Can migration mitigate the effects of ecosystem change? Patterns of dispersal, energy acquisition and allocation in Great Lakes lake whitefish (*Coregonus clupeaformis*)

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with 7 figures, 3 tables and 2 appendices

Abstract: Migration can be a behavioural response to poor or declining home range habitat quality and can occur when the costs of migration are overcome by the benefits of encountering higher-quality resources elsewhere. Despite dramatic ecosystem-level changes in the benthic food web of the Laurentian Great Lakes since the colonization of dreissenid mussels, coincident changes in condition and growth rates among benthivorous lake whitefish populations have been variable. We hypothesized that this variation could be in part mitigated by differences in migratory habits among populations, where increased migration distance can result in an increased probability of encountering high-quality habitat (relative to the home range). Results from four Great Lakes populations support this hypothesis; relative growth rates increased regularly with migration distance. The population with the largest average migration distance also had the least reduction in size-at-age during a period of significant ecosystem change and among the highest estimated consumption and activity rates. In comparison, the population with the greatest declines in size-at-age was among the least mobile, demonstrating only moderate rates of consumption and activity. The least mobile population of lake whitefish was supported by a remnant *Diporeia* population and has experienced only moderate temporal growth declines. Our study provides evidence for the potential role of migration in mitigating the effects of ecosystem change on lake whitefish populations.

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Introduction

Migratory behaviour should evolve in organisms when the high energetic costs of activity and movement associated with migration are offset by the added benefits conferred through the exploitation of heterogeneous habitats (GROSS et al. 1988). This link between migration and energetics suggests that migration is likely a state-dependent process. FORSETH et al. (1999) showed that a critical size or condition level must be attained before the costs of migration can be offset. Further, fishes of larger body sizes are also more likely to display migratory behaviour than smaller fishes (ROFF 1988, JONSSON & JONSSON 2006), due primarily to increasing mass-specific bioenergetic costs of mobility with decreasing body size (ROFF 1991). Additionally, the prospect of "greener pastures" can also explain migration, where dispersal is driven by gradients of prey abundance or density of conspecifics (JONSSON & JONSSON 2006, HAUGEN et al. 2007).

The ability of migratory populations to exploit many potential habitats increases the probability of encountering high-quality patches and may prove beneficial in ecosystems undergoing significant food web changes, such as those experiencing species invasions. Behaviours associated with activity (e.g., the extent of migratory behaviour) also have direct consequences on growth and life history patterns (ROFF 1988), and on the susceptibility of populations to tolerate ecosystem change. For example, Atlantic cod (*Gadus morhua*) populations displaying homing behaviour (i.e., always returning to same spawning site) showed a greater evolutionary response to fishing disturbance (e.g., earlier maturation at smaller size, poor condition) compared with roaming cod populations that selected spawning sites adaptively (JORGENSEN et al. 2008).

The Great Lakes ecosystem has undergone significant changes since the establishment of dreissenid mussels, including substantial changes to the structure and function of benthic communities. For example, densities of the deep-water amphipod *Diporeia* have declined by orders of magnitude in all of the Great Lakes since the early 1990s, except Lake Superior (DERMOTT & KEREC 1997, MCNICKLE et al. 2006, NALEPA et al. 2009). The result of this community-scale change in the benthos has led to an overall reduction in the energy available to benthivorous fish (MCNICKLE et al. 2006, NALEPA et al. 2009, RENNIE et al. 2009b). These changes in the benthic community have been cited as a primary contributor to coincident declines in growth rates and body condition of some populations of lake whitefish (*Coregonus clupeaformis*), a common hypolimnetic benthivore (HOYLE et al. 1999, POTHOVEN et al. 2001, RENNIE et al. 2009b), as well as declines in the abundance and condition of other hypolimnetic species such as alewife (*Alosa pseudoharengus*), deepwater sculpin (*Myoxocephalus thompsoni*) and bloater (*Coregonus hoyi*; HONDORP et al. 2005). However, changes in lake whitefish populations have not been as consistent as have ecological changes observed in the benthos; while some populations demonstrated sudden and dramatic declines in growth, condition and abundance (e.g., Lake Ontario, HOYLE et al. 1999), others display more gradual declines in growth and condition (e.g., Lake Huron populations in South Bay, Georgian Bay and Southampton; RENNIE 2009). Others still appear to have been largely unaffected (e.g., Lake Erie, LUMB et al. 2007). Further, some populations with declining growth and condition have demonstrated increases in catch rates (DEBRUYNE et al. 2008, RENNIE et al. 2009a), which seems an unlikely consequence of changes in the benthic community from high- (*Diporeia*) to low-quality (dreissenids) forage items.

A possible explanation for the variation in response among whitefish populations to ecosystem change might be among-population differences in their degree of migratory behaviour. For example, populations of lake whitefish in Lake Erie, which appear to be largely unaffected by the loss of *Diporeia,* also undergo annual migrations from the deep eastern basin to the more shallow western basin. If these large-scale migrations provide access to otherwise unavailable high-quality food (ROFF 1991), then the growth rates of migrating fish might be less affected by local ecosystem changes than non-migrating fish. This pattern might be further reflected in more efficient rates of energy conversion in migrating fish compared to non-migratory populations (FORSETH et al. 1999).

In this study, we describe long-term changes in growth of four lake whitefish populations in northern Lakes Huron and Michigan during a period of significant ecosystem change. We then evaluate the degree to which migratory differences among these populations might explain differences in their response to ecological change. Finally, we evaluate the degree to which migratory patterns explain contemporary differences in growth, consumption, activity and conversion efficiency among populations. We predict that populations demonstrating broader migratory behaviour will be less susceptible to large-scale ecosystem change in the Great Lakes compared with non-migratory populations.

Methods

Study site

We compared patterns of growth (size-at-age), migration and bioenergetics among four populations of Great Lakes lake whitefish; Big Bay de Noc (BD) and Naubinway (NB) in Lake Michigan and Cheboygan (CH) and Detour-Cedarville (DC) in Lake Huron (Fig. 1). Recent genetic evidence supports the designation and management of the Lake Michigan populations studied here as separate entities (VANDEHEY et al. 2009). We assumed our Lake Huron populations were similarly discrete (EBENER et al. 2010a). These populations were sampled for four years (2003–2006) as part of a multi-agency study to evaluate spatial and temporal variation among populations addressing fish health and other factors influencing natural rates of mortality (EBENER et al. 2010a). Populations were sampled quarterly to obtain diet information. Otoliths were collected for age determination; size, sex and maturity of all fish were recorded and tissue samples were collected for various purposes.

Size-at-age estimates

To evaluate temporal changes in size-at-age among the four populations, we examined trends in weight at age 4 and age 5 lake whitefish. Weights-at-age were taken from statistical catch-at-age models developed for each of the four populations (see EBENER et al. 2005). Ages in this analysis were determined using scales. We selected age 4 and 5 fish because ages determined from scales for these age classes typically agree best with other more accurate ageing methods using otoliths and fin rays (MILLS & BEAMISH 1980, MILLS & CHALANCHUK 2004, MUIR et al. 2008, RENNIE et al. 2009b), which were not otherwise available to examine historic trends in growth.

Contemporary size-at-age estimates for use in bioenergetic models and for comparisons among populations relied on female otolith ages for fish captured in fall (August–November) 2003–2006. These data were augmented with scale ages of fish younger than age 5 to better describe immature growth rates. Because fish collected in fall were assumed to have completed their growth for that year, we added one year to age estimates for bioenergetic models. Cohort length-at-age of female lake whitefish
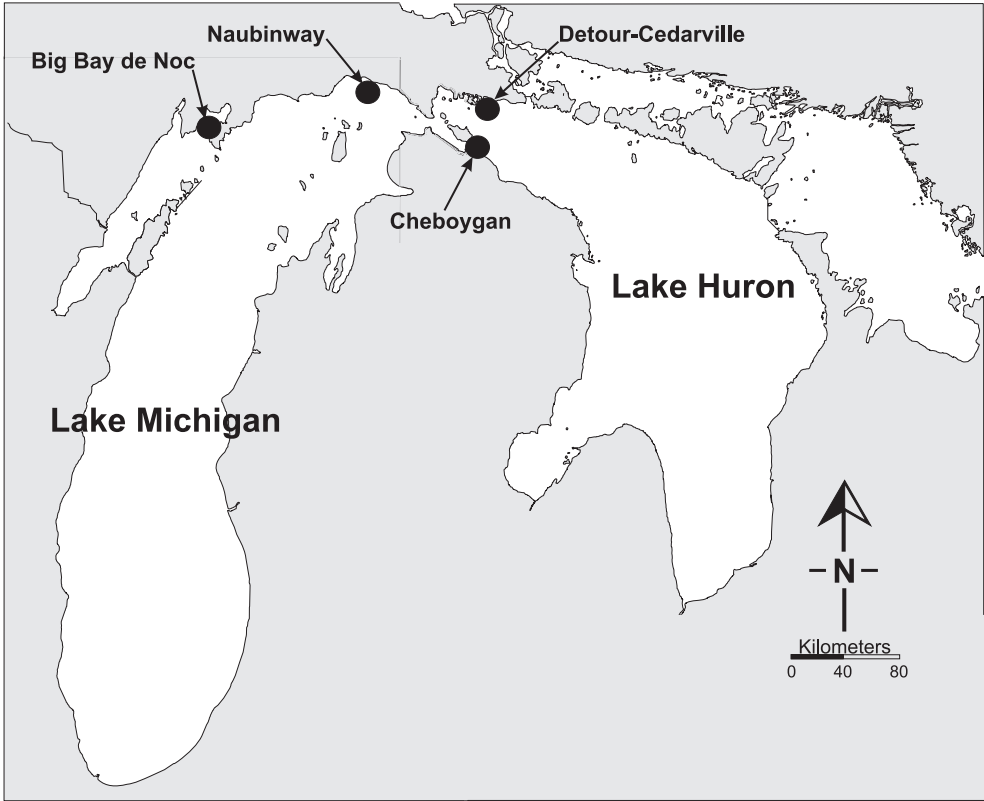
Fig. 1. Locations of lake whitefish populations in this study.

was determined using a standard Von Bertalanffy growth model (VB) fit to individual fish total length and age data in each population (VON BERTALANFFY 1938) and described as:

$$L_t = L_\infty \cdot (1 - e^{-k(t-t_0)}) \qquad \text{eq. 1}$$

where L_∞ = asymptotic length (mm), k = Brody growth coefficient (year^{-1}) and t_0 = the age-intercept (set to zero in our models as per BEAUCHAMP 2002).

Tag and recapture

Tagging was performed during 1–18 November of 2003–2006 to coincide with lake whitefish returning to spawn. In total, 22,416 tagged lake whitefish were released (EBENER et al. 2010a). All fish were captured in commercial-sized trap nets in water <15 m deep and held in aerated water prior to tagging (EBENER et al. 2010a). Fish were tagged with consecutively numbered T-bar anchor tags (Floy Tag, Inc., Seattle, Washington; Model FD-94) near the insertion of the dorsal fin. A US$5 reward was initially offered for the return of each tag, but the reward was increased to US$10 in 2007 to stimulate returns of tagged fish. Tagged lake whitefish were recovered almost exclusively from commercial fishermen (99.9%); the remainder came from recreational anglers or government fishery agencies. Based on these

returns, we were able to assign a statistical grid location of recapture to 1,588 of 2,153 tag recoveries from December 2003 through January 30, 2009.

Estimating Distance Travelled

We conducted comparisons among populations of distance traveled from spawning shoals. We calculated the distance moved by individual lake whitefish as the Euclidean distance between the latitude and longitude coordinates of tag and release point to the latitude and longitude coordinates describing the center of the statistical grid where the fish was recaptured (KAPUSCINSKI et al. 2005). Recapture grids that we used were the 10 min by 10 min latitudinal and longitudinal statistical grids used to compile commercial fishery statistics in the Great Lakes. For incomplete grids that were cutoff by land (about 30%), we chose the center of the partial grid or the center of the known fishing grounds as the latitude and longitude coordinates. Our estimated distances travelled are therefore conservative, since migration distances are not straight and fish obviously could not travel overland between their release and recapture sites.

Estimation of food consumption and activity in lake whitefish

To estimate lake whitefish food consumption and activity, we used an approach combining the mass balance formulae for fish contaminants and weight from a mercury (Hg) mass balance model (MMBM) described by TRUDEL et al. (2000) with the mass balance of fish energy budgets from a bioenergetics model (MADENJIAN et al. 2006). The MMBM models the mass balance of methylmercury (MeHg) in fish, the form of Hg that is most readily bioaccumulated (MASON et al. 1995, LAWSON & MASON 1998, LAWRENCE et al. 1999). The primary mode for MeHg uptake in fish from uncontaminated waters is through absorption in the gut from diet (HALL et al. 1997, LAWSON & MASON 1998, LEANER & MASON 2002). The accumulation of MeHg in fish is described by:

$$\frac{dHg}{dt} = (a \cdot M_d \cdot C) - (E + G + N) \cdot Hg \qquad \text{eq. 2}$$

where Hg is MeHg concentration ([MeHg]) of the fish (μg Hg·g^{-1} wet weight), α is the assimilation efficiency of MeHg from food (0.8 was used in this study, TRUDEL et al. 2000), M_d is [MeHg] in food (μg Hg·g^{-1} wet weight), C is the mass-specific food consumption rate (g prey ·g fish^{-1}·day^{-1} expressed as day^{-1} hereafter), 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 time steps such as one day, differences between parameters such as E and N will be small and can be treated as constants. Integration of eq. 2 then yields the following (rearranged to solve for consumption):

$$C = \frac{Hg_t - Hg_0 \cdot e^{-(E+G+N)t}}{\alpha \cdot M_d \cdot [1 - e^{-(E+G+N)t}]} \cdot (E + G + N) \qquad \text{eq. 3}$$

where Hg_0 and Hg_t are the [MeHg] in fish at time 0 and time t, respectively. Losses due to elimination and spawning (N) are as described by equations in Appendix 1.

The MMBM (eq. 3) is solved over a daily time step and combined with a bioenergetic model (BM) for lake whitefish (MADENJIAN et al., 2006) 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 BM can be expressed simply as:

$$W_t = W_0 + [C - (F + U + R_T)]/ED_{fish} \qquad \text{eq. 4}$$

where W_t is the final fish weight (g), W_0 is the initial fish weight (g), C is ingestion rate (J·day^{-1}) at time t, ED_{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 BM is a function of temperature and an allometric function describing maximum consumption determined from laboratory experiments. Losses from metabolism, R_T from eq. 4, can be further subdivided into three components:

$$R_T = ACT \cdot R_s + R_d \qquad \text{eq. 5}$$

where R_d is specific dynamic action (SDA, 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 $1 \leq ACT \leq \infty$.

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

$$W_t = W_{t-1} - W_{t-1} \cdot (GSI \cdot ED_g) \qquad \text{eq. 6}$$

where W_t is the fish weight after spawning, W_{t-1} is the fish weight the day previous, GSI is the gonadosomatic index (weight of spawning gonads/weight of fish, g) and 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. 2005b).

By iterating on a daily basis both equations 3 and 4, which are linked through the common term C, the unique solution of C and ACT that achieved the observed final weight and [MeHg] was obtained through an optimization routine. The optimization minimized error between observed W_t and Hg_t, and modelled W_t and Hg_t, such that the average difference between observed and modelled W_t and Hg_t was less than 0.1%.

Parameterization of models

Unless otherwise indicated, all model parameters for the MMBM were those reported in Rennie et al. (2008). Functions describing daily MeHg elimination and losses to gonads are reported in Appendix 1. BM parameters for lake whitefish are from Madenjian et al. (2006). Temperatures encountered by fish over the modelled period were based on data from archival tags recovered from lake whitefish in northern Lakes Michigan and Huron, reported in Madenjian et al. (2006). Data points between biweekly means were estimated using linear interpolation. As a coldwater fish, lake whitefish have the ability to thermoregulate during stratification by adjusting their position in the water column relative to thermal gradients with depth. Therefore, we assumed that the temperature data obtained from archival tags described the seasonal thermal preferenda of lake whitefish in the region under study. We modelled growth and mercury 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, weight-at-age, diet [MeHg] and diet ED are described below. Because of potential biases of bioenergetic estimates associated with fish sex (Rennie et al. 2008), we only modelled female lake whitefish.

Lake whitefish size and [MeHg] were based on 1–5 years of data from each population, and used to build statistical models of size and [MeHg] with age specific to each population (described previously and below). These models were used to predict [MeHg]- and size-at-age for MMBM and BM input parameters. Input parameters of modelled cohorts were not extended beyond the age or size range observed in the population to avoid erroneous extrapolation.

Characterization of fish diets

Stomach contents from fish sampled throughout the year 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 of prey taxa found in each fish by weight was estimated. Energy densities (ED) for diets from individual fish were estimated by applying energy densities for various prey taxa (Appendix 2) to weight-based proportional composition estimates of diets. Because our data showed no relationship between fish size and estimated diet EDs, we estimated the mean ED of all fish for which data were available in each sampling period (Table 1). Fish diet ED between sampling periods was estimated using linear interpolation. To characterize proportional composition of diets in each population, we estimated the mean proportion for each taxonomic group and reported results for all organisms ≥1%; all other organisms and those unidentifiable to more specific taxonomic groups were assigned to "other" (Fig. 2).

Methylmercury in fish and diets

A minimum of 40 fish from across the size range that was sampled were analyzed for [Hg] on a Milestone DM-80 direct mercury analyzer following United States Environmental Protection Agency (US-EPA) method 7473 (SW-846). Repeatability of DM-80 results was determined by analyzing 3–5 standard reference material samples per run (TORT-2). Mean estimates 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 was modelled using the mercury mass balance model. Whole body [Hg] in lake whitefish is 82% of tissue [Hg] (Rennie 2009). The proportion of total Hg as MeHg was 65% (Rennie 2009). Fish [Hg] measured from muscle tissues was adjusted to reflect whole body [MeHg] using these correction factors. Within each population, mean fish mercury for each age class was estimated using functions that best described the relationship between mean [Hg] and age (Table 2). These estimates were used to parameterize [MeHg]-at-age for MMBM inputs.

A previous study demonstrated that [MeHg] of diet items harvested directly from yellow perch stomachs were similar to those sampled from the lake (Rennie et al. 2005a). Based on this observation, sub-samples of lake whitefish stomach contents from 1–5 fish were combined into composite samples based on 10 cm length classes for each population. Between 3 and 7 composites were analyzed for each

Table 1. Dietary energy densities of lake whitefish sampled from four populations, 2004–2005. Values in italics are number of fish from which diets were examined in each time period. *nc* = none collected.

Population	Season		
	Spring (Apr.–May)	**Summer (June)**	**Fall (Sept.–Oct.)**
Big Bay de Noc	1769.7	1898.4[a]	2027.0
	28	*nc*	*20*
Naubinway	2483.1	1810.6	3178.9
	17	*16*	*30*
Cheboygan	3068.9	2582.4	1945.7
	10	*22*	*20*
Detour-Cedarville	1698.7	3465.8	2780.4
	13	*2*	*19*

[a] Estimated from mean of spring and fall diets.
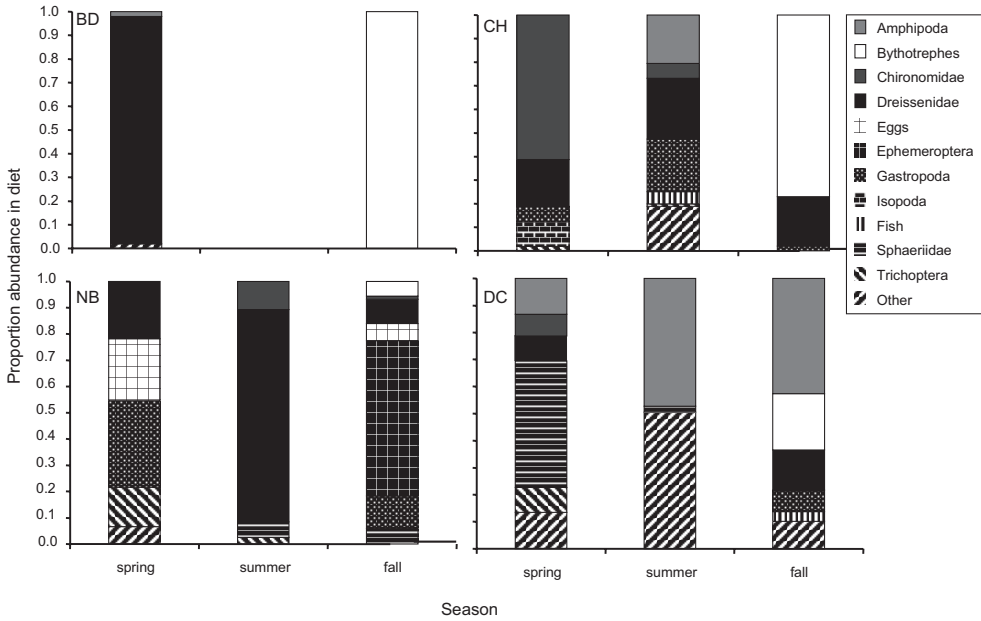
Fig. 2. Diets of lake whitefish from four populations collected during 2004–2005. Lake Michigan stocks are BD (Big Bay de Noc) and NB (Naubinway). Lake Huron stocks are CH (Cheboygan) and DC (Detour-Cedarville).

population. Stomach composites were analyzed for [MeHg] as described in RENNIE (2009). 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. Unlike previous studies, [MeHg] of diet items sampled from the lake were on average 52% lower than those harvested from lake whitefish stomachs (RENNIE 2009). Therefore, diet MeHg of stomach contents determined analytically were multiplied by 0.52 before being applied to our models (Table 2).

Lake whitefish weight-at-age

Cohort weights used in bioenergetic models were estimated from the predicted lengths in each cohort from VB models using a weight-length relationship specific to female lake whitefish for each population (Table 2).

Maturation and costs of reproduction

The size and age at which 50% of females reached maturity was estimated for each population using logistic regression (Table 2) and rounded to the nearest whole number to determine the year of first spawning in bioenergetic models. Modelled cohorts were assumed to spawn every year after first spawning. Female GSI estimates were taken from BEAUCHAMP (2002). Models ran September 1 to August 31 of the following year and losses due to spawning occurred on November 15 (MADENJIAN et al. 2006).

Table 2. Parameters describing life history, growth, size, energy density (ED) and methylmercury (MeHg) dynamics of lake whitefish from four populations under investigation. b_W, a_W are parameters of female weight at length, given by the equation $\log_{10}(\text{weight}) = a_W \cdot \log_{10}(\text{length}) + b_W$. a_{Hg}, b_{Hg} are parameters of female methylmercury (MeHg, $\mu g \cdot g^{-1}$ wet weight) at age, given by the equation MeHg= $a_{Hg} \cdot e^{(bHg \cdot age)}$.

Population	Age at maturity (years)	Length at maturity (mm)	b_W	a_W	Fish ED function[1,2]	a_{Hg}	b_{Hg}	Diet MeHg ($\mu g \cdot g^{-1}$)
Big Bay de Noc	5.8	375.6	-6.00492	3.35375	1	0.0193	0.0639	0.0014
Naubinway	5.8	394.9	-5.64729	3.21031	1	0.0064	0.1340	0.0014
Cheboygan	6.0	380.7	-5.51055	3.16439	2	0.0377	0.0216	0.0017
Detour-Cedarville	5.6	397.8	-5.34211	3.10007	2	0.0240	0.0412	0.0049

[1] MADENJIAN et al. (2006), [2] RENNIE & VERDON (2008).

Fish energy density

Relationships of lake whitefish energy density with body size vary greatly among populations (RENNIE & VERDON 2008). To best reflect the ED for a particular population, we used previously published relationships of ED with body mass thought to best characterize that population (Table 2).

Statistical analysis

We compared patterns in mass-specific bioenergetic estimates among populations, specifically, consumption (C, day^{-1}), activity multipliers (ACT, unitless), conversion efficiency (V, day^{-1}) and growth (G, day^{-1}). For each population, weighted means of mass-specific bioenergetic parameters were estimated where each modelled age class was weighted by its numerical proportional representation in the catch. This was done to represent the "realized" mean consumption for a specific population by emphasizing bioenergetics of common age classes and de-emphasizing uncommon age classes. Standard errors around weighted means were estimated according to COCHRAN (1977), a method that provided similar estimates of variance around weighted means to those of more intensive bootstrapping estimation methods (GATZ & SMITH 1995).

Estimates of migration distances based on tag-recapture data were highly non-normal (Fig. 3), as were weighted estimates of lake whitefish bioenergetics. This is a violation of traditional parametric statistics. Therefore, we employed a randomization-based approach to evaluate differences among populations. Briefly, we began by performing a one-way ANOVA comparing mean migration or bioenergetic estimates among the four populations under investigation. The F-ratio from this analysis was saved. We then randomly assigned the response variable of interest among the four populations and re-calculated the F-ratio for the randomized dataset. This process was repeated 9,999 times. We report our randomization P-values (P_{rand}) as the proportion of F-ratios due entirely to random association that exceeded the initial observed F-ratio. We followed up significant one-way ANOVAs with *post-hoc* comparisons among groups using t-tests based on the same randomization procedure described above, adjusting our critical P-values for all possible *a posteriori* comparisons among the four groups (P_{crit}= 0.05/6= 0.0083).

For bioenergetic estimates, we evaluated significant differences among weighted means by randomly assigning both the response variable and its respective weighting to a given population. Pair-wise follow-up tests among populations were made using ANOVA and compared to adjusted critical P-values as described above.
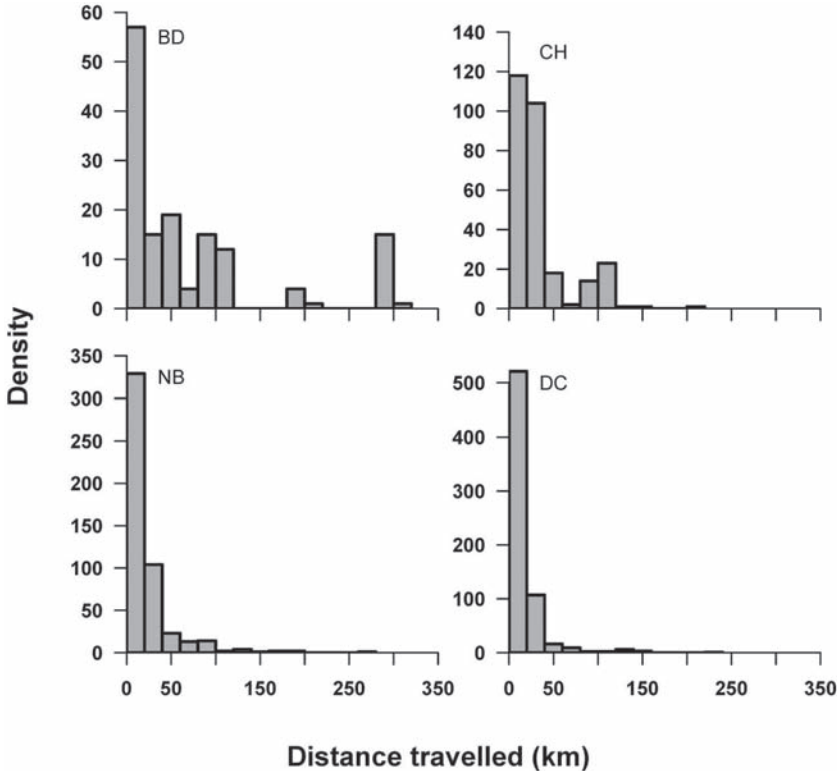
Fig. 3. Histograms of distances travelled between marking and recapture for Lake Huron and Lake Michigan lake whitefish. Abbreviations as in Fig. 2.

## Results

Growth and life histories

All populations demonstrated relative stability in size-at-age 4 and 5 between 1980–1991 (pre-*Diporeia* decline), followed by a significant decline in growth rates between 1992–2000 (Fig. 4). This coincides with the timing of major *Diporeia* declines in Lake Michigan (NALEPA et al. 2006). ANOVA comparing size-at-age 4 between time periods (pre-invasion, 1980–1991 and post-invasion, 2000–2005) among the four populations revealed significant differences among sites ($F_{3,88} = 8.99$, $P < 0.0001$) and between time periods ($F_{1,88} = 41.74$, $P < 0.0001$). Size-at-age 5 showed a significant interaction between time period and population ($F_{3,88} = 4.37$, $P = 0.006$). Generally, size-at-age for both age 4 and 5 fish was lower during 2000–2005 than during 1980–1991 (Fig. 4). However, average declines in size-at-age between 1980–1991 and 2000–2005 were greatest in the NB population and least pronounced in BD fish (Table 3).
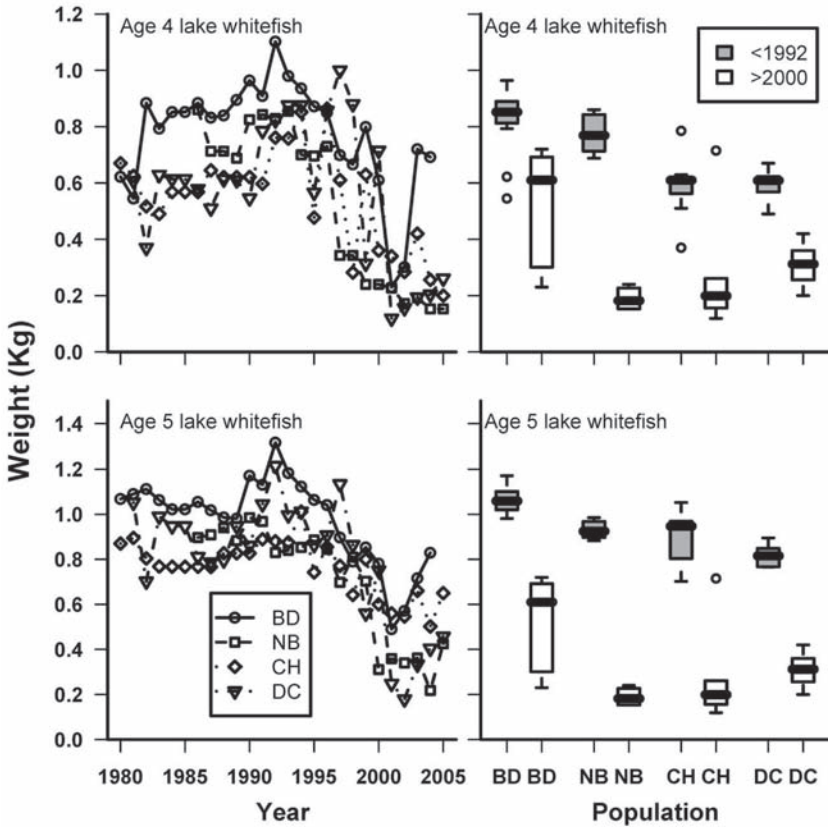
Fig. 4. Weight-at-age for age 4 and 5 lake whitefish. Age determined from scales. Left-hand panels are mean weights. Right-hand panels are boxplots contrasting growth before and after growth declines observed during the 1990s; horizontal lines represent medians, boxes show interquartile ranges and error bars are 95% confidence intervals. Outliers are represented by open circles. Abbreviations as in Fig. 2.

Table 3. Percent decline in mean size-at-age among four lake whitefish populations 1980–1991 vs. 2000–2005.

| Population	Size-at-age 4 decline (%)	Size-at-age 5 decline (%)
Big Bay de Noc	-27.3	-10.3
Naubinway	-58.1	-39.4
Cheboygan	-44.0	-29.1
Detour-Cedarville	-49.3	-27.9
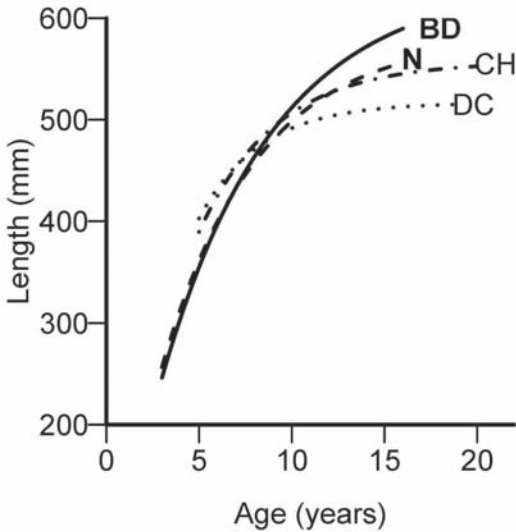
Fig. 5. Von Bertalanffy growth curves fit to length-at-age data (determined from otoliths) for Lake Huron and Lake Michigan lake whitefish populations in this study. Abbreviations as in Fig. 2. Growth parameters (± standard errors) are as follows (see eq. 1 in text for details): BD, $k = 0.163$ (±0.009) year^{-1}, $L_\infty = 636.6$ (±15.0) mm; NB, $k = 0.194$ (±0.007) year^{-1}, $L_\infty = 582.3$ (±9.5) mm; CH, $k = 0.240$ (±0.013) year^{-1}, $L_\infty = 557.1$ (±8.5) mm; DC, $k = 0.302$ (±0.020) year^{-1}, $L_\infty = 516.8$ (±6.2) mm.

Contemporary growth patterns were most similar among populations from the same lake. The BD and NB populations from Lake Michigan were smaller at younger ages, with slower approaches to asymptotic size but larger asymptotic sizes than Lake Huron populations (DC, CH; Fig. 5).

Diets of fish from Lake Michigan had the largest proportions of invasive species (Fig. 2). Diets of BD fish were heavily dominated by dreissenids and *Bythotrpehes*. Dreissenids were a large proportion of NB fish diets in the summer, though were a smaller proportion in the fall and spring. Amphipods (primarily *Diporeia*), though virtually absent from diets of Lake Michigan fish, were present in the guts of Lake Huron whitefish. While amphipods were present all year in DC lake whitefish, they were only detected in the summer diets of CH fish, which also had a greater proportion of invasive species than fish from the DC population.

Patterns of dispersal

Distances travelled from tagging/spawning locations were significantly different among populations (randomization ANOVA [RANOVA hereafter], $F_{3,1583} = 89.8$, P_{rand}, < 0.0001; Fig. 3). Migrations were greatest for fish from the BD population ($n = 143$, mean = 69.5 km, Fig. 3), followed by CH ($n = 282$, mean = 36.8 km) and NB ($n = 495$, mean = 25.0 km). Fish from DC did not disperse widely and were typically caught within 20 km of where fish were tagged and released ($n = 667$, mean = 16.7 km, Fig. 3). Differences among all populations were significant (randomization t-tests, all < $P_{crit} = 0.0083$).
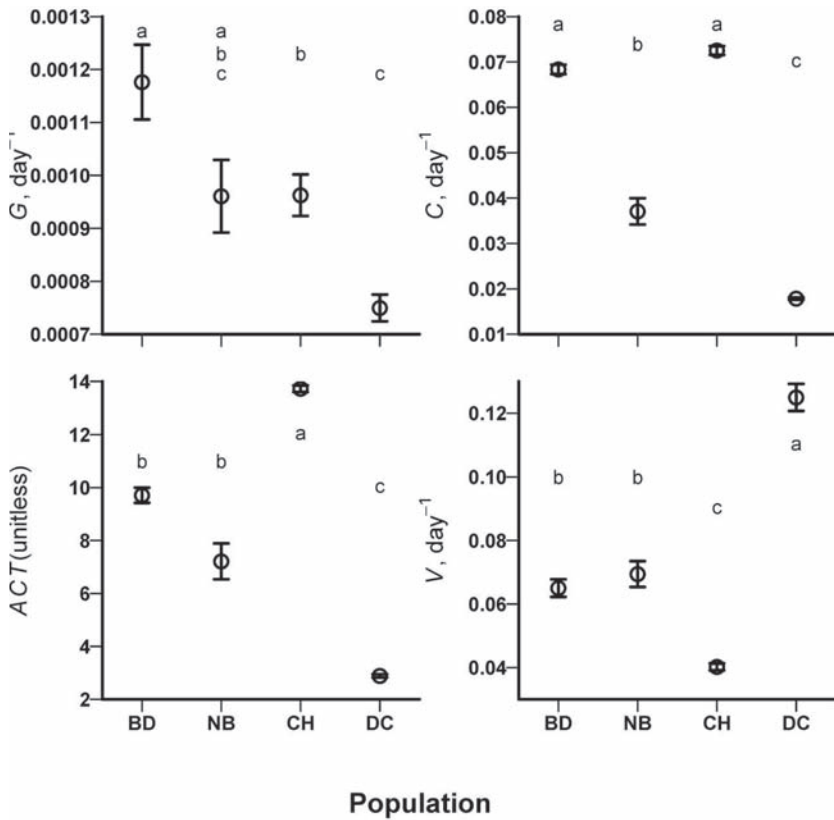
Fig. 6. Instantaneous rates of growth (G), consumption (C), conversion efficiency (V) and activity (ACT) of Lake Michigan and Lake Huron lake whitefish populations in this study. Values are weighted means and standard errors. Values in each panel sharing the same letter are statistically indistinguishable at $P_{crit} = 0.0083$. Population abbreviations as in Fig. 2.

Bioenergetics

Bioenergetic rates were significantly different among populations (RANOVAs, growth, $F_{3,49} = 14.2$, $P_{rand} < 0.0001$; consumption, $F_{3,49} = 281.9$, $P_{rand} < 0.0001$; activity, $F_{3,49} = 148.71$, $P_{rand} < 0.0001$; conversion efficiencies, $F_{3,49} = 127.70$, $P_{rand} < 0.0001$; Fig. 6). Growth was fastest in BD lake whitefish, but not statistically distinguishable from NB fish ($F_{1,25} = 7.43$, $P = 0.0373$, $P_{crit} = 0.0083$). Growth was slowest in DC fish, though not statistically different from NB fish ($F_{1,24} = 12.17$, $P = 0.0118$). Growth was intermediate for NB and CH fish (Fig. 6). Consumption was similarly high for both BD and CH lake whitefish ($F_{1,25} = 7.51$, $P = 0.0154$), intermediate for NB fish and lowest for the DC population (Fig. 6). A similar pattern emerged for activity rates, though activity rates of CH lake whitefish were significantly higher than those from BD (Fig. 6). Activity rates between BD and NB lake whitefish were not statistically different ($F_{1,25} = 12.13$, $P = 0.0109$). Conversion efficiencies were highest for DC lake whitefish, lowest for CH fish and intermediate for BD and NB fish (Fig. 6).
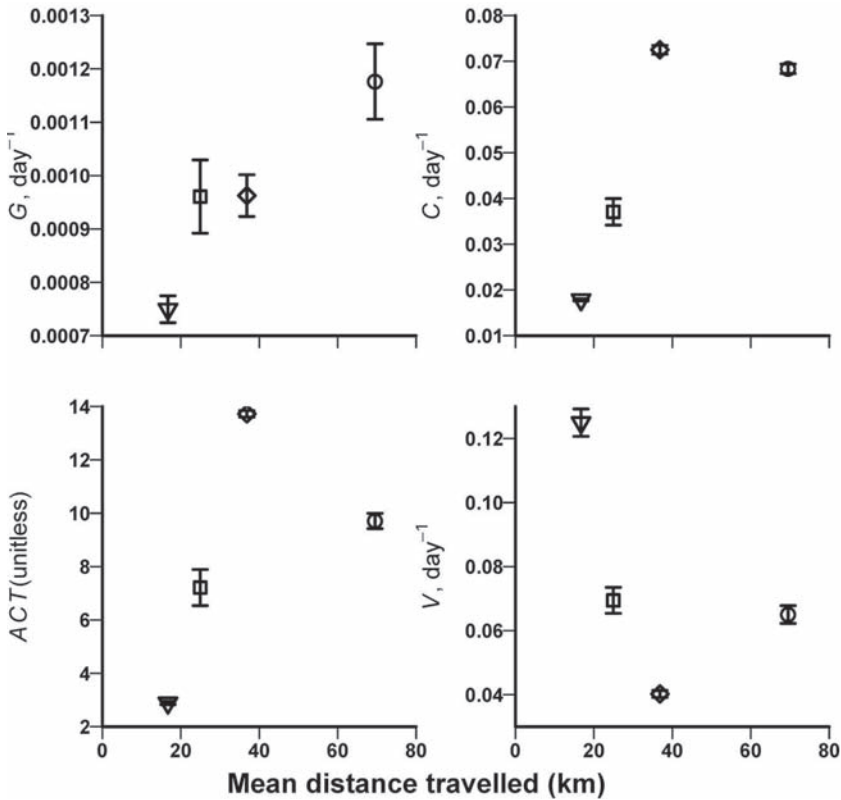
Fig. 7. Comparisons of bioenergetic estimates (weighted means and standard errors) with mean travel distance between mark and recapture in lake whitefish populations. Symbols as in Fig. 4.

Based on visual inspection, rates of growth, activity and consumption appeared to scale positively with mean dispersal distance, while conversion efficiency tended to decline with increasing dispersal distance (Fig. 7). Due to our relatively small sample sizes and lack of expectations about the possible nature of the relationships between dispersal distance and bioenergetics (e.g., linear, asymptotic, etc.), we did not conduct statistical tests about these patterns.

Discussion

Generally, lake whitefish migration distance scaled positively with bioenergetic estimates of activity, consumption and growth, and scaled negatively with conversion efficiency for the four populations that we investigated. Lake whitefish that migrated greater distances from their spawning shoals ate more and grew faster than those that stayed close to their spawning grounds, despite the reduction in conversion efficiency caused by the increased dispersal range. As these trends are based on only four populations, associations between

lake whitefish movement patterns with bioenergetics should be considered carefully. However, the patterns we report here are supported by similar results that demonstrate positive relationships between growth rate and migration distance (ROFF 1991, OLSSON et al. 2006). These observations combined with our results lead us to propose that migration in lake whitefish populations might mitigate the effects of prey community changes occurring in the Great Lakes. Longer migrations increase the probability of exposure to better feeding opportunities (GROSS et al. 1988, ROFF 1991) and/or regions of reduced intraspecific competition (OLSSON et al. 2006, HAUGEN et al. 2007).

An example from our study of the benefits of migration can be seen comparing the two Lake Michigan lake whitefish populations. While the areas enclosed by BD and NB management areas both lack *Diporeia* (NALEPA et al. 2006, KRATZER et al. 2007), BD fish demonstrated the greatest dispersal distance, but the smallest percent change in size-at-age of age 4 and 5 fish from 1980 to 2005. In comparison, most NB fish were recaptured within 40 km of where they were tagged, but demonstrated the largest percent decrease in size-at-age from 1980 to 2005. While both populations had statistically indistinguishable activity rates and conversion efficiencies, greater declines in historic size-at-age of NB fish were due to significantly lower consumption rates. Thus, a wider dispersal range may have allowed BD fish to exploit more high-quality foraging habitats than NB fish. Indeed, the greatest concentrations of *Diporeia* exist along the western shores of Lake Michigan (NALEPA et al. 2006, 2009), which follow the path of dispersal for the BD population (EBENER et al., 2010b).

Size-at-age of BD lake whitefish declined the least, even though their home range diet was dominated by the energetically deficient invasive dreissenids and *Bythotrephes*. Diets of migrating fish could therefore reflect a more energetically rich mix of taxa when compared to those captured within the home range. In contrast, contemporary *Diporeia* populations within the range of NB fish are uniformly depauperate (NALEPA et al. 2006, 2009) and lake whitefish diets are dominated most of the year by shelled prey such as gastropods, dreissenids and sphaerids. This assumed difference in foraging quality between these populations is further supported by fatty acid methyl ester (FAME) profiles—which reflect differences in foraging patterns—examined in the polar lipid fraction of dorsal muscle tissue from these same populations. Based on these FAME profiles, NB fish may be consuming more bivalves (both native and invasive) than other populations, which are deficient in several essential fatty acids when compared to *Diporeia* (WAGNER et al. 2010).

Our study showed that populations with longer-range dispersal were more resilient to ecosystem changes within the Great Lakes. High activity rates in our study were either directed to long-range migration or activity within a smaller home range. Each of these choices appears to have very different consequences for growth responses to ecosystem disturbance. While BD and NB populations showed statistically indistinguishable activity rates, consumption rates in the population with a wider dispersal range (BD) were significantly higher. In this case, directing activity towards exploiting more distant habitats further from the home range resulted in increased food intake, likely due to increased encounters with patches of good quality food (i.e., regions which continue to support *Diporeia*, NALEPA et al. 2006, 2009). In contrast, CH fish dispersed half as far as BD fish and had the highest activity and consumption rates, but had the lowest conversion efficiencies, grew slower and showed greater declines in size-at-age than BD fish. It is possible that the remnant population of *Diporeia* near the spawning grounds of the CH population keeps the whitefish in the region, despite

our bioenergetic evidence (i.e., low conversion efficiencies) that feeding opportunities in the region are suboptimal.

The differences between CH lake whitefish compared to those from DC suggest that there is a point at which a remnant *Diporeia* population may be enough to sustain the local white-fish population given contemporary growth rates. Among all populations, the DC fish were least active, dispersed the least, ate the least and grew slowest, despite having the highest conversion efficiencies of all other populations. A high conversion efficiency combined with a diverse diet rich in amphipods (*Diporeia*) may indicate that slow growth rates in this population are less of a sign of stress compared with the other populations investigated here. Instead, the slower growth observed might indicate a healthy population where exploitation is lower and adequate resources are available. However, growth in both these populations (CH, DC) might continue to decline with *Diporeia* abundance unless they increase their foraging ranges.

The patterns identified in this study ultimately raise the question about what might happen if *Diporeia* populations reach a critically low level throughout the Great Lakes. Continued *Diporeia* declines would likely diminish benefits of migration by making all potential foraging habitats more homogeneous. The sudden crash in the *Diporeia* population in Lake Ontario appears to have caused an equally devastating decline in lake whitefish growth, condition and abundance. Within a two-year period, lake whitefish abundance had decreased by 50% (Hoyle et al. 1999). This rapid die-off was further evidenced by the capture of dead and decomposing fish from bottom gillnet sets (J. Hoyle, personal communication). Die-offs of lake whitefish have occurred in other situations where food resources have suddenly declined (Mills et al. 1998, Mills et al. 2007). Such a scenario does not bode well for continued declines of *Diporeia* on the Great Lakes, particularly given recent reports of increasing lake whitefish catch-per-unit-effort (CPUE) in the face of *Diporeia* declines (DeBruyne et al. 2008, Rennie et al. 2009a). Previous to the collapse of Lake Ontario whitefish, CPUE had roughly doubled from the time of dreissenid establishment (Hoyle et al. 1999).

Recently reported increases in CPUE could reflect some component of dispersal observed in our northern Lake Michigan populations, but not those studied here from Lake Huron. Both gradients of prey density and density of conspecifics can influence dispersal patterns of fishes (Olsson et al. 2006, Haugen et al. 2007). In our Lake Michigan populations, increases in CPUE were coincident with declines in *Diporeia* and lake whitefish growth (Wright & Ebener 2007), making these two potentially separate drivers of dispersal difficult to separate. If increased CPUE is indicative of increased population size, this increased competition for simultaneously declining resources may represent an added pressure for migration on lake whitefish populations. Indeed, increases in lake whitefish abundance, as indicated by increased CPUE, has been proposed to have played a role in depressing *Diporeia* abundance in the Great Lakes (Kratzer et al. 2007). However, Nalepa et al. (2007) showed that declines in *Diporeia* abundance in Lake Huron were not a density-dependent response to lake whitefish. In contrast to the Lake Michigan populations, the estimated biomass and CPUE in both our Lake Huron populations declined rather than increased during the period of *Diporeia* and lake whitefish growth declines (Bence et al. 2003, Kratzer et al. 2007).

Catch rates of lake whitefish in the Great Lakes have been shown to dependent on factors entirely unrelated to population size (Deroba & Bence 2009). For example, CPUE of stationary sampling gear such as gillnets and trap nets are dependent on encounter rates with target

species and can change as a result of changes in fish behaviour. One possible explanation for increased CPUE observed in Great Lakes lake whitefish populations is that increased activity rates caused by increased foraging in dreissenid-disturbed communities has increased whitefish encounter rates with passive capture gear on which CPUE estimates are based, without any actual change (or even masking decreases) in population size. Therefore, the correspondence between lake whitefish CPUE and abundance is less clear in the present situation.

Overall, our study is more consistent with the hypothesis that migration is driven by heterogeneity in spatial patterns of resource availability (Gross et al. 1988, Roff 1991, Olsson et al. 2006). The declines in fish size-at-age in these populations are consistent with the timing of declines in *Diporeia* abundance (Nalepa et al. 2009) and lake whitefish growth (Pothoven et al. 2001, this study) reported in Lake Michigan between the early 1990s and early 2000s. Based on contemporary estimates (2000–2003), regions near the BD and NB populations have undetectable populations of *Diporeia*, but regions near the CH population have *Diporeia* densities of 457 m^{-2} (Nalepa et al. 2007) and regions near the DC population have approximately 1,000 m^{-2} (Kratzer et al. 2007). As such, one might expect the DC fish to have only minor declines in growth and the BD and NB fish to show the greatest declines. This is the opposite of what we observed; the NB and CH populations appear to have suffered as *Diporeia* populations have declined, whereas the BD fish appear to have mitigated the loss of *Diporeia* through migration, providing more beneficial foraging opportunities. Further, *Diporeia* densities observed in the area of the DC fish, while highest among the regions investigated here, are still 4–10 times lower than those observed historically (Nalepa et al. 2007). Forseth et al. (1999) showed that brown trout with high metabolic demands were more likely to migrate to satisfy their energetic requirements than those with lower metabolic demands. Thus, prior metabolic differences among populations might also play a role in the need for fish to migrate when resources are limiting, as might occur during ecosystem disturbance caused by invasive species.

While our study examines patterns in whitefish populations at the edge of their biogeographical range, we believe these patterns have significance in forecasting the ability of other populations' ability to cope with changing ecosystems. Climate is predicted to have a much more profound effect on northern regions (IPCC et al. 2007). The results of our study suggest that as ecosystems respond to environmental change, the migratory predisposition of other, more northern lake whitefish populations may play a significant role in their adaptive capacity to deal with large-scale climate-induced changes.

Acknowledgements

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Appendix 1

Relationship describing MeHg elimination from fish and relationship between fish mercury concentration and gonadal mercury concentration.

Daily elimination of MeHg (E in eq. 2 of text) was modelled as a function of fish size (W) and temperature (T), as described in TRUDEL & RASMUSSEN (1997):

$$E = \phi W^{\beta} e^{\gamma T} \qquad \text{eq. A1.1}$$

where ϕ, β and γ are empirically derived constants (0.0029, -0.20, and 0.066 respectively, corresponding to chronic Hg exposure in TRUDEL & RASMUSSEN (1997).

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:

$$N = \frac{Q \cdot GSI}{365} \qquad \text{eq. A1.2}$$

and:

$$Q = \frac{C_g}{C_f} \qquad \text{eq. A1.3}$$

where GSI is the gonadosomatic index of the fish, or gonad weight expressed as a percentage of the body weight 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 concentrations in gravid female fish (C_g) varied with fish Hg concentration (HAMMERSCHMIDT et al. 1999) according to the following relationship ($r^2 = 0.92$):

$$Log_{10} C_g = 0.884 + 9.03 \times 10^{-4} \cdot C_f \qquad \text{eq. A1.4}$$

where C_g and C_f are in ng·g^{-1} dry weight. Values obtained from equation A1.4 were multiplied by 0.00015 to obtain µg·g^{-1} wet weight (Rennie 2003).

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Appendix 2

Energy densities of lake whitefish prey items as reported from literature sources.

Organism	Energy density (J/g wet weight)	Energy density source
Bythotrephes	2027	8
Chironomidae	3730	1,2,3
Dreissena	1703	6
Diporeia	3625	6
Eggs[A]	5000	1
Ephemeroptera	3791	1,2
Gastropoda	1559	2
Isopoda	2807	4
Sphaeriidae	606	1,3
Fish	4435	5
Trichoptera	3791	1,4
Other	3535	9

[1]Cummins & Wuycheck 1971; [2]Driver et al. 1974; [3]Eggleton & Schramm 2004; [4]Johnson et al. 2006; [5]Lantry & Stewart 1993; [6]Madenjian et al. 2006; [7]Rudstam et al. 1989; [8]Storch 2005; [9]Mean of all values from a larger database of lake whitefish diets (M.D. Rennie, unpublished data). [A]Value from Storch (2005) was reduced to account for spine weight (measured to be 16% of *Bythotrephes* wet body mass, Rennie et al. 2009), because *Bythotrephes* spines are observed to pass unprocessed through the digestive tracts of lake whitefish (M. Rennie, personal observation).

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