

An evaluation of the diet of *Mysis relicta* using gut contents and fatty acid profiles in lakes with and without the invader *Bythotrephes longimanus* (Onychopoda, Cercopagidae)

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Abstract Diets of *Mysis relicta* from four lakes in central Ontario that had been invaded by *Bythotrephes longimanus* and three lakes that had not been invaded were investigated using gut content analysis and fatty acid (FA) composition. Gut content analysis of *M. relicta* revealed a high incidence of cannibalism in all lakes, and consumption of *B. longimanus* and native zooplanktivorous midges in the genus *Chaoborus* in lakes where these were present. Cladocera other than *B. longimanus* were present in the guts of all *M. relicta* examined except those from Bernard Lake, the lake with the most *B. longimanus*. In that lake, *B. longimanus* was the most frequent diet item. Copepod remains were found in 60–100% of *M. relicta* guts with the lowest frequency occurring in Bernard Lake. Fatty acids (FA) that contributed strongly to the variation in FA composition in *M. relicta*, as revealed by a principal component analysis, were C16:0 (palmitic acid), C16:1n7 (palmitoleic acid), C18:1n9c

(oleic acid), C20:4n6 (arachidonic acid), C20:5n3 (eicosapentaenoic acid), and C22:6n3 (docosahexaenoic acid). Significant differences in FA amount and composition of *M. relicta* were found between invaded and non-invaded lakes, and among lakes within these groups. Generally, *M. relicta* in non-invaded lakes had higher concentrations of C16:0, C18:1n9c, C18:2n6c (linoleic acid), C18:3n3 (α -linolenic acid) and C20:4n6, while *M. relicta* in invaded lakes had higher concentrations of C22:6n3. Two of the non-invaded lakes had lower water transparency, as measured by Secchi depth, which may be the reason why mysids and abundant populations of *Chaoborus* spp. could be found in the water column during the day. However, differences in FA profiles and gut contents of *M. relicta* between invaded and non-invaded lakes are consistent with competition for Cladocera in the presence of the invader rather than pre-existing differences among lakes. We conclude that the diet of *M. relicta* is affected by the invasion of *B. longimanus*.

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Introduction

Mysis relicta, the opossum shrimp, occupies an important position in the food webs of many Ontario lakes. By utilizing both the pelagic and benthic zones,

it functions as a link between the two environments, transferring energy and nutrients from one region to the other. This is particularly valuable to fish that eat mysids but do not have access to resources in both areas (Wojcik et al. 1986; Rand et al. 1995; Johannsson 1995). *M. relicta* is a glacial relict native to many northern lakes that were created after the last ice age. Its persistence and success may be attributed, in part, to its euryphagous nature and ability to readily change its diet as food resources fluctuate (Bowers and Vanderploeg 1982; Folt et al. 1982; Grossnickle 2001). It is an opportunistic omnivore whose diet ranges from zooplankton and phytoplankton (Grossnickle 1982; Langeland 1988; Johannsson et al. 2001) to benthic invertebrates (Parker 1980) and detritus (Lasenby and Langford 1973). Although *M. relicta* may consume a wide range of foods, the quality of its diet could have implications for growth, survival, and reproduction (Beeton and Gannon 1991) that may, in turn, affect higher trophic levels.

There is reason to suspect that the diet of *M. relicta* could be affected by the presence of *Bythotrephes longimanus* (previously known as *B. cederstroemi*, see Grigorovich et al. 1998), an exotic predatory cladoceran. *B. longimanus* has been implicated as the reason for changes in zooplankton communities in Lake Michigan (Makarewicz et al. 1995; Lehman 1991; Lehman and Caceres 1993; Barbiero and Tuchman 2004), Lake Huron (Munawar et al. 2001), and in Canadian Shield lakes (Yan and Pawson 1997; Boudreau and Yan 2003; Hovius et al. 2006; Strecker et al. 2006). It may reduce zooplankton species richness, especially for cladocerans (Yan et al. 2002; Strecker et al. 2006). Feeding studies have identified small cladocerans and copepod nauplii as the major food items for *B. longimanus* (Vanderploeg et al. 1993) and Muirhead and Sprules (2003) concluded that small, slow-moving prey have the greatest risk of predation from *B. longimanus*. Because *M. relicta* also consumes these food items (Bowers and Vanderploeg 1982), the invasion of *B. longimanus* may redirect and/or dissipate some of the energy and nutrients that otherwise would be available to *M. relicta*, thereby altering foodweb structure.

In this study we compared patterns of zooplankton composition and biomass amongst seven lakes in central Ontario, which included lakes that had been invaded for at least 5 years, lakes that have not yet

been invaded, and some that became invaded during our study. We examined stomach contents of *M. relicta* sampled from these lakes in mid-August, a time when *B. longimanus* had been feeding for approximately 8 weeks in invaded lakes, to determine whether any resulting differences in zooplankton composition are reflected in the feeding patterns of *M. relicta*. We also compared the fatty acid (FA) composition of *M. relicta* for all sampling periods in 2003 to get a more comprehensive representation of diet differences among lakes. This technique has been applied to krill (Cripps and Atkinson 2000; Virtue et al. 2000), zooplankton (Ahlgren et al. 1997; Desvillettes et al. 1997), and halibut larvae (Evjemo et al. 2003). Last, we examined several fatty acids singly, including ones thought to be essential, in order to determine where possible differences lie, and related these to the composition of prey that had been observed in the guts of *M. relicta*.

Materials and methods

Site description and sampling design

Invasion by *B. longimanus* was occurring in central Ontario lakes even as we conducted the study (see Strecker et al. 2006) and therefore our sampling strategy had to adapt to the continuously expanding distribution of *B. longimanus*. In the end, we collected information on diet of *M. relicta* from seven lakes differing in *B. longimanus* invasion status (Table 1). Three lakes had been invaded for at least 5 years, and will hereafter be referred to as Bernard Lake_(I), Harp Lake_(I), and Skeleton Lake_(I) with the subscript indicating their invasion status. Two lakes were without *B. longimanus* prior to and during our study, and will hereafter be referred to as Buck Lake_(N) and Pickerel Lake_(N). Two lakes were found to contain *B. longimanus* for the first time in 2003 during our study: Gull Lake and Boshkung Lake. Although both Gull and Boshkung lakes contained small populations of *B. longimanus*, the distribution of the invader with respect to our sampling stations within the two lakes differed. A few *B. longimanus* were discovered ~2 km away from our sampling site in Gull Lake and we did not collect any during our regular sampling. Gull Lake_(N) was therefore designated as a non-invaded lake for the comparison

Table 1 Location and history of *B. longimanus* invasion in the sample lakes

Lake	Lat.	Long.	Area (ha)	Mean depth (m)	Max depth (m)	Mean Secchi depth (m)	<i>B. longimanus</i> documented	Source
Harp	45.23	79.07	71	13.3	37.5	4.5	1993	OMOE
Bernard	45.45	79.23	2058	15.1	47.9	3.6	1998	OFAH
Skeleton	45.15	79.27	2156	28.9	64.7	7.3	1998	OFAH
Boshkung	45.04	78.44	716	23.1	71.0	4.8	2003	This study
Gull	44.51	78.47	995	16.5	49.1	6.6	2003	This study
Pickereel	45.41	79.18	513	8.6	38.1	2.1	Not Invaded	OMOE
Buck	45.25	79.23	266	9.9	23.5	1.7	Not Invaded	OMOE

Lake morphometric information provided by Robert Girard, Ontario Ministry of Environment (OMOE), Dorset Environmental Science Centre, Dorset, Ontario. Data on Secchi depth were provided by A. Strecker and J. Hovius. Sources of invasion records include OMOE and Ontario Federation of Anglers and Hunters (OFAH), Peterborough, Ontario

between invaded and non-invaded lakes. However, individual *B. longimanus* were occasionally present in our samples from Boshkung Lake_(I) during mid-summer and thus it was treated as an invaded lake.

Zooplankton and *M. relicta* were sampled once in early June 2003, a period that precedes peak abundance of *B. longimanus* in this region. Samples were then taken every 2 weeks from the beginning of July 2003 until the end of August 2003 in order to track changes during the time *B. longimanus* was active, with the exception of Pickereel Lake_(N). The discovery of *B. longimanus* in some of the lakes previously thought to be non-invaded resulted in changes to the sampling design and, as a result, Pickereel_(N) was not added until 24 July 2003. *M. relicta* and zooplankton were also collected in all lakes in October 2003 and May 2004. Sample sites were located at the deepest basins of each lake. Basins > 60 m were sampled at a location where the depth was 60 m due to limitations of the sampling gear. *M. relicta* were collected at two or more sites in each lake, depending on the number of individuals captured at each site. The same sites were re-visited throughout the study.

Net hauls for *M. relicta* and zooplankton were taken at or just after sunset with the exception of Buck_(N) and Pickereel_(N) lakes where *M. relicta* could be found in the water column during the day, likely because light penetration (measured as Secchi depth) was less in these lakes. *M. relicta* were caught using a 0.75-m diameter, 400- μ m mesh net towed either vertically or obliquely through the water column. Sampling stopped after either 100 *M. relicta*, includ-

ing least 75 mature adults, were caught or 2 h had passed. This kept the time until freezing at <4 h. Approximately 20 *M. relicta* from mid-August were preserved in a sugared and buffered 8% Formalin solution for gut content analysis. *M. relicta* that were captured at sunset for gut content analysis were on the ascent portion of their migrations, so that food items in the gut represented both benthic and pelagic feeding. *M. relicta* that were captured in Buck_(N) and Pickereel_(N) lakes were caught in the water column, and we do not know whether they descend to the bottom. However, our samples were assumed to be representative of the feeding behaviour of the population. Animals to be used for FA analysis were kept in hypolimnetic water on ice until they could be frozen in liquid nitrogen. Before freezing, *M. relicta* \geq 13 mm in body length (from the tip of the rostrum to the proximal end of the telson) were separated by sex. Individuals between 9 mm and 12 mm were grouped as juveniles. Samples were maintained in a cryogenic freezer (-80°C) until FA analysis.

One quantitative zooplankton haul from 2 m above the bottom to the surface was done immediately prior to the *M. relicta* collections using a 0.5-m diameter, 110- μ m mesh net in order to evaluate the density and species composition of potential prey for *M. relicta*. Net efficiency was measured with a flow meter (Rigosha Ltd. model #5571A) and zooplankton abundance and biomass were corrected for net efficiency. Zooplankton samples were preserved with a sugared and buffered 4% Formalin solution.

Chaoborus spp. were noted as being absent, present, or abundant in each lake based on observations throughout the entire sampling period.

Sampling for *B. longimanus* in Bernard_(I), Skeleton_(I), and Harp_(I) lakes was performed concurrently by other researchers (Angela Strecker, Dept. of Biol., Queens Univ., Kingston, Ont., and Jonathan Hovius, Dept. of Integrative Biol., Univ. of Guelph, Guelph, Ont.). Five vertical net hauls were taken from each lake approximately every 2 weeks starting in June 2003. At each lake, an initial net haul was performed at a deep central location, then four additional net hauls were collected along a transect towards shore. Sites were verified with a GPS and re-visited throughout the summer. Hauls were taken with a 0.5-m diameter, 400- μ m mesh net starting from 5 m off of the lake bottom. Sampling time ranged from 9 a.m. to 3 p.m., but was consistent for each lake. The newly invaded lakes, Boshkung_(I) and Gull_(N), were not sampled quantitatively for *B. longimanus*.

Zooplankton measurement and enumeration

Zooplankton were identified according to Balcer et al. (1984). Counts and measurements were processed using the Zebra II software package (Ontario Ministry of the Environment and Energy 1994). At least 250 animals from each sample were measured to achieve an adequate representation of zooplankton community composition and size structure for each lake. Additional details may be found in Nordin (2005).

Mysis relicta gut analysis

Stomach contents of *M. relicta* were examined from the sampling period in mid-late August, a time when *B. longimanus* had been actively feeding for ~8 weeks in the invaded lakes and was still present. A total of 15 adult mysids consisting of both males and females were examined from each lake. Mysid stomachs were removed, spread onto a glass slide with a drop of water, topped with a coverslip, and examined under a phase-contrast microscope. Adult insect leg parts and chironomid mandibles were grouped under the category of “Other insects”. Desmids, rotifers, *Bythotrephes* spines, and other Cladocera (using mandibles and postabdominal claws) were counted. Unidentifiable organic matter,

algae other than Desmidiaceae, copepods fragments, and body parts belonging to *Chaoborus* spp., other insects and *M. relicta* were scored as present/absent or present/absent/abundant.

Fatty acid analysis

Each sample for FA analyses was separated and grouped by sex/life stage (males, females, or juveniles) and consisted of 1–5 whole, freeze-dried mysids, with a total sample weight of between 10 mg and 15 mg. Depending on the quantity of mysids, 2–3 samples of each males, females, and juveniles were analyzed for a total of 6–9 samples from each lake on every sampling day in 2003. Mysid FA were quantified using a three-step process: (a) triplicate extractions in a 2:1 chloroform:methanol solution for gravimetric determination of total lipid (Bligh and Dyer 1959); (b) derivitization of fatty acid methyl esters (FAME) using the Morrison and Smith (1964) boron trifluoride (BF₃-methanol; 10% w/w) method and; (c) identification and quantification of FAME on a Hewlett Packard 6890 Series gas chromatograph (GC). The GC was configured as follows: splitless injection; column = Supelco model SP-2560; 100 m \times 0.25 mm ID \times 0.20 μ m thick film; oven = 140°C (hold 5 min) to 240°C at 4°C min⁻¹, hold for 12 min; carrier gas = helium; detector = FID at 260°C; injector at 260°C; total run time = 42 min sample⁻¹. A known quantity of an internal standard (5 α -cholestane) was added to each sample prior to extraction to provide an estimate of extraction efficiency. A 37-component FAME standard (Supelco #47885-U) was used to identify individual FAME in the samples and to produce separate 4-point calibration curves for each FAME for quantification purposes. All FA results are reported as μ g FAME mg⁻¹ lipid-free dry weight.

Statistical analysis

All statistical analyses were done using SYSTAT version 10.2 (Systat Software Inc., Richmond, California). Pearson’s correlations were used to identify relationships between zooplankton biomass and abundance of *B. longimanus*. A non-parametric Kruskal–Wallis one-way ANOVA was used to compare gut contents of mysids among lakes, which were

binary, multi-state or counts for the different food items. Results of analyses using binary data were confirmed with χ^2 tests.

We performed a principal component analysis (PCA) on a covariance matrix to examine patterns of variation in FA composition. Lakes grouped by invasion status were graphically displayed as Gaussian bivariate ellipses representing one standard deviation from the mean placed around the centroid of each invasion class. To examine differences between invaded and non-invaded lakes on the principal components, and among lakes within each of these lake groups, we used nested ANOVAs. Factor scores were transformed ($\log(x + 10)$). To look for effects of sex/maturity (male, female, juvenile) we used simple one-way ANOVAs. Bonferroni post-hoc tests were performed to identify where differences lay, and significance was assessed at $P = 0.05$. To determine which FA were most able to distinguish between invaded and uninvaded lakes, we used a discriminant function analysis on the log-transformed FA data.

Two-way ANOVAs were used to examine differences due to sex/maturity and lake invasion status for individual FA highlighted by the multivariate analyses. These data were transformed ($\log(x + 1)$). Ratios of arachidonic acid (ARA = 20:4n6) to eicosapentaenoic acid (EPA = 20:5n3) were transformed similarly and the results were used in a two-way ANOVA to look for differences among lakes defined by invasion status and sex/maturity. A Bonferroni post-hoc test was used to identify differences among the groups.

Results

Zooplankton communities in the lakes

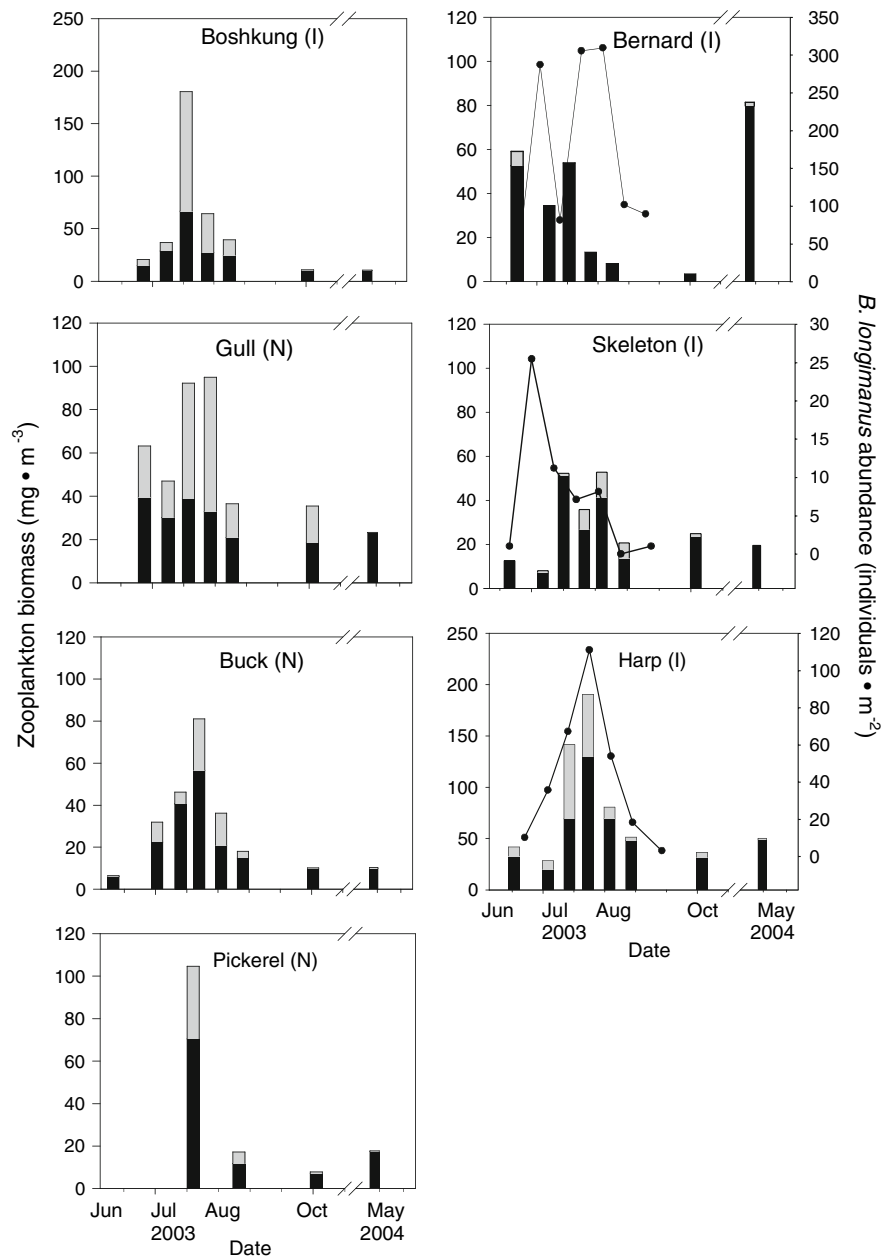
In the invaded lakes, generally, *B. longimanus* was at low densities in late June, increased to maximum density in mid-summer and declined by September (Fig. 1). The abundance of *B. longimanus* surpassed 300 m^{-2} in Lake Bernard_(I) in August, reached 110 m^{-2} in Harp Lake_(I) in late July, and reached 25 m^{-2} in Skeleton Lake_(I) in late June. Although sampling for *B. longimanus* was not performed in Boshkung Lake_(I), it was obvious that densities were lower than in the three lakes above; individuals were seen on occasion in entire samples, but were too few

to occur in the sub-samples that we counted for zooplankton

We tested for correlations between *B. longimanus* abundance and total zooplankton biomass and/or cladoceran biomass throughout the summer sampling periods in individual lakes. Although the biomass of cladocerans in Skeleton Lake_(I) was low at the peak of *B. longimanus* abundance and did not seem to increase until *B. longimanus* was in decline (Fig. 1), the correlation was not significant (Pearson correlation $r = -0.13$, $df = 4$, $P > 0.05$). Total zooplankton biomass and *B. longimanus* abundance had a stronger negative relationship but was also non-significant ($r = -0.30$). It is not possible to assign a meaningful correlation to the relationship between cladoceran biomass and *B. longimanus* abundance in Bernard Lake_(I) because of the absence of cladocerans throughout the summer in this lake. Considering the preference *B. longimanus* has for other cladocerans, their scarcity may be a result of the high density of the invader. The correlation between total zooplankton biomass and *B. longimanus* abundance in Bernard_(I) was significant and negative (Pearson correlation $r = -0.92$, $df = 3$, $P < 0.05$). In sharp contrast, Harp Lake_(I) cladoceran biomass showed a positive correlation with *B. longimanus* ($r = 0.89$, $df = 4$, $P < 0.05$). Total zooplankton had a weaker correlation ($r = 0.75$, $P < 0.10$). Because the positive relationship seen in Harp Lake_(I) was unexpected, we examined the zooplankton community composition. The cladoceran composition in Harp Lake_(I) was mainly *Daphnia galeata mendotae*, with some *Holopedium* during the months when *B. longimanus* was abundant.

Knowing the preference of *B. longimanus* for cladocerans, we examined the cladoceran community in mid-August after the population peak in *B. longimanus* in all of the lakes (Table 2). In the invaded lakes, Bernard_(I), Harp_(I), Skeleton_(I) and Boshkung_(I), only 0–2 cladoceran species/genera were observed within each lake compared to 4–5 species/genera in each of the non-invaded lakes. Cladoceran biomass varied amongst the lakes with no consistent separation between invaded and non-invaded lakes, although the lowest biomass occurred in Bernard_(I), the lake with the highest densities of *B. longimanus* (Fig. 1). Buck_(N) and Pickerel_(N) lakes had abundant *Chaoborus* in late summer. The only other lake in which *Chaoborus* were observed was

Fig. 1 Zooplankton biomass and *B. longimanus* abundance for sampling periods between June 11, 2003 and May 14, 2004. *B. longimanus* data were provided by Emily Parrott and Norman Yan, York University. The line indicates *B. longimanus* abundance; copepod biomass bars are black; herbivorous cladoceran biomass bars are grey. Note differences in scale. Letters in parenthesis denote invasion status



Harp_(I), but densities appeared to be much lower. Zooplankton biomass declined in all lakes in late summer, regardless of invasion status.

Gut contents

Most adult *M. relicta* in these lakes contained cladoceran (87%) and copepod (85%) remains, as expected (Table 3). Rotifers were found in 45% of the

stomachs. Adult mysids were cannibalistic, and the percentage of mysids containing parts of conspecifics averaged 28% across the lakes. Cannibalism was significantly different among lakes ($\chi^2 = 12.87$, $P = 0.05$, $df = 6$) and highest (33–47%) in the three non-invaded lakes. *Mysis* also consumed large, planktivorous invertebrates; *Chaoborus* larvae were frequently found in the guts of *M. relicta* from the two lakes (Buck_(N) and Pickerel_(N)) where they were

Table 2 Zooplankton biomass (mg m^{-3}), and presence/absence of *Chaoborus* spp. in mid-August 2003

Plankton Groups/Species	Bernard _(I)	Skeleton _(I)	Harp _(I)	Boshkung _(I)	Gull _(N)	Buck _(N)	Pickereel _(N)
Calanoids	0.70	9.02	45.49	21.93	18.46	13.47	8.69
Cyclopoids	7.63	4.75	2.49	2.71	2.44	1.42	3.19
Total Copepods	8.33	13.77	47.99	24.64	20.90	14.88	11.88
Bosminids	0	0	0	0.06	0.51	0.35	1.27
<i>Daphnia</i> spp.	0	6.91	3.61	14.81	14.14	1.59	2.66
<i>Diaphanosoma</i> spp.	0	0	0	0	0.86	1.16	0.31
<i>Chydorus</i> spp.	0	0	0	0	0.03	0	0
<i>Holopedium</i> spp.	0	0	0.03	0	0.19	0.04	1.12
<i>Polyphemus pediculus</i>	0	0	0	0	0	0.13	0
Total Cladocera	0	6.91	3.64	14.88	15.72	3.3	5.37
Biomass total	8.33	20.67	51.62	39.51	36.62	18.14	17.25
<i>Chaoborus</i> spp.	Absent	Absent	Present	Absent	Absent	Abundant	Abundant

Table 3 Percentage of *M. relicta* containing the various food items in each lake

Food Item	Lake							All lakes
	Bernard _(I)	Skeleton _(I)	Harp _(I)	Boshkung _(I)	Gull _(N)	Buck _(N)	Pickereel _(N)	
Cladocerans	6.7	100.0	100.0	100.0	100.0	100.0	100.0	86.7
Copepods	60.0	86.7	80.0	86.7	93.3	100.0	86.7	84.8
<i>M. relicta</i>	20.0	20.0	13.3	13.3	46.7	33.3	40.0	27.6
<i>B. longimanus</i>	100.0	33.3	33.3	13.3	0.0	0.0	0.0	25.7
<i>Chaoborus</i> spp.	0.0	0.0	0.0	0.0	0.0	26.7	40.0	9.5
Rotifers	53.3	66.7	20.0	33.3	60.0	46.7	33.3	44.8
Other insects	13.3	0.0	6.7	40.0	26.7	20.0	60.0	23.8
Desmidiaceae	20.0	100.0	13.3	40.0	0.0	46.7	0.0	31.4
Other Algae	53.3	53.3	46.7	13.3	46.7	53.3	26.7	41.9
Organic matter	26.7	100.0	13.3	46.7	13.3	40.0	6.7	35.2

Cladocerans excludes *B. longimanus*. Fifteen *M. relicta* were examined per lake, and the final column is based on all 105 specimens examined. 'Other insects' include adult insects and or insect pupae and chironomid larvae

abundant, and *B. longimanus* was found in *M. relicta* stomachs in all four of the invaded lakes, ranging from 13% in Boshkung_(I) to 100% in Bernard_(I). Insect remains other than *Chaoborus* larvae were a common item in some lakes. A few were from chironomid larvae, while the rest appeared to be legs of adult insects although they could be from emerging pupae. Algae were also common, especially desmids which were found in high numbers in mysids from Skeleton Lake_(I). Unidentifiable organic matter was present in all of the lakes, but most common in Skeleton_(I).

The frequency of cladocerans other than *B. longimanus* (*Daphnia* spp., bosminids, *Polyphe-*

mus pediculus, *Diaphanosoma* spp.), insects, rotifers, *B. longimanus*, *Chaoborus* spp., detritus, and Desmidiaceae in the stomachs of mysids were significantly different among lakes (Table 3; Kruskal–Wallis non-parametric one-way ANOVA $P < 0.01$). Only 0.2% of the cladocerans we found in *M. relicta* were from Bernard Lake_(I) (Table 4) so this lake was removed from the analysis and the ANOVA was run again, after which the occurrence of cladocerans in the guts of mysids among remaining lakes was not significantly different ($P = 0.221$). However, mysids from two other invaded lakes, Boshkung_(I) and Skeleton_(I), contained fewer Cladocera than the remaining 4 lakes

Table 4 Occurrence of each food item in each lake as a percentage of the total occurrences for that food item

Food Item	Lake							Total
	Bernard _(I)	Skeleton _(I)	Harp _(I)	Boshkung _(I)	Gull _(N)	Buck _(N)	Pickereel _(N)	
Cladoceran parts	0.2	13.6	18.8	13.5	18.8	18.1	17.0	1,231
Copepods	10.1	14.6	13.5	14.6	15.7	16.9	14.6	89*
<i>M. relicta</i>	10.3	20.3	5.1	7.7	30.8	15.4	20.5	39
<i>Bythotrephes setae</i>	94.4	2.0	2.3	1.2	0.0	0.0	0.0	642
<i>Chaoborus</i> spp.	0.0	0.0	0.0	0.0	0.0	46.7	53.3	15
Rotifers	17.7	17.7	3.1	6.3	29.2	20.8	5.2	96
Other Insects	8.0	0.0	4.0	24.0	16.0	12.0	36.0	25*
Desmidiaceae	0.8	91.2	1.4	1.9	0.0	4.7	0.0	363
Other Algae	18.2	18.2	15.9	4.5	15.9	18.2	9.1	44*
Organic matter	10.7	48.2	3.6	19.6	3.6	12.5	1.8	56

The final column gives the total number for food items that were counted, or the total number of individuals in which the food type was seen (indicated with an asterisk) for those items that were simply scored as present/absent. *M. relicta* and *Chaoborus* remains, and organic matter were scored as absent (0), present (1), or abundant (2), and the total reported is the total of those multistate scores

(Table 4). The occurrence of copepods in *Mysis* guts was also lowest in Bernard_(I).

Fatty acids

The variation in FA composition of *M. relicta* was examined first using a principal component analysis (PCA); an unconstrained ordination maximizing variation displayed on successive orthogonal axes. We used a covariance matrix that included 22 out of 37 FA for the PCA. The 15 FA that were left out of the analysis had concentrations totalling < 0.1 µg FAME mg⁻¹ lipid-free dry weight of tissue extracted, and thus they were considered to be negligible constituents of total FA. The first principal component was positively related to all 22 FA (Table 5) so was a measure of total FA, but was largely determined by C16:0 (palmitic acid), C16:1n7 (palmitoleic acid), C18:1n9c (oleic acid), EPA, and C22:6n3 (docosahexaenoic acid = DHA). The second principal component was bipolar, separating lakes by FA composition rather than amount. It was primarily influenced by EPA and DHA (negatively), and oleic acid and ARA (positively). The variance explained by these first two principal component axes was 74% and 13%. Differences between adult males and females were non-significant on both axes (ANOVA; $P > 0.05$). Juveniles had a lower mean score (less FA) on axis 1 (ANOVA; $P = 0.036$), but were not different on axis

2 (ANOVA; $P = 0.090$). Although juveniles tended to have lower FA, the difference was small and the overlap large. Adults and juveniles were grouped together and Gaussian bivariate ellipses representing one standard deviation around the mean for invaded and non-invaded lakes were overlaid on site scores to visualize the differences between invasion classes (Fig. 2). There were significant differences between the two groups of lakes for principal component 1 (nested ANOVA, $P = 0.023$) indicating *M. relicta* from invaded lakes tended to have lower FA concentrations. The greater difference was on principal component 2 ($P < 0.001$) indicating that *M. relicta* tended to differ more in quality than quantity of FA between invaded and non-invaded lakes. There were also significant differences among lakes within the two groups for both principal components (both $P < 0.000$).

Next we used a discriminant function analysis to highlight the strongest differences (Table 5) in FA composition of *M. relicta* among lakes and how these differences varied in time (Fig. 3). The FA contributing most to the separation were EPA, which did not vary with invasion, and C16:0 (palmitic acid), C16:1n7 (palmitoleic acid), and C22:5n3 (docosapentaenoic acid = DPA), which were higher in uninvaded lakes. Three of the four invaded lakes had the highest discriminant function scores in July, while Harp_(I) had highest scores in mid-June (Fig. 3). There was some indication that differences between

Table 5 Loadings for the first 2 principal components (PC Loadings) of the PCA of fatty acid composition of *M. relictus* (Fig. 2) and the standardized discriminant function (Std DF) used to create Fig. 3

Fatty Acid Molecular Formula	Common name	PC loadings		Std. DF
		1	2	
C12:0	Lauric acid	0.086	0.044	0.087
C14:0	Myristic acid	0.830	0.237	−0.147
C15:0	Pentadecanoic acid	0.098	0.058	−0.439
C16:0	Palmitic acid	3.409	0.407	−0.853
C16:1n7	Palmitoleic acid	1.025	0.112	0.816
C17:0	Heptadecanoic acid	0.081	0.037	−0.042
C18:0	Stearic acid	0.255	0.066	−0.240
C18:1n9c	Oleic acid	2.996	0.991	−0.495
C18:2n6c	Linoleic acid (LIN)	0.628	0.214	−0.429
C20:0	Arachidic acid	0.044	0.012	−0.384
C18:3n6	γ -Linolenic acid	0.070	0.058	0.370
C20:1n9	Eicosenoic acid	0.252	0.018	0.259
C18:3n3	α -Linolenic acid (ALA)	0.795	0.489	−0.383
C20:2	Cis-11,14-eicosadienoic acid	0.257	−0.075	0.002
C20:3n6	Homo- γ -linolenic acid	0.032	0.016	−0.003
C22:1n9	Eicosenoic acid	0.252	0.018	0.074
C20:3n3	Eicosatrienoic acid (ETA)	0.156	0.031	0.489
C20:4n6	Arachidonic acid (ARA)	0.959	0.665	0.059
C20:5n3	Eicosapentaenoic acid (EPA)	2.179	−0.535	1.206
C24:1n9	Nervonic acid	0.038	−0.020	0.244
C22:5n3c	Docosapentaenoic acid (DPA)	0.153	0.006	−0.798
C22:6n3	Docosahexaenoic acid (DHA)	2.410	−1.944	0.547
Eigenvalue (%)		73.9	12.7	

The strongest contributions to principal components and the discriminant function are bolded

non-invaded and invaded lakes were becoming smaller by the fall.

We then examined particular FA that were highlighted by the multivariate analyses or that are often essential FA in animals (Fig. 4). We included C18:3n3 (α -linolenic acid) and C18:2n6c (linoleic acid) because some animals may be able to elongate and desaturate these FA to synthesize EPA, DHA, and ARA, and thus they may become essential when the longer chain EFA are in short supply (Von Elert 2002; Ballantyne et al. 2003; Kainz et al. 2004). We also categorized ARA as an essential FA even though the role of this FA has not yet been clearly established for zooplankton (Kainz et al. 2004). Significant differences among males, females, and juveniles were found with ARA, DHA, α -linolenic,

oleic, palmitic, and palmitoleic acids (ANOVA; $P < 0.05$). Concentrations of all FA singly were significantly higher in *M. relictus* from the non-invaded lakes compared to invaded lakes with the exception of EPA, DHA, and palmitoleic acid. The interaction of sex and status was found to be non-significant for all FA (ANOVA; $P > 0.05$).

To assess possible differences in carnivory, we examined the amount of ARA with respect to EPA. The ARA:EPA ratio was significantly higher in non-invaded lakes than in the invaded lakes (ANOVA; $P < 0.001$), as would be expected from the results for ARA and EPA singly. There was no significant difference among males, females and juveniles, and the interaction of sex and invasion status was also non-significant (ANOVA; $P > 0.05$).

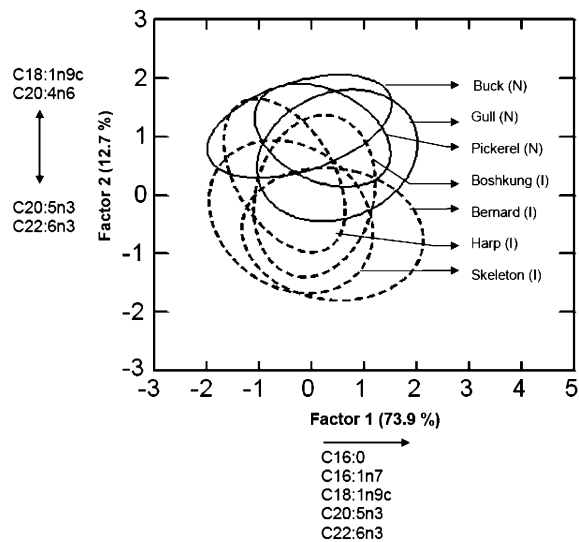


Fig. 2 Principal component analysis of fatty acids for all sampling periods in 2003. Ellipses represent one standard deviation around the centroid of each class: Non-invaded lakes are represented by solid lines and invaded lakes by dashed lines. Percent variance explained by each axis is denoted in parentheses

Discussion

Our analyses of gut contents and of fatty acids suggest that invasion by *B. longimanus* alters the diet of *M. relictus*. However, we must be cautious because our sample size of lakes was small, and also because we discovered during our study that *M. relictus* in two of the uninvaded lakes behaved differently. Pickerel_(N) and Buck_(N) lakes had shallower mean Secchi

depths (1.7 m and 2.1 m, respectively) relative to the other lakes (3.6–7.3 m). While Pickerel Lake_(N) has the highest chlorophyll *a* concentration among our lakes, 4.4 mg m⁻³ (Strecker et al. 2006), we believe the lower Secchi depth in these two lakes is due to coloured DOC. In these two lakes, *M. relictus* could be found in the water column during the day and these lakes also had abundant *Chaoborus*. While these factors make us cautious of our interpretation, there is no indication either in the principal components analysis (Fig. 2) or the discriminant function analysis (Fig. 3) that the differences between invaded and uninvaded lakes are driven by these two lakes; Gull Lake_(N) is a clear-water lake (mean Secchi depth = 6.6 m) and demonstrates the same differences in FA composition. Further, both clear-water and coloured lakes can be invaded by *B. longimanus* (D. Branstrator, Dept. of Biol., Univ. of Minnesota-Duluth, Duluth, Minnesota; pers. comm.).

There are other shortcomings of both gut content analysis and FA analysis. Gut content analysis may be biased by digestibility, and prey with indigestible elements may contribute disproportionately to gut contents. In our data, some prey could only be scored as present (e.g., copepods) while others could be counted (e.g., rotifers); and no inferences on their relative importance can be drawn. Similarly, indigestible prey may contribute to FA results even though they are not assimilated. Therefore, the data we present here should only be interpreted in terms of what prey are consumed, and how their occurrence in *M. relictus* varies among lakes.

Fig. 3 Discriminant function scores for invaded and uninvaded lakes, plotted for each lake against day of the year. Note that the top cluster are invaded lakes, the bottom cluster uninvaded lakes

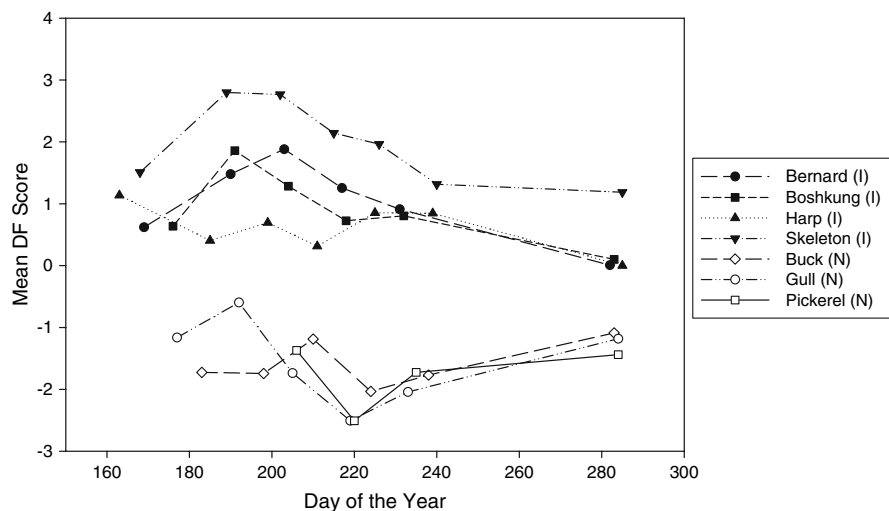
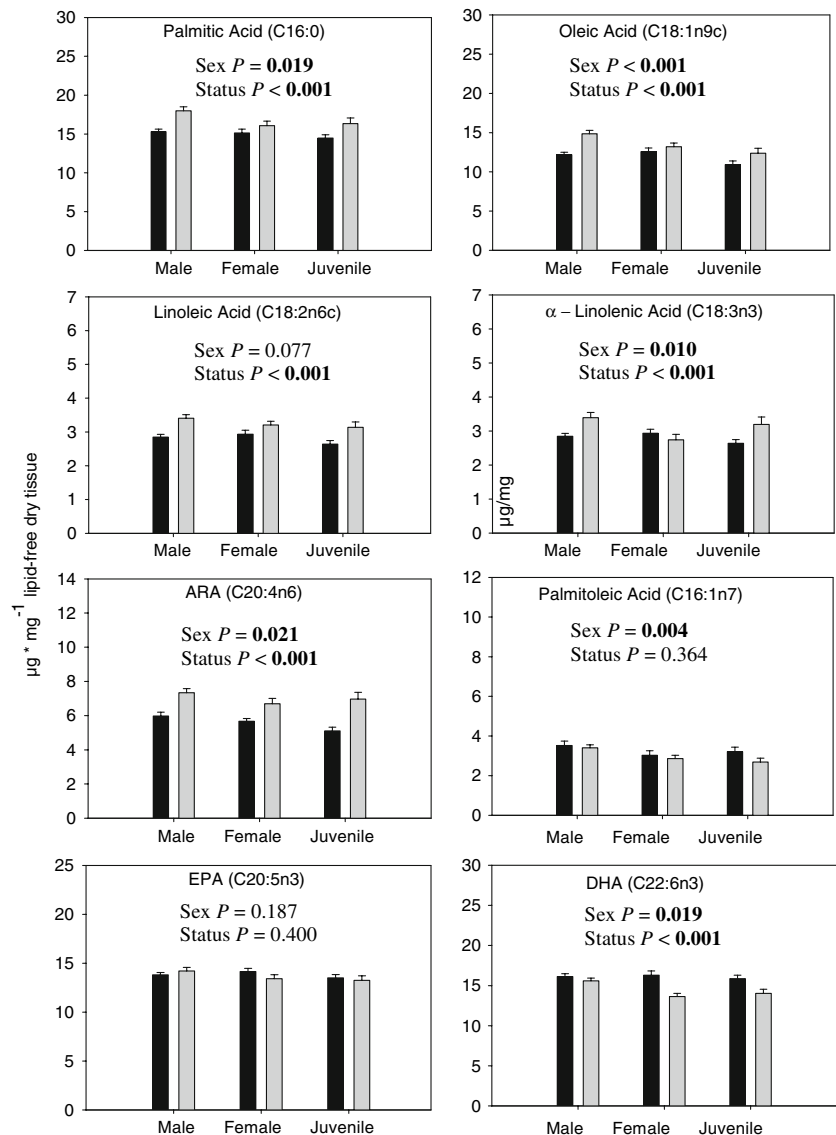


Fig. 4 Means and standard errors of individual fatty acids. Results of factorial ANOVAs for the effect of invasion status (invaded = black, non-invaded = grey) and sexes/ life stage are also indicated. There was no significant interaction between lake and sex/life stage for any of the fatty acids ($P > 0.05$). The bar graphs illustrate μg FAME mg^{-1} lipid-free dry weight, while ANOVAs were performed on $\log(x + 1)$ transformed data. Note differences in scale



Zooplankton prey and *M. relicta* gut contents

The relationships between *B. longimanus* abundance and zooplankton abundance or composition are complex. Research done on lakes in the same region that had been invaded by *B. longimanus* found that crustacean populations were lower in species richness, abundance and biomass (Boudreau and Yan 2003; Strecker et al. 2006; Hovius et al. 2006). Lehman and Cáceres (1993) described a logistic or threshold relationship between zooplankton abundances and *B. longimanus* biomass in Lake Michigan, and similar relationships have been observed in Lake

Erie (O. Johannsson; unpublished data). Small lakes also show a steep negative response of crustacean biomass to abundance of *B. longimanus* (Hovius et al. 2006). *B. longimanus* abundances in our invaded lakes differed in peak densities and seasonal timing. Their impacts on the cladoceran community also differed among lakes. Such differences likely indicate a similar variability exists in the response of *M. relicta* to the invasion of inland lakes by *B. longimanus* further modified by differences in cladoceran abundance, species composition and availability.

Total zooplankton biomass was negatively correlated with *B. longimanus* abundance during the

summer in Bernard_(I), the most heavily invaded lake. Lehman and Càceres (1993) found similar reciprocal relationships between populations of *B. longimanus* and the cladocerans *Daphnia pulicaria*, *D. retrocurva*, and *Leptodora kindtii*. Skeleton Lake_(I), an oligotrophic lake with low abundance of *B. longimanus*, showed a suggestive but non-significant relationship.

In contrast, Harp Lake_(I) cladoceran biomass climbed steadily until August, then decreased suddenly and concurrently with a decrease in *B. longimanus*. Of all our study lakes, Harp Lake_(I) has had the longest history of invasion and zooplankton species richness has declined to the point where the dominant species contributing to cladoceran biomass other than *B. longimanus* are *Daphnia g. mendotae* and *Holopedium gibberum* (Yan and Pawson 1997). *B. longimanus* was cited as the cause of the loss of zooplankton biodiversity in Harp Lake (Yan et al. 2002) and appears to select prey other than the now dominant herbivorous cladoceran species. This agrees with a study by Dumitru et al. (2001) that found larger-bodied *D. g. mendotae* and *H. gibberum* had the smallest fractional losses due to *B. longimanus* in Harp Lake_(I) during the summer of 1995. The sudden concurrent decline of *B. longimanus* and other cladocerans in Harp Lake_(I) during this study may be related to fish predation. Coulas et al. (1998) showed that lake herring (*Coregonus artedii*) in Harp Lake_(I) preferred to prey on *D. g. mendotae* and *B. longimanus*. Another explanation for the different zooplankton dynamics in Harp Lake_(I) compared to the other invaded lakes may be that its large populations of zooplankton reproduce quickly and are largely unaffected by predation until predator densities reach a threshold. Sprules et al. (1990) suggested that this was the case with *B. longimanus* and *Daphnia* spp. populations in Lake Michigan.

Zooplankton biomass in Bernard Lake_(I) increased substantially during winter 2003–2004. *B. longimanus* typically spends the colder months as resting eggs (de Bernardi and Guissani 1975; Herzig 1985) and its absence from the water column during this time may have contributed to the rapid growth of the remaining zooplankton population. In 2003, we first detected *B. longimanus* in mid-June when epilimnetic water temperatures were 17.5–20°C. We did not observe *B. longimanus* in our nets in May 2004. This is consistent with a multi-year study conducted by

Pothoven et al. (2001) that did not report *B. longimanus* in the water column of Lake Michigan until June or July when water temperatures reached 17–20°C. The large winter increase in zooplankton biomass observed in Bernard Lake_(I) was not evident in Skeleton_(I) or Harp_(I) lakes.

Differences in the diet of *M. relicta* among the study lakes were suggested by both FA analysis and by direct examination of gut contents from mid-August. In all lakes, mysids ingested many different prey and differences in diet appeared to depend on the presence/absence of *Chaoborus* spp. and *B. longimanus* as alternative food sources in some lakes, the degree of cannibalism, and the abundance of native crustacean zooplankton. Several studies on the feeding habits of *M. relicta* suggest that their diet can vary from month to month and is a function of selectivity and the relative abundance of prey species that are available for a given size of mysid (Bowers and Vanderploeg 1982; Folt et al. 1982; Viherluoto and Viitasalo 2001). *M. relicta* were observed to eat *B. longimanus* in the lakes where it was present. However, the frequency of *B. longimanus* found in the guts of *M. relicta* varied greatly and appeared to be related to the abundance of both the invader and alternate prey. For example, lower concentrations of native prey combined with high densities of *B. longimanus* could be the cause of the high frequency of the invader in the guts of *M. relicta* from Bernard Lake_(I). Although Skeleton Lake_(I) also has relatively low zooplankton biomass, *B. longimanus* also has a much lower population density in this lake than in Bernard_(I), likely resulting in reduced encounter rates with *M. relicta*. The lower density of both zooplankton and *B. longimanus* may be the reason *M. relicta* seems to be primarily herbivorous in this lake. Grossnickle (2001) found that when zooplankton abundance is low, *M. relicta* will switch to a mainly algal diet.

Chaoborus spp. and *M. relicta* are both zooplanktivorous and their combined planktivory in Buck_(N) and Pickerel_(N) lakes may contribute to the low abundance of cladocerans and copepods observed in August. Although zooplankton biomass was lower in these two non-invaded lakes compared to Gull_(N), Boshkung_(I), Skeleton_(I) and Harp_(I) lakes, the relatively high occurrences of cladoceran body parts in mysid guts suggests that cladocerans are relatively vulnerable to predation by *M. relicta*. In addition, the

frequency of *Chaoborus* larvae and other insect remains in the guts of these mysids indicates that these alternative prey are being consumed when zooplankton are less abundant. Consumption of emerging *Chaoborus* or other pupae could account for some or all of what appeared to be parts of adult insects in *M. relicta*. Without this compensation of alternative prey, mysids may be forced to switch to a more herbivorous diet, as may be the case in Skeleton Lake₍₁₎, to minimize the energetic consequences of additional search effort required to encounter cladoceran prey when biomass is low.

There were few *B. longimanus* in the guts of *M. relicta* from Harp Lake₍₁₎, and the large biomass of native zooplankton is likely the reason *M. relicta* are not consuming the invader in larger quantities. This possibility concurs with a study by Cooper and Goldman (1980) who found a decrease in *M. relicta* consumption of *Diaptomus*, an alternative food source, when *Epischura*, a preferred prey item, increased. In addition, the long spine of *B. longimanus* may be a deterrent, and the cost of handling this animal may only be offset when alternative prey are scarce. The tail spine of *B. longimanus* was not found in the guts of *M. relicta* from any of the invaded lakes, which may mean that it is manipulated in such a way that only the soft body portion is consumed. Laboratory observations later confirmed that *M. relicta* does not ingest the spine of *B. longimanus* during feeding (Kelly Bowen, Department of Fisheries and Oceans, Burlington; pers. comm.).

Mysis relicta remained in the water column with *Chaoborus* spp. in two of the non-invaded lakes instead of undergoing its usual migration to the bottom. Usually, *M. relicta* is benthic during the day and migrates vertically to feed on zooplankton in the upper part of the water column at night, when predation by fish is less intense (Rudstam et al. 1989; Johannsson et al. 2001). These diel migrations would limit the time spent searching for planktonic food, especially in summer when nights are shorter. During these times, animals may trade selection of higher quality foods for lower quality, more abundant prey to meet their energy needs (Pastorok 1981). The daytime presence of *M. relicta* in the water column of these two lakes suggests that there was adequate cover during the day for mysids to forage under reduced fish predation. It is possible that the presence of *Mysis* and *Chaoborus* in the water column prevents

Daphnia from using the metalimnion and hypolimnion as a daytime refuge, causing them to suffer greater fish predation as well as invertebrate predation.

Fatty acids

The most abundant and most variable FA measured in *M. relicta* in this study were C16:0, C18:1n9c, EPA, and DHA. These findings are not unusual, as the same FA have been found to occur in large amounts in krill and their zooplankton prey (Virtue et al. 2000), Antarctic zooplankton (Phleger et al. 1998), polar copepods (Kattner et al. 2003), halibut larvae (Ejemo et al. 2003) and some species of algae (Napolitano 1999). Furthermore, C16:0 and C18:1n9c can be synthesized de novo in animals. Concentrations of FA were, on average, lower in the invaded lakes. However, concentrations of the essential fatty acid EPA in *M. relicta* from the invaded lakes was not lower than in mysids from the non-invaded lakes, and the DHA concentration was actually higher. This suggests that the alternative sources of prey in invaded lakes can provide similar or greater amounts of EPA and DHA relative to animals in non-invaded lakes

Some highly unsaturated fatty acids accumulate in food webs and therefore may be used as an index of trophic position (Goedkoop et al. 2000; Hebert et al. 2006). The ratio of ARA:EPA has been suggested as an index of trophic position based on the observation that, while some algae (e.g., diatoms) are rich in EPA, ARA accumulates in carnivores (Kainz et al. 2004). It has been used previously to help assess the trophic position of fish (Kuusipalo and Käkälä 2000) and birds (Hebert et al. 2006). Other studies have found high proportions of ARA in fish that were known to consume large quantities of aquatic insects, gammarids, and oligochaetes relative to the ARA content of aquaculture fish (Ackman and Takeuchi 1986; Bell et al. 1994). In invaded lakes, increased herbivory should reduce this ratio, while increasing consumption of *B. longimanus* rather than rotifers and herbivorous *Cladocera* should increase it. While EPA was not significantly different between invaded and uninvaded lakes, most other fatty acids including ARA were reduced in invaded lakes. Therefore, ARA:EPA was also lower in invaded lakes. Among the omega-3 fatty acids, DHA was higher in invaded

lakes. The effect of *B. longimanus* on trophic position could be obscured by the presence of *Chaoborus* in two of the uninvaded lakes. That omega-3 FA are similar (EPA) or higher (DHA) in invaded lakes, while most other fatty acids are reduced, could indicate that these are conserved in food-stressed animals or that mysids in invaded lakes are eating proportionately more of food items that contain higher concentrations of DHA (e.g., copepods and/or dinoflagellates).

Conclusions

The gut content and fatty acid analyses both revealed differences in *M. relictus* diet between lakes invaded by *B. longimanus* and non-invaded lakes. Gut content analysis showed a diverse diet for *Mysis* in these lakes. Cannibalism was observed in all lakes, and consumption of the planktivores *B. longimanus* and *Chaoborus* occurred when they were available. The observed large densities of *Chaoborus* spp. in the two non-invaded lakes may not only be an additional food source for *M. relictus*, but may also keep *B. longimanus* from becoming established. There was reduced frequency of Cladocera and Copepoda in the guts of *M. relictus* in lakes with the most *B. longimanus*. Fatty acid analysis revealed differences in both quantity and quality of FA between invaded and non-invaded lakes, but we found that the essential fatty acids DHA and EPA were not reduced by invasion. Fortunately, mysids are opportunistic omnivores and can adapt to changes in the food supply in order to survive; for example the high frequency of *B. longimanus* in their guts in Bernard Lake₍₁₎, although growth and reproduction may be sacrificed (Beeton and Gannon 1991; Chess and Stanford 1998). Johannsson et al. (1994, 2003) found that interactions among fish, *M. relictus*, and zooplankton are complex, and that *M. relictus* from lakes Ontario and Michigan may consume a variety of food over the course of a year to meet their energy and nutritional demands. Further research is necessary to determine the extent to which *B. longimanus* affects the growth and reproduction of *M. relictus*.

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