

HABITAT SHIFTS OF *MYISIS RELICTA* (DECAPODA, MYSIDACEA) IN THE LAKES BREITER AND SCHMALER LUZIN (NE GERMANY)

BY

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ABSTRACT

Between spring 2001 and autumn 2004, the habitat use, vertical migration, and density of *Mysis relicta* in the lakes “Breiter Luzin” and “Schmaler Luzin” in northeastern Germany were investigated by horizontal net hauls, epibenthic sledge hauls, and SCUBA diving. On 3-4 July 2001 we estimated a density of 466.03 ind./m² in the water column of lake “Breiter Luzin”, but in April of 2002 population density was only 5.26 ind./m². In October 2004 the observed densities increased with depth, starting at the lower sublittoral down to the upper profundal on about 1000 ind./m². Downward from 22 m, densities fluctuated around this value up to 30 m depth. During daytime, mysids were never observed above 9 m. Below this limit all suitable parts of both lakes were occupied. We found no evidence for a preference of different sediment types as mud or sand. During daytime mysids showed a strong affinity for the lake bottom, and adults tend to live in deeper areas than juveniles. At night this distribution seems to be inverted. In July 2001 the proportion of adults (especially females) was highest in the metalimnion and the upper hypolimnion, whereas the proportion of juveniles increased with depth.

ZUSAMMENFASSUNG

In den im Nordosten Deutschlands gelegenen Seen Breiter und Schmaler Luzin wurde die Habitatnutzung, vertikale Migration und Dichte von *Mysis relicta* zwischen Frühjahr 2001 und Herbst 2004 mit einer epibenthischen Dredge, mit Horizontalnetzen und Taucheinsätzen untersucht. Im Breiten Luzin wurde in der Nacht vom 3. zum 4. Juli 2001 im Freiwasser eine Dichte von 466,03 Ind./m² ermittelt. Im April 2002 betrug die Dichte lediglich 5,26 Ind./m². Die Dichte der sich am Tage dicht über dem Boden aufhaltenden Tiere stieg vom Sublittoral zum oberen Profundal hin auf ca. 1000 Ind./m² an. Unterhalb 22 m blieb diese Dichte bis in 30 m Wassertiefe mit geringen Schwankungen konstant. Oberhalb 9 m konnten am Tag keine *Mysis*-Individuen nachgewiesen werden. Unterhalb dieser Grenze wurden dagegen alle geeigneten Benthalthbereiche besiedelt. Eine

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Substratpräferenz für Mudde oder sandige Sedimente konnte nicht festgestellt werden. Am Tage bevorzugt *Mysis* die Bodenoberfläche und adulte Tiere halten sich tendenziell in größerer Tiefe als Jungtiere auf. Nachts wurden im Metalimnion und im oberen Hypolimnion dagegen größere Konzentrationen von adulten, besonders weiblichen, Tieren gefunden, während der Anteil von Jungtieren mit der Tiefe zunahm.

INTRODUCTION

Mysis relicta Lovén, 1862 is an epibenthic-pelagic crustacean of marine origin. According to Väinölä et al. (1994) four sibling species in northern Europe and North America are described as the *Mysis relicta* species group. The population we investigated in the Luzin lakes belongs to a species widespread around the Baltic Sea, in many Fennoscandian, German, and Polish lakes (Väinölä et al., 2002).

The occurrence of populations of *M. relicta* in the Luzin lakes and in other lakes in Germany and Poland was an important element for the explanation of the dispersal of glacial marine relicts in fresh water. According to the theory of Thienemann (1950), the species entered the Baltic Sea area during the Yoldia period from the White Sea, and was sluiced during the Pomerian stage of Vistula glaciations up to those levels where the lakes harbouring relicts are situated today (Seegerstråle, 1957, 1962). Other glacial marine relicts, like the amphipods *Pallasiola quadrispinosa* (G. O. Sars, 1867) and *Pontoporeia affinis* Lindström, 1855, and the fish *Cottus poecilopus* Heckel, 1836, settled in the lakes of the south Baltic area (Köhn & Waterstraat, 1990) and are now isolated from the main distributional area of the species. Most of these populations are endangered or extinct.

In the Luzin lakes, the populations of *M. relicta* and *C. poecilopus*, as well as of the endemic *Coregonus lucinensis* Thienemann, 1933, were strongly affected by eutrophication in the last century (Thienemann, 1933; Waterstraat, 1988; Winkler et al., 2002; Kotusz et al., 2004). The species were temporary lost in lake Schmaler Luzin and neighboring lake Zansen, and were also endangered in the larger lake Breiter Luzin. In order to reduce the harmful influence of human activity in the region, restoration measures in the catchment area, but especially in that of lake Schmaler Luzin (Koschel et al., 2001), have been brought into effect in recent years.

Analysis of the distribution (Samter, 1905; Thienemann, 1950), experiments to introduce the species in new localities (Fürst, 1981; Fürst et al., 1985), ecological studies to investigate density and abundance (Hakala, 1978; Morgan & Beeton, 1978; Pothoven et al., 2000; Johannsson et al., 2003), population structure (Pothoven et al., 2000), and the importance of mysids in the food web (Rudstam et al., 1999; Spencer et al., 1999; Johannsson et al., 2001) were in the focus of

attention in the past. Also, in the Luzin lakes new data about the recolonization of lake Schmalter Luzin and the density and population structure of *M. relictata* were collected (Scharf & Koschel, 2004). Information about the spatial distribution and the habitat preference of *Mysis* in the Luzin lakes is as yet not available.

In the past, these lakes were oligotrophic, but at present they are mesotrophic. The eutrophication processes in the lakes affected both the habitats of the mysids on the benthic sediments, and the pelagial, especially by oxygen depletion. This results in a reduction of usable hypolimnetic water and bottom areas. That is why the aim of our investigations was to collect new information about habitat use and spatial distribution during daytime and at night in the lakes, and to enhance our knowledge about the density and structure of these mysid populations.

STUDY SITE

The Luzin lakes are part of the Feldberg lake area in the district Mecklenburg-Strelitz of the state Mecklenburg-Vorpommern in northeastern Germany (fig. 1). The Lake District was influenced by the Saale glaciations and formed by the glaciers of the Vistulian glaciations (Schmidt, 1997). This resulted in a large litho-littoral zone, which is unusual for lowland lakes of Central Europe.

Lake Breiter Luzin is the deepest lake of the district, with a maximum depth of 58.3 m. According to the digital map, the lake's surface area and volume reach 345 ha and 77 mill. m³, respectively. From May to October, the thermocline was found mostly at a depth between 4 and 12 meters. Lake Schmalter Luzin, connected by a small channel to lake Breiter Luzin, has a surface area of 145 ha, a volume of 21 mill. m³, and a maximum depth of 34 m.

The littoral of both lakes is dominated by geogenic sandy and stony sediments. Between a depth of 14 and 26 m, mud is predominating with 70-90% and below 25 m this is the only sediment occurring (table I).

TABLE I
Characteristics of the lakes "Breiter Luzin" and "Schmalter Luzin"

Depth layer	Depth	Pelagial volume (mill. m ³)		Benthic area (mill. m ²)		Percentage of mud	
		Breiter Luzin	Schmalter Luzin	Breiter Luzin	Schmalter Luzin	Breiter Luzin	Schmalter Luzin
Epilimnion	0-9 m	26.2	11.1	1.064	0.382	14.7	2.2
Metalimnion	9.1-14 m	10.3	4.3	0.453	0.313	35.6	9.0
Upper hypolimnion	14.1-26 m	18.8	5.2	0.498	0.439	70.8	89.4
Lower hypolimnion	26.1-59 m	21.7	0.8	1.333	0.223	99.2	100

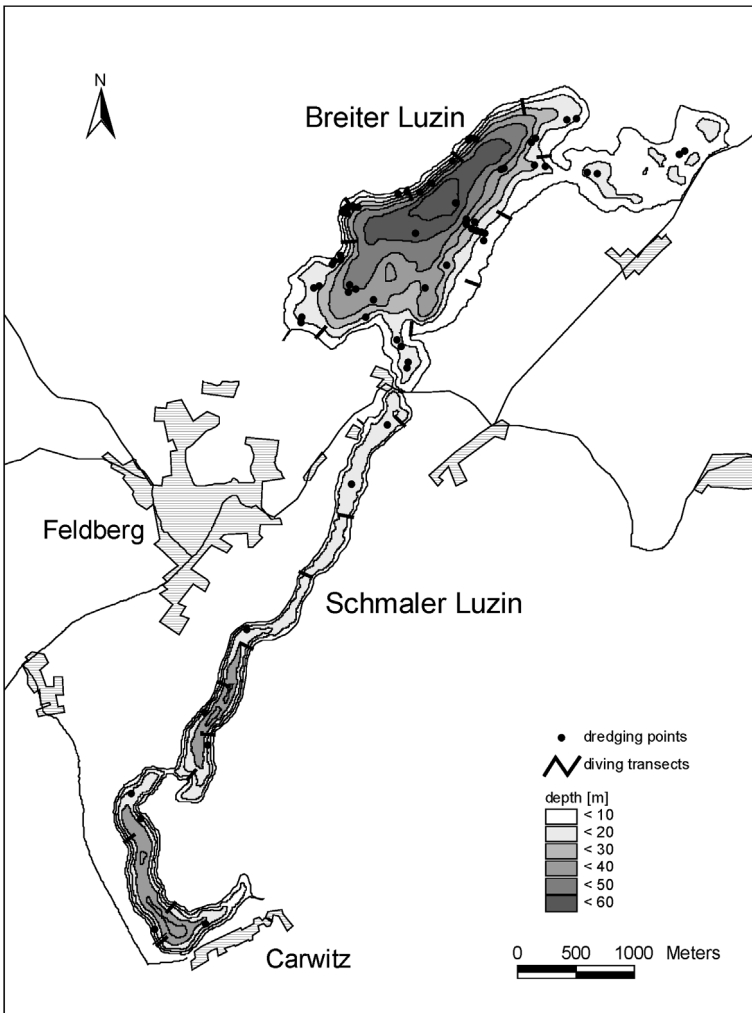


Fig. 1. Map of the location of the Luzin lakes and the investigation sites in them.

SCUBA diving was used to investigate the sublittoral and profundal sediment structure in the lakes: the sediment composition of the lakes was estimated visually each 10 m on standardized line transects (perpendicular to the shore) of 100 m (fig. 2).

METHODS

During daytime, mysids were caught with an epibenthic sledge (0.6×1 m; mesh size 0.5 mm). The length of each of the 73 hauls between April and October 2001 in both lakes were 50-80 m and the area sampled by a single haul about 40-50 m².

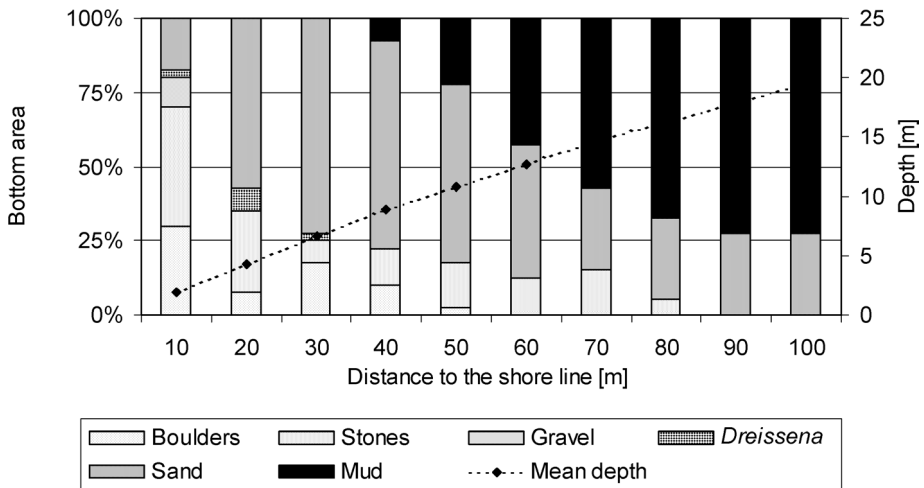


Fig. 2. Distribution of different sediment classes dependent on depth in 20 transects of 100 m length each in the lakes Breiter and Schmalzer Luzin.

The samples were preserved in 70% ethanol. Most of the samples were counted entirely. Only samples of >5,000 specimens were counted by large random sub-sampling. Body length and sex were recorded of all individuals counted. Length was measured from the tip of the rostrum to the base of the telson to the closest millimeter. Males were identified by the presence of thickened and bifurcated fourth pleopods and females by the presence of a marsupium. Specimens without these characteristics were classified as juveniles.

Between 2001 and 2004, the occurrence of mysids in the Luzin lakes was observed by SCUBA diving at daytime (nine times) and at night (six times). In October 2004, the autumn vertical distribution was investigated by SCUBA diving in the "Schlossbergbucht" of Lake Breiter Luzin. At daytime five standardized line transects up to a depth of 30 m were inspected by divers. The number of *Mysis* found within one square meter bottom was registered with regard to the depth and the dominating substrate type of the site.

In July 2001, April 2002, and July 2002, horizontal bongo net trawls were hauled at different depths during nighttime at new moon. Two bongo nets (mesh size 500 μm) with a diameter of 0.6 m each (together 0.565 m^2) were trawled about 1000 m with a speed of 2 m/s.

Water temperature and oxygen concentration were measured in situ (WTW Oxi 197 S) at 1 m intervals. For statistical analysis, the program Statistica 5.01 (© StatSoft Inc.) was used.

Digital lake maps were provided by the Ministry of the Environment of the Federal State Mecklenburg-Vorpommern. The geographic informationsystem ArcView 3.1 (© Environ. Syst. Res. Inst. Inc.) was used to analyse these maps.

RESULTS

Vertical and horizontal distribution of mysids during daytime

Mysids were never caught or observed above 9 m during daytime with the epibenthic sledge (fig. 3), and by SCUBA diving. According to both methods, *Mysis relicta* occurs more frequently in the upper profundal areas (14-26 m) than in the sublittoral areas (9-14 m) of both lakes. The deepest epibenthic catch was done in lake Breiter Luzin in October 2001, between 35 and 43.2 m (mean 39.1 m, fig. 3). The oxygen concentration at this depth was 4 mg/l.

Not only the frequency of occurrence but also the density of mysids increased in the deeper bottom areas of the lakes (fig. 4). The first mysid occurrence in the SCUBA diving transects at 13 m was deeper than expected, but the water transparency (more than 4 m) was much higher than usual. The mean *Mysis*-density in the transects increased to about 1000 ind./m² at a depth of 22 m, and fluctuated around this value up to 30 m. With increasing depth, a higher proportion of large mysids was visually observed.

Estimated densities of mysids based on epibenthic dredging hauls were substantially lower. They increased significantly from the sublittoral to the upper profundal area ($p = 0.02$, Mann-Whitney U -test). In the upper profundal area the median of all hauls was below 10 ind./m². A quarter of all samples contained more than 25 ind./m² and only in one haul more than 1500 ind./m² could be counted. Samples of April of 2001/2002 were excluded for this analysis because of very low densities of mysids in lake Breiter Luzin at this time of year (Scharf & Koschel, 2004).

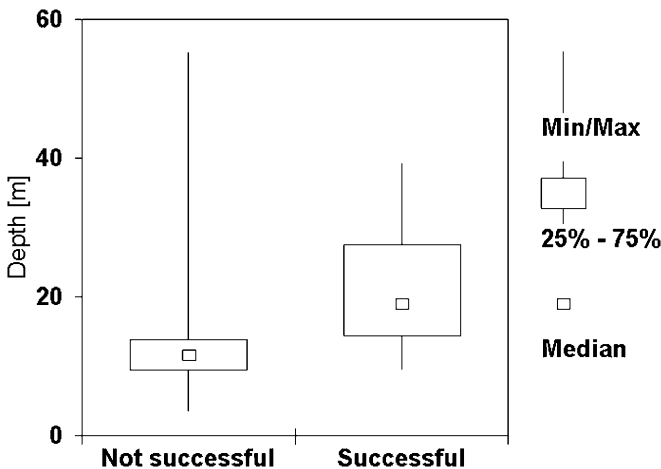


Fig. 3. Depth of successful and unsuccessful epibenthic hauls for mysids: number of hauls with *Mysis relicta* Lovén, 1862, $n = 38$; number of hauls without *M. relicta*, $n = 25$; differences between groups are significant with $p < 0.01$, Mann-Whitney U -test.

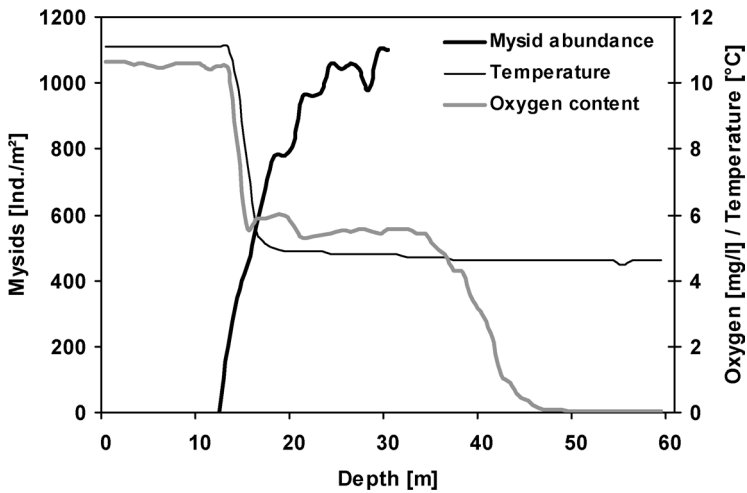


Fig. 4. Mean density of *Mysis relicta* Lovén, 1862 at five diving line transects in the Schlossbergbucht of lake Breiter Luzin on 13 October 2004, related to depth, temperature, and oxygen content.

In the deeper profundal area (below 26 m) the density of mysids in our dredging hauls decreased again. This result is inconsistent with our diving results, and mainly describes a lower catch efficiency of epibenthic dredging on mud in deeper lake areas (see below). Larger individuals could be caught much more frequently at deeper bottom areas (fig. 5). The proportion of juveniles was much higher in the sublittoral and upper profundal zone than in the deeper profundal zone. The number of small juveniles was very low in October 2001. In the deeper profundal area, adults were dominating in the spring and autumn of 2001. Especially in deeper bottom areas of the lake, the proportion of females increased.

Mysids could be found during daytime with diving and epibenthic hauls in almost all areas of lake Breiter Luzin. In the shallow southeastern and northeastern bay (“Lütter See”) mysids were absent for most of the year. But also there, divers could detect some individuals between 10 and 12 meters in October 2004. In lake Schmaler Luzin, the population of *M. relicta* appeared to be concentrated in both deep basins of that lake.

Habitat use during daytime

During our daylight SCUBA diving, all mysids were found directly on the sediment. In the line transects, sediments dominated by sand and stones were replaced for mud at a depth of 20.5–21.5 m. The lowest densities of mysids could be found on sublittoral sand (Mann-Whitney *U*-test, $p = 0.01$; fig. 6). Densities of mysids on mud did not differ between upper and deeper profundal areas. The density on sand in the upper profundal was only a little bit lower than that on mud.

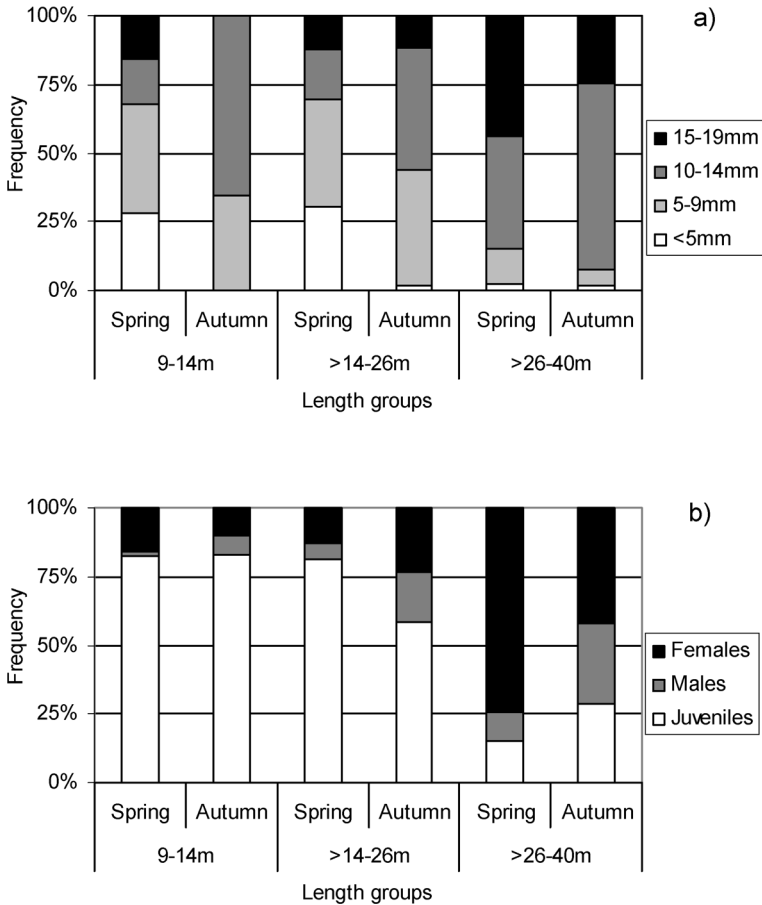


Fig. 5. Vertical distribution of: a, length groups; and, b, sex categories of *Mysis relicta* Lovén, 1862 from daytime dredge hauls in spring and autumn 2001 in lake Breiter Luzin (spring/autumn: 9-14 m, $n = 780/400$ ind.; >14-26 m, $n = 1812/3159$ ind.; >26-40 m, $n = 39/187$ ind.).

In fact, this difference is only caused by the shallower presence of sand in this zone. We conclude that there is no difference in habitat use of mud and sand, although this was suggested by the results of epibenthic dredging. By this method, the mean catch on mud was significantly lower (Mann-Whitney U -test, $p = 0.01$) than on sand, or on a mixture of sand and stones. This must be explained by a differential catch probability on different kinds of bottom substrate.

Vertical distribution at night

With SCUBA diving, we could confirm, that mysids did not occur on the bottom at night. Most of the specimens were observed in the water column, only occasionally some were found near the bottom.

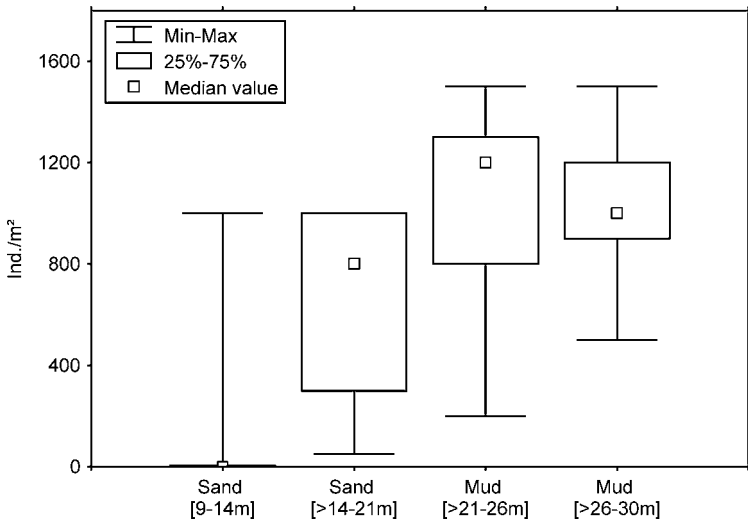


Fig. 6. Mean densities of *Mysis relicta* Lovén, 1862 of five SCUBA diving line transects in the Schlossbergbucht of lake Breiter Luzin on 13 October 2004 in relation to sediment depth.

Bongo net trawling at night was used to estimate the densities of mysids in the water column of lake Breiter Luzin. In the night from 3 to 4 July 2001, we estimated a density of 466.03 ind./m². In the night from 18 to 19 April 2002, only 5.27 ind./m² were counted. Unfortunately, only the water column between 0 and 30 meters could be checked at this date.

In July 2001 and 2002, the epilimnion and the upper part of the thermocline were not or only scarcely used by mysids. The highest density during July was observed immediately below the thermocline at a depth of 11-15 m. In spring 2002, specimens were distributed regularly in the pelagial. The epilimnion was also used (fig. 7).

In July 2001, the proportion of just hatched and small juveniles decreased with increasing depth (fig. 8). Only one-third of all juveniles could be found in the metalimnion and upper hypolimnion (9-16 m), but half of the males and more than 60% of all females occurred there. In regard to the fact that this represents a reversal of the relations during daylight, adults and especially females must have carried out larger vertical movements than juveniles.

DISCUSSION

Mysis relicta is a semipelagic species. Therefore, different methods are necessary to study its population structure and dynamics, as well as its density and movements in the water column and on the bottom. Densities of *M. relicta* were

recorded effectively with vertical nets at night (Grossnickle & Morgan, 1978; Bagge et al., 1996). Scharf & Koschel (2004) successfully used these methods in the Luzin lakes. We reached similar densities of *M. relicta* with our horizontal net catches. The advantage of horizontal catches is the larger haul distance. This may be important if densities are very low. For instance, in early spring 2002, Scharf & Koschel (2004) observed very low densities of mysids in lake Breiter Luzin. They could find only a few specimens in the middle-deep layer (10-25 m). Our estimated density of 5.3 ind./m² from April 2002 is based on a much larger data set of 595 specimens caught. On the other hand, deep lakes are more difficult to investigate with horizontal net hauls.

The catch efficiencies of most of the epibenthic methods are quite lower than those of vertical or horizontal pelagic hauls. Only by SCUBA diving, we could estimate the real mysid density during daytime on the bottom in the Luzin lakes. The high effort and a maximum investigation depth of 40 m restrict the use of this method, however. That is why Morgan & Beeton (1978) used a submarine for visual observations of *M. relicta* at greater depths. Bagge et al. (1996) could not effectively catch mysids on the bottom of two Finnish lakes with plexiglass traps or Eckman-grabs. Their epibenthic dredge catches at depths of 250-300 m were also much poorer than the comparable vertical haul catches (0.5 ± 0.5 to 119.5 ± 111.1 ind./m² in lake Paasivesi and 0.8 ± 1.0 to 4.4 ± 14.7 ind./m² in lake Puruvesi). On the other hand, Grossnickle & Morgan (1978) could not find significant differences between epibenthic dredge hauls during daytime and vertical hauls at night in medium depths (115 m) of Lake Michigan. They assumed

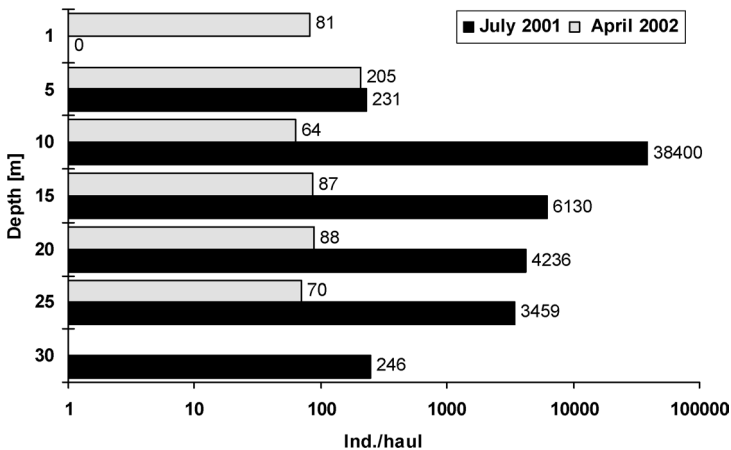


Fig. 7. Distribution of *Mysis relicta* Lovén, 1862 at different depths by Bongo net trawling at night in July 2001 and April 2002.

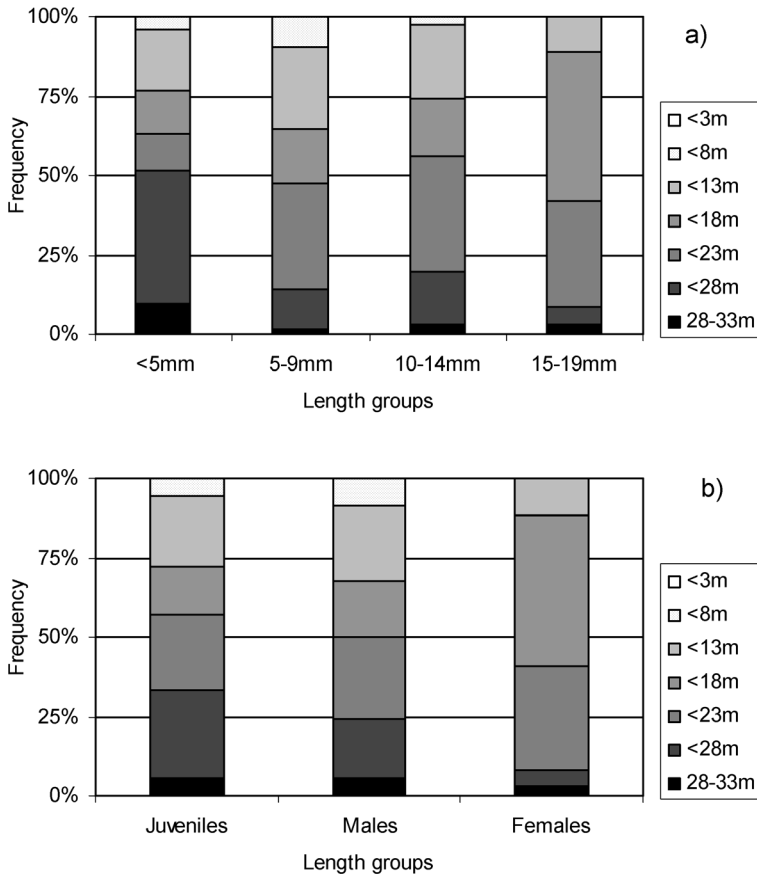


Fig. 8. a, Length distribution; and, b, sex distribution of *Mysis relicta* Lovén, 1862 in Bongo-hauls of 4 July 2001 (<5 mm, $n = 1990$; 5-9 mm, $n = 1465$; 10-14 mm, $n = 702$; 15-19 mm, $n = 256$).

that the used epibenthic sledge underestimated densities in shal lower depths of 20-40 m, where mysids stay directly on the bottom. In the Luzin lakes, we could not effectively catch total mysid density with an epibenthic sledge either. The mean calculated density ($<10 \text{ ind./m}^2$) reached only 10% of those of the vertical hauls (Scharf & Koschel, 2004). The catch efficiency of the sledge was mainly reduced on mud.

However, dredging and SCUBA diving are useful methods to investigate spatial pattern and habitat use during daytime. In the diving observations by Morgan & Beeton (1978), mysids were found to settle strongly on the sediment during daytime. Our diving observations confirm this. According to this fact, *M. relicta* does not have a preference for sand or mud in lake Breiter Luzin. Unfortunately, only some reports describe the sediment use of mysids. Song & Breslin (1999) observed the occurrence of mysids in Lake Ontario both on mud

and on anthropogenic sediments formed by coal mining. Bagge et al. (1996) also caught *Mysis* on mud.

Detrimental light-, temperature-, or oxygen conditions are the expected reasons for permanent or temporary mysid absence on parts of the bottom during daylight in spring and autumn in our investigations. At this time, littoral areas above 9 m were avoided by mysids. At higher water transparencies as in October 2004, sublittoral areas above 13 m were also avoided. This is clear evidence that not only temperature but also light gradients are responsible for the depth distribution of mysids in our lakes. Mysids ascent at night and their distribution during daytime is reported to be limited by light as low as 10^{-2} to 10^{-4} Lux (Rudstam et al., 1989). In lakes with high water transparency like Lake Ontario, *M. relicta* does not occur above 20 m (Johannsson, 1995). Gal et al. (1999) observed this light avoidance by *M. relicta* at any time of the day or night. They estimated a limit of 3.4×10^{-7} to 2.1×10^{-6} mylux (1 mylux = 157 lux or 0.46 W/m²).

Density of mysids in lake Breiter Luzin increased regularly on the bottom below the thermocline and reached about 1000 ind./m² at 20 to 25 m in October 2004. We assume that large densities occur also in deeper bottom areas, like in other lakes (Morgan & Beeton, 1978). The reduced oxygen concentration in the depth of our lakes probably restricts settlement on deeper bottom areas during summer and autumn. Before the restoration of lake Schmaler Luzin by the end of the 1990s, the majority of the hypolimnion was totally lacking oxygen during summer (Koschel et al., 2001). In this lake, *Cottus poecilopus* (cf. Kotusz et al., 2004) and *M. relicta* (cf. Waterstraat, 1988) have gone extinct. In order to reduce the harmful influence of human activity in the Feldberg region, a restoration program for lake Schmaler Luzin has been brought into effect in recent years. As a result of this, the oxygen concentration in the hypolimnion recorded during the summer stagnation season has rapidly increased (Koschel & Dietrich, 2000; Koschel et al., 2001). The first recovered species in the lake is *M. relicta* (Waterstraat & Krappe, 2003; Scharf & Koschel, 2004). The same process of oxygen loss has been taking place in lake Breiter Luzin. Simultaneously, H₂S-formations at the bottom have been reported since 1976 (Richter, 1982). Currently, at the end of the summer stratification period, the maximum O₂-concentration in the hypolimnion falls below 6 mg/l and no oxygen can be detected below 45 m. According to Sherman et al. (1987), who described a minimum oxygen-level of 1 mg/l for *M. relicta*, in lake Breiter Luzin insufficient conditions for this species occur below a depth of 40 m from September to December. In accordance with this fact, Scharf & Koschel (2004) observed a lower density at four stations at a depth of 25 meters on the deepest location, with bad oxygen conditions, in vertical net hauls at night.

In our investigations, mysids were never found above 15°C on the bottom during daylight. At night, in July 2001 and 2002 we could find a small proportion of

the population at a depth from 5 to 6 meters at 17-20°C. The epilimnetic layer between 0 and 1 m with temperatures above 20°C was free of mysids in July. Nevertheless, most of the population did not migrate across the thermocline in July. The highest densities were found directly below the thermocline. The thermocline has often been noted as the upper limit of mysid migration (Beeton, 1960). Scharf & Koschel (2004) found the highest densities in lake Breiter Luzin in the upper and middle depth layers. Because of larger depth intervals of their nets (10 and 15 m) they were not able to prove concentration effects at the thermocline. In April 2002, at a homoeothermic state, some individuals of *M. relictata* moved close to the surface at night, but the population of lake Breiter Luzin was distributed over all layers. Thienemann (1925, 1928) already knew the influence of temperature on the settlement of mysids in the Luzin lakes. He described that mysids avoided layers with temperatures above 15°C. If temperatures were slowly increased by 1 to 5°C per day, DeGraeve & Reynolds (1975) reported, the mortality of mysids increased above 13°C. However, this is not dangerous for short time migrations: according to Rudstam et al. (1999) daily (short time) vertical migrations between 4 and 15°C are possible. *M. relictata* survival (over 8 hours) was high up to 17°C (93%) and decreased rapidly with increasing temperatures to 0% at 26°C. Yet, feeding rates for adult mysids were highest at 12°C and for juveniles at 14°C (Rudstam et al., 1999).

At day- and nighttime, we could find a different depth distribution of juveniles and adults in the Luzin lakes. During daytime, the proportion of larger individuals, among the adults more females than males, increased in the deeper profundal. At night, we could find the opposite result. Beeton (1960) discovered the same result during daytime. At night, he could not find differences between the depth distributions in the pelagial.

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