
Impact of predation by *Mysis relicta* on zooplankton in Flathead Lake, Montana, USA

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Abstract. We documented major changes in the zooplankton community of Flathead Lake following the appearance of *Mysis relicta*. The three common cladocerans found in the lake decreased in abundance, most notably *Daphnia longiremis* which virtually disappeared from the lake. Copepods were also affected by *M.relicta*, especially *Diacyclops thomasi* which decreased in abundance by an order of magnitude. The only macrozooplankton species which seemed to benefit from the presence of *M.relicta* was *Leptodiaptomus ashlandi*. The varied responses of dominant zooplankton species appeared to be the result of a combination of factors. Laboratory feeding studies indicate that *M.relicta* preferred Cladocera over Copepoda, with the following order of feeding preference: *Bosmina longirostris* > *D.longiremis* > *Daphnia thorata* > *L.ashlandi* > *D.thomasi*. The two zooplankton species which declined most following the appearance of *M.relicta* showed the greatest degree of habitat overlap with *M.relicta*. *Daphnia longiremis* and *D.thomasi*, together with *M.relicta*, are cold stenotherms and were concentrated in the hypolimnion during the summer. Finally, another trait shared by *D.longiremis* and *D.thomasi* was the absence of a diapause stage, which made them vulnerable to predation by *M.relicta* throughout the year.

Introduction

Fisheries biologists introduced *Mysis relicta* into >100 large oligotrophic lakes throughout the NW USA and British Columbia, Canada, during the 1960s and early 1970s in the hopes of stimulating production of salmonids, especially kokanee salmon (*Oncorhynchus nerka*) (Gosho, 1975; Lasenby *et al.*, 1986). In many instances, these introductions did not stimulate fish production as expected, and in some cases, such as Flathead Lake, were followed by dramatic declines in the target fish species (Morgan *et al.*, 1978; Rieman and Falter, 1981; Beattie and Clancey, 1991; Northcote, 1991; Spencer *et al.*, 1991). These results have been attributed largely to unanticipated alteration in lake trophic structure, and in particular to reductions in cladoceran zooplankton abundance owing to predation by *M.relicta* (see reviews by Lasenby *et al.*, 1986; Martinez and Bergersen, 1989; Northcote, 1991).

Among zooplankton, Cladocera are preferred prey of *M.relicta* (Cooper and Goldman, 1980; Grossnickle, 1982; Nero and Sprules, 1986b). Copepods, though less preferred, may also serve as prey for *M.relicta* (Cooper and Goldman, 1980; Grossnickle, 1982; Nero and Sprules, 1986b). Several studies report some change in copepod populations associated with predation by *M.relicta* (Goldman, 1981; Nero and Sprules, 1986a), but none to the extent found in Flathead Lake, NW Montana. However, the response was not uniform across all copepod taxa in Flathead Lake, as one species appeared to benefit from the appearance of *M.relicta*.

In addition to differences in prey electivity by *M.relicta*, studies indicate that the extent of habitat overlap between *M.relicta* and its various potential prey may also help explain post-mysid changes in the abundance of various zooplankton species. Cladoceran species most likely to persist in lakes containing *M.relicta* are those concentrated in the epilimnion, which may serve as a thermal refuge relatively free from predation by *M.relicta* (Rieman and Falter, 1981; Martinez and Bergersen, 1989, 1991). Nero and Sprules (1986a) compiled data on the distribution and abundance of various zooplankton taxa in lakes without *M.relicta* compared with similar lakes in which *M.relicta* are endemic. Their results corroborate the importance of thermal preferences and vertical distribution in the vulnerability of various macrozooplankton to predation by *M.relicta*. However, we have found no studies which present detailed vertical distribution data on cladocerans and copepods in a lake before and after the introduction of *M.relicta*.

In addition to vertical distribution, another factor which may affect the vulnerability of various zooplankton to predation by *M.relicta* is the presence of a diapause stage. Certain cladocerans and copepods produce resting eggs which may remain dormant in the sediments for some time, while other species do not produce resting eggs (Pennak, 1989). Production of resting eggs is commonly attributed to the onset of stressful conditions such as declining water temperature, crowding, or drying (Pennak, 1989). A few studies suggest a link between predation and resting egg production in copepods (Hairston and Olds, 1984; Hairston, 1987). However, we have found no studies which explore the potential role of resting eggs in reducing the predation risk from *M.relicta*.

In the present study, we make detailed comparisons of the zooplankton community of Flathead Lake before and after the appearance of *M.relicta*. Flathead Lake is a large (surface area 482 km²), deep (mean depth 52 m), oligotrophic lake located in NW Montana. *Mysis relicta* was first noted in the lake in 1981, the result of downstream dispersal from several lakes which were stocked with *M.relicta* between 1968 and 1975 (Leathe, 1984). Previous studies have presented some information on zooplankton abundance in Flathead Lake following the appearance of *M.relicta* (Beattie and Clancey, 1991; Spencer *et al.*, 1991); however, these studies focused primarily on higher trophic level interactions.

In the present study, pre-*Mysis* zooplankton conditions in Flathead Lake were based upon extensive zooplankton collections made in 1972 that formed the basis of a PhD dissertation (Potter, 1978). These zooplankton collections were repeated again in 1988 after *M.relicta* had become well established in Flathead Lake. In the ensuing analysis, we attempt to link the post-mysid response of various zooplankton in Flathead Lake to three main factors: prey electivity by *M.relicta*, differences in the spatial and temporal distribution of various zooplankton taxa, and the extent of resting egg production.

The present study focuses on gross changes in macrozooplankton populations in Flathead Lake through 1988, as a consequence of the *Mysis* introduction. A more complete time series of zooplankton and phytoplankton dynamics including data from 1998 are presented elsewhere (Stanford and Ellis, in preparation).

Method

Field studies

Vertical profiles of *M. relicta* and zooplankton were taken each month from May through November 1988 at a sampling site located in the deepest part of Flathead Lake in the south-central region of the lake. *Mysis relicta* were sampled with a 1-m-diameter closing net (mesh size 500 μm) while zooplankton were collected using a 30-cm-diameter, 64- μm -mesh closing net. Duplicate vertical hauls were made with both nets over the following depth intervals: 0–5 m, 5–10 m, 10–20 m, 20–30 m, 30–40 m, 40–50 m, and 50 m to the bottom (~100 m). Collections were made both during the day (between 11:00 and 15:00 h) and on moonless nights (with sample collections commencing at least 1 h after dark and finishing at least 1 h before dawn). We did not complete the full set of vertical hauls from January through April 1988. Sampling during these months consisted of duplicate 0–50 m zooplankton hauls which were used to estimate total abundance of the various taxa.

Juvenile *M. relicta* were separated from adults based upon obvious differences in size and cohort analysis (Spencer, 1991). *Mysis relicta* have a 1.5 year life span in Flathead Lake, with the vast majority of juveniles released in early spring and the parental generation disappearing by the following fall (Spencer, 1991; Chess and Stanford, 1998).

The zooplankton data collected in 1988 were compared with similar data collected in 1972 by Potter (1978). The sampling site and sampling techniques used in our 1988 studies were similar to those used in 1972; however, the earlier work included more intensive sampling of the deeper strata. Whereas Potter (1978) included discrete 10 m plankton tows at depths below 50 m, during the 1988 sampling period, all depths below 50 m were combined into a single sampling zone due to the scarcity of zooplankton at these depths.

Duplicate 1 ml aliquots were taken from each zooplankton sample using a Hensen–Stempel pipette and zooplankton were enumerated using a Sedgewick–Rafter counting cell and a compound microscope at $\times 100$. All zooplankton data are reported in units of organisms l^{-1} . No corrections were made to account for net sampling efficiency. Since the present research focuses on relative changes in zooplankton abundance over time, any such correction for sampling efficiency would have little, if any, effect on the inferences drawn in this study.

Laboratory feeding studies

We focused our laboratory feeding experiments on the common Cladocera and Copepoda species found in Flathead Lake. Nauplii and rotifers were present in our experiments, but are not included in the present analysis. Feeding experiments were conducted in the dark at 12°C using large carboys (20–25 l) housed in Forma Scientific 38604-1 environmental chambers. Zooplankton for the carboys were collected by vertical haul in the epilimnion with a 64- μm -mesh net. Initial zooplankton concentrations in the carboys approximated ambient lake conditions. Feeding experiments were conducted on 24 July 1986 using zooplankton collected

from Flathead Lake. A second experiment was conducted on 10 July 1986 using zooplankton collected from Lake McDonald. Zooplankton were collected from Lake McDonald because it is similar to Flathead Lake and still contains *Daphnia longiremis*, which disappeared from Flathead Lake following the appearance of *M.relicta*.

A stock population of *M.relicta* from Flathead Lake was maintained in the laboratory with a flow-through water system and maintained on a diet of live zooplankton from Flathead Lake together with crushed commercial fish food pellets. Approximately 12 h prior to the initiation of the feeding experiments, a number of adult *M.relicta* (16–19 mm in length) were gently captured and placed in the environmental chambers. As *M.relicta* often suffer damage to sensory appendages during collection, the study organisms were examined for damage in order that the best available organisms were used in the feeding experiments.

Each experiment included four control carboys without mysids and four experimental carboys containing 6–8 mysids. The feeding experiments were run for ~9 h duration. Feeding rates were determined by dividing the difference between the number of prey species present in the controls and the experimental chambers at the end of an experiment by time and the number of mysids in the experimental chamber. Clearance rates were calculated following standard methods described by Vanderploeg *et al.* (1982).

Results

Zooplankton: seasonal abundance

We concentrated our analysis on five dominant zooplankton species which historically accounted for >95% of the macrozooplankton in the pelagic zone of Flathead Lake (Potter, 1978). These included two copepods, *Diacyclops thomasi* and *Leptodiatomus ashlandi*, which together accounted for >75% of the macrozooplankton, and three species of Cladocera, i.e. *Daphnia thorata*, *D.longiremis* and *Bosmina longirostris*. These five common macrozooplankters each responded differently to the appearance of *M.relicta* in Flathead Lake (Figure 1). Four of them showed evidence of decline, while the fifth species, *L.ashlandi*, appeared to become more abundant.

All three cladoceran species declined following the appearance of *M.relicta* (Figure 1a–c). The most dramatic decline involved *D.longiremis* which disappeared completely from our plankton hauls in 1988 (Figure 1a). In 1972, *D.longiremis* was present throughout the year in Flathead Lake, with peak abundances just above 1.0 organism l⁻¹ during the spring and early summer. A second species of *Daphnia*, *D.thorata*, persisted in Flathead Lake following the appearance of *M.relicta*, but its period of dominance during the year was truncated by several months (Figure 1b). In 1972, *D.thorata* first appeared in the water column in early April, and persisted until late December. In 1988, the springtime increase in *D.thorata* was delayed for 2 months until early June, while the annual fall decline in abundance began a month earlier in 1988 compared to 1972.

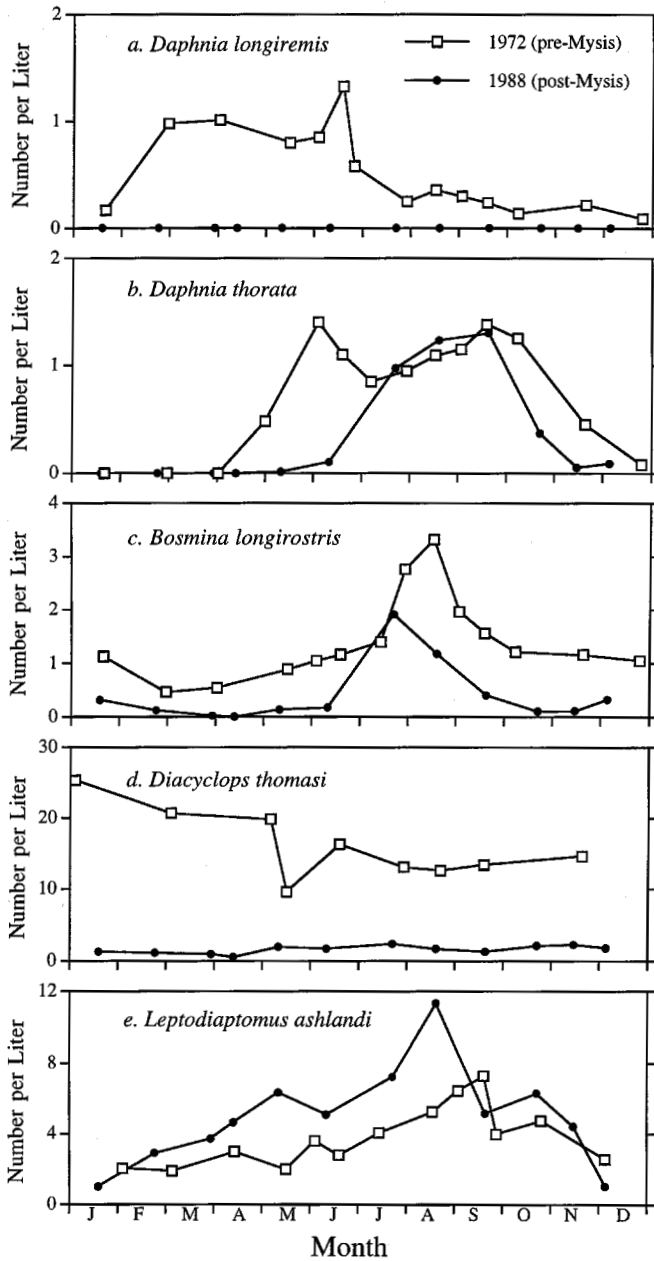


Fig. 1. Seasonal abundance of the five common macrozooplankton species in Flathead Lake in 1972, prior to the appearance of *M. relicta*, and in 1988 after *M. relicta* had become well established in the lake. Densities were calculated by summing up incremental 10 m hauls from 50 m to the surface.

Nevertheless, peak summer densities of *D.thorata* measured in 1988 were nearly identical to densities measured in 1972, ranging from 1 to 1.5 organisms l⁻¹.

The response of *B.longirostris* appeared to be intermediate between the other two cladocerans (Figure 1c). The abundance of *B.longirostris* was reduced throughout the year in 1988 compared to 1972 with the greatest declines occurring from fall through spring (Figure 1c). Densities fell below 0.2 organisms l⁻¹ for most of this time period in 1988, compared to densities around 1 organism l⁻¹ in 1972. However, substantial numbers of *B.longirostris* still appeared in mid-summer of 1988, peaking at 1.9 organisms l⁻¹ in July of 1988. Nevertheless, this peak density was nearly 50% lower than the maximum of 3.3 organisms l⁻¹ measured in August of 1972.

Like the Cladocera, the dominant copepod species also exhibited varied responses to *M.relicta* (Figure 1d and e). Prior to the appearance of *M.relicta*, the cyclopoid copepod *D.thomasi* was the most abundant species of macrozooplankton in Flathead Lake, with densities for adults plus copepodites ranging from 10 to 25 organisms l⁻¹ throughout the year (Figure 1d). Following the introduction of *M.relicta*, the density of *D.thomasi* declined dramatically, with the mean annual abundance declining 10-fold: from 16.17 organisms l⁻¹ in 1972 to only 1.6 organisms l⁻¹ in 1988. The peak annual abundance of *D.thomasi* declined from 25.4 organisms l⁻¹ in January of 1972 to only 2.4 organisms l⁻¹ in July of 1988.

The only common macrozooplankton species which appeared to benefit from the appearance of *M.relicta* was the calanoid copepod, *L.ashlandi* (Figure 1e). The mean annual density increased slightly from 3.7 organisms l⁻¹ in 1972 to 4.9 organisms l⁻¹ in 1988. The maximum annual density measured for *L.ashlandi* increased from 7.3 organisms l⁻¹ in 1972 to 11.4 organisms l⁻¹ in 1988.

The post-mysid changes in zooplankton abundance noted in our detailed data set from 1988 (Figure 1) were also readily apparent in Flathead Lake zooplankton data from every other year from 1986 through 1998 (Stanford and Ellis, in preparation). *Daphnia longiremis* was not found in any of these years. Winter macrozooplankton densities remained severely depressed (<5 organisms l⁻¹), while maximum summer densities remained below 20 organisms l⁻¹ in all post-mysid years.

Vertical distribution

Mysis relicta. During the daylight hours, *M.relicta* was concentrated on the bottom of Flathead Lake; at night, this species migrated up into the water column (Spencer, 1991). The extent of vertical migration varied depending upon the time of year as well as age of the mysids (Figure 2). During the spring and fall, when lakewide water temperatures were cool, *M.relicta* migrated throughout the water column. Maximum night-time abundances were found in the top 5–10 m of the water column during these seasons (Figure 2). During the summer months when water temperatures rose above 15°C in the upper water column, few *M.relicta* migrated into the epilimnion. Maximum night-time densities were found just below the thermocline, at depths from 15 to 25 m.

Juvenile *M.relicta* seemed to have wider temperature tolerances than adults.

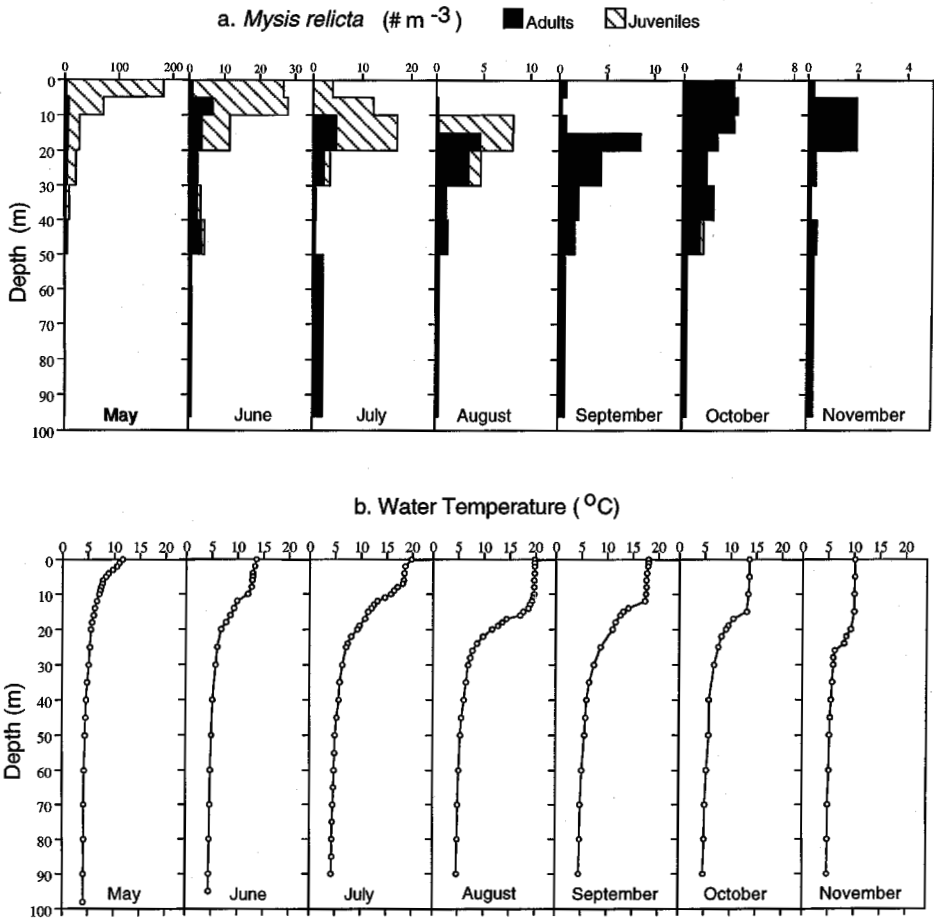
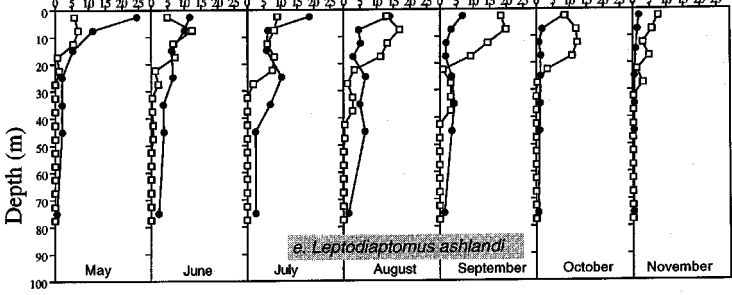
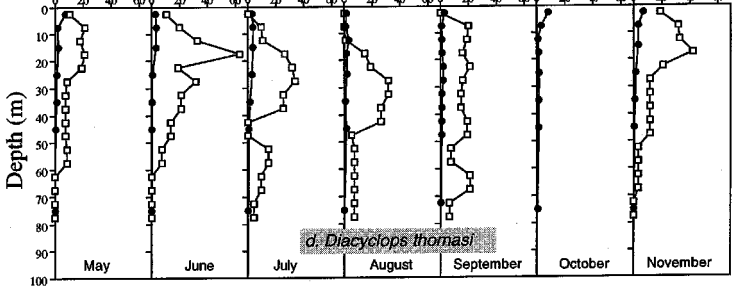
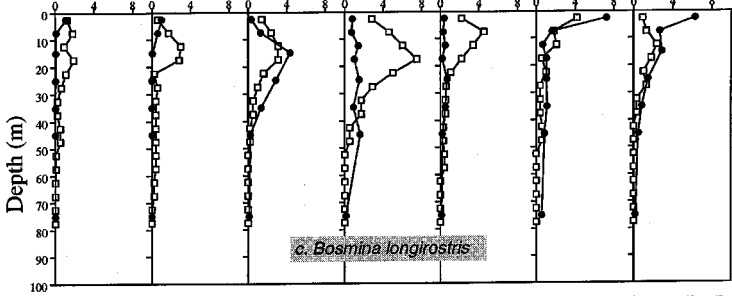
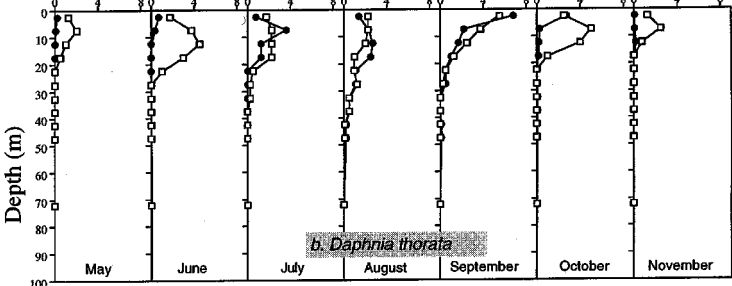
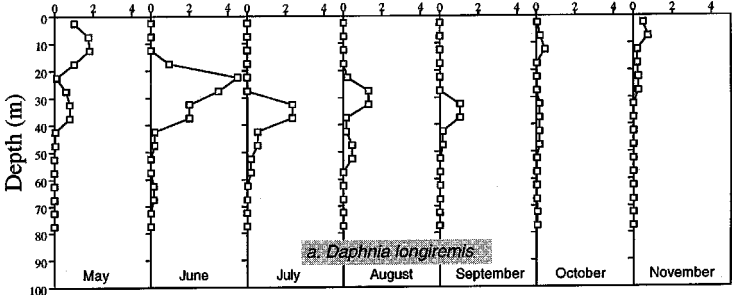


Fig. 2. (a) Vertical distribution of juvenile and adult *M. relicta*. (b) Temperature profiles in Flathead Lake, from May through October 1988.

During July, substantial numbers of juveniles migrated into the epilimnion of Flathead Lake where temperatures exceeded 18°C (Figure 2). However, as the lake became more deeply stratified during August and September, almost all *M. relicta* remained below the thermocline.

Zooplankton. The five dominant macrozooplankton species showed differences in habitat preference in Flathead Lake (Figure 3). *Daphnia longiremis* and *D. thomasi* seemed to favor thermal zones with cooler water temperatures (Figure 3a and d). During periods of thermal stratification in the summer time, these two species had peak abundances just below the thermocline. Peak abundances were located closer to the surface during the spring and fall. The distribution pattern exhibited by these two species was quite similar to the night-time distribution of *M. relicta* (Figure 2).

Organisms per Liter □1972 (pre-Mysis) ●1988 (post-Mysis)



Daphnia thorata and *L.ashlandi* had vertical distributions indicating a preference for warmer water temperatures. During the summer months, these two species were most abundant in the epilimnion, with maximum densities found in the upper 5–10 m of the water column (Figure 3b and e). Although *L.ashlandi* was most abundant near the surface, its summer distribution appeared bimodal, with evidence of a smaller peak at depths from 25 to 45 m, well below the thermocline. The vertical distribution of *B.longirostris* seemed to be intermediate between the two patterns described above, with peak summer densities located in the lower portion of the epilimnion (Figure 3c). Although *M.relicta* underwent marked diel vertical migrations in Flathead Lake, the five common zooplankters show little evidence of diel vertical migration (Spencer, 1991).

Laboratory feeding experiments

Mysis relicta preyed on all five common macrozooplankton species in our feeding experiments, reducing initial prey densities by 18–69%, depending on the prey species (Table I). Clearance rates were higher for the cladocerans than the copepods, with the following order of prey preference: *B.longirostris* > *D.longiremis* > *D.thorata* > *L.ashlandi* > *D.thomasi* (Table I). Clearance rates ranged from a high of 358 ml⁻¹ h⁻¹ mysid⁻¹ for *B.longirostris* to a low of 60.5 ml⁻¹ h⁻¹ mysid⁻¹ for *D.thomasi*.

Discussion

The five common macrozooplankton species dominating the pelagic waters of Flathead Lake exhibited markedly different responses to the appearance of *M.relicta* (Figures 1 and 3). The varied impacts can best be explained by a combination of factors, including well-known differences in prey selectivity and vertical distribution as well as the extent of seasonal diapause.

The post-mysid decline in Cladocera in Flathead Lake (Figure 1a–c) closely resembles cladoceran declines reported in other lakes following the introduction

Table I. Results of laboratory feeding experiments with *M.relicta* and various zooplankton prey

Prey species	Average initial prey density (no chamber ⁻¹)	Mean % of prey consumed by <i>M.relicta</i>	Mean (SD) clearance rate (ml h ⁻¹ mysid ⁻¹)
<i>Bosmina longirostris</i>	40.8	69	358 (78.7)
<i>Daphnia longiremis</i>	90.0	38	244 (189)
<i>Daphnia thorata</i>	182	51	221 (56.1)
<i>Leptodiaptomus ashlandi</i>	291	35	133 (34.7)
<i>Diacyclops thomasi</i>	218	18	60.5 (22.1)

Fig. 3. Vertical distribution of the five common macrozooplankton species in Flathead Lake in 1972, prior to the appearance of *M.relicta*, and in 1988 after *M.relicta* had become well established in the lake. No *D.longiremis* were collected in 1988.

of *M.relicta* (Richards *et al.*, 1975; Lasenby and Furst, 1981; Rieman and Falter, 1981). Cladocera are preferred prey for *M.relicta*, as shown in our laboratory feeding experiments (Table I), and other studies (Cooper and Goldman, 1980; Grossnickle, 1982; Nero and Sprules, 1986b). Furthermore, among Cladocera it is well known that deep-dwelling species such as *D.longiremis* (Figure 3a) are most susceptible to predation due to extensive habit overlap with *M.relicta* (Threlkeld *et al.*, 1980; Nero and Sprules, 1986a; Martinez and Bergersen, 1989, 1991).

The 10-fold decline in the abundance of the cyclopoid copepod *D.thomasi* in Flathead Lake (Figure 1d) was unexpected. We have only found a few studies which report declines in copepod abundance following other introductions of *M.relicta*. Koksvik *et al.* (1991) documented an 80% decline in biomass of *Cyclops scutifer* following the appearance of *M.relicta* in a shallow embayment of Lake Jonsvatn in Norway, although little reduction was noted in the main part of the lake. Nero and Sprules (1986a) reported a negative association between *M.relicta* and *C.scutifer* in several Canadian lakes. However, a number of studies report no such declines in copepod abundance following the introduction of *M.relicta*. Martinez and Bergersen (1989, 1991) noted that *D.thomasi* remained the most abundant macrozooplankton in Lake Granby following the introduction of *M.relicta*. Nero and Sprules (1986a) reported that densities of *D.thomasi* appeared to be unaffected by the presence or absence of *M.relicta* in a number of lakes in Canada. Goldman (1981) reported wide fluctuations in copepod densities following the introduction of *M.relicta* in Lake Tahoe, but no obvious reduction in abundance.

Though less preferred than Cladocera, *M.relicta* nevertheless will feed on copepods (Table I) (Cooper and Goldman, 1980; Nero and Sprules, 1986b). In a review of feeding habits of *M.relicta*, Grossnickle (1982) concluded that: 'Mysis are potentially voracious predators upon copepods'. Based upon laboratory feeding studies, Folt *et al.* (1982) predicted that *M.relicta* may shift to a less preferred prey species if its density is increased relative to a more preferred species. *Diacyclops thomasi* was the most abundant macrozooplankton species in Flathead Lake prior to the appearance of *M.relicta*, frequently outnumbering the combined total of all other macrozooplankton taxa (Figure 1). Furthermore, *D.thomasi* was found primarily below the thermocline and, similar to *D.longiremis*, appeared vulnerable to predation by *M.relicta* throughout the summer (Figures 2 and 3a and d).

In addition to predation, it is possible that interspecific competition with *M.relicta* could also have contributed to the decline in *D.thomasi* in Flathead Lake. *Diacyclops thomasi*, like most cyclopoid copepods, is a predator and feeds primarily on small zooplankton (McQueen, 1969) which also serve as food resources for *M.relicta* (Grossnickle, 1982). Thus, *D.thomasi* likely was subject to double jeopardy following the appearance of *M.relicta* in Flathead Lake, with *M.relicta* acting as a predator as well as a competitor for food resources.

One additional factor which likely contributed to differences in the response of various zooplankton to *M.relicta* in Flathead Lake is a difference in life history attributes, namely the presence or absence of an overwintering stage. Among

Cladocera in Flathead Lake, *D.thorata* exhibited the greatest winter diapause, and this trait likely contributed to its enhanced ability to co-exist with *M.relicta* in Flathead Lake. *Daphnia thorata* begins to produce ephippia in the fall and by early winter the species disappears completely from the water column, re-appearing in the spring as the ephippia hatch and re-seed the water column. Thick-walled ephippia typically overwinter in lake sediments where they appear to be relatively free from predation risk by *M.relicta*. We have found no reports of ephippia being consumed by *M.relicta*, and in cases where ephippia have been consumed by other predators, some remain viable even after passing through the predator's digestive tract (Pennak, 1989). Thus, *D.thorata* seemed to be effectively immune from predation by *M.relicta*, both in winter during their diapausal stage and again in summer due to the thermal refugia found in the epilimnion.

Daphnia thorata were vulnerable to predation by *M.relicta* for only a few months each year, during periods of turnover or weak thermal stratification occurring in the spring and fall. The abundance of *D.thorata* was reduced substantially during these seasons following the appearance of *M.relicta* in Flathead Lake (Figure 1b). Rieman and Falter (1981) reported a similar truncation in the period of dominance of *D.thorata* in Lake Pend Oreille following the introduction of *M.relicta*.

Given the present truncated period of dominance by *D.thorata* during the summer, we expect there has been strong selection within this population for early production of ephippia in the fall and also for late hatching of ephippia in the spring. Hairston and Walton (1986) demonstrated that the timing of diapause in copepods in a small pond can shift significantly within a few generations following changes in predator abundance; however, we do not have sufficient data to evaluate this hypothesis concerning *D.thorata* in Flathead Lake.

The zooplankton which declined most in the presence of *M.relicta* was *D.longiremis* and this result is consistent with the fact that *D.longiremis* does not appear to have a winter resting stage. Potter (1978) reported collecting only one ephippial female during 3 years of intensive sampling on Flathead Lake. Brooks (1957) also reported that production of ephippia is extremely rare in this cladoceran. Thus, for all intents and purposes, it seems that *D.longiremis* reproduced almost entirely by parthenogenesis in Flathead Lake. Lacking an ephippial resting stage, adult *D.longiremis* remained in the water column year round (Figure 1a) and thus, unlike *D.thorata*, this doomed species was exposed to predation by *M.relicta* throughout the winter.

Among the three cladocerans, the intermediate response of *B.longirostris* to *M.relicta* appears to be the result of several factors. Although *B.longirostris* does produce ephippia, it shows evidence of only a weak winter diapause in Flathead Lake. Whereas the entire population of *D.thorata* disappeared from the water column after ephippia production in the fall, substantial numbers of adult *B.longirostris*, ranging from 0.5 to 1.0 organism l⁻¹, overwintered in the lake prior to the appearance of *M.relicta* (Figure 1c). In addition to a weak winter diapause, *B.longirostris* appeared to make only partial use of the epilimnetic refuge (Figure 1b and c). Other studies report post-mysid declines in *B.longirostris*, including Richards *et al.* (1975) who noted that *B.longirostris* initially disappeared from

Lake Tahoe following the introduction of *M.relicta*, but this species later reappeared periodically at reduced densities (Threlkeld, 1981).

Differences in life history traits also likely contributed to the varied post-mysid response of Copepoda in Flathead Lake. *Diacyclops thomasi*, like *D.longiremis*, showed no evidence of a winter resting stage. Pennak (1989) indicates that cyclopoid copepods do not produce resting eggs and some are known to reproduce year round. Such appears to be the case for *D.thomasi* as the maximum abundance of this cyclopoid in 1972 occurred during the winter (Figure 1d). Consequently, *D.thomasi*, like *D.longiremis*, appeared vulnerable to mysid predation throughout the year, which likely contributed to its marked post-mysid decline in abundance.

By contrast, the calanoid copepod *L.ashlandi* showed evidence of a wintertime decline in abundance in 1972, and this trend became more pronounced following the appearance of *M.relicta* (Figure 1e). As with many Cladocera, some calanoid copepods are known to produce resting eggs (Pennak, 1989). However, we have not confirmed any examples of resting eggs in *L.ashlandi* through the course of our work on Flathead Lake.

Thus, a combination of factors likely contributed to the post-mysid success of *L.ashlandi* in Flathead Lake, including reduced vulnerability to mysid predation during winter due to decreased population size, reduced predation risk during summer due to a favorable vertical distribution (Figure 3e), and its status as a less preferred prey species (Table I). Other studies of prey selectivity by *M.relicta* report that adult calanoid copepods are the least preferred of all zooplankton prey (Grossnickle, 1982; Vanderploeg *et al.*, 1982).

The fact that densities of *L.ashlandi* seemed to increase slightly after the appearance of *M.relicta* may have resulted from a competitive release following mysid-induced reductions in potential competitors. Like other calanoid copepods, *L.ashlandi* is a filter feeder (Pennak, 1989), likely competing with other filter feeders in Flathead Lake, including *D.thorata*, *D.longiremis* and *B.longirostris*. Thus, *L.ashlandi* could well have benefited from reduced competition in Flathead Lake after abundances of these other filter feeders became reduced following the appearance of *M.relicta*. A similar competitive release mechanism has been suggested for increases in the abundance of *Diaphanosoma* following the appearance of *M.relicta* in several other lakes (Nero and Sprules, 1986a).

Flathead Lake is one of many lakes showing evidence of significant declines in cladoceran abundance following the appearance of *M.relicta*. The unexpected decline in cyclopoid copepods is more difficult to explain. It is possible that predation on zooplankton was especially intense following the mysid invasion in Flathead Lake, and this might explain the 10-fold decline in *D.thomasi*, a less preferred mysid prey. However, the density of *M.relicta* was not unusually high in Flathead Lake; in fact, it was relatively low compared to other well-studied mysid lakes including Pend Oreille, Kootenay and Tahoe (Lasenby, 1991; Spencer *et al.*, 1991). Nevertheless, the total extent of predation on zooplankton in these lakes is determined not only by the abundance of *M.relicta*, but also by the abundance of other planktivores including various fish species. Unfortunately, we do not have quantitative data on other planktivores.

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