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Life history, habitat utilisation, and biomass of introduced *Mysis relicta*

T. F. Næsje*, R. Saksgård, A. J. Jensen & O. T. Sandlund

Norwegian Institute for Nature Research (NINA), Trondheim, Norway

Abstract

Life history, habitat utilisation, and biomass of benthic and pelagic opossum shrimp (*Mysis relicta*) were studied in the oligotrophic Lake Jonsvatn, central Norway. Sampling in the pelagic zone was done by means of a closing zooplankton net; in the benthic zone by means of a benthic beam trawl.

M. relicta had a mixed one or two year life cycle. In the autumn, the proportion of mature females and males were larger in the pelagic than in the benthic habitat. Copulation took place in late autumn, and the first females with eggs occurred in November. In February, the first juvenile *M. relicta* were released in the benthic habitat. In May and July, however, juveniles were found in large numbers in all parts of the lake. The length distribution of *M. relicta* indicates that juveniles partly segregate between benthic and pelagic habitats.

Both juvenile and adult *M. relicta* performed vertical diel migrations in the pelagic habitat. In the benthic habitat, diel vertical migrations along the bottom were not as pronounced as vertical migrations in the pelagic habitat. In the benthic habitat, major migrations were performed only by adults in the autumn. Our results indicate that the light intensity in the green part of the spectrum gives the proximate cue for regulation of vertical distribution of *M. relicta*.

The mean total biomass varied between 288 and 1576 kg dry weight, corresponding to 23.2–127.1 mg dry weight m^{-2} surface area. *M. relicta* had smallest biomass during late spring/early summer and largest biomass during autumn and early winter. Estimated pelagic biomasses were largest in February, August, October and November, while benthic biomasses were largest in May and July. Estimated biomass of pelagic *M. relicta* during autumn was approximately 1/10 of the estimated biomass of zooplankton in this lake.

Key words: Diel migration – life cycle – habitat shifts – population growth

Introduction

The opossum shrimp (*Mysis relicta* LOVÉN) is a key species in many lakes where it acts as an opportunistic omnivore, feeding on zooplankton, phytoplankton and detritus (GROSSNICKLE 1982). In its natural range, *M. re-* *licta* is recognised as an important prey item for fish (e.g. TATTERSAL & TATTERSAL 1951; NORTHCOTE 1970; LASENBY et al. 1986; GROSSNICKLE 1982). Their relatively large size (maximum body length 20 mm) and distribution throughout the water column led many to consider *M. relicta* to be an ideal food source for many

*Corresponding author: Tor F. Næsje, Norwegian Institute for Natural Research (NINA), Tungasletta 2, NO-7485 Trondheim, Norway; e-mail: tor.naesje@nina.no

salmonids (CLEMENS et al. 1939; SPARROW et al. 1964; FÜRST 1972; NORTHCOTE 1972). This resulted in widespread introductions of *M. relicta* to North American and Scandinavian lakes and reservoirs from the mid-1960s through the 1970s (NESLER & BERGERSEN 1991).

Mysis relicta turned out to be a successful invader, as it established viable populations in most new localities. Moreover, it spread to downstream localities with apparent ease, and has frequently utilized man-made water transfer tunnels among lakes for further invasions. In terms of fish enhancement, however, results were often the opposite of those expected, as the abundance of planktivorous fish frequently declined sharply soon after *M. relicta* was introduced. While the rationale behind the introductions was the assumed herbi- and detritivory of *M. relicta*, it turned out that the species is also an efficient zooplanktivore. Thus, the introduction of *M. relicta* has established an additional trophic link between zooplankton and zooplanktivorous fish. *M. relicta* has also reduced the abundance of zooplankton, particularly larger cladoceran species which are important food items for fish (e.g. RICHARDS et al. 1975; MORGAN et al. 1978; KINSTEN & OLSEN 1981; SPENCER et al. 1999). In addition, their diurnal migratory behaviour limits their availability as food for pelagic fish that search visually for food (NÆSJE et al. 1991). Introductions have been reported beneficial to fisheries when benthivorous fish species, such as lake trout (*Salvelinus namaycush*), brown trout (*Salmo trutta*), lake whitefish (*Coregonus clupeaformis*) and burbot (*Lota lota*) have been targeted for enhancement (MORGAN et al. 1978; FÜRST et al. 1986).

The diurnal vertical migration of *M. relicta* in the pelagic habitat has been well documented, but little is known about their benthic habitat utilisation, and studies analysing habitat use in both major habitats are few. Such studies, however, are important for a better understanding of the function of *M. relicta* in the aquatic ecosystem.

The success of *M. relicta* as an invading species is an indication of a highly adaptable habitat utilisation and life history (CHESS & STANFORD 1998). The ecology of the species was very poorly known in the 1960 s and 1970 s, a fact which was not heeded by fish managers promoting *Mysis* introductions as a management tool. Additional complexity emerges from the fact that the impact of the introduced *M. relicta* may vary among different lakes. The higher productivity of eutrophic lakes, for example, may reduce the impact on zooplankton communities, compared to what has been recorded in oligotrophic lakes (MORGAN et al. 1978; GOLDMAN et al. 1979). In shallow lakes, the possibility of vertical diurnal migration is reduced, increasing the vulnerability of *M. relicta* to visually hunting predators (MORGAN et al.

1978). Therefore, the most serious negative impacts on planktivorous fish from *Mysis* introductions are most often reported from cold, deep and oligotrophic lakes such as Lake Jonsvatn studied in this paper.

Because of the serious implications of *Mysis* introductions, it is important to better understand the life history and habitat utilisation of the species, and to document its role in the ecosystem. This may also add to the general understanding of the process of exotic species invasions (WILLIAMSON 1999). The aims of this paper are: (1) to analyse the life history of *M. relicta* in order to detect possible differences between the sub-populations utilising the benthic and pelagic habitats, respectively; (2) to analyse the population and biomass development of *M. relicta* in the benthic and pelagic habitat throughout the year; and (3) to reveal the diurnal migration patterns of *M. relicta* in the two habitats.

Study area

The oligotrophic Lake Jonsvatn (63° 22′ N 10° 37′ E) is used as water reservoir for the city of Trondheim, Norway (Fig. 1). In 1978, *M. relicta* was introduced into the lake, and in 1981, densities of 2–3 mysids m^{-2} surface area were observed in the pelagic zone.

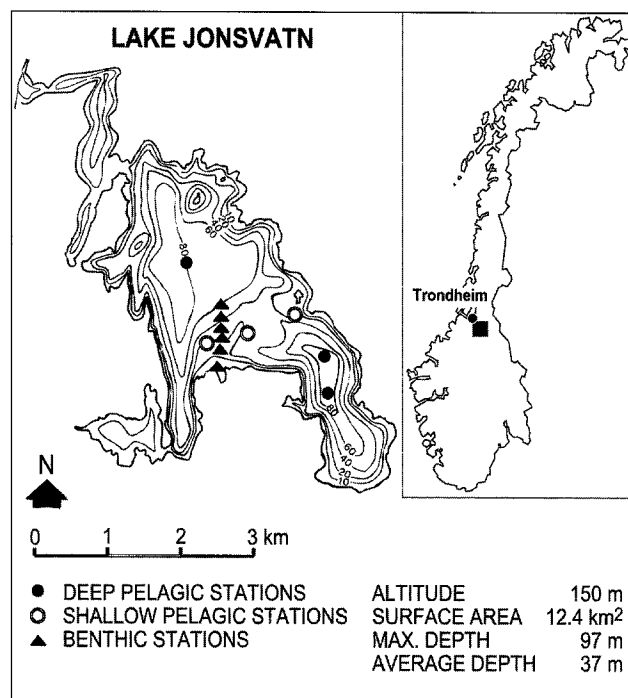In 1986–1987, when our study was performed, the crustacean zooplankton community was still dominated

LAKE JONSVATN

Trondheim

N

0   1   2   3 km

● DEEP PELAGIC STATIONS   ALTITUDE   150 m
O SHALLOW PELAGIC STATIONS   SURFACE AREA   12.4 km²
▲ BENTHIC STATIONS   MAX. DEPTH   97 m
                             AVERAGE DEPTH   37 m

Fig. 1. Map of Lake Jonsvatn with morphometric data indicating locations of the deep pelagic stations (0–80 m), shallow pelagic stations (0 –20 m) and benthic stations (0–65 m).

by the cladocerans *Bosmina longispina, Daphnia galeata* and *Holopedium gibberum*, and the copepods *Cyclops scutifer, Arctodiaptomus laticeps* and *Heterocope appendiculata* (KOKSVIK et al. 1991). With the exception of August, copepods were the most common zooplankters throughout the year, accounting for 70–99% of the biomass (NÆSJE.et al. 1991). In August, cladocerans were most abundant and constituted 61% of the zooplankton biomass. Zooplankton was most numerous in the upper part of the pelagic zone and exhibited small diel vertical migrations (NÆSJE et al. 1991). The fish fauna consisted of Arctic charr (*Salvelinus alpinus*), brown trout, northern pike (*Esox lucius*) and three-spined stickleback (*Gasterosteus aculeatus*) (NÆSJE et al. 1991).

Methods

Mysis relicta were sampled at six pelagic stations and one benthic station (Fig. 1) seven times from December 1986 to November 1987. Three of the pelagic stations were at 80 m depth and the other three stations at 20 m depth. Quantitative samples of pelagic *M. relicta* were taken with a net (500 μm mesh size, frame opening 1 m²) equipped with a closing mechanism (DE BERNARDI 1984). Samples were collected from the following depth intervals: 0–5, 5–10, 10–15, 15–20, 20–30, 30–40, 40–50, 50–60, 60–70, and 70–80 m. The pelagic catches

were taken down to 0.5 m above bottom. At each of the six pelagic stations, four parallel vertical hauls were taken with 2 parallel nets. The replicability of the vertical net hauls was good, as the average coefficient of variation (CV%) for the parallel hauls (>10 ind.) at each 0–80 m station was 26.9% (5.1–56.5). The average CV% between the three 0–80 m stations was 44.8% (14.3–98.5) indicating a more homogeneous distribution of *M. relicta* within, than between the three stations.

Benthic dwelling mysids were sampled with a benthic beam trawl with a frame opening of 1 m × 0.2 m, and mesh sizes of 1 mm along the sides and 200 μm in the bag (FÜRST 1965). The following depths were sampled: 0–10, 10–20, 20–30, 30–40, 40–50, and 55–65 m. The trawl was pulled at a speed of 0.4–0.6 m s⁻¹ and the length of each trawl transect was approximately 60 m. In February, the trawl was pulled 45 m under the ice at the following depths: 5, 30 and 55 m. Three parallel hauls were taken in each depth zone. The replicability of benthic hauls was not as good as for the vertical net tows. Average CV% for the 3 parallel trawls in each depth zone was 42.1% (3.6–85.4). The higher CV% might be due to a clustered distribution of mysids on the bottom, also found by GREGG (1976) in Twin Lakes, Colorado. In all sampling periods, both pelagic and benthic *M. relicta* were sampled during light and dark hours. Sampling took place from 09.00 to 15.00 h, and 21.00 to 03.00 h Norwegian Standard Time.
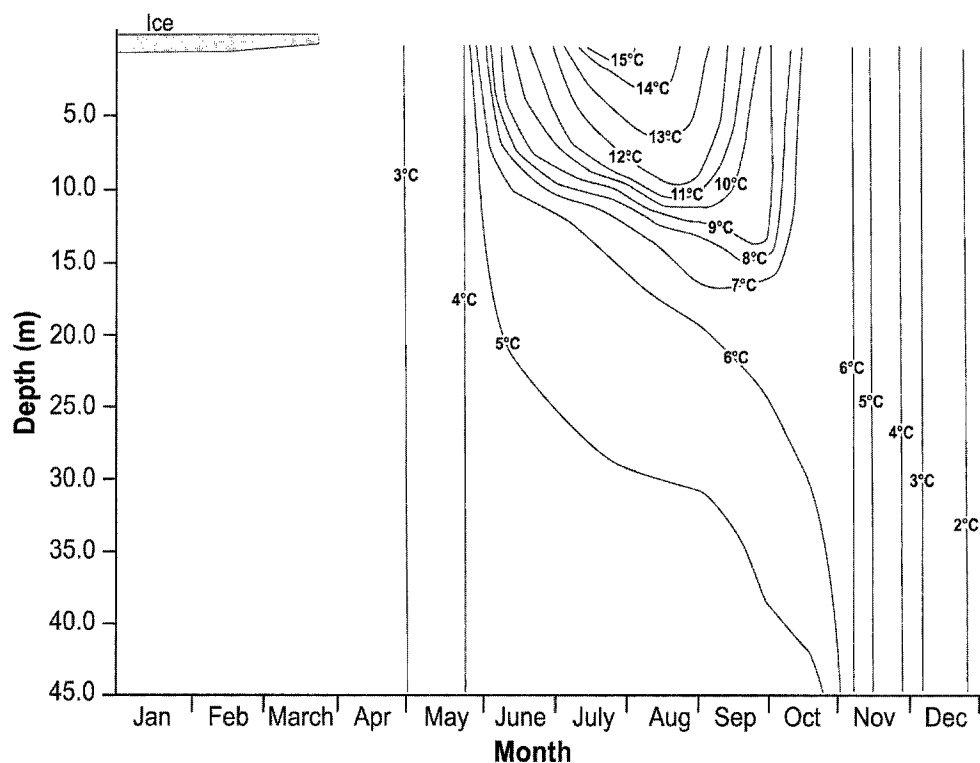
Fig. 2. Isothermic diagram of the deep pelagic stations (0–80 m) in Lake Jonsvatn, based on data from December 1986 to November 1987.

Determinations of sex and developmental stages were made according to FÜRST (1972) and BERILL (1969). Individuals with no externally differentiated sex organ were termed juveniles. Dependent on the length of the exopods on the third pleopod, males were separated into five stages (A–E). Males copulate in stage E (FÜRST 1972), and individuals in the developmental stages C–E were defined as mature males. Females were separated into nine developmental stages (α, β, μ_{1-7}). In the α stage the oostegites do not overlap ventrally. In β the oostegites overlap ventrally, but the marsupium is not fully developed. Stage μ_1 are females with eggs, and stage μ_{2-7} are females carrying embryos at different developmental stages (BERILL 1969).

Water temperature and oxygen were measured with a YSI-meter, registered concurrently with the vertical net hauls and benthic trawl samples of *M. relicta*. Oxygen varied between 7.4 mg l⁻¹ (56.5% saturation) and 12.2 mg l⁻¹ (104.2% saturation) and was always higher than critical values for *M. relicta* (SHERMAN et al. 1987). Survival of *M. relicta* is high up to 17 °C, and decreases with increasing temperature to 0% at 26 °C (RUDSTAM et al. 1999). At depths greater than 3 m, water temperature in Lake Jonsvatn was lower than 14 °C for the entire year (Fig. 2). Hence, during our study the water temperature should not put any significant limit to the habitat use of *M. relicta*.

During the day, between 10.00 and 14.00 h Norwegian Standard Time, light profiles in the water were measured with a light-meter consisting of a photoconductive cell, type LI–192S (Lambda Instruments Corp.). The photocell measured the photosynthetically active radiation (PAR) in μE m⁻²s⁻¹. Quantitative measurements of blue, green and red light were made using different filters of the following wavelengths: 400–510 nm, 480–590 nm, and 600–700 nm, with maximum absorption at 450, 525 and 620 nm, respectively. The filters were mounted on an underwater cell, and light measurements were made just above and in the water column down to 7 m. The extinction coefficients calculated for the upper 7 m were assumed to apply for greater depths (MOEN & LANGELAND 1989). After recalculating light intensity to photons (1 μE cm⁻²s⁻¹ = 6.02 x 10¹¹ photons mm⁻²s⁻¹), light intensity of different light qualities at different depths could be estimated by using the formula: $\ln I_z = \ln I_0 - Kz$; where I_z is the light intensity at depth z, I_0 is the light intensity just below the water surface and K is the attenuation coefficient.

Calculation of body length and weight of *M. relicta* was done using the length of the antennal scale, measured in a stereoscopic microscope. The length of the antennal scale of *M. relicta* is correlated to total body length and body weight (GROSSNICKLE & BEETON 1979; MOEN & LANGELAND 1989).

Biomass of pelagic *M. relicta* has been estimated by calculating number of individuals per m⁻³ in each depth zone based on the mean number of all parallel net hauls. These densities were multiplied with the total volume of the respective depth zone in Lake Jonsvatn. Biomass was estimated by taking the mean weight of 100 pelagic individuals multiplied with the number of individuals in the respective zone. Total biomass of pelagic *M. relicta* during day or night was calculated by adding the biomass in each pelagic depth zone. Biomass of benthic *M. relicta* was estimated after similar procedures as the number of individuals per m⁻² were estimated for each depth zone, multiplied with total area of that depth zone and the mean weight of 100 benthic individuals. Biomass during day or night was estimated by adding the biomass of each depth zone down to 65 m. For the area of depths larger than 65 m, the densities of *M. relicta* in the 55–65 m depth zone have been used.

Results

Life history

In Lake Jonsvatn, *M. relicta* had a mixed one or two year life cycle (Figs. 3 and 4). Based on estimates of number of individuals in the benthic and pelagic habitats, the proportion of individuals from December 1986 still alive and immature in July 1987 was estimated. These estimates indicate that approximately 14% of the female and 9% of the male *M. relicta* had a two year life cycle. The size distribution of mature *M. relicta* indicates that most males die during winter (December–February), while most females die in late spring or during summer (February–July) (Figs. 3 and 4).

Juvenile *M. relicta* were released from females' brood pouches (marsupium) during a period of several months from late in winter to summer (Figs. 3 and 4). The first juveniles occurred in February in the benthic habitat, but from May onwards they were found in large numbers in all parts of the lake (Fig. 3 and 4). In May, juveniles constituted 100, 75, and 58% of the individuals caught in the shallow pelagic (0–20 m total depth), benthic (0–65 m depth) and deep pelagic (0–80 m depth) habitats, respectively.

Mean size of juveniles varied between habitats. From May to August juveniles living in the pelagic zone at the 0–80 m stations were smaller than both benthic and shallow pelagic juveniles (t-tests, P < 0.001) (Table 1). In May, shallow pelagic juveniles (0–20 m stations) were larger than both the deep pelagic and benthic ones (t-tests, P < 0.001). In August, however, benthic juveniles were the largest (t-tests, P < 0.05).

In August, the first mature males (stage C) were observed in both benthic and pelagic habitats (Figs. 3 and 4). The mean length of these individuals was 13.3 ± 0.09
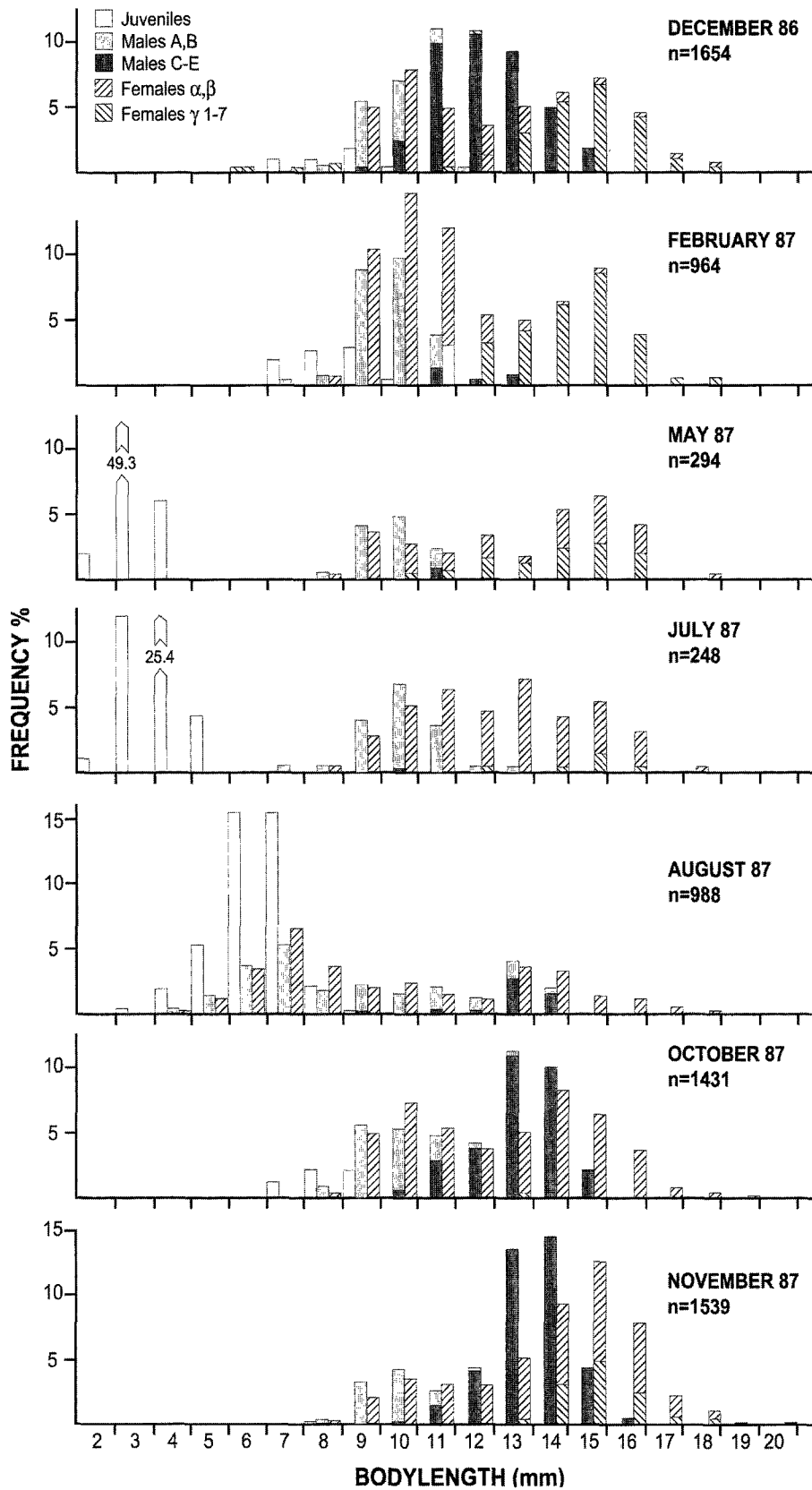
Fig. 3. Length frequency of juvenile (≤ 8 mm), male stage A and B, and C–E, and female α and β, and γ_{1-7} of *M. relicta* in Lake Jonsvatn in the deep pelagic habitat (0–80 m) in the period from December 1986 to November 1987.
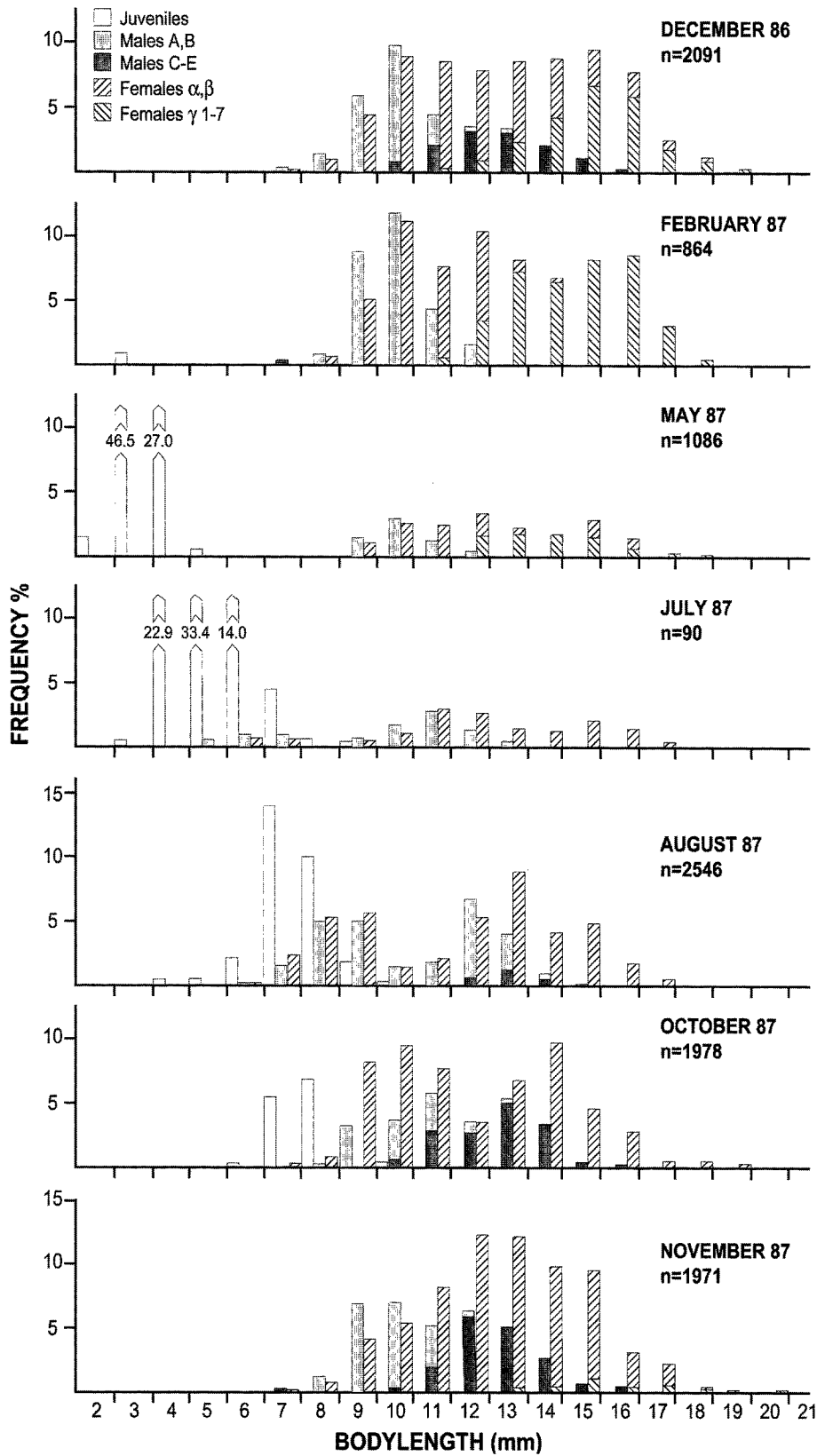
Fig. 4. Length frequency of juvenile (≤ 8 mm), male stage A and B, and C–E, and female α and β, and γ₁₋₇ of *M. relicta* in Lake Jonsvatn in the benthic habitat (0–65 m) in the period from December 1986 to November 1987.

Table 1. Mean length of juveniles (all individuals ≤ 8mm) in the deep pelagic (0–80 m), benthic, and shallow pelagic habitat (0–20 m) in Lake Jonsvatn in May, July and August 1987. Abbreviations: L = mean length (mm), SE = standard error, n = sample size.

	Deep pelagic			Benthic			Shallow pelagic		
	L	SE	n	L	SE	n	L	SE	n
May	3.10	0.045	170	3.35	0.010	2787	3.71	0.066	49
July	3.83	0.079	107	5.03	0.012	5714			
August	6.42	0.038	683	7.37	0.022	1071	7.24	0.068	162
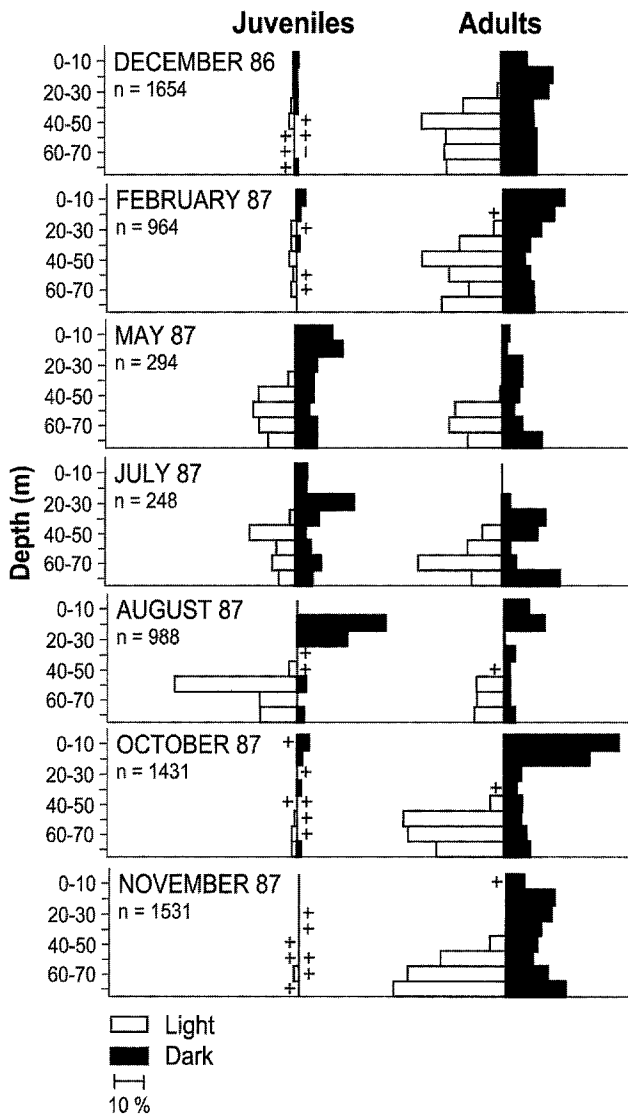
Fig. 5. Diel vertical distribution of juvenile (≤ 8 mm) and adult (> 8 mm) *M. relicta* in the deep pelagic habitat (0–80 m) of Lake Jonsvatn in the period from December 1986 to November 1987. "+" indicates that animals were collected, but in too low numbers to show on the figure.

mm (SE) and the minimum length was 10.0 mm. In October, the first males with sperm in their testes (stage E: mean length 14.1 ± 0.23 mm, minimum length 12.7 mm) were caught only at the deep pelagic stations where they

constituted approximately 3% of the individuals. The size difference between stage E males in October and November in the pelagic habitat was not significant (t-test, P > 0.05). Stage E males in December 1986 were 12.7 ± 0.05 mm (SE). However, the body size of individuals caught in December 1986 and November 1987 was not directly comparable due to different growth conditions. The proportion of mature males (stage C–E) in the deep pelagic habitat was 2.0–3.4 times larger than in the benthic habitat (December 1986, October and November 1987) (Figs. 3 and 4).

In Lake Jonsvatn, copulation in the *Mysis* population took place in late autumn (October-December), and the first females with eggs were caught in November (stage μ_1: mean size 15.6 ± 0.08 mm, minimum size 13.4 mm). During this period stage μ_1 females constituted a 7 times larger proportion of the total female population in the deep pelagic than they do in the benthic habitat (23% and 3%, respectively).

The mean size of females in stage μ_{1-7} decreased from December to February, from 15.7 ± 0.015 mm to 15.2 ± 0.040 mm in the benthic habitat, and from 15.1 ± 0.003 mm to 14.6 ± 0.052 mm in the deep pelagic habitat (t-tests, P < 0.001). Based on these results, the largest mature females were living in the benthic habitat during this period (t-tests, P < 0.001).

Migrations

The spatial distribution of juvenile and adult *M. relicta* varied through the year in the benthic and pelagic habitats and also between the two habitats (Figs. 5 and 6). Throughout the year, but to a varying degree, both juvenile and adult *M. relicta* performed vertical diel migrations in the deep pelagic habitat (0–80 m stations) (Fig. 5). The most pronounced diel migration took place in August and October. During this period most of the pelagic juvenile and adult *M. relicta* abandoned the 0–50 m zone during light, but stayed in the 0–20 m zone during dark. Darkness during this period is considerably longer and greater than during May and July where only a few adult *M. relicta* stayed in the upper pelagic zone (0–20 m and 0–30 m, respectively). During light hours in winter, both before ice cover in December and during
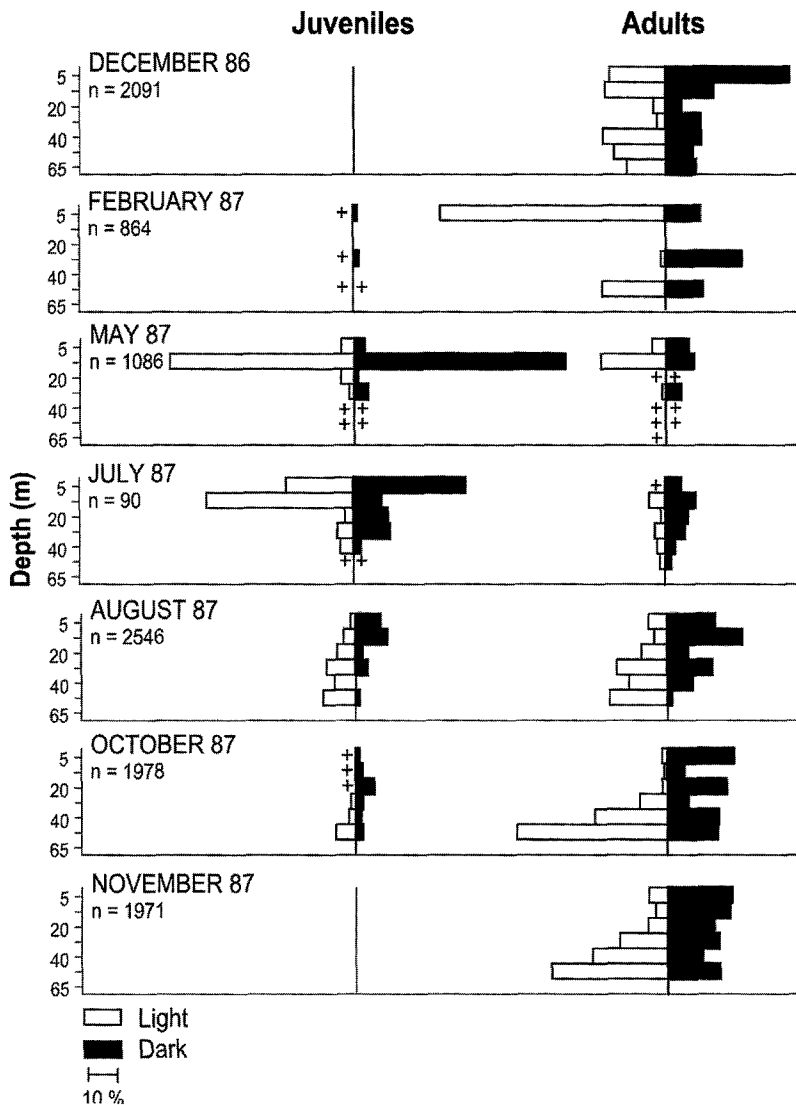
Fig. 6. Diel vertical distribution of juvenile (≤ 8 mm) and adult (> 8 mm) *M. relicta* in the benthic habitat (0–65 m) of Lake Jonsvatn in the period from December 1986 to November 1987. "+" indicates that animals were collected, but in too low numbers to show on the figure.

ice cover in February, *M. relicta* stayed somewhat higher in the water column than during autumn, and were caught up to 30 m depth. Pelagic habitat utilisation also varied between juvenile (≤ 8 mm) and adult *M. relicta*. Both during light and dark (in May–August), some juveniles stayed 10–20 m higher up in the water column than the adults (Fig. 5).

No *M. relicta* stayed in the water column during light in the shallow pelagic habitat (0–20 m stations). During dark, however, the distribution of *M. relicta* was similar to the distribution in the upper 0–20 m at the deep pelagic stations.

The catches of benthic *M. relicta* were high during both day and night. In the benthic habitat (0–65 m depth), the vertical migrations along the bottom of both juveniles and adults were not as pronounced as in the pelagic habitat (Fig. 6). In February and May, most benthic *M. relicta* were living in the littoral habitat (0–10

m), and adult *M. relicta* only performed large vertical migrations (< ca. 30 m) from August to November (Fig. 6). However, during daylight in this period, they did not descend to as great depths as in the pelagic habitat, and during dark they were more evenly dispersed along the vertical depth profile, as they never totally abandoned the littoral zone. Juveniles (≤ 8 mm) stayed in shallow benthic waters (0–10 m) both during day and night in May and July, and they only showed a minor tendency towards vertical migrations in August and October.

The Secchi disk transparency of Lake Jonsvatn was 6.7 ± 0.6 m (n = 14), and the transparency was greatest in the green part of the spectrum (Table 2). In spite of large variations at the surface, the light intensity was quite stable in the deep regions, with the mean depth of 1000 photons $mm^{-2} s^{-1}$ by day for blue, green and red light at 30.1 m, 54.3 m and 44.8 m, respectively. During light, the majority (90%) of the adult *M. relicta* was

Table 2. Mean attenuation coefficient (K), and mean depth (± standard error, n = 10) for the 1000 and 1 photon mm^{-1} s^{-2} levels in Lake Jonsvatn by day for PAR, blue, green, and red light. Average values for December 1986 and May to November 1987.

		K (m^{-1})	1000 photons (mm^{-2} s^{-1})	1 photon (mm^{-2} s^{-1})
PAR	(400–700 nm)	0.487 ± 0.023	53.4 ± 2.0	67.9 ± 2.7
Blue	(400–510 nm)	0.776 ± 0.021	30.1 ± 0.7	39.0 ± 1.0
Green	(480–590 nm)	0.437 ± 0.013	54.3 ± 1.0	69.9 ± 1.5
Red	(600–700 nm)	0.545 ± 0.017	44.8 ± 1.0	57.6 ± 1.3

Table 3. Depth at which the majority (90%) of juvenile (≤ 8 mm) and adult *M. relicta* stayed below during daylight from December 1986 to November 1987, and the intensity (photons mm^{-2} s^{-1}) of blue, green and red light at that depth.

	Juveniles				Adults			
Month	Depth	Blue	Green	Red	Depth	Blue	Green	Red
Dec.	35	136	1.8×10^6	2.9×10^5	37	36	7.9×10^5	1.1×10^5
May	42	0	3.6×10^5	15646	53	0	2154	34
July	41	0	3.5×10^5	4298	49	0	10405	45
Aug.	51	0	3328	47	53	0	1373	16
Oct.	54	0	1959	44	52	0	4447	119
Nov.	46	0	6292	30	52	0	372	0

Table 4. Estimated total biomass (kg dry weight for the whole lake) of *M. relicta* in pelagic and benthic habitats during day (D) and night (N), and density (measured as mean biomass in mg dry weight m^{-2} lake surface area) in Lake Jonsvatn, December 1986–November 1987. "Mean total biomass" is the mean of day and night samples in the benthic and pelagic habitats combined. "Mean D N pelagic" and "Mean D N benthic" are the mean density of day and night samples in the benthic and pelagic habitat, respectively. "Mean total density" is the sum of the mean pelagic and benthic densities.

Dec.	Feb.	May	Jul.	Aug.	Oct.	Nov.	
Total biomass, Day							
D: Pelagic kg	723 ± 114	332 ± 50	43 ± 9	46 ± 6	198 ± 18	330 ± 53	730 ± 195
D: Benthic kg	786 ± 98	212 ± 23	217 ± 25	232 ± 73	43 ± 6	93 ± 12	101 ± 15
D: Total kg	1509	544	260	278	241	423	831
Total biomass, Night							
N: Pelagic kg	1128 ± 97	448 ± 41	117 ± 27	72 ± 14	622 ± 118	1392 ± 212	599 ± 84
N: Benthic kg	515 ± 168	137 ± 17	198 ± 74	255 ± 50	153 ± 4	65 ± 13	174 ± 2
N: Total kg	1643	585	315	327	775	1457	773
Mean total biomass	1576	565	288	303	508	940	802
Density, mg m^{-2}							
Mean D N pelagic, mg m^{-2}	74.6	31.5	6.5	4.8	33.1	69.4	53.6
Mean D N benthic, mg m^{-2}	52.5	14.0	16.7	19.6	7.9	6.4	11.0
Mean total density, mg m^{-2}	127.1	45.5	23.2	24.4	40.9	75.8	64.6

found deeper than 49–53 m in May-September. At this depth the light intensities of green light varied between 372 and 10405 photons mm^{-2} s^{-1} (Table 3). The corresponding value of blue light was zero and the intensity of red light was also negligible (0–119 photons mm^{-2} s^{-1}). In December, the majority of adult *M. relicta* during light was found deeper than 37 m, where the light intensities were 7.9 · 10^5 1.1 · 10^5 and 36 photons mm^{-2} s^{-1} of green, red and blue light, respectively (Table 3). In May and July, juveniles stayed higher up in the water column and at higher light intensities, especially for green light, than adult *M. relicta* (Table 3).

Biomass

The mean total biomass of *M. relicta* in Lake Jonsvatn varied between 288 and 1576 kg dry weight throughout the year (Table 4). In all months but November, pelagic biomass was larger during night than during day. In the benthic habitat, biomass was higher during day in December, February, May, and October, but higher during night in July, August and November. However, with the exception of August and October, estimates of total biomass (pelagic and benthic combined) during day and night were very similar. The larger differences in biomass in August and October may be due to the patchy distribution during night in the pelagic zone, leading to large variation between parallel samples. This may have caused overestimation of the biomass in these months. Total mean biomass (day and night) of *M. relicta* in Lake Jonsvatn was highest in December 1986 (total 1576 kg or 127.1 mg m^{-2}), decreasing to approximately 300 kg (24 mg m^{-2}) in May-July. The biomass subsequently increased during autumn, reaching 800–940 kg (65–75 mg m^{-2}) in October and November 1987.

Pelagic biomass was largest in October, November and December, at 54–75 mg m^{-2} dry weight. During February to August, pelagic biomass varied between 5–33 mg m^{-2} dry weight. In the benthic zone, biomass was largest in December at 53 mg m^{-2} dry weight, while biomass during the rest of the year varied between 6–20 mg m^{-2} dry weight.

Discussion

Life history

The ultimate cause of the development of different life history characteristics is the maximisation of lifetime reproductive success, or fitness (DARWIN 1859). After the introduction of animals into a new environment, traits such as timing of reproduction and size or age at maturation are likely to come under strong selection resulting either in a phenotypically plastic or genetic response. Phenotypic plasticity leading to different reactions norms (cf. STEARNS 1992) is shown in the timing of reproduction by *M. relicta*, as some populations reproduce throughout the year, while others reproduce only in winter and spring (SAMTER & WELTNER 1904; THIENEMANN 1925; LARKIN 1948; FÜRST 1972). In Lake Jonsvatn, copulation took place in late autumn. Juveniles were released from the brood pouch over a period of approximately six months, and newly released young-of-the-year were caught from February to July. This long period of release gave rise to a combined one and two year life cycle. Similar life histories are found in other lakes with both natural (KJELLBERG et al. 1991) and introduced populations of *M. relicta* (MORGAN 1980; MOEN & LAN-

GELAND 1989; CHESS & STANFORD 1998), and demonstrate the flexible life history of the species.

The reason for the combined life cycle might be that the juveniles which were released towards the end of the season, in June-July, will experience only a short growth period during the first year of life. Because the timing of maturation is size dependent (FÜRST 1972; MORGAN 1980), these juveniles may not reach the minimum size for maturity during the first year of life. In Lake Jonsvatn this minimum size was approximately 13 mm for both males and females, and approximately 14% of the females and 9% of the males had to complete a two year life cycle to reach this size, and thereby sexual maturity.

The annual growth of *M. relicta* depends on the time of release from the brood pouch and growth conditions, i.e., water temperature and food availability (MORGAN 1980). The fecundity of females increases with body size (FÜRST 1972; KJELLBERG et al. 1991), and the lower limit for size at maturation might have evolved as a trade-off between size dependent fecundity and mortality rate. With respect to fitness, the increased fecundity due to larger size might compensate for the increased mortality prior to reproduction among individuals with a two year life cycle.

In Lake Jonsvatn, the largest females became sexually mature before smaller ones, which led to a decrease in the mean size of mature females through the autumn. Among the mature males, however, there was no decrease in size during autumn of 1987. This is in accordance with FÜRST (1972), who found that the older and larger females copulated three weeks before the younger and smaller ones, while the length of males in stage E was constant or decreased only slightly with time. Hence, the frequency of large, two year old *M. relicta* will be higher among early than later maturing individuals. These early reproducing individuals will in turn give rise to a new generation released early in the next spring. Given stable temperature and food availability the cohort of two year old *M. relicta* will therefore produce individuals that become earlier sexually mature as one year olds.

The mean size of juveniles living in the benthic and shallow pelagic habitats (0–20 m total depth) was significantly larger than of juveniles living in the deep pelagic habitats (0–80 m total depth). There might be two reasons for this. First, the size difference may be due to a migration of juveniles, with either larger individuals migrating from the deep pelagic habitat to benthic and shallow areas, and/or smaller individuals migrating in the opposite direction. This hypothesis is supported by MORGAN & THRELKELD (1982), who suggested that juveniles are released in deep regions of the lake and migrate into shallower areas during early spring. An alternative explanation might be that mature females in the benthic habitat may release their young earlier than females in the pelagic habitat, giving rise to two partly

separated populations of juveniles. This may explain the size difference observed between benthic and pelagic juveniles observed in Lake Jonsvatn. Our study supports the second hypothesis, as the difference in length distributions of juveniles from the two habitats is maintained from February through August. Furthermore, mature females (stage μ_7) ready to release their young are present in both habitats in May. The reason for the earlier release of young by *M. relicta* in the benthic habitat might be a better availability of food in this zone. Our results indicating that juveniles also are released in the pelagic habitat are contradictory to earlier studies, which only have reported releases of young *M. relicta* in either the benthic or littoral areas (e.g. HAKALA 1978; MORGAN & THRELKELD 1982; MOEN & LANGELAND 1989).

Migrations

Animals face trade-offs between benefits and costs in different habitats (STEPHENS & KREBS 1986). Predation risk and the presence of competitors may force an individual to stay away from habitats that otherwise would have been profitable (WERNER et al. 1983; MITTELBACH 1984; HOLBROOK & SCHMITT 1988). In Lake Jonsvatn, *M. relicta* exploit both benthic and pelagic habitats. The utilisation of different parts of the lake, however, varied between light and dark periods.

In the pelagic habitat, *M. relicta* performed diel vertical migrations of approximately 40 to 50 m, ascending in dark and descending in light. Diel migrations were small in December and February and larger from August to November. Pelagic migrations of *M. relicta* are well documented and the amplitude of the diel vertical migrations may vary between 2 and 300 m (e.g. DAKIN & LATARCHE 1913; SOUTHERN 1932; BEETON 1960; TERAGUCHI et al. 1975; MORGAN et al. 1978; NERO & DAVIS 1982).

During night in May and July (i.e. when there is some light also during night at 63°22′N), larger *M. relicta* were more restricted in their pelagic habitat use than smaller ones. During this period most of the larger *M. relicta* stayed deeper than 20 m, while juveniles were found all the way to the surface. Broader habitat use by pelagic juveniles than adults has been reported in several studies (e.g. LARKIN 1948; BEETON 1960; LASENBY 1971). From August to October, when nights were darker, adult *M. relicta* were also found in the upper zone of the pelagic habitat, i.e. above the thermocline. Later in the autumn, when the thermocline became weak and disrupted, we found *M. relicta* to be more evenly distributed among the different depth zones.

In the pelagic zone, the most important prey species of *M. relicta* are cladocerans, copepods and rotifers (e.g. LASENBY & LANGFORD 1973; RICHARDS et al. 1975; BOWERS & VANDERPLOEG 1982; GROSSNICKLE 1982). In Lake Jonsvatn, these species showed only a minor ten-

dency towards vertical migrations (NÆSJE et al. 1991), and they were always most numerous in the 0-30 m zone. Thus, habitat overlap between *M. relicta* and their food was low during day, and the daytime descent of *M. relicta* in Lake Jonsvatn can not be explained as a migration to more profitable feeding areas. However, *M. relicta*'s main predator in Lake Jonsvatn, Arctic charr, also performs diel migrations, descending during light to 30–40 m depth and ascending during dark. NÆSJE et al. (1991) found that during most periods the pelagic habitat overlap between *M. relicta* and Arctic charr in Lake Jonsvatn was low during light and high during dark. In addition, the proportion of *M. relicta* eaten by Arctic charr was only significantly correlated with the degree of habitat overlap during light hours (NÆSJE et al. 1991). The vertical migrations of *M. relicta* in the pelagic habitat can therefore be explained as an adaptation to the conflicting needs to maximise energy intake and minimise predation risk. By descending into darkness during day, and during light summer nights, *M. relicta* avoid predation by Arctic charr (FABRICIUS 1953), and by ascending during night they are able to feed in the highest densities of zooplankton. This hypothesis is also supported by, e.g., ZARET & SUFFERN (1976) and GLIWICZ (1986) who concluded that predation risk is the most important factor for the development and regulation of diurnal migration of zooplankton. Furthermore, NEILL (1992) found that the diurnal vertical migration of zooplankton (copepods) was locally adapted to their size or stage selective predators. Timing, phototaxis and transit distance in the pelagic habitat may change during the ontogeny of *M. relicta*, reflecting changes in their vulnerability to predation. Such variation in the risk of predation might explain the broader habitat use of pelagic juveniles.

Predation risk is one of the most important ultimate factors regulating the diel vertical migrations of *M. relicta*. Light, however, appears to be the most important proximate cue in regulating the amplitude of the migrations (BEETON 1960; TERAGUCHI 1969; TERAGUCHI et al. 1975; BEETON & BOWERS 1982; MOEN & LANGELAND 1989). In Lake Jonsvatn, the majority (90%) of the adult *M. relicta* were found deeper than 49–53 m in the deep pelagic habitat during daytime in summer. At this depth the intensity of green light was below 1373–10405 photons $mm^{-2} s^{-1}$, and blue and red light was negligible (Table 3). The same level of green light (e.g. about 1000 photons $mm^{-2} s^{-1}$) was observed at the modal depth of *M. relicta* in Lake Snåsavatn, in Norway by MOEN & LANGELAND (1989), in spite of higher intensities of red than green light at that depth. While the transparency of Lake Jonsvatn is greatest in the green part of the spectrum, the peak of the transmission curve in Lake Snåsavatn is in the red. The combined data for these two lakes strongly suggest that light intensity in the green part of the spectrum is the proximate cue for regulating vertical distribution of *M. relicta* during light

hours. This agrees with BEETON (1959) and GAL et al. (1999), who established through experimental studies that *M. relicta* has a peak sensitivity to light at 515 and 520 nm (green), respectively, and is almost completely insensitive to the red region above 620 nm.

Diel variations in habitat utilisation by *M. relicta* within the benthic habitat were not as pronounced as within the pelagic habitat (0–80 m stations). In May and July most benthic *M. relicta* in Lake Jonsvatn consisted of juveniles (2–6 mm), living mainly in shallow waters (0–10 m) during day and night. Only during late summer and autumn (August–November) did *M. relicta* show a tendency towards diurnal migration in this habitat. The transit distance, however, was not as great as in the pelagic zone and *M. relicta* was always found in the littoral zone during daylight. In the shallow benthic habitat *M. relicta* is an important food for both littoral brown trout and Arctic charr (NÆSJE et al. 1991; NÆSJE 1995). As benthic Arctic charr also utilise deep (30–80 m) waters along the bottom, *M. relicta* constituted an important part of the diet of charr in the deep benthic habitat (NÆSJE et al. 1991). In the pelagic zone, however, Artctic charr are restricted to the upper 30–40 m. Deep pelagic waters thus constitute a predation refuge for *M. relicta*. The smaller amplitude in diel vertical migration in the benthic habitat may be explained by higher predation risk in the deeper parts of the benthic than the pelagic habitats.

Biomass

The total biomass of *M. relicta* in Lake Jonsvatn varied in accordance with its life history. Maximum biomass, 1576 kg or 127 mg m^{-2} (dry weight), was found in December. Similar high biomasses were found also in late autumn. This is when early born young-of-the-year had reached the size of sexual maturity, but before most males had finished copulation and died. There was a sharp decline in biomass from December to February. This is most likely due to high mortality among adult males during winter. Lowest biomass, approximately 300 kg (or 24 mg m^{-2}), was found during summer after the release of young individuals from the marsupium and a period of high mortality of sexually mature females.

Mean biomass of *M. relicta* in the pelagic zone varied from 54–74 mg m^{-2} during winter to 4–7 mg m^{-2} during early summer. KOKSVIK et al. (1991) studied the zooplankton community in Lake Jonsvatn from 1977, before the introduction of *M. relicta* in 1978, until 1987. In 1977, mean zooplankton biomass (June–September) was approximately 525 mg m^{-2}. In 1987, i.e. 10 years after the introduction of *M. relicta*, zooplankton biomass was still relatively large (450 mg m^{-2}). The amount of pelagic *M. relicta* during autumn in 1987 was approximately 1/10 of their most important prey category, zooplankton.

Mysis relicta, however, is an opportunistic omnivore, also feeding on detritus (GROSSNICKLE 1982). In periods with low density of preferred zooplankton (May–July), the major part of the *M. relicta* population in Lake Jonsvatn stayed at the bottom both during day and night. During the rest of the year, pelagic biomasses were similar or larger than benthic biomasses of *M. relicta*.

Conclusions

Mysis relicta in Lake Jonsvatn demonstrates a flexible life history and habitat use. There is a mixture of one and two year life cycles, and every available lake habitat is utilised. The species also has a rather extreme omnivory, being able to thrive on detritus and phytoplankton as well as zooplankton. During early summer, when there is a low density of the preferred zooplankton prey, newly released juveniles are able to grow on detritus and phytoplankton. This ecological flexibility is the main reason that *M. relicta* is such a successful invader in most lake types.

The diel migrations of the species are closely related to the risk of predation in the pelagic habitat. Large *M. relicta* utilise the fishless deep pelagic habitat during light hours. Small *M. relicta* are less vulnerable to fish predation, and do not perform vertical migration to the same extent. Along the bottom, predation risk is present in the form of Arctic charr at all depths. Consequently, migrations between depth zones are less pronounced in this habitat.

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