Energy acquisition and allocation patterns of lake whitefish (*Coregonus clupeaformis*) are modified when dreissenids are present

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Abstract: We evaluated the effects of dreissenid-induced food web changes on rates of lake whitefish (*Coregonus clupeaformis*) energy acquisition and allocation in North American populations. We used mass-balance models of lake whitefish growth and methylmercury accumulation in 17 populations with and without dreissenids present to estimate and contrast rates of activity (ACT), consumption (*C*) and conversion efficiency (*V*). Historical estimates were also generated for a single lake whitefish population during dreissenid establishment. Bioenergetic estimates from both scenarios were compared with densities of *Diporeia*, a historically important diet component of lake whitefish. Mean lake whitefish ACT and *C* estimates in populations with dreissenids were significantly greater: 1.3–2 times those of populations without dreissenids. Conversion efficiencies scaled positively and significantly, while *C* and ACT varied negatively and significantly with *Diporeia* abundance. Our results suggest that changes in lake whitefish activity may affect density estimates — and ultimately sustainable management quotas — for this species. Our results also show that reported declines in lake whitefish individual growth rates in South Bay, Lake Huron, can be explained by increased activity rates due to increased foraging activity in an energetically depleted prey community.

Résumé : Nous évaluons les effets des changements dans les réseaux alimentaires occasionnés par les dreissénidés sur les taux d'acquisition et d'allocation de l'énergie chez le grand corégone (*Coregonus clupeaformis*) dans des populations nord-américaines. Des modèles de bilans massiques de la croissance et d'accumulation de méthylmercure chez des grands corégones de 17 populations avec et sans présence de dreissénidés nous ont servi à estimer et comparer les taux d'activité (ACT), de consommation (*C*) et d'efficacité de conversion (*V*). Nous avons aussi produit des estimations historiques pour une seule population de grands corégones durant l'établissement des dreissénidés. Nous avons comparé les estimations bioénergétiques des deux scénarios en fonction des densités de *Diporeia*, une composante historiquement importante du régime alimentaire des grands corégones. Les estimations moyennes des ACT et de *C* des grands corégones dans les populations avec dreissénidés sont significativement plus grandes, 1,3–2 plus élevées, que celles des populations sans dreissénidés. Les efficacités de conversion se cadrent de façon positive et significative, alors que *C* et ACT varient de manière négative et significative, en fonction de l'abondance des *Diporeia*. Nos résultats indiquent que les changements dans l'activité des grands corégones peuvent affecter les estimations de densité — et en bout de compte les quotas de gestion durable — chez cette espèce. Nos résultats montrent aussi que les déclins dans les taux de croissance individuelle des grands corégones signalés dans South Bay, au lac Huron, peuvent s'expliquer par les taux accrus d'activité à cause d'une recherche plus importante de nourriture dans une communauté de proies appauvrie en énergie.

[Traduit par la Rédaction]

Introduction

Changes in the North American Great Lakes ecosystem associated with the establishment of dreissenid mussels (the zebra mussel *Dreissena polymorpha* and the quagga mussel *Dreissena bugensis*) have been profound. The decline of the deepwater amphipod *Diporeia* (Nalepa et al. 1998, 2007; McNickle et al. 2006) has been linked to decreasing pelagic algal biovolume and productivity as well as increasing water clarity during this time (Barbiero et al. 2006; Fahnenstiel et al. 2010). As important benthic–pelagic couplers, *Diporeia* assimilate a large proportion of offshore energy by feeding on settled pelagic algae (Flint 1986) and have traditionally been key prey items to many fish species (Nalepa et al. 2006). Dreissenids are thought to have disrupted this energetic pathway by concentrating production and mineralizing

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nutrients in nearshore and benthic environments, thus limiting offshore production and, in turn, rates of profundal algal deposition (Hecky et al. 2004; Nalepa et al. 2006; Watkins et al. 2007).

Resource managers have expressed concern that these ecosystem changes may threaten the sustainability of the Great Lakes fishery, a cornerstone of the regional economy worth nearly US$50 million in 2000 (Kinnunen 2003). *Diporeia* declines have already been implicated in population declines of offshore fish such as alewife (*Alosa pseudoharengus*) in Lake Michigan (Madenjian et al. 2006*b*) and benthic fish in Lake Ontario such as sculpin (*Cottus* spp.; Owens and Dittman 2003) and lake whitefish (*Coregonus clupeaformis*; Hoyle et al. 1999). Lake whitefish are the primary catch of the Great Lakes commercial fishery, where they are harvested primarily from the upper Great Lakes. Concern exists over noted declines in individual growth and condition of lake whitefish during the past 2 to 3 decades (Pothoven et al. 2001; Lumb et al. 2007; Rennie et al. 2009*a*). Because of their dominance in commercial catches, the future of the upper Great Lakes fishery lies in great part on the successful and sustainable management of lake whitefish.

While numerous recent changes in Great Lakes ecosystems can be attributed to the establishment of dreissenids (Higgins and Vander Zanden 2010), recent evidence has also identified alternative explanations for lake whitefish growth and condition declines. Lake whitefish body condition appears to be affected by fish density and climate-related environmental change (Rennie et al. 2009*a*) and has declined in inland and Great Lakes populations throughout Ontario (Rennie et al. 2010*a*). Lake whitefish growth rate declines in Lake Michigan (DeBruyne et al. 2008) as well as Lakes Superior and Huron and inland Ontario lakes (Rennie 2009) appear at least in part to be a response to increases in density. Increased lake whitefish density is further suggested to have contributed to *Diporeia* declines in northern Lake Michigan and Lake Huron (Kratzer et al. 2007). However, studies reporting increased lake whitefish density have primarily relied on passive sampling gear (i.e., gillnets), which is stationary and depends on the movement of target species for encounter and capture. Thus, changes in fish behaviour (e.g., activity rates) could potentially affect encounter rates with passive gear (Biro and Post 2008; Biro and Dingemanse 2009) and therefore density estimates, which are ultimately used to determine commercial harvest quotas.

Lake whitefish have been shown to undergo behavioural changes following dreissenid invasion (Rennie et al. 2009*b*); depth distributions and diets of lake whitefish in South Bay, Lake Huron, showed evidence of increased reliance on nearshore resources after the establishment of dreissenids. As a result, energy densities of lake whitefish diets were 15%–30% lower than before dreissenids entered the system (Rennie et al. 2009*b*). Declines in diet quality will require fish to spend more time foraging to sustain energetic costs of basic metabolism, growth, and reproduction (Weatherley 1966). Increased activity allocated to foraging will itself impose greater metabolic costs, further exacerbating the effect of foraging in an energy-depleted prey community (Sherwood et al. 2002).

Field-based activity rates have been difficult to estimate accurately in the past, and current approaches of tracking fish with various transmitters can require a large initial investment in both capital and human resources. In contrast, contaminant modelling (Forseth et al. 1992; Rowan and Rasmussen 1996; Trudel et al. 2000) when combined with bioenergetic models (e.g., Kitchell et al. 1977) can provide a relatively inexpensive means for researchers to estimate activity of fish in the wild. Further, modelled activity estimates using this method have been shown to agree with both behavioural and enzymatic measures of activity (Rennie et al. 2005*b*).

The primary goal of this study was to consider the effects of food web changes associated with dreissenid establishment on energy allocation patterns in lake whitefish. To do this, we used an existing methylmercury (MeHg) contaminant accumulation model (Trudel and Rasmussen 2001) combined with a lake whitefish bioenergetics model (Madenjian et al. 2006*a*). Modelled bioenergetic estimates of consumption, activity, and conversion efficiency were compared among invaded and non-invaded populations. Further, we investigated correlations among lake whitefish bioenergetic parameters with *Diporeia* density, an important component of lake whitefish diets historically (Hart 1931; Ihssen et al. 1981; Rennie et al. 2009*b*). Second, we evaluated bioenergetics over a time series of observations spanning dreissenid establishment in South Bay, Lake Huron, to determine if changes in bioenergetics could explain documented declines in growth in this population (Rennie et al. 2009*a*).

Materials and methods

Sampling

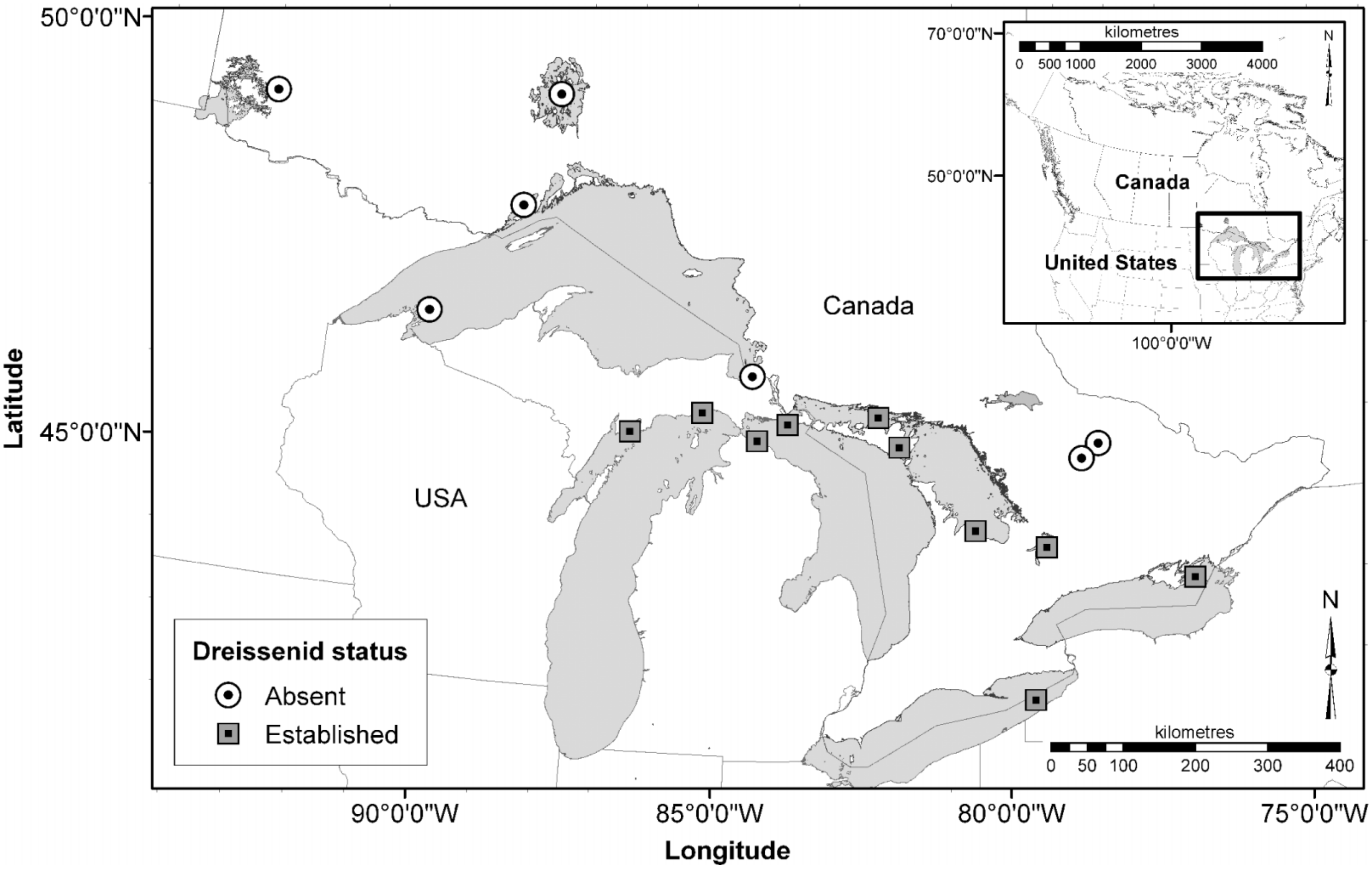
Fish were collected in conjunction with collaborating agencies during 2001–2007 from 17 different populations (Fig. 1) using standardized index gear specific to each particular population or through commercial harvest (Table 1). Bony structures (otoliths, scales) were removed for ageing. A skinless, boneless sample of muscle tissue was taken subdorsally, above the lateral line of the fish to be analyzed for mercury (Hg).

Characterization of fish diets

Lake whitefish stomachs collected during sampling (July–September) were used to describe diets. While fish diets may vary seasonally within populations, seasonal diet estimates were not available for all stocks. Therefore, while the magnitude of our bioenergetics estimates may be slightly biased, as they do not take into account potential seasonal variation (e.g., Rennie et al. 2009*b*), the sampling period among all stocks is temporally coherent.

Stomach contents were thawed and inspected in deionized water. Identifiable items were separated into broad taxonomic groups. Animals were then dabbed with an absorbent wipe to remove excess moisture and weighed. Proportional composition by mass of prey taxa in each fish examined was estimated. To characterize proportional composition of diets in each population, we estimated the mean proportion for each taxonomic group over all fish from a population and reported results for all organisms ≥ 1%; all other organisms and those unidentifiable to more specific taxonomic groups were assigned to "Other" (Table 2). For purposes of statistical analysis, we further summarized these data into three broad groups: shelled prey (dreissenids, gastropods, and sphaeriids), soft-

Fig. 1. Locations of North American lake whitefish populations under study. Outlined squares are stocks where dreissenids are established, outlined circles are stocks where dreissenids were not present at the time the study was conducted.



bodied prey (amphipods, ceratopogoniids, chironomids, eggs, Ephemeroptera, fish, isopods, oligochaetes, ostracods, plant material, trichopterans, insects, and other), and zooplankton (*Bythotrephes*, *Chaoborus*, *Mysis*, other zooplankton).

Estimation of consumption and activity in lake whitefish

To estimate lake whitefish consumption and activity, we used an approach combining the mass balance formulae for fish contaminants and mass from a mercury mass balance model (MMBM) described by Trudel et al. (2000) and modified in Rennie et al. (2005*b*), with the mass balance of fish energy budgets from a bioenergetics model (Madenjian et al. 2006*a*). The MMBM models the mass balance of MeHg in fish, the form of Hg that is most readily bioaccumulated (Mason et al. 1995; Lawson and Mason 1998; Lawrence et al. 1999). The primary mode for MeHg uptake in fish is through absorption in the gut from diet (Hall et al. 1997; Lawson and Mason 1998; Leaner and Mason 2002). The accumulation of MeHg in fish is described by

$$(1) \qquad \frac{\mathrm{dMeHg}}{\mathrm{d}t} = (\alpha \cdot M_{\mathrm{d}} \cdot C) - (E + G + N) \cdot \mathrm{MeHg}$$

where MeHg is [MeHg] of the fish (μg Hg·g^{-1} wet mass), α is the assimilation efficiency of MeHg from food, M_{d} is [MeHg] in food (μg Hg·g^{-1} wet mass), C is the mass-specific food consumption rate (g prey·g fish^{-1}·day^{-1}, or day^{-1}), E is the instantaneous elimination rate of MeHg (day^{-1}), G is the mass-specific growth rate (day^{-1}), and N is the instantaneous loss rate of MeHg to gonads (day^{-1}). If modelled over small (i.e., 1 day) time steps, differences between parameters such as E and N will be small and can be treated as constants. Integration of eq. 1 then yields the following (rearranged to solve for consumption):

$$(2) \qquad C = \frac{\mathrm{MeHg}_t - \mathrm{MeHg}_0 \cdot \mathrm{e}^{-(E+G+N)t}}{\alpha \cdot M_{\mathrm{d}} \cdot [1 - \mathrm{e}^{-(E+G+N)t}]} \cdot (E + G + N)$$

where MeHg_0 and MeHg_t are the [MeHg] in fish at time 0 and time t, respectively. Losses due to elimination (E), growth (G), and spawning (N) are described by equations in Appendix A.

The MMBM (eq. 2) is solved over a daily time step and combined with a bioenergetics model for lake whitefish (Madenjian et al. 2006*a*) through the common term, C (C above can be converted from units of day^{-1} to J·day^{-1} by multiplying C by prey energy density and W_{t-1}). The bioenergetics model can be expressed simply as

$$(3) \qquad W_t = W_0 + [C - (F + U + R_T)]/\mathrm{ED}_{\mathrm{fish}}$$

where W_t is the final fish mass (g), W_0 is the initial fish mass (g), C is ingestion rate (J·day^{-1}), $\mathrm{ED}_{\mathrm{fish}}$ is the energy density of fish (J·g^{-1}), F is loss due to egestion (J·day^{-1}), U is loss due to excretion (J·day^{-1}), and R_T is loss due to metabolism (J·day^{-1}).

Consumption rate in the bioenergetics model is a function of temperature and an allometric function describing maximum consumption determined from laboratory experiments.

Table 1. Populations of lake whitefish (*Coregonus clupeaformis*) included in the study.

Dreissenid status	Lake	Population	Location (N, W)	Years sampled	Year dreissenids established	*Diporeia* abundance (no.·m^{-2})	Collection method
Established	Erie	East basin	42°31′, 79°34′	2004	1989	177[a]	Index
	Huron	Cape Rich, Georgian Bay	44°32′, 80°37′	2003–2006	1996	99[b]	Index
		Cheboygan	45°42′, 84°27′	2003–2006	2000	457[c]	Commercial
		Detour Village	45°55′, 83°55′	2003–2006	2000	1000[d]	Commercial
		North Channel	46°02′, 82°18′	2004	1993[e]	2097[f]	Index
		South Bay, Manitoulin Island	45°40′, 81°55′	1965–2005[g]	1997	194[h]	Index
	Michigan	Big Bay de Noc	45°44′, 86°43′	2003–2006	1994	0[d]	Commercial
		Naubinway	46°01′, 85°27′	2003–2006	1994	0[d]	Commercial
	Ontario	Kingston basin	43°60′, 76°47′	2004	1993	304[i]	Commercial
	Simcoe	Lake Simcoe	44°25′, 79°20′	2003–2006	1995	0[j]	Index
Absent	Lake of the Woods	Whitefish Bay	49°24′, 93°53′	2005–2006	NA	817[k]	Index
	Nipigon	Lake Nipigon	49°50′, 88°30′	2006–2007	NA	2610[l]	Index
	Opeongo	Lake Opeongo	45°42′, 78°23′	2005–2007	NA	0[j]	Index
	Smoke	Smoke Lake	45°31′, 78°41′	2005–2007	NA	0[j]	Index
	Superior	Apostle Islands	47°00′, 90°30′	2004	NA	1470[m]	Index
		Thunder Bay	48°25′, 89°00′	2005	NA	2449[n]	Commercial
		Whitefish Bay	46°30′, 84°35′	2004	NA	1119[o]	Commercial

Note: NA, not applicable.

[a]Dermott and Kerec (1997).

[b]Rennie and Verdon (2008); value for 2003 only.

[c]Pothoven and Nalepa (2006).

[d]Kratzer et al. (2007).

[e]Date reported by Ontario Ministry of Natural Resources at Espanola; Nalepa et al. (2007) reported only very low densities of dreissenids in 2002.

[f]Nalepa et al. (2007).

[g]Only years 2001–2005 used for cross-population study, using ages based on otoliths.

[h]Rennie et al. (2009*a*); average of values 2001–2005.

[i]Dermott (2001).

[j]*Diporeia* absence confirmed in Lake Opeongo and Smoke Lake historically based on absence in benthic samples taken in the 1970s (Dadswell 1974); current absence confirmed based on benthic sampling in 2007 (M. Rennie, unpublished data). *Diporeia* are absent from Lake Simcoe (Rawson 1930; Kilgour et al. 2008).

[k]T. Mosindy, unpublished data, Ontario Ministry of Natural Resources, P.O. Box 5080, Kenora, ON P9N 3X9, Canada.

[l]Based on amphipod counts in >15 m depth (Bentz et al. 2002).

[m]Mean value for sites west of Keweenaw Peninsula (Scharold et al. 2004).

[n]J.V. Scharold, unpublished data, United States Environmental Protection Agency, 6201 Congdon Boulevard, Duluth, MN 55804, USA.

[o]Mean value for sites east of Keweenaw Peninsula (Scharold et al. 2004).

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Table 2. Mean proportional composition of lake whitefish diet items by mass.

(*a*) Populations with dreissenids.

Taxa	Erie	Cape Rich	Cheboygan	Detour	North Channel	South Bay	Bay de Noc	Naubinway	Ontario	Simcoe
Amphipoda				**0.39**	0.10	0.01				
Bythotrephes	0.05	**0.25**	**0.77**	**0.19**	**0.23**	**0.13**	**1.00**			
Ceratopogoniidae		0.01								
Chaoborus										
Chironomidae	**0.16**	0.06		0.01	0.04	**0.24**		**0.11**		**0.39**
Dreissenids	0.08	0.04	**0.21**	0.14		0.11		**0.80**	**0.90**	0.12
Fish eggs	0.03									
Ephemeroptera		0.07			**0.13**	0.02				0.01
Fish	0.06	0.02		0.03	0.03	0.04			**0.04**	0.05
Gastropoda		**0.12**	0.02	0.07	0.03	0.06		0.01	0.01	0.15
Isopoda										0.04
Mysis		0.06				0.01				
Oligochaete	0.03				0.01					
Ostracoda		0.04			0.03	0.01				
Plant	**0.35**	0.02		0.01		0.02			0.01	0.02
Sphaeriidae	0.15	0.09		0.01	0.07	0.07		0.06		**0.21**
Trichoptera								0.02		
Other zooplankton						0.01				0.01
Insecta	0.03	0.03				0.06			0.04	
Other	0.05	0.08		0.06	0.21	0.05				
Shelled	0.23	0.25	0.23	0.22	0.10	0.24	0.00	0.87	0.91	0.48
Soft-bodied	0.71	0.33	0.00	0.50	0.55	0.45	0.00	0.13	0.09	0.51
Zooplankton	0.05	0.31	0.77	0.19	0.23	0.15	1.00	0.00	0.00	0.01

(*b*) Populations without dreissenids.

Taxa	Lake of the Woods	Nipigon	Opeongo	Smoke	Apostle Islands	Thunder Bay
Amphipoda	**0.52**	0.08			**0.25**	**0.55**
Bythotrephes		**0.38**			**0.19**	
Ceratopogoniidae		0.04			0.01	
Chaoborus			0.01	0.03		
Chironomidae	0.12	0.11	**0.34**	**0.48**	0.04	0.04
Dreissenids						
Fish eggs						
Ephemeroptera		0.01	0.06			
Fish						
Gastropoda		0.01		0.01		
Isopoda						
Mysis	0.01				0.09	**0.25**
Oligochaete	0.01					
Ostracoda						
Plant	0.03				0.06	0.05
Sphaeriidae	**0.20**	**0.22**	0.14	0.10	0.07	0.10
Trichoptera			0.05	0.08		
Other zooplankton	0.03		**0.30**	**0.14**		
Insecta				0.06		0.01
Other		0.02	0.01		0.06	0.01
Shelled	0.20	0.23	0.14	0.11	0.07	0.10
Soft-bodied	0.68	0.26	0.46	0.63	0.42	0.65
Zooplankton	0.04	0.38	0.31	0.16	0.28	0.25

Note: Only organisms consisting of >1% of the total diet are shown; the sum of those <1% are grouped into "Other". Shelled, Soft-bodied, and Zooplankton summarize information across these groups from the taxa-specific data listed above. Taxa with first- and second-highest proportion by mass (excluding "Other") for each population are shown in bold. Values may not sum to 1 because of the presence of inorganic material (e.g., rocks, sand, etc.), not listed.

Losses from metabolism (R_T from eq. 3) can be further subdivided into three components:

$$(4) \qquad R_T = \mathrm{ACT} \cdot R_s + R_d$$

where R_d is specific dynamic action (J·day^{-1}) and varies proportionally with C; R_s is loss due to standard metabolism (J·day^{-1}) and is an allometric function based on temperature and body mass, and ACT (unitless) represents energy lost to active metabolism as a multiple of standard metabolism, where $1 \leq \mathrm{ACT} \leq \infty$.

Losses to reproduction are modelled as a one-time annual loss:

$$(5) \qquad W_t = W_{t-1} - W_{t-1} \cdot (\mathrm{GSI} \cdot \mathrm{ED_g})$$

where W_t is the fish mass after spawning, W_{t-1} is the fish mass the day previous, GSI is the gonadosomatic index (mass of spawning gonads/mass of fish, g), and $\mathrm{ED_g}$ is the ratio of the energy density of the gonads to that of the whole fish (1.2 for female fish; Rennie et al. 2005*b*).

By iterating on a daily basis both eqs. 2 and 3, which are linked through the common term, C, the unique solution of C and ACT that achieved the observed final mass and [MeHg] was obtained through an optimization routine. The optimization minimized the average difference between observed W_t and MeHg_t and modelled W_t and MeHg_t.

Parameterization of models

Subequations describing daily MeHg elimination, mass, and MeHg losses are based on those presented in Trudel and Rasmussen (1997) (described in Appendix A). Assimilation efficiency in the MMBM was set to 0.8 (Trudel and Rasmussen 2006). Parameters and subequations for the bioenergetics model are those described for the generalized coregonid model (Rudstam et al. 1994) with two exceptions. First, we used the revised value of 0.00085 for the intercept of the allometric mass function proposed by Madenjian et al. (2006*a*). Second, we replaced the term relating activity based on swimming speed with one that expresses activity as a multiple of standard metabolism as per eq. 4 (because we could solve directly for this parameter using consumption estimates from the MMBM). All other inputs for both models are detailed in Appendix B. Though the MMBM models MeHg dynamics, we measured Hg in individual whitefish and converted [Hg] to [MeHg] using a conversion factor appropriate for this species (65%, see Appendix B for details). While the entire age distribution from each population was used to generate von Bertalanffy fits (Appendix B), we applied MMBM and bioenergetic models to cohorts arising from the age range of fish detected in each population, to a maximum of 20 years of age.

Historic bioenergetics of lake whitefish in South Bay, Lake Huron

To determine if reported growth declines in lake whitefish from South Bay (Rennie et al. 2009*a*) could be explained by bioenergetic processes, we modelled bioenergetics of South Bay whitefish during three pre-invasion time periods (1965–1969, 1980–1984, and 1988–1992) and compared them with a single postinvasion time period (2001–2005). South Bay was selected to examine temporal bioenergetic patterns, as it had the longest and most complete time series of the populations considered in this study. Size-at-age for all time periods was estimated using scale ages, as these were the only structures aged in South Bay prior to 2001 (ages were determined using both scales and otoliths for South Bay lake whitefish sampled 2001–2005). Estimates of fish [MeHg]-at-age from 2001 to 2005 (described above) were applied to pre-invasion fish. Diet ED was taken from Rennie et al. (2009*b*), and diet [MeHg] was estimated from [MeHg] of prey items (Appendix C) and applied to proportions used to generate diet ED (pre-invasion diet MeHg = 2.70 ng·g^{-1}, postinvasion = 2.04 ng·g^{-1}). Thus, any changes in the bioenergetics of the population over time would be due to changes in size-at-age of the fish, and differences in diet ED and MeHg would result from changes in diet composition only. Size-at-age of modelled cohorts was estimated from fish across all years in each time period, and predicted mass-at-age was generated using mass–length relationships specific to female lake whitefish in each time period.

MeHg concentrations of lake whitefish and their diets were all based on contemporary [MeHg] in the South Bay temporal analysis. We believe this is a reasonable assumption, since the goal of this modelling exercise was to determine differences in bioenergetics due primarily to differences observed in lake whitefish growth rates and diet composition in the different time periods, all else being equal. While [Hg] in some fish species have declined over time (e.g., French et al. 2006), many have not (Rennie et al. 2010*a*). An examination of tissue [Hg] from 10 lake whitefish collected from South Bay in 1987 was not different from contemporary measurements reported here. Concentrations of MeHg in fish and invertebrates may change as a function of water chemistry (Rennie et al. 2005*a*), which has remained relatively stable in South Bay over the course of dreissenid invasion (Fernandez et al. 2009). Further, changes in Hg deposition over time because of increased environmental regulation would have the effect of altering Hg concentrations at all trophic levels (e.g., in both fish and their prey). Therefore, the relative difference between lake whitefish [MeHg] and that of any particular prey item should be similar, regardless of change in the actual values due to changes in Hg deposition over time. It is the relative differences between fish and prey [MeHg] that are important in the MMBM formulations, and these only change in the above modelling exercise as a result of changes in diet composition. While it is possible that dreissenids have affected the [MeHg] of other benthic invertebrates, we know of no published work on dreissenid effects on benthic invertebrate [MeHg] where this has been demonstrated. Thus, we could not account for possible taxa-specific modulations due to dreissenids in our historical estimates of lake whitefish prey [MeHg].

Statistical analysis

To determine the effect of dreissenid establishment on lake whitefish, we evaluated mass-specific bioenergetic rates. Estimates of interest were rates of consumption (C, $\mathrm{g_{food} \cdot g_{fish}^{-1} \cdot day^{-1}}$, or day^{-1}), activity multipliers (ACT, unitless), and conversion efficiency (V, unitless). We also estimated mass-specific growth rates (G, $\mathrm{g_{growth} \cdot g_{fish}^{-1} \cdot day^{-1}}$, or day^{-1}) across time periods for the South Bay, Lake Huron, population. Mass-specific rates may require adjustment to permit comparisons among different sized cohorts if rates deviate from isometry (i.e., allometric exponent of mass-relative rate with body size is different from 1; Hewett and Kraft 1993; Jobling 1994). The mean mass exponent for mass-relative rates of consumption ($g_{food}·day^{-1}$) with body size among the populations included in this study were not significantly different from 1 (mean ± standard error (SE) = 1.10 ± 0.07, one-sample *t* test of mean equal to 1, $t_{[16]}$ = 1.4, p = 0.17), confirming other reports that consumption rates for lake whitefish generally vary isometrically with body size (Trudel et al. 2001). The allometric exponent of mass-relative growth ($g_{growth}·day^{-1}$) with body mass for lake whitefish was significantly different from 1 (mean ± SE = 0.75 ± 0.07, one-sample *t* test of mean equal to 1, $t_{[16]}$ = 3.7, p = 0.002). This value is slightly higher than that reported for various salmonids (Jobling 1994) but comparable to female yellow perch (*Perca flavescens*) (Rennie et al. 2010*b*). We therefore estimated mass-specific estimates of growth as $g_{growth}·g_{fish}^{-0.75}·day^{-1}$ for the South Bay population.

For comparisons among lake whitefish stocks with and without dreissenids present (either temporally in South Bay or among contemporary populations), weighted means of *C*, ACT, and *V* were also estimated where each age class modelled was weighted by its numerical proportional representation in the catch. Weighted means of *G* were similarly estimated for all time periods in South Bay. This was done to represent the "realized" means of bioenergetic estimates for a specific population by emphasizing bioenergetics of common age classes and de-emphasizing uncommon age classes. Weighted means were compared among invaded and non-invaded populations using two sample *t* tests, with a Welch correction on degrees of freedom to account for differences in variance between groups (Zar 1999). We also examined relationships among the weighted means of bioenergetic estimates with *Diporeia* density using linear regression. Multiple comparisons were evaluated against sequential Bonferroni-corrected *p* values (Rice 1989). Diet proportions among stocks with and without dreissenids were compared using *t* tests using arcsine-square-root-transformed data.

Model sensitivity to temperature variation and length of growing season

All populations investigated in this study occupy lakes that stratify, and none experienced substantial deepwater oxygen depletion over the period of study. Thus, whitefish in all our systems have the ability to thermoregulate behaviourally by occupying preferred temperatures (Edsall 1999). Even so, whitefish may show some variability in their thermal preferences that are not well reflected by the mean temperatures used in our simulations (Madenjian et al. 2006*a*). To investigate this possibility, we simulated various temperature regimes for lake whitefish bioenergetic models for South Bay postdreissenid invasion. First, we increased or decreased lake whitefish water temperatures by two standard deviations above and below the mean temperatures reported from thermal tags in Madenjian et al. (2006*a*). Second, we evaluated the effects of changes in growing season on results by comparing a representative minimum (Lake of the Woods) and maximum (Lake Erie) season length on our bioenergetic estimates. To determine the length of the growing season at these two sites, we obtained online historic water temperature data from buoys deployed in both areas from Fisheries and Oceans Canada (http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/waves-vagues/index-eng.htm; Lake of the Woods centre buoy 45148; Lake Erie Port Colborne buoy 45142). We defined the growing season at each site as the number of days where surface water temperatures were recorded above 4 °C, indicative of a thermal switch-point in the density gradients of lakes towards stratification of warmer waters over cooler waters. We examined 2004 data at both sites; other years in the record were excluded because of incomplete annual data for one or the other buoys. Also, these data are within 1 year of the thermal tag data used in our models (Madenjian et al. 2006*a*). The growing season was estimated as 223 days in Lake Erie and 203 days in Lake of the Woods, compared with 212 from Lake Michigan archival whitefish tag data. Based on this finding, we removed the 10 warmest days in our models and extended the coldwater period by 10 days to simulate our northernmost environment (Lake of the Woods). Similarly, we extended the warmest period by 10 days and removed the 10 coldest days to simulate our southernmost environment (Lake Erie). We assumed that whitefish would otherwise thermoregulate similar to the Lake Michigan stock. We then compared differences between bioenergetic estimates from these simulated temperature regimes with our initial model using *t* tests.

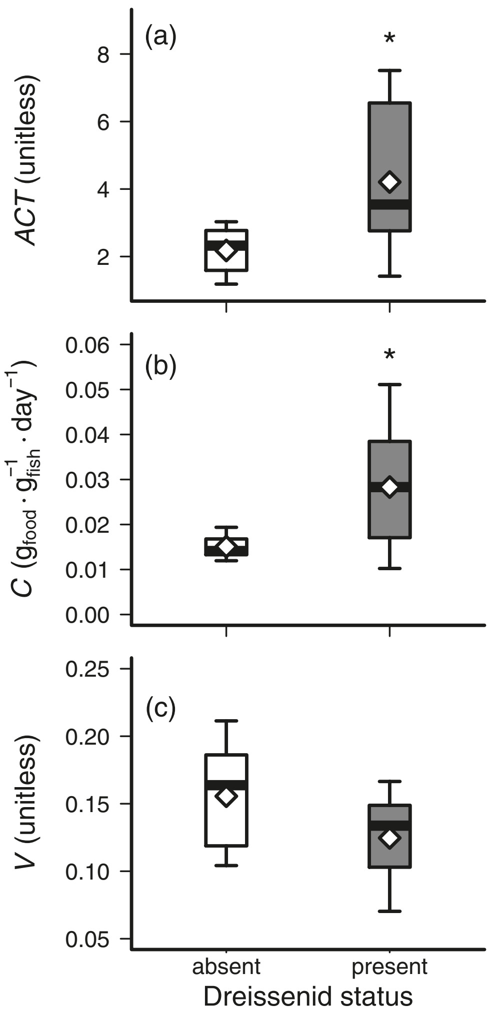
Results

Bioenergetics among populations

Weighted means of mass-specific bioenergetic estimates were significantly different between lake whitefish populations with and without dreissenids (Fig. 2). Lake whitefish ACT was twice as high in populations with dreissenids (mean = 4.2) compared with populations without dreissenids (mean = 2.18; Fig. 2*a*; two sample *t* test, $t_{[11.8]}$ = 2.99, p = 0.016, p_{crit} = 0.025), as was *C* (Fig. 2*b*; mean *C* with dreissenids = 0.028; mean *C* without dreissenids = 0.015; $t_{[10.7]}$ = 2.93, p = 0.014, p_{crit} = 0.0167). Differences in conversion efficiencies were not significant between invaded and non-invaded populations (*V*, p = 0.15). Analysis of diet data showed that the proportion of amphipods (typically *Diporeia*) were significantly greater (two-sample *t* test, $t_{[5.3]}$ = 3.25, p = 0.02) in non-invaded populations (0.61 ± 0.11) compared with those where dreissenids were established (0.06 ± 0.4). Though they bordered on statistical significance, mean proportions of soft-bodied prey in lake whitefish stomachs tended to be lower (invaded, 0.33 ± 0.08; non-invaded, 0.52 ± 0.07; p = 0.085) and those of shelled prey higher (invaded, 0.35 ± 0.1; non-invaded, 0.14 ± 0.03; p = 0.061) in dreissenid-invaded populations compared with non-invaded populations (Table 2). A similar pattern was found for mean diet energy densities (Appendix B, Table B1; invaded, 2.3 ± 0.1 kJ; non-invaded, 2.6 ± 0.2 kJ, p = 0.2), but again the pattern was nonsignificant.

Lake whitefish *C* and ACT decreased significantly (following sequential Bonferroni corrections) with increasing *Diporeia* abundance when only whitefish populations that previously supported *Diporeia* were considered (Fig. 3*a*: *C*, p = 0.0132, p_{crit} = 0.025; Fig. 3*b*: ACT, p = 0.049, p_{crit} = 0.05). *Diporeia* abundance was positively related to *V* over

Fig. 2. Boxplots comparing modelled mass-specific lake whitefish (*a*) activity (ACT), (*b*) consumption (*C*), and (*c*) conversion efficiency (*V*) between populations with dreissenids (shaded symbols) and populations without (open symbols). Significant differences after sequential Bonferroni corrections are denoted with an asterisk. Dark portions of bars are medians, boxes are interquartiles, and error bars are 95% confidence intervals. Open diamonds are means.

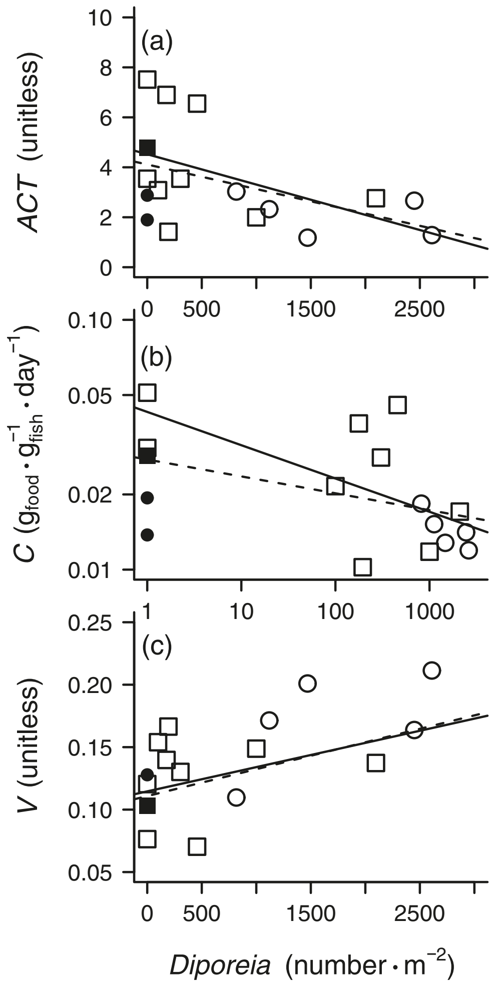


all populations considered (Fig. 3*d*; linear regression, $F_{[1,15]} = 9.9$, $p = 0.0072$, $p_{crit} = 0.0167$).

Bioenergetics over time in South Bay

To better standardize temporal comparisons in South Bay, only those age classes that were observed in each time period (ages 2–12) were used for comparison. Temporal changes in weighted means of mass-specific *C*, ACT, and *V* estimates were consistent with the comparison of contemporary lake whitefish populations with and without dreissenids. Mean ACT estimates in years before the invasion of dreissenids were significantly lower than that observed after dreissenid establishment (Table 3; one-sample *t* test, $t_{[2]} = -9.69$, $p = 0.01$). Similarly, *C* was lower before the invasion of dreissenids (one-sample *t* test, $t_{[2]} = -33.9$, $p = 0.0009$), whereas *V* was higher prior to the invasion of dreissenids (one-sample *t* test, $t_{[2]} = 8.8$, $p = 0.013$). Growth rate (*G*) was also significantly higher prior to dreissenid invasion in South Bay (one-sample *t* test, $t_{[2]} = 16.2$, $p = 0.004$).

Fig. 3. Relationships of weighted means of modelled mass-specific lake whitefish (*a*) activity (ACT), (*b*) consumption (*C*), and (*c*) conversion efficiency (*V*) with *Diporeia* density. Bioenergetic means are weighted by the proportional contribution of modelled age classes in each population. Squares are populations with dreissenids established, circles are those without. Filled symbols are populations in which *Diporeia* were historically absent or where their absence preceded the appearance of dreissenids. The dashed line shows the relationship among all populations; the solid line shows the relationship excluding filled symbols. Note logarithmic *Diporeia* axis in panel (*b*).



Sensitivity to water temperature and growing season

Whitefish bioenergetic estimates (*C*, ACT, *V*) based on water temperatures two standard deviations above and below values used in our study were not significantly different from our initial estimates (*t* tests, all $p >> 0.05$). Similarly, bioenergetic estimates (*C*, ACT, *V*) yielded from extending or shortening the warmwater period by 10 days were not significantly different from those estimated from the initial model (*t* tests, all $p >> 0.05$). Percent differences between reported model estimates with alternative temperature regimes were all less than 7%, and in most cases within 2% of the reported estimates (Table 4).

Discussion

Based on either historical reconstruction or comparisons among contemporary populations, lake whitefish activity and

Table 3. Mean mass-specific bioenergetic estimates of lake whitefish consumption (*C*), activity (ACT), conversion efficiency (*V*), and growth (*G*) weighted by relative abundance of age classes 2–12 within time periods modelled for South Bay, as well as *Diporeia* abundance in each time period.

Years modelled	*C*	ACT	*V*	*G*	*Diporeia* density (no.·m^{-2})
1965–1969	0.0136	2.30	0.152	0.0053	1937.5[a]
1980–1984	0.0133	2.10	0.163	0.0051	1971.9[b]
1988–1992	0.0138	2.29	0.145	0.0052	ND
2001–2005	0.0181	2.87	0.107	0.0042	194.4[c]

Note: ND, no data.

[a]Average of years 1959–1962, data from McNickle et al. (2006).

[b]Average of years 1980–1982, data from McNickle et al. (2006).

[c]Average of years 2001–2005, data from Rennie et al. (2009*a*).

Table 4. Percent difference in modelled temperature exposure of lake whitefish on bioenergetic parameters estimated from mercury mass-balance (consumption *C*)) and bioenergetic models (activity multipliers (ACT) and conversion efficiency (*V*)) compared with reported model estimates.

Variable	Extended growing season	Reduced growing season	Increased water temperature	Decreased water temperature
C	–0.7%	1.0%	6.7%	–5.2%
ACT	–1.7%	2.0%	–1.6%	2.0%
V	–0.6%	0.5%	–4.8%	3.5%

Note: Extended and reduced growing seasons represent a 10-day lengthening and shortening of the warmest temperatures used to generate reported model estimates, respectively. Increased and decreased water temperatures represent temperature exposure based on the upper and lower bounds (95% confidence intervals) reported by Madenjian et al. (2006*a*).

consumption estimates were elevated and conversion efficiencies were depressed in the presence of dreissenids. Additionally, the abundance of *Diporeia* had a significant effect on lake whitefish bioenergetics; in the absence of dreissenids, lake whitefish diets had a greater proportion of *Diporeia* and demonstrated higher conversion efficiencies and lower consumption and activity when *Diporeia* were abundant. We believe that these results interpreted together provide strong evidence that elevated consumption and activity in lake whitefish populations exposed to dreissenids are a result of a depleted prey community associated with dreissenid establishment. Further, our study shows that increased allocation of energy to activity provides a proximate explanation for growth declines in lake whitefish from South Bay, Lake Huron. Growth declines have been well documented elsewhere in Great Lakes lake whitefish populations coincident with the establishment of dreissenids (e.g., Pothoven et al. 2001; DeBruyne et al. 2008; Rennie 2009).

Higher consumption rates in the presence of dreissenids suggest that fish may increase foraging activities in response to an energetically depleted prey community (McNickle et al. 2006; Rennie et al. 2009*a*). Considered with our observations of higher activity rates and reduced conversion efficiency in populations with dreissenids present, this suggests that there is a combined effect of reduced prey quality, increased allocation of energy towards foraging, and potential increases in the energy required to process large-bodied shelled prey like dreissenids. In contrast with our investigation, a recent study found no change in the total consumption or conversion efficiency of lake whitefish in Lakes Huron and Michigan (Pothoven and Madenjian 2008). However, their study employed models that assumed fish activity as a largely size-dependent process and did not consider the potential for differences in activity rates before and after dreissenid invasion. Our detection of significant differences in consumption and conversion efficiencies when allowing for potential activity differences stresses the importance of estimating field-based activity estimates, particularly when scaling individual-level consumption estimates to whole-ecosystem processes (e.g., Pothoven and Madenjian 2008).

Conversion efficiency scaled positively with *Diporeia* density, whereas activity and consumption rates declined as *Diporeia* densities increased, suggesting that *Diporeia* densities likely play a major role in moderating lake whitefish bioenergetics. However, changes in *Diporeia* reflect just one aspect of the community changes experienced by lake whitefish prey during the establishment of dreissenids in aquatic ecosystems, and changes in the distribution and abundance of other prey items may contribute to lake whitefish growth declines and changes in bioenergetics. An examination of seasonal lake whitefish diets collected in 1947 suggested that while *Diporeia* was an important prey item (Rennie et al. 2009*b*), pre-invasion diets were far more diverse than previously described (Hart 1931; Ihssen et al. 1981). Following dreissenid invasion in South Bay, Lake Huron, lake whitefish appear to be more reliant on nearshore organisms (Rennie et al. 2009*b*), which are frequently shelled (e.g., dreissenids) and likely more energetically costly to process than the soft-bodied prey once common at deeper waters (Owens and Dittman 2003). Chironomids, sphaeriids, and oligochaetes have all declined dramatically in deeper waters (regions in which lake whitefish forage during summer stratification when they

Table 5. Increase in lake whitefish catch per unit effort (CPUE), expressed as a multiple of pre-invasion lake whitefish densities.

Population	Increase in lake whitefish CPUE (as multiple of pre-invasion CPUE)	Source
Central Lake Michigan[a]	3.69	DeBruyne et al. 2008
Southern Lake Michigan[a]	3.10	DeBruyne et al. 2008
Big Bay de Noc, Lake Michigan	1.50	Kratzer et al. 2007
Naubinway, Lake Michigan	2.39	Kratzer et al. 2007
Alpena, Lake Huron	1.20	Kratzer et al. 2007
Bay Port, Lake Huron	2.05	Kratzer et al. 2007
South Bay, Lake Huron	1.37	Rennie et al. 2009*a*
Cape Rich, Lake Huron	1.15	Rennie 2009
Lake Simcoe[a]	2.08	Rennie 2009
Average among populations listed above	2.06	This study

[a]CPUE is numeric. CPUE for all other sites is based on biomass.

accumulate most of their growth annually) since the establishment of dreissenid mussels in Lake Huron (McNickle et al. 2006; Nalepa et al. 2007; Watkins et al. 2007).

It is unlikely that potential differences in water temperatures or growing seasons experienced by the populations we considered affected our bioenergetic estimates. Lake whitefish bioenergetic estimates (*C*, ACT, *V*) did not differ between our initial model with either warmer or cooler temperature exposure (plus or minus two standard deviations of estimates reported by Madenjian et al. 2006*a*) or with the extension or reduction of the growing season by 10 days. These findings are consistent with previously published sensitivity analysis on consumption estimates from both the MMBM and bioenergetics models that revealed that temperature is among the less influential parameters on model outcomes (Kitchell et al. 1977; Trudel et al. 2000); 10% variation in temperature tended to result in only 2%–3% differences in consumption estimates from the MMBM when applied to lake whitefish, and sensitivity of temperature-dependent consumption and respiration parameters were ranked as medium to low in the bioenergetics model.

The possibility of increased lake whitefish activity rates in the presence of dreissenids could have major implications for the correct interpretation of temporal changes in lake whitefish catch-per-unit-effort (CPUE) data that are collected using passive collection gear. Our results suggest that activity rates (and therefore potentially gear encounter rates) could be as much as two times higher in the presence of dreissenids. Studies that have employed passive sampling gear reported increases in lake whitefish CPUE of a similar magnitude during the establishment of dreissenids on the Great Lakes (Table 5). Recent experimental studies have highlighted inherent bias of passive sampling gear towards more active individuals e.g., (Biro and Post 2008) and the lack of attention this issue has received in the recent literature (Biro and Dingemanse 2009) despite the fact that it has been recognized for decades (Rudstam et al. 1984). CPUE of more active populations are expected to be higher when population sizes are similar (Radabaugh et al. 2010). If lake whitefish activity scales positively with gear encounter rates and therefore also with CPUE, then our estimates of activity increases are of a similar magnitude as CPUE increases in seven of nine populations, and approximately 65% of CPUE increases in the two populations in central and northern Lake Michigan. Under this scenario, increases in CPUE may not reflect actual increases in population size, but rather result from increased lake whitefish activity due to food web changes associated with the establishment of dreissenids.

If activity rates of lake whitefish are indeed greater in populations with dreissenids, as our model estimates suggest, this could have serious implications for the successful sustainable management of these stocks. Many management organizations frequently employ passive gear to generate CPUE estimates. These data are used to set fishing quotas for the following year by commercial fleets and to set fishing regulations for recreational fisheries. If population estimates are overestimated by two times as a result of sampling bias related to increased activity, then harvest rates set for populations with dreissenids could be set well beyond what management organizations have deemed to be sustainable. Clearly, more work is needed to establish the exact relationship between activity rates and gear encounter rates in this species, but our study at the very least provides justification for additional research on this topic and on the need to account for behavioural change related to catchability in quantitative fishery assessment models given the gravity of the potential consequences of not doing so for the sustainability of the fishery.

Changes in the distribution of benthic invertebrates might also affect lake whitefish by making consumption more variable. Very high variability in resource availability can in some cases lead to compensatory growth. Studies have shown that consumption estimates from traditional bioenergetic models do not perform well under variable resource availability (Bajer et al. 2003, 2004). Unlike traditional bioenergetic models, we estimated consumption from the mercury mass-balance model and used this in the bioenergetics model to estimate lake whitefish activity. Under compensatory growth, standard metabolic rate would be slower than described in our bioenergetics model. If this is occurring in our populations, then activity estimates reported here might be lower than would be expected under a scenario of compensatory growth. No studies currently exist that document the degree of variability in lake whitefish consumption or resource availability nor how this variability may differ between the stocks we have evaluated here. As such, we must accept this variability as uncontrolled error in our bioenergetic estimates. Despite this potential source of error, we still detect significant differences between stocks where dreissenids are present and those where they are absent. Further, activity rates estimated using the same methods we have employed here have been shown to be consistent with other independent methods of estimation (Sherwood et al. 2002). We argue that higher whitefish activity rates observed in the presence of dreissenids reported here, considered alongside the apparent increase in CPUE following dreissenid invasion, should certainly warrant additional study regarding the dependence of passive gear selectivity on lake whitefish in the presence of dreissenids. Investigations into fish movement patterns can be expensive and require specialized equipment (e.g., hydroacoustic arrays or survey equipment, surgical implants, etc.). We hope this work provides justification for pursuing future study on the effects of dreissenids on lake whitefish movement patterns, given the potential consequences that changes in fish behaviour might have for biasing abundance estimates and the consequences this may have on the successful and sustainable management of the resource.

In conclusion, our results show clear and consistent differences in consumption, conversion efficiency, and activity rates among lake whitefish populations with and without dreissenids present. Declines in *Diporeia* in the presence of dreissenids appear to have played a major role in reshaping lake whitefish energetics. Greater proportions of shelled prey may be more energetically costly to process and may require fish in the presence of dreissenids to spend more time foraging to maintain the same basal metabolic costs as fish not exposed to dreissenids. Further, our findings suggest that reported increases in lake whitefish CPUE where dreissenids have established should be interpreted cautiously and that current population estimates (and therefore harvest quotas set by management agencies) based on passive sampling gear could be inflated because of increased lake whitefish activity rates. Finally, our study shows that food web changes associated with the establishment of dreissenids in South Bay, Lake Huron, have led to declines in lake whitefish growth through increased lake whitefish activity and decreased conversion efficiency, despite higher rates of consumption. The application of our models to historic data from South Bay also provides further evidence for trade-offs between activity and growth rates in fish, despite elevated consumption (e.g., Rennie et al. 2005*b*). The results of this study illustrate the importance of estimating field rates of activity when considering proximate explanations for changes in growth rate or bioenergetic differences among populations.

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Appendix A. Relationship describing methylmercury (MeHg) elimination from fish and the relationship between fish MeHg and gonadal mercury concentrations

Daily elimination of MeHg (E in eq. 2 of text) was modelled as a function of fish mass (W) and temperature (T), as described in Trudel and Rasmussen (1997):

$$\text{(A.1)} \qquad E = \varphi W^{\beta} e^{\gamma T}$$

where φ, β, and γ are empirically derived constants (0.0014, –0.20, and 0.066, respectively, corresponding to the acute Hg exposure model in Trudel and Rasmussen 1997). Recent work has shown that Hg elimination rates of lake whitefish in the lab (Madenjian and O'Connor 2008) and other fish species in the wild (Van Walleghem et al. 2007) are most closely described by the acute elimination model reported by Trudel and Rasmussen (1997).

Growth in the mercury mass-balance was modelled as described in Trudel et al. (2000):

$$\text{(A.2)} \qquad G = \Delta t^{-1} \cdot \ln \left(W_{t+\Delta t} \cdot W_t^{-1} \right)$$

where W_t and $W_{t+\Delta t}$ are fish mass at times t and $t + \Delta t$, respectively.

Calculating consumption using the mercury mass-balance model also requires an estimate of the loss of MeHg to reproductive tissues at spawning, N, defined by the following equation:

$$\text{(A.3)} \qquad N = Q \cdot \text{GSI} \cdot 365^{-1}$$

and

$$\text{(A.4)} \qquad Q = C_g \cdot C_f^{-1}$$

where GSI is the gonadosomatic index of the fish, or gonad mass expressed as a percentage of the body mass of the fish; 365 is the number of days in a year, and Q is the ratio of MeHg in the gonads at spawning (C_g) to Hg in the fish (C_f).

Gonad [MeHg] in gravid female fish (C_g) varied with fish [Hg] (Hammerschmidt et al. 1999) according to the following relationship ($r^2 = 0.92$):

$$\text{(A.5)} \qquad \log_{10} C_g = 0.884 + 9.03 \times 10^{-4} \cdot C_f$$

where C_g and C_f are in units of ng·g^{-1} dry mass. Values obtained from eq. A.4 were multiplied by 0.00015 to obtain µg·g^{-1} wet mass (Rennie 2003).

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Appendix B. Estimation of input parameters for the mercury mass balance and bioenergetic models

We modelled growth and methylmercury (MeHg) accumulation of lake whitefish over the course of a year, using size- and MeHg-at-age of adjacent cohorts as parameter inputs. Parameter estimates for fish energy density (ED), [MeHg]-at-age, mass-at-age, diet [MeHg], and diet ED are described below. Because of potential biases of bioenergetic estimates associated with fish gender (Rennie et al. 2008), we modelled female lake whitefish only.

Size- and [MeHg]-at-age for each population were summarized from data collected over 1–5 years. Size- and [MeHg]-at-age data were used to build statistical models specific to each population (described below). These models were used to predict [MeHg]- and size-at-age for MMBM and bioenergetic model input parameters. Input parameters of modelled cohorts were not extended beyond the age or size range observed in the population sample to avoid extrapolation.

Estimating diet inputs for models

Energy densities (EDs) for diets from individual fish were estimated by applying EDs for various prey taxa (Appendix C) to mass-based proportional composition estimates of diets. As our data showed no relationship between fish size and estimated diet EDs (M. Rennie, unpublished data), we estimated the mean prey ED of all fish for which data were available (minimum 20 fish per population). This value was used to inform bioenergetic models (Appendix B, Table B1).

MeHg in fish and diets

A minimum of 40 fish from each population across the size range sampled were analyzed for total mercury (Hg). For a subset of populations, the Ontario Ministry of Environment (OMOE) analyzed fish Hg for up to 30 individuals. Additional samples were analyzed on a Milestone DM-80 direct mercury analyzer following United States Environmental Protection Agency (USEPA) method 7473 (SW-846). Paired comparisons between tissues analyzed using both methods indicated no systematic differences between procedures (Rennie et al. 2010). Methodology and quality assurance of OMOE methods are reported in detail elsewhere (French et al. 2006; Goulet et al. 2008; Choy et al. 2008). Repeatability of DM-80 results was determined by analyzing three to five standard reference material samples per run (TORT-2). The mean estimate of TORT-2 across 28 runs was 0.275 µg·g^{-1} (±0.007 µg·g^{-1} standard deviation), and all measures were well within the error reported by the National Research Council of Canada (0.27 ± 0.06 µg·g^{-1}). The whole MeHg burden of fish is modeled using the mercury mass balance model. To determine the relationship between contaminants in whole body and muscle, [Hg] in both muscle tissue and whole body homogenates were determined. Whole body [Hg] was 82% of tissue [Hg] averaged across fish from four populations (n = 106). To determine the proportion of total Hg as MeHg, we analyzed [MeHg] for a subsample of 14 fish from three populations (Round Lake; Apostle Islands, Lake Superior; Lake of the Woods) using USEPA method 1630 (stomach contents and invertebrates were also analyzed using this method). Standard reference material samples (NIST 1974b) were analyzed to ensure repeatability of results. Mean standard reference material values (±SD) over nine runs were 6.71 ± 1.2 ng·g^{-1}, within the standard deviation reported by the National Institute of Standards and Technology (7.05 ± 0.44 ng·g^{-1}). A subset of five additional samples from a fourth population (South Bay, Lake Huron) was sent to an independent lab to verify our results. [MeHg] averaged over all 19 samples was 57% ± 8% (1 standard error) of estimated total [Hg] (our results, n = 14, 55%; independent lab, n = 5, 63%). Grey et al. (1995) reported [MeHg] in lake whitefish from Arctic populations as 72% ± 5% of total [Hg] (n = 14).

We used a Kruskal–Wallis test to determine whether there were significant differences in percent [MeHg] as total [Hg] among populations from both our study and that of Grey et al. (1995), using the raw data presented in their report. Only those lakes with more than three observations were evaluated, allowing for a comparison among six populations in total. A nonparametric test was selected because of unequal sample sizes among groups and non-normal distributions of the raw data. We found no significant differences among populations (χ^2_5 = 7.38, p = 0.19). The grand mean from our study and those of Grey et al. (1995) was 65% [MeHg] as total [Hg]. We interpreted this as a value applicable to the species within our study region, and this value was applied to our fish [Hg] data to estimate lake whitefish [MeHg] estimates in models.

Fish [MeHg] estimated from muscle tissues was adjusted to reflect whole body [MeHg] using the correction factors described above. Within each population, mean fish [MeHg] for each age class was estimated using functions that best de-

Table B1. Parameter values and functions describing methylmercury (MeHg) and energy density (ED) of lake whitefish and their diets.

Dreissenid status	Population	Corrected diet MeHg (μg·g^{-1})	Diet ED	Fish ED function[a]	Fish MeHg function (μg·g^{-1})[b]
Present	Lake Erie	[MeHg] = 3.7385·(length)$^{-1.2956}$	2554.4	2	[MeHg] = 0.0067·age$^{0.5422}$
	Cape Rich	0.0027	2636.9	3	[MeHg] = 0.009·e$^{\text{age}\cdot 0.1539}$
	Cheboygan	0.0017	1945.7	3	[MeHg] = 0.0377·e$^{\text{age}\cdot 0.0216}$
	Detour	0.0049	2780.4	3	[MeHg] = 0.0240·e$^{\text{age}\cdot 0.0412}$
	North Channel	0.0026	2701.0	3	[MeHg] = 0.0099·e$^{\text{age}\cdot 0.0874}$
	South Bay	0.0037	2484.9	3	[MeHg] = 0.01·e$^{\text{age}\cdot 0.0737}$
	Big Bay de Noc	0.0014	2027.0	4	[MeHg] = 0.0193·e$^{\text{age}\cdot 0.0639}$
	Naubinway	0.0014	1810.6	4	[MeHg] = 0.0064·e$^{\text{age}\cdot 0.1340}$
	Lake Ontario	0.0020	1868.9	1	[MeHg] = 0.003·age$^{0.9147}$
	Lake Simcoe	0.0019	2467.6	5	[MeHg] = 0.0087·age$^{0.557}$
Absent	Lake of the Woods	[MeHg] = 0.0009·e$^{\text{age}\cdot 0.0027}$	2653.1	5	[MeHg] = 0.0169·e$^{\text{age}\cdot 0.0356}$
	Lake Nipigon	<400 mm, 0.0044; >400 mm, [MeHg] = 0.0001·e$^{\text{age}\cdot 0.0092}$	2170.3	6	[MeHg] = 0.0128·e$^{\text{age}\cdot 0.0973}$
	Lake Opeongo	0.0086	2488.6	7	[MeHg] = 0.0396·e$^{\text{age}\cdot 0.052}$
	Smoke Lake	0.0061	2827.7	5	[MeHg] = 0.0367·mass$^{0.0025}$
	Apostle Islands	0.0056	2239.2	6	[MeHg] = 0.0162·age$^{0.3242}$
	Thunder Bay	0.0085	3316.3	6	[MeHg] = 0.0067·age$^{0.8327}$
	Whitefish Bay	0.0070[c]	2777.8[c]	6	[MeHg] = 0.0199·e$^{\text{age}\cdot 0.0742}$

[a]Functions as reported in Appendix D.
[b]Concentrations reported are per gram wet mass of fish tissue.
[c]Estimated as mean of all Lake Superior sites.

scribed the relationship between mean [MeHg] and age or [MeHg] and mass, depending on the data available (Appendix B, Table B1). These estimates were used to parameterize [MeHg]-at-age for MMBM inputs.

Subsamples of lake whitefish stomach contents (all prey combined) from one to five fish were combined into a composite sample based on 10 cm lake whitefish length classes in each population. Between three and seven composites were analyzed for each population. Stomach composites were analyzed for MeHg as described above. For populations demonstrating no relationship between fish size class and diet [MeHg], we averaged values over all length classes. Where a significant trend in diet [MeHg] with size was observed, we estimated diet [MeHg] based on the best relationship describing diet [MeHg] with fish size or age.

To determine the validity of [MeHg] estimated directly from fish stomach contents in lake whitefish as a reasonable representation of diet [MeHg], stomach content [MeHg] was analyzed from 64 individual fish collected from South Bay in 2002 and 2003. Measured [MeHg] of stomach contents were compared with [MeHg] estimated from the proportional diet composition for the same fish and [MeHg] of invertebrates collected from South Bay (Appendix C). On average, [MeHg] estimated from diet composition and invertebrate [MeHg] were 52% of that measured directly from stomach contents (standard error = 1.3%). Based on this evidence, diet [MeHg] of stomach contents determined analytically were multiplied by 0.52 before being applied to our models (Appendix B, Table B1).

Lake whitefish size-at-age

Fish age was determined primarily using otoliths. Only two stocks were aged using scales (Appendix B, Table B2): one dreissenid invaded and one not. As such, we assumed that any potential bias due to aging using scales (vs. otoliths) would be equally represented in the two groups under comparison. Assuming that fish collected in late summer had accumulated the majority of their growth for the calendar year, we added 1 year to estimated fish ages (Beauchamp 2002).

Cohort length-at-age of female lake whitefish was determined using a biphasic von Bertalanffy growth model (BVB) fit to individual fish length and age data in each population (Lester et al. 2004). Under the BVB, prematuration growth is linear with age, and declines in growth rate occur with the onset of maturity owing to allocation of energy to reproductive tissues. By assuming that investment in reproduction is proportional to somatic mass, the model predicts that postmaturation growth is described by the von Bertalanffy growth equation.

We used immature fish to estimate a prematuration growth rate:

$$L_t = h \cdot (t - t_1) \tag{B.1}$$

where L_t is length (mm) at age t, h is the growth rate (mm·year^{-1}), and t_1 is the age intercept (year). We then used a von Bertalanffy model to describe the postmaturation growth of males and females:

$$L_t = L_\infty \cdot \left[1 - e^{-k(t-t_0)}\right] \tag{B.2}$$

where L_∞ is asymptotic length (mm), k is Brody growth coefficient (year^{-1}), and t_0 is the age intercept (year). In estimating these parameters, we used the biphasic model to justify the following constraints:

$$L_\infty = 3h/g \tag{B.3}$$

$$k = \ln(1 + g/3) \tag{B.4}$$

where g measures gonadal investment, and h is the potential growth rate (estimated from prematuration growth). Values of

Table B2. Characteristics of populations under study.

Location	Age range	Age at 50% maturity (years)	Length at 50% maturity (mm)	GSI	h (mm·year^{-1})	t_1 (years)	t_0 (years)	g	b	a
Lake Erie	2–23	5.0	425	0.19[b]	95.3	0.631	–5.86	0.49	–5.5480	3.2716
Cape Rich[a]	2–10	6.9	466	0.13[c]	57.7	–1.162	–3.19	0.10	–5.4209	3.1828
Cheboygan	5–17	6.0	381	0.16[d]	69.2	–0.422	–7.36	0.35	–5.5105	3.1644
Detour	5–15	5.6	398	0.16[e]	141.1	2.94	–3.78	0.83	–5.3421	3.1001
North Channel	2–17	5.6	359	0.11[f]	54.5	–1.183	–8.08	0.30	–6.1188	3.4583
South Bay	1–29	9.0	362	0.11[c]	29.8	–4.116	–15.69	0.17	–5.5793	3.2583
Big Bay de Noc	3–14	5.8	376	0.15[g]	61.6	–0.337	–6.22	0.27	–6.0049	3.3537
Naubinway	3–17	5.8	395	0.15[e]	63.9	–0.396	–8.27	0.33	–5.6473	3.2103
Lake Ontario	6–19	4.7	360	0.17[b]	75.0	–0.001	–3.64	0.39	–4.8211	2.9704
Lake Simcoe	1–50	5.8	375	0.14[h]	47.2	–2.731	–13.41	0.24	–5.7906	3.3427
Lake of the Woods	2–35	7.1	287	0.11[i]	33.9	–2.743	–6.67	0.17	–5.5507	3.2598
Lake Nipigon	2–33	7.0	364	0.11[f]	41.2	–2.457	–10.64	0.23	–5.6533	3.2910
Lake Opeongo	2–33	4.8	131	0.13[h]	25.5	–5.945	–10.76	0.16	–5.2616	3.1158
Smoke Lake[a]	2–15	4.0	181	0.13[j]	29.8	–2.346	–5.98	0.26	–5.8349	3.3766
Apostle Islands	1–20	10.8	333	0.14[f]	20.6	–4.317	–40.46	0.15	–5.8778	3.3786
Thunder Bay	6–26	6.1	337	0.14[k]	58.0	–0.002	–6.31	0.32	–6.0135	3.4131
Whitefish Bay, Lake Superior	3–14	7.0	338	0.14[e]	62.9	0.426	–5.86	0.37	–5.9374	3.3933

Note: Age range is of fish encountered in catch; GSI refers to gonadosomatic index; h, t_1, t_0, and g are biphasic von Bertalanffy growth parameters (see text); b and a are parameters of female mass-at-length, given by the equation $\log_{10}(\text{mass}) = a{\cdot}\log_{10}(\text{length}) + b$.

[a]Ages determined from scales.

[b]Lumb et al. (2007).

[c]Estimated directly from fall spawning fish.

[d]Value from Detour stock.

[e]Beauchamp (2002).

[f]Estimate based on summer samples, adjusted to reflect fall spawning GSI (see text).

[g]Value from Naubinway stock.

[h]Ihssen et al. (1981).

[i]Value from Lake Nipigon.

[j]Value from Lake Opeongo.

[k]Mean of values from Lake Superior populations.

g and t_0 that best described the postmaturation growth pattern were estimated using nonlinear fitting methods applied to individual observations of length and age (Appendix B, Table B2).

Cohort masses used in bioenergetic models were estimated from the predicted lengths in each cohort from BVB models using a mass–length relationship specific to female lake whitefish for each population (Appendix B, Table B2).

Maturation and costs of reproduction

The size and age at which 50% of females reached maturity was estimated for each population using logistic regression (Appendix B, Table B2) and rounded to the nearest whole number to determine the year of first spawning in bioenergetic models. Where data were insufficient to apply logistic regression models, values were taken from the literature (Beauchamp 2002). Modelled cohorts were assumed to spawn annually after first spawning.

Female GSI from fish collected in the summer and during fall spawning in South Bay in 2005 indicated that summer GSI was approximately ½ of spawning GSI. For populations in which only summer GSI data were available, this value was doubled to estimate spawning GSI of female cohorts in bioenergetic models. Close agreement of values estimated in this manner with spawning GSI reported elsewhere for the same stocks (Beauchamp 2002) suggested this approach was valid. Values for populations where no GSI data were available were taken from the literature or estimated based on values of neighbouring populations (Appendix B, Table B2). Models ran 1 September to 31 August of the following year, and losses due to spawning occurred on 15 November (Madenjian et al. 2006).

Fish energy density

Relationships of lake whitefish energy density with body size vary greatly among populations (Rennie and Verdon 2008). To best account for this variation among populations, we used previously published relationships of ED with body mass (Appendix D) and further supplemented this information with ED vs. body mass relationships for three inland populations. ED for inland populations without sufficient data were estimated from a general ED vs. body mass relationship for inland populations (Appendix B, Table B1; Appendix D).

Environmental temperatures encountered by fish

Temperatures encountered by fish over the modelled period was based on data from archival tags recovered from lake whitefish in northern Lake Michigan and Lake Huron, reported in Madenjian et al. (2006). Data between reported biweekly means were estimated using linear interpolation. As a coldwater fish, lake whitefish have the ability to behaviourally thermoregulate during stratification by adjusting their position in the water column relative to thermal gradients with depth.

We therefore assumed that temperature data obtained from archival tags described the seasonal thermal preferendum of lake whitefish generally in the region under study.

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Appendices C and D

Appendices C and D appear on the following pages.

Appendix C

Table C1. Methylmercury (MeHg) concentrations and energy densities of lake whitefish prey items.

Organism	MeHg (ng·g wet mass^{-1})	Energy density (J·g wet mass^{-1})	Energy density source[a]
Bulk zooplankton	0.34	2170	10
Bythotrephes	2.17	2027	8
Ceratopogoniidae	0.72	3730	—[b]
Chaoborus	NC	1837	1
Chironomidae	1.98	3730	1, 2, 3
Cladocera	0.26	2200	10
Copepoda	0.49	2440	10
Decapoda	7.76	3686	3
Dreissena	1.44	1703	6
Diporeia	2.50	3625	6
Eggs[c]	NC	5000	1
Ephemeroptera	2.13	3791	1, 2
Gastropoda	1.16	1559	2
Holopedium	0.30	2222	10
Insecta[d]	2.42	3176	1
Isopoda	4.26	2807	4
Megaloptera	2.90	2753	4
Mysis	3.67	3783	1, 6, 7
Oligochaeta	4.52	3347	3
Ostracoda	0.21	6639	1
Plant[e]	NC	2243	3
Sphaeriidae	4.58	606	1, 3
Fish[f]	6.79	4435	5
Trichoptera	0.25	3791	1, 4
Other[d]	2.42	3535	9

Note: NC, not collected. MeHg concentrations are from organisms collected from South Bay, Lake Huron, in September 2005.

[a]Energy densities are literature values and are taken from the source referenced as follows: 1, Cummins and Wuycheck 1971; 2, Driver et al. 1974; 3, Eggleton and Schramm 2004; 4, Johnson et al. 2006; 5, Lantry and Stewart 1993; 6, Madenjian et al. 2006; 7, Rudstam 1989; 8, Storch 2005, where the value from Storch (2005) was reduced to account for spine mass (measured to be 16% of *Bythotrephes* wet body mass; this study), because *Bythotrephes* spines are observed to pass unprocessed through the digestive tracts of lake whitefish (M. Rennie, personal observation); 9, Mean of all values from a larger database of lake whitefish diets (M.D. Rennie, unpublished data); 10, Fernandez et al. 2009, summarized from Cummins and Wuycheck 1971.

[b]Chironomid energy density applied to Ceratopogoniidae.

[c]Assumed [MeHg] of fish.

[d]Average value for all organisms was applied for MeHg estimate.

[e]Assumed [MeHg] was negligible (i.e., = 0).

[f]Fish MeHg value is for stickleback collected in South Bay, Lake Huron, September 2005.

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Appendix D

Table D1. Lake whitefish energy density (J·g^{-1} wet mass) relationships with round mass of fish (g).

Function	Relationship	Source	df	F	p	R^2
1	1.9398·mass + 4445.7	Lumb 2005	1,19	14.6	0.0013	0.45
2	1.8476·mass + 6605.1	Lumb 2005	1,19	49.2	<0.0001	0.73
3	0.565·mass + 5233.7	Rennie and Verdon 2008	1,37	17.83	0.0002	0.33
4	<886 g: 2.543·mass + 5211; ≥886 g: 0.3078·mass + 7192	Madenjian et al. 2006	NR	NR	NR	NR
5[a]	2.4846·mass + 5132.9	This study	1,58	10.3	<0.0001	0.49
6[b]	2.1370·mass + 5472.4	This study	1,19	57.8	0.005	0.36
7[c]	2.4096·mass + 4865.6	This study	1,18	4.54	0.048	0.21

Note: NR, not reported.

[a]Relationship among three inland stocks of lake whitefish (Smoke, Opeongo, Nipigon).

[b]Relationship specific to Lake Nipigon.

[c]Relationship specific to Lake Opeongo.

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