The dominant invertebrate zooplanktivore in Lake Baikal, Russia, is the pelagic amphipod Macrohectopus branickii. We followed the dynamics of an aggregation of this amphipod in Barguzin Bay, middle Lake Baikal, between 27 and 30 September 1989, using a 200 kHz echosounder and vertical net tows. Correlations between amphipod biomass and volume backscattering yielded a target strength of -66.8 dB/g or -82 dB/individual (15 mm, 30 mg animal). This is similar to results from theoretical scattering models. Macrohectopus were aggregated in a 29 km$^2$ large patch over bottom depths of 150 to 200 m (density 73 g/m$^2$) during the day. This patch spread out to 40 km$^2$ during the night (density 64 g/m$^2$). Density estimates for the whole bay were 9.1 g/m$^2$ (night) and 8.9 g/m$^2$ (day). Total area surveyed was 415 km$^2$. The amphipod migrated from daytime depths of 100-200 m to nighttime depths of 20-70 m. Both the evening ascent and the morning descent lasted about 1.5 h, corresponding to a migration velocity of 1 m/min. Larger females were found deeper than smaller females both day and night. Reaction of Macrohectopus to a flood light suggested that the animals avoided light levels brighter than 0.0001 lux. The prey of Macrohectopus (smaller zooplankton) were primarily distributed above 50 m depth both day and night. These data indicate remarkable similarities with the migration patterns of mysids, the ecological analog to Macrohectopus in many large northern lakes. This is the first study to continuously follow the diet dynamics of the amphipod and to map the size of an amphipod aggregation using hydroacoustics.

INDEX WORDS: Lake Baikal, Macrohectopus, diel migration, acoustics, aggregations, light.
Introduction

Diel migrations of aquatic organisms is a common phenomenon both in marine and freshwater systems (Kerfoot 1985, Mangel and Clark 1988, Haney 1988). Evidence is mounting that these migrations are a response to the compromise between maximizing ingestion, digestion or egg development rates, and minimizing predation risk (Stich and Lampert 1981, Luecke 1986, Vuorinen 1987, Wurtsbaugh and Neverman 1988, Clark and Levy 1988, Ohman 1990). Diel vertical migrations are often regulated by light (Blaxter 1974, Teraguchi et al. 1975, Rudstam et al. 1989, Haney et al. 1990), although the extent of the migrations can be limited by other factors, such as temperature, food availability, or the distribution of predators (Beeton and Bowers 1982, Levy 1990, Barange 1990).

In Lake Baikal, Russia, the common pelagic invertebrate predator is an endemic amphipod, *Macrohectopus branickii* (Dyb.) (maximum body length 38 mm). This amphipod is one of the major predators on zooplankton and an important prey of fish (omul, *Coregonus autumnalis migratorius*, and adult pelagic sculpins — family Cottoidei: Kozhov 1963, Melnik 1978, Volerman 1983). The amphipod performs extensive diel vertical migrations (Zakhvatkin 1932, Vilisova 1962, Bekman and Nagorny 1985) to feed on zooplankton and phytoplankton in the upper water layers during the night. *Macrohectopus* is known to form large aggregation in relatively shallow water (150-250 m depth) in the more productive bays (Barguzin Bay and Chivyrykuy Bay) of middle Lake Baikal during late summer (Bekman and Nagorny 1985). In this paper we report the result from a study of one such aggregation in Barguzin Bay (53°30'N, 108°60'E) at the end of September, 1989, using a combination of hydroacoustics (200 kHz) and vertical tows with closing nets. These observations are the first to continuously follow the diel migration of the *Macrohectopus* and to map the spatial extent of an aggregation.

Hydroacoustic sampling is often an integral part of studies on the distribution and migrations of pelagic animals and has been used for measuring biomass, distribution, and patchiness of similar sized euphausiids and mysids (Teraguchi et al. 1975, Greenlaw 1979, Sameoto 1983, Greenlaw and Pearcy 1985, Simard et al. 1986, Stanton et al. 1987, Greene et al. 1988, Rudstam et al. 1989, Nero and Magnuson 1989, Smith et al. 1992). However, quantitative estimates of abundance and biomass are directly dependent on the target strength relationships of the animals and available equations for crustaceans vary substantially (Ever-son et al. 1990). An additional goal of this research was to continue the work of Melnik et al. (1992) of assessing the possibilities for using acoustics for quantitative estimates of *Macrohectopus* in Lake Baikal.

Materials and Methods

The data were collected during a research cruise from 25 September to 30 September 1989, with the R/V Vereschagin in middle Lake Baikal. *Macrohectopus* in different depth layers were sampled with an 82 cm diameter DJOM closing net (mesh size 160 µm). This net is about 4 m long and has a large filtering area compared to its opening. We assumed that the efficiency of the net was 100%. The animals were preserved in 4% formalin and
measured and counted in the laboratory. *Macrohectopus* biomass was determined from length measurements using the regression $W = 0.047 \times L^{2.39}$ (Melnik et al. 1992, derived from data in Bekman and Afanasyeva 1977. $W$ is wet weight in mg and $L$ is total length in mm). Zooplankton were sampled with a 36 cm diameter Juday closing net (mesh size 77 µm, depth layers 70-50 m, 50-20 m, 20-10 m, 10-2 m, and 2-0 m). All zooplankton were preserved in 4% formalin and identified and counted in the laboratory. Both *Macrohectopus* and zooplankton were collected at eight stations along the survey grid (stations 1 to 8) and on six occasions at the diel station (station 9, Fig. 1).

**FIG. 1.** Day and night distribution of *Macrohectopus* in Barguzin Bay, 28-29 Sept/89, estimated with acoustics. The isolines are area back-scattering. Sonar transects are indicated with solid lines (night) and dashed lines (day). Station locations are also given (the star is the stationary station). The 50, 100, 500, and 1,000 m depth contours are included on the day distribution map.

Acoustic data were collected with a 200 kHz single-beam echo-sounder (Simrad EK400, half power beam width 6°, pulse length 1 ms, TVG of 20 log R with an attenuation of 15.2 dB/km). The transducer was calibrated during the survey using copper sphere with a target strength of -44.7 dB at 200 kHz. Acoustic data and net samples were obtained both from a night (28 Sept/89 1803-29 Sept/89 0535) and a day survey (29 Sept/89 0535-1800) of the whole bay and from a 30 h (29 Sept/89 1800-30 Sept/89 2400) stationary station within the main patch of *Macrohectopus* identified during the whole bay surveys. A SIORS integrator provided continuous shipboard echo integration data in five depth layers. The areal back scattering strength from this integrator was used to map the extent of the aggregation (using Surfer software for PC). Echo signals were also recorded on digital cassette tapes and later processed using the HADAS acoustic data acquisition program (Lindem 1990). Volume back scattering was measured in 2-m depth intervals at the stationary station.

Surface temperature and Secchi depth were measured at the net sampling stations. Light levels at the surface were calculated using a program by Janiczek and DeYoung (1987) which gives illumination from the sun and moon at any time and location on earth. There was no cloud cover during the cruise and these light estimates should therefore be reasonably accurate. Light at a specific depth was calculated assuming that the Secchi
depth represented the depth of 10% of surface light (Wetzel 1983) and no change in transparency throughout the water column. A temperature profile was obtained at the stationary station using repeated casts with a reversing thermometer.

Results and Discussion

Hydroacoustics and vertical net tows revealed a large aggregation of *Macrohectopus* along the northern shore of Barguzin Bay in 150-200 m deep water (Fig. 1, stations 1-4, 8, and 9). This aggregation consisted of primarily immature females (70%, animals less than 15 mm long) and mature females (27%, animals larger than 15 mm), with smaller numbers of males (3%) and juveniles (< 1 %) (Fig. 2).

*Fig. 2.* Length and biomass distribution of *Macrohectopus* caught in Barguzin Bay, 28-30 Sept/89. A *Macrohectopus branickii* female is inserted (after Kozhov 1963).
Males made up a larger proportion of the samples taken in the southern Bay (station 6, Table 1). Females generally dominate Macrohectopus population in late summer and autumn (Bekman and Nagorny 1985, Melnik et al. 1992). The average length was 12 mm but the biomass distribution was centered around a 15-mm, 30-mg animal (Fig. 2). In addition to Macrohectopus, the DJOM net samples contained some nektobenthic amphipods and sculpins (primarily golomyanka Comephorus dybowskii, Pisces, Cottoidei).

The relationship between volume back-scattering and Macrohectopus biomass was similar to the results from the 1988 cruise (Melnik et al. 1992, Fig. 3). Samples that only included the top 50 m or less of the water column (1989 shallow in Fig. 3) were considered outliers and not included in the regressions. Fish (primarily omul) were common in this depth layer (evidenced from hook and line catches by the crew of the R/V Vereshagin and the appearance of echoes on the charts) which resulted in high volume back-scattering compared to Macrohectopus biomass in net samples. Log-log linear regression of volume back-scattering strength ($S_v$, dB) on biomass ($W$, g/m$^3$) yielded $S_v = -65.4 + 11.2 \cdot \log_{10} W$ ($r^2 = .682, N = 14$). This regression is similar to a regression for Macrohectopus based on Melnik et al.’s (1992) data from 1988: $S_v = -63.9 + 10.1 \cdot \log_{10} W$ ($r^2 = .764, N = 19$). Melnik et al. (1992) used the same closing net and echosounder to sample an aggregation of Macrohectopus in Chivyrkuy Bay, 1-2 Oct/88. The combined data from 1988 and 1989 yield:

$$S_v = -65.8 + 10.9 \cdot \log_{10} W \ (r^2 = .721, N = 33). \ (1)$$

Sameoto (1980, 1983) obtained similar relationships for euphausiids of about 18 mm lengths at 120 kHz ($S_v = -63.8 + 10 \log_{10} W$). For a 15-mm, 30-mg animal, equation (1) predicts an individual target strength of -82 dB. Average biomass target strength for the densities observed in this study was -66.8 dB/g.

Theoretical scattering models yield similar values. Melnik et al. (1992) derived a target strength of -82 dB for a 15-mm (30-mg) Macrohectopus (or -66.8 dB/g) based on scattering models in Clay and Medwin (1977). Stanton (1989) presented general models of acoustic scattering from different shaped objects. Stanton's high pass solution for a bent cylinder give similar values (a target strength of -82.4 dB for a 15-mm-long euphausiids at 200 kHz). Greene et al. (1989) measured target strength of 10 to 10,000 mg wet weight (4 to 100 mm) crustaceans with a 420 kHz echosounder in the laboratory. Their relationship ($S_v = -62.8 + 10.3 \log_{10} W$) shows somewhat higher target strengths for a 30 mg animal (-79.4 dB) than ours. Greene et al.’s (1989) values may be higher than target strengths for natural populations because of differences in orientation of animals between experimental conditions and the field (Sameoto 1980, Cochrane et al. 1991). Our results support the new, lower target strength estimates suggested by Everson et al. (1990) for euphausiids. The results also show that meaningful quantitative estimates of Macrohectopus biomass in Lake Baikal can be made with the 200 kHz echosounder. For more details on derivations of Macrohectopus target strengths see Melnik et al. (1992). The relationship -66.8 dB/g is used for biomass estimates in this paper.
The day and night survey of Barguzin Bay (areas with bottom depths of more than 50 m) showed that the aggregation was more restricted during the day (approximate size 28.7 km$^2$) than during the night (39.7 km$^2$) (Fig. 1). Apparently, the animals disperse horizontally during the night. Secchi disk depths were similar across the bay (5.5-6.5 m), but surface temperatures were higher in the patch (9.3-11.3 °C) than at the western end of the bay (8.0°C). This temperature difference is caused by the Barguzin River plume which flows primarily along the northern shore of the bay. The aggregation of *Macrohectopus* in the northern part can be a response to increased food availability associated with the river plume. Net samples from the aggregation yielded an average biomass of 30.2 g wet weight/m$^2$ (SE = 9.2, N = 11). From the acoustic data we estimated that the aggregation contained 2.54 $10^6$ kg during the...
night (density 64 g/m²) and 2.10 10⁶ kg during the day (density 73 g/m²) of Macrohectopus. The acoustic density estimates are higher than the net estimates because the diel station where most samples were collected was not located in the most dense part of the aggregation (see Fig. 1). The estimated biomass of Macrohectopus in the whole bay was 3.7 10⁶ kg (area surveyed 407 km², density 9.1 g/m²) during the night and 3.8 10⁶ kg (area surveyed 426 km², density 8.9 g/m²) during the day. Thus, 69% (night) and 55% (day) of the Macrohectopus biomass in the bay was found in the aggregation. Estimates of average biomass of Macrohectopus for the entire Lake Baikal are 4 g/ m² during August (Bekman and Nagorny 1985). The similarity between the day and night estimates indicate that the whole population of Macrohectopus remained in the water column both day and night.

The amphipod is known to form late summer aggregations in Barguzin and Chivyrkuy Bays (Bekman and Nagorny 1985) In 1988, a large aggregation was found in Chivyrkuy Bay (Melnik et al. 1992), but large aggregations were not present in that bay in 1989. Densities of pelagic mysid shrimps rarely exceed 5 g/m² (Nero and Sprules 1986, McDonald et al. 1990, Rudstam and Hansson 1990) although densities of euphausiids can be much higher (Sameoto 1983).

FIG. 3. Comparison of Macrohectopus biomass obtained with vertical net tows and volume back-scattering from a 200 kHz echosounder. Data from 1-2 Oct/88 (Chivyrkuy Bay, Melnik et al. 1992) and from the present study (Barguzin Bay) are included. The “1989 shallow” data points include only depths shallower than 50 m and are excluded from the regression (see text). The line represents equation 1 in the text.
The amphipod performed marked diel vertical migrations (Figs. 4 and 5). Vertical net hauls showed good agreement with the hydroacoustic depth profiles for data collected at our 30 h stationary station (Fig. 4). Larger mature females were found deeper than smaller immature females both day and night. Males appeared to migrate less than females. We generally observed an increase in the proportion of males in deep water at night when most females had migrated to the upper water layers (Table 1). During the migrations, most amphipods were concentrated in a narrow scattering layer moving rapidly (vertical velocity of 1 m/min) up to 50-20 m depth at dusk and back down to over 100 m depth at dawn (Fig. 5). The ascent started when surface light levels were below 2,000 lux and the descent began as the surface light increased above 0.2 lux. This represents a light level of about 0.0001 lux at 20 m depth. Many fish species stop feeding between 0.01 and .0001 lux (Blaxter 1974, Batty et al. 1990). Our observations on the descent is based on the echo chart and echo integration from the SIORS integrator (five depth layers) because of a malfunctioning tape recorder. Both the ascent and the descent took about 1.5 hours and each was tightly correlated with the fast change in light levels at dusk and dawn. The amphipod spread out vertically in the top 100 m after the initial ascent and concentrated again closer to the surface before the morning descent. This is probably the cause for the two peaks in abundance (at 2100 and 0300) in the upper layers observed for immature Macrhectopus by Zakhvatkin (1932) and Vilisova (1962).

During the first night at the stationary station, we used the flood lights of the vessel to observe the behavior of the amphipod. This light was directed toward the suspended transducer and emitted a light intensity of 8 PAR (µE m⁻² s⁻¹ measured the following week by R. Back and D. Bolgrien during a study of primary production, see Back et al. 1991). This light intensity corresponds roughly to 400 lux (Biggs and Hansen 1979). With the light turned off, we observed the animals at about 20 m depth. When the light was turned on, Macrhectopus instantaneously disappeared from the echo chart in the top 40 m of water and were restricted to depths below 40 m as long as the light was on (Fig. 6). This immediate disappearance is probably a result of a vertical and horizontal escape response.
that moves the animals out of the acoustic beam. It could also be the result of changed orientation and associated reduction in target strength (observed for euphausiids by Sameoto et al. 1985) or a combination of the two processes. But we did not observe the almost immediate return of scatterers shown by Sameoto et al. (1985) when the light was switched off. Macrohectopus appeared to regain their vertical position in the water column through upward migration (Fig. 6). Calculated light level at 40 m depth was 0.0001 lux, the same light level as estimated for 20 m depth at the start of the descent. Similar light levels restrict vertical migrations of Mysis mixta in the Baltic Sea (Rudstam et al. 1989). This sensitivity to light should cause the vertical distribution of Macrohectopus to depend on the phase of the moon. There was no moon during our study.

**FIG. 5.** Vertical distribution of volume back-scattering from 1800, 29 Sept/89 to 2300, 30 Sept/89. The gray scale indicates different intensity of back-scattering and ranges from less than -110 dB (white) to -60 dB and higher (black). Data are missing for the beginning of the evening descent (0430-0630).

Although it is clear that the migration of the amphipod is associated with the fast changes in light levels at dawn and dusk, we are less confident about whether a particular light level restricts their vertical distribution throughout the 24 hour cycle. We do see a slow upward movement of the Macrohectopus scattering layer during the afternoon as light levels decrease (Fig. 5), indicating a possible association of the upper edge of the Macrohectopus scattering layer with an absolute light level. Our calculated light levels were lower at the upper edge during the day (about $10^{-9}$ lux, 80 m depth) than during the night (about $10^{-6}$ lux, 20 m depth) but these light levels are inferred from Secchi depths which reflect transparency in the top meters of water. Transparency probably inc-
Light is the only factor we could identify that restricted the upward migration of the amphipod. There were no temperature discontinuities at this time of the year (Fig. 4) and no correlation of Macrohectopus distributions with a particular temperature. Surface temperatures rarely exceed 12°C in the open water of Lake Baikal (Kozhov 1963) and temperature is therefore unlikely to restrict the vertical distribution of the am-
phipod in Lake Baikal. The zooplankton species present, the copepods *Epischura baicalensis* and *Cyclops kolensis*, the cladoceran *Bosmina longirostris* and *Daphnia longispina* and several species of rotifers, are all prey of this amphipod (Vilisova 1962). At this time of the year, most of the zooplankton are found in the upper water layers. At our diel station, 85% of *Epischura*, and over 99% of *Cyclops*, cladocerans, and rotifers were found in the upper 90 m of water. Ranges of areal zooplankton densities in the upper 70 m of water were 271,000-663,000 copepods/m$^2$, 134,00-400,000 cladocerans/m$^2$, and 333,000-1,905,000 rotifers/ m$^2$. All three zooplankton groups were most dense in the upper 10 m of water both day and night (Fig. 7). Thus, there was no deep water concentration of prey that could have affected the distribution of the amphipod. However, we cannot rule out that direct avoidance of predators (e.g, omul) restricted the upward movement of the amphipod.

![Graph showing depth distribution of zooplankton](image)

**FIG. 7.** Day and night depth distribution of zooplankton (copepods, cladocerans, and rotifers) at the stationary station. Night samples were collected 1800-1830, 2230-2310, and 0120-0210, day samples were collected 0850-1000 and 1420-1510.

The migration patterns of *Macrohectopus* are very similar to those observed for mysids (Beeton and Bowers 1982, Rudstam et al. 1989). *Macrohectopus* could be considered a "mysid equivalent" in Lake Baikal. Both groups are of approximately the same size, are predators on zooplankton, and are themselves major prey species for fish. Further, both groups need to avoid visual feeding predators during the day and move up to feed on concentrations of zooplankton prey closer to the surface during the night, resulting in similar migration patterns. Given the high abundance of *Macrohectopus* in Lake Baikal it is likely that the amphipod, like mysids (see review by Lasenby et al. 1986), is an important regulator of the abundance and distribution of their zooplankton prey.
Acknowledgments

We thank Dr M. Grachev for suggesting and supporting this research cooperation, Dr V. Sideleva for further support in Irkutsk, Tatyana Vasilyeva, Pavel Azarkov, Captain Oleg Kalinin and the crew of the R/V Vereschagin for help during field sampling, Daniel Schindler, Redwood Nero, Marlene Evans, D. Sameoto and N.G. Granin for helpful suggestions. Mike Jech and Bill Feeney assisted with figure preparations. The study was supported by the Institute of Limnology of the Siberian Branch of the Russian Academy of Sciences in Irkutsk, the Swedish and Russian Academy of Sciences exchange program, the Swedish Council for Forestry and Agricultural Research (to LGR), the Swedish National Science Research Council (to SH), and the University of Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and from the State of Wisconsin (NA90AA-D-SG469).