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AB THEME SECTION 2

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**Advances in
the ecology of
freshwater mysids**



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Female *Mysis diluviana* (formerly *M. relicta*).

Photo: NOAA, Great Lakes Environmental Research
Laboratory, Ann Arbor, MI, USA

THEME SECTIONS of Aquatic Biology (AB) present integrated multi-author syntheses initiated and coordinated by acknowledged experts. They highlight cutting-edge research areas or problems and/or bring together cogent bodies of literature on all aspects of the biology of organisms in freshwater and marine habitats.

AB Theme Section 2 presents advances in the ecology of freshwater mysids, the opossum shrimp. Mysids are an important component of many aquatic food webs. They are relatively small omnivores (up to 30 mm length) that perform extensive diel vertical migrations and are an

important prey of fishes. They are a dominant taxon in many lake ecosystems.

The contributions to AB Theme Section 2 examine questions ranging from the control of vertical migration, to conditions affecting growth rates, variation in the role of mysids in different food webs, and impacts of mysid introductions.

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THEME SECTION

Advances in the ecology of freshwater mysids

Idea and coordination: Lars G. Rudstam, Ora E. Johannsson

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Introduction

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ABSTRACT: Mysids can be considered the krill of lakes. These crustaceans are relatively small (<30 mm), omnivorous, perform extensive vertical migrations, are a major food source for fishes, and can be the dominant species by mass in lakes. This Theme Section comprises 4 papers that represent significant advances in the study of these ecologically important animals, including techniques that were not available 20 years ago, such as DNA:RNA:protein ratios, fatty acids and stable isotopes as growth indicators, quantitative analysis of acoustics data and vertical migration models. The Theme Section thus represents a step forward towards better understanding long-term zooplankton time series, mysid omnivory, and the mysid ecological role in lake food webs.

KEY WORDS: *Mysis relicta* · *Mysis diluviana* · Zooplankton · Lakes · Food web

Mysids, or opossum shrimps, are members of the mostly marine order Mysidacea. There are some 30 species occurring in freshwater lakes and rivers, and the group has a worldwide distribution. Of these species, members of the *Mysis relicta* species complex

have received the greatest attention because of their high abundance in some lakes (reported densities >1000 ind. m⁻²), their importance as a food source for fishes, and their sometimes large effect on food web dynamics. The *Mysis relicta* species complex consists of

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4 species, 1 in North America (*M. diluviana*) and 3 in Eurasia (*M. relicta*, *M. segerstralei*, *M. salemaai*) (Audzijonyte & Väinölä 2005). The complex is a glacial relict with circumpolar distribution in deep, cold lakes of the Northern Hemisphere. The biomass of mysids can exceed that of planktivorous fishes, with which they compete for zooplankton prey (Gal et al. 2006). Their potential effect on food webs was not fully appreciated until they were introduced into new lake habitats in an attempt to promote fish growth. Mysids often had strong negative effects on zooplankton and their introduction led to decreases in some of the fish species they were supposed to enhance (Lasenby et al. 1986, Nesler & Bergersen 1991). Effects can cascade through ecosystem food webs to top predators such as bears and eagles (Spencer et al. 1991).

Mysid growth rate is a key component in calculating productivity of the mysid population and mysid consumption of various prey items (Johannsson et al. 2003), which are needed for inferences on the role of mysids in the food web. Growth rates vary widely, and are highest in highly productive lakes. Growth rates range from 0.2 mm mo^{-1} in Lake Tahoe to 1.5 mm mo^{-1} in mesotrophic lakes (review in Rudstam 2009), but they are difficult to measure *in situ*, especially when generations overlap. Johannsson et al. (2008) used nucleic acids and protein ratios as indicators of mysid growth and condition in laboratory experiments. Johannsson et al. (2009, this Theme Section) use this method to investigate inter-annual and spatial growth rate differences in Lake Ontario. The indices demonstrate differences in condition and growth rate, and suggest that certain essential fatty acids may be limiting in Lake Ontario.

Mysis spp. perform diel migrations at dusk and dawn from their daytime refuge in dark, deep water to the meta- or epilimnion, where they feed on zooplankton and algae. These migrations can be over 100 m and are limited by temperatures above 12 to 16°C and light levels above 10^{-4} lux, i.e. light levels that limit fish visual feeding. Boscarino et al. (2009a, this Theme Section) show that the actual distributions, not just the mean depth, can be predicted from the response of mysids to these variables in the laboratory (Boscarino et al. 2007, 2009b). Including the distribution of mysid prey and predators did not improve the predicting ability of the models. Because most of the interactions between mysids and their prey and predators likely occur at the edges of their vertical distributions, a better understanding of the whole distribution, not only the mean depth, is essential for adding a spatial dimension and more realism to predator-prey models. Diel vertical migrations are common in zooplankton (DeMeester 2009), and the approach by Boscarino et al. should also be useful for understanding the distribution of other migrating organisms.

Mysids are omnivores and capable of both filter-feeding and raptorial feeding. Mysids also feed on benthic prey, detritus and sediment during the day (Van Duyn-Henderson & Lasenby 1986). Diets of mysids can vary greatly between neighboring lakes (Nordin et al. 2008). Whall & Lasenby (2009, this Theme Section) examined the trophic role of *Mysis diluviana* in 2 neighboring lakes, one in which the introduction of mysids was associated with the collapse of kokanee salmon *Oncorhynchus nerka* (Okanagan Lake), and the other, in which it was not (Kalamalka Lake). They predicted that zooplankton would form a greater proportion of the diet of mysids in Okanagan Lake, where they were expected to compete more strongly with kokanee for zooplankton prey. However, comparison of mysid diets and clearance rates together with stable isotope signatures suggested that this was not the case. The study by Whall & Lasenby (2009) shows how these different techniques can be combined to investigate mysid prey choice. The reason for the different food web effects in the 2 lakes, however, remains unknown.

Mysids were introduced in 1949 to Kootenay Lake, BC, Canada, and are thought to be responsible for a large increase in growth rate of kokanee salmon and the spectacular fishery that developed after the introduction. After this reported success, mysids were introduced to many lakes and reservoirs in North America and Scandinavia to increase fish growth and production. However, results were not often those intended, as mysid predation caused declines in cladocerans, in particular in *Daphnia*. Koksvik et al. (2009, this Theme Section) show that an initial decline in cladocerans can be a transitory phenomenon. In Lake Lille Jonsvatn, the cladocerans returned after a period of 11 yr with depressed *Daphnia* abundance. Koksvik et al. (2009) think that this may be due to increased water clarity, which limits mysid migration into shallower water and provides a refuge for cladocerans in the epilimnion. This study highlights the importance of long-term studies.

The contributions to this Theme Section represent the state of the art in mysid ecology. The papers are based on a symposium on mysid biology organized by Lars Rudstam, Ora Johannsson and Michael Arts at the International Society of Limnology meeting in Montreal in 2007. The mysid symposium represented an update of similar symposia held in the 1980s and 1990s (Morgan 1982, Nesler & Bergersen 1991). The contributions to the present Theme Section include the use of techniques that were not available 20 years ago, such as DNA:RNA:protein ratios, fatty acids and stable isotopes as growth indicators, as well as quantitative analysis of acoustics data and vertical migration models, and thus represent a step forward towards better understanding the ecology of mysids in freshwater systems.

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Field assessment of condition indices (nucleic acid and protein) in *Mysis diluviana*

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ABSTRACT: *Mysis diluviana*, the opossum shrimp, is a key link between offshore benthic and pelagic foodwebs in the Laurentian Great Lakes. Nucleic acid and protein indices (RNA/DNA, DNA/protein, %protein, DNA/weight), which have been related to growth and protein synthesis rates, were assessed as measures of mysid condition. We examined autumn inter-annual and spatial patterns in these metrics in juvenile and adult female *M. diluviana* in Lake Ontario from 2001 to 2005. Males were not included because initial results of the present study indicated that larger, mature males entered a physiological decline in autumn. Nucleic acid/protein indices had a sufficient range and sensitivity to detect differences among years and habitats. In years when *M. diluviana* was in poor condition, nucleic acid and protein indices were similar to laboratory values of animals with low growth rates, values which were slightly above the nucleic acid and protein values of fasting animals. Mysids which were deemed to be in better condition in Lake Ontario had similar condition indices to those in Lake Huron. When differences existed, inshore mysids tended to be in poorer condition than offshore mysids, supporting the hypothesis that improved food resources may encourage offshore movement of mysids during the growing season. Zooplankton areal biomass, and female % total lipids and fecundity were not correlated with the nucleic acid and protein condition indices. However, key essential fatty acids and total saturated fatty acids had significant associations with nucleic acid and protein indices; this indicates that food quality is an important determinant of condition in *M. diluviana*.

KEY WORDS: *Mysis relicta* · *Mysis diluviana* · Great Lakes · RNA · Monitoring · Lake Ontario

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INTRODUCTION

In 2002, Fisheries and Oceans, Canada, in partnership with Environment Canada, initiated a monitoring program for *Mysis diluviana* (formerly *M. relicta*, Audzijonyte & Väinölä 2005) in Lake Ontario. The lake was changing rapidly with the arrival and expansion of several aquatic invasive species: dreissenid mussels *Dreissena polymorpha* and *D. bugensis*, predatory cladocerans *Bythotrephes longimanus* and *Cercopagis pengoi*, and the round goby *Neogobius melanostomus* (Dermott & Geminiuc 2003, Johannsson 2003, Dermott et al. 2005, Warner et al. 2006, Walsh et al. 2007, Wat-

kins et al. 2007), all of which could potentially impact mysid populations. In the Laurentian Great Lakes (Superior, Michigan, Huron, Ontario, but excluding Erie), *M. diluviana* and *Diporeia* spp. are the dominant large native macroinvertebrates. Historically, these species funneled the majority of zooplankton and phytoplankton production to the fish community in the offshore regions. In the 1990s, *M. diluviana* consumed as much, or more, of the offshore zooplankton production in Lake Ontario as the dominant planktivore, the alewife *Alosa pseudoharengus* (Gal et al. 2006). In 1990, prior to the invasive species impacts, mysids composed ~20% of the biomass consumed by alewife

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in spring and fall (Rand et al. 1995). Dreissenid mussels now also help to move phytoplankton production to the fish community in Lakes Ontario, Erie, Michigan and Huron, where they are replacing *Diporeia* spp. (Dermott et al. 2005, McNickle et al. 2006, Nalepa et al. 2006). In response, the distributions and diets of fish such as alewife and lake whitefish *Coregonus clupeaformis* have been shifting, and diets have been broadening to include alternative prey such as dreissenids and mysids (O’Gorman et al. 2000, Pothoven et al. 2001, Hoyle et al. 2003, Hondorp et al. 2005). Mysids are also an important component of the diet of a recent invader, the round goby (Walsh et al. 2007). With the loss of *Diporeia* and the arrival of round goby, the role of *M. diluviana* in the offshore food web is enhanced.

The ongoing monitoring program examines the mysid population throughout Lake Ontario in late October to early November, when the best estimates of density and biomass are obtained and when the population is reproducing (Johannsson 1992, 1995). In the spring, when the water column is totally mixed, mysids feed equally well at the bottom (in the 2 m of water above the bottom sediment not sampled by the net) and in the upper water column (Johannsson et al. 2001). Many individuals do not undertake vertical migrations at this time, rendering estimates of abundance and biomass unreliable. In summer and fall however, the majority of the mysid diet is upper water column zooplankton. Thus, reliable estimates of abundance and biomass can be obtained at least until fall turnover in December. The generation time of *Mysis diluviana* in Lake Ontario is 2 yr. The principal reproductive period commences in early October and young are carried until mid-winter or early spring. In autumn, mature *M. diluviana* contain 20 to 40% lipids by dry weight (dry wt) (Adare & Lasenby 1994). Thus, fecundity and % total lipid content at maturity can also be monitored in the fall.

A physiological measure of mysid condition as an early warning indicator of poor health or poor food quality or availability was a desirable addition to the ecological parameters in our monitoring program. In this respect, growth rate is an excellent integrative measure of condition in organisms. While it is not possible to determine the growth rate of individuals in an annual survey, biochemical indices, such as nucleic acid and protein ratios, correlate with growth rate and hence can serve as surrogate measures of growth.

Growth rates and protein synthesis rates in both vertebrates and invertebrates have been correlated with ribonucleic acid (RNA) content or ratios of ribonucleic acid/deoxy-

ribonucleic acid (RNA/DNA) (Buckley 1979, Houlihan et al. 1993, Bergeron 1997, Dahloff & Menge 1996, Saiz et al. 1998, Wagner et al. 1998, 2001). In order to make comparisons between groups, total RNA must be normalized to a single cell or to a measure of body size, usually expressed as total DNA; hence, the frequent use of the RNA/DNA ratio. Larger cells, which contain more structural protein, tend to be metabolically more active and have more RNA than smaller cells (Schmidt & Schibler 1995). Consequently, protein/DNA—a measure of cell size—has also been observed to correlate with growth rates (Foster 1990). If more active cells are larger, then there should be fewer of them per unit body weight, and therefore, DNA/dry wt and DNA/carbon content have been suggested as additional measures of condition (Bergeron 1997). In laboratory studies of *Mysis diluviana* growth rates under different conditions, Johannsson et al. (2008) observed corresponding increases in RNA and protein relative to DNA and of protein relative to wet weight (%protein) with increases in growth rate, while the number of cells per unit of weight (DNA per unit wet weight) decreased. Changes in temperature can alter the relationship between RNA and growth rate. RNA is more efficient at higher temperatures, and concentrations of RNA decline as temperatures increase (Buckley 1982, Foster et al. 1992). We propose that all 4 indices (RNA/DNA, protein/DNA, %protein, DNA/weight) should be examined simultaneously when assessing changes in growth rate (Fig. 1).

Therefore, the primary purpose of the present study was to assess the potential usefulness of these nucleic acid and protein indices in monitoring the condition of *Mysis diluviana* in the field. This includes: (1) examining the range of inter-annual variation in the indices, (2) determining whether spatial variability is important and, if present, its patterns and consistency, (3) comparing field and experimental indices for *M. diluviana*,

	RNA/DNA ↓	RNA/DNA ↑
Protein/DNA ↑	A Temperature may be increasing	B Higher metabolic activity Larger cells Likely growing more rapidly
%Protein ↓		
Protein/Weight ↓	C Lower metabolic activity Smaller cells Likely growing more slowly	D Temperature may be decreasing Growth may be limited by nitrogen
Protein/DNA ↓		
%Protein ↓		
DNA/Weight ↑		

Fig. 1. Interpretation of nucleic acid and protein indices to determine relative condition factors. If the ratios are analyzed using ANCOVA, the black component of the index is the dependent variable and the gray component is the covariate. Arrows indicate direction of change of parameters

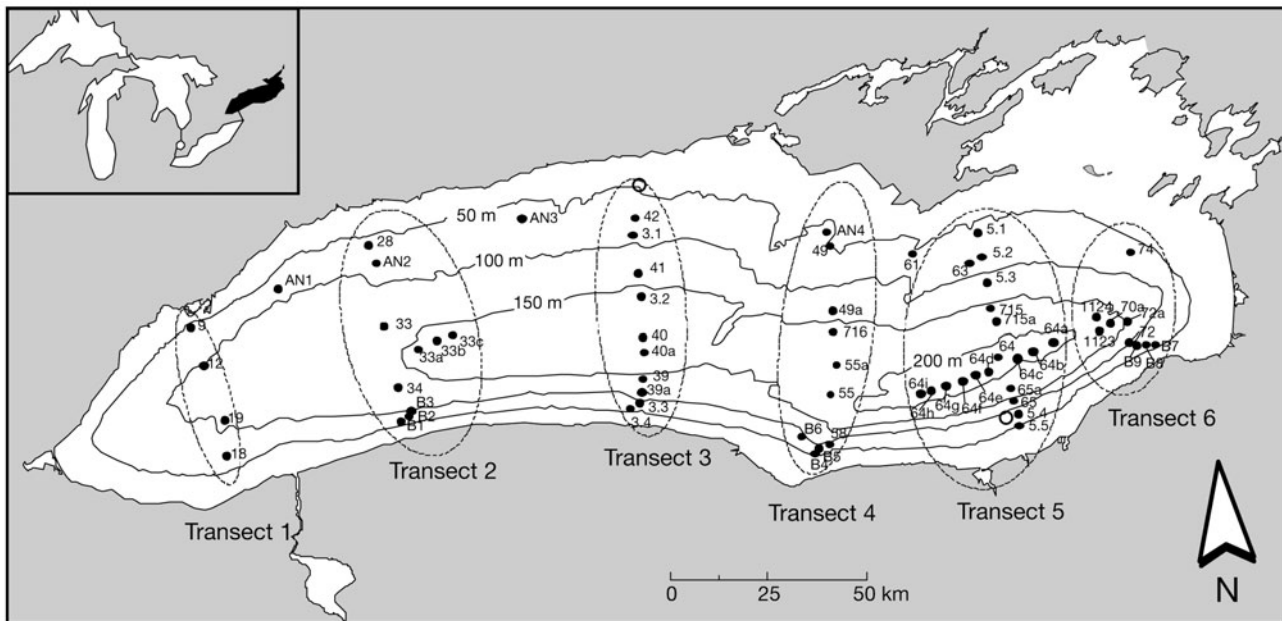


Fig. 2. Map of the 2001 to 2005 sampling stations in Lake Ontario showing the 6 cross-lake transects, the transect down the length of the deep hole, and additional stations (AN series and B series) used to augment samples in the depauperate 50 to 100 m bottom depth region. ○: 2 shallow stations sampled only in 2001

and (4) comparing the response of the indices to other measures of mysid condition, i.e. fecundity, total lipid (mature, non-gravid females) and omega-3 essential fatty acid (EFA) concentrations (Schlechtriem et al. 2008a). By examining these growth indices along the inshore–offshore mysid abundance gradient, we assessed whether the actively maintained pattern of increasing mysid density with depth, especially of larger animals, might be a response to better conditions in offshore areas.

MATERIALS AND METHODS

Field studies. The nucleic acid and protein indices, lipid and zooplankton data were generated during 2 studies on Lake Ontario. The first, carried out in October 2001, collected mysids from 4 sites: 2 in the central region of the lake at 128 m (Station 41) and at 45 m (open circle north of Station 41) bottom depth, and 2 in the southeastern portion of the lake at 118 m (Station 65) and 63 m (open circle south of Station 65) bottom depth (Fig. 2).

The second ongoing study, of which the 2003 to 2005 data are reported here, monitors the *Mysis diluviana* population in Lake Ontario between late October and early November (Table 1). No zooplankton or nucleic acid data are available for 2002. Mysids were sampled along a total of 6 north–south transects, weather permitting, replicating the 1990 mysid sampling pattern of

Johannsson (1995) (Fig. 2). Sampling stations were located such that 10 stations fell within each of the 50 m bottom depth ranges except for 0 to 50 m, and equal numbers of stations occurred in each quadrant of the lake. An additional transect was conducted through the ‘deep hole’ to adequately sample the 200 to 250 m depth range. Additional stations were added in the 50 to 100 m depth range where mysid densities were very low (Fig. 2).

Mysids were collected by vertical net haul at night. A rectangular, 1 m² net constructed of 1 mm Nitex mesh with a 250 µm cod end was lowered to within 2 m of the bottom, allowed to rest for 30 s to enable the mysids to redistribute, and then raised at 0.33 m s⁻¹. All samples were collected between 1 h after dusk and 1 h before dawn. The net was fitted with a darkened plastic bottle at the cod end to ensure that the mysids remained in cold water and were not compressed on their ascent through the water column. Mysids were kept cool and

Table 1. Sampling dates and number of stations sampled annually for *Mysis diluviana* in Lake Ontario. Data originated from 2 different programs (2001 and 2003 to 2005); during the later study, stations were distributed across the lake

Year	Date range	Stations
2001	2 to 3 October	4
2003	27 to 30 October	55
2004	26 to 28 October	26
2005	7 to 12 November	47

examined immediately. Gravid females were placed individually in 0.5 ml bullet tubes containing 8% sugar-buffered formalin. Mysids for lipid or nucleic acid and protein analyses were sexed, assigned to 1 of 3 size groups (4 to 8 mm, 9 to 12 mm, ≥ 13 mm body length) and frozen in cryovials in liquid nitrogen, either individually for nucleic acid and protein analyses or in small groups (10 to 30, 5 to 10, 3 to 5 animals per vial for the 3 size classes, respectively) for lipid analyses. However, mysids in the smallest size group were often not abundant enough for fatty acid analyses. The samples were stored at -85°C until analysis. The remaining mysids were preserved in 8% sugar-buffered formalin.

In the 2001 study, 2 vertical zooplankton tows through the hypolimnion were conducted using a 64 μm mesh closing net at each of the deeper stations. In the 2003 to 2005 study, two 153 μm mesh zooplankton tows were conducted during the day through the entire water column at 6 to 9 locations spaced east to west, along transects running above and below the centre line of the lake. The positions of the sites were not fixed but opportunistic, with the intent of capturing all regions of the lake inhabited by mysids, both shallow and deep.

Zooplankton analyses. The 2 samples from each site were combined and analyzed to species level using a randomized, weighted counting procedure to ensure adequate counting of rare species (Cooley et al. 1986). Biomass was calculated from length–weight relationships derived from the literature (Johannsson et al. 2000). The areal biomass of the water column was calculated *in toto*. The 2001 hypolimnetic biomass data were extrapolated to the entire water column for comparison with the biomass estimates from the later years. The 2001 biomass calculations may underestimate total zooplankton, and, in particular, cladoceran biomass. Zooplankton biomass is greater per cubic meter in the epilimnion than in the meta- and hypolimnion in the fall at deep stations (data reworked from appendices, in Mills et al. 2006).

Nucleic acid and total protein determination. RNA and DNA contents of individual mysids were determined spectrophotometrically using the UV dual absorbance method (232 and 260 nm) according to the protocols developed by Schmidt & Thannhauser (1945) and modified by Munro & Fleck (1966) and Buckley & Bulow (1987). The method is described in detail in Schlechtriem et al. (2008b). These methods have been used for fish, crustacean and mammalian assays, and the advantages, in terms of accuracy, have been summarized by Smith et al. (1999). For example, RNA recovery efficiencies are between 95.4% (Mathers et al. 1993) and 100% (Munro & Fleck. 1966). Two standards prepared previously from fresh and frozen Lake Ontario mysids and stored at -85°C were run with

each batch of samples to check consistency of sample processing.

Protein was determined using the method of Lowry et al. (1951). Standard 5-point concentration curves were created with bovine serum albumin.

Lipid determinations. Total lipid content and fatty acid methyl esters (FAME) of freeze-dried *Mysis diluviana* were obtained in a 3-step process: extraction and weighing of 2 subsamples for total lipid estimation, derivatization of the remainder, and quantification of FAME on a gas chromatograph (GC) as in Schlechtriem et al. (2008a). A 37-component FAME standard (Supelco #47885-U) was used to identify FAME by comparison of retention times. The FAME of interest to this study were: (1) eicosapentaenoic acid (EPA; 20:5n-3) and docosahexaenoic acid (DHA; 22:6n-3), 2 essential fatty acids (EFA) needed for proper immunological (EPA) and neurological (DHA) function, (2) their precursor α -linolenic acid (ALA; 18:3n-3), and (3) the sum of saturated fatty acids (SAFA; a source of energy).

Statistical treatment of data. Data are reported as mean \pm 2 SE and a significance level of $p \leq 0.05$ was used throughout unless otherwise noted. All statistical analyses were performed with SYSTAT (11.0).

The nucleic acid and protein indices examined were RNA/DNA, protein/DNA, %protein and DNA/wet weight. The ratios change with body size in mysids (Nordin 2005, Schlechtriem et al. 2008b), with the exception of %protein, and thus must be standardized to a common body size before they can be compared across 'treatments' (years, lakes, locations, etc.). The ratios already contain a measure of body size (DNA or weight), and thus, the indices are more sensitive if the ratios are split into their component parts (e.g. RNA vs. DNA instead of RNA/DNA vs. weight) for analysis because there is one less source of error variability. In addition, interaction terms between body size and factors are often significant when the indices are expressed as ratios, but not when the indices are split. All data were examined and, if necessary, transformed to ensure linearity and homogeneity. This meant that we examined log RNA and log protein relative to log DNA, and DNA^2 relative to wet weight (females only).

Juveniles and adults exhibited considerable morphological overlap when the division was defined purely by body length. Females were first identified at a DNA content of 23 $\mu\text{g ind.}^{-1}$. However, the variability and slope of the relationship between log RNA and log DNA changed at a DNA content of 26 $\mu\text{g ind.}^{-1}$. Therefore, for analytical purposes, juveniles were defined as having a DNA content $\leq 26 \mu\text{g ind.}^{-1}$, while adults had DNA content $> 26 \mu\text{g ind.}^{-1}$. There was no break in the data between the 2 juvenile size classes; therefore, they were combined.

The indices were first examined for variability among years using ANCOVA, or ANOVA for %protein. Tukey's

honestly significant difference (HSD) multiple comparison test was employed to determine significant differences between pairs of years. Next, the indices were examined for differences between inshore and offshore habitats within each year, again using ANCOVA or ANOVA. The division between inshore and offshore was set at 120 m bottom depth, based on the distribution of the benthic invertebrate and fish communities. In order to directly compare data that included both annual and, when significant, inshore and offshore estimates of adjusted means, we divided them into year-depth categories; i.e. 2001-Inshore, 2001-Offshore, 2003-Inshore, etc., and reanalyzed the data to produce comparable, adjusted means across the years. Finally, we compared our yearly indices from Lake Ontario with those from Lake Huron (October 2002) and with from laboratory experiments during which mysid growth rates were measured using the same methods as in the present study (Johannsson et al. 2008). The Lake Huron data were included to provide a reference to mysid nucleic acid and protein indices from another field site because the higher growth rates observed in the field have not yet been attained in laboratory experiments. These data were included directly in the ANCOVA and ANOVA analyses. The experimental data did not include mysids from as wide a size range as the field data. Therefore, we ran a separate analysis restricting the size range of the field-caught animals to match that of the experimental animals (high growth treatments, $<7^{\circ}\text{C}$). A correction was then calculated for the experimental data by subtracting the adjusted means of the indices for the same-size selected field data from those determined for the entire set of field data. This difference was then added to the adjusted means of the experimental data so that they could be compared visually with the complete Lake Ontario data.

Upwelling events during the summer and fall often push colder waters into the northwest and southwest of the lake, decreasing epilimnetic productivity in this region through thinning of the epilimnion and increasing it in the southeast, which then has a deeper epilimnion (Patalas 1969, Johannsson 2003). Other factors, such as the Niagara River inflow along the south shore, and differential depth gradients between the north and south shores, also affect habitat characteristics in the different regions of the lake. Therefore, we divided the lake into 4 quadrants: NW, NE, SE and SW. This allowed us to examine the importance of possible habitat differences through the analysis of the association of geolocation with the nucleic acid and protein indices, both within each year and across all years, using ANCOVA or ANOVA.

To assess possible associations between EFA and nucleic acid and protein indices, Pearson correlation coefficients were calculated.

RESULTS

Nucleic acid and protein indices

Nucleic acid and protein index relationships differed between males and females. Male DNA content was 8% higher than that of females (Fig. 3A). The relationship between log RNA and log DNA also differed between the sexes (Fig. 3B), being positive and significant in females and non-existent in males. When RNA was plotted against protein, males separated into 2 groups at a protein content of 3.8 mg ind.^{-1} (Fig. 3C). The separation was associated with body size: the group of males with lower RNA (cov protein) values was generally $>35 \text{ mg}$ wet weight and the group with higher values $<35 \text{ mg}$ wet weight. The RNA/DNA ratios of the larger males were also lower (1.55 to 2.05) than those of the smaller males (2.0 to 2.5) (Fig. 3D). However, the ratios normally increase with body size (Schlechtriem et al. 2008b, Fig. 3D). For these reasons, we concluded that males were in physiological decline. Consequently, males were not collected after 2003 and only females and juveniles were analyzed for inter-annual and spatial patterns.

Relatively consistent trends were observed across years in juveniles and females. Adjusted means of log RNA with log DNA as the covariate (cov log DNA), log protein (cov log DNA), and %protein (for females only) were higher in 2003 and 2005, while adjusted means of DNA² (for females) or DNA (for juveniles) with weight as the covariate (cov weight) were lower (Fig. 4). An exception was log RNA (cov log DNA) in juveniles in 2005, which was intermediate and similar to that of individuals from the offshore area in 2004. The reverse was true for 2001 and 2004. The adjusted means of log RNA (cov log DNA) and log protein (cov log DNA) of offshore juveniles in 2003 were particularly high (Fig. 4A,B), while that of DNA (cov wet weight) was particularly low (Fig. 4D). The adjusted means of the later 2 indices (log protein, cov log DNA and DNA, cov wet weight) were similar to those observed in Lake Huron (Fig. 4B&D). Juvenile adjusted mean log RNAs in Lake Ontario were significantly lower than those in Lake Huron (Fig. 4A). The experimental data indices of Johannsson et al. (2008) were similar to those observed in 2001 and 2004 in all cases (Fig. 4A): log RNA (cov log DNA) experimental data were also similar to 2005 data. These results place the condition of juvenile mysids in 2003 in Box (B) of Fig. 1. The condition of mysids in 2005 is also in Box (B); however, it would be ranked lower than 2003 based on the slightly lower log RNA (cov log DNA) and log protein (cov log DNA). The condition in 2001 was similar to that in 2004 and both fell in Box (C) of Fig. 1.

All 4 nucleic acid and protein indices of females were similar in 2003 and 2005, and in 2001 and 2004. In

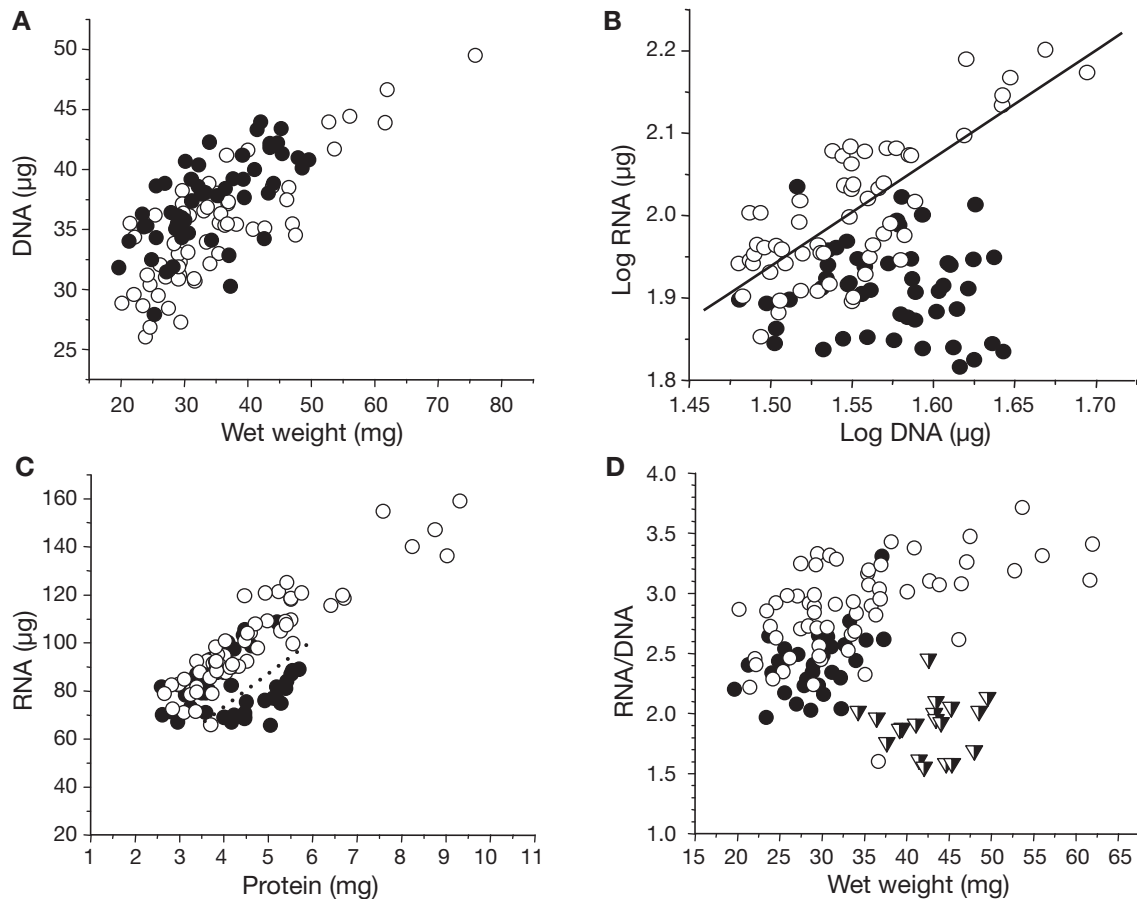


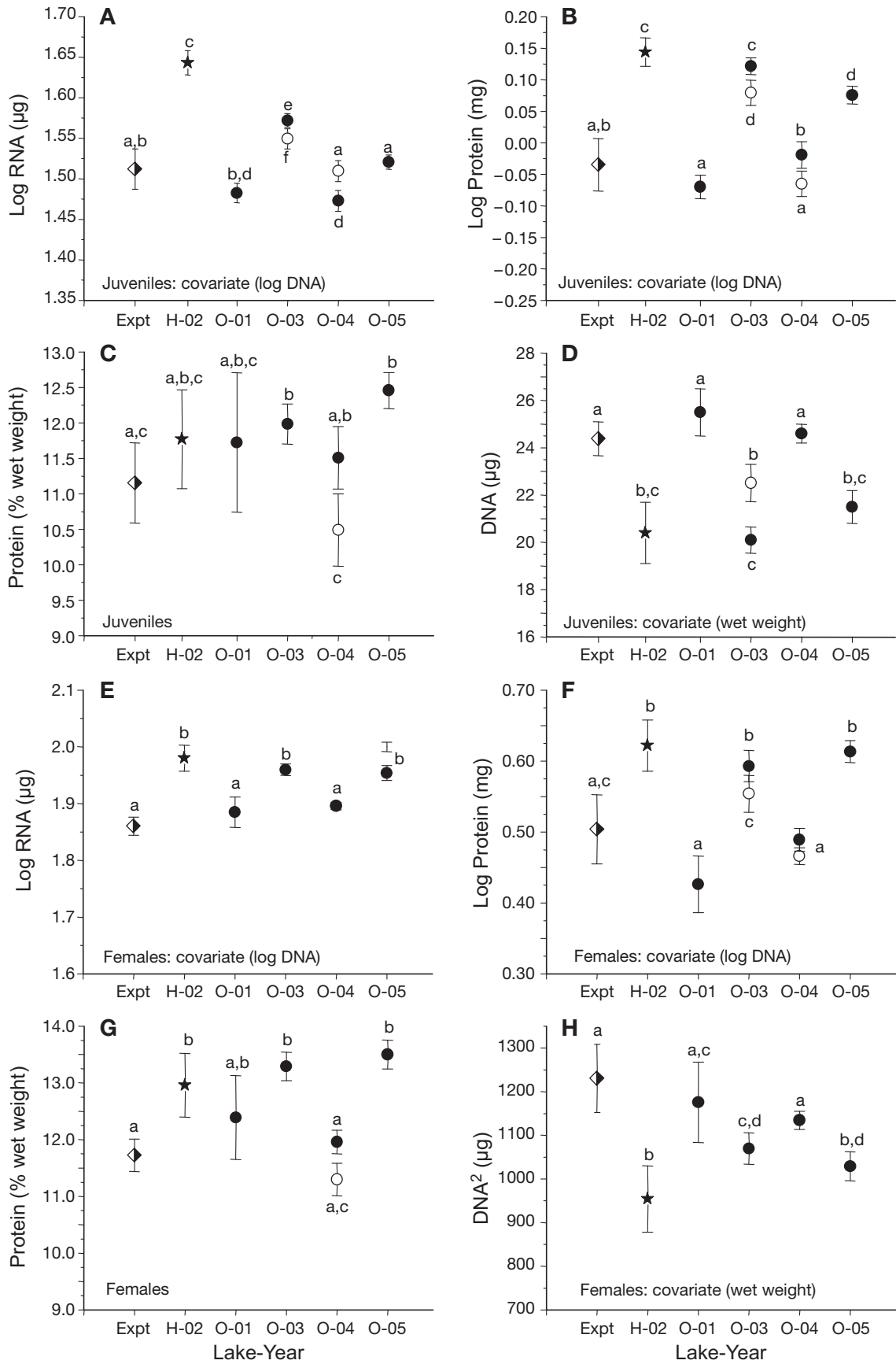
Fig. 3. *Mysis diluviana*. Nucleic acid and protein indices of male and female individuals in autumn. (A) Relationships between DNA content (μg) and wet weight (mg) of males (\bullet) and females (\circ). (B) \log RNA (μg) vs. \log DNA (μg) of males (\bullet) and females (\circ). No relationship exists in males. For females, $\log \text{RNA} = 0.0283 + 1.312 \log \text{DNA}$ ($r = 0.775$, $p < 0.001$, $n = 58$). Data suggest one misidentification of a male. (C) RNA (μg) vs. protein (mg) content of males (\bullet) and females (\circ). Dotted line indicates separation of males into 2 groups. Females overlap with the higher RNA group of males. (D) RNA/DNA ratio vs. wet weight (mg) of females (\circ) and both groups of males defined in (C), with high RNA/protein ratio males (\bullet), low RNA/protein ratio males (\blacktriangledown)

females, all 3 adjusted means and %protein in 2003 were similar to those in 2005 (Fig. 4E–H). In addition, the 2003 and 2005 values of \log RNA, \log protein and %protein were similar to those in Lake Huron (Fig. 4E–G): the Lake Huron adjusted mean DNA² was lower than that in Lake Ontario (Fig. 4H). Again, the experimental data indices of Johannsson et al. (2008) were similar to the Lake Ontario indices for females in 2001 and 2004 (Fig. 4E–H). The condition of female mysids in 2003 and 2005 was similar and fell in Box (B) of Fig. 1, while the condition of female mysids in 2001

and 2004 was similar and poorer than in 2003 and 2005; thus, they fell in Box (C) of Fig. 1.

Inshore–offshore trends were clearly identified only in 2003 and 2004. In 8 of the 9 instances where significant differences between inshore and offshore areas occurred in the indices, the mysids were in better condition in the offshore areas; that is, the adjusted means of \log RNA (cov \log DNA), \log protein (cov \log DNA) and %protein were higher offshore while DNA (cov weight) was lower (Fig. 4A–D, F&G). Only 2004 juvenile \log RNA did not follow this pattern (Fig. 4A).

Fig. 4. *Mysis diluviana*. Nucleic acid and protein indices in juvenile (A–D) and adult female (E–H) individuals (autumn adjusted means \pm 2 SE). In all cases, Lake Ontario indices (\bullet) for each year (O-01, O-03, O-04, O-05 for years 2001 to 2005) are compared with autumn indices from Lake Huron (\star) from 2002 (H-02), and with laboratory experimental indices (\blacklozenge) with known growth rates (Exp; data from Johannsson et al. 2008). See text for details of experimental animals. Where inshore and offshore values were significantly different, they are displayed separately: inshore (\circ), offshore (\bullet). Significantly different values have been assigned different letters (a,b,c,d)



No inshore–offshore trends were observed in 2005. In 2001, the data were insufficient to test for spatial patterns.

Other habitat differences were captured by dividing the lake into quadrants along the main north–south and east–west axes of the lake. Data for all years were combined and the similarity of each index across quadrants assessed. In juveniles, log RNA (cov DNA) showed some differences between the east and west of the lake in 2004, and between the north and south in 2005 (Fig. 5); however, no general pattern was observed among the quadrants. The NE log protein (cov log DNA) was high and the corresponding DNA (cov weight) low, compared with the other quadrants (Fig. 5B,D). These latter 2 patterns were not dependent on a single year. %protein was lowest in the SE quadrant (Fig. 5C), but was driven solely by the 2004 data. In females, all indices differed significantly. Indices indicating better mysid condition tended to occur in the north, particularly the northeast, and those indicating poorer condition in the south, particularly the southeast (Fig. 5E–H). However, the 2004 data drove the patterns, which disappeared if these data were removed.

Lipids. Mature, non-gravid females had a similar total lipid content (% dry wt) in 2001 and 2003: $36.1 \pm 4.5\%$ ($n = 10$) and $36.8 \pm 1.0\%$ ($n = 91$), respectively. Lipid content decreased significantly in 2004 and again in 2005 to $35.3 \pm 1.5\%$ ($n = 29$) and $31.5\% \pm 1.9\%$ ($n = 31$), respectively.

No significant correlations were observed between the 4 nucleic acid and protein indices and the 4 individual FA in adult females (Table 2). However, the sum of EPA + DHA was significantly associated with the adjusted means of log RNA (cov log DNA), and closely related to log protein (cov log DNA) ($0.05 < p < 0.10$). Significant correlations were observed in juvenile mysids between the adjusted means of log RNA (cov log DNA) and EPA and SAFA; ALA was also close ($0.05 < p < 0.10$). Log protein (cov log DNA) approached significant associations with EPA ($0.05 < p < 0.10$) and SAFA ($0.05 < p < 0.10$) and was significantly correlated with the sum of EPA + DHA. DNA (cov wet weight)

Table 2. *Mysis diluviana*. Pearson Correlation Coefficients (r) between the adjusted means of the nucleic acid and protein indices and key essential fatty acids (EPA, 20:5n-3; DHA, 22:6n-3; ALA, 18:3n-3) and total saturated fatty acids (SAFA) in juveniles and adult females from Lake Ontario in late autumn 2001 and 2003 to 2005. Significant values are **bold**; * $p < 0.1$, ** $p < 0.05$

Life stage	Indices	EPA	DHA	ALA	SAFA	EPA + DHA
Juvenile	RNA (cov DNA)	0.966**	0.012	0.928*	0.995**	0.808
	Protein (cov DNA)	0.920*	0.362	0.787	0.910*	0.957**
	%protein	0.504	0.438	-0.092	0.315	0.653
	DNA (cov weight)	-0.898	-0.408	-0.769	-0.888	-0.963**
Female	RNA (cov DNA)	0.692	0.652	0.729	0.71	0.985**
	Protein (cov DNA)	0.52	0.798	0.676	0.59	0.924*
	%protein	0.652	0.516	0.347	0.449	0.869
	DNA ² (cov weight)	-0.443	-0.848	-0.637	-0.528	-0.886

had a significant negative association with EPA + DHA and strong, negative but not significant, associations with EPA ($r = -0.898$) and SAFA ($r = -0.888$).

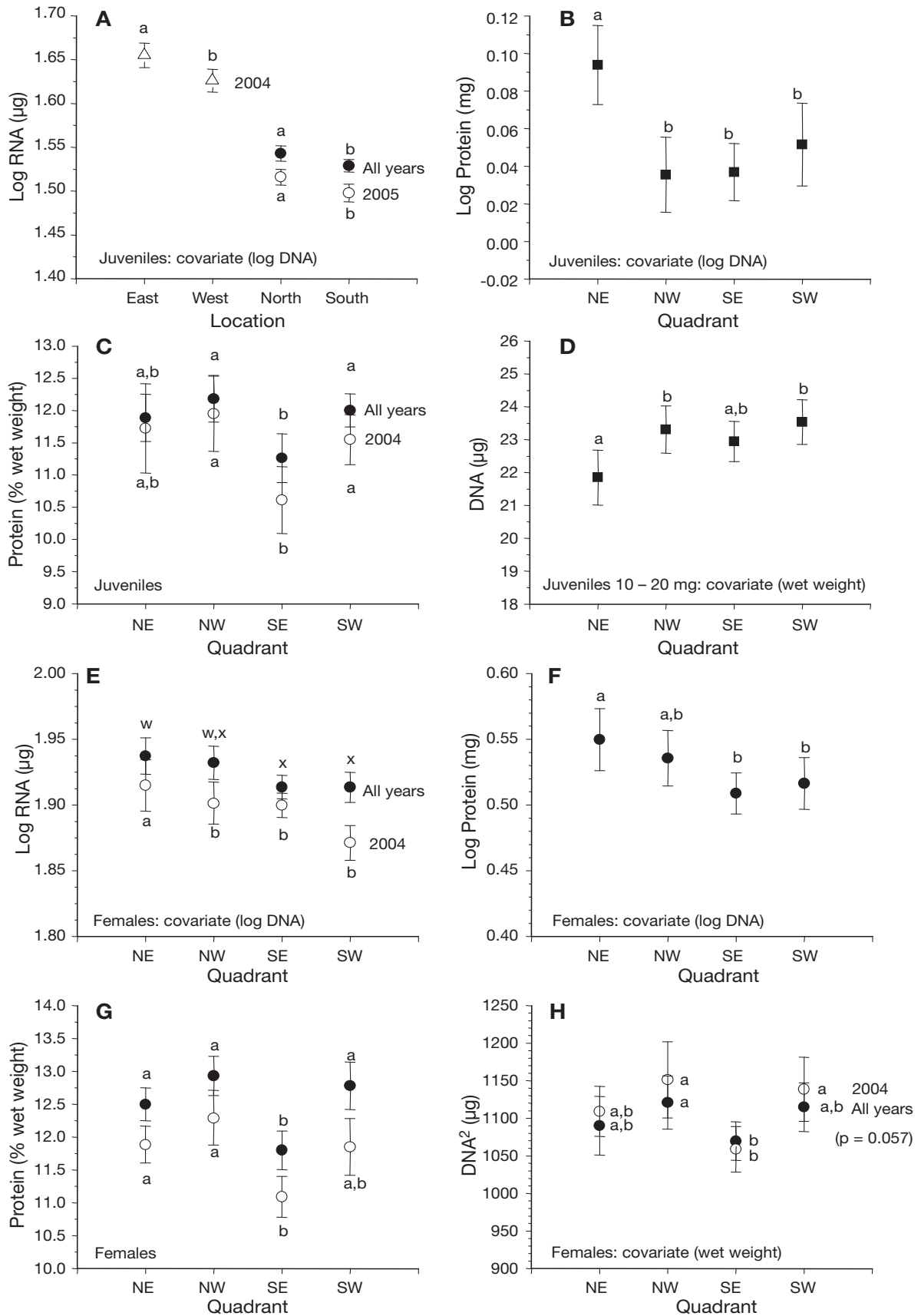
Mysid autumn egg ratios

The adjusted mean number of eggs carried by the same size female, as determined by ANCOVA, declined from a high of 33.0 ± 0.7 in 2003 to 28.7 ± 0.9 in 2004 and 27.7 ± 0.8 in 2005. Tukeys post-hoc comparisons indicated that the decline was significant at each step.

Zooplankton biomass

When total water column biomass was plotted against bottom depth, zooplankton biomass increased sharply to ~ 1.5 g dry wt m^{-2} at stations located beyond the 120 m bottom depth contour (Fig. 6). Of the 7 zooplankton biomass estimates for locations beyond bottom depths of 120 m, 6 were between 1.3 and 2.1 g dry wt m^{-2} while 1 was low at 0.5 g dry wt m^{-2} . No striking inter-annual differences were observed across the 2001 to 2005 time period, suggesting that total zooplankton biomass did not differ greatly amongst these years. A variation on this pattern did occur in 2004: zooplankton biomass at half of the inshore stations (north shore) was high and equivalent to that offshore, a result of strong upwelling events around the lake in October of that year (GLSEA 2007).

Fig. 5. *Mysis diluviana*. Nucleic acid and protein indices (autumn adjusted means ± 2 SE) of juveniles (A–D) and adult female (E–H) individuals from the geographical quadrants of Lake Ontario: NE (northeast), NW (northwest), SE (southeast), and SW (southwest). The significant trends are presented for each nucleic acid and protein index. The effect of geoposition (quadrant) was tested within each year (2003 to 2005) and across all years. The log RNA with the covariate log DNA of juvenile mysids did not show significant differences among quadrants, but did show significant differences between the northern and southern halves of the lake and, in 2004, the eastern and western sides of the lake (A). Significantly different values have been assigned different letters (a, b, w, x)



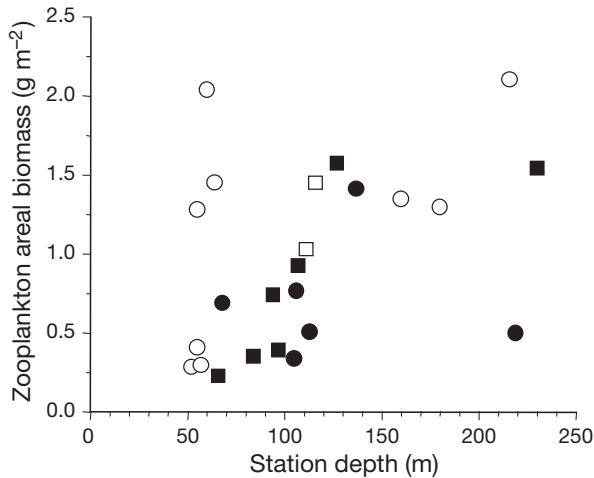


Fig. 6. Zooplankton biomass (g m^{-2}) in the entire water column across the bottom-depth gradient of Lake Ontario; changes in October to early November. Samples were collected with duplicate, vertical net hauls ($153 \mu\text{m}$ mesh) from both northern and southern sites either along the length of the lake (2003 to 2005) or only from the hypolimnion at 2 deep sites (2001). The 2001 data were extrapolated to the entire water column. \square : 2001, \bullet : 2003, \circ : 2004, and \blacksquare : 2005

DISCUSSION

Biochemical growth indices

Nucleic acid and protein measures are good indices for the assessment of *Mysis diluviana* condition in field situations. The Lake Ontario autumn field data demonstrate that RNA (cov DNA), protein (cov DNA) and DNA (cov wet weight) have a sufficient range and sensitivity to reveal a gradient of conditions in metabolic activity. Over the 4 yr of the study, significant differences were detected in these indices among years and among locations in the lake within years. %protein, however, did not show similarly clear differences among years. Only juveniles in the inshore regions in 2004 and adult females in both the inshore and offshore regions in 2004 had a significantly lower protein content than in other years. Data from the laboratory growth experiments by Johannsson et al. (2008) were also lower and similar to our 2004 values. The %protein data from Lake Ontario were variable, likely due to the process of 'growth by moulting', where individuals expand their new exoskeleton with water when they moult and then replace the water with tissue as they grow. %protein showed promise as an indicator in the experimental work by Johannsson et al. (2008), as it increased significantly from 11.3% under low growth rates to 12.8% with higher growth rates. The high variability in %protein observed, which is likely related at least in part to the manner of growth, reduces the potential of %protein to detect finer differences in condition; however, it is still important in detecting or

confirming particularly poor growth conditions. Although not expressly studied, Johannsson et al. (2008) did not observe moult stage-related changes in the other variables.

RNA/protein has also been used as an index of potential growth, but we have not included it in the recommended suite of indicators (Fig. 1). RNA/protein has shown significant relationships with protein synthesis and growth rates (Houlihan et al. 1993, Smith et al. 2000); however, the response is not always observed (Smith et al. 2000) and laboratory studies with *Mysis diluviana* provide further cause for caution in using this index. Mysids fasted for 11 d exhibited no decline in RNA/protein although RNA/DNA and protein/DNA ratios fell during this period (Schlechtriem et al. 2008b), indicating that RNA and protein fell in tandem. Ratios in which both components can fluctuate can be misleading. Similarly, in *M. diluviana* feeding experiments over a range of low growth rates, RNA/protein and specific growth rate showed no correspondence (Johannsson et al. 2008).

Mysid condition was not constant throughout the lake, but could vary between inshore (<120 m bottom depth) and offshore regions and among different quadrants of the lake. Johannsson (1995) observed a movement of mysids from shallower (<100 m bottom-depth) to deeper water as the growing season (May to November) progressed, and proposed 2 hypotheses to explain this pattern: (1) higher size-selective fish predation in the inshore regions may have depressed mysid abundance and selected for smaller-sized individuals, and (2) mysids may have emigrated offshore. Emigration could be a response to predation pressure or a food resource gradient. Similar increases in offshore density and biomass were observed during the 2002 to 2005 study (O. E. Johannsson & K. L. Bowen unpubl. data). The condition indices presented here may shed some light on the second hypothesis. Generally, the nucleic acid and protein indices indicated that mysids were in better condition in the offshore regions. The 2 exceptions involved measures of log RNA (cov log DNA). Temperature differences can alter RNA concentration (Buckley 1982), with RNA increasing linearly as temperature decreased between 12.7 and 4.2°C in *Mysis diluviana* (Johannsson et al. 2008). Low N/P food resources (Acharya et al. 2004) can also induce increases in RNA without concomitant growth. Therefore, differences in RNA must be substantiated by examining trends in the other indicators. The higher RNA levels in inshore females in 2005 are not substantiated by any of the other indices, and likely do not indicate an enhanced condition.

Similarly, in the case of juveniles in 2004, the other condition indices suggest that animals were in better condition in the offshore regions, although higher RNA content was observed in inshore mysids. Upwelling was persistent and circled much of the lake in October 2004, pushing cooler hypolimnetic water into the inshore

areas (GLSEA 2007). Juvenile mysids have a temperature preference of $\sim 12^{\circ}\text{C}$ (B. Boscarino, pers. comm.), which takes them into the metalimnion at night in the summer and into surface waters in the autumn. With cold waters near the surface in the inshore regions in October 2004, juvenile mysids in inshore regions likely experienced lower mean diel temperatures than those in the offshore regions, and correspondingly had higher RNA levels than those offshore. Adults, however, may not have been affected to a significant degree, as they have a lower temperature preference (6 to 8°C) and generally remain deeper in the water column than juveniles (Boscarino et al. 2007). Therefore, they are normally found in cooler waters, inshore and offshore. Overall, the data indicate that mysid condition in the offshore regions is better than inshore in some but not all years. The potential of improved condition, likely through access to better food resources, may provide an incentive for mysids to move offshore. Whether this is sufficient to promote a general pattern of movement offshore in all years is not clear. It may reinforce other pressures which encourage migration. Thus, food resources may play a role in this behaviour, at least in the autumn, and mysids which move offshore have a statistically higher probability of being in better condition. Additional confirmation should now be sought from spring and summer samples.

Overall, across years, juvenile mysids in the northern half of the lake, particularly the NE quadrant, were in better condition, as indicated by all 4 indices, than mysids in the southern part of the lake. It is not clear why the northern side of the lake was more favorable to juvenile mysids in autumn. On the other hand, location within the lake only affected adult females in 2004. These females were in poorer condition in the southern part of the lake, particularly the SE quadrant. Both the juvenile and female nucleic acid data from 2004 were more variable than those from other years. It would appear that 2004 was a difficult year for many mysids, particularly in the southern part of the lake.

Females exhibited strong north–south differences in condition only in 2004; thus, the cause should be unique to that year. 2004 was marked by strong upwelling throughout October. Cold hypolimnetic waters were forced up the northern side of the lake and zooplankton accumulated in these waters, reaching a total biomass similar to that offshore (Fig. 6). In these cold waters, the vertical ascent of larger mysids would have been limited by light (and/or predators) but not by temperature. Therefore, mysids at all bottom depths potentially had access to high levels of zooplankton biomass. At the same time, epilimnetic water would have been pushed to the south, deepening the epilimnion on the southern side of the lake. This may have presented a thermal barrier to larger mysids,

which prefer waters of 6 to 8°C (Boscarino et al. 2007), limiting their vertical migration. Light diminishes with depth and mysid feeding efficiency diminishes with the loss of light (Ramcharan & Sprules 1986). Thus, the feeding potential of adult mysids may have increased in the north and decreased in the south. We cannot dismiss the possibility that upwelling influenced the spatial patterns in mysid condition in 2004.

Thus, distinct spatial patterns in condition indices can occur in *Mysis diluviana* in Lake Ontario between (1) the inshore and offshore, (2) the northern and southern reaches of the lake, and (3) in response to upwelling events. These patterns need to be taken into account in setting the objectives of and design any future monitoring of the lake.

Maturation can affect the nucleic acid ratios (e.g. reviewed in Bulow 1987) and October/November is the dominant reproductive period for mysids in Lake Ontario (Johannsson 1992). Males contained 8% more DNA, or cells, than females of the same size. This value is in the range expected for species where males mate with numerous partners during the reproductive period and, consequently, invest substantial resources in sperm production (e.g. Stockley et al. 1997). However, the RNA content per cell of larger (older?) males declined, as indicated by the low RNA concentrations relative to protein and the lower than expected RNA/DNA ratios. Schlechtriem et al. (2008b) described the decline in RNA/DNA and RNA/protein with fasting in juvenile mysids. Normally, RNA/DNA ratios increase with body size (see also Nordin 2005). RNA/DNA ratios ≤ 2 , as seen in the field data of the present study, were associated with prolonged fasting at the largest body size observed (24 mg) in the study of Schlechtriem et al. (2008b). Two possible explanations exist: either the larger males contain a lot of sperm, which has a low RNA content, or the larger males are senescing after reproduction. Since (1) the higher DNA content of males is consistent across all body sizes, (2) the drop in RNA/DNA is greater than could be accounted for if all of the additional cells were sperm and had little or no RNA, and (3) no decline occurred in mature females, the second hypothesis is supported. The decline in RNA in larger males indicates a marked decrease in cellular activity, growth and protein synthesis; symptoms characteristic of a physiological decline. This conclusion is consistent with the observation of Morgan & Beeton (1978) in Lake Michigan that, after males reproduce, they do not moult again and eventually die off. Therefore, if males were to be included in a monitoring program which involved assessing their physiological condition, their reproductive period, state of maturation and decline would have to be taken into account.

Sample size and distribution are important considerations in designing a monitoring program. We found that

20 to 30 individuals could define the status of a group, as was demonstrated in the geolocation comparisons for each life stage. Thus, the total number of mysids that should be examined in a lake is a function of the number of life stages examined and potential spatial variation within the lake. For Lake Ontario, a minimum of 160, but preferably 200 to 240 individuals, can capture mysid condition and its spatial variability, including 2 life stages within 4 quadrants distributed over the depth range of the mysid distribution. The mysids should also be collected over the whole size range present in order to improve the sensitivity of the ANCOVA.

Comparisons with other mysid nucleic acid studies

How do the field data of the present study correspond with laboratory studies on the response of nucleic acid and protein indices to a range of experimental feeding regimes, including fasting, in *Mysis diluviana*? Schleichriem et al. (2008b) described declines in RNA and protein relative to DNA with fasting in juvenile mysids, the declines increasing with time and temperature. Schleichriem et al. (2008b) gave the relationships between RNA/DNA and protein/DNA ratios with body wet weight for both the day of capture and 11 d fasted animals at 3 and 8°C. Mean diel temperature experience of juvenile mysids in October to early November in Lake Ontario is between 5 and 7°C, depending on the epilimnetic temperature (GLSEA 2007), and time in the upper water column was estimated as 12 h d⁻¹. Ratios in the study by Schleichriem et al. (2008b), recalculated to 6°C, were: 2.34 and 1.95 for RNA/DNA, and 0.079 and 0.066 for protein/DNA in freshly caught and fasted individuals, respectively. In the present study, ratios for individuals weighing between 14.5 and 16.5 mg were averaged for each year in Lake Ontario. Ratios for 2003 were similar to those of the 'freshly caught' mysids (RNA/DNA = 2.28, protein/DNA = 0.083, n = 20), while individuals in 2004 had ratios of 2.06 (RNA/DNA) and 0.069 (protein/DNA) (n = 27): the former index was still significantly higher than that of the fasted mysids, while the latter was not. In 2001, only 5 individuals fell in this size range and the large error term ensured that the index values were not significantly different from fasted or normal animals: 2.11 (RNA/DNA) and 0.07 (protein/DNA). In 2005, the RNA/DNA (2.06) ratio was intermediate and significantly different from both the freshly caught and fasted mysids, while the protein/DNA (0.086) ratio was higher than that of the freshly caught mysids (n = 11). These comparisons confirm the normal condition of mysids in 2003 and the poor condition of mysids in 2004.

Johannsson et al. (2008) examined responses of nucleic acid and protein indices of *Mysis diluviana* fed

Artemia or Cyclop-eeze® (freeze dried copepods) for 3 to 6 wk to changes in temperature and feeding regime. We compared the nucleic acid and protein indices of the study by Johannsson et al. (2008) to those from the present study (Fig. 4A,B). For both females and juveniles, the experimental indices from well-fed animals experiencing mean diel temperatures between 4.2 and 6.7°C were similar to those observed in the present study in 2001 and 2004, with the exception of juvenile log RNA (cov DNA). In the experimental study, RNA had increased at the highest food ration without a concurrent increase in growth rate, and this may explain the discrepancy. Johannsson et al. (2008) observed that experimental *ad libitum* fed mysids had lower than expected growth rates based on field estimates over the April to October period: e.g. 0.41 % d⁻¹ (10 mg juvenile) and 0.15 % d⁻¹ (30 mg young adult) compared to 1.0 to 0.6 % d⁻¹ for 10 and 30 mg mysids in the field. These comparisons suggest that the animals in 2004, and perhaps 2001, of the present study were growing at similarly low rates. This result is in agreement with the comparisons to the fasting experiments above. We do not yet know the growth rates associated with the 2003 and 2005 mysid condition indices; however, the similarity of these indices to those from Lake Huron 2002 suggest that these values are within the normal range.

Given that mysids exhibit distinct patterns in nucleic acid and protein indices over the years, do we see similar patterns in their food supply or food quality? In addition, are there similar patterns in egg production as observed by Saiz et al. (1998) in the copepod *Acartia grani*? Over 90 % of the biomass consumed by mysids in the autumn is composed of zooplankton (Johannsson et al. 2001). No distinct difference occurred in the areal biomass of zooplankton across the years of this study. Percent total lipid of mature, non-gravid females, another index of food quantity, declined from 2003 through 2004 and 2005. Neither food quantity pattern across years fits that of the nucleic acid and protein indices, suggesting that food quantity alone was not responsible for the inter-annual patterns in these indices. Food quality may differ across years in a pattern similar to that observed in nucleic acid and protein indices. Pearson's correlations indicated a number of significant and nearly significant (0.05 < p > 0.1) associations between nucleic acid and protein indices and concentrations of EPA, SAFA and (EPA + DHA).

Schleichriem et al. (2008a) recently showed that DHA is conserved during fasting, which may explain its lack of strong direct associations with nucleic acid and protein indices. Relationships between nucleic acid and protein indices and EFA composition require more study to determine whether these associations hold and which lipid profiles are most correlated with somatic growth. The trends in nucleic acid and protein

indices did not extend to patterns in egg production per female mysid. Egg production was high in 2003 and declined through 2004 and 2005, roughly mirroring the pattern in % total lipids, while nucleic acid and protein indices in mature, non-gravid females were high in 2003 and 2005. More years of data are needed to confirm the relationships between fecundity and total lipids and between nucleic acid and protein indices and EFA, and the lack of correspondence between the 2 groups. However, if they hold, this brings into question inter-annual variation in egg quality.

In conclusion, nucleic acid and protein indices are suitable for monitoring the condition of *Mysis diluviana* in the field. They express a sufficient range and sensitivity to detect differences among years and different habitats within Lake Ontario. Years with *M. diluviana* in 'poor condition' had nucleic acid and protein indices similar to laboratory values of animals with low growth rates, values which were slightly above the indicators of fasting but below 'normal' values found in the lake. The normal values were similar to those in years with putative 'good condition'. Inshore mysids tended to be in poorer condition than offshore mysids in 2 of the 3 yr for which we have sufficient data. This supports the hypothesis that improved food resources may be partly involved in the movement of mysids offshore. Neither total zooplankton areal biomass and % total lipids in mature, non-gravid females (2 measures of food quantity), nor number of eggs per female were related to nucleic acid and protein-based indices of mysid condition; however, key EFA and SAFA had interesting associations which suggest the importance of food quality and the need for further study.

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Importance of light, temperature, zooplankton and fish in predicting the nighttime vertical distribution of *Mysis diluviana*

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ABSTRACT: The opossum shrimp *Mysis diluviana* (formerly *M. relicta*) performs large amplitude diel vertical migrations in Lake Ontario and its nighttime distribution is influenced by temperature, light and the distribution of its predators and prey. At one location in southeastern Lake Ontario, we measured the vertical distribution of mysids, mysid predators (i.e. planktivorous fishes) and mysid prey (i.e. zooplankton), in addition to light and temperature, on 8 occasions from May to September, 2004 and 2005. We use these data to test 3 different predictive models of mysid habitat selection, based on: (1) laboratory-derived responses of mysids to different light and temperature gradients in the absence of predator or prey cues; (2) growth rate of mysids, as estimated with a mysid bioenergetics model, given known prey densities and temperatures at different depths in the water column; (3) ratio of growth rates (g) and mortality risk (μ) associated with the distribution of predatory fishes. The model based on light and temperature preferences was a better predictor of mysid vertical distribution than the models based on growth rate and $g:\mu$ on all 8 occasions. Although mysid temperature and light preferences probably evolved as mechanisms to reduce predation while increasing foraging intake, the response to temperature and light alone predicts mysid vertical distribution across seasons in Lake Ontario.

KEY WORDS: *Mysis relicta* · Modeling · Migration · Zooplankton · Vertical distribution · DVM

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INTRODUCTION

Diel vertical migration (DVM) of invertebrates is a widespread phenomenon in both freshwater and marine systems, and probably evolved as a mechanism for maximizing food intake in upper, food-rich waters during periods of low risk from visual predators (Gliwicz & Pijanowska 1988, Lampert 1993, Hays 2003). Most vertical movement into warmer, more productive waters to feed therefore occurs between dusk and dawn, when light levels are too low for efficient visual predation by planktivores. The vertical distribution of a migrating population at night is therefore either directly or indirectly influenced by the organisms' abiotic (i.e. light and temperature) and biotic (i.e. predator and prey distribution) environment.

The opossum shrimp *Mysis diluviana* (formerly *M. relicta*; Audzijonyte & Väinölä 2005—hereafter referred to as 'mysids' unless otherwise noted), undergoes DVM in most of the deep lakes where it occurs, including Lake Ontario, one of the Laurentian Great Lakes of North America (Beeton & Bowers 1982). In Lake Ontario, mysids ascend from their daytime benthic habitat into the water column at dusk, when they are both prey and competitors of planktivorous fishes such as alewife *Alosa pseudoharengus* and rainbow smelt *Osmerus mordax* (Johannsson et al. 2003).

The factors shaping the nighttime distribution of mysids are still poorly understood. Laboratory-derived temperature (Boscarino et al. 2007) and light preference (Boscarino et al. 2009) functions have been used to predict mysid vertical distributions when either tem-

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perature or light was the dominant environmental factor. However, little is known about how the relative influence of temperature or light on mysid distribution will vary across different seasons. Moreover, it is unclear as to how fish and zooplankton distributions modify the temperature and light preferences of mysids, because the preference functions derived by Boscarino et al. (2007, 2009) were developed in the laboratory in the absence of predators and prey.

In Lake Ontario, the zooplankton prey of mysids is concentrated in the upper portion of the water column (Gal et al. 2006) and their distribution may influence the nighttime habitat selection of mysids. Larsson (1997) demonstrated that a population of *Daphnia pulex* was distributed throughout different sections of an experimental chamber in direct proportion to the relative abundance of algal food resources, and argued that the distribution approximated an ideal free distribution (Fretwell & Lucas 1969). Lampert et al. (2003) expanded this approach by predicting the distribution of a population of *Daphnia hyalina* × *galeata* in combined food and temperature gradients in large plankton towers based on growth rates at each depth in the column (ideal free distribution with costs model; Lampert et al. 2003). In the present study, we use a modified version of Lampert et al.'s (2003) model to predict mysid vertical distribution based on estimated growth rates of mysids at each depth as a function of both food availability and temperature.

In addition to growth rate, mortality risk is commonly invoked in models of vertical migration. The distribution of alewives, the most abundant fish in Lake Ontario (Owens et al. 2003), changes seasonally (Mills et al. 1992, Rand et al. 1994) and could also influence mysid nighttime distribution, particularly because alewives feed at night (Janssen & Brandt 1980) and are able to feed in total darkness (Janssen 1990, Janssen et al. 1995). Mysids may respond to predation risk by avoiding waters inhabited by alewives, because they sense fish kairomones (Hamrén & Hansson 1999, Gal et al. 2004, Boscarino et al. 2007).

The potential effect of both predator and prey distributions can be combined by calculating the ratio of gain (typically estimated by either gains in growth, g , or in foraging, f ; e.g. Werner & Gilliam 1984) to mortality risk (μ). Ratios between gain and risk have been used to predict both the timing and amplitude of migration in a variety of fish (Scheuerell & Schindler 2003, Jensen et al. 2006) and invertebrate species (Fiksen 1997, Liu et al. 2003). These models assume that an organism will always choose a depth that minimizes the ratio between growth gains and perceived mortality risks. In order to predict entire distributions based on this ratio, one needs to either (1) have prior knowledge of an organism's preference for different combinations of $g:\mu$,

or (2) assume that a population is distributed in direct proportion to its $g:\mu$ profile and test this assumption empirically. Given the absence of laboratory-derived data on the preference of mysids to different $g:\mu$ ratios, we compared predictions based on the magnitude of difference between risk and gain at each depth to observed distributions of mysids in the field.

We tested 3 different models of the nighttime vertical distribution of mysids, based on: (1) laboratory-derived light and temperature preferences (e.g. Gal et al. 2004, Boscarino et al. 2007, 2009), (2) mysid growth rate (e.g. Lampert et al. 2003), and (3) ratio between growth rate and mortality risk. We elected not to test a model based on mortality risk alone, since alewife densities drop markedly beneath the thermocline in the offshore part of Lake Ontario (Gal et al. 2004), and this would ensure minimization of predation pressure at the deepest depth evaluated if foraging gains in shallower waters were not considered. We have already shown that this is an unrealistic prediction for mysids in Lake Ontario (Gal et al. 2004, 2006). The objective of this study is to test whether mysid distribution can be predicted based on adult light and temperature preferences alone, or whether predator and prey distributions must be invoked to predict their distribution. We compare predictions made by all 3 models to observed mysid vertical distributions measured on 8 nights in southeastern Lake Ontario in 2004–2005.

MATERIALS AND METHODS

Sampling design. We conducted 8 research cruises on Lake Ontario on May 19, August 16, August 27, and September 30 in 2004 and May 5, June 20, July 7 and September 27 in 2005 aboard the United States Geological Survey's RV 'Kaho' (we refer to these sampling nights by the date on which we left the harbor, even though we did not return until the following morning at dawn). Sampling dates were selected to measure the nighttime distribution of mysids under 'high' and 'low' light intensities (full moon or new moon) in each of 3 seasons (spring, summer, fall). During most cruises we (1) used acoustics data with at least 1 or some combination of 3 different frequencies (70, 123 and 430 kHz) to determine the vertical distribution of mysids and fishes (Table 1); (2) deployed plankton, mid-water trawl, and gill nets to identify acoustic targets and capture fishes for diet analysis; (3) collected zooplankton at discrete depths to determine zooplankton vertical distribution; and (4) collected depth profiles of light and temperature with a combination of a SeaBird instrument and a high-sensitivity light meter. All night sampling was conducted at or near a 170 m depth station located 11.1 km NNW of Oswego, New York (Table 1).

Table 1. Sampling times, dates, acoustics equipment and calibration settings used in analysis. Detection limits for mysids with 430 kHz and 123 kHz represent the depth at which background noise is equal to a density of 5 mysids m^{-3} . Detection limits for fish at 70 kHz and 123 kHz represent the depth at which background noise is equal to the backscattering produced by a single alewife with an average target strength of -54 dB. Noise: volume backscattering strength (S_v) at 1 m depth

Year	Date	Time of day	Bottom depth (m)	Frequency (kHz)	Noise at 1 m (dB)	Detection limit (m)	
						Mysids	Fishes
2004	19 May	3:37–3:55	120–170	430, 70	$-116.7^a, -119.0^b$	58	93
	16 Aug	2:44–4:00	116–170	430, 70	$-117.2^a, -125.0^b$	68	133
	27 Aug	1:29–2:52	110–170	430, 70	$-116.4^a, -124.5^b$	64	127
	30 Sep	0:44–1:39	150–170	430, 70	$-117.0^a, -115.2^b$	67	75
2005	5 May	3:14–3:39	116–170	430, 70	$-116.9^a, -113.0^b$	67	66
	20 June	22:18–23:41	165–170	123	-134.7^c	Bottom	Bottom
	7 July	22:00–23:45	165–170	123	-135.9^c	Bottom	Bottom
	27 Sep	12:00–3:12	165–170	123	-131.0^c	Bottom	165

^a430 kHz; ^b70 kHz; ^c123 kHz

Temperature and light profiles. Temperature data were collected at 1 m intervals with a SeaBird profiler lowered to the bottom. In 2004, light extinction was obtained with a PAR light meter that integrated the total light available between 400 and 700 nm (PAR range). We measured light extinction during the day, because our SeaBird was not sensitive enough to measure light at night. For each sampling date, we calculated the average extinction coefficient values ($k_{\text{PAR}}, \text{m}^{-1}$) at 20 m intervals and used the relationships in Jerome et al. (1983) to calculate wavelength-specific extinction coefficients for each 20 m depth interval of the water column (see Gal et al. 1999, 2004). These extinction coefficients were then combined with the calculated nighttime surface irradiance (see below), to derive wavelength-specific irradiance values at 1 m depth intervals in the water column at night. These calculations assumed a moonlight spectrum at the surface (see Gal et al. 1999). Following Gal et al. (1999, 2004) and Boscarino et al. (2007), we calculated light at depth in ‘mylux’ by applying the normalized mysid visual sensitivity curve (ranging from 0 to 1 after Gal et al. 1999) to the estimated total amount of light available at each depth and wavelength (Gal et al. 1999). The concept of mylux units is similar to the concept behind lux in that it is a scale adjusted to an organism’s relative spectral sensitivity. Mysid visual pigments retain the same absorbance characteristics regardless of season or developmental stage (Lindström & Nilsson 1988), so we assumed that all mysids had identical spectral sensitivities.

Surface irradiance in lux was predicted with the moonlight illuminance modeling program of Janiczek & DeYoung (1987) for all full moon nights. The Janiczek & DeYoung model is not capable of predicting light levels at new moon, and we therefore used values reported by Austin et al. (1976) for new moon nights and times when the moon was below the horizon. These 2 studies yield illuminance values within a factor of 2 of each other

when moon phase and zenith angles are the same (B. T. Boscarino, unpubl.). All predicted surface values, in lux, can be converted to mylux using the conversions of Gal et al. (1999), which are valid for a moonlight spectrum: $1 \text{ mylux} = 175 \text{ lux} = 0.51 \text{ W m}^{-2}$.

In 2005, we collected light data using a specially designed light meter (mk9 archival tag, Wildlife Computers), which we equipped with a Rosco® Roscolux® filter # 91 (peak transmission between 510 and 520 nm) that closely resembles the spectral sensitivity of the mysid eye (wavelength of maximum absorbance, $\lambda_{\text{max}} = 520 \text{ nm}$; Gal et al. 1999). Differences in λ_{max} between the filter and the mysid eye pigment were reconciled by applying a correction factor to measurements obtained with the mk9 tag, which thus measured light in units directly proportional to mylux (see Boscarino et al. 2009).

The mk9 tag was calibrated to a Gamma Scientific light source, which has an accuracy of $\pm 2\%$ of the international light calibration transfer standards ($\pm 2\%$ for NIST transfer). This tag is capable of storing light levels in millisecond intervals, and this allowed us to measure light at 1 m depth intervals throughout the water column.

Because we did not have the mk9 tag in 2004, we compared light level estimations using both techniques in 2005 to check for any inconsistencies between the 2 methods. Differences were less than a factor of 5, even as far as 50 m below the surface. These discrepancies would result in a maximum change of 5 m in the predicted peak mysid distribution on June 20, 2005 (differences on all other dates were $< 2 \text{ m}$). Although we consider the mk9-derived light profiles to be a better representation of the light perceived by mysids, we did not adjust the 2004 light profiles, because there were no consistent directional differences between the 2 methods in the 2005 surveys.

Hydroacoustic data. Mysid distributions: Mysid vertical distributions were measured by hydroacoustics at

night along a transect from the 170 m station to a bottom depth no less than 110 m (2004) or while stationary at the 170 m station (2005) (Table 1). Ship lights were minimized during data collection; 2 transducers were mounted on a tow body positioned 5 m away from the starboard side of the boat and towed with the transducer face at a depth of 1.5 m. The tow body was balanced to remain horizontal when the ship was stationary. We used a 70 kHz unit (11.4° beam width; Simrad EY500 split beam) and a 430 kHz unit (6° beam width; Biosonics DtX single beam) in 2004. In 2005, the 70 kHz unit was replaced by a 123 kHz unit (7.8° beam width; Biosonics DtX split beam). We initially expected to use the 430 kHz data for mysids following Gal et al. (2004) and the lower frequency (70 or 123 kHz) for fishes. Rudstam et al. (2008a) showed that mysid target strength (TS) is about 5 dB higher at 430 kHz than at 123 kHz. However, the higher TS of a mysid at 430 kHz does not compensate for the increased sound absorption at the higher frequencies, and frequencies between 120 and 200 kHz are better for detecting mysids in deep water than 430 kHz (Rudstam et al. 2008a). All data analysis was done with EchoView 3.4.

The 430 kHz single beam unit was calibrated by the manufacturer on April 4, 2004, May 25, 2005 and February 20, 2007; source levels ranged from 218.55 to 218.18 dB and no additional corrections were applied to the 430 kHz data. The 123 kHz unit was calibrated by the manufacturer in May 2005, and was within 0.1 dB of the previous calibration in October 2005 using a -40.4 dB standard copper sphere. The 70 kHz unit was calibrated before each survey with a standard -39.2 dB copper sphere and adjusted as necessary. Calibration varied less than ± 1 dB on this unit during 2004 and 2005. All acoustics data were collected at a pulse duration of 0.6 ms and a ping rate of 1 ping s^{-1} . Biosonics data (123 and 430 kHz) were collected with a square threshold of -130 dB; no lower threshold was applied to the 70 kHz data.

Hereafter, we refer to any acoustic scattering layer as the 'mysid layer' if the layer (1) was not apparent before sunset, (2) stabilized within a distinct depth range within 1 to 2 h after sunset, and (3) was no longer observed at depths <50 m in the water column at dawn; these observations are consistent and unique to mysids in Lake Ontario (Johannsson et al. 2003). Net samples (conical opening and closing net, 1 m diameter, mesh size: 1 mm) were obtained at the 170 m station on each night to confirm that this scattering layer was primarily composed of mysids. Replicate tows were made 'above', 'through', and 'below' the mysid layer after visual inspection of acoustic echograms. All sampling was done under minimal red light. Mysids were preserved in 95% alcohol in the field and later enumerated and measured in the laboratory.

Lengths were converted to biomass using a length to dry weight regression originally derived by Johannsson et al. (1995) and modified by Rudstam et al. (2008b):

$$\ln DW = -12.55 + 2.72 \ln L \quad (1)$$

where DW is dry wt in g, and L is length from the tip of the rostrum to the cleft of the telson in mm. Biomass values were converted to wet weight (WW; Morgan 1976), as the bioenergetics applications used in this study are based on mysid WW (Rudstam 1989; see present study, 'Materials and methods—Models—Growth (*g*) model'). Total mysid abundance (ind. m^{-2}) was estimated by dividing the total number of mysids caught in a net haul by the area of the net opening. Mysid net tows were not taken on August 16, 2004, due to time constraints.

Fish echoes were defined as data pixels with echo returns > -60 dB in the uncompensated TS domain of the 70 or 123 kHz data and the corresponding pixels were replaced by 'no data' tags in the 430 or 123 kHz dataset. We used this threshold for all surveys based on inspection of echograms. We removed ambient noise by subtraction of the expected noise level at each depth calculated from the noise levels at 1 m (Korneliusson 2000). The depth limit for detection of a density of 5 mysids m^{-3} was calculated using a TS of a single mysid of -80.1 dB at 430 kHz and -84.9 dB at 123 kHz (12 mm mysid; Rudstam et al. 2008a), sound absorption, and measured noise level (Table 1). Acoustic data from the mysid layer was exported at 1 m intervals after removing noise and contributions from fishes. Sound scattering from above the mysid layer was excluded, as that depth layer includes backscattering from other zooplankton and from larval fishes that would not have been removed by the fish exclusion threshold chosen here. The method is described in detail in Rudstam et al. (2008b).

Fish densities: These were obtained for the same transects and time periods as the mysid densities with the 70 or 123 kHz data. We first applied a data threshold in the uncompensated TS data of -60 dB and converted this filtered dataset to volume backscattering strength (S_v). This will exclude most mysid backscattering (see above) and include most backscattering from fishes with a TS > -54 dB (see Rudstam et al. 2008b). Fish density at depth was calculated by scaling the volume backscattering coefficient (s_v) with the *in situ* backscattering cross section σ_{bs} , calculated separately for the epilimnion and meta/hypolimnion (the mysid layer) for targets > -54 dB. Fish density was calculated for each 2 m depth interval from 2 m below the transducer (depth of 3.5 m in most surveys and 2.5 m in June 2005) to 2 m above the bottom of the lake. Total fish abundance in ind. ha^{-1} was calculated for depths

from 3 or 4 m to 60 m. We summed all estimates down to 60 m so that we could make direct density comparisons between sampling dates that may have had different detection limits. The depth of maximum mysid density was shallower than 60 m on all sampling dates.

Fish species identification was verified based on either mid-water trawls or gillnetting conducted at each station, with the exception of May 19, 2004 (nets not available) and July 7, 2005 (when emphasis was on mysid TS estimations). Each gillnet set consisted of a series of 7 separate 3 m wide by 20 m deep nets, each tied together by a 15 m rope. Each net had a different mesh size (6.25, 8, 10, 12.5, 15, 18.5 and 25 mm bar mesh). This range of mesh sizes catches alewife from 50 to 250 mm total length with similar efficiencies (Warner et al. 2002). Each gillnet set was allowed to drift several hundreds of meters away from the boat for at least 5 h. Gillnets were suspended between 15 and 35 m in the water column. Decisions on the depth of the set were made prior to each sampling night and were based on the likely depth ranges associated with the upper edge and peak of the main mysid scattering layer. The fishes were identified to species, their depth in the net was noted, and total length was measured to the nearest mm. We also determined presence/absence of mysids in the gut contents of all fishes caught. The number of fishes caught per hour of gillnet set was also recorded, to compare catch per hour across dates in which gillnets were used. Gillnet and trawl catches (see below) were not used to derive overall abundance estimates.

Mid-water trawling was conducted on June 20, 2005, and September 27, 2005. Trawls were conducted through the mysid layer, as determined by visual inspection of echograms. Trawls through the mysid layer were between 23 and 51 m depth on June 20, 2005, and between 22 and 60 m depth on September 27, 2005. Fishes caught in each trawl haul were identified to species, enumerated, measured (nearest mm total length), and evaluated for presence/absence of mysids in the gut. The number of alewives caught per hour trawled was also recorded to compare abundance between the 2 dates in which mid-water trawling was used.

Zooplankton distribution. Samples were obtained at the 170 m station with a submersible pump (Dayton® submersible sump pump) for all dates in 2004 and on the May, June and October 2005 cruises. We did not take zooplankton pump samples during the July 2005 sampling trip, due to time constraints, and instead relied on 2 replicate stratified net tows for every 10 m depth interval down to a depth of 50 m. Pump samples on all other nights were taken at 2 m intervals from the surface down to 30 m (the length of our hose) and at 4 m intervals on the way back to the surface; 100 l of water were strained through a 64 µm mesh net for each

depth interval and samples were immediately preserved in 95 % ethanol.

Stratified net tows (0.5 m diameter opening/closing, 64 µm mesh nylon net) through the 30 to 40 m and 40 to 50 m depth strata were also collected in 2005 to assess zooplankton community structure at depths >30 m. These net tows were not taken in 2004 and we assumed the density of zooplankton in the deepest depth sampled (30 m) was representative of depths down to 50 m (see 'Discussion'). Because pump and net sampling may have different sampling efficiencies for size groups and species (Johannsson et al. 1992, Masson et al. 2004), we performed net tows through the top 22 m of the water column on September 27, 2005 to compare the species composition and absolute density estimates obtained by the 2 gears.

All zooplankton were categorized into 9 major groups: daphnids, nauplii, *Cercopagis pengoi*, *Bythotrephes longimanus*, cyclopoid copepods, calanoid copepods, bosminids, *Holopedium gibberum* and *Limnocalanus macrurus*. We counted and measured at random 100 or more organisms from each sample using a compound microscope at 10 to 40× magnification. *C. pengoi* and *B. longimanus* were sieved out separately from smaller zooplankton and the entire sample was counted, given these larger organisms' propensity for clumping together and biasing subsamples. We used length:dry weight (L:DW) regression equations previously used for Lake Ontario zooplankton (see Benoit et al. 2002) to estimate total zooplankton biomass and the biomass of each group for each depth interval. This procedure follows the standard methods used by the Lake Ontario biomonitoring program (e.g. Warner et al. 2006). Biomass was averaged down to 30 m to arrive at a mean zooplankton biomass estimate for each night.

Models. Temperature-light model (TLM): We used the model of Boscarino et al. (2009) to predict the vertical distribution of mysids on each of the 8 nights. This model uses laboratory-based light and temperature preferences, derived in the absence of predator or prey cues, to yield an index of habitat preference for each 1 m depth interval given ambient temperature (°C) and light levels (mylux) by depth. The 2 preference curves are assumed to be independent and have equal weight—assumptions based on experiments by Boscarino et al. (2009). The probability of finding a mysid at depth z [$P_{\text{TLM}}(z)$] and the distribution of mysids in the water column can be described by:

$$P_{\text{TLM}}(z) = \frac{h(L_z) \times f(T_z)}{\sum_{z=1}^{z_{\text{max}}} h(L_z) \times f(T_z)} \quad (2)$$

where $f(T_z)$ and $h(L_z)$ represent the value of the temperature and light functions at depth z , respectively, and z_{max} is the maximum depth included in the analy-

sis. The denominator is the sum of this product over all depths considered. The light preference function $h(L)$ and the temperature preference function, $f(T)$, are defined in Boscarino et al. (2007, 2009) and reproduced here:

$$h(L) = 0.10 \text{ for } L \leq 10^{-10} \text{ and} \quad (3)$$

$$h(L) = e^{-0.5 \left\{ \frac{\log_{10}(L) - [-7.53]}{0.76} \right\}^2} \text{ for } L > 10^{-10}$$

$$f(T) = e^{-0.5 \left\{ \frac{\ln(T) - [\ln(6.07)]}{0.23} \right\}^2} \quad (4)$$

Direct comparisons were made between differences in predicted versus observed depth of peak mysid density, whereas the percent overlap between predicted and observed mysid distributions was assessed by the Czekanowski index of overlap: $|1 - (0.5 \times \Sigma(\text{observed} - \text{predicted})| \times 100$ (Feinsinger et al. 1981). A perfect fit of predicted to observed distributions would therefore result in an index of 100%.

Growth (g) model: The second model is based on calculating the estimated growth rate of an individual mysid at each depth of the water column and assumes that mysids are distributed in proportion to their depth-specific growth rates (e.g. Lampert et al. 2003). Growth rate was estimated as the difference between energy intake and physiological costs. Energy intake is based on a functional response model (Cooper & Goldman 1980) modified by temperature (Rudstam et al. 1999). Physiological costs were calculated for a mysid with a length of 12 mm and are temperature dependent following a bioenergetics model for mysid growth and consumption by Rudstam (1989), which was independently validated for *Mysis relicta* by Chipps & Bennett (2002).

Depth-specific consumption was estimated by applying the Type I functional response curve published in Cooper & Goldman (1980, their Fig. 2) for *Mysis relicta* feeding on *Epischura nevadensis* in the laboratory. Applying a Type I functional response curve to our field data is reasonable, given the low to medium zooplankton densities observed in this study and others (e.g. Johannsson et al. 1994). Prey densities reported in Cooper & Goldman (1980) were converted into dry weight (DW) to derive a functional response equation relating prey biomass to the total zooplankton biomass consumed per day (C). The regression was forced through the origin, so that feeding rate would be zero if no prey were available. This relationship is expressed as follows:

$$C = 2 \times 10^{-5} \times (\text{prey biomass}); r^2 = 0.99, n = 5 \quad (5)$$

where C is consumed biomass (g zooplankton DW) per (g mysid WW) d^{-1} , and prey biomass is zooplankton DW (in $\mu g l^{-1}$). This consumption relationship was evaluated for all measured prey densities and temperatures from the surface down to 50 m at 1 m intervals on each of the 8 nights sampled. Because ingestion

and gut evacuation rates vary with temperature, we applied a temperature-specific multiplier (based on the feeding rates of mysids on *Artemia* spp. at different temperatures; Rudstam et al. 1999, Gal et al. 2004) to account for variations in food intake rate with temperature. The peak of this feeding curve occurs at 9°C, representing a temperature-specific multiplier of 1. The multiplier at other temperatures ranged from 0 to 1 following the curve of Gal et al. (2004). Thus, total consumption at any depth was calculated as the functional response (dependent on prey abundance) and this multiplier (dependent on temperature). Although feeding rate may decrease in the presence of conspecifics (Hansson et al. 2001), we did not include this effect in the model. Caloric intake was calculated from zooplankton biomass consumed using a value of 5411 cal per g DW (Johannsson et al. 1994).

Each depth-specific growth value was then used to construct a vertical growth profile from the surface down to 50 m on each of the sampling nights. The probability of observing a mysid at any given depth z , [$P_g(z)$], is described by the following equation:

$$P_g(z) = \frac{g(z)}{\sum_{z=1}^{z_{\max}} g(z)} \quad (6)$$

where $g(z)$ represents the value of the growth function at depth z , and z_{\max} is the maximum depth included in the analysis. Direct comparisons were made between differences in predicted versus observed depths of peak mysid density and the percent overlap between predicted and observed mysid distributions was assessed by the Czekanowski index.

Growth:mortality risk ($g:\mu$) model: We modeled the vertical change in the ratio of estimated growth rate of mysids to the perceived mortality risk—hereafter referred to as the ' $g:\mu$ model'—with respect to temperature, predator abundance and prey biomass at 1 m depth increments in the water column for each of the 8 sampling nights. Mortality risk is modeled as fish abundance multiplied by a light dependent function relating the proportion of fishes that are feeding to ambient light levels.

Because no data currently exist on alewife reaction distance at the low light levels experienced by fishes that are feeding in the mysid layer at night, mortality risk was estimated by deriving a best-fit linear equation through data for a related clupeid (herring *Clupea harengus*) in Batty et al. (1990, their Fig. 2A); the figure describes the relationship between light levels (0 to 270 lux) and the proportion of herring feeding on zooplankton in the laboratory. We converted all lux values presented by Batty et al. (1990) to mylux using the conversions of Gal et al. (1999) and log-transformed all light levels to linearize the relationship. A third-order

polynomial curve was fitted to the data describing the proportion of fishes that are feeding as a function of log-transformed light values, between $10^{-1.24}$ to $10^{-5.24}$ mylux, such that the sums of squares of differences between observed and predicted proportions of fishes that are feeding were minimized (third-order polynomial regression; Microsoft Excel Version 12.0; adjusted $r^2 = 0.72$, $n = 31$). For all light levels at least one order of magnitude lower than the visual threshold of 10^{-3} lux, (or $10^{-5.24}$ mylux), the function was set to 0.1, which represents the proportion of fishes that are feeding in complete darkness. The equation for this light-dependent multiplier, $n(L)$, evaluated at all light levels $L < 0.058$ mylux [$\log(L) < -1.24$] is:

$$n(L) = -0.009(\log L)^3 - 0.0979(\log L)^2 - 0.1777(\log L) + 0.6181$$

$$\text{for } -6.24 < \log L < -1.24. \tag{7}$$

$$n(L) = 0.10 \text{ for } \log L \leq -6.24$$

We assumed mortality risk μ to be proportional to the density of fishes (ρ , in ind. m^{-3}) multiplied by the proportion of fishes that are feeding at light level L [$n(L)$], such that:

$$\mu(\rho, L) = \rho n(L) \tag{8}$$

Growth:mortality risk ratios were then constructed by dividing the value of the growth function g , by the value of the risk function μ , evaluated for each depth z in 1 m depth intervals. Therefore, the probability of finding a mysid at any depth z [$P_{g:\mu}(z)$], given all available depths (1, z_{max}) equals:

$$P_{g:\mu}(z) = \frac{g(z)}{\sum_{z=1}^{z_{max}} \mu(z)} \tag{9}$$

Comparisons with observations were done in the same manner as the other 2 models.

RESULTS

Light and temperature conditions

Average k_{PAR} in the top 20 m of the water column varied seasonally with the highest k_{PAR} values found in the summer and the lowest values in the fall and spring. Surface irradiance was about 2 orders of magnitude higher on full moon compared to new moon nights (Table 2).

Thermal conditions ranged from isothermal at 3.5°C in May 2004 and 2005 to a strongly stratified water column during the summer of 2004 and 2005. The depth of the thermocline (defined as the depth at which the rate of temperature change with increasing depth is maximized) ranged from 7 m in June, 2005 to 27 m in September, 2005 (Table 2).

Mysid vertical distribution, length and abundance

Mysid vertical distribution varied with moon phase. Mysids were consistently found deeper in the water column on full moon versus new moon nights, when temperature conditions were similar, i.e. when surface temperature was within 2°C and thermocline depth was within 5 m (Fig. 1, Table 2). Light levels at the peak of the mysid distribution were also consistently higher on full moon versus new moon nights, when temperature conditions were similar. We never found more than 10% of the population above 1×10^{-7} mylux in any season.

Temperatures associated with the peak of the mysid layer during stratified conditions varied from 4.1°C in September 2004 to 6.4°C on August 16, 2004 (Table 2). Temperatures at the peak of the mysid distribution were significantly higher on new moon versus full moon nights during periods of thermal stratification (2-tailed t -test, $t = 2.95$, $p = 0.04$, $n_{new} = 3$, $n_{full} = 3$).

Table 2. Light, temperature and depth representing the shallowest 10 and 90% of the mysid population as well as the peak of the mysid distribution. The thermocline depth is defined as the depth at which temperature change is fastest. Depth range of mysid layer: difference between the depth of the shallowest 10 and 90% of the mysid distribution; k_{PAR} : 0 to 20 m

Year	Date	Moon phase	Mysid layer depth (m)				Light (mylux)					Temperature ($^\circ\text{C}$)			Thermocline depth (m)
			10%	Peak	90%	Range	Surface	10%	Peak	90%	k_{PAR}	Surface	10%	Peak	
2004	19 May	New	25	45	-	-	5×10^{-6}	1×10^{-7}	9×10^{-9}	-	0.21	3.8	3.5	3.5	-
	16 Aug	New	25	30	46	21	5×10^{-6}	1×10^{-8}	6×10^{-9}	1×10^{-9}	0.32	21.0	9.3	6.4	21
	27 Aug	Full	30	36	53	23	1×10^{-4}	4×10^{-7}	2×10^{-7}	2×10^{-8}	0.24	21.5	5.6	4.5	19
	30 Sep	Full	45	58	-	-	5×10^{-4}	2×10^{-7}	2×10^{-8}	-	0.13	17.4	4.1	4.1	15
2005	5 May	New	26	46	53	27	5×10^{-6}	2×10^{-7}	3×10^{-8}	1×10^{-8}	0.16	3.6	3.5	3.5	-
	20 Jun	Full	24	29	36	12	2×10^{-4}	2×10^{-7}	8×10^{-8}	3×10^{-8}	0.21	18.5	6.2	5.0	7
	7 Jul	New	21	24	30	9	5×10^{-6}	4×10^{-8}	2×10^{-8}	8×10^{-9}	0.23	21.7	6.9	5.5	19
	27 Sep	New	29	35	47	18	5×10^{-6}	2×10^{-8}	9×10^{-9}	1×10^{-9}	0.13	20.0	10.2	5.4	27

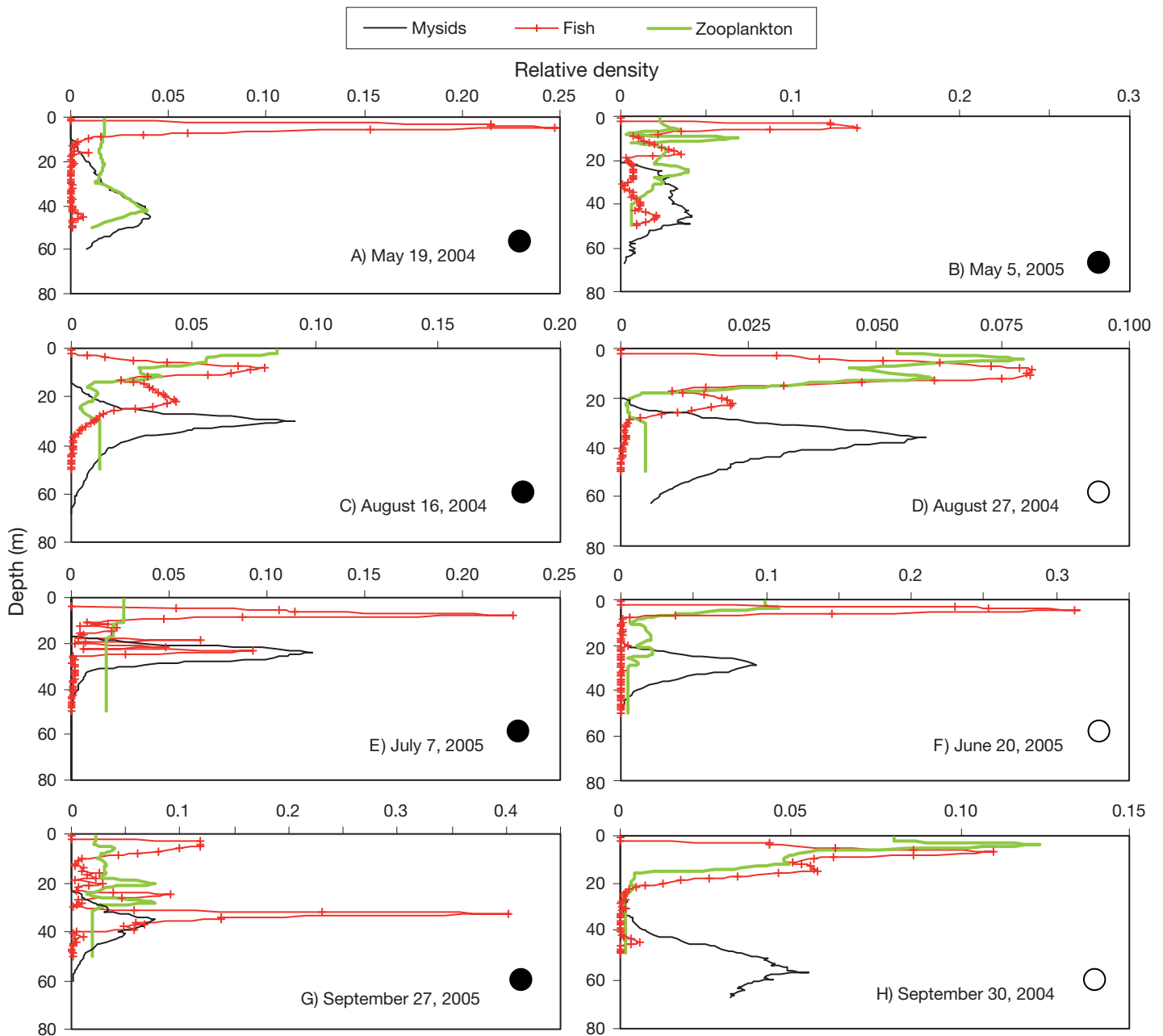


Fig. 1. Vertical distribution of mysids, zooplankton and fishes on 8 sampling nights on Lake Ontario. (●) New moon; (○) full moon. Total density for each profile equals 1. Note the different x-axis scales

The peak of the mysid layer was significantly deeper during spring, when the lake was isothermal (May 2004, 2005), than during early summer (June and July 2005), when a shallow thermocline was present ($t = 7.45$, $p = 0.02$). This was independent of moon phase. Furthermore, mysids were spread over a significantly larger range of depths during spring (mean depth range = 33 m, $SE = 5.0$) than at all other times of the year for which data were available (mean depth range = 17 m, $SE = 3.0$) ($t = 3.0$, $p = 0.03$, $n_{\text{spring}} = 2$, $n_{\text{other}} = 5$).

Mysid depth distributions obtained with the 430 kHz unit were very similar to the depth distributions obtained with the 123 kHz unit. For example, for the July 07, 2005 data, we found a highly significant relationship between mysid density estimates obtained with the 123 and 430 kHz units ($r^2 = 0.90$, slope = 0.99; evaluated for all depths between 20 and 50 m) (see Rudstam et al. 2008b for detailed discussion).

Mean size of mysids ranged from a minimum of 8.0 mm on May 5, 2005 to a maximum of 11.4 mm on

May 19, 2004 (Table 3). Mean abundance, as estimated through net tows, ranged from 71 mysids m^{-2} on September 27, 2005 to 801 mysids m^{-2} on July 7, 2005 (Table 3). Acoustically derived densities were somewhat lower than net tow estimates and ranged from 44 to 290 mysids m^{-2} ; however, no significant differences were found when acoustic and net tow estimates were compared across all dates in which net tows were taken (Paired *t*-test, $t = 1.85$, $p = 0.11$, $n = 7$). The correlation between acoustic and net hauls in July 2005 using a larger data set was high ($r^2 = 0.68$; Rudstam et al. 2008b).

Fish vertical distribution, length and abundance

Fish vertical distribution tended to be bimodal when the lake was thermally stratified, with a large peak in the epilimnion and a smaller peak in the metalimnion. The upper peak tended to coincide with high zooplankton biomass in epilimnetic waters and the lower peak with the upper edge of the mysid layer in metalimnetic waters (Fig. 1). An exception to this bimodal pattern during stratified conditions occurred in June 2005, when there was only one epilimnetic peak between 5 and 10 m, which coincided with the zooplankton peak.

Fishes were found deepest in the water column in May 2005. On this sampling date, fishes had a bimodal distribution with one peak between 45 and 50 m (which coincided with the peak of the mysid distribution), and a shallower peak between 8 and 10 m, which coincided with the zooplankton peak (Fig. 1). We did not observe a bimodal distribution in May 2004, when there was only one peak between 8 and 10 m (Fig. 1).

We did not notice any effects of moon phase on the vertical distribution of fishes. The depth of the main peak was nearly identical during new and full moons in August 2004 and in June (full) and July (new) 2005. Fish distributions were quite different in the September new moon–full moon comparison, but this was likely due to the higher contribution of rainbow smelt below the thermocline in 2005 (see below).

Fish abundance estimates near our 170 m sampling station in 2004 ranged from 462 ind. ha^{-1} on August 16 to 5761 ind. ha^{-1} on September 30 (Table 3). The majority of these fishes were found in the upper epilimnion, as total abundance dropped sharply below the thermocline. Abundance estimates were significantly lower in 2005 (range = 36 ind. ha^{-1} in July to 462 ind. ha^{-1} in May), and a larger proportion were found below the thermocline than in 2004. Gillnet and trawl catch through the mysid layer indicated that nearly 100% of the fishes sampled through the mysid layer were alewives on 5 of the 6 nights in which fish sampling was conducted (mean fish length = 162 mm,

Table 3. Fish and mysid abundances and lengths (mean \pm SD) and zooplankton biomass. Mysid abundance was determined by either full water column net tows or acoustic sampling. Fish abundance below the thermocline was summed for all depths from the thermocline down to 60 m during stratified conditions, and between 10 and 60 m for both May 2005 and 2004, when the water column was isothermal. Presence: percentage of the total fish catch (gillnet or trawl — see text) from within the mysid layer that had mysids in their stomachs. Alewife: percentage of total catch

Year	Date	Peak of mysid layer (m)	Mysid length (mm)	Mysid abundance (ind. m^{-2})		Zooplankton biomass ($\mu g l^{-1}$)	Fish length (mm)	Fish abundance (ind. ha^{-1})		Gut samples (n)	Presence (%)	Alewife (%)	
				Net	Acoustics			Total	Below thermocline				
2004	19 May	45	11.4 \pm 3.1	167	155 ^a	2.5	N/A	2520	130	N/A	N/A	N/A	
	16 Aug	30	N/A	N/A	125 ^a	24.7	163 \pm 13	462	148	74	14	5	98
	27 Aug	36	11.3 \pm 4.3	392	290 ^a	60.3	161 \pm 16	1852	313	30	5	55	96
	30 Sep	58	11.1 \pm 3.3	185	46 ^a	19.0	160 \pm 7	5761	1303	85	11	28	100
2005	5 May	46	8.0 \pm 3.0	174	44 ^a	1.8	160 \pm 22	462	183	34	16	26	100
	20 Jun	29	10.7 \pm 3.1	386	162 ^b	70.0	163 \pm 13	208	12	34	36	0	100
	7 Jul	24	9.5 \pm 3.2	801	202 ^b	33.0	N/A	36	15	N/A	N/A	N/A	N/A
	27 Sep	35	10.9 \pm 3.2	71	182 ^b	31.0	166 \pm 10	108	60	31	46	64	30

^a430 kHz; ^b123 kHz

range of sizes = 50 to 190 mm; Table 3). These results confirm that alewives frequently occur within the mysid layer during all 3 seasons. Gut content analyses confirmed that alewives and smelt were feeding on mysids on all nights sampled, with the exception of June 20, 2005 (Table 3).

We saw no consistent patterns in alewife length by depth on any of the sampling nights in which gillnets were used and no differences in mean alewife length on June 20, 2005 among fishes caught in and above the mysid layer. These results indicate that alewives were not segregated by size within the mysid layer (i.e. between 15 and 35 m) and were not segregated in epilimnetic waters at night during June 2005. The one exception to alewives dominating our gillnet and mid-water trawl catches occurred in September, 2005, when over half of the trawl catch through the mysid layer (22 to 60 m) was rainbow smelt. It was during this time period that a larger proportion of the fish backscattering occurred below the thermocline, relative to the other sampling nights (Fig. 1, Table 3). We assume that the fish in this deeper layer in September 2005 were primarily rainbow smelt, while fish caught above the thermocline (<27 m) were primarily adult and juvenile alewives (see discussion in Gal et al. 2006). Because so few alewives were caught in our trawls in September, 2005, we cannot draw conclusions about segregation of alewife age classes on this date.

Zooplankton vertical distribution and total biomass

Zooplankton vertical distributions varied seasonally and by moon phase. Zooplankton biomass generally peaked in the top 10 m of the water column and dropped off considerably at depths below the thermocline (Fig. 1). One notable exception was September 2005 when the thermocline was at 27 m and there was a substantial *Limnocalanus* peak below it. Results from net tows below 30 m in 2005 suggest that zooplankton biomass remains low and relatively constant in hypolimnetic waters (biomass estimates in the 30 to 40 m depth stratum were nearly identical to estimates in the 40 to 50 m stratum for all nights in 2005). Zooplankton biomass peaks were slightly deeper in the spring (Fig. 1). Mean zooplankton biomass down to 30 m depth was 11 to 32 fold higher during summer than during spring and varied nearly 3 fold during June to August (Table 3). Mean biomass in September 2005 was about 60% higher than in September 2004.

Comparisons of our net and pump samples failed to show any significant differences between the 2 techniques. Estimates for mean zooplankton biomass down to 22 m were identical between the 2 techniques ($26 \mu\text{g l}^{-1}$) and species composition of the integrated samples was also similar (percent biomass ratios for pump:net = 41:42 for cyclopoids, 31:39 for calanoids, 17:9 for *Bythotrephes* spp., 9:5 for *Daphnia* spp., 2:5 other).

Model performance

Temperature-light model (TLM)

The TLM predicted the peak of the mysid distribution to within 5 m on 7 of the 8 nights sampled, and within 10 m in May 2004. Overlap between TLM predictions and observed mysid distributions was >74% on all sampling nights (84% on August 16, 2004), indicating that the model is a good predictor of both the peak and range of the mysid distribution in the field (Fig. 2, Table 4).

Growth (*g*) model

The model based on mysid growth at depth predicted the peak of the mysid layer to within 10 m on 3 of the 8 nights, but vastly underestimated the observed peak in May 2005 (Fig. 3, Table 4). Overlap between growth model predictions and observed mysid distributions ranged from 39% in May 2005 to 79% in September 2005. There were no significant differences in percent overlap (2-tailed *t*-test, $t = 0.14$, $p = 0.19$) or difference from observed peak ($t = 0.81$, $p = 0.45$) predictions when means were compared on new moon versus full moon nights ($n_{\text{new}} = 5$, $n_{\text{full}} = 3$), or between stratified ($n_{\text{strat}} = 6$) and isothermal ($n_{\text{iso}} = 2$) conditions

Table 4. Comparison of the mysid temperature-light (TLM), growth (*g*) and growth:mortality risk (*g*: μ) models to observed mysid distribution. Means with different superscript letters are significantly different (pairwise comparisons with Tukey-Kramer HSD post-hoc test; $\alpha = 0.05$)

Year	Date	Peak (m)	Difference from peak (m)			Overlap (%)		
			TLM	<i>g</i>	<i>g</i> : μ	TLM	<i>g</i>	<i>g</i> : μ
2004	19 May	45	9	2	18	80	68	65
	16 Aug	30	0	19	20	84	68	22
	27 Aug	36	5	13	13	76	75	49
	30 Sep	58	3	9	8	75	53	48
2005	5 May	46	0	36	15	75	39	45
	20 Jun	29	1	5	7	74	52	22
	7 Jul	24	2	26	25	76	39	12
	27 Sep	35	1	15	12	78	79	28
Mean	—	—	2.6 ^A	15.6 ^B	14.8 ^B	77.2 ^A	59.0 ^B	36.4 ^C
SE	—	—	1.1	4.0	2.1	1.2	5.5	6.4

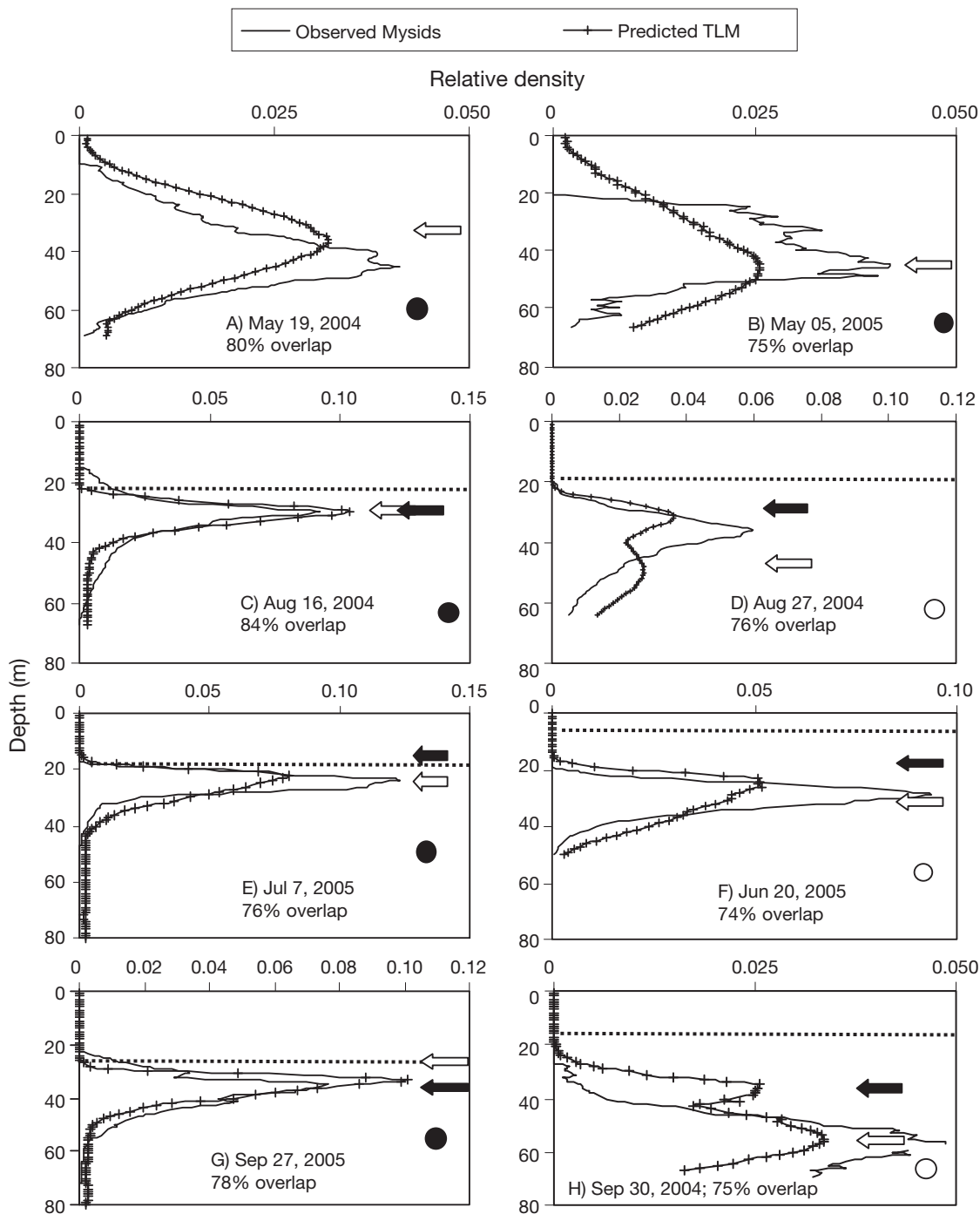


Fig. 2. Observed mysid distributions versus temperature-light model (TLM) predictions during full moon (○) and new moon (●) nights. Dashed line: thermocline. May profiles were isothermal. Black arrows: depth at which the temperature preference function is maximized; open arrows: depth at which the light preference function is maximized. Total density for each profile equals 1. Note the different x-axis scales

($p > 0.50$ when both percent overlap and differences from observed peak means were compared). These results indicate that the growth model was not a better predictor of mysid distribution under any particular light or seasonal temperature conditions.

Growth:mortality risk ($g:\mu$) model

The $g:\mu$ model predicted the peak of the mysid distribution to within 10 m on only 2 of the 8 nights sampled (Table 4). Overlap ranged from 12% in July 2005 to

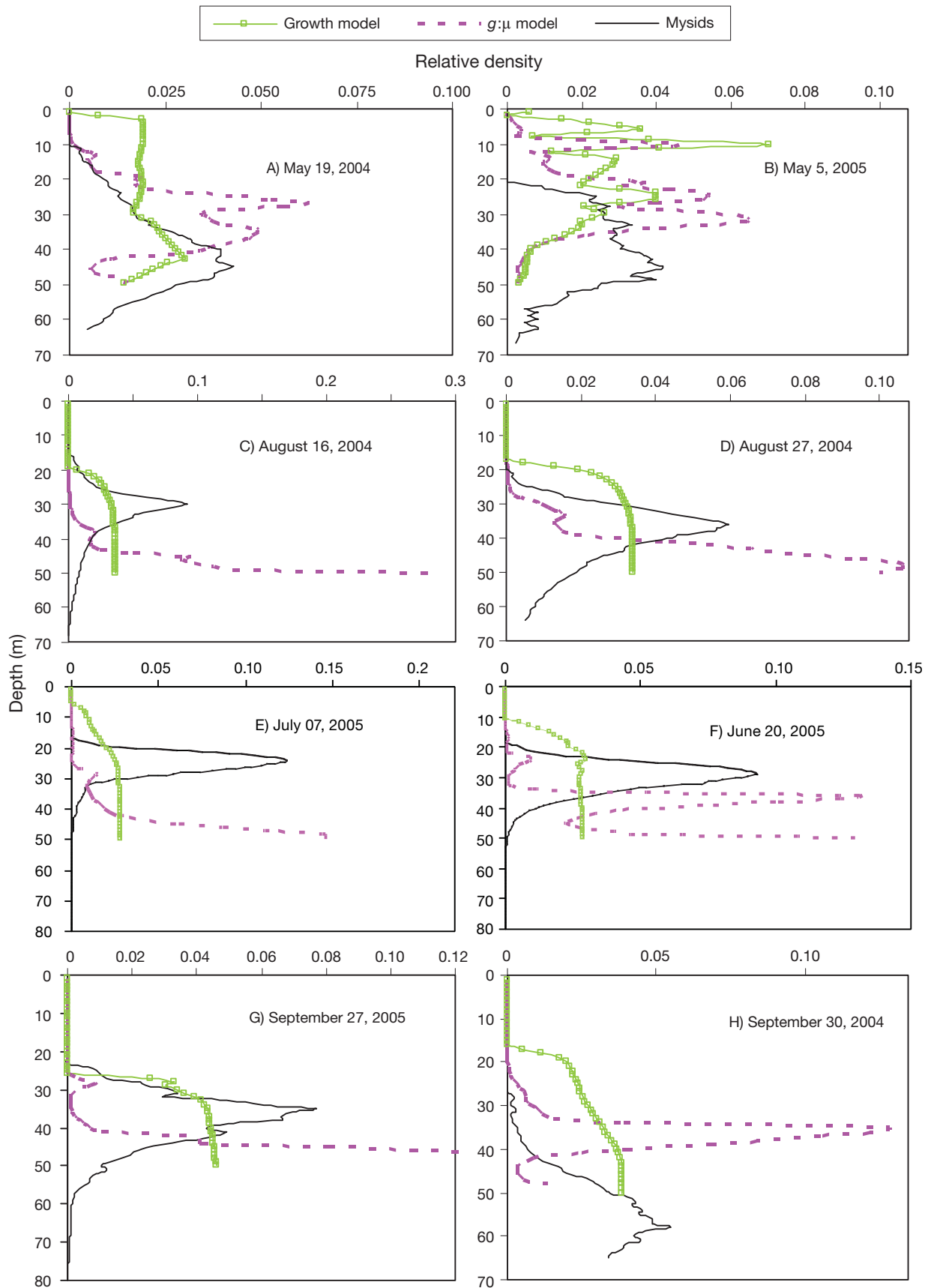


Fig. 3. Observed and predicted mysid distributions for the growth model and the growth:mortality risk ($g:\mu$) model

65% in May 2004, and was not significantly higher during the spring, isothermal months than during stratified conditions (2-tailed t -test, $t = 0.43$, $n_{\text{spring}} = 2$, $n_{\text{stratified}} = 6$, $p = 0.68$) or on new moon versus full moon nights ($t = 0.17$, $n_{\text{new}} = 5$, $n_{\text{full}} = 3$, $p = 0.87$).

Comparison of all models

The TLM was a significantly better predictor of the depth of peak mysid density (Table 4; 1-way ANOVA, $F_{2,21} = 8.2$, $p = 0.002$) and the range of depths occupied by the mysid layer, as approximated by percent overlap ($F_{2,21} = 14.2$, $p < 0.0001$) than either the growth or $g:\mu$ models, when the respective mean values were compared across all dates. Tukey-Kramer HSD post-hoc tests (JMP Version 5.1) revealed significant differences between all 3 models in terms of mean percent overlap (TLM $> g > g:\mu$; all $p < 0.02$), but between the TLM and growth model and the TLM and $g:\mu$ model only when comparing difference from peak means ($g > g:\mu > \text{TLM}$; for g to $g:\mu$, $p = 0.84$; for TLM to g , $p = 0.0020$, for TLM to $g:\mu$, $p = 0.0027$).

DISCUSSION

We show that a model based on 2 readily measured environmental factors, temperature and light, provides reasonable predictions of the entire nighttime distribution of mysids during the spring, summer and fall in Lake Ontario. In contrast, the models based on estimated growth rate and on the ratio of growth rate to predation risk did not accurately predict the depth of maximum mysid density or the range of depths occupied by mysids (less overlap between predicted and observed distributions). We conclude that the response to temperature and light alone is sufficient for predicting mysid vertical distribution across seasons in Lake Ontario.

Abundance estimates

We do not think that our mysid acoustic returns were biased due to backscattering contributions of other species. Net samples taken above, through, and below the mysid layer confirmed acoustic returns in both 2004 and 2005, with greater than 85% of the catch occurring at depths deemed to be the 'mysid scattering layer' (as determined through visual inspection of acoustic echograms) on all dates. Estimates were likely not confounded by smaller zooplankton, as invertebrates < 4 mm are weak scatterers and likely do not contribute substantially to backscattering in the mysid

layer (see Rudstam et al. 2008b). In addition, very few juvenile fishes were found within the mysid layer in our gillnets; this should decrease the probability of including fish scattering in our mysid distribution analyses.

Differences in absolute mysid and fish abundance between years were likely due to sampling variance, given that we only surveyed a relatively small region of the lake. These estimates should therefore not be extrapolated to lake-wide abundances and we present them only as a means of describing densities near our 170 m sampling station. Our abundance estimates for mysids are reasonable, compared to literature estimates at similar times of the year (Johannsson et al. 2003). Fish density at our sampling station, however, was lower on all but one date than the mean alewife density in Lake Ontario. In 2004 and 2005, numbers of alewives in the USA sector of the lake averaged 4329 ind. ha⁻¹, as estimated from area swept by bottom trawls in early spring, when alewives are close to bottom (R. O'Gorman, unpublished data). The lower fish densities at our station are not surprising, given that there are large differences in alewife density along the southern shoreline in early spring, and the geographic region with peak density varies from year to year, suggesting that alewives are highly mobile. Moreover, alewives move seasonally between off-shore and near-shore, migrating nearshore in spring and spawning there in summer.

Comparison of model predictions

We never found more than 10% of the mysid population at depths with $> 10^{-7}$ mylux, regardless of moon phase, depth of the thermocline, or relative predator and prey abundances. These results indicate that mysids do not move into light levels $> 10^{-7}$ mylux, even if abundant food is available in brighter light. This is similar to earlier observations in Lake Ontario (Gal et al. 1999, 2004) and elsewhere (Janssen & Brandt 1980, Moen & Langeland 1989, Rudstam et al. 1989). However, mysids were found deeper (and thus at lower temperatures) on full moon nights and at slightly higher light levels than the light preference function alone would predict on nights with shallow thermoclines. Despite these substantial differences in temperature and light preference predictions on some nights, the TLM was able to predict the depth of peak mysid density to within 10 m on all sampling occasions and to within 3 m on 6 of the 8 nights we sampled. These results support our light and temperature preference functions and indicate that the model, which assumes that light and temperature functions are independent and have equal weight, yields reasonably accurate

predictions of distribution even when light and temperature functions predict peak depth distributions several meters apart.

Although we did not test the models in the winter, the ability of the TLM to predict both the range and peak depths occupied by the mysid layer across such a wide variety of environmental conditions from spring to late fall shows that mysid distribution can be predicted based on temperature and light alone during most of the year. This result is somewhat surprising, given that the light and temperature preference functions were derived based on adult mysid behavior only. Juvenile mysids are typically found higher in the water column than adults (Grossnickle & Morgan 1979, Bowers 1988, Rudstam et al. 1989), indicating that smaller mysids may have higher light and temperature tolerances than larger mysids. An alternative explanation is that our acoustic sampling procedure did not accurately detect smaller mysids. Mysids <7 mm made up a large proportion of the overall mysid catch in May through July 2005, suggesting a large brood release in spring 2005. Given that small mysids are relatively weak scatterers, they will contribute less to the overall mysid backscattering than adult individuals (Rudstam et al. 2008b). However, we were able to accurately predict both the range and peak of mysid vertical distribution in Lake Ontario for most of the sampling nights, suggesting that mysid size differences may not be playing a large role in structuring the overall distribution.

There are several potential explanations as to why both the growth and the $g;\mu$ models were not as strong predictors of mysid distribution as the TLM. We did not have zooplankton biomass data through the peak of the mysid layer on several occasions in 2004 (August 16, August 27 and September 30), and on those sampling dates we assumed that zooplankton biomass in the mysid layer was the same as at the deepest sampled depth of 30 m. This assumption was supported by our data collected in May, June, July and September 2005, when zooplankton was sampled down to 50 m depth (through at least 90% of the mysid layer on these nights). Even if we exclude the 3 profiles in 2004 for which we do not have zooplankton data down to 50 m, the TLM was a better predictor of peak mysid density than either the growth or $g;\mu$ models. However, the observed mysid distribution in September 2004 was several meters deeper than the 50 m depth limit of the growth and $g;\mu$ models, and this made it impossible to accurately predict the actual depth of peak mysid density on this date. If we assume similarly low zooplankton densities past 50 m on this date (as we assumed between 30 and 50 m), the model would still predict the peak of the mysid distribution to be 8 m shallower than was observed.

It is unlikely that zooplankton peaks in the 30 to 50 m depth stratum would be significant enough to alter our predictions of the depth of maximum growth. Zooplankton densities are typically very low below the thermocline in Lake Ontario (Johannsson et al. 1994, Gal et al. 2006) and remain at constant, low-density levels below 30 m (see Benoit et al. 2002 for discussion). Given (1) that the thermocline was shallower than 30 m in all 8 profiles, and (2) the similarity in zooplankton density estimates in the 40 to 50 m and 30 to 40 m stratified net tows in 2005, we do not think that there would have been a substantial peak in zooplankton density below 30 m that is correlated with the mysid peak; however, we cannot exclude this possibility, and future investigations may provide further insight into the prevalence and importance of deep zooplankton layers on mysid behavior.

One possible explanation for why the $g;\mu$ model did not provide better predictions of mysid distribution is that predation risk may be better approximated with a model based on reaction distance or feeding rate, rather than a model based on the product of predator abundance and proportion of fishes that are feeding. Batty et al. (1990) based their estimates of the proportion of fishes that are feeding entirely on the number of fishes displaying feeding-oriented swimming behavior, and they did not measure capture success or feeding rate. However, it is possible that the proportion of fishes engaged in feeding-oriented swimming behavior does not translate proportionally into foraging success. For example, alewives may switch between different types of searching behavior, depending on the light level present, particularly given that alewives are capable of feeding in complete darkness, using lateral line sensitivity (Janssen et al. 1995).

Another possible explanation why the growth and $g;\mu$ models were not better predictors of mysid distribution relates to the main assumption of both models—that mysid distribution is directly proportional to growth or growth:mortality risk. Lampert et al. (2003) reported that *Daphnia pulex* × *galeata* were distributed vertically in experimental plankton towers in direct proportion to their growth profiles. They described the resulting distribution as approximating an ideal free distribution, given known concentrations of (and predicted gains and losses associated with) food and temperature at 1 m depth intervals in the water column. A true ideal free distribution, however, assumes that organisms select habitat in proportion to the supply rate of resources, so that each animal receives identical food resources regardless of their location. Lampert et al. (2003) argued that in filter-feeding daphnids, feeding rate is directly related to food concentration, and therefore that a relatively constant food gradient (owing to daily replenishment) should mimic a con-

stant supply rate. However, these assumptions may not hold for mysids in the same way as they do for filter-feeding daphnids.

Implications

We are not implying that mysid distributions are unaffected by predators and prey. Our results suggest that mysid distribution is best approximated by absolute light and temperature preferences, but these preferences likely evolved as mechanisms to increase food intake during periods of low predation risk. Constantly searching for the exact optimum depth that would maximize $g:\mu$ (i.e. displaying direct responses to relative prey and predator abundances over a short time period) may be too risky for *M. diluviana*. Mysids have slow growth rates, long generation times and low life-time fecundity, which should lead to a strong selection for avoiding predators by staying in colder and darker waters. *r*-selected species with high clearance rates, such as daphnids, can more effectively exploit higher prey concentrations over short time periods in shallow waters, and this could explain why daphnids are more plastic in their depth selection than mysids.

The ability to model entire distributions of a migrating population based on relatively simple parameters, such as light and temperature, has important ecological and management implications. The success of the TLM in predicting mysid distribution across 3 different seasons and 2 different moon phases suggests that we should be able to forecast distributional shifts resulting from long-term environmental changes such as global warming or increased light penetration, observed in Lake Ontario and other North American lakes (Anderson et al. 1996, Magnuson et al. 2000, Mills et al. 2003). Similar models have been used to forecast impacts of climate change on vertical and horizontal distributions of migrating organisms (DeStasio et al. 1996, McDonald et al. 1996, Schindler et al. 2005). Given the direct link between mysids, alewife and salmonids, the ability to predict vertical distributions also has important implications for both the current and future management of salmonid fisheries in the Great Lakes and other systems inhabited by both mysids and salmonids.

This study also provides one of the first accounts of a bimodal distribution of alewives in the pelagic waters of Lake Ontario—with an upper peak that appears to coincide with the main zooplankton layer and another, deeper peak which overlaps with the upper edge of the mysid layer. By extension, we demonstrate that much of the interaction between mysids and their fish predators and zooplankton prey is occurring at the upper edge of the mysid distribu-

tion. If an assessment of the contribution of mysids to the pelagic food web were based on the 'average' mysid alone, we would underestimate the significance of mysid feeding and their availability as a food resource to alewives over the deeper waters of the lake during thermal stratification.

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Differences in the trophic role of *Mysis diluviana* in two intermontane lakes

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ABSTRACT: The trophic role of the freshwater shrimp *Mysis diluviana* was compared between 2 neighbouring lakes in British Columbia to investigate its possible role in the collapse of the Okanagan Lake kokanee salmon *Oncorhynchus nerka* population. Stable isotopes of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) were used to compare the trophic relationships of mysids within the pelagic food web and between lakes. Mid-summer $\delta^{15}\text{N}$ signatures suggested that adult mysids in Okanagan Lake were acting more as primary consumers, and Kalamalka Lake mysids were acting as secondary consumers. *M. diluviana*'s predatory capacity was also assessed through *in situ* clearance rate feeding experiments and examination of gut contents. *M. diluviana* <1 yr old in Okanagan Lake were capable of clearing a greater volume of prey, but there was no difference between lakes for *M. diluviana* >1 yr old. Gut contents confirmed *M. diluviana* in both lakes were consuming copepod and cladoceran prey. All 3 techniques demonstrated ontogenetic diet shifts, with larger mysids obtaining more energy from zooplankton prey. Although mysids in feeding experiments actively consumed the same zooplankton prey as kokanee, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios suggest that mysids in Okanagan Lake were not feeding at the same trophic level as kokanee, which indicates that there may have been less competition for food sources than previously thought. These differences in results suggest that predatory capacity, as indicated by *in situ* feeding experiments or gut content analysis, should not be used in isolation to establish trophic roles for omnivorous animals.

KEY WORDS: *Mysis relicta* · *Mysis diluviana* · Stable isotopes · Trophic position · Okanagan Lake · Clearance rates

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INTRODUCTION

The role of the opossum shrimp *Mysis diluviana* (formerly *M. relicta*; Audzijonyte & Väinölä 2005) in the decline of native planktivorous fish stocks in lakes into which it has been introduced is well documented. In particular, predation by *M. diluviana* on zooplankton has been implicated in the elimination or temporal displacement of cladoceran populations and subsequent disruption of energy flow to planktivorous fishes (Lasenby et al. 1986, Bowles et al. 1991, Martinez & Bergersen 1991, and others). As mysids increase the length of food chains in their native glacial-relict lakes through their omnivorous feeding habits (Sprules & Bowerman 1988), their introduction into non-glacial food webs may effectively increase the number of

trophic linkages in the new system. The consumption of lower trophic levels by introduced *M. diluviana* may divert food resources that were previously available to the native planktivorous fish.

In North American intermontane lakes where *Mysis diluviana* has been introduced, significant population reductions of kokanee salmon *Oncorhynchus nerka* have been documented (Morgan et al. 1978, Beattie & Clancey 1991, Ashley et al. 1997, Spencer et al. 1999). Kokanee are planktivorous forage fish that play a key role in energy transfer to piscivorous fish such as lake trout *Salvelinus namaycush*, and they can provide an economically valuable sportfishery. It has been assumed that *M. diluviana* has a similar trophic role and competes with kokanee for food. However, in 2 neighbouring lakes in British Columbia, Okanagan

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and Kalamalka Lakes, where mysids were introduced in the 1960s, kokanee populations have responded quite differently to the introduction of *M. diluviana*.

Since the mid-1980s, Okanagan Lake has undergone a significant loss of kokanee stocks, which forced the closure of the sportfishery for this species in 1995 (Ashley et al. 1997), whereas neighbouring Kalamalka Lake is able to support a viable kokanee population and sportfishery. Acoustic surveys of both lakes in 1996–1997 suggested that kokanee densities in Kalamalka Lake (~ 700 fish ha^{-1}) were approximately 3.5 times higher than in Okanagan Lake (~ 200 fish ha^{-1}) (Sebastian & Scholten 1998). A prominent theory regarding the loss of kokanee in Okanagan Lake is that the introduced *Mysis diluviana* were outcompeting these planktivorous forage fish for pelagic zooplankton (Ashley et al. 1998). However, zooplankton abundance does not appear to account for the sustained Kalamalka Lake kokanee fishery. Average total zooplankton densities remained similar between the 2 lakes during the 1996 to 1998 sampling seasons, ranging from 1.2 to 2.8 ind. l^{-1} (McEachern 1999). The proportion of cladocerans, which are the preferred food source for kokanee, was only slightly higher in Kalamalka Lake (~ 4 to 8% of total zooplankton) than in Okanagan Lake ($\sim 3\%$ of total) (McEachern 1999). In addition, mean population estimates for *M. diluviana* from deep sampling stations were greater in Kalamalka Lake (418 ± 43 ind. m^{-2}) than in Okanagan Lake (300 ± 24 ind. m^{-2}) over the same sampling period (Whall 2000). Therefore, the loss of kokanee stocks in Okanagan Lake is unlikely to be due to mysid population impacts on zooplankton abundance alone. A possible explanation for the difference in kokanee abundance in the 2 lakes could be that the mysids have different trophic roles in the 2 lakes and are competing less or not at all with kokanee for food in Kalamalka Lake.

Mysis diluviana is omnivorous and goes through ontogenetic shifts in its diet, becoming more predatory with increasing age (Branstrator et al. 2000). This life history adaptability improves the success of young mysids born early in the summer, when zooplankton abundance is minimal (Naesje et al. 2003), and could lead to variability in mysid trophic position between lakes. We hypothesized that if *M. diluviana* were diverting a significantly greater proportion of the zooplankton prey resources from the planktivorous fish communities in Okanagan Lake than Kalamalka Lake, then mysids in Okanagan Lake would be incorporating a greater proportion of zooplankton in their diet, relative to mysids in Kalamalka Lake.

We examined the pelagic feeding habits of *Mysis diluviana* and its trophic role in the 2 lakes using the trophic position model of food web structure (Vander Zanden & Rasmussen 1996, Post 2002). This model pro-

vides a continuous estimate of energy transfer from primary producer to top consumer by tracking relative differences in stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) between prey and predators within the food web. The model is especially useful for understanding energy transfers for omnivorous animals, such as *M. diluviana*, that do not belong to a rigid trophic guild. To provide supporting evidence for the stable isotope analyses and confirm *M. diluviana*'s pelagic feeding habits in the 2 lakes, we also examined *M. diluviana*'s gut contents and compared prey removal rates in the 2 lakes.

MATERIALS AND METHODS

Study lakes. Okanagan Lake ($50^{\circ} 14' \text{N}$, $119^{\circ} 21' \text{W}$; 351 km^2 , $z_{\text{max}} = 242 \text{ m}$) and Kalamalka Lake ($50^{\circ} 14' \text{N}$, $119^{\circ} 16' \text{W}$; 26 km^2 , $z_{\text{max}} = 142 \text{ m}$) are the largest of the Okanagan Drainage Basin lakes located in the south-central interior of British Columbia. Both are oligotrophic steep-sided valley lakes with narrow littoral zones (Andrusak 2000).

Specimen collections and experiments outlined in the methods below were carried out in both lakes within days of each other, unless otherwise indicated.

Stable isotope analysis and food web structure. Samples for stable isotope analysis were obtained in August 1997 and June 1998. Food web energy linkages were explored between sediment, phytoplankton, benthos, zooplankton, mysids and fish.

As mysids feed on lake sediment (Johannsson et al. 2001, Lasenby & Shi 2004), representative samples were obtained from a depth of 15 m in August 1997 using an Ekman dredge, and from a depth of 70 m in June 1998 using a K-B corer (Wildlife Supply Company). When using the K-B corer, the top 1 cm of sediment was siphoned off and collected using water from the sediment–water interface. All sediment was sifted through a $500 \mu\text{m}$ mesh nylon screen, collected in sterile 250 ml plastic bags and stored on ice until rinsed with 10% HCl and distilled deionized water (ddH_2O) (Estep & Vigg 1985, Keough et al. 1996). The water/sediment slurries were then collected on $1 \mu\text{m}$ Gelman GF/F discs that had been precombusted at 400°C for 2 h. Sediment was then removed from the filter and dried at 60°C in pre-acid-rinsed borosilicate glass vials for a minimum of 72 h.

Particulate organic matter (POM), consisting mainly of phytoplankton (Kling et al. 1992), was assumed to form the base of the food chain for pelagic primary consumers, and may serve as a food source for mysids. To isolate POM from the metalimnion, which was the depth at which mysids fed during the night (Whall 2000), water was collected using a submersible pump, then filtered ($64 \mu\text{m}$ mesh) and stored in 20 l opaque plastic carboys. POM was filtered from the stored

water within 2 h by passing the sample through a 1 µm GF/F in-line 47 mm diameter filter disc to obtain isotope signatures for POM in the 1 to 64 µm size range. Following filtration, POM on the 1 µm GF/F filters was rinsed with 10% HCl, rinsed again with ddH₂O and then dried at 60°C for a minimum of 72 h.

Zooplankton was collected from 30 m depth to the surface using a Wisconsin plankton net and sorted by size fraction (295, 210, 110 and 64 µm) using a series of nylon mesh sieves. Each size fraction was then concentrated and transferred to 64 µm filtered metalimnetic water. Zooplankton were kept alive on ice until separated by taxa, then rinsed with 10% HCl, placed in 5 ml glass vials and dried. A minimum of 500 individuals of *Daphnia* spp. and calanoid and cyclopoid copepods were isolated from the 295 and 210 µm fractions for analysis.

Mysids were collected from deep-water stations (>100 m depth) between 23:00 and 01:00 h, during their nighttime vertical feeding migration into the metalimnion. Hauls were made with a 1 m² Wisconsin plankton net from ~2 m off the bottom to the surface. Mysids were placed in pre-filtered (64 µm) metalimnetic water and sorted according to size: small juveniles born that year (Year 0), intermediate immature animals (late Year 0 or early Year 1 cohorts) and large adults (mature Year 1 cohort); 10 to 15 animals of each class were measured to the nearest 0.1 mm, rinsed with 10% HCl and ddH₂O and dried in glass vials.

Kokanee, lake trout, rainbow trout *Oncorhynchus mykiss* and whitefish *Coregonus clupeaformis* samples were obtained from both Okanagan and Kalamalka Lakes to show possible food web linkages for potential predators of mysids. Samples were provided by the BC Ministry of Environment, Lands and Parks (MELP). In all cases, fish had been frozen intact within a few hours of being caught. Muscle tissue samples (~1 cm³) were extracted from just behind the operculum and above the lateral line. All skin, scales, subcutaneous adipose tissue and bones were removed from the samples. The remaining sections of tissue were rinsed with ddH₂O, placed in glass vials and dried at 60°C.

With the exception of zooplankton (which was scraped from the sides of the glass containers), all samples were homogenized using a porcelain mortar and pestle, transferred to ultra clean aluminum foil weighing capsules, weighed to the nearest 0.0001 mg and sealed for analysis. Blank GF/F discs were also prepared for analysis by rinsing with 10% HCl and ddH₂O before drying.

Triplicate samples of each homogenized sample type were analyzed using a Finnigan-Mat continuous flow-isotope ratio mass spectrometer (CF-IRMS) to determine δ¹⁵N and δ¹³C. Analytical precision was ±0.3‰ for δ¹⁵N and ±0.1‰ for δ¹³C (G. St. Jean pers. comm.). Standard errors around triplicate samples of the same

homogenized material were ≤0.2‰ for δ¹⁵N and δ¹³C signatures of food web organisms.

Isotope ratios of tissue samples were determined as:

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C}\text{‰} = [(R_{\text{sample}} - R_{\text{standard}})(R_{\text{standard}})^{-1}]1000 \quad (1)$$

where R is the ratio of ¹⁵N/¹⁴N or ¹³C/¹²C, 'sample' is the tissue sample analyzed, and 'standard' are the international standards of VPDB limestone (for δ¹³C) and N_{air} (for δ¹⁵N) (Fry 1991).

Trophic positions (TP) of consumers were determined from an assumed δ¹⁵N difference of 3.4‰ between predator and prey (Minagawa & Wada 1984, Wada et al. 1993, Cabana & Rasmussen 1994, Vander Zanden et al. 1997, Post 2002), with the first trophic position being equal to the δ¹⁵N signature of phytoplankton in the lake:

$$\text{TP}_{\text{consumer}} = [(\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{phytoplankton}}) + 1]3.4^{-1} \quad (2)$$

To determine which proportion of the mysid diet was made up of benthic sediment organic material versus planktonic (e.g. phyto- and zooplankton) sources, the relative amounts of benthic and pelagic carbon (δ¹³C) assimilated by the mysids were determined using a 2-source mixing model modified from Vander Zanden & Rasmussen (2001):

$$\% \text{ Benthic carbon} = [(\delta^{13}\text{C}_{\text{mysid}} - \text{TP}_{\text{mysid}} \times 0.47 - \delta^{13}\text{C}_{\text{pelagic}}) / (\delta^{13}\text{C}_{\text{benthic}} - \delta^{13}\text{C}_{\text{pelagic}})^{-1}]100 \quad (3)$$

and

$$\% \text{ Pelagic carbon} = 100 - \% \text{ Benthic carbon} \quad (4)$$

where δ¹³C_{mysid} is the mean ¹³C/¹²C ratio for *Mysis diluviana*, δ¹³C_{benthic} the mean ¹³C/¹²C ratio for sediments, δ¹³C_{pelagic} the mean ¹³C/¹²C ratio for POM and pelagic zooplankton, TP_{mysid} the trophic position estimate for *M. diluviana* (assumed to be 1.0 relative to mean pelagic and benthic carbon sources) and 0.47 the average δ¹³C fractionation factor between predator and prey (including herbivores), as described in Vander Zanden & Rasmussen (2001). The trophic position correction factor (i.e. TP_{mysid}0.47) was added to the model to account for expected fractionation of carbon isotope ratios due to trophic transfer.

Mysid gut contents. To verify prey items in the diet of mysids in the 2 lakes, mysids were collected in August 1997 from the meta- and epilimnia at 04:00 h at the end of the diurnal migration cycle. Stomachs of 10 mysids from each of Year 0 and Year 1 cohorts were extracted, placed on a glass microscope slide in a drop of glycerine, teased apart and viewed under 100× magnification. Rotifer genera and zooplankton mandible type (calanoid, cyclopoid, *Daphnia* spp. and *Diaphanosoma* spp.) were enumerated for each stomach.

Mysid clearance rate experiments. To support stable isotope evidence for mysid diet and determine if mysid predation on zooplankton was similar between lakes,

we conducted clearance rate experiments during June and August 1997. In these controlled feeding experiments, mysids were offered a natural zooplankton assemblage from their respective lakes.

For each trial, mysids were collected at night and held in unfiltered metalimnetic water for 24 h. Approximately 3 h prior to the experiment, all mysids were transferred to filtered (64 μm mesh) metalimnetic water to avoid introducing any additional zooplankton to the feeding chambers. Translucent 20 l polyethylene plastic containers filled with filtered metalimnetic water were used for feeding chambers; 5 containers contained zooplankton only (controls), 5 contained 10 small Year 0 cohort mysids and zooplankton, and 5 contained 10 large Year 1 cohort mysids and zooplankton. Zooplankton was collected by taking multiple vertical hauls through the metalimnion using a Wisconsin closing net (120 μm mesh). Zooplankton was placed in filtered metalimnetic water and randomly transferred to feeding chambers at densities approximating those found within each lake. Mysids were then added to the experimental chambers and suspended in the metalimnion for approximately 8 h, after which the chambers were retrieved and the contents of each was filtered through a 64 μm mesh and preserved in 95 % ethanol for zooplankton identification and enumeration. Mysids from each chamber were measured to the nearest 0.1 mm.

Mysid clearance rates, F ($\text{ml mysid}^{-1} \text{h}^{-1}$), were calculated for each zooplankton taxon found and for the total zooplankton assemblage present as follows:

$$F = [1000V \times \ln(CZ^{-1})](tn)^{-1} \quad (5)$$

where V is the chamber volume (l), C the prey concentration in the control chamber remaining at the end of the experiment, Z the prey concentration in the experimental chamber remaining at the end of the experiment, t the time spent feeding (h) and n the number of mysids in the chamber (modified from Bowers & Vanderploeg 1982).

Statistical analyses. Mysid isotope signatures and clearance rates were compared conducted using 1-way ANOVA. Trophic position estimates for individual size classes of mysids were compared between lakes using Student's t -test. All statistical analyses were conducted using SigmaStat computer software.

RESULTS

Mysid trophic position and food web structure from stable isotopes

Stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) for all members of the food webs sampled are presented in Table 1. POM, which forms the base of the pelagic food web,

had very similar $\delta^{15}\text{N}$ values between lakes, indicating little difference in pelagic nitrogen sources between lakes for the higher trophic levels. In both lakes, POM was a key food source for *Daphnia* spp., which were enriched by 1.8 to 4.8‰ $\delta^{15}\text{N}$ and 0.6 to 1.6‰ $\delta^{13}\text{C}$ relative to POM (insufficient quantities of *Daphnia* spp. were available for a sample in Okanagan Lake in June 1998). Copepods were between 2.8 and 3.9‰ more enriched in $\delta^{15}\text{N}$ than *Daphnia* spp., although they maintained similar $\delta^{13}\text{C}$ signatures, indicating that they were feeding approximately about 1 trophic level above *Daphnia* spp. Bulk zooplankton collections showed increasing nitrogen enrichment and carbon depletion with increasing size fractions. Zooplankton collections from Kalamalka Lake were enriched by up to 3.8‰ in $\delta^{15}\text{N}$ relative to those in Okanagan Lake.

Average $\delta^{15}\text{N}$ signatures for *Mysis diluviana* were consistently higher in Kalamalka lake than in Okanagan Lake over the 2 study periods. Within each lake, $\delta^{15}\text{N}$ values were similar to or slightly less than those of copepods, while being enriched over *Daphnia* spp. and POM (Table 1), suggesting that mysids were feeding primarily on the latter 2 food types.

Nitrogen isotope signatures for mysids in August 1997 were more similar to those of copepods in Kalamalka Lake (mean difference = 0.9‰ $\delta^{15}\text{N}$) than in Okanagan Lake (mean difference = 2.0‰ $\delta^{15}\text{N}$). The average mysid $\delta^{15}\text{N}$ enrichment over *Daphnia* in Kalamalka Lake (mean difference = 1.9‰) was also slightly higher than in Okanagan Lake (mean difference = 1.3‰); therefore, it appears that mysids in Kalamalka Lake may be incorporating more zooplankton in their diet than those in Okanagan Lake.

Mysid $\delta^{15}\text{N}$ signatures increased with animal size in both lakes, and this increase was significant ($p \leq 0.004$) in 3 of 4 comparisons (the exception being Okanagan Lake mysids in August 1997, $p = 0.152$). However, mysids in Kalamalka Lake exhibited a greater range in isotope signatures between size classes over the 2 sampling periods (2.6‰ $\delta^{15}\text{N}$) than mysids in Okanagan Lake (1.9‰ $\delta^{15}\text{N}$). Across all size classes, Kalamalka Lake mysid $\delta^{15}\text{N}$ signatures were 1.2 to 3.7‰ higher than in Okanagan Lake. Mysid size, however, did not account for the higher nitrogen enrichment in Kalamalka Lake, as the mean sizes of mysids from each size class were within 1.1 mm of each other (June 1998 collections) (Table 1).

Calculations of mean mysid trophic position based on differences in $\delta^{15}\text{N}$ between mysids and phytoplankton showed that for both sampling periods, Kalamalka Lake mysids occupied a significantly higher trophic position than those in Okanagan Lake over all size categories ($p \leq 0.005$) (Table 1). Estimates of trophic position tended to increase with mysid size category.

Table 1. Stable isotope signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and trophic position estimates (TP) for members of Okanagan (OL) and Kalamalka Lake (KL) food webs August 1997 and June 1998. Data are mean (SD). n/a: not available, insufficient numbers of individuals for analysis

Size	Okanagan Lake			Kalamalka Lake			
	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	TP	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	TP
August 1997							
POM	3	3.2 (0.58)	-32.8 (0.74)	1.0 (0.17)	3.5 (0.72)	-32.2 (0.09)	1.0 (0.21)
<i>Daphnia</i> spp.	1 ^a	6.4 (0.07)	-31.2 (0.20)	1.9	8.3	-31.8	2.4
Calanoid copepods	1 ^a	9.5 (0.24)	-31.6 (0.09)	2.9	11.0 (0.13)	-31.6 (0.10)	3.2
Cyclopoid copepods	1 ^a	9.8 (0.03)	-30.5 (0.13)	2.9	11.2 (0.11)	-31.6 (0.13)	3.3
Zooplankton	1 ^b	5.9 (0.06)	-20.3 (4.57)	1.8	9.2 (0.05)	-30.5 (0.02)	2.7
	1 ^b	8.5 (0.21)	-24.9 (0.02)	2.6	11.2 (0.06)	-30.8 (0.21)	3.3
	1 ^b	10.1 (0.10)	-32.0 (0.14)	3.0	11.5 (0.09)	-31.8 (0.12)	3.3
	1 ^b	8.7 (0.20)	-32.1 (0.13)	2.6	10.6 (0.09)	-32.3 (0.10)	3.1
<i>Mysis diluviana</i>							
small	3 ^c	7.5 (0.08)	-29.3 (0.11)	2.3 (0.02)	8.7 (0.09)	-29.0 (0.09)	2.5 (0.03)
medium	3 ^c	7.7 (0.10)	-29.9 (0.30)	2.3 (0.03)	10.6 (0.58)	-30.6 (2.71)	3.1 (0.17)
large	3 ^c	7.8 (0.30)	-30.8 (0.39)	2.4 (0.09)	11.2 (0.45)	-32.6 (1.17)	3.3 (0.13)
Rainbow trout (OL)	3	12.2 (1.42)	-25.7 (0.67)	3.7 (0.42)	n/a	n/a	n/a
Lake trout (KL)	3	n/a	n/a	n/a	15.2 (0.36)	-29.1 (0.50)	4.4 (0.11)
Kokanee (OL)	3	10.6 (0.30)	-27.0 (0.25)	3.2 (0.09)	n/a	n/a	n/a
Whitefish (OL)	2	9.7 (0.64)	-26.3 (0.42)	2.9 (0.19)	n/a	n/a	n/a
Clams	3	5.8 (0.09)	-27.6 (0.13)	1.8 (0.03)	6.0 (0.18)	-30.7 (0.15)	1.7 (0.05)
Chironomids	3	4.3 (0.50)	-29.8 (0.59)	1.3 (0.15)	6.2 (0.53)	-31.2 (3.08)	1.8 (0.16)
Sediment	3	1.6 (0.28)	-25.6 (0.05)	0.8 (0.08)	1.5 (0.21)	-13.9 (0.77) ^d	0.4 (0.06)
June 1998							
POM	3	3.6 (0.21)	-30.9	1.0 (0.06)	3.7 (0.21)	-30.3 (0.14)	1.0 (0.06)
<i>Daphnia</i> spp.	1 ^a	n/a	n/a	n/a	5.5 (0.15)	-30.9 (0.10)	1.6
Calanoid copepods	1 ^a	8.5 (0.23)	-32.6 (0.26)	2.4	9.3 (0.15)	-31.5 (0.23)	2.7
Cyclopoid copepods	1 ^a	7.4 (0.35)	-30.0 (1.34)	2.1	9.4 (0.20)	-31.3 (0.17)	2.7
Zooplankton	1 ^b	2.0 (0.21)	-29.9 (0.21)	0.5	5.3 (0.92)	-28.5 (0.07)	1.5
	1 ^b	4.5 (0.55)	-28.2 (0.44)	1.3	8.3 (0.35)	-30.4 (0.06)	2.4
	1 ^b	7.1 (0.06)	-30.7 (0.25)	2.1	8.6 (0.64)	-31.0 (0.15)	2.5
	1 ^b	7.4 (0.06)	-31.9 (0.06)	2.1	8.7 (0.81)	-31.5 (0.10)	2.5
<i>Mysis diluviana</i>							
small	3 ^c	6.7 (0.46)	-29.8 (0.44)	1.9 (0.13)	8.7 (0.40)	-29.7 (0.12)	2.5 (0.12)
medium	3 ^c	6.5 (0.30)	-28.2 (0.57)	1.9 (0.09)	10.2 (0.25)	-32.0 (0.57)	2.9 (0.07)
large	3 ^c	8.6 (0.21)	-29.7 (0.35)	2.5 (0.06)	11.3 (0.70)	-32.1 (0.86)	3.3 (0.21)
Kokanee - Age 2+ (OL)	3	11.3 (0.45)	-26.6 (0.21)	3.3 (0.13)	n/a	n/a	n/a
Kokanee - Age 1+ (OL)	3	11.3 (0.45)	-27.2 (0.17)	3.3 (0.13)	n/a	n/a	n/a
Whitefish (OL)	3	12.0 (0.59)	-27.9 (0.89)	3.5 (0.17)	n/a	n/a	n/a
Clams	3	5.8 (0.49)	-26.1 (0.51)	1.7 (0.15)	7.1 (0.17)	-28.4 (0.15)	2.0 (0.05)
Sediment	3	3.0 (0.83)	-26.9 (0.75)	0.8 (0.24)	4.9 (0.21)	-13.9 (0.77)	1.4 (0.06)

^aComposite of approximately 500 individuals (triplicate analysis); ^bBulk sample analyzed in triplicate; ^cComposite of 10-15 individuals per sample; ^dSediment carbon isotope ratio for Okanagan Lake in August 1997 was substituted with June 1998 results due to an uncharacteristically enriched $\delta^{13}\text{C}$ value of -2.7‰

To examine potential food sources for the mysids, carbon isotope signatures in mysids were compared to those for pelagic POM and zooplankton, and benthic sediment material. With the exception of August 1997 collections in Kalamalka Lake, $\delta^{13}\text{C}$ signatures differed significantly between size classes of mysids ($p \leq 0.010$) and tended to become more depleted with increasing mysid size. Mean mysid $\delta^{13}\text{C}$ signatures were similar to, or slightly enriched, over other pelagic zooplankton and POM $\delta^{13}\text{C}$ values, while being more depleted than the sediments (Table 1). For Kalamalka Lake, the August 1997 sediment signatures ($-2.7 \pm 0.2\%$ $\delta^{13}\text{C}$) were not used to determine benthic carbon sources, as these samples had not been acidified, and as such were most likely artificially enriched due to the presence of calcium carbonate in the matrix. Instead, the June 1998 mean sediment values of $-13.9 \pm 0.77\%$ were used as a surrogate estimate for comparing benthic carbon sources.

Mean $\delta^{13}\text{C}$ signatures from benthic (sediment) and pelagic sources (phyto- and zooplankton) indicated that mysids were assimilating $\geq 70\%$ of their carbon from pelagic sources, regardless of mysid size class (one exception being medium-sized mysids in Okanagan Lake in June 1998) (Table 2). There was a difference in dietary carbon sources between lakes, however, with *Mysis diluviana* in Okanagan Lake incorporating more benthic carbon into their diet (mean = 26.0%, range = 4 to 59%) than those in Kalamalka Lake (mean = 3.7%, range = 0 to 13%) (Table 2).

The fish analyzed from Okanagan Lake were spatially separated from the pelagic zooplankton by both their $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures (Table 1). Kokanee $\delta^{15}\text{N}$ values were enriched by up to 4.2‰ relative to copepods and *Daphnia* spp. However, as kokanee $\delta^{13}\text{C}$ values were highly enriched relative to the pelagic zooplankton sampled, it appears that kokanee (and

whitefish and rainbow trout) were not incorporating carbon from the pelagic zooplankton sampled here. Collections from June 1998 showed that kokanee $\delta^{15}\text{N}$ signatures were identical for both small and large fish, and $\delta^{13}\text{C}$ values were also similar, suggesting that there is little difference in trophic status or food sources for Okanagan Lake kokanee related to age.

Mysid gut contents

Nearly all mysid stomachs from both size classes contained zooplankton mandibles, rotifer remains (*Keratella* spp. and *Kellicottia* spp.) and detrital material. There was little difference in mandible abundance between lakes for Year 0 mysids, while Year 1 mysids in Okanagan Lake contained 63% more mandibles per gut than similarly sized mysids in Kalamalka Lake (Table 3). The greater number of prey items in large mysids in Okanagan Lake relative to Kalamalka Lake corresponds to higher zooplankton densities for the sampling stations in Okanagan Lake ($19.6 \pm 0.9 \text{ l}^{-1}$) relative to Kalamalka Lake ($15.8 \pm 0.7 \text{ l}^{-1}$) (Table 3). Larger Year 1 mysids contained approximately twice as many mandibles as the smaller Year 0 mysids in both lakes.

Despite lower concentrations of *Daphnia* spp. in both lakes, their mandibles were found in quantities similar to or higher than those of calanoids and cyclopoids, indicating that mysids were preferentially selecting the larger cladocerans. Depending on the time and mysid age, *Diaphanosoma* spp. mandibles were found in numbers similar to those of the calanoid mandibles (Table 3) and *Bosmina* spp. mandibles were low in number or not found. Cyclopoid mandibles were 12 to 14 times more abundant in the guts of larger Year 1 mysids than calanoids in both lakes, reflecting the greater densities of cyclopoids in both lakes.

Mysid clearance rates

Clearance rates varied with mysid age, prey type and lake (Fig. 1). In Okanagan Lake there was no significant difference in mysid clearance rates on the total zooplankton assemblage or individual taxa between cohorts ($p \geq 0.058$). However, in Kalamalka Lake the average Year 1 mysid clearance rate was significantly higher than that of the Year 0 mysids on the total zooplankton assemblage and for all individual taxa, with the exception of *Diaphanosoma* spp. ($p < 0.001$). In general, mysids from both cohorts had higher clearance rates for cladoceran prey (47 to 467 $\text{ml mysid}^{-1} \text{ h}^{-1}$) than copepod prey (9 to 125 $\text{ml mysid}^{-1} \text{ h}^{-1}$) (Fig. 1).

Table 2. *Mysis diluviana*. Proportions of benthic and pelagic carbon (%) assimilated in mysid diet based on mean $\delta^{13}\text{C}$ signatures. Sediment $\delta^{13}\text{C}$ values from August 1997 in Kalamalka Lake were substituted with June 1998 signatures because of highly enriched $\delta^{13}\text{C}$ signatures

Mysid size class	Okanagan Lake		Kalamalka Lake	
	Benthic	Pelagic	Benthic	Pelagic
August 1997				
Small	30	70	13	87
Medium	19	81	4	96
Large	4	96	0	100
June 1998				
Small	21	79	5	95
Medium	59	41	0	100
Large	23	77	0	100

Table 3. *Mysis diluviana*. Zooplankton densities and mandible abundance in gut contents of mysids from Okanagan and Kalamalka Lakes, August 1997 (n = 10 mysids per group). Data are mean (SE)

Prey type	Zooplankton density (ind. l ⁻¹)		Zooplankton mandibles (no. per mysid)			
	Okanagan Lake	Kalamalka Lake	Okanagan Lake Year 0	Okanagan Lake Year 1	Kalamalka Lake Year 0	Kalamalka Lake Year 1
Calanoids	5.5 (0.4)	2.5 (0.3)	0.3 (0.4)	1.1 (0.9)	2.5 (0.8)	1.3 (2.0)
Cyclopoids	12.2 (0.8)	12.2 (0.6)	0.3 (0.2)	12.9 (3.3)	0.9 (0.9)	17.7 (4.6)
<i>Daphnia</i> spp.	1.7 (0.2)	0.4 (0.1)	5.6 (1.7)	37.5 (5.5)	0.8 (0.6)	9.7 (2.9)
<i>Diaphanasoma</i> spp.	0.2 (0.02)	0.5 (0.07)	0.0 (0.0)	0.0 (0.0)	3.3 (0.8)	2.4 (2.5)
<i>Bosmina</i> spp.	0.0 (0.0)	0.2 (0.04)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.5 (0.4)
Total	19.6 (0.9)	15.8 (0.7)	6.1 (1.8)	51.5 (6.4)	7.4 (1.5)	31.6 (6.4)
Mean mysid length (mm)			6.5 (0.2)	15.4 (0.4)	7.5 (0.2)	15.4 (0.2)

Between-lake comparisons showed that average Year 0 mysid clearance rates on the total available zooplankton assemblage were significantly higher in Okanagan Lake than in Kalamalka Lake ($p < 0.001$) (Fig. 1a). For

the larger Year 1 mysids, however, clearance rates were not significantly different between lakes ($p = 0.299$) (Fig. 1b). Mysid size ranges within each cohort during the study (mean lengths of Year 0 = 5.0 to 7.1 mm, Year 1 = 14.1 to 16.5 mm) did not appear to influence clearance rates. No significant relationships were found between average clearance rates on the total zooplankton assemblage and mean body length, with either the Year 0 (ANOVA, $r^2 = 0.07$, $p = 0.40$) or Year 1 mysid cohorts ($r^2 = 0.08$, $p = 0.20$; $n = 12$ for both cohorts).

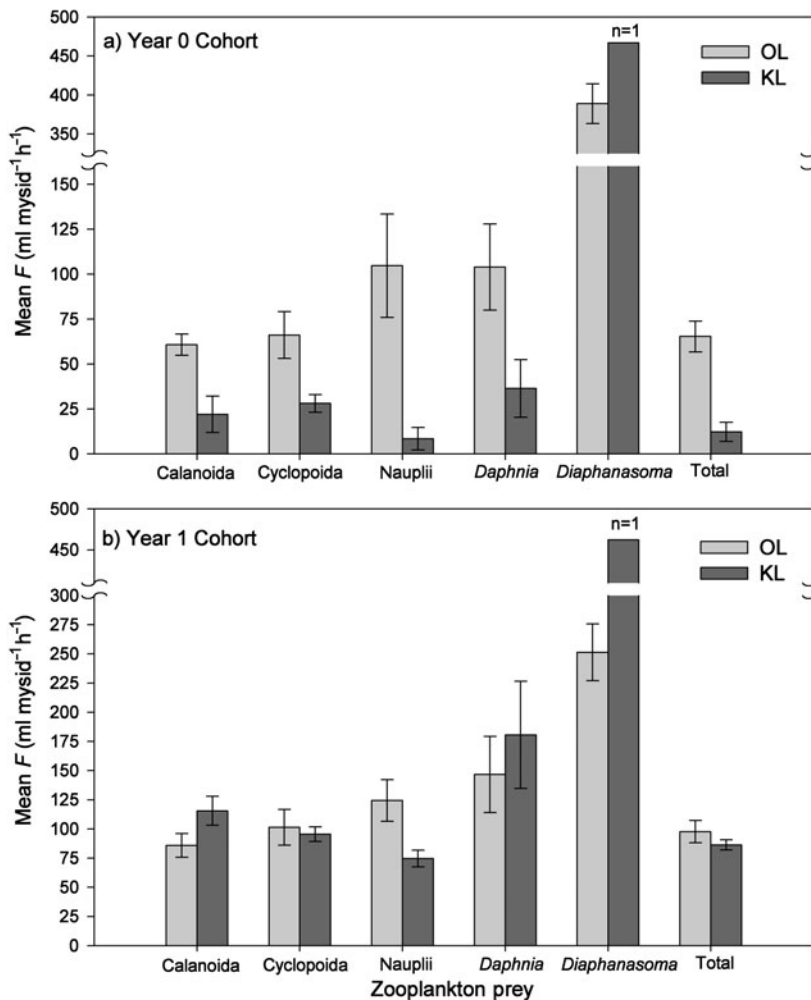


Fig. 1. *Mysis diluviana*. Clearance rates (F) on zooplankton (mean \pm SE) for the (a) Year 0 and (b) Year 1 cohorts in Okanagan (OL) and Kalamalka Lakes (KL) in June and August 1997. Copepods and nauplii were present in all 6 trials in both lakes, while *Daphnia* were present for 3 trials in both lakes

DISCUSSION

Although *Mysis diluviana* in both Okanagan and Kalamalka Lakes originate from the same Kootenay Lake, British Columbia, stock, the mysid populations in these 2 lakes appear to occupy different trophic levels. This plasticity in food selection has allowed the species to colonize many large oligotrophic lakes in North America and northern Europe (Lasenby et al. 1986). We hypothesized that mysids in Okanagan Lake should have been incorporating a greater proportion of zooplankton into their diet relative to mysids in Kalamalka Lake, which contained a much larger kokanee population. Examination of mysid gut contents and clearance rate experiments demonstrated that *M. diluviana* in both lakes were consuming similar proportions of zooplankton prey. Stable isotope analysis revealed that Okanagan mysids did not occupy an elevated trophic position relative to those from Kalamalka Lake.

Trophic position of *M. diluviana*

Trophic position estimates suggested that adult mysids tended to occupy primary and secondary consumer roles in the planktonic food webs of Okanagan and Kalamalka Lakes, respectively. However, stable isotope analyses did not support the original hypothesis that the trophic position of mysids in Okanagan Lake is higher; rather, the mysids' higher trophic position in Kalamalka Lake indicated that their diet contained a greater proportion of zooplankton than the diet of those in Okanagan Lake.

Estimates of trophic position for mysids were determined as the difference in $\delta^{15}\text{N}$ signatures in mysids relative to POM (1 to 64 μm size range), which is assumed to be predominantly composed of phytoplankton (Kling et al. 1992, Keough et al. 1996). The estimated error variance in trophic position estimates in lake food webs is very small (± 0.045 TP) when primary consumers such as mussels or clams are used as a baseline $\delta^{15}\text{N}$ signature compared to primary producers (± 0.16 TP) (Vander Zanden & Rasmussen 2001). However, primary producers were used as baseline trophic position estimates in the present study due to the lack of long-lived primary consumers in the deep pelagic zones. Although clams were available from the littoral zone of both Okanagan and Kalamalka Lakes, the potential for distinct isotopic ratios between littoral and pelagic consumers (France 1995, Keough et al. 1996, Fry 1999) precluded their use for estimating primary producer isotope signatures in the pelagic food web.

Elevated trophic positions for mysids in Kalamalka Lake correspond to higher $\delta^{15}\text{N}$ signatures of sediments in this lake. However, it is not clear to what extent mysids were incorporating the nitrogen-enriched sediments in Kalamalka Lake, as carbon mixing model results suggest Kalamalka Lake mysids were obtaining the majority of their nutrition from pelagic sources. Trophic position estimates for mysids were not calculated using sediment $\delta^{15}\text{N}$ ratios as a baseline because benthic nitrogen sources for mysids would include a mixture of primary and secondary productivity.

Although differences in nitrogen isotope ratios between predator and prey range from +3 to 5‰ (Peterson & Fry 1987), the value of 3.4‰ from Minagawa & Wada (1984) was used to calculate mysid trophic position. A literature review of the change in $\delta^{15}\text{N}$ values for 20 species between consumers and prey in 22 studies revealed an overall enrichment of $3.46 \pm 0.23\%$ (Vander Zanden & Rasmussen 2001). This value is also very close to the mean trophic enrichment of +3.2‰ between a frozen cladoceran food source and *Neomysis integer* in controlled laboratory feeding experiments (Toda & Wada 1990). In Lake Ontario, a trophic enrichment factor of 2.2‰ $\delta^{15}\text{N}$ provided the best cor-

respondence between observed stable isotope signatures for *Mysis diluviana* and those expected based on dietary composition and a 100% nitrogen tissue turnover rate (Johannsson et al. 2001). Our assumed fractionation factor of 3.4‰ is higher than that of Lake Ontario mysids; however, the mean trophic enrichment factor between *Daphnia* spp. and POM in the present study was $+3.3 \pm 0.4\%$, suggesting that an assumed transfer of +3.4‰ $\delta^{15}\text{N}$ between trophic levels was appropriate.

Food sources of *Mysis diluviana*

There is isotopic evidence that mysids are feeding on different food sources according to their stage in life. With the exception of Okanagan Lake in August 1997, large mysids were enriched in $\delta^{15}\text{N}$ relative to small mysids by approximately 2‰, which resulted in an elevated trophic position estimate for large mysids of 0.6 to 0.8. This nitrogen isotope enrichment in the larger mysids suggests an ontogenetic shift in diet to incorporate a greater proportion of the more enriched zooplankton food source relative to POM. Similar ontogenetic shifts in nitrogen isotopic enrichment for *Mysis diluviana* have been reported in eastern North American lakes (Branstrator et al. 2000). Here, seasonal $\delta^{15}\text{N}$ values also increased by approximately 2‰ (range = 1.7 to 3.1‰) between small and large mysids, representing an increase in trophic elevation of 0.6 to 0.9 (Branstrator et al. 2000).

Mysid $\delta^{13}\text{C}$ values also indicate a potential shift in food resources with age. The 2-stage mixing model comparing mean pelagic and benthic $\delta^{13}\text{C}$ signatures showed that mysids assimilated most of their carbon from planktonic rather than benthic sources. The relative proportions of more depleted planktonic $\delta^{13}\text{C}$ to more enriched benthic $\delta^{13}\text{C}$ tended to increase with increasing mysid size class, suggesting that the mysids relied more extensively on plankton with increasing age.

Mysis diluviana is omnivorous and may change its diet with seasonal changes in food availability (Johannsson et al. 2001). Gorokhova & Hansson (1999) demonstrated that for *M. mixta* and *Neomysis integer*, different foods with different isotopic ratios give rise to different isotopic composition in the mysid tissue. They also showed that the isotopic composition of different tissues depends on the growth and turnover rate of the tissue. Isotopic ratios in muscle tissue reflected food sources obtained over the previous 6 to 8 wk for $\delta^{15}\text{N}$ and up to 3 mo for $\delta^{13}\text{C}$. In the present study, we used similarly sized mysids collected at the same time of year and analyzed whole animals from both lakes. We examined gut contents and carried out clearance rate

experiments to confirm that mysids from both lakes had similar diets at the time of collection. However, seasonal variation may occur and further studies should be undertaken to address this.

Mysids can obtain a substantial portion of their energy from sediments during the daylight hours, when they are not foraging in the pelagic zone (Parker 1980, Johannsson et al. 1994, Leggett 1998). In Okanagan Lake, *Mysis diluviana* appeared to be obtaining more of its diet from the sediments, as benthic carbon contributed up to 59% compared to $\leq 13\%$ in Kalamalka Lake. This does not support the hypothesis that mysids in Okanagan Lake incorporate a greater proportion of zooplankton prey if they outcompete kokanee for zooplankton resources.

Acoustic echograms of mysids in Okanagan Lake from a 150 m deep station showed that a large portion of the population remained at between 100 and 120 m during the day (Levy 1991), which would reduce potential feeding time on sediment detrital organic matter. Although mysids in both lakes were restricted to >50 m depth after sunrise (Whall 2000), it is not known what proportions of the population were located at the sediment–water interface. Kalamalka Lake mysids may remain higher off the sediments because of the reduced water transparency from the high carbonate levels in the water column. Mysids remain elevated in the water column in the Armstrong Arm region of Okanagan Lake, which has greatly reduced water transparency relative to the main basins (McEachern 1999). As transparency in Kalamalka Lake (as measured by Secchi depth) was 1 to 3 m lower than in Okanagan Lake during the sampling periods (McEachern 1999), mysids may not have been migrating as deeply in the less transparent Kalamalka Lake, and therefore not incorporating as much sediment detrital matter in their diets.

Mysids were obtained in night-time vertical hauls from ~2 m off the bottom to the surface. Therefore, if a proportion of the population remained at the sediment–water interface during the nightly migration, they would not have been included in our stable isotope analyses. It is unlikely, however, that these animals would have distinctly different diets, as Johannsson et al. (2001) found no consistent differences in $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ isotope ratios for ascending, descending or benthic *Mysis diluviana* in Lake Ontario.

Lipids of aquatic consumers can be depleted in $\delta^{13}\text{C}$ relative to body tissues, and intensive lipid storage may result in lower $\delta^{13}\text{C}$ signatures than an organism's diet (Gu et al. 1994, 1996, Leggett 1998). In a comparison of lipid-extracted and non-lipid-extracted mysids from Lake Ontario, Leggett (1998) found that the mean $\delta^{13}\text{C}$ of mysids with lipids removed (-28.9 ± 0.58) was enriched relative to non-treated mysids (-32.2 ± 0.67).

However, Adare & Lasenby (1994) found that between several lakes spanning a range of trophic states, similarly sized mysids had similar lipid contents. As mean size of mysids in Okanagan and Kalamalka Lakes sampled for stable isotopes was within 1 mm of each other (Table 1), we do not expect significant differences in lipid-related carbon depletion between them. Smyntek et al. (2007) established a correction factor for $\delta^{13}\text{C}$ enrichment in lake zooplankton based on their C/N ratios. In the future, species-specific $\delta^{13}\text{C}$ value lipid-correction factors based on measured C/N ratios (as established for mysids by Leggett 1998) may be necessary for all members of the food web being studied.

The lack of increase in $\delta^{15}\text{N}$ signatures in mysids relative to copepods is puzzling. Although selectivity coefficients have shown that cladocerans are selected over copepods, mysids readily consumed copepods in experimental chambers and in gut content analysis in the present study. Toda & Wada (1990) also found that mysid $\delta^{15}\text{N}$ signatures were on average ~1‰ lower than those of zooplankton and ~3.7‰ enriched relative to POM (mostly phytoplankton), despite being an assumed predator on the zooplankton. The authors suggested that zooplankton did not constitute a major source of the mysid diet, but rather that mysid $\delta^{15}\text{N}$ signatures tracked the seasonal changes in POM more closely. Branstrator et al. (2000) also found that fractionation factors (i.e. trophic elevations) for *Mysis diluviana* relative to bulk zooplankton samples were <1 (range = 0.1 to 0.89), implying that for their study lakes in eastern North America, mysids had diets similar to that of bulk zooplankton.

Another potential food source for *Mysis diluviana* are benthic invertebrates. Due to difficulties in recovering benthos from the deep mysid sampling stations (generally >150 m), representative chironomid samples were obtained from shallower littoral regions (<40 m) in August 1997. Mysid $\delta^{15}\text{N}$ ratios were enriched by 3.2 to 5.0‰ relative to chironomids, while $\delta^{13}\text{C}$ values were nearly equivalent to those of mysids (Table 1), suggesting that chironomids may also make up part of the diet of *M. diluviana* in the 2 lakes. Although chironomid mandibles were not found in the guts of the mysids examined, this may have been due to the relatively small sample size ($n = 10$ per lake) or the result of rapid gut passage times (generally between 1 and 6 h for *M. diluviana*; Chipps 1998) and the fact that the animals were retrieved several hours after migrating off the lake bottom and feeding in the metalimnion.

Interactions between mysids and kokanee

Stable isotopes suggest that in Okanagan Lake there may be more separation in the trophic and feeding

relationships between the deep-water mysids and kokanee than previously thought. Based on $\delta^{15}\text{N}$ values, kokanee salmon are occupying a higher trophic position (3.2 to 3.3) than *Mysis diluviana* (1.9 to 2.5). In addition, kokanee $\delta^{13}\text{C}$ values are enriched relative to pelagic zooplankton in Okanagan Lake by more than the mean trophic enrichment factor of 0.8‰ observed for aquatic consumers (herbivores excluded; Vander Zanden & Rasmussen 2001). Spatial separation within the lake can lead to differences in carbon signatures: $\delta^{13}\text{C}$ signatures in both POM and zooplankton from the littoral zone can be enriched relative to those in the pelagic zone (Fry 1991). This separation in $\delta^{13}\text{C}$ was found for alewife *Alosa pseudoharengus* in Lake Superior; Keough et al. (1996) found that the $\delta^{13}\text{C}$ signature of the alewife was more closely linked with the enriched carbon isotopes found in the shallow wetland ecosystem than the more ^{13}C -depleted pelagic system, suggesting that alewife may have spent more time feeding in the shallower regions of the lake. Therefore, kokanee, which are primarily planktivorous (Foerster 1968), may be consuming zooplankton that are spatially distinct from the pelagic zooplankton consumed by the deep-water mysids. Evidence from stable carbon isotope studies with $\delta^{13}\text{C}$ has indicated that dual trophic pathways from benthic and pelagic production to consumer biomass can be important in lakes (Vadeboncoeur et al. 2002, Vander Zanden & Vadeboncoeur 2002). It is possible that both benthic and pelagic pathways play a significant role in kokanee production in Okanagan Lake.

Supporting evidence for mysid predatory capabilities

Clearance rates represent the ability of a predator to remove prey items from its environment within a given amount of time. Higher clearance rates for particular prey items reflect a more efficient predatory capacity and imply selection pressure on those prey species. In both study lakes, clearance rates were highest for cladocerans and copepod nauplii, followed by adult copepods. Bowers & Vanderploeg (1982) reported a

similar order of preference for mysids feeding on a natural zooplankton assemblage from Lake Michigan, where cladocerans are preferred, followed by copepod copepodites and nauplii, and lastly adult copepods. Adult mysid clearance rates for copepods in the present study were generally similar to those found in other central and western North American lakes (Table 4). Clearance rates on cladocerans however, were markedly lower than those found for mysids in Lake Michigan and central Ontario lakes. The significantly higher clearance rates for larger mysids >1 yr old over smaller mysids <1 yr old in Kalamalka Lake supports the isotopic evidence for increased predatory capacity with size. Further support comes from gut contents, where larger mysids >1 yr old from both study lakes contained twice the number of zooplankton mandibles in their guts as mysids <1 yr old (Table 3).

The variability in clearance rates between the present and other studies suggests that the ability of a mysid to search for, secure and ingest its prey will be influenced by lake-specific factors such as temperature, light availability, productivity and prey assemblage (Nero & Sprules 1986, Smokorowski 1998). The relatively low variability surrounding the clearance rate estimates for both lakes over 2 sampling months indicates that mysid populations within each lake have generally consistent feeding preferences.

By conducting clearance rate experiments and gut content analysis concurrently with nitrogen and carbon isotope analyses, the present study has demonstrated the advantages of using multiple lines of evidence in assessing the diets of omnivorous zooplankton such as *Mysis diluviana*. Basing trophic role estimates only on clearance rate data or gut contents would have overestimated the contribution of zooplankton to mysid diets, without being able to quantify the amount of primary production being assimilated. Likewise, caution must be used when interpreting stable isotope data, because signatures can be confounded by physiological and environmental factors; temporal trends in isotopic ratios of consumers can arise due to differences in animal growth rates, lipid content, degree of fractionation and seasonal changes

Table 4. *Mysis diluviana*. Comparison of adult mysid clearance rates ($\text{ml mysid}^{-1} \text{h}^{-1}$) between the present study and selected North American lakes

	Calanoids	Cyclopoids	Copepod nauplii	<i>Daphnia</i> spp.	<i>Diaphanosoma</i> spp.	Source
Okanagan and Kalamalka Lakes	22–116	28–101	8–124	47–181	251–467	This study
Kootenay Lake	50–110	50–120	–	10–80	110–232	Smokorowski (1998)
Central Ontario lakes	42–110	–	75–167	392–801	452–1019	Nero & Sprules (1986)
Lake Michigan	40–113	0–339	294	870 ^a	–	Bowers & Vanderploeg (1982)
Flathead Lake	–	61–133	–	221–244	–	Spencer et al. (1999)

^acombined Cladocera (*Daphnia* and *Bosmina*)

in isotope ratios of primary producers (Leggett 1998, Johannsson et al. 2001, Vander Zanden & Rasmussen 2001). In the present study, stable isotopes demonstrated that mysids were not occupying the same trophic position in both lakes, but clearance rate and gut content data confirmed the importance of dietary food sources, such as copepods, that were not reflected in the isotope signatures of the mysids.

In summary, our hypothesis that *Mysis diluviana* in Okanagan Lake should be occupying a relatively higher trophic position than mysids in Kalamalka Lake was not supported, since stable isotopes indicated that Kalamalka Lake mysids were acting as secondary consumers or true carnivores, whereas Okanagan Lake mysids were closer to primary consumers, incorporating a greater proportion of their energy from primary producers. These results demonstrate the benefits of using both assimilated nutrient content (i.e. stable isotope analysis) and direct dietary assessments (i.e. *in situ* feeding experiments and gut content analysis) in establishing trophic roles for omnivorous animals.

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Plankton development in Lake Jonsvatn, Norway, after introduction of *Mysis relicta*: a long-term study

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ABSTRACT: Quantitative sampling of phyto- and zooplankton has been carried out for 25 yr in Lake Jonsvatn, Norway, in order to assess changes after the introduction of *Mysis relicta*. In Lille Jonsvatn, the outlet basin, the cladoceran populations collapsed 7 yr after the mysid introduction. The mean cladoceran biomass was reduced by 95 to 99% for a decade before *Bosmina longispina*, *Holopedium gibberum* and *Daphnia galeata* developed new populations. *B. longispina* and *H. gibberum* almost disappeared again after a few years, while *D. galeata* was replaced by *D. longispina*, which unexpectedly maintained a relatively dense population in the presence of high mysid abundance. Rotifers declined significantly in Lille Jonsvatn after the mysid establishment, whereas copepod biomass did not change. Phytoplankton biomass increased during the first years after the cladoceran collapse, but declined later to levels lower than in pre-mysid years. The changes were probably a combined effect of reduced nutrient loads and grazing pressure. In the main basin, Store Jonsvatn, there were no detectable effects on the zooplankton community during the first 10 to 15 yr after the introduction, in spite of development to common densities of mysids within 8 yr. Over time, cladocerans decreased significantly, however, and mean biomass for the last 5 yr showed a 60% reduction compared with the first 10 yr. No significant long-term changes were detected in copepods, rotifers or phytoplankton biomass in Store Jonsvatn. Differences in temperature, stratification, light transmission and depth may partly explain the different plankton development in the 2 basins.

KEY WORDS: *Mysis relicta* · Long-term study · Phytoplankton biomass · Zooplankton biomass

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INTRODUCTION

From 1954 to 1975 the opossum shrimp *Mysis relicta* was introduced in many lakes in Scandinavia in order to serve as a supplementary food for fish. In Sweden, introductions took place in 61 lakes (Fürst et al. 1984), and in Norway in 9 lakes. The Norwegian introductions all took place between 1968 and 1974, and through downstream dispersal *M. relicta* established populations in 6 additional lakes. The introductions in Scandinavia were specifically performed in lakes that were regulated for hydroelectric power production, where production of fish food organisms was reduced because of large fluctuations in water level. Before and

concurrently with the Scandinavian introductions, the species was also introduced to a large number of North American lakes (Lasenby et al. 1986, Nesler & Bergersen 1991).

Mysis relicta was assumed to feed mainly on dead organic matter from the bottom in the deeper parts of the lakes, and through extensive diurnal vertical migrations it would act as an energy elevator by serving as fish food in the upper water layers (Fürst et al. 1984). The dietary habits of *M. relicta* turned out to be quite complex, however. Grossnickle (1982) showed in an overview that *M. relicta* is capable of both filter-feeding and raptorial feeding, eating phytoplankton, zooplankton, benthos, detritus and sediments. More re-

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cent studies have added nuanced information to the omnivorous feeding habits of *M. relicta* (Branstrator et al. 2000, Johannsson et al. 2001, Lasenby & Shi 2004, Ikonen et al. 2005, Scharf & Koschel 2005). After introductions both in North America and Scandinavia, it gradually became evident that *M. relicta* had the ability to reduce zooplankton abundance and change species composition through its predatory behavior (Lasenby & Langford 1973, Threlkeld et al. 1980, Kinsten & Olsén 1981, Lasenby et al. 1986, Nero & Sprules 1986a, Langeland et al. 1991, Spencer et al. 1999). In many of the target lakes, *M. relicta* turned out to be an effective competitor with planktivorous fish for zooplankton prey. Because of its diurnal migratory behaviour, *M. relicta* avoided, to a large extent, predation by pelagic fish that search visually for food (Næsje et al. 1991).

The knowledge of effects from mysid introductions in Scandinavia is mainly restricted to oligotrophic regulated lakes (Fürst et al. 1984, Langeland et al. 1991). Lake Jonsvatn is unregulated and consists of basins that differ with respect to morphometry and water quality. Some studies indicate that increased lake productivity may reduce the adverse effects of *Mysis relicta* on the plankton populations (Nesler & Bergersen 1991). In the present study, special attention was given to the basin called Lille Jonsvatn, which had a higher nutrient level than typical lakes with introduced mysids in Norway, and was therefore hypothesized to be less negatively affected.

The introduction of *Mysis relicta* to Lake Jonsvatn was due to a water diversion tunnel from the neighbouring Lake Selbusjøen where mysid introduction took place in 1973. Most probably, *M. relicta* was swept into Lake Jonsvatn when the tunnel was opened for the first time in 1978. The tunnel is normally closed. An investigation in 1981 showed that *M. relicta* was by then established in Store Jonsvatn. As water flows from Store Jonsvatn through Lille Jonsvatn into the outlet river, *M. relicta* most likely developed populations almost simultaneously in the 2 basins.

The present study deals with the long-term development of phyto- and zooplankton in Lake Jonsvatn after introduction of *Mysis relicta*. It is based on data from 1980 to 2006. The Lake Jonsvatn study represents the longest continuous data series in Scandinavia on the development of the plankton communities after introduction of *M. relicta*. It has been classified by the Norwegian Research Council as especially valuable to maintain.

MATERIALS AND METHODS

Study site. Lake Jonsvatn (63° 22' N, 10° 37' E) is located 150 m above sea level in central Norway (Fig. 1). It is an oligotrophic lake that serves as a drinking water

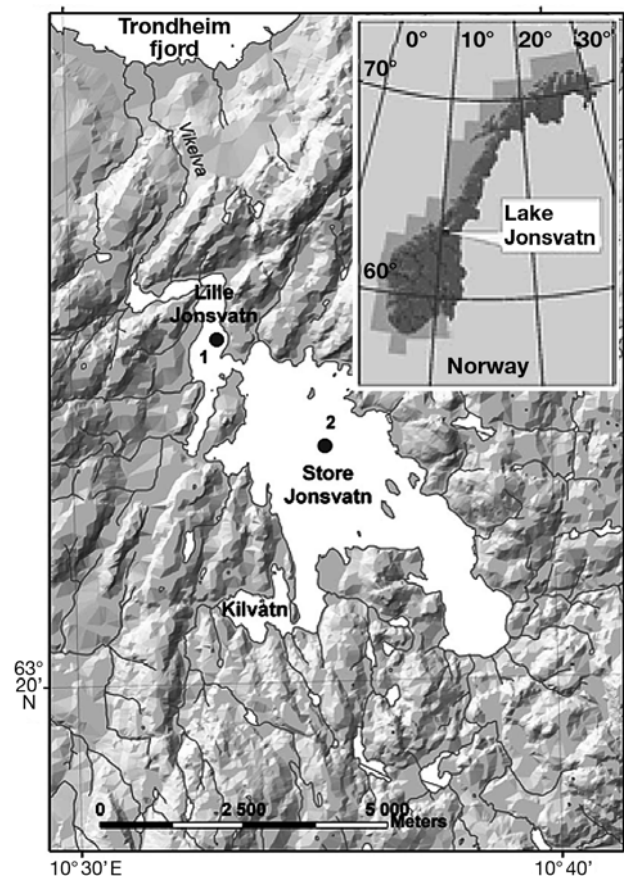


Fig. 1. Lake Jonsvatn, Norway, and sampling stations in Lille Jonsvatn (1) and Store Jonsvatn (2)

reservoir for the city of Trondheim (160 000 inhabitants). The surface area is 15 km², maximum depth 97 m and mean depth 37 m. In addition to the main basin—Store Jonsvatn (12.4 km²)—the lake has 2 nearly disconnected basins, Lille Jonsvatn (1.6 km²) and Kilvatn (0.8 km²). There are narrow sounds with depths of 1 to 3 m between the main lake and the embayments. The maximum depth in Lille Jonsvatn is 37 m and in Kilvatn 34 m.

The chemical data of Lille Jonsvatn and Store Jonsvatn are characteristic for oligotrophic conditions (Table 1). However, both total P (Mann-Whitney *U*-test,

Table 1. Physical and chemical characteristics (range of annual means) of surface waters (0 to 5 m) of Lille Jonsvatn and Store Jonsvatn between 1989 and 2006. Data provided by the Environmental Division, Municipality of Trondheim

	Annual mean range	
	Lille Jonsvatn	Store Jonsvatn
pH	7.1–7.5	7.2–7.4
Conductivity (μS cm ⁻¹)	64–74	51–64
Total P (μg l ⁻¹)	4.6–10.6	2.4–7.4
Total N (μg l ⁻¹)	311–428	297–419

$p = 0.001$) and total N ($p = 0.045$) are significantly higher in Lille Jonsvatn. The P content (average of mixed samples from 0 to 5 m from all seasons) has significantly decreased in both Store Jonsvatn and Lille Jonsvatn during the investigation period (Fig. 2).

Epilimnetic summer temperatures normally reach 15 to 20°C in both basins, whereas temperatures at 20 m depth reach 5 to 7°C (Fig. 3). Temperatures closer to the bottom stay at 4 to 6°C throughout the summer. Due to a higher degree of wind exposure, the thermocline lies deeper in Store Jonsvatn than in Lille Jonsvatn (Fig. 3). Secchi depth observations show that light transmission is highest in Store Jonsvatn (Table 2).

The drainage area mainly consists of coniferous forests and some cultivated farmland, especially around Lille Jonsvatn. Restrictions on farming and development have been imposed since the early 1990s in order to reduce the runoff of nutrients from human activities.

Arctic char *Salvelinus alpinus*, brown trout *Salmo trutta*, northern pike *Esox lucius* and three-spined stickleback *Gasterosteus aculeatus* are the only fish species that occur in Lake Jonsvatn. Brown trout, northern pike and three-spined stickleback occurred only in the littoral zone in Store Jonsvatn, whereas Arctic char utilized both the littoral and the pelagic

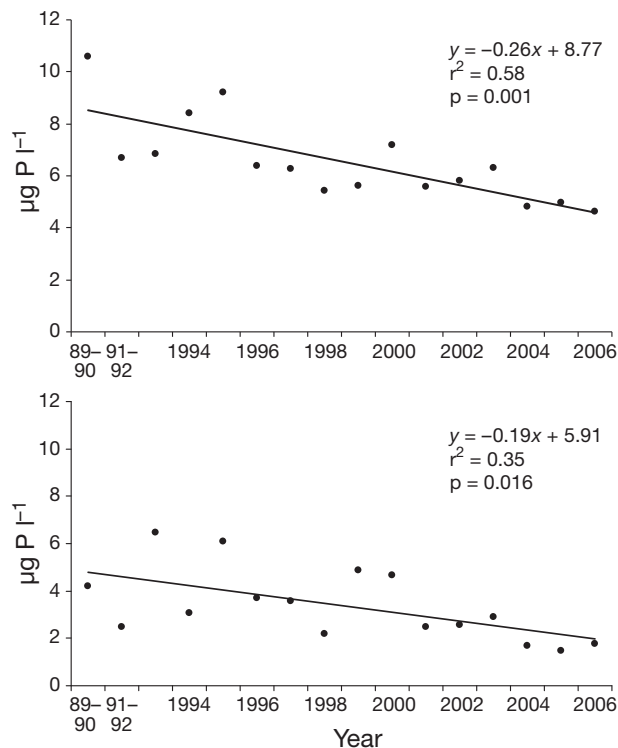


Fig. 2. Regression of total P ($\mu\text{g l}^{-1}$) versus sampling year in Lille Jonsvatn (top) and Store Jonsvatn (bottom). Only pooled data were available for the years 1989–1990 and 1991–1992. Data provided by the Environmental Division, Municipality of Trondheim

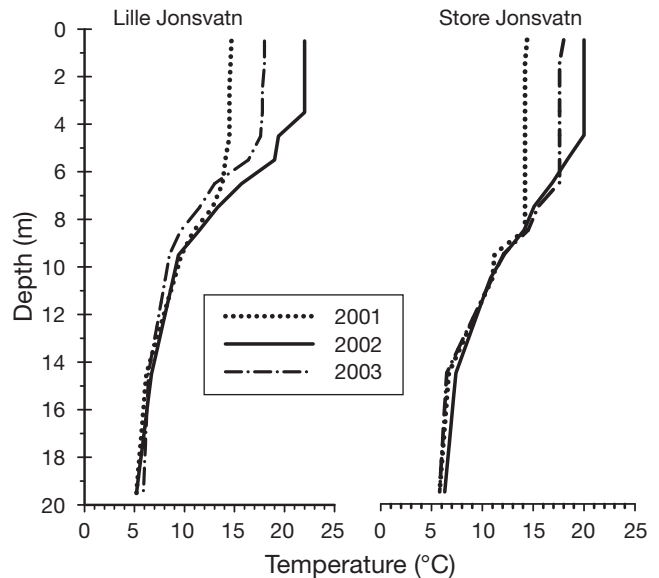


Fig. 3. Temperature profiles in Lille Jonsvatn and Store Jonsvatn. Early August data from 3 subsequent years with different summer temperatures

zones (Næsje et al. 1991). An investigation of the fish populations in Lille Jonsvatn in 1999 gave an extremely low yield of Arctic char and brown trout both in the littoral zone, along the bottom in deeper areas and in the pelagic zone, whereas northern pike were exclusively caught along the bottom (Koksvik 2000). We have observed three-spined stickleback only along the shore. In Store Jonsvatn, the catch per unit effort (CPUE, 24 h fishing, 0 to 10 m depth) in floating gillnets was <1 to 5 Arctic char per 100 m² net area in the pelagic zone (Næsje et al. 1991), while the corresponding yield (0 to 6 m depth) was 0.4 Arctic char and 0.2 brown trout in Lille Jonsvatn (Koksvik 2000). According to local fishermen, the populations of Arctic char and brown trout have been very small for several decades in Lille Jonsvatn.

Table 2. Secchi depths (m) in Lille Jonsvatn and Store Jonsvatn. Data are June–September averages for 2001 to 2006

Year	Secchi depth (m)	
	Lille Jonsvatn	Store Jonsvatn
2001	4.3	5.5
2002	5.5	6.7
2003	5.4	6.8
2004	5.0	6.8
2005	5.3	6.9
2006	5.3	6.2
Mean	5.1	6.5

Plankton sampling. Plankton was sampled at Stns 1 & 2 (Fig. 1). Zooplankton was sampled with a 1 m long plexiglass tube sampler. Each sample contained 5 l of water. A vertical column extending from 0 to 20 m depth was consistently sampled every 1 m. Samples from 5 m layers were mixed and treated as one sample. Additional zooplankton sampling was carried out by vertical net hauls (90 μm mesh) to secure sufficient material for length measurements and biomass calculations. The net was hauled vertically from 20 m to the surface. Zooplankton samples were preserved with Lugol's solution in the field and later transferred to 70% ethanol for permanent storage.

All zooplankton samples were identified to species and enumerated. Counts were carried out on the total samples or subsamples containing $\frac{1}{10}$ of the total sample. On each sampling date, length measurements were made on 30 to 50 individuals of each cladoceran species from each station. Copepods were distinguished to the instar level when counted. Biomass calculations for cladocerans and copepods (with fixed individual weights for different instars) were made according to length/weight regressions from Bottrell et al. (1976) and Langeland (1982). Rotifer biomass was calculated using individual weights given in Bottrell et al. (1976). The zooplankton material has been incorporated into the collections of the Museum of Natural History and Archaeology at the Norwegian University of Science and Technology.

Integrated phytoplankton samples from 0 to 5 and 5 to 10 m were collected in Lille and Store Jonsvatn with a plexiglass water sampler (volume = 1.6 l). Phytoplankton samples of 200 ml were taken from the pooled samples and preserved with Lugol's solution. The samples were analysed according to the Utermöhl settling technique. For each sample a minimum of 200 cells or colonies was counted and identified to genus or species. Volume of counted cells was calculated using simple geometric models, and the biovolume was converted to wet weight assuming a specific gravity of 1.0 mg mm^{-3} . Wet weights for algal groups and total algal biomass are given as means of biomass of the 2 integrated samples, i.e. mean biomass of 0 to 10 m.

Mysis relicta was sampled by vertical net hauls in Lille Jonsvatn in 1996 and 1999–2006. The net had a frame opening of 1 m^2 , a mesh size of 500 μm and was equipped with a lead weight at its mouth, sinking upside down before being hauled up again vertically. Each sample thus consisted of 2 vertical hauls, between 1 m above the bottom (30 m) and the surface. Sampling was performed on the plankton station in the dark in October–November, which is within the period when *M. relicta* is most abundant in the pelagic zone in Lake Jonsvatn (Næsje et al. 1991, 2003); 3 replicate hauls were performed on every sampling occasion.

The present study did not include sampling of mysids in Store Jonsvatn.

In 1980, zooplankton was sampled on 3 occasions within the June–September period, and in 1983 to 1987, monthly from June to September. From 1988 onwards, zooplankton samples were collected 6 times per year (monthly sampling in June and September, twice monthly in July and August). Both plankton stations were always sampled simultaneously. Phytoplankton was sampled at the same stations and dates as zooplankton in Lille Jonsvatn in 1980, 1983, 1985, 1986 and 1988–2006, and in Store Jonsvatn in 1980, 1983, 1985, 1987, 1994 and 1996–2006. Biomass means of both phytoplankton and zooplankton are given as estimated averages of all samples in the particular year. The change in sampling intensity from 1988 onwards might have led to a slight increase of mean zooplankton biomass and for some years a decrease in mean phytoplankton biomass, but not to an extent that has influenced the trends of development in either group.

RESULTS

Zooplankton

In Lille Jonsvatn, a mean biomass (June–September) of 1100 to 1650 mg m^{-2} (dry weight) was recorded until 1985, when a dramatic decline took place (Fig. 4). The cladoceran biomass was then reduced to less than 5% of the mean for 1980–1984, and in 1986–1987 the cladocerans had become virtually extinct (mean biomass = 2 and 9 mg m^{-2} , respectively). Extremely low biomasses of cladocerans were recorded for 10 yr. The previously dominant species, *Bosmina longispina*, had a mean biomass in 1985–1994 that was less than 1% compared with the estimates for years prior to 1985, and the other common species, *Daphnia galeata* and *Holopedium gibberum*, were irregularly found in low numbers throughout this period. In 1995, a moderate recovery of *B. longispina* was recorded (140 mg m^{-2}). In 1996, the mean biomass of *B. longispina* increased to almost 600 mg m^{-2} , and *D. galeata* and *H. gibberum* also developed populations with mean biomasses of 170 and 320 mg m^{-2} , respectively (Fig. 5). Total cladoceran biomass was again on the level recorded before the collapse in 1985. After 1996, the mean biomass of cladocerans has varied between 230 and 540 mg m^{-2} . Since 1998, *B. longispina* has been virtually absent, and *H. gibberum* has also been recorded in extremely low numbers except for a moderate abundance in 2000. The daphnids continued to increase until 2000, and have afterwards fluctuated in abundance. The highest daphnid biomass (540 mg m^{-2}) in the entire investigation period was recorded in 2006. *D. galeata*

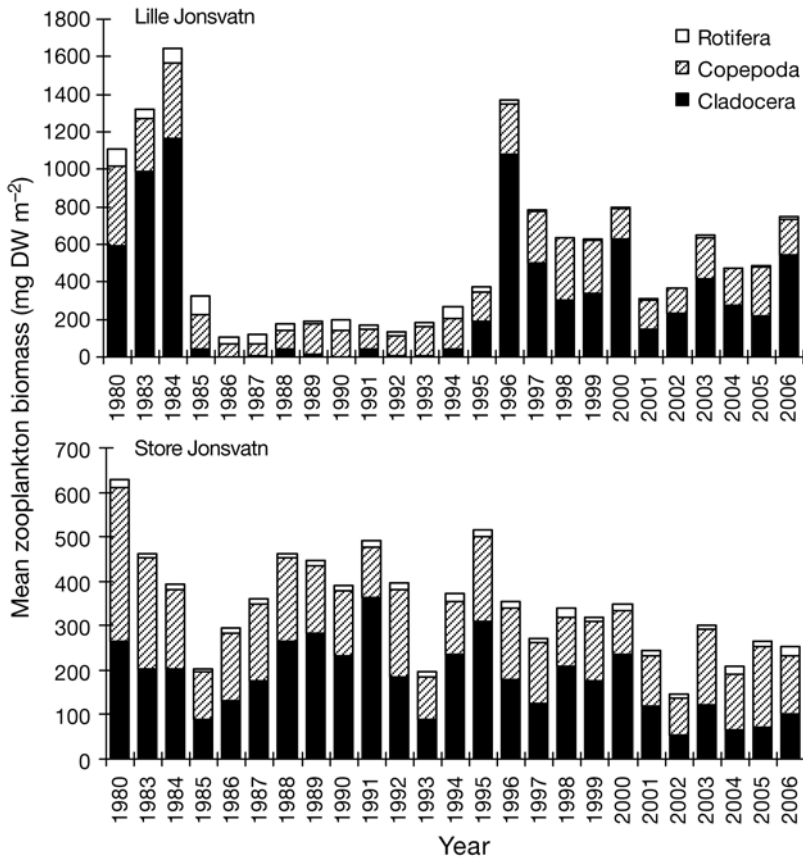


Fig. 4. Mean June–September biomass (mg dry weight m⁻² over 20 m) of zooplankton in Lille Jonsvatn (top) and Store Jonsvatn (bottom) in the period 1980–2006. The lake was not sampled in 1981 and 1982

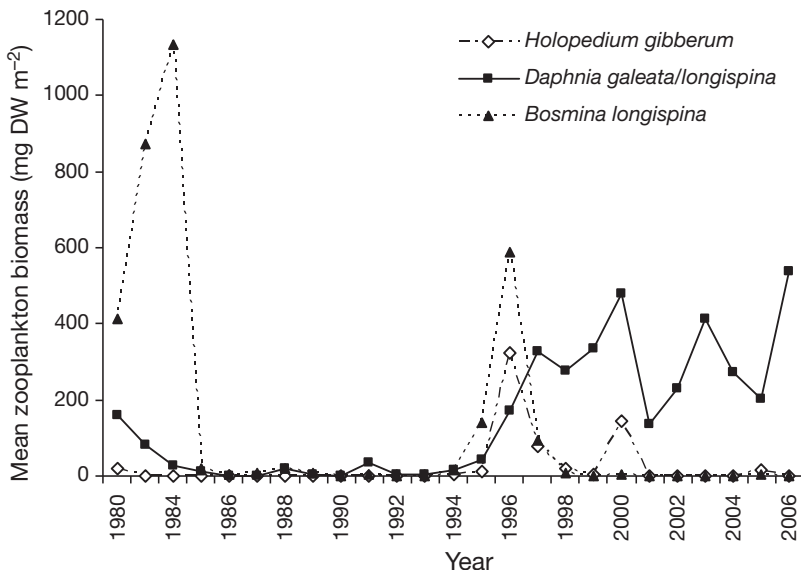


Fig. 5. *Holopedium gibberum*, *Daphnia galeata/longispina* and *Bosmina longispina*. Development of zooplankton biomass (mg dry weight m⁻² over 20 m) in Lille Jonsvatn over the period 1980–2006. The lake was not sampled in 1981 and 1982

was the only daphnid in the samples until 1998, when *Daphnia longispina* turned up, and became the dominant species from 1999 onwards. The biomass of *D. galeata* after the appearance of *D. longispina* was extremely low (<1 to 6 mg m⁻² in 2004–2006).

Total biomass of copepods also declined in Lille Jonsvatn after 1984 (Fig. 4), but not to the same extent as cladocerans. Mean biomass for the years 1985–1995 was 129 ± 12 (SE) mg m⁻², compared to 369 ± 43 mg m⁻² for the years prior to 1985; copepod biomass was significantly different in the 2 periods (Mann-Whitney *U*-test, $p < 0.01$). The biomass reduction in copepods was mainly due to the dominant species *Cyclops scutifer*. The other copepods in question, *Heterocope appendiculata*, *Arctodiaptomus laticeps* and *Mesocyclops leuckarti*, showed no clear trend in biomass between 1985 and 1995. In 1996, copepods developed the highest biomass since 1984, and a level of 270 to 330 mg m⁻² was maintained until 2000. Mean biomass for the period 1996–2006 was 224 ± 18 mg m⁻², which is 73% higher than for 1985–1995. The difference in biomasses between the 2 periods was highly significant ($p < 0.001$). *C. scutifer* was the dominant species through the entire period. *Acanthodiptomus denticornis* turned up as a new copepod species in 1999, and maintained the second highest biomass for all but one year afterwards, closely followed by *A. laticeps*.

Rotifer biomass was relatively high (55 to 95 mg m⁻²) in 1980–1984 and dominated by the colony forming *Conochilus* sp. that made up 50 to 75% of the total. *Asplanchna priodonta*, *Polyarthra* sp., *Keratella cochlearis* and *Kellicottia longispina* also made up a significant share of the biomass. After 1984, *Conochilus* sp. biomass dropped to almost zero for a 10 yr period; after that, it varied at very low levels. *Kellicottia longispina* was also strongly decimated after 1984. From 1996 on, all species had very low biomass, and total rotifer biomass averaged 2 to 12 mg m⁻² in 1997–2006. *Keratella cochlearis* had the highest biomass most years during this period. The development of rotifers through the entire investigation period fits an exponential regression (Fig. 6).

In Store Jonsvatn, zooplankton biomass decreased between 1980 and 1985, but then increased again until 1988 (Fig. 4). The changes were caused by the cladocerans *Bosmina*

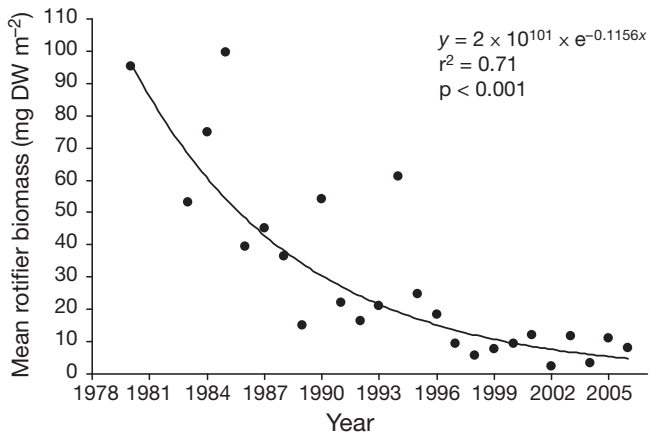


Fig. 6. Regression of mean rotifer biomass (mg dry weight m^{-2} over 20 m) versus sampling year (1980–2006) in Lille Jonsvatn. The lake was not sampled in 1981 and 1982

longispina and *Daphnia galeata* and the copepods *Cyclops scutifer* and *Heterocope appendiculata*. After 1988 there was a long-term decrease in cladoceran biomass (Fig. 7). The change fits a linear regression. The most pronounced decline was found in *B. longispina* and *D. galeata*. Mean biomass of cladocerans in 1998–2006 was $128 \pm 22 \text{ mg m}^{-2}$ compared to $226 \pm 27 \text{ mg m}^{-2}$ in 1988–1997. The difference in biomass was highly significant (Mann-Whitney *U*-test, $p < 0.01$), and 4 of the last 5 years studied represent the lowest biomasses of Cladocera in the entire investigation period.

A corresponding decline in copepod biomass was not detected in Store Jonsvatn. Mean biomass in 1998–2006 was $127 \pm 11 \text{ mg m}^{-2}$ compared to $150 \pm 11 \text{ mg m}^{-2}$ in 1988–1997 (not significant; Mann-Whitney *U*-test, $p = 0.14$). *Cyclops scutifer* was the dominant species in most years, constituting a mean of 55% of the total copepod biomass in 1988–2006. *Heterocope*

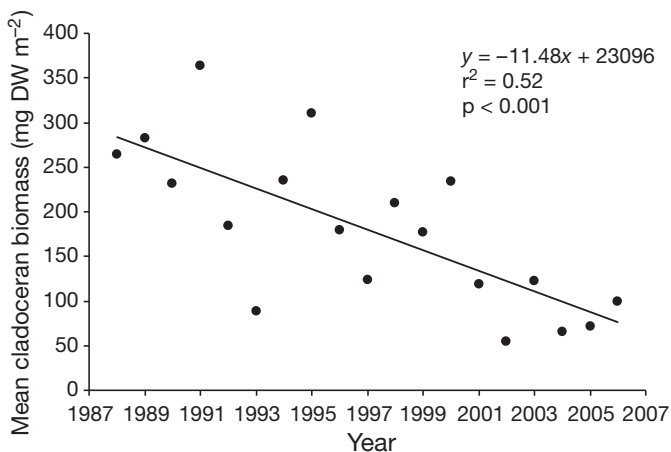


Fig. 7. Regression of mean cladoceran biomass (mg dry weight m^{-2} over 20 m) versus sampling year (1988–2006) in Store Jonsvatn

appendiculata and *Arctodiaptomus laticeps* were present with moderate abundance in all years and did not show any significant trend in biomass. As in Lille Jonsvatn, *Acanthodiaptomus denticornis* was recorded as a new species in Store Jonsvatn in 1999, and was found in very low numbers most years afterwards.

Rotifer biomass was low in Store Jonsvatn throughout the entire investigation period. Yearly means varied between 7 and 20 mg m^{-2} and there was no long-term trend in biomass change. *Conochilus* sp. was the dominant rotifer most years and constituted an average of 61% of the total rotifer biomass. The next most abundant rotifers were *Polyarthra* sp. with 20% and *Asplanchna priodonta* with 8% of the total rotifer biomass.

Phytoplankton

In Lille Jonsvatn, the maximum annual peak biomass reached 2020 and 2150 mg m^{-3} (wet weight) in 1989 and 1994, respectively, and values $>1000 \text{ mg m}^{-3}$ were recorded in 1980–1989 (Fig. 8). Except for 1994, the spring peak biomass gradually declined from 1989 onwards, to maximum values near 300 mg m^{-3} at the end of the investigated period. Diatoms constituted 60 to 90% of the recorded maximum biomass in 1980–1990 and 1994, and *Asterionella formosa* and *Synedra* spp. were the dominant species.

The mean June–September biomass showed a significant decline from 1000 to 1100 mg m^{-3} in 1985, 1986 and 1989 to about 200 mg m^{-3} at the end of the investigation (Fig. 9). Diatom biomass declined from 293 mg m^{-3} or 41% of the mean total biomass in 1985–1995 to 73 mg m^{-3} or 23% of the mean biomass in 1995–2006. The diatoms made up a significantly lower proportion of the total algal biomass in the latter period (Mann-Whitney *U*-test, $p = 0.02$). *Asterionella formosa* and *Synedra* spp. were also recorded in the summer samples, and in the later phase of the investigation *Rhizosolenia eriensis*, *R. longiseta* and a small *Cyclotella* species (5 μm diameter) became more frequent diatom species.

The biomass of cryptophytes, the second most important algal group, changed from a mean of 170 mg m^{-3} in 1985–1995 to 110 mg m^{-3} in 1996–2006. However, their proportion of the total biomass increased significantly (Mann-Whitney *U*-test, $p = 0.007$), from about 23 to 36% from the former to the latter period, respectively, and cryptophytes constituted in 1996–2006 up to 60% of the biomass during summer and autumn samples. *Rhodomonas lacustris* was the most frequent cryptophyte species.

Chrysophytes constituted close to 24% of the mean biomass in all investigated years. *Dinobryon sociale* var. *americanum* was the dominant species during the

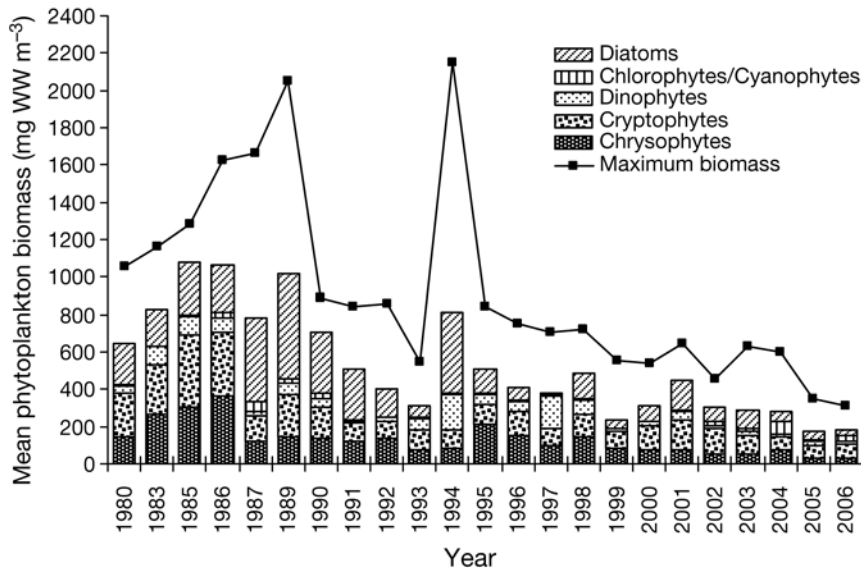


Fig. 8. Mean ($\text{mg wet weight m}^{-3}$ over 10 m) and maximum biomasses of phytoplankton groups in Lille Jonsvatn over the period 1980–2006. There are no data from 1981, 1982, 1984 or 1988

spring period and was also frequently recorded in the summer and autumn periods together with other *Dinobryon* species and individuals of *Bitrichia chodati*, *Pseudochephyron entchii*, *Chrysoikos skujai*, *Mallomonas crassisquamma*, *M. akrokomos* and *Chrysochromulina parva*.

Three dinophyte species, *Gymnodinium lacustre*, *Peridinium inconspicuum* and *Ceratium hirundinella*, constituted about 10 % of the total biomass in all years. Chlorophytes, usually *Scenedesmus* sp., *Monoraphidium dybowski*, and *M. griffithii*, were recorded in low numbers. However, from 2002 on, gelatinous chlorophytes such as *Sphaerocystis Schroeteri* and *Willea irregularis* were also included in the biomass estimates,

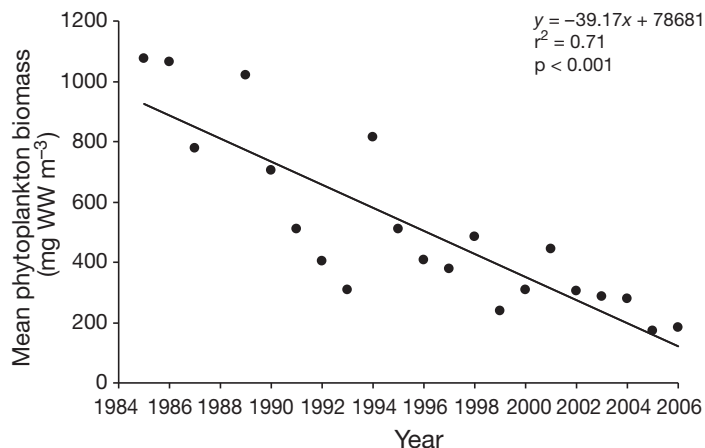


Fig. 9. Regression of mean phytoplankton biomass ($\text{mg wet weight m}^{-3}$ over 10 m) versus sampling year (1985–2006) in Lille Jonsvatn. There are no data from 1988

and a maximum biomass was recorded in August 2004, when gelatinous chlorophytes constituted 22 % of the total biomass. The colony-forming cyanophyte *Coelosphaerium kuetzingianum* was recorded in the late summer samples from 1996, and it was sufficiently abundant to be included in the biomass estimates from 2003 onwards. In 2004 this species constituted close to 60 % of the recorded biomass in August samples. However, on an annual (June–September) basis the species never exceeded 12 % of the biomass, and for the investigated period cyanophytes did not exceed 1 % of the total biomass.

In Store Jonsvatn, a maximum phytoplankton biomass of 450 to 500 mg m^{-3} was recorded in June 2001 and 2002, and diatoms constituted 30 and 45 % of the biomass, respectively. The highest mean seasonal biomass, 370 and 270 mg m^{-3} , were recorded in the same years. In

all other years, mean seasonal biomasses varied from 130 to 230 mg m^{-3} , and no specific trend in biomass development was recorded during the investigated period. The mean biomass for 1980–2006 was 190 mg m^{-3} , or about one-fourth of the mean biomass recorded for Lille Jonsvatn in the same period. However, in 2005 and 2006 the mean June–September biomass was similar in the 2 lakes.

Cryptophytes and chrysophytes each constituted about 30 % of the mean June–September biomass in Store Jonsvatn, whereas the biomass shares of diatoms and dinophytes were close to 19 and 16 %, respectively. Chlorophytes accounted for 3 % of this biomass. The taxa mentioned for Lille Jonsvatn were also the most frequent ones in Store Jonsvatn, except for gelatinous chlorophytes and cyanophytes that were present in very low numbers and not included in the biomass estimates in the latter basin.

Phytoplankton–zooplankton relationships

Biomass relationships between phytoplankton (0 to 10 m) and herbivorous zooplankton (0 to 20 m) have changed significantly in Lille Jonsvatn (Fig. 10). In the first years of the investigation, 1980 and 1983, the mean biomass of herbivorous zooplankton was larger than that of phytoplankton (1.6 and 1.4 times, respectively). This situation changed to an inverse relationship after 1984, with a phytoplankton biomass that was 4 to 12 times larger than that of zooplankton in 1986–1990. From 1996 onwards, the biomass of herbi-

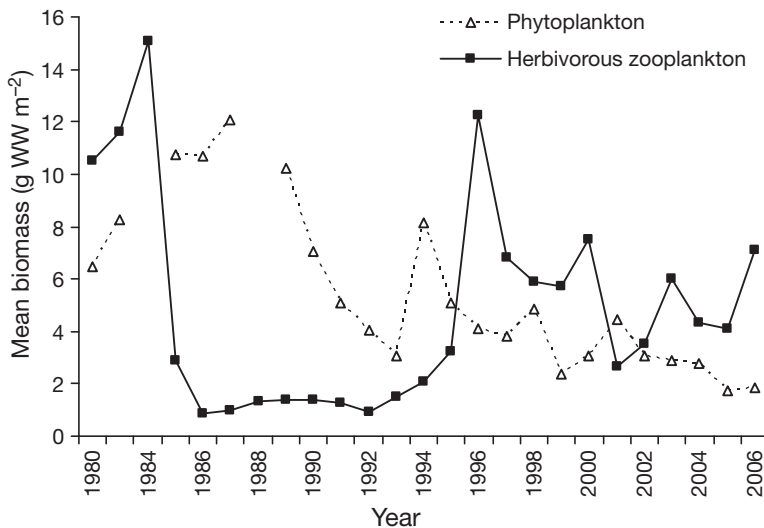


Fig. 10. Comparison of phytoplankton and herbivorous zooplankton biomass (g wet weight m⁻²) development in Lille Jonsvatn from 1980 to 2006. There are no data from 1981 or 1982 and only zooplankton data from 1984 and 1988

vorous zooplankton was on average 2.2 times higher than that of phytoplankton (except for 2001) for the period 1996–2006. In Store Jonsvatn, the mean biomass of herbivorous zooplankton was on average 1.8 times higher than that of phytoplankton in all years, except for 2001 and 2002.

Mysis relicta

Mysid data from Lille Jonsvatn in 1996 and yearly from 1999 to 2006 indicate 2.5 to 4.5 times higher abundance in 2003–2006 compared to 2000–2002 and 1996 (Fig. 11). The highest abundance was recorded in 2003 with 252 ind. m⁻². In 1999, *Mysis relicta* was very scarce, with an abundance of only 3 ind. m⁻². The first attempt to collect mysids in Store Jonsvatn was in

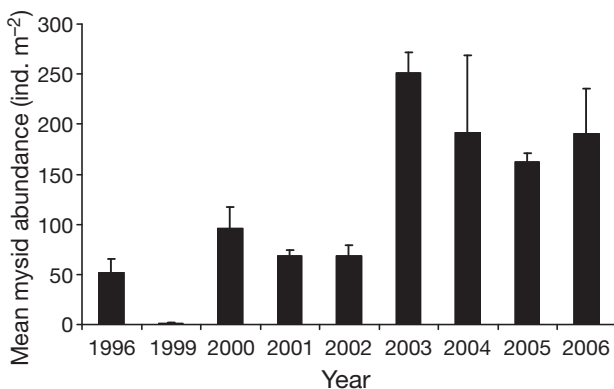


Fig. 11. *Mysis relicta*. Abundance (ind. m⁻²; mean ± SD) in Lille Jonsvatn in 1996 and 1999–2006

November 1981, when the mean abundance was estimated at 2.7 ind. m⁻² in vertical hauls from 50 to 0 m (Koksvik et al. 1991). Næsje et al. (1991) recorded 50 to 110 ind. m⁻² in Store Jonsvatn in 1986–1987 (August–December samples), and in 2000, the average of 3 vertical hauls (50 to 0 m) in November was 31 ind. m⁻² (J. I. Koksvik unpubl. data).

DISCUSSION

The results of the present long-term study reveal large differences in the plankton development in 2 basins of Lake Jonsvatn after introduction of *Mysis relicta*. In Lille Jonsvatn, the cladoceran populations collapsed about 7 yr after the introduction that likely took place in 1978 in another basin of the lake, about 6 km from Lille Jonsvatn.

Bosmina longispina was the strongly dominating cladoceran in Lille Jonsvatn before the collapse, followed by *Daphnia galeata*. The preference for cladocerans in the diet of *Mysis* spp. is well documented (Lasenby & Langford 1973, Richards et al. 1975, Kinsten & Olsén 1981, Langeland 1981, 1988, Bowers and Vanderploeg 1982). In Lake Tahoe, the dominant zooplankters *Bosmina* and 2 species of *Daphnia* virtually disappeared after the introduction of *M. diluviana* (formerly *M. relicta*) (Richards et al. 1975), and *Bosmina* and *Daphnia* were the preferred prey in Flathead Lake (Spencer et al. 1999). In Lake Selbusjøen, the source lake for mysids in Lake Jonsvatn, cladocerans were reduced to a very low biomass 5 to 6 yr after the introduction of *M. relicta* in 1973. The mysids had then developed an abundance of 200 to 600 ind. m⁻² based on vertical haul samples. *B. longispina*, *Holopedium gibberum* and *D. longispina* were the most severely decimated cladoceran species (Langeland 1981, Langeland et al. 1991).

In another lake in the same region, Lake Stugusjøen, a similar development took place (Langeland 1981, 1988). *Mysis relicta* was introduced in 1973, and from 1978 the 3 most abundant planktonic cladocerans, *Bosmina longispina*, *Daphnia galeata* and *Holopedium gibberum*, were almost absent in the samples. From 1980, vertical hauls showed a mysid abundance of 30 to 100 ind. m⁻². In 2 mysid-free neighbouring lakes, Lakes Møsjøen and Grønsjøen, no significant decrease in the zooplankton populations was recorded for the same period. These lakes have similar environmental conditions as Lake Stugusjøen, and the only fish species in all 3 lakes were Arctic char and brown trout.

The cladoceran numbers decreased dramatically for a period of 10 yr in Lille Jonsvatn, and the low abundance was considered permanent until the numbers again began to increase in 1995. In 1996, the mean biomass of cladocerans very surprisingly developed to the same level as before the collapse. *Bosmina longispina* was again the dominant species, followed by *Holopedium gibberum* and *Daphnia galeata*. The causes for the sudden return of cladocerans are unclear. Threlkeld et al. (1980) reported a reappearance of *Bosmina* in Lake Tahoe for a short period with low *Mysis diluviana* density. In the present study, mysid density in Lille Jonsvatn was low in 1996 and considerably lower than the 4 last years of the investigation (2003 to 2006). Unfortunately, *M. relicta* was not sampled in Lille Jonsvatn prior to 1996; however, from frequent occurrence in the plankton samples, the existence of the species in this part of the lake was well known. The new collapse of *B. longispina* and *H. gibberum* in 1998–1999 did not coincide with a recorded increase in *M. relicta* abundance, as the mysid density was extremely low in 1999. Interspecific competition with the rapidly increasing *Daphnia* populations may have played an important role for the reduction of *B. longispina* and *H. gibberum*. The *Daphnia* populations continued to increase until 2000, and afterwards varied considerably, with the highest mean density occurring in 2006, when the second highest density of *M. relicta* was recorded.

There is no coincidental long-term study of the development of planktivorous fish in Lake Jonsvatn. In 1999, however, a survey of the fish populations in Lille Jonsvatn, performed by series of floating and bottom-set gill nets (10 to 45 mm mesh size), revealed that the population of Arctic char, the only planktivorous fish species, was very small (Koksvik 2000). Gut analysis showed that *Mysis relicta*, *Daphnia galeata* and *D. longispina* were the most important food items. Arctic char has also been found to prey extensively on *M. relicta* and cladocerans in Store Jonsvatn (Næsje et al. 1991). However, since Arctic char was reported by local fishermen to have been scarce in Lille Jonsvatn from pre-mysid years and up to the present, it is unlikely that this species was an important agent in the development of zooplankton and *M. relicta* in Lille Jonsvatn.

In 1998–1999, *Daphnia galeata* was replaced by *D. longispina*. This development is the opposite of what Riemann & Falter (1981) reported from a study in Pend Oreille Lake in Idaho, where only the round-headed *D. thorata* was present before the introduction of mysids, whereas a pointed-helmet form, *D. galeata mendotae*, gained numerical dominance after the introduction. Summer forms of *D. galeata* in Lake Jonsvatn typically have pointed helmets, whereas *D. longispina* is round-

headed. Protuberances such as spines and pointed helmets may be important in preventing predation from other invertebrates, and was discussed as a defence against mysid attacks in Pend Oreille Lake.

The ability of *Daphnia longispina* to develop and sustain a population at a relatively high biomass level in Lille Jonsvatn in the presence of the dense *Mysis relicta* population recorded in 2003–2006 is puzzling. Both *D. longispina* and *D. galeata* mainly inhabited the upper 10 m of the water column and the size of the 2 species was about equal. It is difficult to see what anti-predator strategies *D. longispina* might have developed that made it more competitive and viable than *D. galeata*, and why Store Jonsvatnet or other mysid lakes in the same district have not experienced an equivalent development. In Store Jonsvatn, *D. galeata* was the strongly dominating daphnid through the entire investigation. In Lake Selbusjøen, *D. longispina* was more negatively affected than *D. galeata* (Langeland et al. 1991), and in Lake Stugusjøen *D. galeata*, the only daphnid in the lake, completely disappeared 5 yr after the introduction of *M. relicta* (Langeland 1981).

In Lille Jonsvatn, the 10 yr period with extremely low cladoceran biomass may also have affected the dominant copepod species, *Cyclops scutifer*, which showed a significant biomass decrease. It is reasonable that the predation pressure by *Mysis relicta* became stronger on copepods when cladocerans were scarce or absent. When cladoceran abundance increased again from 1995 to 1996, *C. scutifer* did as well. The assumption that the decrease in *C. scutifer* was caused by mysid predation is supported by a study of Canadian lakes by Nero & Sprules (1986b), where *C. scutifer* abundance was found to be much lower in 2 mysid lakes than in 2 similar lakes without mysids. *Heterocope appendiculata* and *Arctodiaptomus laticeps* decreased after *M. relicta* introduction in the nearby Lakes Selbusjøen (Langeland et al. 1991) and Stugusjøen (Langeland 1988), but in Lake Jonsvatn no such long-term trend was found, although both species have varied considerably within periods of a few years. Rybock (1978) reported a consistently negative selection for the copepod *Diaptomus* in Lake Tahoe.

Among the rotifers, *Conochilus* sp. strongly dominated the biomass in Lille Jonsvatn for the first years of the present study; however, it collapsed concurrently with the cladocerans and did not recover again. An equivalent development did not take place in Store Jonsvatn, where *Conochilus* sp. also was the dominant rotifer. It is plausible that *Conochilus* sp. was decimated by *Mysis relicta* predation in Lille Jonsvatn, although it might be a difficult prey as it forms colonies of considerable size. Rotifers have been paid less attention than cladocerans and copepods, but in some studies are reported to be part of the mysid diet

(Lasenby & Langford 1973, Bowers & Grossnickle 1978, Johannsson et al. 2001, Ikonen et al. 2005). Lasenby & Langford (1973) reported *Kellicottia* to be an important prey in Stony Lake, Ontario. Additionally, after the disappearance of *Daphnia* and *Bosmina* in Lake Tahoe in 1970–1971, densities of *Kellicottia longispina* varied inversely with estimates of *M. diluviana*, and gut analysis showed intensive use of *Kellicottia* as prey (Threlkeld et al. 1980). Rybock (1978) found positive selection for *Kellicottia* in Lake Tahoe and showed in an experiment that large *M. diluviana* were able to eat 3.5 *K. longispina* per hour. Based on these studies, it seems reasonable that the decrease in *K. longispina* density in Lille Jonsvatn after 1984 also was a result of increased predation by *M. relicta* after the cladoceran collapse. The very low rotifer biomass in Lille Jonsvatn for the 10 last years of the investigation could be a combined effect of *M. relicta* predation and interspecific competition among the herbivorous zooplankton. An increase in abundance of large daphnids has led to a decrease in rotifers in other lakes in the region (Reinertsen et al. 1990, 1997), and is in accordance with the much debated size efficiency hypothesis (Brooks & Dodson 1965).

The recorded cladoceran collapse in Lille Jonsvatn in 1985 was not clearly reflected in the development of algal biomass and composition during the grazing-free period 1985–1994. High maximum and mean annual algal biomasses were recorded in the years following 1985, but the decline in peak biomasses started from 1989 onwards, and mean biomass showed a significant decline from the late 1980s, i.e. before the reappearance of the cladocerans in 1995–1996. Although phytoplankton may be an important part of the *Mysis* spp. diet (Grossnickle 1982, Johannsson et al. 2001), it has not been shown that *M. relicta* by its herbivory has influenced phytoplankton biomass in lakes. As the total P content in Lille Jonsvatn showed a significant decrease from $\sim 11 \mu\text{g l}^{-1}$ in 1989–1990 to $5 \mu\text{g l}^{-1}$ in 2006 (Fig. 2), this may have been a major reason for the phytoplankton biomass decline. When comparing data from a large number of north temperate lake ecosystems, Mazumder (1994) found a strong positive response of algal biomass to total phosphorus in ecosystems where grazers are controlled by planktivores (odd-link ecosystems). The extremely low abundance of large cladocerans, the most important grazers, in Lille Jonsvatn from 1985 to 1995, indicates very strong planktivore control. It is also obvious that a change in grazing pressure after 1995, as indicated by the higher zooplankton (than phytoplankton) biomass (Fig. 10), affected the phytoplankton development in Lille Jonsvatn for the last 10 yr of the present study. The ratio of herbivorous zooplankton to phytoplankton in most years after 1995 reflects an intensive grazing

pressure, which is also shown by the significant increase in cryptophytes in the biomass share of rapidly growing algae, i.e. *Rhodomonas lacustris* (Fott 1975, Cronberg 1980, Reinertsen et al. 1990). Due to increased turnover rate of the phytoplankton, less biomass is produced per unit P, as the P:C ratio of algae increases with increasing growth rate (Olsen et al. 1983). The presence of gelatinous chlorophytes and cyanophytes also confirms a high grazing pressure (Porter 1977, Reinertsen 1982). A significant decrease in total P was also found in Store Jonsvatn in 1989–2006 (Fig. 2), but no change in total algal biomass or algal composition was recorded.

The sudden collapse in cladoceran populations recorded in Lille Jonsvatn did not take place in Store Jonsvatn, where attractive prey and mysids have coexisted for many years; however, there has been a long-term, slow decline in the density of the most attractive cladocerans. The decrease in cladoceran biomass in Store Jonsvatn has been less dramatic and taken considerably longer than in other lakes with introduced *Mysis relicta* in the same area. In Lakes Selbusjøen and Stugusjøen, the cladoceran populations were strongly reduced 5 to 6 yr after the mysid introduction (Langeland 1988, Langeland et al. 1991). No long-term trends in biomass change in copepod or rotifer species were detected in Store Jonsvatn.

The large differences in zooplankton development in the 2 basins of Lake Jonsvatn may be explained by differences in temperature and light conditions. In controlled laboratory experiments, Boscarino et al. (2007) found that *Mysis diluviana* preferred temperatures between 6 and 8°C and had limited movement into water of 12°C or higher. Martinez & Bergersen (1991) found that temperatures above 14°C excluded *M. diluviana* from the epilimnion of Lake Granby, Colorado, and Rudstam et al. (1999) stated that mysids seldom occur in temperatures above 15°C. Summer temperatures in the epilimnion normally exceed 14 to 15°C in all parts of Lake Jonsvatn. Due to a higher degree of wind exposure, the thermocline is often 1 to 2 m deeper in Store Jonsvatn than in Lille Jonsvatn. This might give the zooplankton a greater vertical refuge for population development in Store Jonsvatn. The duration of egg development in Daphniidae at 15°C is 5 to 7 d (Bottrell et al. 1976) and post-embryonic development (the time from hatching to attaining maturity) was, in an *in situ* experiment in Lake Haugatjern, not far from Lake Jonsvatn, 6 d at 13°C (Langeland et al. 1985). The period with sufficiently high temperatures to establish zooplankton refuges will normally last 1 to 2 mo in Lake Jonsvatn and provide enough time for development of several new generations. The larger refuge in Store Jonsvatn may be an important factor in explaining the differences in zooplankton development between the 2 basins.

Differences in Secchi disc transparencies of 1 to 2 m show lower light transmission in Lille Jonsvatn than in Store Jonsvatn. This might result in acceptable light conditions for *Mysis relicta* to feed in the upper water layers for longer time periods at night in Lille Jonsvatn than in Store Jonsvatn in periods with acceptable temperatures (<14 to 15°C), and it may also contribute to a more sheltered environment for the zooplankton populations in the productive layers in Store Jonsvatn. Næsje et al. (2003) found that 90% of adult *M. relicta* stayed deeper than 49 to 53 m during light hours in May–September in Store Jonsvatn in a cool summer (maximum temperature 15°C at 1 m depth). Some juveniles (<8 mm) stayed 10 to 20 m higher up. During dark hours, both adults and juveniles performed vertical migrations and were found in all layers up to the surface. However, from mid-May to mid-July the nights are short at the high latitude of Lake Jonsvatn, and the period with acceptable light conditions for mysids to feed near the surface is quite limited. The shorter distance of vertical migration in Lille Jonsvatn (the maximum depth is 37 m and there are large areas with depths ≤30 m) might also contribute to easier access for *M. relicta* to the zooplankton in the upper layers in this part of the lake.

The present long-term study in Lake Jonsvatn revealed an unexpected plankton development in both investigated basins. In Store Jonsvatn, the zooplankton biomass was unaffected for a longer time than in other regional lakes with introduced *Mysis relicta*, and the eventual decline in cladocerans was less pronounced. In Lille Jonsvatn, the mysid introduction was expected to give reduced negative effects due to the higher nutrient level in this part of the lake. However, the cladocerans collapsed almost totally in this basin. The most diverging result from earlier documentation of mysid impacts was the development of *Daphnia longispina* in Lille Jonsvatn after a depletion of cladocerans that had lasted for 10 yr. The documented ability of a large daphnid to develop and sustain a relatively high population density for years in the presence of a relatively high mysid abundance adds new knowledge to interactions in mysid lakes, and shows the importance of long-term studies.

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