

## *Mysis relicta* in a eutrophic lake: Consequences of obligatory habitat shifts

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### Abstract

Low numbers of mysids in eutrophic lakes have usually been related to their poor tolerance to low oxygen. In eutrophic Lake Hiidenvesi, we studied the possibility that water quality indirectly affects mysids by forcing them to habitats where they are vulnerable to fish predation. *Mysis relicta* was absent from basins that did not stratify (water depth < 10 m). In the deep basin, as the summer progressed, *M. relicta* was concentrated in the deepest areas and moved upward in the water column as water temperature increased and dissolved oxygen decreased. Between mid-August and mid-September, only a thin water layer was habitable; the rest had either intolerably low oxygen concentration or too high of a temperature. *M. relicta* abundance decreased from  $2.72 \times 10^8$  individuals on 3 June to  $3.72 \times 10^6$  individuals on 19 October, with the sharpest decrease taking place in August. At the same time, the vertical distribution of smelts shifted downward and the percentage of mysids in the stomach contents of smelts increased steeply. The consumption rate by smelts was high enough to explain the collapse of the *M. relicta* population; during 18 August–2 September, smelts consumed 5.6 times the mysid production. The results suggested that unfavorable physicochemical conditions did not directly cause the drastic reduction of the population abundance of *M. relicta* but indirectly facilitated predation by smelts, which was the final cause of the collapse. The high predation rate by smelts was probably accelerated by the emergence of chaoborid larvae, which were important food items for smelts in early summer.

Pelagic invertebrate predators (predatory cladocerans and copepods, insect larvae, and mysids) are important components in lake ecosystems. They may regulate zooplankton communities, thus competing with fish for food (e.g., Dodson 1974; Ramcharan et al. 2001). On the other hand, many invertebrate predators are important food items for fish, which makes their interactions with fish and planktonic assemblages very complex (Johannsson et al. 1994). The opossum shrimp, *Mysis relicta* (Lovén) (Malacostraca, Mysidacea), is distributed widely over the northern hemisphere (Segerstråle 1966). The distribution of the species has been widened through introductions, which have been conducted widely in North America and Fennoscandia to enhance the food supply for fish (Lasenby et al. 1986; Northcote 1991). *M. relicta* is capable of using various food resources, including zooplankton, benthos, phytoplankton, and detritus (Grossnickle 1982, with references). Numerous studies have shown that predation by mysids may depress zooplankton and consequently affect the growth and survival of zooplanktivorous fish (Lasenby et al. 1986; Langeland et al. 1991; Richards et al. 1991; Johannsson et al. 1994).

High densities of mysids are usually found in oligotrophic waters, and they become less abundant with increasing eutrophication (Beeton 1969; Gannon et al. 1978; Köhn and Waterstraat 1990; Żmudziński 1990). How eutrophication negatively affects mysids is not clear. The most common interpretation is that mysids cannot tolerate low oxygen (Judson and Birge 1927; Foulds and Roff 1976; Sandeman and

Lasenby 1980). In lakes that undergo oxygen depletion, *M. relicta* tends to move upward in the water column (Sherman et al. 1987). Other factors, such as temperature and light, limit the upward movement, finally leading to extinction (Teraguchi et al. 1975; Sherman et al. 1987). Other possible effects of eutrophication are declining availability of high-quality food and increased fish predation. Mysids are preferred food items for many fish species (McDonald et al. 1990; Johannsson et al. 1994), and it is possible that mysids are forced by low oxygen into habitats where they are more vulnerable to predation. Connections between obligatory seasonal habitat shifts and predation mortality of mysids have not been thoroughly documented, although earlier studies have demonstrated that restriction of the habitable water volume due to changing physical-chemical conditions can increase the predator-mediated mortality of aquatic animals (Fast 1971; Wright and Shapiro 1990; Tessier and Welser 1991; Eby and Crowder 2002).

The aim of the present study was to find out whether seasonal changes in water temperature and oxygen concentration affect fish-mediated mortality of *M. relicta*. We examined the abundance of the *M. relicta* population in separate basins of eutrophic Lake Hiidenvesi. According to earlier studies (Carpenter et al. 1974; Sherman et al. 1987), it was expected that, with rising water temperature and declining hypolimnetic oxygen concentration, mysids would be concentrated in the deepest areas of the lake and move upward in the water column. To explore whether such habitat shifts affected predation pressure on mysids, seasonal variations in the distribution, food quality, and predation on *Mysis* by the most abundant planktivorous fish species, smelt (*Osmerus eperlanus* (Linnaeus)) were studied. Smelt is the dominant planktivore in numerous eutrophic lakes and forages intensively on *M. relicta* when the two species occur in the same habitat (Kjellberg et al. 1991; Johannsson et al.

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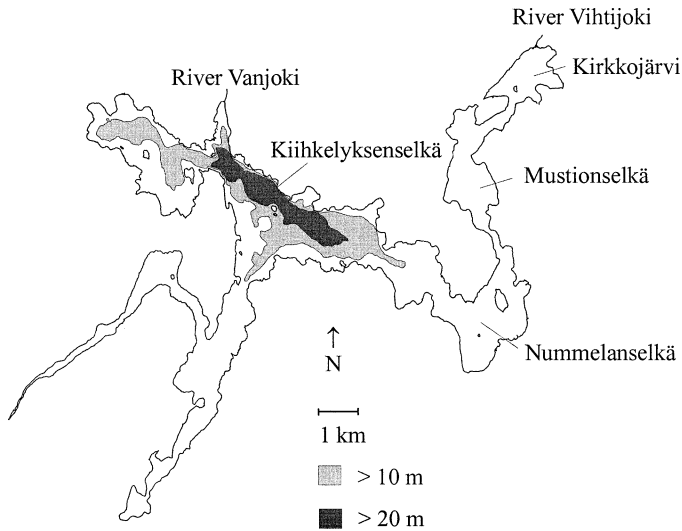


Fig. 1. Lake Hiidenvesi and the main sampling stations.

1994). To evaluate the role of food availability for mysids, seasonal changes in the food composition of *M. relicta* were also studied.

## Methods

**Study area**—Lake Hiidenvesi is situated in southwestern Finland and has a surface area of 30.3 km<sup>2</sup>. The lake is made up of several basins (Fig. 1). In the most shallow basins, Kirkkojärvi (mean depth 0.9 m, maximum depth 3.5 m) and Mustionselkä (mean depth 2.0 m, maximum depth 4 m), the total phosphorus (P) concentration frequently exceeds 90 µg L<sup>-1</sup> and Secchi depth is usually below 0.5 m (Tallberg et al. 1999). The Nummelanselkä basin (mean depth 2.6 m, maximum depth 6 m) has a total P concentration of 50–70 µg L<sup>-1</sup> and Secchi depth between 0.5 and 1 m. In these shallow basins, copepods dominate the zooplankton community, constituting >80% of the crustacean zooplankton biomass, which remains below 300 µg carbon (C) L<sup>-1</sup> (Tallberg et al. 1999). The biomass of cladocerans is below 80 µg C L<sup>-1</sup> in most years. The most abundant cladocerans are *Daphnia cristata* Sars and *Limnosa frontosa* Sars (Tallberg et al. 1999). The fish community is dominated by cyprinids, with white bream (*Abramis björkna* (Linnaeus)), bleak (*Alburnus alburnus* (Linnaeus)), and roach (*Rutilus rutilus* (Linnaeus)) being the most abundant species (Vinni et al. 2000).

The largest basin of the lake, Kiihkelyksenselkä, has mean and maximum depths of 11.2 and 33 m, respectively. Average total P concentration is 40–50 µg L<sup>-1</sup>. The maximum biomass of cladocerans is 50 µg C L<sup>-1</sup>. Larvae of the phantom midge *Chaoborus flavicans* (Meigen) inhabit the areas of the basin that stratify (water depths >10 m); densities are 5,000–10,000 individuals m<sup>-2</sup>, and they are important food for many fish species (Vinni et al. 2000). The distribution and seasonal dynamics of the *C. flavicans* population have been described in Liljendahl-Nurminen et al. (2002). Planktivorous smelt is the dominant fish species in this area, making up >95% of the trawl catches (by number; Uusitalo et al. 2003). Several cyprinid species, including bleak and

roach, as well as percids, perch (*Perca fluviatilis* Linnaeus), and pikeperch (*Sander lucioperca* (Linnaeus)) are present in lower numbers (Vinni et al. 2000).

**Distribution, population size, production, and food composition of *M. relicta***—The density of the *M. relicta* population was determined fortnightly from 18 May to 19 October 1999 at four sampling stations located in the deepest part of the four different basins (Fig. 1). In waters having a low water transparency, *M. relicta* occupies the pelagic instead of benthic habitat (Beeton 1960; Hakala 1978). Thus, sampling was conducted by vertical net hauls (net diameter 50 cm, mesh size 183 µm) (Carpenter et al. 1974; Hakala 1978). In the deep Kiihkelyksenselkä basin (water depth 30 m), three replicate net hauls were conducted from four different depths (0–8 m, 8–16 m, 16–24 m, 24–28 m). In the shallow Kirkkojärvi, Mustionselkä, and Nummelanselkä basins, three replicate vertical net hauls from the bottom to the surface were performed. Additionally, three replicate bottom samples were taken from each station with an Ekman sampler (area 279 cm<sup>2</sup>) and washed through a 500-µm sieve. Water temperature, concentrations of dissolved oxygen, total P, and total nitrogen (N) were measured in each sampling station with methods described in Tallberg et al. (1999).

All *M. relicta* individuals were measured from the tip of the rostrum to the telson bend (Kjellberg et al. 1991). The dry weights of the animals were calculated using the length–dry weight relation  $W = 0.00345L^{2.84}$  (Lasenby and Langford 1972), where  $W$  is the dry weight (mg) and  $L$  is the length (mm) of an individual. The production of mysids was calculated with the Allen curve method (Hakala 1978; Kjellberg et al. 1991), the production of a cohort in a period of time being the average number of individuals in the period multiplied by the change of mean weight during the period. The carbon content of mysids was assumed to be 50% of dry weight, and dry weight was 16% of wet weight (Salonen et al. 1976; Downing and Rigler 1984). To determine their diets, mysids were dissected and their stomach contents placed on a glass slide and analyzed with an inverted microscope (Viherluoto et al. 2000).

Detailed studies on the horizontal distribution of the population were conducted in Nummelanselkä and Kiihkelyksenselkä (Fig. 1). The two basins (areas > 3 m depth) were divided into 53 squares 500 m × 500 m in area. On 3 June, 6 July, and 19 October, a plankton net sample (one haul from the bottom to surface) and a bottom sample with an Ekman sampler were taken from each station and *M. relicta* in the samples were counted. The first sampling occasion took place at the early stage of the summer stagnation, the second during the stagnation, and the third after the autumn overturn. Profiles of water temperature and the concentration of dissolved oxygen were measured from each of the 53 locations on 3 June and 6 July with a YSI-95 meter. On 19 October, when temperature and oxygen concentrations were homogeneous throughout the water column, such areal measurements were not conducted. Total abundance of the *M. relicta* population and 95% confidence limits were calculated with equations for poststratified sampling (depth zones as strata) (Cochran 1977). The abundance of *M. relicta* in each depth zone was calculated by multiplying the area of each

depth zone by the average density of mysids in that zone (Wood 1956).

*Distribution and abundance of smelts*—The horizontal and vertical distributions of smelts were studied by echosounding with a SIMRAD EY-500 echosounder that was equipped with a split-beam transducer ES120-7F (operating frequency 120 kHz and beam opening angle 7° at -3 dB level) on 3 June, 6 July, 3 August, 6 September, and 19 October. Pulse duration was set to 0.3 ms and ping interval to minimum value. Equidistant transects were made from north to south at intervals of 500 m in June, July, and October and from northeast to southwest at intervals of 700 m in August and September. The location of the first transect was randomized.

The transects were divided into elementary sampling distance units (ESDUs) about 500 m in length. The fish density of ESDUs was computed as follows. First, the echo integral (area backscattering coefficient,  $s_a$ ) from smelts was computed with EP 500 software in two to four vertical layers with time-varied gain  $20 \log R$ . Integration threshold ( $s_v$  threshold) was set to -60 dB in shallow layers (<14 m deep) and to -62 dB in deep layers ( $\geq 14$  m deep). These threshold values were determined to be low enough to contain practically all  $s_a$  from smelts and to be high enough that noise from *Chaoborus*, e.g., was still negligible. This was accomplished by thresholding the data with various thresholds (Eckmann 1998). Second, the  $s_a$  from smelts was converted to fish density by dividing the  $s_a$  by the mean backscattering cross-section ( $\sigma_{bs}$ ) of smelt. This was determined with the trace-tracking option of EP 500 software (time-varied gain  $40 \log R$ ). However, in some water layers, the proportion of  $s_a$  from single fish echoes to total  $s_a$  was so low that  $\sigma_{bs}$  could not be reliably computed. In these cases,  $\sigma_{bs}$  was computed with the length- $\sigma_{bs}$  relationship, which was determined from 21 trawl hauls conducted during 1998–2001 (T. Malinen unpubl. data). The mean length of smelt in each water layer was calculated from trawl catches of the present study (see below).

Smelt density was computed as the weighted mean smelt density values in ESDUs with ESDU lengths as weights. The weighted variance of mean density ( $\bar{y}$ ) was calculated as (Shotton and Bazigos 1984)

$$\text{var}(\bar{y}) = \frac{\sum_{i=1}^n [(y_i - \bar{y})^2 l_i]}{\sum_{i=1}^n l_i (n - 1)}$$

where

- $y_i$  = smelt density in the  $i$ th ESDU
- $\bar{y}$  = mean smelt density
- $l_i$  = length of the  $i$ th ESDU
- $n$  = number of ESDUs

The population size of each age group of smelts was calculated for the areas where the water depth was >10 m by multiplying the mean smelt density by the surface area. The 95% confidence limits for the population size were calculated assuming a Poisson distribution (Jolly and Hampton

1990). Young-of-the-year smelts were excluded from the calculations because they inhabited the uppermost three meters and could not be reliably detected by the echosounder.

*Food quality and consumption by smelts*—Food consumption rate by smelts was determined using a bioenergetics model (Kitchell et al. 1977; Hewett and Johnson 1992). This model uses temperature, growth history, diet composition, and the energy content of both predator and prey to estimate food consumption using a mass balance equation (consumption = respiration + waste + growth).

Fish for diet-content analysis were collected in Kiihkelyksenselkä on 7–8 June, 13–14 July, 10–11 August, and 7–8 October with a pelagic trawl (height 5 m, width 8 m, 3 mm cod end). Trawling was carried out both in the epilimnion and in the hypolimnion in full daylight (1300–1600 h), during darkness (2300–0200 h), and at the time of sunrise and sunset to account for the possible diurnal changes in food composition. Catches were analyzed for species composition, and from each haul a random subsample of 200 smelts was taken (or all smelts if the catch was less than 200 individuals). In the laboratory, the smelts were weighed to the nearest gram and measured for total length to the nearest millimeter; age was determined from otoliths ( $n = 1,249$  in June, 1,335 in July, 1,525 in August, and 1,768 in October). For stomach content and fullness, 1,892 smelts were microscopically analyzed ( $n = 689, 416, 373,$  and  $414$  in June, July, August, and October, respectively). In each month, data on the different sampling times were pooled by weighting by the number of smelts captured at each time.

The species-specific physiological parameters of the bioenergetics model were taken from Lantry and Stewart (1993). Water temperature experienced by smelts was adjusted according to the vertical distribution of the population at different times of the summer. The energy content of smelts was assumed to be  $4,814 \text{ J g}^{-1}$  (Lantry and Stewart 1993) and the energy content of *M. relicta*, copepods, cladocerans, and *Chaoborus flavicans* 4,604, 2,300, 1,674, and  $1,837 \text{ J g}^{-1}$ , respectively (Cummins and Wuycheck 1971; Stewart and Binkowski 1986). The food consumption rate by the smelt population at different dates (excluding young of the year) was calculated using the population abundance given by echosounding and the age-group composition obtained from the trawl catches.

## Results

*Water quality*—The surface-water temperature reached 20°C in early June and remained above 18°C until September. In the shallow Kirkkojärvi and Mustionselkä basins no stratification developed, but Nummelanselkä was stratified in late June-early July, when the water temperature declined from 22°C at 4 m to 16°C at a 6-m depth. The concentration of dissolved oxygen stayed above  $3 \text{ mg L}^{-1}$  in all the three basins throughout the water column. The average Secchi depth was 40 cm in Kirkkojärvi, 50 cm in Mustionselkä, and 75 cm in Nummelanselkä, and the average total P concentrations were 106, 104, and  $62 \mu\text{g L}^{-1}$ , respectively.

In the deep Kiihkelyksenselkä, a thermocline developed by the beginning of July, with temperature falling from

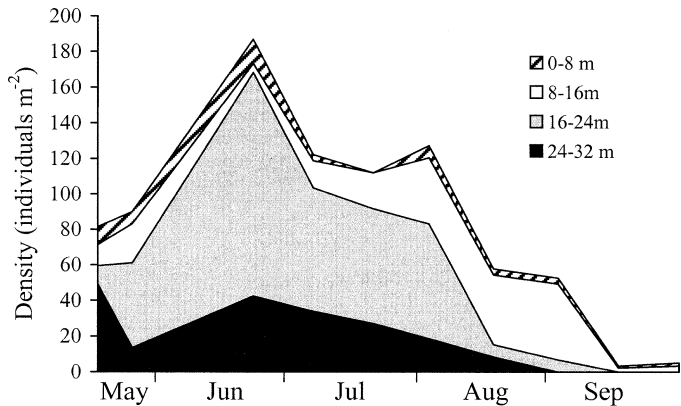


Fig. 2. The density of *Mysis relicta* at different depths in the deepest sampling station (Kiihkelyksenselkä basin) in 1999.

above 20°C to below 10°C in 5–10-m depth. Autumn overturn started in early October. Oxygen concentration in the deepest layers (>25 m) was above 6 mg L<sup>-1</sup> until early July, but during August–September, it fell below 2 mg L<sup>-1</sup>. In late August and September, the concentration of dissolved oxygen was above 4 mg L<sup>-1</sup> only in the uppermost 15 m. The average total P concentration in the epilimnion was 49 µg L<sup>-1</sup> and average Secchi depth was 90 cm.

**Abundance and distribution of *Mysis relicta* and smelts**—In the shallow Kirkkojärvi and Mustionselkä, no *M. relicta* were found, and in Nummelanselkä, only two individuals were captured (3 August and 30 September). In Kiihkelyksenselkä, mysids were absent from the bottom samples, but with net hauls, representatives of two clearly distinguishable cohorts were captured. On 23 June, the population density reached its maximum of 186 individuals m<sup>-2</sup> (117 mg C m<sup>-2</sup>) (Fig. 2). The population was dominated by young of the year, which reached a density of 175 individuals m<sup>-2</sup> on 23 June. In July, the density of mysids rapidly declined to 120 individuals m<sup>-2</sup>, and in August, it dropped to below 60 individuals m<sup>-2</sup>. By the end of September, the density fell below 10 individuals m<sup>-2</sup> (Fig. 2). The density of mysids older than young of the year remained below 15 individuals m<sup>-2</sup> throughout the study period.

The vertical distribution of the population changed clearly in the course of the summer. In the beginning of the study period, the majority of mysids inhabited the water layers below 24 m, whereas in June–July, the population density was highest at 16–24-m depth (Fig. 2). After mid-August, >50% of the population occurred at 8–16-m depth, and in September, no mysids were found in the deepest layer.

Horizontally, on 3 June, the population was distributed evenly in >10-m deep areas, with density fluctuating mostly between 40 and 100 individuals m<sup>-2</sup> (Fig. 3). Mysids were found also in six stations shallower than 10 m and in three stations where water depth was less than 7 m. The estimated total population size was  $2.72 \pm 0.70 \times 10^8$  individuals. On 6 July, the population was concentrated in areas deeper than 20 m. In stations shallower than 20 m, the population density was below 40 individuals m<sup>-2</sup>, and no mysids were found from stations where water depth was less than 7 m. The total

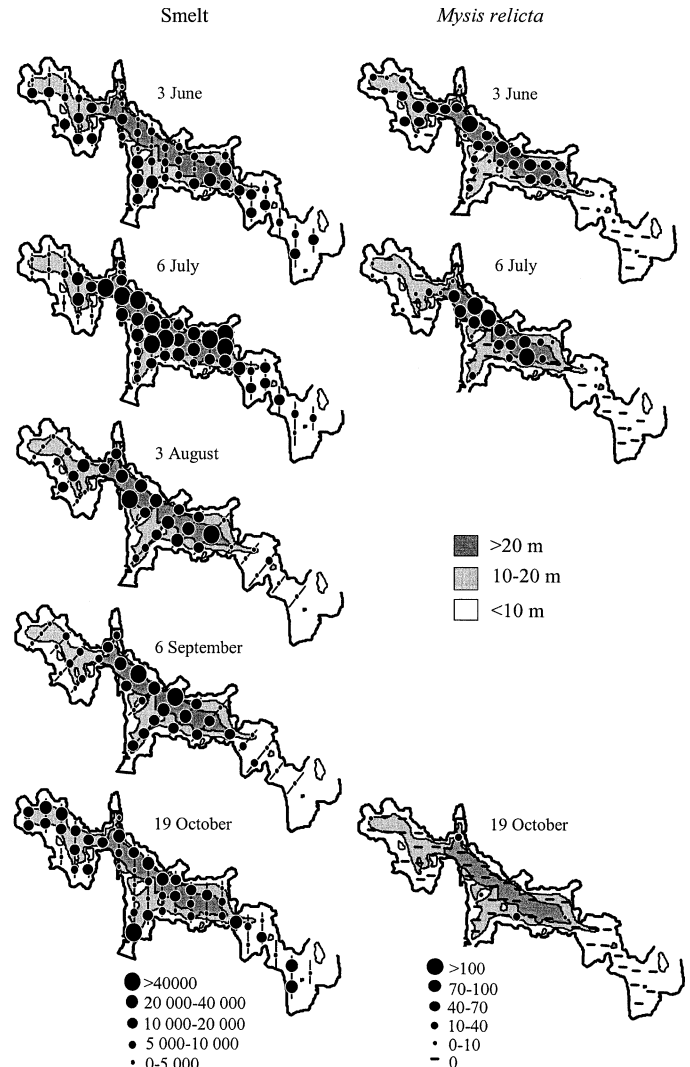


Fig. 3. The horizontal distribution of *Mysis relicta* (individuals m<sup>-2</sup>) and smelts (age 1 and older, fish ha<sup>-1</sup>) in Lake Hiidenvesi in June–October 1999.

population abundance was  $2.43 \pm 0.46 \times 10^8$  individuals. On 19 October, *M. relicta* were found in only 5 of the 53 sampling stations, and density nowhere exceeded 15 individuals m<sup>-2</sup> (Fig. 3). The total population abundance was  $3.72 \pm 3.48 \times 10^6$  individuals. Throughout the study period, only young-of-the-year mysids were found in stations shallower than 10 m, older individuals staying exclusively in the part of the lake that was stratified.

Smelts were evenly distributed over the whole study area in June, with fish density varying mostly between 5,000 and 20,000 individuals ha<sup>-1</sup> (on average, 10,375 fish ha<sup>-1</sup>; 95% confidence limits 7,787–13,335 fish ha<sup>-1</sup>) (Fig. 3). The highest densities were observed in regions shallower than 10 m. In July, smelts were concentrated in the deepest areas of the basin, with smelt density frequently exceeding 40,000 individuals ha<sup>-1</sup> (average 32,962 fish ha<sup>-1</sup>; 95% confidence limits 21,177–47,343 fish ha<sup>-1</sup>). In August (average 18,952 fish ha<sup>-1</sup>; 95% confidence limits 14,471–24,036 fish ha<sup>-1</sup>) and September (average 17,021 fish ha<sup>-1</sup>; 95% confidence limits

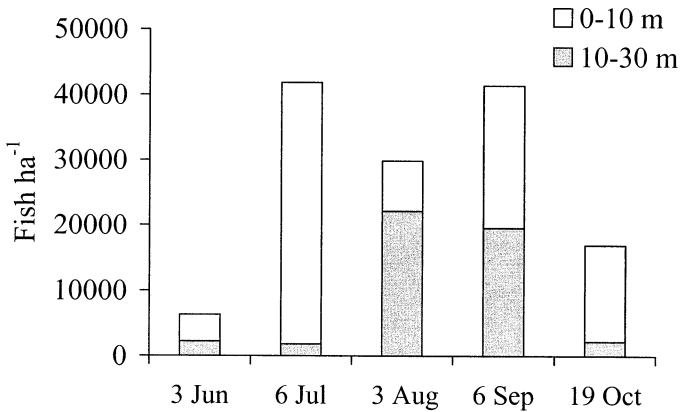


Fig. 4. The vertical distribution of smelts in the Kiihkelyksen-selkä basin in 1999.

11,698–23,339 fish ha<sup>-1</sup>), horizontal distribution was similar to that in July. In October, the smelt population was again dispersed evenly throughout the whole basin (average 12,528 individuals ha<sup>-1</sup>; 95% confidence limits 9,479–16,001 fish ha<sup>-1</sup>) (Fig. 3).

Vertically, in June and July, most smelts of age 1 and older were concentrated in the epilimnion (Fig. 4). In August and September, almost 80 and about 50%, respectively, of the population were found in the metalimnion and hypolimnion. In October, most fish were in the epilimnion. Young-of-the-year smelts almost exclusively inhabited the epilimnion.

**Growth, food quality, and production of *Mysis relicta***—During the study period, the mean individual length of young-of-the-year mysids increased from 3.9 to 12.8 mm and individual weight from 0.16 to 4.81 mg dry weight (dw) (Table 1). The mean individual length of older individuals fluctuated between 15.5 and 17.8 mm and mean individual weight between 8 and 12 mg dw (Table 1). Due to individual growth, the highest biomass of the population, 2.5 g wet weight (ww) m<sup>-2</sup> (0.2 g C m<sup>-2</sup>), was reached on 3 August.

Cladocerans were 33–86% of the stomach contents of young-of-the-year mysids. In older individuals, cladocerans constituted 40–75% of stomach contents. For both cohorts, rotifers, especially *Kellicottia longispina* Kellicott, were also an important food category. Diatoms were found in the guts to a considerable extent in May and in August–September.

Production of the *M. relicta* population was calculated starting 23 June, when the horizontal migration toward the sampling station had ceased. In late June and July, the production rate was between 0.03 and 0.04 g ww m<sup>-2</sup> d<sup>-1</sup> (2.4–3.2 mg C m<sup>2</sup> d<sup>-1</sup>) (Fig. 5). In August, production rate decreased to below 0.01 g ww m<sup>-2</sup> d<sup>-1</sup> (<0.8 mg C m<sup>2</sup> d<sup>-1</sup>). During the period 23 June–30 September, the total production of the population was 1.97 g ww m<sup>-2</sup> (0.16 g C m<sup>-2</sup>).

**Food quality and consumption of smelts**—Young-of-the-year smelts appeared in the samples in July and foraged exclusively on zooplankton (mainly copepods) (Fig. 6). In late summer and autumn, *C. flavicans* and few mysids appeared in diet, but zooplankton still made up >85% of the stomach contents. The daily individual food consumption

Table 1. The individual mean length ( $\pm 95\%$  confidence limits) and weight of *M. relicta* in Lake Hiidenvesi during the growing season 1999.

	Young of the year		Older	
	Length (mm)	Dry weight (mg)	Length (mm)	Dry weight (mg)
18 May	3.9 $\pm$ 0.04	0.16	16.7 $\pm$ 0.55	10.24
26 May	4.1 $\pm$ 0.03	0.19	15.5 $\pm$ 1.18	8.29
23 Jun	6.4 $\pm$ 0.02	0.67	16.5 $\pm$ 0.28	9.90
7 Jul	7.8 $\pm$ 0.03	1.18	17.0 $\pm$ 0.21	10.77
21 Jul	9.0 $\pm$ 0.03	1.77	17.8 $\pm$ 0.28	12.27
3 Aug	10.0 $\pm$ 0.03	2.39	16.4 $\pm$ 0.24	9.73
18 Aug	10.5 $\pm$ 0.06	2.74	17.3 $\pm$ 0.24	11.32
2 Sep	10.9 $\pm$ 0.05	3.05	17.1 $\pm$ 0.83	10.95
16 Sep	11.8 $\pm$ 0.51	3.82		
30 Sep	12.8 $\pm$ 0.92	4.81		

reached 0.09 g ww at its highest. In 1-yr-old smelts, zooplankton was still the main food, but *C. flavicans* constituted a considerable percentage of the diets in June and October (Fig. 6), and *M. relicta* was consumed in the hypolimnion in August. The maximum individual food consumption rate was 0.12 g ww d<sup>-1</sup>. In age 2 and older smelts, *C. flavicans* was the primary food in June and July, constituting 60–70% of the stomach contents, whereas *M. relicta* and zooplankton dominated the diets in August. *M. relicta* was preyed almost exclusively in the hypolimnion (Fig. 6). In October, *C. flavicans* together with zooplankton made up >90% of the stomach contents. The food consumption rate reached 0.12 g ww d<sup>-1</sup> individuals<sup>-1</sup> in age groups 2 and 3 and 0.14 g ww d<sup>-1</sup> individuals<sup>-1</sup> in older smelts.

For the whole smelt population, consumption of *M. relicta* was below 0.01 g ww m<sup>-2</sup> d<sup>-1</sup> in June and increased moderately toward midsummer (Fig. 7). In early August, it increased steeply, reached 0.05 g ww m<sup>-2</sup> d<sup>-1</sup> on 12 August, and decreased thereafter. One-year-old smelts constituted >65% of the consumption throughout the summer. Consumption of zooplankton peaked in early July and exceeded 0.18 g ww m<sup>-2</sup> d<sup>-1</sup>. In August–October, zooplankton consumption stabilized between 0.09–0.12 g ww m<sup>-2</sup> d<sup>-1</sup>. The consumption of *C. flavicans* peaked in early July at 0.06 g

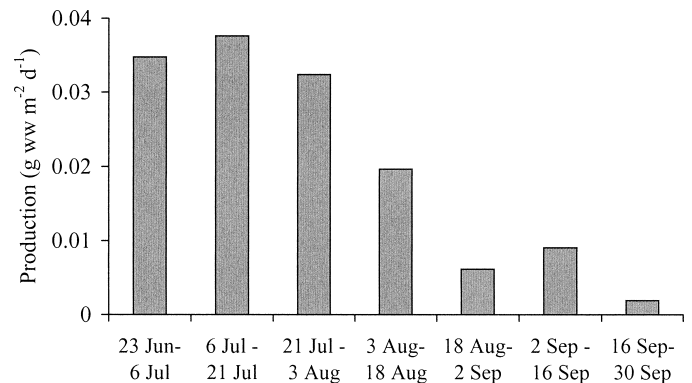


Fig. 5. The average daily production rate of the *Mysis relicta* population during the growing season 1999.

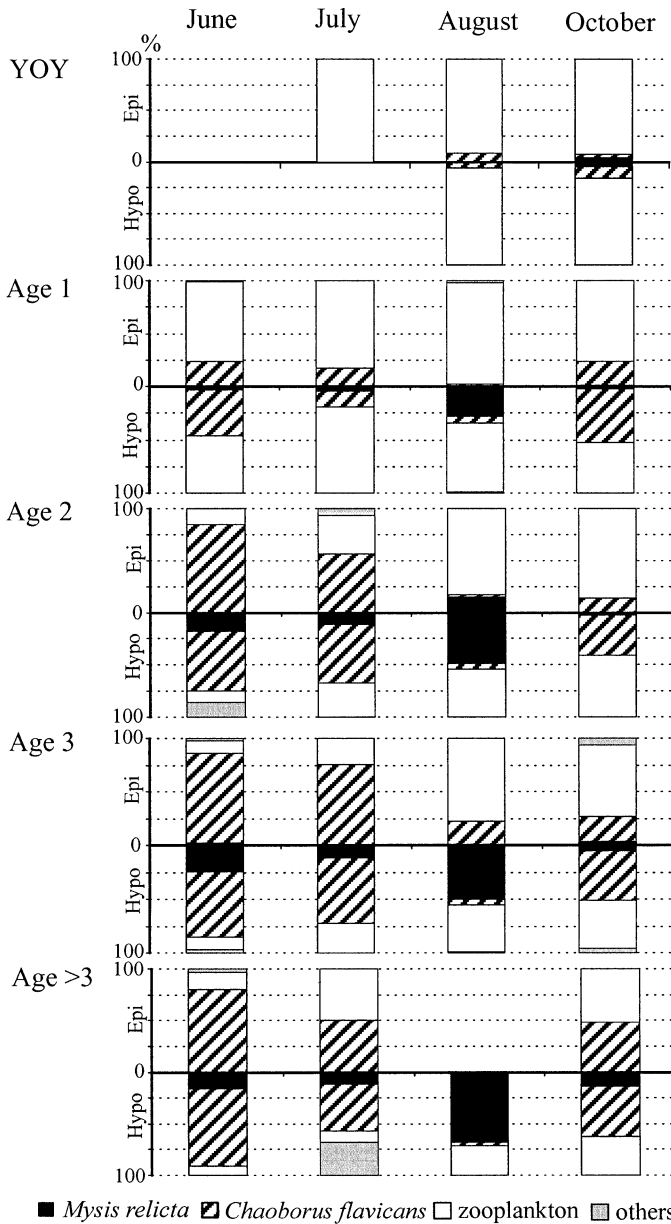


Fig. 6. The food composition of the different smelt age groups in the hypolimnion and in the epilimnion in June, July, August, and October 1999.

ww m<sup>-2</sup> d<sup>-1</sup>, fell to below 0.01 g ww m<sup>-2</sup> d<sup>-1</sup> in August, and again reached 0.06 g ww m<sup>-2</sup> d<sup>-1</sup> in October (Fig. 7).

Discussion

In Finland, most lakes inhabited by *M. relicta* have a maximum depth of more than 10 m (Särkkä et al. 1988); thus, its absence from the unstratified (shallow) basins of Lake Hiidenvesi could be expected. Probably due to several factors, shallow basins are unfavorable for mysids. During winter under the ice cover, oxygen may be depleted. The density of planktivorous and benthivorous fish is high (Vinni et al. 2000), and avoidance of predation by vertical migrations

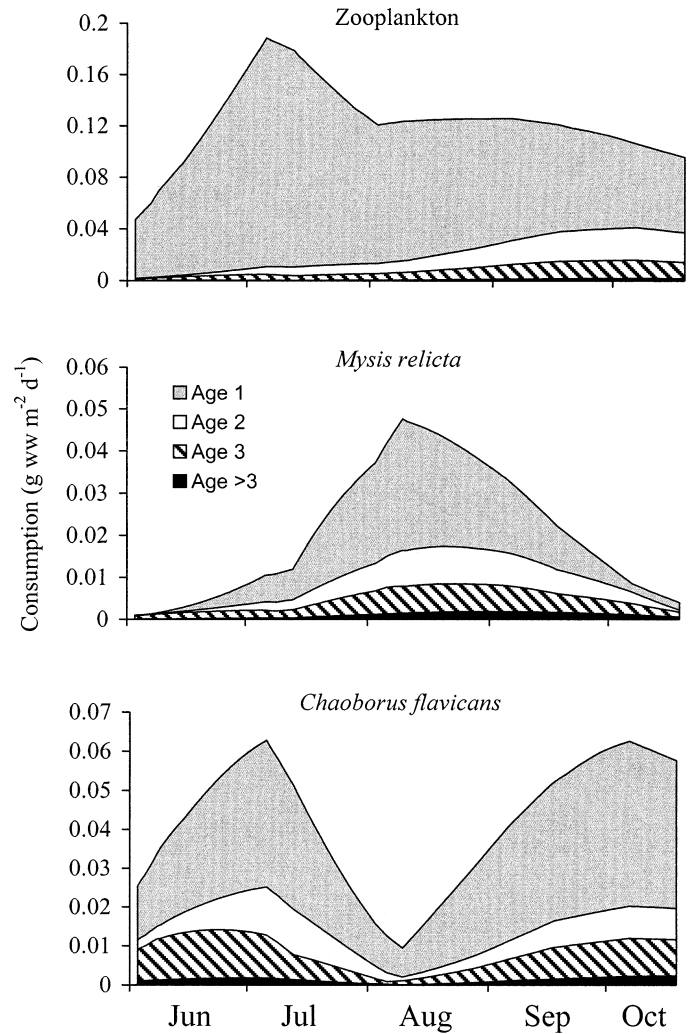


Fig. 7. The total daily consumption rate of zooplankton, *Chaoborus flavicans*, and *Mysis relicta* by the smelt stock (age 1 and older) in the stratifying areas (water depth > 10 m) of Lake Hiidenvesi. Note different scales on the y-axis.

(Bowers and Vanderploeg 1982; Rudstam et al. 1989) is not possible. Additionally, during midsummer, water temperature is often intolerably high (>18°C) throughout the water column (*M. relicta* can tolerate a wide range of temperatures, but the upper limit for long exposure times is 10–14°C [Smith 1970; Pennak 1978]). Thus, *M. relicta* inhabits the deepest regions of lakes and migrates horizontally in response to changing water temperatures (Carpenter et al. 1974; Hakala 1978; Morgan et al. 1978). In Lake Hiidenvesi, when water temperature increased, *M. relicta* population was concentrated in the deepest regions. On 3 June, when mysids inhabited sampling stations shallower than 7 m, 14°C was reached only in the surface water. On 6 July, when mysids were found only from stations deeper than 10 m, the 14°C isotherm was situated at 7-m depth and the 10°C isotherm was at 12-m depth. Additionally, young-of-the-year mysids have a tendency to migrate toward the pelagic zone as they grow (Moen and Langeland 1989), which contributed to the increasing density in the deepest area.

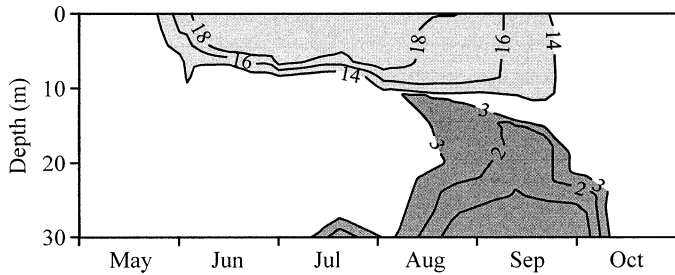


Fig. 8. The water layers unavailable for *Mysis relicta* due to low concentration of dissolved oxygen ( $<3 \text{ mg L}^{-1}$ , dark shading) or high temperature ( $>14^\circ\text{C}$ , light shading).

The vertical distribution of mysids corroborated the findings of Hakala (1978); in waters having a low transparency, *M. relicta* prefers the pelagic habitat throughout the day instead of staying near the bottom, as is common in clear-water lakes (Beeton 1960; Carpenter et al. 1974). In such situations, vertical net hauls are a reliable method for estimating abundance (Nero and Davies 1982). Only in May, when a considerable part of the population inhabited water layers below 24 m, would net hauls have underestimated the density of mysids. However, the total absence of mysids from bottom samples suggested that their density near and in the sediment was low. During the summer, the population moved upward in the water column, most likely in response to declining oxygen concentration in the deepest waters. The most distinct change of the vertical distribution of the population took place in August, when the concentration of dissolved oxygen in the hypolimnion was rapidly decreasing. The reported oxygen tolerance limits of *M. relicta* have varied between 1 and 4  $\text{mg L}^{-1}$  (Juday and Birge 1927; Dadswell 1974; Sherman et al. 1987). In Kiihkelyksenselkä, by the beginning of August, oxygen concentration at a 20-m depth had fallen below 3  $\text{mg L}^{-1}$ . On the other hand, water temperatures in the uppermost 10 m were unfavorably high; thus, *M. relicta* was restricted to a thin layer of water. Beeton (1960) found that *M. relicta* do not migrate through the metalimnion if the temperature gradient is above  $0.94^\circ\text{C m}^{-1}$ ; on 12 August, the temperature gradient in the metalimnion of Lake Hiidenvesi was  $1.8^\circ\text{C m}^{-1}$ . Mysids are also sensitive to light, and their daytime depth may be regulated by light intensity in the surface layers (Beeton 1960; Teraguchi et al. 1975). According to Teraguchi et al. (1975), *M. relicta* avoids light intensities above 0.02–0.05 lux. In Lake Hiidenvesi, due to the turbidity of the water, such intensities are reached only in the uppermost 2 m (Horppila et al. 2000 and unpublished). Additionally, mysids are most sensitive to light in the blue and green wavelength regions (Beeton 1959; Gal et al. 1999), while in the turbid water of Lake Hiidenvesi, red light penetrates deepest. It is therefore unlikely that light prevented mysids from ascending further than they did. The almost total absence of mysids in the stomachs of smelts captured from the epilimnion suggested that mysids did not enter the epilimnion even during the night.

Assuming that the tolerance limit of *M. relicta* is 3  $\text{mg L}^{-1}$  in dissolved oxygen and  $14^\circ\text{C}$  in water temperature, only a 1–3-m water layer (10–13 m) was available for *M. relicta* from mid-August to mid-September (Fig. 8). In this partic-

ular water layer, the density of mysids increased despite the declining total population abundance. On 6 July, when the whole hypolimnion was available for mysids, the estimated density of mysids was 2.4 individuals  $\text{m}^{-3}$ , assuming that the population was evenly distributed to the hypolimnion. On 18 August, the density of mysids in the 10–13-m layer was 17.0 individuals  $\text{m}^{-3}$ . If the oxygen tolerance limit was 2  $\text{mg L}^{-1}$ , the thickness of the available layer would have been lowest in September. However, in August, the vertical distribution of the smelt population changed downward and the percentage of mysids in the food of smelts increased steeply. The occurrence of some mysids in the unfavorable physical-chemical conditions below 24-m depth in August may have been due to the heavy predation pressure higher in the water column. Many planktivorous fish positively select large-sized invertebrate predators when they are available (Johannsson et al. 1994; Herzig 1995). Accordingly, in Lake Hiidenvesi, *Chaoborus flavicans* was the main prey for smelts in June and July. In August, the fraction of chaoborid larvae in the diet of smelts declined steeply due to the emergence of the adults. In summer 1999, the density of the large fourth instar larvae of *C. flavicans* fell to 2,000 individuals  $\text{m}^{-2}$  in mid-July–mid-August, while in June and September, it exceeded 5,000 individuals  $\text{m}^{-2}$  (Liljendahl-Nurminen et al. 2002). Thus, in August, a logical strategy for smelts was to shift their predation toward mysids, which became readily available due to their ascent in the water column and concentration in a small volume of water. The downward movement of smelts was probably accelerated by the tendency of smelts to avoid temperatures above  $15^\circ\text{C}$  (Nellbring 1989). Increasing water temperature was also a factor behind the avoidance of the shallow, nonstratifying regions by smelts during midsummer. Due to their higher abundance compared with older fish, the predation pressure on mysids was mainly by 1-yr-old smelts. Young-of-the-year smelts did not consume mysids in June–August because they inhabited the surface water layers, where mysids were absent. Thus, their omission from the smelt stock estimate did not bias the estimation of predation rate on mysids. The precision of the smelt-density estimates was relatively good, as indicated by the narrow confidence limits. Spatial autocorrelation, a common problem in acoustic data (Jolly and Hampton 1990), may cause underestimation of variance. However, in the present study, on most occasions, the critical level ( $r = 0.25$ ) presented by Williamson (1982) was not exceeded.

The predation rate by smelts alone was enough to account for the collapse of the mysid population. In June–July, production by mysids clearly exceeded the consumption rate by smelts. But in the first half of August, daily consumption by smelts was on average 1.5 times the production of mysids, and from 18 August to 2 September, smelts consumed 5.6 times the mysid production. It thus seems likely that smelt predation was the main cause of the drastic drop in the population density of *M. relicta* in late summer. Lack of suitable food was not a likely cause for the collapse. Food composition of mysids in Lake Hiidenvesi followed earlier findings. Cladocerans are often preferred over other prey (Bowers and Vanderploeg 1982; Johannsson et al. 1994). Individual growth rates were also comparable with those re-

ported from other lakes (Lasenby and Langford 1972; Kjellberg et al. 1991; Johannsson et al. 1994).

Our results suggest that unfavorable physicochemical conditions did not directly cause the drastic reduction of the population of *M. relicta*. Indirectly, however, seasonal water-quality changes facilitated effective predation by smelts, which was the final cause of the collapse. Without predation by smelts, a larger part of the mysid population would probably have survived in the narrow corridor between the layers of too low oxygen and high temperature. The predation by smelts was accelerated by the emergence of chaoborid larvae, which were important food items for smelts in early summer.

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