

Energetic consequences of diet shifts in Lake Erie rainbow smelt (*Osmerus mordax*)

S.L. Parker Stetter, L.D. Witzel, L.G. Rudstam, D.W. Einhouse, and E.L. Mills

Abstract: The diet of eastern Lake Erie rainbow smelt (*Osmerus mordax*) has changed since the 1960s, reflecting food resource shifts due to phosphorus reductions and the invasion of exotic species (dreissenid mussels and *Bythotrephes longimanus*). Since rainbow smelt growth was lower in the 1990s than in the 1960s, we considered diet changes as an explanation. A decrease in the proportion of zooplankton occurred in the summer (May–August) diet of two size classes (63–88 and 89–114 mm fork length) between 1961 and 1999. Within the zooplankton, the proportion of *Bythotrephes* increased. In spite of these changes, energy density (joules per gram) of the summer (June–August) diet has not changed since 1961. However, during the late-summer and fall, predation on *Bythotrephes*, and therefore the proportion of indigestible spines in the stomach, increases. Using bioenergetics models, we show that Lake Erie rainbow smelt could achieve 66%–155% greater growth between June and October if *Bythotrephes* spines were replaced with digestible prey items, resulting in end-of-season weights and lengths similar to the 1985–1990 period. Our results indicate that indigestible *Bythotrephes* spines may reduce growth by occupying space in the stomach but providing no nutritional value to the fish, thereby reducing the realized daily ration for rainbow smelt.

Résumé : Le régime alimentaire des éperlans arc-en-ciel (*Osmerus mordax*) de l'est du lac Érié s'est modifié depuis les années 1960, reflétant ainsi les changements des ressources alimentaires dus aux réductions du phosphore et à l'invasion d'espèces exotiques (les mollusques dreissenidés et *Bythotrephes longimanus*). Comme la croissance des éperlans arc-en-ciel est plus faible dans les années 1990 que dans les années 1960, nous avons examiné le rôle possible des changements de régime alimentaire dans ce phénomène. Il s'est produit une diminution de la proportion du zooplancton dans le régime alimentaire d'été (mai à août) des poissons de deux classes de taille (longueurs à la fourche, 63–88 mm et 89–114 mm) entre 1961 et 1999. La proportion de *Bythotrephes* dans le zooplancton a augmenté. Malgré ces changements, la densité énergétique (joules par gramme) du régime d'été (juin à août) n'a pas changé depuis 1961. Cependant, durant la fin de l'été et l'automne, la consommation de *Bythotrephes* augmente et, par conséquent, il y a une plus grande proportion d'épines indigestes dans l'estomac. Des modèles bioénergétiques montrent que les éperlans arc-en-ciel du lac Érié pourraient atteindre une croissance de 66 à 155 % plus élevée entre juin et octobre si les épines de *Bythotrephes* étaient remplacées par des proies digestibles, ce qui donnerait des masses et des longueurs à la fin de la saison semblables à celles observées en 1985–1990. Nos données indiquent que les épines non assimilables de *Bythotrephes* peuvent réduire la croissance en occupant de l'espace dans l'estomac sans apporter de bénéfice nutritionnel au poisson et en réduisant ainsi la ration quotidienne réalisée de l'éperlan arc-en-ciel.

[Traduit par la Rédaction]

Introduction

Growth rates of eastern Lake Erie rainbow smelt (*Osmerus mordax*) began to decline in the 1960s (Henderson and Nepszy 1989). During the early 1980s, yearling size

continued to decrease but also showed a strong 2-year cycle associated with yearling abundance (Einhouse et al. 1998). This pattern continued until 1994 when the 2-year cycle disappeared and a progressive decrease in yearling size began (Einhouse et al. 1998; Johnson et al. 2000) (Fig. 1). Changes in the yearling rainbow smelt diet have been suggested as an explanation for their decreased growth (Dermott et al. 1999). Interestingly, young-of-the-year growth rates did not change during the same time period (Fig. 1).

Three important ecosystem changes, with the potential to affect the rainbow smelt prey base, have occurred in eastern Lake Erie since rainbow smelt growth began to decline in the 1960s: reductions in phosphorus, the invasion of *Bythotrephes longimanus*, and the invasion of dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*).

Reductions in phosphorus concentrations began in 1972 and continued until the late 1980s (Dolan 1993), decreasing the productivity of the system. As a result, zooplankton production and mean body size decreased (Johannsson et al.

Received 7 October 2003. Accepted 16 September 2004.
Published on the NRC Research Press Web site at
<http://cjfas.nrc.ca> on 5 March 2005.
J17777

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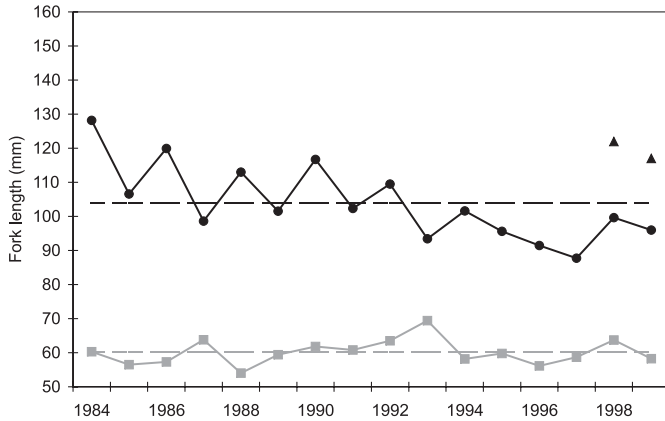
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Fig. 1. Fall fork lengths of yearling (solid circles) and young-of-the-year (shaded squares) rainbow smelt from Ontario Ministry of Natural Resources 10-m index trawl in Long Point Bay, Ontario, 1984–1999. Figure modified from Johnson et al. (2000). Long-term average line for yearling (black broken line) and young-of-the-year (shaded broken line) rainbow smelt added. Results from predicted growth bioenergetic simulations (solid triangles) are presented for 1998 and 1999.



2000) and the community shifted toward more calanoid copepods relative to other crustaceans (Johannsson et al. 1999). A significant decrease in rainbow smelt abundance also occurred during this time period (Ryan et al. 1999).

In 1985, as phosphorus levels were near target levels (Dolan 1993), the exotic cladoceran *B. longimanus* was confirmed in the eastern basin zooplankton assemblage (Bur et al. 1986). In spite of its large indigestible caudal spine, it is a major prey item for rainbow smelt (Parker et al. 2001).

Dreissenid mussels were found in the eastern basin in 1989 (Dermott et al. 1993) and had little effect on the rainbow smelt prey base. Zooplankton biomass in the offshore region where rainbow smelt forage did not change significantly following the dreissenid invasion (Johannsson et al. 1999, 2000). In the profundal zone of eastern Lake Erie, density of nondreissenid benthic invertebrates increased, and biomass of nondreissenid benthic invertebrates decreased, following the dreissenid invasion (Dermott and Kerec 1997). Biomass and density of nondreissenid benthic invertebrates did not change further between 1993 and 1998 (MacDougall et al. 2001), although the spatial distribution of benthic invertebrates may have changed in the presence of dreissenid druses (Botts et al. 1996; Dermott and Kerec 1997).

Reduced rainbow smelt growth could result from changes in prey quantity or type. Lower daily consumption, decreased energy density of prey, or the expenditure of additional energy to find scarce prey items would reduce growth. Decreased growth could also result from the loss of large prey items that were previously important to rainbow smelt as they grew (Dermott et al. 1999). Although these are likely explanations for decreased growth during phosphorus reductions in the 1960–1980s, rainbow smelt growth continued to decline through the 1990s in spite of reduced smelt density (Ryan et al. 1999) and a relatively stable invertebrate prey base (Dermott et al. 1993; Johannsson et al. 1999; MacDougall et al. 2001).

The objective of this study was to examine alternative explanations for decreased rainbow smelt growth during the 1990s focusing on changes in composition and energy density of the diet. Our approach used rainbow smelt diet data from 1961, 1994, 1998, and 1999. Specifically, we (i) examined the summer (May–August) diet of two size classes to determine whether significant shifts in prey composition or energetic content have occurred as a result of ecosystem change and (ii) constructed a seasonal diet for 1998 and 1999 to determine if indigestible *Bythotrephes* spines found in rainbow smelt stomachs decreased the energy density of the diet enough to reduce seasonal growth.

Materials and methods

1998 and 1999 rainbow smelt collection and diet analyses

Rainbow smelt were obtained from 35 midwater trawl samples collected in 1998 (11 June, 2 July, 1 August, 6 October) and 1999 (6 June, 7 July, 3 October) in the eastern basin of Lake Erie. All fish were from night or sunrise collections with the exception of two daytime collections in June 1998. Nighttime collections were made in June between 2 h 10 min and 8 h 52 min (sunrise) after sunset, in July–August between 2 h 24 min and 8 h 20 min after sunset, and in October between 2 h 24 min and 10 h 52 min after sunset. Daytime collections were made in early afternoon. Trawling was concentrated in the southern half of the basin due to hazards such as gas wells and commercial fishing gear in Canadian waters. A four-seam midwater trawl with 6-mm² cod-end mesh and average fishing dimensions of 6.0 m vertical gape and 6.0 m horizontal spread was used. Trawls lasted 20 min at an average velocity of 1.5 m·s⁻¹. A subsample of yearling and older fish was measured for fork length (millimetres) prior to processing specimens for diet analysis. From each trawl catch, we randomly selected 50 rainbow smelt from the yearling size class (≤120 mm) and actively selected up to 50 larger (>120 mm) rainbow smelt to ensure that all life stages were represented in the diet analyses. The body cavity of each fish was slit prior to preservation in 95% ethanol.

At the laboratory, rainbow smelt from each trawl were processed until at least 20 fish (10 yearling size class, 10 larger size class) with stomach contents, not including those containing only *Bythotrephes* spines, were examined. Fork length and total length measurements were made to the nearest millimetre on each fish. The stomach was then removed and assessed for degree of fullness based on a modification of the Hynes–Thompson method (Hynes 1950; Thompson 1959), a volumetric diet estimate that assigns points to prey items found in the stomach. Each stomach was emptied into a petri dish and inspected under a dissecting scope to ensure that no food items were missed. Prey items were identified to major groups, calanoid copepods, cyclopoid copepods, unknown copepods or copepodites, nauplii, *Bosmina* or *Eubosmina*, *Daphnia*, *Bythotrephes* bodies, *Bythotrephes* spines, benthic or emergent invertebrates, fish, and unknown or digested material, and assigned a proportion of the degree of stomach fullness based on their estimated volume. *Bythotrephes* spines and *Bythotrephes* bodies were considered separately because of the longer retention time of caudal spines in rainbow smelt (Parker et al. 2001). Because of classifica-

tion differences among studies, prey categories were grouped as copepods, cladocerans, *Bythotrephes* bodies, *Bythotrephes* spines, benthos, fish, and unknown or digested material. The proportion of unknown or digested material (ranging from 0.01 to 0.11) was partitioned among all prey categories except *Bythotrephes* spines. Zooplankton proportion was defined as copepods plus cladocerans including *Bythotrephes*.

1961 and 1994 rainbow smelt collections and diet analyses

Rainbow smelt from the 1961 (Bidgood 1961) and 1994 (Dermott et al. 1999; L.D. Witzel, unpublished data) studies used fish from the central and eastern basins of Lake Erie. In 1961, central basin rainbow smelt were collected with a 12-mm cod-end midwater trawl and eastern basin smelt were collected with a commercial Texas bottom trawl. The 1994 collections (2 May, 2 July) were made in the eastern and central basins using commercial Texas bottom trawls or a standard 10-m index trawl. In both 1961 and 1994, collections were primarily made during early daylight hours. During both years, specimens were packed on ice immediately upon landing and transferred to freezers upon arrival at the dock. In 1961 and 1994, the Hynes–Thompson method (Hynes 1950; Thompson 1959) was used to estimate the volumetric composition of the diet.

Summer diet of rainbow smelt (1961–1999)

Summer diet information for individual yearling and older rainbow smelt was available between the last week of May and the first week of August for 1994, 1998, and 1999. Bidgood (1961) generated size-class diets based on an amalgamation of data for May, June, July, and August. Of the fish examined by Bidgood (1961), 67% (1306 of 1936) of all fish with stomach contents and 72% (19 100 of 26 678) of all prey points assigned under the Hynes–Thompson method (Hynes 1950; Thompson 1959) were obtained between the last week of May and the first week of August. Diet data were available in 2-week intervals for the 1961 and 3- to 4-week intervals for 1994, 1998, and 1999. Fork length categories were defined at natural breaks in the diet identified by Bidgood (1961) at 63–88 and 89–114 mm. To remain consistent with methodologies used in Bidgood (1961), averages were calculated based on diets for individual fish. A May–August summer diet was determined by calculating a grand mean proportion for each prey type from the mean proportion of each prey type from individual months in rainbow smelt diets from 1994, 1998, and 1999.

Generalized linear models, with a binomial family and logit link, and F tests were used to test the significance of year as (i) a predictor of the proportion of zooplankton in the summer diet of rainbow smelt in 1961, 1994, 1998, and 1999 and (ii) a predictor of the proportion of *Bythotrephes* in the summer diet of rainbow smelt in 1994, 1998, and 1999. Two size classes of rainbow smelt were included for each year in these analyses. As differences between size classes were expected, the effect of year was tested in the presence of size class. All analyses were completed with S-Plus (Math-Soft, Inc. 1999) and considered significant at the $p < 0.05$ level. A mean percent (± 2 SE) of summer stomach fullness (including empty stomachs) was calculated for both rainbow smelt size classes in 1994, 1998, and 1999 using in-

dividual trawls. Results were compared with a mean value calculated from Bidgood (1961) for all size classes during the same time period.

A comparison was made of the energy density of the summer diet of rainbow smelt in 1961, 1994, 1998, and 1999. Summer diets for the two rainbow smelt size classes were taken from the previous analysis. All prey energy density values were based on Cummins and Wuycheck (1971) as implemented in prior bioenergetics models. Prey energy densities for fish ($4435 \text{ J}\cdot\text{g}^{-1}$), benthos ($3138 \text{ J}\cdot\text{g}^{-1}$), and *Bythotrephes* ($1674 \text{ J}\cdot\text{g}^{-1}$) were taken from Lantry and Stewart (1993). However, because Lantry and Stewart (1993) used an amalgamated energy density for copepods and cladocerans, individual energy densities for copepods ($2300 \text{ J}\cdot\text{g}^{-1}$) and cladocerans ($1674 \text{ J}\cdot\text{g}^{-1}$) were based on Stewart and Binkowski (1986). As *Bythotrephes* spines are indigestible, we assigned spines an energy density of $0 \text{ J}\cdot\text{g}^{-1}$. The energy density of the summer diet for both rainbow smelt size classes was calculated by multiplying the proportion of each diet item by its energy density.

A generalized linear model was used to test the significance of year as a predictor of summer diet energy in two size classes of rainbow smelt in 1961, 1994, 1998, and 1999. As differences between size classes were expected, the effect of year was tested in the presence of size class.

Temporal patterns in stomach fullness during 1998 and 1999 were considered by expressing mean percentage of stomach fullness (including empty stomach) for each trawl sample as a function of time of collection in minutes after sunset. Only those midwater trawls performed between dusk and dawn were included in the analysis. The relationship between stomach fullness and time of collection was investigated with a correlation analysis. Data were also plotted and fit with a second-order polynomial curve, as rainbow smelt are expected to have their highest feeding rates at dusk and dawn crepuscular periods.

Energetics of *Bythotrephes* spine consumption (1998 and 1999)

The potential effect of *Bythotrephes* spines on yearling rainbow smelt growth (1 June – 31 October) in 1998 and 1999 was investigated using a bioenergetics model. The mean fork lengths of yearling rainbow smelt were calculated from midwater trawl samples for June, July–August, and October of 1998 and 1999. For diet calculations, the size ranges were defined as the mean yearling fork length ± 5 mm. As no diet information was available for September, the results of the July–August diet were used for 1–15 September and the results of the October diet were used for 16–30 September. Kozuchowski (1996) found increased consumption of *Bythotrephes* by rainbow smelt during the month of September, a condition that is similar to October diet observations in our study.

Fish Bioenergetics 3.0 (Hanson et al. 1997) was used for the 1 June – 31 October growth simulations. Model parameters, including the summer simulation temperature value of 10°C , were taken from Lantry and Stewart (1993). Weights for 1 June and 31 October of each year were calculated from the mean fork length in June and October of each year using a wet weight (grams) versus fork length (millimetres) regression equation developed for eastern Lake Erie rainbow smelt

from 1984–2001 (L.D. Witzel, unpublished data). The regression was

$$\log_{10}(\text{wet weight}) = 3.16 \log_{10}(\text{fork length}) - 5.52$$

$$(R^2 = 0.93, N = 4428)$$

Given the observed start and end weights and the observed diet, the year-specific simulations were run to determine the proportion of maximum consumption (p value) needed for rainbow smelt to achieve the observed growth in 1998 and 1999. Diet proportions for these simulations included the indigestible *Bythotrephes* spines with an energy density of $0 \text{ J}\cdot\text{g}^{-1}$. Seasonal diet proportions and the total energy density of the diet are presented in Table 1.

A second set of year-specific bioenergetic simulations was used to predict rainbow smelt growth if the indigestible *Bythotrephes* spines were replaced with nutritional prey items. *Bythotrephes* spines were reassigned an energy density value equivalent to the mean of other prey items weighted by their proportion in the diet in a given month. The models were initiated with the observed starting weight on 1 June and run to 31 October, using the p values determined from the first bioenergetics simulations, to predict the new seasonal weight gains. Predicted weight gains were then converted to their corresponding fork length using the length–weight regression equation presented above for comparison with observed growth.

Results

Summer diet of rainbow smelt (1961–1999)

The generalized linear models indicated that the proportion of zooplankton in the diet of rainbow smelt has decreased since 1961. Year was a significant predictor of zooplankton proportion in the diet ($p = 0.05$, $F = 9.56$, $N = 8$). In the second generalized linear logistic model, year was a significant predictor of *Bythotrephes* proportion in the diet ($p = 0.01$, $F = 70.06$, $N = 6$). In both analyses, size class was retained as an explanatory variable even though it was not significant ($p > 0.07$) to remove any effect of size class on the analyses. Mean percentage of summer stomach fullness (± 2 SE) for 63- to 88-mm fork length rainbow smelt in 1994 (46 ± 28 , $N = 5$), 1998 (59 ± 14 , $N = 13$), and 1999 (62 ± 10 , $N = 12$) and for 89- to 114-mm fork length rainbow smelt in 1994 (40 ± 26 , $N = 4$), 1998 (52 ± 14 , $N = 13$), and 1999 (55 ± 12 , $N = 8$) did not differ significantly from the mean percentage of fullness of 66 calculated for the same time period in Bidgood (1961). The total number of specimens examined by Bidgood (1961) was 1388; however, no sample sizes were given for individual time periods and the data were an amalgamation of all size classes.

The energy densities (joules per gram) of rainbow smelt diets in 1994, 1998, and 1999 were not significantly different from those of the 1961 diet. After controlling for the effect of size class, year was not a significant predictor of energy density in the diet ($p = 0.41$, $F = 1.31$, $N = 8$). Size class was retained as an explanatory variable even though it was not significant ($p > 0.21$) to remove any effect of size class on the analysis. The diets of the 63- to 88-mm fork length rainbow smelt in 1994, 1998, and 1999 were within 6% of the energy density of the 1961 diet. The diets of 89-

Table 1. Proportion of fullness by volume of diet items and mean energy density used in 1998 and 1999 Lake Erie yearling rainbow smelt bioenergetics simulations (1 June – 31 October).

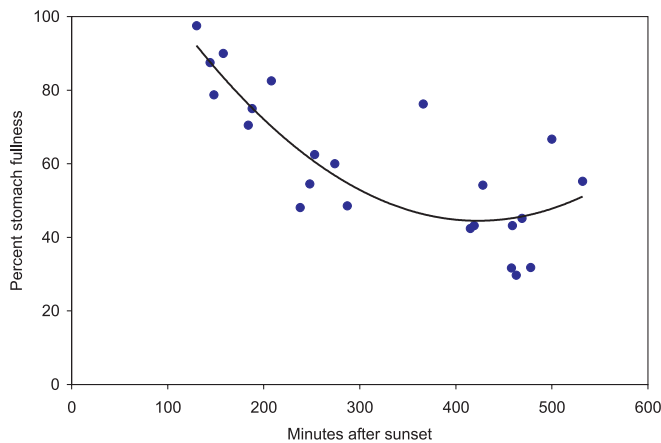
Date	Size range (mm)	N	Bythotrephes			Fish	Energy ($\text{J}\cdot\text{g wet weight}^{-1}$)	Energy* ($\text{J}\cdot\text{g wet weight}^{-1}$)
			Cladocerans	bodies	spines			
1998								
1 June – 30 June	82–92	71	0.64	0.09	0.04	0.02	0.21	2403
1 July – 15 Sept.	88–98	16	0.19	0.17	0.39	0.11	0.00	2247
16 Sept. – 31 Oct.	99–109	20	0.09	0.01	0.47	0.43	0.00	1774
1999								
1 June – 30 June	67–77	40	0.47	0.31	0.00	0.00	0.22	2299
1 July – 15 Sept.	79–89	30	0.33	0.21	0.32	0.10	0.04	1964
16 Sept. – 31 Oct.	94–104	31	0.18	0.02	0.30	0.29	0.14	2399

Note: Energy of the diets with $0 \text{ J}\cdot\text{g wet weight}^{-1}$ spines for observed growth (Energy) and for simulations with spines assigned the mean energy density of other items in the diet for predicted growth (Energy*) is presented. N is the number of individual fish.

Table 2. Proportion of fullness by volume of diet items and mean energy density for two size classes (63–88 and 89–114 mm fork length) of Lake Erie rainbow smelt in summer (May–August) of 1961, 1994, 1998, and 1999.

Year	Size range (mm)	N	Copepods	Cladocerans	<i>Bythotrephes</i> bodies	<i>Bythotrephes</i> spines	Benthos	Fish	Energy (J·g wet weight ⁻¹)
1961	63–88		0.78	0.19	0.00	0.00	0.03	0.00	2206
	89–114		0.14	0.75	0.00	0.00	0.08	0.03	1962
1994	63–88	77	0.79	0.13	0.00	0.00	0.08	0.00	2286
	89–114	110	0.57	0.13	0.01	0.00	0.29	0.00	2455
1998	63–88	82	0.42	0.26	0.19	0.03	0.06	0.04	2085
	89–114	76	0.35	0.19	0.21	0.06	0.14	0.05	2136
1999	63–88	135	0.43	0.24	0.15	0.04	0.14	0.00	2081
	89–114	54	0.03	0.10	0.19	0.11	0.55	0.02	2369

Note: Indigestible *Bythotrephes* spines were assumed to have no digestible energetic value (0 J·g wet weight⁻¹). *N* is the number of individual fish. The total number specimens examined by Bidgood (1961) was 1388; however, no sample sizes were given for individual size classes.

Fig. 2. Percent stomach fullness for rainbow smelt in 1998 and 1999 as a function of time of collection (minutes after sunset). A second-order polynomial line ($y = 0.0006x^2 - 0.4693x + 143.77$; $R^2 = 0.69$, $N = 23$ trawls) is fit to the data, as peak feeding is expected at sunset and sunrise.

to 114-mm rainbow smelt in 1994, 1998, and 1999 were within 25% of the energy density of the 1961 diet (Table 2).

Stomach fullness of rainbow smelt in 1998 and 1999 was significantly negatively correlated with time of collection ($p < 0.01$, $r = -0.76$, $N = 23$). Stomach fullness was highest near sunset, decreased through the night, and began increasing near dawn (Fig. 2). The data were fit with a second-order polynomial curve ($R^2 = 0.688$, $N = 23$) (Fig. 2).

Energetics of *Bythotrephes* spine consumption (1998 and 1999)

The bioenergetic simulations for observed growth provided consumption estimates for seasonal growth in 1998 and 1999 with 0 J·g⁻¹ *Bythotrephes* spines in the diet. A *p* value of 0.58 was calculated for the 1998 simulation in which rainbow smelt fork length increased from 87 to 104 mm over the season, an increase in wet weight from 4.1 to 7.2 g. Similarly, a *p* value of 0.60 was calculated for the 1999 simulation in which rainbow smelt fork length increased from 72 to 99 mm, an increase in wet weight from 2.2 to 6.2 g.

We also used the energetics model to predict growth of rainbow smelt when *Bythotrephes* spines were assigned a weighted energy density based on other prey items in the

diet. In the 1998 predicted growth simulation, rainbow smelt wet weight increased over the season from 4.1 to 12.0 g, an increase in fork length from 87 to 122 mm. These results were 155% (weight) and 106% (length) greater than observed growth when *Bythotrephes* spines had 0 J·g⁻¹. In the 1999 predicted growth simulation, rainbow smelt wet weight increased over the season from 2.2 to 10.5 g, an increase in fork length from 72 to 117 mm. The 1999 simulation results were 108% (weight) and 67% (length) greater than for observed growth in the 0 J·g⁻¹ simulation. Total energy density in the diet during predicted growth simulations was greater than for those that used observed growth in all months except June 1999 when no *Bythotrephes* were present in the diet (Table 1).

Discussion

The composition of the diet of eastern Lake Erie rainbow smelt has changed since the 1960s; however, these changes have not decreased average energy density of the summer diet or the ability of rainbow smelt to fill their stomachs during peak feeding.

The proportion of zooplankton in the rainbow smelt summer diet has decreased and trends in the diet parallel changes that occurred in eastern Lake Erie associated with decreasing phosphorus levels (Dermott et al. 1999), the invasion of dreissenids, and the invasion of *Bythotrephes*. The 1960s diet of 89- to 114-mm rainbow smelt had a high proportion of cladocerans and reflected the dominance of the eastern basin ecosystem by large-bodied cladocerans and cyclopoid copepods (Davis 1968; Patalas 1972). Following phosphorus reductions, the eastern basin ecosystem shifted toward a higher number of calanoid copepods relative to other crustaceans (Johannsson et al. 1999) and copepods subsequently replaced cladocerans as the dominant prey item of rainbow smelt. A greater proportion of benthic or emergent invertebrates is present in the 1990 diets than in the 1961 diets of both size classes. Increased exploitation of both benthic and ephemeral prey items, such as chironomid pupae, may have resulted from increased water clarity (Mayer et al. 2001) or localized concentrations of benthic prey associated with dreissenid druses (Botts et al. 1996). In their review of the influence of zebra mussels on European aquatic systems, Karatayev et al. (1997) found no evidence of dreissenid effect, positive or negative, on planktivorous

fish species. However, evidence indicates that fish capable of benthic feeding may be positively affected by an increased biomass of benthic invertebrates associated with zebra mussels (Karatayev et al. 1997).

The proportion of *Bythotrephes* in the diet of eastern Lake Erie rainbow smelt increased from 1994 to 1998–1999. Interestingly, density estimates for *Bythotrephes* are consistently low (e.g., Johannsson et al. 1999). Several explanations for the apparent increase in consumption of *Bythotrephes* by rainbow smelt are possible. The reduction in the size of other zooplankton prey items (Johannsson et al. 1999), or increase in water clarity that enhances visibility, may make *Bythotrephes* a more attainable prey item for rainbow smelt. Alternatively, *Bythotrephes* densities may be poorly represented by conventional zooplankton sampling methods and may have increased more than suggested by the available data. *Bythotrephes* move rapidly and may avoid sampling gear (Johannsson et al. 1999). Studies in European lakes suggest that *Bythotrephes* may be undetectable in zooplankton tows but present in the stomachs of fish (e.g., de Bernardi 1981; Manca and Ruggiu 1998).

The compositional shift in the summer (May–August) diet of rainbow smelt during the 1990s did not significantly change energy density of the diet as compared with 1961. In spite of the presence of *Bythotrephes*' indigestible caudal spine, the summer diet of the 89- to 114-mm rainbow smelt size class during the 1990s contained between 8% and 25% more energy per unit volume than the diet in 1961. This is due to the inclusion of more energy-rich benthic or emergent invertebrates and fish in the 1990s summer diets of both size classes. Thus, decreased growth and condition of yearling rainbow smelt in eastern Lake Erie through the 1990s does not appear to be caused by decreased energy density of the summer diet.

Although the summer diet analysis suggested that indigestible *Bythotrephes* spines were not compromising the energy density of the summer diet in the 1990s, consumption of *Bythotrephes* increases dramatically late in the growing season (Parker et al. 2001). It is also during the late summer and early fall that *Bythotrephes* spines are differentially retained, being present in higher numbers than would be expected based on the number of *Bythotrephes* bodies (Parker et al. 2001). Indigestible spines accounted for 43% and 29% of yearling rainbow smelt stomach volume in October of 1998 and 1999, respectively. If rainbow smelt were able to replace *Bythotrephes* spines with prey items of the average energy density observed in the diet, the same rate of consumption (p value) would predict growth for yearling rainbow smelt to be 2–2.5 times greater than observed growth. Our p values (~ 0.60) suggest relatively high food intake, as wild fish seldom consume prey at rates higher than 30%–40% of maximum rates observed in the laboratory (Walters 2000). Similarly, our p values are equivalent to those found for fast-growing largemouth bass (*Micropterus salmoides*) (Irwin et al. 2003) and higher than those found for bloater (*Coregonus hoyi*) (Rudstam et al. 1994). Predicted seasonal weight gains of 7.9 g (1998) and 8.3 g (1999) with final fall weights of 12.0 g (1998) and 10.5 g (1999) were similar to observed growth in the 1985–1990 period (Dermott et al. 1999). Predicted fall lengths of 122 and 117 mm are similar

to those observed for yearling rainbow smelt during 1984–1990 (Dermott et al. 1999).

Bythotrephes spines will only affect rainbow smelt growth if their presence in the gut decreases intake of nutritional food. If food availability has declined, rainbow smelt may not be able to find additional food. Results indicate that, although variable, the mean percentage of stomach fullness for rainbow smelt in both size classes in 1994, 1998, and 1999 was not significantly different than the mean value for the same time period in 1961. Variability in data from 1994, 1998, and 1999 likely resulted from sampling across periods of low and peak feeding. Rainbow smelt caught shortly after dusk had percent stomach fullness values of 80%–100%, suggesting that food was not limiting peak feeding. Such discrete diel peaks in feeding rates are common in many fish species including smelt (Ferguson 1965; Walters 2000). Thus, spines present in the stomach will likely decrease the quantity of digestible food present in the stomach during peak dusk and dawn feeding periods. Our analysis shows that if these fish could replace the *Bythotrephes* spines with nutritional prey, their growth rate would be similar to observed growth prior to the *Bythotrephes* invasion. This is, of course, only one of several hypotheses for effects of diet on growth rates. It is also possible that *Bythotrephes* are harder to catch and therefore require increased activity by the fish, that the energy density of benthic and (or) zooplankton prey has decreased over time, or that the nutritional quality rather than energy has decreased. However, if the energetic or nutritional quality of benthic or zooplankton prey has decreased, the growth rates of young-of-the-year rainbow smelt should also have decreased. This has not been observed. Fall fork length of young-of-the-year rainbow smelt has remained relatively constant since 1984. Young-of-the-year rainbow smelt also prey upon *Bythotrephes* during the fall but consume far fewer individuals than yearling and older rainbow smelt and contain significantly fewer excess *Bythotrephes* spines (Parker et al. 2001).

Giussani and de Bernardi (1977) observed a similar trend in *Bythotrephes* consumption and coregonid growth in Lago Maggiore. Although *Bythotrephes* had the highest energy density per individual of all zooplankton prey species in Lago Maggiore, the assimilation efficiency of this prey item was significantly lower than that of other prey types. *Coregonus* species were unable to use many of the ingested *Bythotrephes* calories, and it was during the midsummer to early-fall period of high predation on *Bythotrephes* that *Coregonus* species had the lowest seasonal growth rate (Giussani and de Bernardi 1977). However, in Harp Lake, Ontario, a system invaded by *Bythotrephes*, Coulas et al. (1998) found no decrease in lake herring (*Coregonus artedii*) condition as compared with neighboring uninvaded lakes. The comparison of growth rates between invaded and uninvaded lakes may have been complicated by differences in the abundance of other preferred prey types in the zooplankton assemblages of individual lakes (Coulas et al. 1998). Similarly, seasonal patterns in growth may not have been apparent, as collections for herring condition took place between mid-April and late May (Coulas et al. 1998), prior to the period of highest predation on *Bythotrephes*.

Collection methods differed between past and present

Lake Erie rainbow smelt diet studies. In particular, rainbow smelt were collected during the day with bottom trawls in 1961 (Bidgood 1961) and 1994 (Dermott et al. 1999) and during the crepuscular period and at night with midwater trawls in 1998 and 1999. However, we felt that the comparison of diet information was acceptable for several reasons. Differences in diel composition of rainbow smelt diets are particularly large in systems with abundant *Mysis relicta* (e.g., Urban and Brandt 1993); however, eastern Lake Erie has few *Mysis* (Johannsson et al. 1999). Additionally, the proportion of zooplankton in the diet of eastern basin rainbow smelt will increase at night owing to increased overlap with zooplankton prey items resulting from the crepuscular vertical migration of yearling and older rainbow smelt. Our conclusion that energy density in the summer diet of rainbow smelt has not declined will therefore be robust, as nighttime midwater collections of rainbow smelt will provide liberal estimates of zooplankton consumption (with lower energy density) and conservative estimates of benthos consumption (with higher energy density) relative to daytime samples.

Changes in the composition of the summer (May–August) diet of rainbow smelt since the 1960s do not explain the continued decline in rainbow smelt growth through the 1990s. Our analyses indicated that the energy density of the rainbow smelt summer diet during the 1990s was not significantly different from that in 1961 and that prey availability was not limited. Our bioenergetics results indicate that indigestible *Bythotrephes* spines may reduce seasonal growth by occupying space in the stomach but providing no nutritional value to the fish, thereby reducing the realized daily ration for rainbow smelt. Other explanations are possible and should be explored.

Acknowledgements

Insight and project support were provided by Patrick Sullivan, Stacy Vega, and Myron Mitchell. All sampling for this study took place in cooperation with the New York State Department of Environmental Conservation Lake Erie Fisheries Unit in Dunkirk, New York, as part of a multiagency, basinwide hydroacoustics survey in partnership with the Ontario Ministry of Natural Resources and the Pennsylvania Fish and Boat Commission. Special thanks to the crews of the R/Vs *Argo*, *Shepherd*, *Erie Explorer*, and *Perca*. This paper is a result of research funded by a National Oceanic and Atmospheric Administration award NA46RG0090 to the Research Foundation of the State University of New York for New York Sea Grant (R/C-13) and the New York State Department of Environmental Conservation. Additional funding was received from the Great Lakes Research Consortium (Capstone Fellowship to S.L.P.). The US government is authorized to produce and distribute reprints for government purposes, notwithstanding any copyright notation that may appear herein. The views expressed herein are those of the authors and do not necessarily reflect the views of National Oceanic and Atmospheric Administration or any of its sub-agencies. Contribution No. 219 of the Cornell Biological Field Station.

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