

APPLIED ISSUES

Comparative energetics and life cycle of the opossum shrimp (*Mysis relicta*) in native and non-native environments

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SUMMARY

1. Life history, fecundity and energy ingestion were compared for non-native *Mysis relicta* in Flathead Lake, Montana, and in Waterton Lake, Montana/Alberta, where the mysid is native.
2. Based on estimates from stomach contents, *M. relicta* in Flathead Lake consumed three to four times more energy per hour while foraging than *M. relicta* from Waterton Lake. The primary prey of *M. relicta* in Flathead Lake was *Daphnia thorata*. *Diaptomus sicilis* was the primary prey for *M. relicta* in Waterton Lake.
3. *Mysis relicta* in Flathead Lake had a 1-year life history. It took 2 years for *M. relicta* in Waterton Lake to complete a generation. *Mysis relicta* from Flathead Lake produced significantly ($P < 0.05$) more eggs per female (19.9 ± 4.7) compared to *M. relicta* in Waterton Lake (13.7 ± 3.6). The lipid content in eggs from *M. relicta* in Flathead Lake was also significantly ($P < 0.05$) higher than eggs from *M. relicta* in Waterton Lake.
4. In Flathead Lake, *M. relicta* is able effectively to exploit *Daphnia thorata*, consuming greater biomass than *M. relicta* in Waterton Lake. *Mysis relicta* efficiently assimilates the greater biomass, which reduces generation time, increases fecundity, and increases lipid reserves of offspring. These results provide evidence of energetic mechanisms that enable *M. relicta* to colonize and affect foodwebs when introduced into lakes.

Keywords: energy balance, foodweb, lakes, *Mysis relicta*, opossum shrimp, phenology.

Introduction

In an attempt to increase fish production, managers have manipulated lake foodwebs by introducing non-native species. Many of these introductions have produced undesirable results (Li & Moyle, 1981). In the western United States and Canada, probably the most notorious foodweb manipulation is the introduction of the opossum shrimp (*Mysis relicta* Lovén). Clemens, Rawson & McHugh (1939) and Larkin (1948) observed that in lakes where it was native, *M. relicta* composed a large proportion of the fish diet. They

recommended introductions to non-native lakes to enhance fisheries.

On the basis of these recommendations, in 1949 and 1950, Kootenay Lake, British Columbia, Canada, became the first of many lakes in North America to receive *M. relicta*. The source was Waterton Lake, which straddles the U.S.A.–Canadian border in Alberta and Montana. The goal of the mysid introduction was the enhancement of the Gerrard rainbow trout (*Oncorhynchus mykiss* Walbaum) fishery in Kootenay Lake. However, after the mysid introduction, it was the kokanee (*Oncorhynchus nerka* Walbaum) which seemed to benefit most (Sparrow,

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Table 1 Physical and chemical variables of Flathead Lake and Waterton Lake. Means and ranges for chemical variables and Secchi disc are from summer to autumn, for the period of 1985–90

	Flathead Lake	Waterton Lake
Surface area (km ²)	496.00	94.00
Maximum depth (m)	113.00	136.00
Mean depth (m)	50.00	69.0
Total nitrogen (µg L ⁻¹)	92.70 (44.90–137.20)	211.80 (169.00–338.00)
Total phosphorus (µg L ⁻¹)	5.24 (1.70–13.10)	3.40 (1.10–7.00)
Chlorophyll <i>a</i> (mg m ⁻³)	1.02 (0.55–1.79)	0.77 (0.34–1.27)
Secchi disc (m)	11.40 (8.50–16.00)	10.30 (8.00–14.00)
Temperature °C (degree days in epilimnion) 1939.00 (April–October 1993)		1405.00

Larkin & Rutherglen, 1964). From the mid-1960s to 1970s, kokanee stocks in the West Arm of Kootenay Lake grew to unprecedented size (Northcote, 1973), and a sport fishery quickly developed for the large kokanee. Upwelling of deep lake water swept mysids into the shallow West Arm where they could be fed upon by the kokanee (Martin & Northcote, 1991). Because of this apparent success (which later proved to be an anomaly related to the morphometry of Kootenay Lake), mysids were introduced into over 100 lakes in North America (Lasenby, Northcote & Fürst, 1986; Northcote, 1991).

Following the introductions of *M. relicta*, it became apparent the shrimp was altering and disrupting foodwebs in many lake ecosystems (Northcote, 1972; Richards *et al.*, 1975; Threlkeld *et al.*, 1980; Reiman & Falter, 1981; Lasenby, Northcote & Fürst, 1986; Spencer, McClelland & Stanford, 1991). Flathead Lake in north-western Montana is a deep oligotrophic lake of glacial origin (Table 1) and is one of the lakes that received *M. relicta* from Waterton Lake. In the late 1970s, *M. relicta* passively immigrated into Flathead Lake from stocked lakes in the upper Flathead catchment, a common problem associated with *M. relicta* introductions (Lasenby *et al.*, 1986). *Mysis relicta* was first caught in Flathead Lake in the early 1980s and reached a maximum density of 129 m⁻² in 1986. The maximum density coincided with the collapse of the introduced kokanee salmon fishery and an array of

other foodweb changes (Beattie & Clancey, 1991; Spencer *et al.*, 1991) that persist today.

Unfortunately, the ecology of *M. relicta* in Waterton Lake had never been investigated prior to the present study, even though Waterton Lake was the direct or indirect stocking source for all lakes in western North America. Like Flathead Lake, Waterton Lake is a cold, oligotrophic lake of glacial origin (Table 1). The surface temperatures in Waterton are less than 15 °C in midsummer (Anderson & Green, 1976); Flathead Lake, located in a wider, open valley, reaches 20 °C at the surface. Waterton Lake contains a 'glacial relict' crustacean and fish assemblage characteristic of the Canadian Shield, not the Rocky Mountains, suggesting that Waterton was a glacial refugium sometime during the Pleistocene period (Dadswell, 1974; Hocutt & Wiley, 1986). The *M. relicta* population of Waterton Lake apparently has been geographically isolated since then (Väinölä *et al.*, 1994). In Waterton Lake, *M. relicta* evolved in a cold, low productivity environment with zooplankton prey and a fish assemblage that differs substantially from the temperate lakes into which the shrimp were introduced.

Omnivory, diel vertical migration (DVM) and life cycle plasticity are the most studied life history traits of *M. relicta*. These traits probably account for its ability to propagate, persist and alter lake foodwebs. *Mysis relicta* is an omnivore (Grossnickle, 1982), but prefers zooplankton, especially cladocerans (Cooper & Goldman, 1980; Threlkeld *et al.*, 1980; Bowers & Vanderploeg, 1982; Folt, Rybock & Goldman, 1982). The DVM behaviour of *M. relicta* is well documented in native (Beeton, 1960; Beeton & Bowers, 1982) and introduced populations (Morgan, 1980; Moen & Langeland, 1989; Levy, 1991). The introduced *M. relicta* population in Lake Tahoe, California, provides an example of the life cycle plasticity. After introduction of *M. relicta* from Waterton Lake, Morgan (1980) reported a 4-year life cycle in oligotrophic Lake Tahoe, compared to a 1-year life cycle in Emerald Bay, an isolated, more productive embayment of Lake Tahoe.

To examine the mechanisms of life history plasticity of *M. relicta* in relation to its strong influences on foodwebs, the energetics of foraging of *M. relicta* in native Waterton Lake and non-native Flathead Lake were quantified. The approach used in the present study compared the interaction of the spatial distribution of prey, prey preference, energy ingested and energy allocated to growth and fecundity with

M. relicta life cycle duration in the two lakes. Diel vertical migration is an important component of the foraging strategy of *M. relicta*. Therefore, it was essential to quantify the nocturnal spatial distribution of *M. relicta* in relation to zooplankton prey density and temperature. By following this approach, mechanisms that allow *M. relicta* to alter non-native foodwebs became apparent.

Methods

Mysis relicta and zooplankton were routinely collected from 100 to 50 m depth, and from 50 m to the surface in 10-m intervals at night from pelagic sites on Flathead Lake and Waterton Lake. Throughout the study, midday vertical hauls were taken from both lakes to confirm the daytime, benthic distribution of the mysids. Diel sampling in Flathead Lake revealed no evidence of DVM behaviour in the zooplankton (D. W. Chess, unpublished data). In May 1993, zooplankton were sampled throughout a 24-h period in Waterton Lake to determine whether the zooplankton underwent DVM. *Mysis relicta* and zooplankton hauls were replicated ($n=2$ or 3) at each depth stratum. For collection of zooplankton, a 30-cm diameter, 64- μm mesh closing net was used; whereas for *M. relicta*, a 100-cm diameter Puget Sound closing net with 400- μm mesh was used. A Hydrolab Surveyor III or Seabird Model 25 CTD (conductivity, temperature and depth) was used to collect temperature data at each site from 100 m to the surface.

Live *M. relicta* were needed to determine growth and energy accumulation over time. For both lakes, on each sample date, thirty to fifty live *M. relicta* were anaesthetized with carbonated water, separated by gender and measured to the nearest 0.1 mm from the tip of the rostrum to the cleft of the telson. Measured *M. relicta* were placed in scintillation vials and frozen at -20°C for chemical analysis. Biomass was determined after drying individual mysids for 24 h at 60°C , and then weighing them on a Sartorius M2P microbalance to the nearest microgram. Carbon and nitrogen were determined for individual *M. relicta* with a Carlo-Erba Model 1500 CHN (carbon, hydrogen and nitrogen) analyser using acetanilide as the standard. Total lipid was determined for individual

M. relicta by a micromethod (Gardner *et al.*, 1985). Protein content was estimated by assuming a 5.78% nitrogen content (Clarke, Skadsheim & Holmes, 1985). Protein and total lipid content were used to estimate energy content using the conversion values of 23.9 kJ g^{-1} and 39.5 kJ g^{-1} for protein and lipid, respectively (Gnaiger & Bitterlich, 1984). The length and dry weight data from specimens used for chemical analysis were also used to develop the length to dry weight relationship of mysids from Flathead Lake: biomass (mg) = $0.00191 \times \text{length (mm)}^{3.01}$, $r^2 = 0.945$, $n = 237$. The same relationship for *M. relicta* from Waterton Lake: biomass (mg) = $0.00232 \times \text{length (mm)}^{2.91}$, $r^2 = 0.974$, $n = 119$.

Estimates of growth were extrapolated to the population level for *M. relicta* by measuring all individuals to the nearest 0.1 mm from each sample date. Biomass was then estimated from the length to weight relationship from each of the two lakes. Fecundity was quantified by counting eggs and embryos from gravid females. Embryo developmental stage was determined based on yolk sac utilization, eye development and appendage development (Berrill, 1969).

The biomass and chemical content of zooplankton species were determined in order to calculate the energy content of individual zooplankton consumed by *M. relicta*. Live zooplankton samples were collected in hauls from 30 m to the surface. Live zooplankton were separated by size using a series of Nitex mesh sieves from 500 μm to 63 μm . Species and life cycle stages were then separated by hand. Several replicates containing approximately fifty individuals per replicate were frozen in scintillation vials at -20°C . Carbon, nitrogen and total lipid were determined for zooplankton following the same methods used for *M. relicta*. The protein content and energy content were estimated following the same conversions used for *M. relicta*. To estimate copepod biomass, five replicates with ten adults per replicate were dried for 24 h at 60°C and then weighed to the nearest microgram. The same procedure was followed for copepodites. Individual *Daphnia thorata* Forbes were measured to the nearest 0.1 mm from top of helmet to the bottom of the carapace, excluding the tailspine. Individuals were then dried at 60°C for 24 h and weighed to the nearest microgram. A dry weight to total length relationship was developed to estimate *D. thorata*

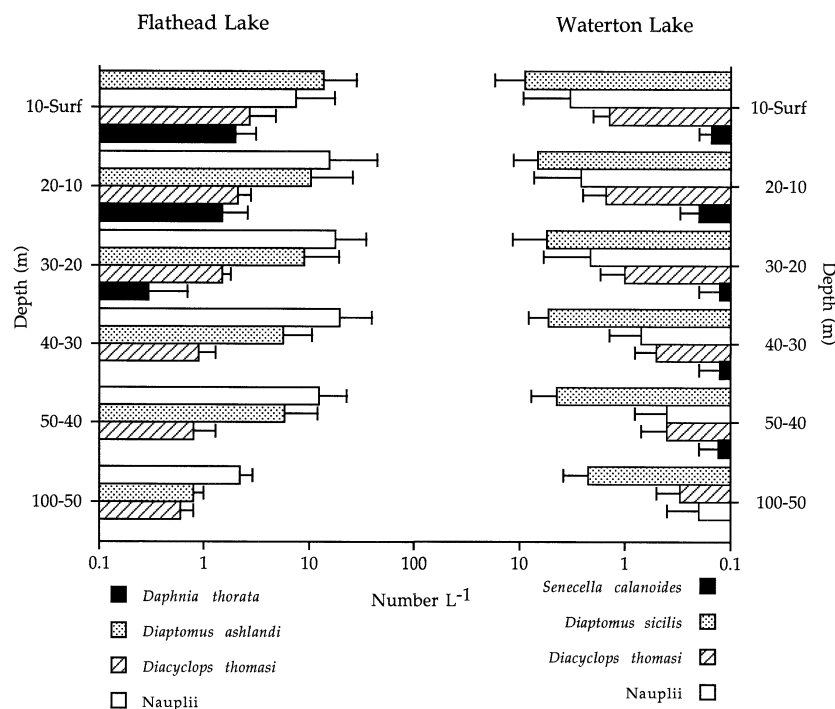


Fig. 1 Crustacean zooplankton density (log transformed) in relation to depth intervals in Flathead and Waterton Lakes. Values are means \pm 1 SE for six dates during summer and autumn.

biomass: $\text{biomass } (\mu\text{g}) = 4.92 \times \text{length}(\text{mm})^{2.24}$, $r^2 = 0.936$, $n = 50$.

Stomach analysis was used to determine prey preference and estimate the amount of energy ingested by mysids. The contents of foreguts of ten to twenty mysids were determined on each of four dates for both lakes during summer and autumn. Mysids preserved in ethanol were placed in glycerine for 24 h before stomach analysis. The foregut was dissected, and the contents were placed on a glass slide, then teased apart in a drop of glycerine. Identification of copepods was accomplished from various body parts, especially mandibles, the modified fifth appendage of male diaptomid copepods and antenna pieces. In many cases, segments of copepod carapace were used to separate adult from copepodid stages. The zooplankton from the mysid foreguts were always damaged enough to prevent accurate measurement of total length. Copepod biomass ingested was estimated from mean biomass of copepods from net hauls, averaged over several dates. It was assumed that the size selectivity of the net and the mysids was similar. In the foreguts of *M. relicta* from Flathead Lake, the only consistently intact body part of *D. thorata* was the mandibles. As each *D. thorata* has two mandibles, it was possible to

quantify the number of *D. thorata* consumed per individual *M. relicta*. To estimate the biomass of *D. thorata* in *M. relicta* foreguts, a mandible length to *D. thorata* weight relationship was developed. *Daphnia thorata* were anaesthetized with carbonated water and mandible length was measured through the carapace to the nearest 0.01 mm at 100 \times . *Daphnia thorata* were then dried individually at 60 $^{\circ}\text{C}$ for 24 h and weighed to the nearest μg . The mandible length to dry weight relationship was: $\text{biomass } (\mu\text{g}) = 4.95 \times 10^4 \times \text{mandible width } (\text{mm})^{2.6}$, $r^2 = 0.869$, $n = 29$.

Hence, the prey estimates were converted from gut content analysis to the amount of energy consumed and that was divided by the estimated time spent foraging to calculate energy consumption by the mysids in Flathead and Waterton Lakes. It was assumed that gut evacuation rates were similar in the two lakes.

Results

Zooplankton dynamics

The crustacean assemblage in Waterton Lake was indeed composed of 'glacial relict' species, including *M. relicta*, *Diaptomus sicilis* Forbes, *Senecella*

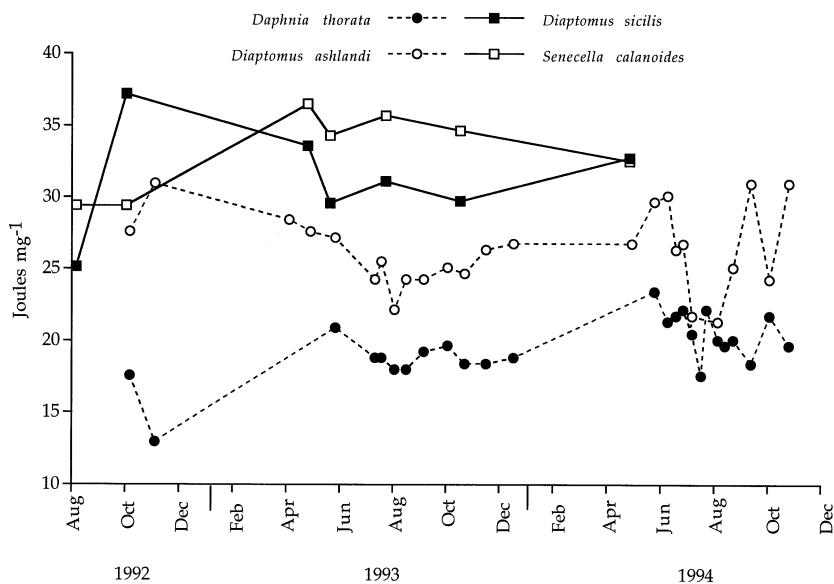


Fig. 2 Energy content of dominant crustacean zooplankton from Flathead and Waterton Lakes.

calanoides Juday, and the amphipod *Pontoporeia affinis* Lindström. *Diaptomus sicilis* was the dominant zooplankton in Waterton Lake throughout the study (Fig. 1). The cyclopoid *Diacyclops thomasi* Forbes was present at lower densities (Fig. 1). Cladocerans and rotifers were rare in the plankton of Waterton Lake. *Daphnia rosea* Sars was present ($<0.1 \text{ L}^{-1}$) in October samples from 1992 and 1993. Anderson & Green (1976) also reported a lack of rotifers in zooplankton samples obtained in the early 1970s. Notably, in samples from the present study the harpacticoid copepod, *Bryocamptus* sp., was consistently present in samples from the upper 50 m at the pelagic site. These copepods are usually found on the bottom or within the substratum (Pennak, 1989).

The Flathead Lake copepod assemblage was composed of (in order of decreasing dominance): *Diaptomus ashlandi* Marsh; *Diacyclops thomasi*; and *Epischura nevadensis* Lilljeborg. *Diaptomus ashlandi* was the dominant zooplankton in Flathead Lake throughout the study (Fig. 1). Compared to Waterton Lake, Flathead Lake had approximately twenty times the density of cladocerans, dominated by *Daphnia thorata* (Fig. 1). *Bosmina longirostris* O.F. Müller, was present throughout the year at less than 0.2 L^{-1} . *Daphnia pulicaria* Forbes was first found in Flathead Lake in samples from 1991 at less than 0.05 L^{-1} but density increased to 0.2 L^{-1} in 1994. The rotifer assemblage of Flathead Lake was more diverse than in Waterton Lake, and, sometimes,

total densities were as high as 50 L^{-1} . Although the zooplankton species composition differed between Flathead and Waterton Lakes (Fig. 1), total zooplankton density was not significantly different ($P = 0.631$, t -test). In both lakes, zooplankton density gradually decreased with depth (Fig. 1).

The energy content per individual of *Diaptomus sicilis* and *Senecella calanoides* from Waterton Lake was higher than *Diaptomus ashlandi* and *Daphnia thorata* from Flathead Lake (Fig. 2). Lipid storage accounted for the difference in energy content. *Senecella calanoides* had the highest lipid per dry weight content (55–68%), followed by *Diaptomus sicilis* at (46–61%). In Flathead Lake, the lipid content of *Diaptomus ashlandi* and *Daphnia thorata* ranged from 20–51% and 12–24%, respectively.

Diel vertical migration

Daytime vertical hauls in Flathead and Waterton Lakes yielded no mysids; they apparently remained on or near the bottom during daylight hours. However, *M. relicta* were present high in the water column in Waterton and Flathead Lakes at night (Fig. 3). On every sampling run diel vertical migration (DVM) by the mysids was observed, characterized by nocturnal ascension towards the lake surface. No evidence for DVM behaviour in the *Daphnia* sp. or the copepods in Flathead Lake was found. *Diaptomus sicilis* in Waterton Lake appeared to undergo weak DVM in the upper water column,

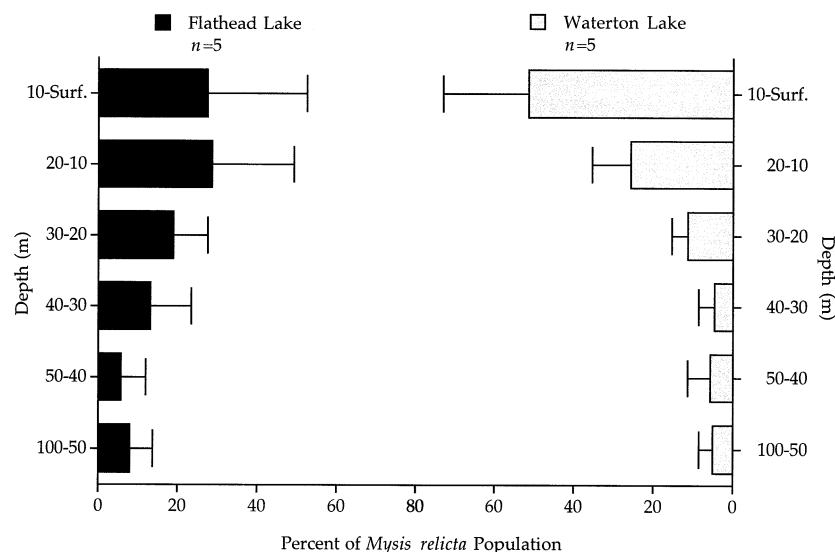


Fig. 3 Nocturnal distribution of *Mysis relicta* from Flathead and Waterton Lakes. Values are means \pm 1 SE for five dates during summer and autumn.

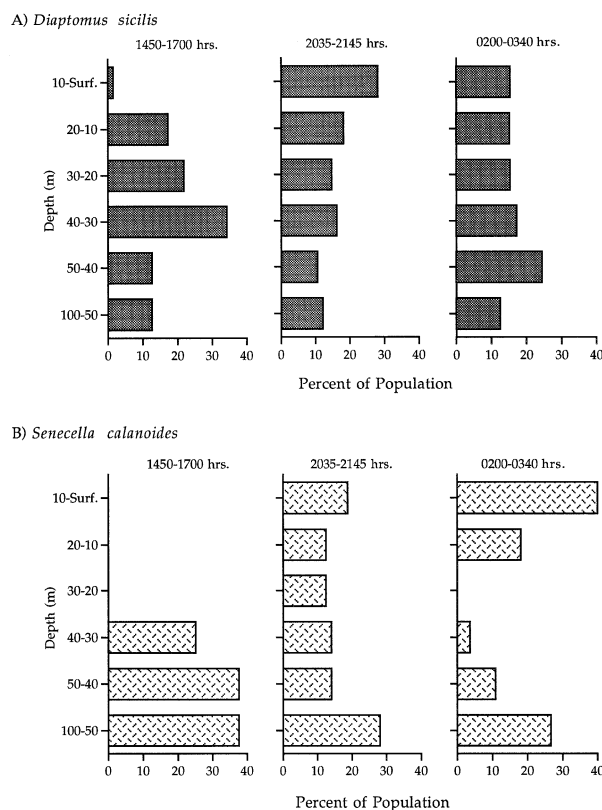


Fig. 4 Diel distribution of *Diaptomus sicilis* and *Senecella calanoides* at a 130-m pelagic site in Waterton Lake on 17–18 May 1993. Values are means from two hauls per time period.

and a large component of the *Senecella calanoides* population ascended from depths greater than 30 m to the surface waters at night (Fig. 4). Hence, the

largest zooplankters, other than *M. relicta*, remained primarily in the upper 30 m throughout the diel cycle in both lakes.

Mysis relicta food habits

Stomach analysis of juvenile *M. relicta*, (<6 mm) from Flathead Lake and Waterton Lake revealed filamentous diatoms, pollen (mostly from local conifers) and amorphous detritus. No attempt was made to quantify the algal or detrital material. *Diaptomus ashlandi* numbers ranged from two to six per gut from Waterton Lake with a few *Diacyclops thomasi*, and *Daphnia rosea* was present in only two of the total fifty-four guts on the four sampling dates from Waterton Lake. *Daphnia thorata* was the dominant prey species of subadult and mature *M. relicta* from Flathead Lake, comprising 90% of the biomass in foreguts. Numbers ranged from one to fourteen *Daphnia* per mysid gut over the four dates that stomach analyses were carried out. *Diaptomus ashlandi*, *Daphnia pulicaria* and *Diacyclops thomasi* made up the other 10% of stomach contents. Detritus was rarely found in stomachs from subadults and adult mysids from Flathead Lake. *Diaptomus sicilis* and *Diacyclops thomasi* comprised 79% and 15% of the identifiable biomass in the foreguts from subadult and adult mysids in Waterton Lake. Numbers ranged from none to six *Diaptomus sicilis* per gut and all but fourteen of fifty-four guts examined on four dates had at least one. Only nine guts contained one or two *Diaptomus thomasi*. One *Daphnia rosea* was present in two mysids.

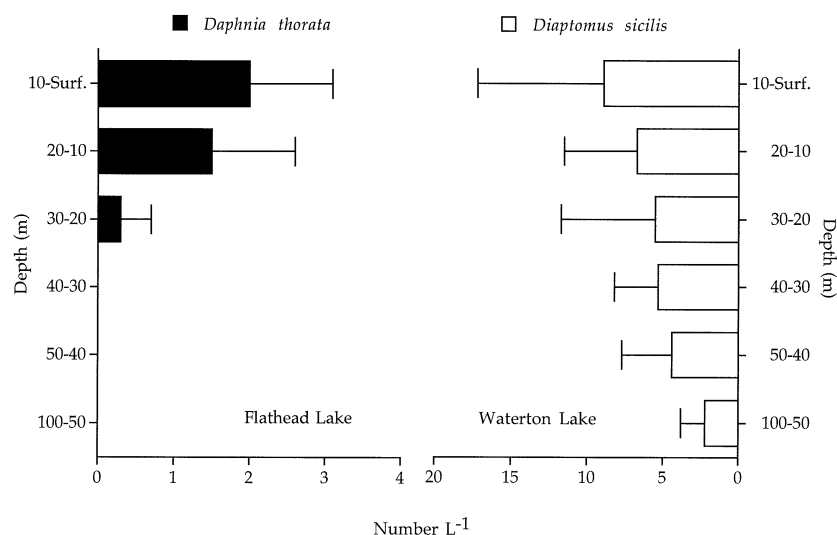


Fig. 5 Nocturnal distribution of dominant prey of *Mysis relicta* from Flathead Lake (*Daphnia thorata*) and Waterton Lake (*Diaptomus sicilis*). Values are means \pm 1 SE for six dates during summer and autumn. Note the difference in scale.

Fig. 5 shows the depth distribution of *Daphnia thorata*, the dominant prey of Flathead Lake mysids, and *Diaptomus sicilis*, the dominant prey of Waterton Lake mysids. The densities of both prey species were higher in the upper 30 m of the lakes. This was especially pronounced in the depth distribution of *Daphnia thorata* in Flathead Lake (Fig. 5). The Flathead Lake mysids consumed approximately three to four times the amount of energy per unit time during migration and while in the upper water column than the Waterton Lake mysids (Fig. 6).

Mysis growth and life history

In Flathead Lake, *M. relicta* completed their life cycle within 1 year. Young were released from the marsupium during March and April. Growth was generally slow during June then increased dramatically from July to October (Fig. 7). The mysids in Waterton Lake completed their life cycle within 2 years and some possibly within 3 years. In Waterton Lake, first-year cohorts were released in May, 1–2 months later than those in Flathead Lake. The growth of the first-year cohort was much slower than that of Flathead Lake juveniles (Fig. 7), forcing the cohort to overwinter. The following spring and summer, growth increased but was still lower than that in Flathead Lake (Fig. 7).

Juveniles in Flathead Lake contained \approx 35% lipid on a dry weight basis (Fig. 8a). The lipid content decreased during the early and midsummer, then increased from midsummer to the autumn until maturation (Fig. 8a). From early October to Nov-

ember, female mysids in Flathead Lake produced eggs, using and allocating lipid to the eggs in the process (Fig. 8a). In May of 1993, the newly released juvenile mysids (1993 cohort) in Waterton Lake contained \approx 25% lipid on a dry weight basis (Fig. 8b). Lipid stores decreased from late May to July, then increased from August to mid-October. Lipid stores also decreased significantly in the winter (October to April) for subadults in the 1992 cohort from Waterton Lake (Fig. 8b). From May to August, the subadults accumulated lipid and allocated it to maturation in mid-October (Fig. 8b). Over the winter, the females used lipid stores while carrying their broods (Fig. 8b). In both lakes, mature male mysids had 15–20% less lipid than mature females.

The percentage lipid of mature females with broods was not significantly different in the two lakes (Fig. 9), but female mysids from Flathead Lake were significantly larger (Fig. 10). In Flathead Lake, the lipid content of stage 5 embryos (Fig. 9) and the number of eggs per female (Fig. 10) were significantly higher than those of Waterton Lake mysids, $P < 0.05$ for an unpaired *t*-test.

Discussion

Non-native *M. relicta* in Flathead Lake consumed more prey, grew faster, were more fecund and allocated more lipid to their progeny than the population in Waterton Lake. *Mysis relicta* in Flathead Lake complete their life cycle within 1 year. In Waterton Lake, it takes at least 2 years to complete

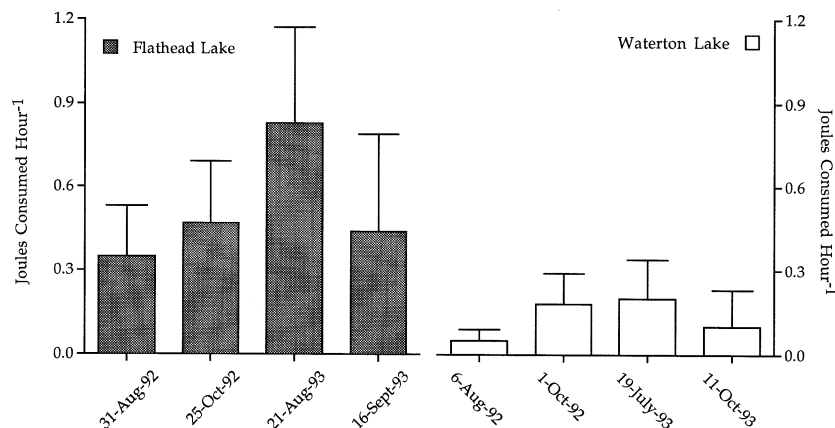


Fig. 6 Total Joules consumed by subadult and mature *Mysis relicta*. Values were estimated from analyses of ten to twenty stomachs per date. Prey energy values (Fig. 2) were used in calculations.

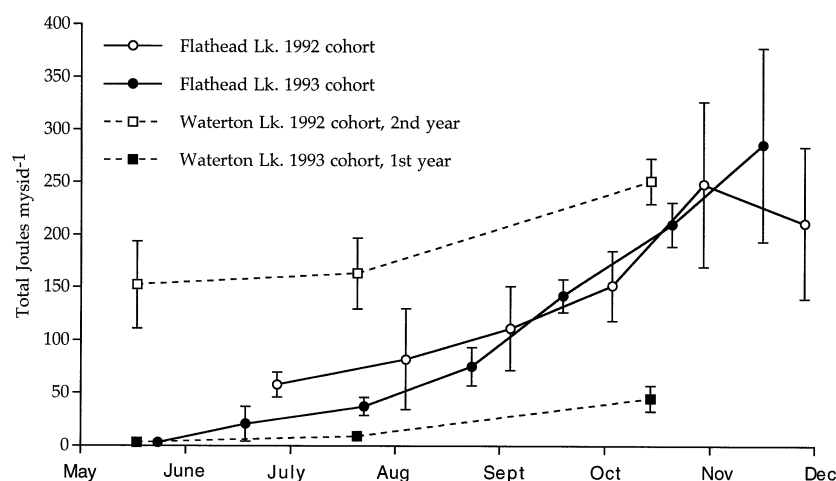


Fig. 7 Total energy content of *Mysis relicta* from Flathead and Waterton Lakes over time. Values were calculated from mean biomass \pm 1SD multiplied by J mg^{-1} for each date.

the life cycle. After the introduction of *M. relicta* from Waterton Lake, Morgan (1980) reported a 4-year life cycle in the main basin of Lake Tahoe and only a 1-year life cycle in the more productive Emerald Bay. Morgan (1980) hypothesized that *M. relicta* had not been in Lake Tahoe long enough to have evolved this difference in life cycle duration, and phenotypic plasticity accounted for the difference in growth rates. Morgan (1980) suggested the difference in life cycle duration was caused by the greater productivity in Emerald Bay. Temperature did not account for the difference because Emerald Bay had a similar summer thermal regime and was cooler than the main body of Lake Tahoe in the winter. The difference in life cycle length of *M. relicta* between Flathead and Waterton Lakes cannot be explained by temperature, because they selected the same temperature strata in the two lakes. During summer, *M. relicta* in Flathead Lake did not exercise DVM into the epilimnion when tempera-

tures reached or exceeded 15°C. In Waterton Lake, the epilimnion was never warmer than 15°C. Hence, in both lakes, the mysids were in water less than 15°C all of the time, and much of the time they were on the bottom, where the temperature was consistently near 4°C in both lakes.

The total energy content and lipid dynamics of *M. relicta* best explain the difference in life cycle length between the two lakes. The total energy content integrates biomass accumulation and lipid storage. In Flathead Lake, the total energy content of *M. relicta* increased steadily from spring through the summer and into the autumn, during maturation and egg production (Fig. 7). In their first year, *M. relicta* in Waterton Lake had a much slower rate of energy increase, did not mature in the autumn and had to overwinter (Fig. 7). In the summer, the energy content of second-year mysids from Waterton Lake gradually increased until maturation. The energy content of

Fig. 8 Temporal dynamics of percentage lipid content of *Mysis relicta* cohorts from (a) Flathead and (b) Waterton Lakes. Values are means \pm 1 SD, $n=3-6$ for each date. Note the dramatic decrease of lipid as females allocate energy to egg development.

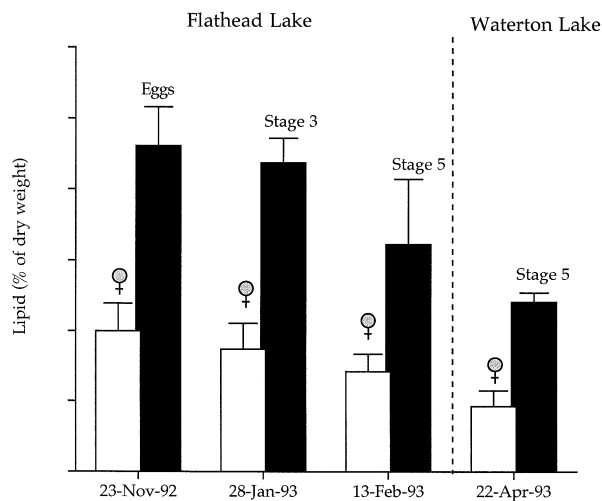
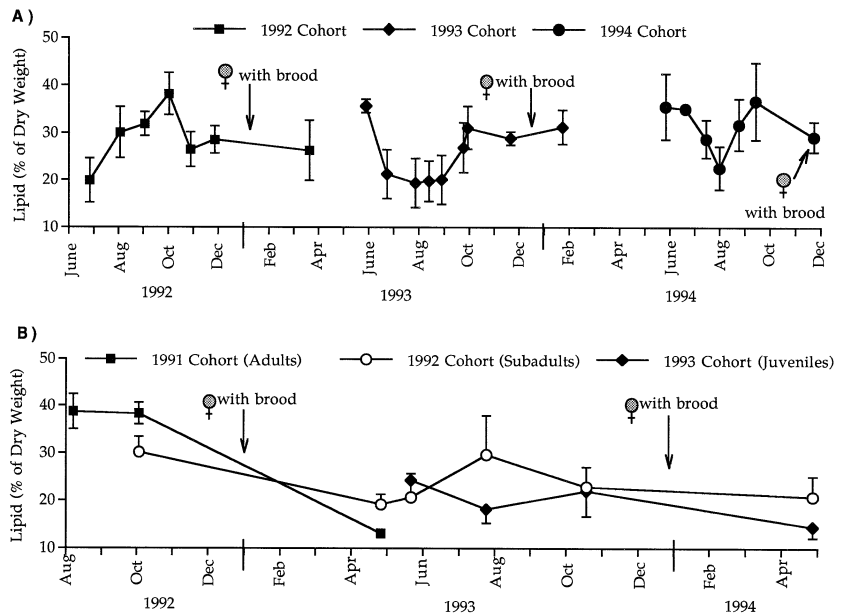


Fig. 9 Per cent lipid content of eggs, developing embryos and female *Mysis relicta* from Flathead and Waterton Lakes. Stage 5 embryos were significantly different between lakes ($P < 0.05$, unpaired t -test).

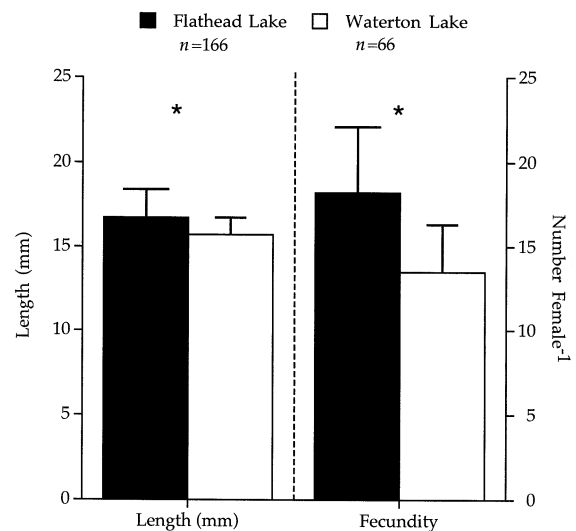


Fig. 10 Number of eggs and embryos per female and total length of gravid female *Mysis relicta* from Flathead and Waterton Lakes. Bars indicate \pm 1 SD. Lakes were significantly different ($P < 0.05$, unpaired t -test).

mature female mysids from Flathead and Waterton Lakes was very similar. This suggests an energy threshold is required for reproduction.

In the spring, Flathead Lake juveniles contained $\approx 35\%$ lipid, which they used for somatic growth in the early summer (Fig. 8a). During this time, the lipid stores decreased until midsummer, then biomass and lipid reserves increased through the autumn. In the autumn, lipid stores were used to synthesize eggs

(Fig. 8a). In May, Waterton Lake juvenile mysids contained less lipid than Flathead Lake mysids but also used lipid for somatic growth. The Waterton Lake juveniles did not accumulate enough biomass and lipid in order to mature and produce eggs in 1 year (Fig. 8b). The Waterton Lake mysids used lipid stores over the winter. In both lakes, the gravid females used lipid while carrying developing broods over the winter. Flathead Lake females did not use as much

lipid, suggesting they were consuming more prey during the winter. In lakes similar to those in the present study, Adare & Lasenby (1994) suggested that juvenile mysids used energy reserves for growth and that a lipid content and biomass threshold must be reached for reproduction. They concluded that 2-year phenology was too short to reach the lipid and biomass threshold. Results from the present study agree with this interpretation, except that the Flathead Lake juvenile mysids allocated more lipid to somatic growth.

Total crustacean density (Fig. 1) in Flathead Lake was slightly higher than in Waterton Lake. However, when comparing the density of the dominant prey species from stomach contents, *Diaptomus sicilis* density in Waterton Lake was approximately four times higher than the density of *Daphnia thorata* in Flathead Lake (Fig. 5). The energy content of *Diaptomus sicilis* in Waterton Lake was approximately one and a half to two times higher than that of *Daphnia thorata* from Flathead Lake (Fig. 2). *Mysis relicta* in Flathead Lake preyed more effectively on *Daphnia thorata* compared to Waterton Lake mysid predation on *Diaptomus sicilis*. The greater predation efficiency on cladocerans agrees with laboratory feeding experiments (Grossnickle, 1978; Cooper & Goldman, 1980; Bowers & Vanderploeg, 1982) and stomach analysis (Lehman *et al.*, 1990).

The lower predation efficiency of Waterton Lake mysids on *Diaptomus sicilis* may be the product of their co-evolution. *Diaptomus sicilis* does not avoid *M. relicta* by vertically migrating to deeper water at night (Fig. 4). Neill (1990) reported that *Diaptomus kenai* underwent reverse DVM when *Chaoborus* were introduced into a British Columbia lake. In Waterton Lake, the lack of spatial avoidance by *Diaptomus sicilis* suggests an effective escape response that explains the lower rate of consumption by *M. relicta*, even though *Diaptomus sicilis* densities in the lake were high. The large calanoid *Senecella calanoides* migrates with *M. relicta* in Waterton Lake (Fig. 4), suggesting the lack of a predator-prey association.

Cladocerans may be rare in Waterton Lake because of the lack of a thermal refuge. The surface temperature of Waterton Lake rarely reaches 15°C and *M. relicta* were frequently seen at the lake surface. In Flathead Lake during summer, the temperature of the epilimnion is 17–20°C to a depth of ≈15 m. The 14–15°C isocline suppresses the ascent of *M. relicta* in

Flathead Lake, providing a thermal refuge for *Daphnia thorata*. Warm-water refuges have been reported for cladocerans in Lake Tahoe (Morgan, 1980; Richards *et al.*, 1991), Lake Michigan (Lehman *et al.*, 1990) and Lake Ontario (Nero & Sprules, 1986). In Flathead Lake, the warm-water refuge for cladocerans, coupled with a productive epilimnion may provide a replenishment of *Daphnia thorata* to the metalimnion during wind events. The importance of temperature as a factor controlling the spatial overlap of *M. relicta* and prey is illustrated by the disappearance of the cold-water stenotherm, *Daphnia longiremis*, in Flathead Lake. *Daphnia longiremis* was frequently sampled from the hypolimnion of Flathead Lake (Potter, 1978), but disappeared after the introduction of *M. relicta*.

When *M. relicta* from Waterton Lake are introduced into a temperate lake, they typically propagate and alter the foodweb. Flathead Lake is a good example of how the adaptations from Waterton Lake enabled *M. relicta* to alter the foodweb. In Flathead Lake, *M. relicta* exercise DVM, ascending at night to capture large amounts of *Daphnia thorata*. *Mysis relicta* then descend to the lake bottom where they assimilate their prey at low temperatures (*sensu* McLaren, 1963), also avoiding predation by pelagic fish. This behaviour has mediated very high growth and fecundity of the mysids at the expense of large zooplankton and, secondarily, pelagic fish.

The establishment of *M. relicta* was the main cause of the collapse of the non-native kokanee fishery. Kokanee were the dominant planktivores in Flathead Lake and the premysid population numbered around one million (Spencer, McClelland & Stanford, 1991). Unfortunately, it appears that as a result of very effective foraging and DVM, the mysids were substantially better competitors for the large zooplankton upon which the kokanee depended. Moreover, as pelagic fish have declined in the decade since the mysid invasion peaked (Montana Fish, Wildlife and Parks, unpublished data), *M. relicta* has enjoyed higher density of preferred prey, especially *Daphnia thorata*. Mysids have become an important prey organism for demersal fishes, especially non-native lake trout [*Salvelinus namaycush* (Walbaum)] and lake whitefish [*Coregonus clupeaformis* (Mitchell)]. Populations of these fish have dramatically increased in the last decade and now dominate gill net catches and hydroacoustic measures (Montana Fish, Wildlife and Parks, unpublished data). A 5-year effort by fisheries

management agencies to re-establish kokanee through a massive stocking effort failed, apparently because of the lack of zooplankton forage coupled with extreme predation by the now very abundant and highly piscivorous lake trout.

Re-establishing kokanee in Flathead Lake is probably impossible without either lake trout or mysid control measures and both of those actions are decidedly problematical from a management perspective. Kokanee, and perhaps other planktivores [e.g. native cutthroat trout (*Oncorhynchus clarki clarki* Richardson)], are pinched between high predation rates from lake trout and competition with *M. relicta* for *Daphnia* prey. Moreover, *M. relicta* will probably remain highly resilient as the foodweb responds to changes in fish populations. The mysids can shorten their life cycle duration and increase in abundance when *Daphnia* density is high and planktivore density is low, or they can lengthen the life cycle and/or shift to copepod prey during periods of low cladoceran availability, should densities of planktivorous fish increase. Indeed, the literature provides no support for the ability of kokanee to be able to complete their life cycle when copepods are their main prey. A similar abundance shift from a planktivorous to demersal fish fauna after *M. relicta* introduction also was documented in a Norwegian lake (Langeland, Koksvok & Nydal, 1991).

It is concluded that *M. relicta* are strong interactors in deep, oligotrophic lakes and foodweb changes will occur when they are introduced into non-native lakes. Their ability to alter foodwebs is explained by a combination of coevolution with fast copepod prey, evolution of DVM and evolution of high phenotypic plasticity associated with life history energetics adapted to cold, low productivity environments like Waterton Lake.

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