer (Fig. 9B,D). Acoustic backscattering in the scattering layer decreased approximately two orders of magnitude during migration, an amount that corresponds to a decrease of almost 100,000 *Daphnia* equivalents m⁻³ in less than 1 h.

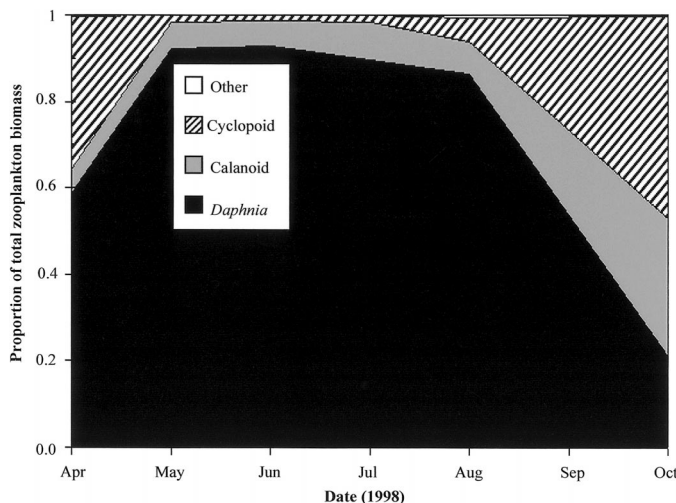


Fig. 4. Proportions of taxa in zooplankton biomass in 1998. *Daphnia* dominated the zooplankton until fall, when copepods became abundant. 'Other' taxa (nauplii, *Bosmina*, and *Diaphanosoma*) never comprised a large portion of the zooplankton biomass.

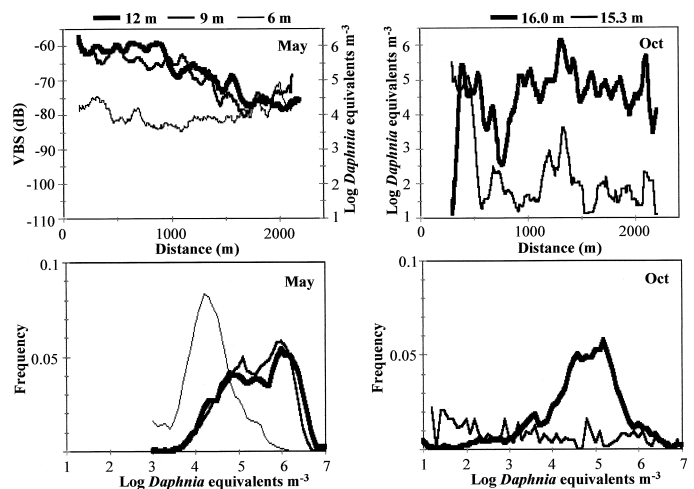


Fig. 5. Spatial variation of volume backscattering strength and equivalent concentration of *Daphnia* at various depths along the long axis of the lake during daylight on 25 May and 24 October 1998 (see echograms in Fig. 2). Volume backscattering was high (> -80 dB) throughout the lake in May (top left) but was especially high at the eastern end of the lake in the deep scattering layer (9- and 12-m profiles). In May, the most frequent concentration of *Daphnia* in the deep scattering layer was about two orders of magnitude greater than at 6 m (bottom left). In October (right panels), the typical concentration of *Daphnia* equivalents was four orders of magnitude greater within the deep scattering layer (16 m) than it was 0.7 m above it (15.3 m).

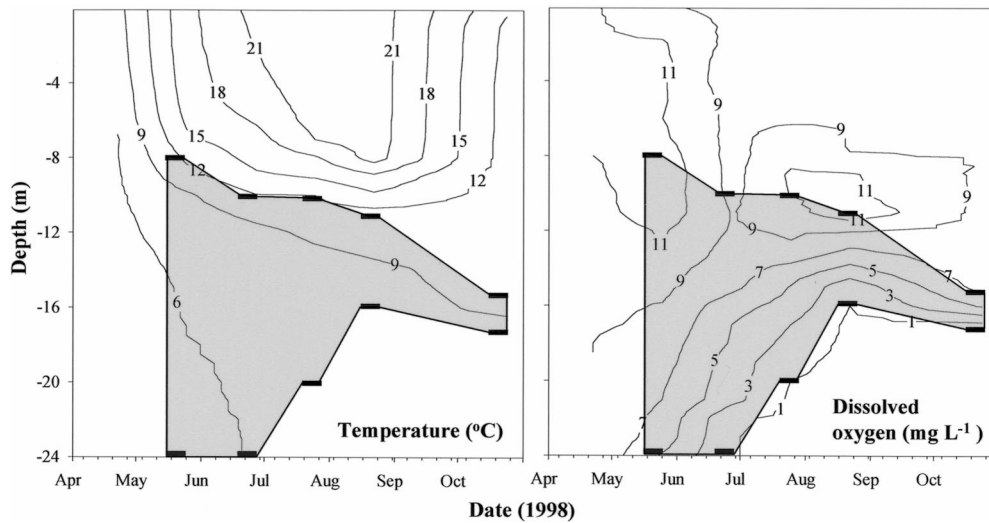


Fig. 6. The spatial extent of the deep scattering layer (shaded) compared with temperature and oxygen isopleths in 1998.

Discussion

Simple single-beam sonar can sample sound-scatterers at high resolution in both vertical and horizontal dimensions and thus provides essential spatial information for mapping plankton distributions rapidly. The locations and boundaries of plankton patches can be related to water masses efficiently, as was observed in this study. Because it is not feasible to collect enough plankton samples with conventional methodology, descriptions of plankton patchiness have been limited until now to statistical indices (*see* Downing 1991 and Pinel-Alloul 1995 for comprehensive reviews). Now we can visualize the locations, boundaries, and internal densities of patches and determine how they are related to underlying mechanisms.

Sonar provides no information about plankton identity, but

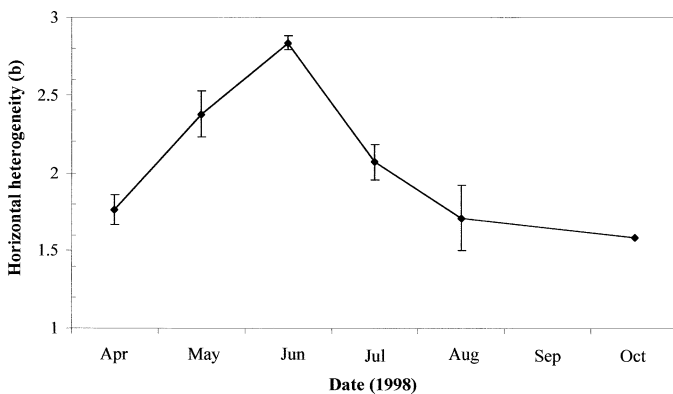


Fig. 7. Horizontal spatial heterogeneity of *Daphnia* equivalents during 1998. Horizontal patchiness (quantified by the slope [b] of the power function of the variance vs. the mean concentration of *Daphnia* equivalents) was highest in May and June, when the population was hypolimnetic. Horizontal heterogeneity decreased significantly later in the year, when the population aggregated at depths in which there was a pronounced temperature gradient. Error bars represent two standard errors of the slope.

it is invaluable for detecting aggregations and for selecting depth increments for precise sampling with plankton nets. Information about the identities, abundances, and sizes of sound-scatterers obtained by coordinated conventional and acoustic sampling can be used with Rayleigh scattering theory to calculate target strengths and thus to calibrate measurements of backscattered sound in terms of concentrations of organisms. Several sources of variation exist between acoustic and net sampling estimates of zooplankton concentration. These include (1) variation in the scattering characteristics of individual animals (Chu et al. 1992), (2) scattering by nonfocal species (Coyle 2000), and (3) net avoidance or inefficiency (Greene et al. 1989). Given these sources of variability, the relationship we found between MVBS and the concentration of large *Daphnia* from net samples was quite strong ($r^2 = 0.63$) and is within the range of relationships ($r^2 = 0.23$ – 0.93) found in other studies of freshwater zooplankton populations (Coyle 2000). The relationship was even stronger for the regression of MVBS on *Daphnia* biomass ($r^2 = 0.73$, Table 5), which depends on both concentration and size. Because backscattering depends strongly on the radius of a target (Clay and Medwin 1977; Megard et al. 1997), backscattering by *D. pulicaria* obscured signals from smaller, co-occurring taxa (Tables 2, 4). Had our focal species been smaller, single-frequency sonar would not have allowed this analysis.

Here, we evaluated the target strength of an important planktonic crustacean, *D. pulicaria*, for the first time (Table 1) and used scattering theory to confirm that the target strength was consistent with the physical size of the organism. The target strength of *Daphnia* enabled us to describe spatial distributions in the entire lake at high resolution on many days (Figs. 5, 7, and 8). This method is relevant for ecological studies of pelagic food webs and could also be used by fisheries managers to aid with decision making regarding the timing and the level of fish stocking (Hembre 2002). Also, because acoustic surveys such as those presented here provide high-resolution, instantaneous data over

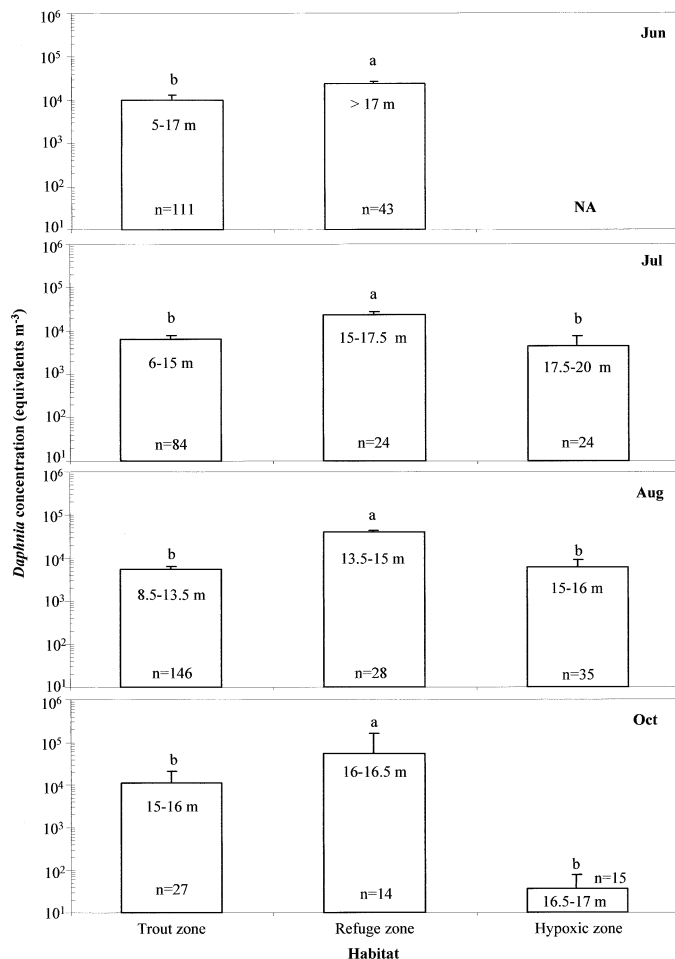


Fig. 8. Mean concentration of *Daphnia* (equivalents m^{-3}) in three different habitat zones from June to October 1998. Lowercase letters (a, b) above bars indicate whether groups differ from each other significantly ($P < 0.05$). In June, concentrations were significantly higher ($t = 4.62$, $df = 152$, $P < 0.0001$) in the refuge zone (O_2 concentrations 3–5 $mg L^{-1}$) than in the trout zone (O_2 concentrations $> 5 mg L^{-1}$). Oxygen concentrations were above 3 $mg L^{-1}$ at all depths on this date, so the hypoxic zone (O_2 concentrations 1–3 $mg L^{-1}$) did not exist. In July, concentrations were significantly higher ($F_{2,129} = 54.95$, $P < 0.0001$) in the refuge zone than in either the trout or hypoxic zones. *Daphnia* were also more abundant in the refuge zone than in other zones in August ($F_{2,206} = 298.7$, $P < 0.0001$) and October ($F_{2,53} = 12.32$, $P = 0.0001$). April and May sampling dates were excluded from this analysis because oxygen concentrations exceeded 5 $mg L^{-1}$ at all depths. Depths of the habitat zones and sample sizes (n) are noted within the bars. Error bars indicate two standard errors of the mean.

large areas, they have utility for detecting sudden zooplankton die-offs caused by pesticides or toxic algae blooms.

Precision sampling—The use of sonar together with conventional sampling revealed extreme levels of patchiness, in which zooplankton densities sometimes varied by as many as four orders of magnitude over very small distances (< 1 m, Fig. 5). Such spatial heterogeneity is usually blurred by plankton samples collected without the aid of sonar, because “blind” net tows can traverse wide ranges of densities. Ac-

cess to this “real time” data showing the location and limits of aggregations was especially useful for a study of habitat partitioning by clones of the Long Lake *D. pulicaria* population (Hembre 2002). By sampling aggregations precisely at specific depths it was possible to document the genetic differentiation of the population with respect to depth and to identify clones with different habitat affinities. Had conventional plankton samples been taken at fixed depth intervals, they would likely have mixed patches that differed genetically, and the ability to detect habitat segregation among clones would have been reduced.

Seasonal patterns of patchiness—Interactions between lake physics and trout predation (or predation risk) shaped the patchiness of *D. pulicaria* seasonally. On 22 April, the day before 14,500 rainbow trout were stocked, *Daphnia* were aggregated in shallow water (< 7 m, Fig. 2), where temperature was somewhat higher than in deeper water (Fig. 6). On all dates after the stocking of trout, the population aggregated in deep water during the daytime. This observation is consistent with the expectations of vertical migration theory. That is, when the risk of predation by fish is low, zooplankton will take advantage of warmer surface waters in which their development (growth and reproduction) is maximized (Dawidowicz 1994; Loose and Dawidowicz 1994). When predation risk is high, zooplankton are expected to migrate downward during the day (Zaret and Suffern 1976).

In May and June, the population resided primarily in the oxic hypolimnion during the day (Fig. 2) and was distributed heterogeneously along the lake’s longest axis (Fig. 7). From July to October, as oxygen concentrations progressively declined in the hypolimnion, the population became more metalimnetic and more uniformly distributed horizontally (Fig. 7). This is consistent with an acoustic study in western Lake Superior (Megard et al. 1997). In that study, zooplankton were found to be strongly aggregated in the thermocline, even when the thermocline was tilted from a depth of 5 m near shore to 15 m five kilometers offshore as a result of coastal upwelling. This indicates that once zooplankton attain their daytime depth, they are more attuned to temperature/density gradients than to other environmental variables, such as light, which would have varied considerably over 10 m of depth. The strong density gradient in the thermocline creates an environment that is less turbulent than the isothermal mixed layer above and the essentially isothermal hypolimnion below, thus reducing the vulnerability of zooplankton to passive dispersal by water movements.

That *Daphnia* were significantly more concentrated at depths at which oxygen concentrations were 3–5 $mg L^{-1}$ (i.e., the refuge zone) further illustrates the effect of predation on population patchiness (Fig. 8). *Daphnia* in water with oxygen levels greater than 5 $mg L^{-1}$ (i.e., the trout zone) were more vulnerable to predation, whereas those at depths with oxygen concentrations below 3 $mg L^{-1}$ were presumably subject to elevated physiological stress (Kring and O’Brien 1976). Oxygen concentrations below 1 $mg L^{-1}$ appeared to set the lower limit of the population’s spatial distribution later in the year (Fig. 6), a finding that is consistent

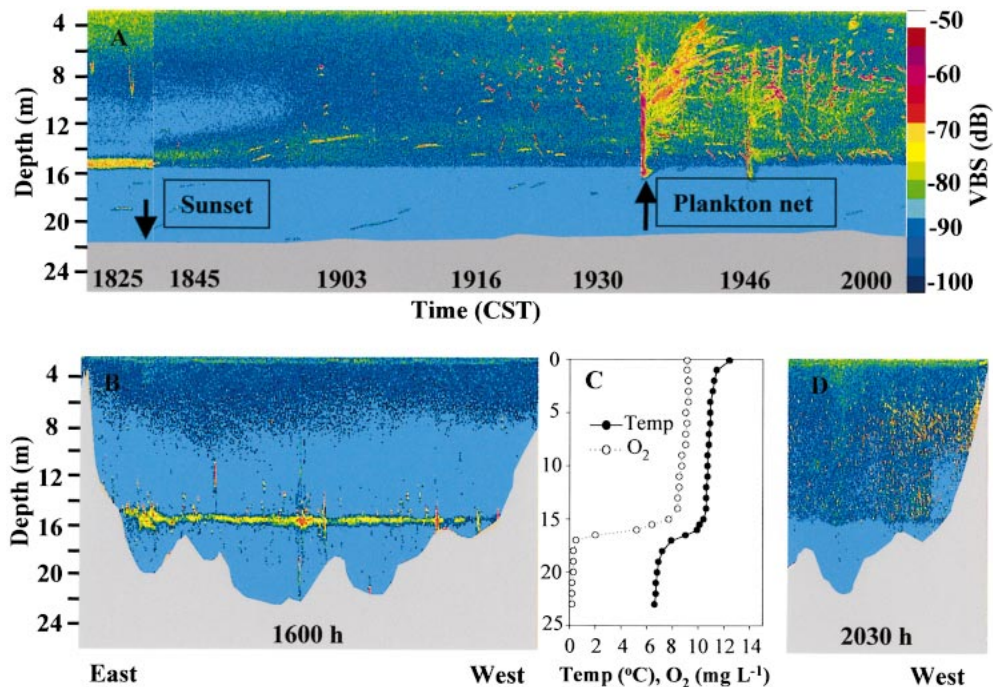


Fig. 9. Composite figure showing diel spatial distribution of zooplankton on 24 October 1998. (A) Backscattered sound recorded while stationary where water depth was 22 m shows that *Daphnia* were aggregated between 15 m and 16 m before sunset and dispersed upward after sunset. Abundant red echotraces after 1916 h are fish (likely cyprinids) that probably dispersed offshore after sunset. (B) *Daphnia* were densely aggregated in a very thin metalimnetic layer across the lake during daylight (1600 h). (C) The layer was bounded by anoxic water at 16 m and by the mixed layer (11°C) above 15 m. (D) Backscattered sound recorded between the sampling location and the west end of the lake after migration shows that upward nocturnal dispersion occurred throughout the lake.

with other studies of *D. pulicaria* (Geedy et al. 1996; Tessier and Leibold 1997).

Diel pattern of spatial distribution—Behavior can offset hydraulic transport processes, which tend to disperse plankton. The effect of passive dispersal where thermal gradients are weak is especially evident when one examines the diel spatial distribution of the *Daphnia* population in October (Fig. 9). At night, migration into the mixing epilimnion dispersed the population nearly uniformly. The dispersion resulted in much lower concentrations, because the volume of the epilimnion was much larger than the metalimnion. Early in the summer stratification period, however, when the volume of the epilimnion is smaller than that below it, *Daphnia* are likely to become more concentrated at night. These high concentrations would likely cause intense grazing on phytoplankton in the epilimnion and clearer water.

This study illustrates the practical utility of sonar for mapping the spatial distribution and abundance of zooplankton. Our analysis also reveals the relative importance of abiotic and biotic drivers of patchiness in structuring the spatial distribution of *D. pulicaria* during the spring, summer, and autumn in a dimictic lake. Oxygen concentrations delimited the range of depths in which *Daphnia* were distributed, and the temperature/density gradients in those depth ranges appeared to control the horizontal patchiness of the population.

The aggregation of *Daphnia* at refuge depths during the day and migration behavior appeared to primarily determine the specific vertical location of the population at any given time.

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