Factors affecting the growth and condition of lake whitefish (*Coregonus clupeaformis*)

Michael D. Rennie, W. Gary Sprules, and Timothy B. Johnson

Abstract: Though declines in the growth and condition of Great Lakes lake whitefish (*Coregonus clupeaformis*) have been largely attributed to food web disruptions caused by invasive dreissenid mussels, a comprehensive evaluation of alternative hypotheses is currently lacking. Using various statistical approaches, we evaluated 69 years of data from the inner basin of South Bay, Lake Huron, considering the role of biological variables (food availability as *Diporeia* abundance and lake whitefish relative abundance as catch per unit effort, CPUE) versus environmental variables (climate change as growing degree days >5 °C and productive habitat capacity as percent epilimnetic volume, EV) on the condition and early growth rates of resident lake whitefish. Consistently, biological variables (*Diporeia* abundance, CPUE) best explained changes in lake whitefish growth and condition, respectively, in years when *Diporeia* data were available. In their absence, environmental variables (EV) best explained early growth rates of lake whitefish, whereas CPUE again best explained lake whitefish condition. Our analysis revealed that environmental change contributed significantly but alone was not sufficient to explain declines in lake whitefish growth after dreissenid establishment, whereas biological variables considered here could account for the majority of growth and condition changes observed in this population.

Résumé : Alors que les déclins de la croissance et de la condition des grands corégones (*Coregonus clupeaformis*) des Grands Lacs ont été en grande partie attribués aux disruptions des réseaux alimentaires causées par les mollusques dreissénidés envahissants, les hypothèses de rechange n'ont pas à ce jour été soumises à une évaluation complète. À l'aide de diverses méthodologies statistiques, nous avons évalué des données sur une période de 69 ans provenant du bassin intérieur de South Bay au lac Huron; nous avons examiné le rôle des variables biologiques (la disponibilité de la nourriture mesurée par l'abondance des *Diporeia* et l'abondance relative des grands corégones exprimée en captures par unité d'effort, CPUE) par rapport aux variables de l'environnement (le changement climatique évalué en degrés-jours de croissance >5 °C et l'habitat productif potentiel représenté par le pourcent du volume de l'épilimnion, EV) sur la condition et les taux de croissance juvénile chez les grands corégones résidants. De manière régulière, les variables biologiques, soit l'abondance de *Diporeia* et les CPUE, expliquent mieux respectivement les changements dans la croissance et la condition des grands corégones, les années pour lesquelles les données sur les *Diporeia* sont disponibles. En l'absence de ces données, les variables du milieu (EV) expliquent le mieux les taux de croissance juvénile des grands corégones, alors que les CPUE expliquent toujours le mieux la condition des grands corégones. Notre analyse démontre que le changement de l'environnement contribue significativement aux déclins de la croissance des grands corégones après l'établissement des dreissénidés, mais qu'il ne suffit pas à les expliquer par lui-même; en revanche, les variables biologiques examinées ici peuvent expliquer la majorité des changements de croissance et de condition observés dans cette population.

[Traduit par la Rédaction]

Introduction

Lake whitefish (*Coregonus clupeaformis*) are an economic and ecological cornerstone of the Laurentian Great Lakes aquatic food web. In 2000, the lake whitefish fishery was worth over $18 million US dollars, roughly one-third of the total value of the entire Great Lakes fishery at the time (Kinnunen 2003). Ecologically, lake whitefish are a major cold-water benthivore and play an important role in coupling nearshore and offshore habitats (Rennie et al. 2009). Lake whitefish also appear to be highly sensitive to food web changes in the Great Lakes. In the early 1950s, lake whitefish populations (and many other cold-water species) declined precipitously as a direct result of mortality imposed

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by invasive sea lamprey (Smith and Tibbles 1980) but later increased after basin-wide lamprey control programs initiated jointly by Canada and the United States (Ebener 1997).

More recently, declines in lake whitefish growth and condition in many Great Lakes populations have been observed (Pothoven et al. 2001; Lumb et al. 2007). These declines have been largely attributed to changes in the food web associated with the appearance of invasive dreissenid mussels in the Great Lakes (Nalepa et al. 2006; Rennie et al. 2009). Since the establishment of these mussels in the Great Lakes, populations of the deepwater amphipod *Diporeia* have declined dramatically (Nalepa et al. 1998; Dermott 2001; McNickle et al. 2006). *Diporeia* were historically an important component of lake whitefish diets (Hart 1931; Ihssen et al. 1981; Rennie et al. 2009), but they have largely disappeared from contemporary diets and been replaced by shelled prey (dreissenids, gastropods), which are energetically inferior (Madenjian et al. 2006) and difficult to process (Owens and Dittman 2003). As a result, energy densities of contemporary lake whitefish diets are estimated to have declined by as little as 13%–29% (Rennie et al. 2009) and as much as 43% (McNickle et al. 2006).

Although dreissenid-related effects have become a widely accepted working hypothesis for declines in Great Lakes lake whitefish growth and condition, recent work has suggested the importance of other factors. Increased catch rates of lake whitefish populations in northern Lake Michigan have been proposed as a major contributor to observed lake whitefish growth and condition declines (DeBruyne et al. 2008). However, it is surprising that alternative explanations (such as density dependence) have only recently been quantified for Great Lakes stocks, given the large body of historic literature describing the importance of food availability, population density, and climate in contributing to growth variation in lake whitefish. Among populations, lake whitefish demonstrate a large degree of plasticity with regards to growth and life history strategies (Healey 1975; Beauchamp et al. 2004; Mills et al. 2004). Both exploitation rate (Healey 1980; Mills et al. 2004) and geographic location (potentially reflecting latitudinal gradients; Healey 1975; Beauchamp et al. 2004) appear to be related to observed rates of growth in this species. Further, early growth rates of lake whitefish have been shown to respond positively to increased resource availability (Mills 1985; Mills and Chalanchuk 1987), where the most dramatic effect of both fish harvest and fertilization was an increase in recruitment and survival of age-0 to age-1 fish. Acidification has also been shown to increase individual lake whitefish growth rates, presumably due to decreased fish density (and therefore competition; K.H. Mills, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada, unpublished data). Though all these factors may be important contributors to recent changes in Great Lakes whitefish populations, no studies to date have considered these factors simultaneously to quantitatively evaluate them as alternatives.

The objectives of this study were therefore (*i*) to document long-term changes in lake whitefish growth and condition before and after the establishment of dreissenid mussels and (*ii*) to identify the degree of influence of multiple potential factors (climate change, thermal habitat volume, population density, food availability) on lake whitefish growth and condition. To address these questions, we examined a 69-year series of data from a geographically isolated Great Lakes lake whitefish population in South Bay, Lake Huron.

Materials and methods

We compiled lake whitefish data reported from fall (late August to early September) index gill-netting from the inner basin of South Bay, Lake Huron (81°53′W, 45°38′N, Appendix A), between 1947 and 2005. Evidence presented previously suggests that lake whitefish from the inner basin of South Bay are resident and do not mix with populations found in the outer basin or main basin of Lake Huron (Casselman et al. 1981; Henderson and Fry 1987). These fish have distinctly slower growth trajectories compared with those captured in the outer basin of South Bay or in the main basin of Lake Huron (Casselman et al. 1981; Henderson and Fry 1987) and are genetically unique compared with whitefish from the same geographic region (Casselman et al. 1981). Further, summer thermocline depths are typically deeper than the maximum depth (12 m) of the outer basin (King et al. 1997; Rennie et al. 2009), which creates a thermal barrier against the movement of cold-water fish between the main basin of Lake Huron and inner basin of South Bay for much of the growing season (Bryson and Stearns 1959). As such, environmental and ecological conditions measured from the inner basin were assumed to be those experienced by fish captured there.

Estimation of growth

We defined the early growth of lake whitefish as the mean size of fish at age 3 in the year of capture minus the mean size of fish at age 2 captured in the previous year. This estimate of growth was chosen for a number of reasons. First, because young fish have no investment into reproduction, all surplus energy should be dedicated to somatic growth. As a result, ecosystem or environmental change that affects fish growth should be expressed most clearly among immature age classes of fish. Second, fish ages were determined using scales for most years. Lake whitefish scale ages typically only agree with other, more reliable ageing structures (fin rays, otoliths) early in life (Mills and Beamish 1980; Barnes and Power 1984; Muir et al. 2008) as they do in South Bay (Rennie et al. 2009). Therefore, our increment of growth was selected to reduce uncertainty in age regardless of the ageing structure used. We used alternate data sources for years when size at age could not be reliably estimated due to small sample sizes or lack of data. For years 1936–1955, we obtained size at age for age 2 and age 3 fish from Reckahn (1986), which were back-calculated from scales of whitefish collected from South Bay in 1947–1982. Lengths were adjusted for fall measurements (Reckahn 1986). To evaluate this data source, we compared estimates of size at age for 2- and 3-year-old fish where both empirical and back-calculated (Reckahn 1986) estimates were available. The line estimating empirical size at age from fall-corrected estimates reported by Reckahn (1986) was statistically indistinguishable from the 1:1 line (Fig. 1; *t* test slope is not different from 1, $t_{54} = -1.94$, $p = 0.97$; *t* test intercept is not different from zero, $t_{54} = 1.82$, $p = 0.07$) and therefore assumed to be a reliable source of size at

Fig. 1. Empirical estimates of size at age for 2-year-old (open circles) and 3-year-old (open diamonds) lake whitefish collected in fall surveys (1947–1982) compared with those estimated from back-calculation of scales reported in Reckahn (1986), corrected for fall growth. Broken line is 1:1; solid line is statistical fit between empirical and back-calculated estimates. Statistical fit is not significantly different from 1:1 line.

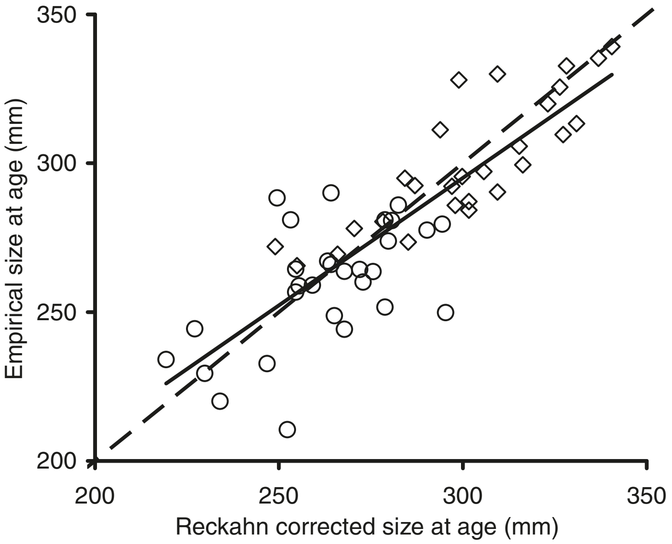
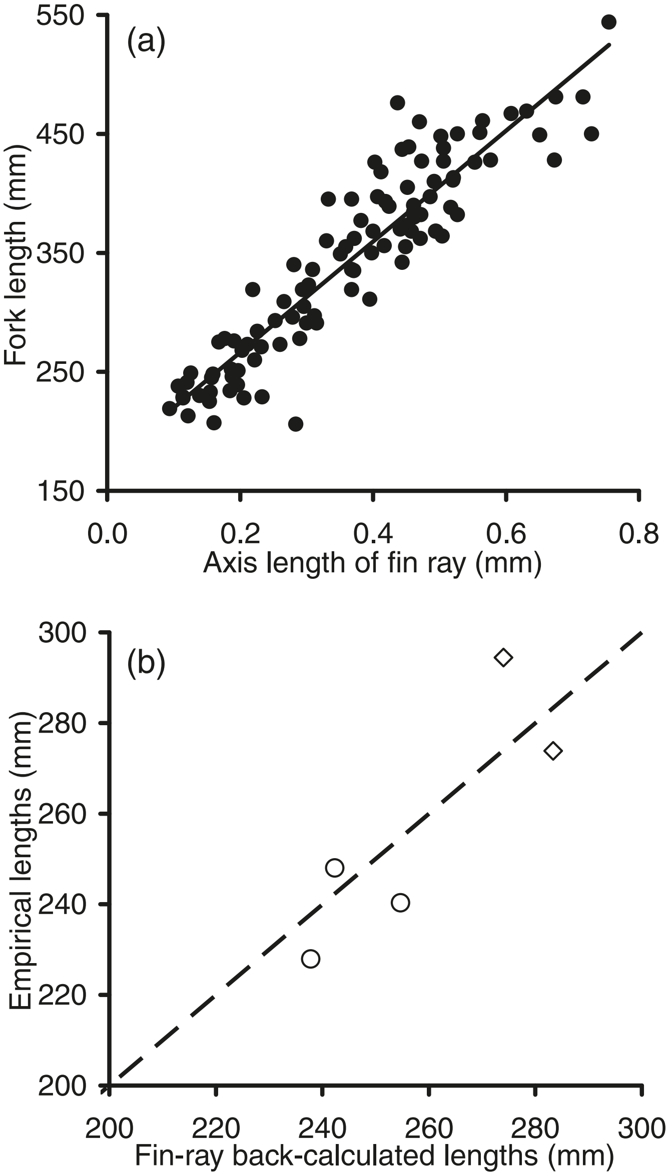


Fig. 2. (*a*) Relationship between fork length (mm) of fish and length (mm) of axis of fin rays measured from the first annulus to the edge of the ray: fork length = 465.5·(fin-ray axis) + 173.4, $R^2 = 0.85$, $F_{[1,101]} = 590.5$, $p < 0.0001$. (*b*) Empirical estimates of size at age for 2-year-old (open circles) and 3-year-old (open diamonds) lake whitefish collected in fall surveys compared with those estimated from back-calculation of fin rays. Broken line is 1:1.



age in the absence of empirical observations. For the time period of 1993–2001, only one survey was conducted (1997). For years 1993–1996 and 1998–2000, size at age for 2- and 3-year-old fish was back-calculated using fin rays from fish collected in 2001, based on a relationship between lake whitefish length and the length of the axis in fin rays from the first annulus to the edge of the fin ray (Fig. 2*a*; Mills and Chalanchuk 2004). Again, we compared back-calculated with empirical estimates. Though based on only five observations, the data fall reasonably around the 1:1 line (Fig. 2*b*), suggesting this was also a reasonable method of estimating size at age.

Estimation of condition

Condition was estimated as relative weight (W_r) using the regression length percentile standard weight for this species (Rennie and Verdon 2008). This estimation method of W_r in lake whitefish has been shown to correlate with other measures of physiological condition while avoiding systematic length-related bias (Rennie and Verdon 2008). Condition estimates were applied only to fish 100–700 mm in length and averaged within each year.

Estimation of lake whitefish catch-per-unit-effort (CPUE)

CPUE was estimated as the geometric mean across all nets set within lake whitefish habitat in a particular fall index. CPUE of each net was estimated as the sum of lake whitefish catch in standard-sized experimental gill nets (52, 64, 76, 89, 102, 114 mm stretched mesh) in overnight sets. Catch was expressed as biomass (kilograms) per kilometre of net per 24-h period. The gill-net material used changed from cotton to multifilament net during 1954–1956 and from multifilament to monofilament in 1986. Catch in all years was converted appropriately to reflect catch in monofilament gear. We standardized lake whitefish CPUE from cotton gear to multifilament gear by multiplying estimates by 2.6 (correction factor used was an average estimated from those reported in Lawler (1950), Atton (1955), and McCombie and Fry (1960)) and from multifilament gear to monofilament gear by a factor of 1.8 (Collins 1979). The sum of whitefish caught in each net was $\log_{10}(x + 1)$-transformed to normalize data and reduce the influence of zero catches on estimates. Further, nets set in water less than 14 m deep were eliminated from the estimation of CPUE as these did not accurately evaluate lake whitefish habitat during the fall based on the thermal structure of the bay at this time (King et al. 1997).

Estimation of environmental correlates

Growing degree days (GDD) were estimated from the annual total degree days greater than 5 °C. Data were compiled from historical weather station data available online (Environment Canada 2008). Thermal habitat volume (EV) was estimated as the volume of the epilimnion using a hypsographic curve (Appendix A), thermocline depth, and lake water levels (Hydrographic Service of Canada 2008). Thermocline depths were those reported from the Ontario Ministry of Natural Resources (OMNR) during fall index netting (1997–2005). Earlier records (1955–1992) were previously summarized and reported in King et al. (1997).

Estimation of *Diporeia* abundance

Diporeia abundance was estimated as annual mean densities from OMNR fall benthic surveys, as reported elsewhere (McNickle et al. 2006; Rennie and Verdon 2008). These data were updated with additional information from benthic surveys conducted in 2005 and 1947. Data from 1947 were reported in archived OMNR records from May samples only. May densities were multiplied by 2.3 as an estimate of fall *Diporeia* abundance. This estimate was based on previously unreported seasonal abundance data collected during an intensive benthic survey of South Bay in 1980 in which September *Diporeia* densities were found to be 2.3 times more abundant than May samples at locations greater than 30 m deep. *Diporeia* abundance was $\log_{10}$-transformed to normalize data.

Evaluation of variables, data set generation

To provide a basic indication of which of our variables were correlated and to help identify multicolinearity among predictor variables, we estimated Pearson's correlation coefficients among all pairwise combinations of observations. Comparison of Pearson and Spearman correlation coefficients was conducted to identify potential nonlinearity in relationships among variables. To illustrate the degree to which all variables (predictor and response) might have changed over the course of dreissenid establishment in South Bay, we conducted independent comparisons of means before (years prior to 1997) and after (1997–2005) dreissenid establishment (McNickle et al. 2006) using two-sample *t* tests with a Welch correction for unequal variances (Zar 1999).

Because further statistical evaluations relied on complete observations for all variables considered (i.e., sampling years with values for all variables), we employed two data sets in each step of the remaining analyses. The first data set (hereafter referred to as D+) included *Diporeia* abundance and possessed the greatest number of variables (two response and four predictor variables), but fewer complete observations (18) with which to generate and evaluate relationships. The second data set (hereafter referred to as D–) excluded *Diporeia* abundance but had over twice the number of complete observations (42) than the previous data set. Correlations among variables in each data set were compared with each other and with pairwise combinations of variables (above) to determine the influence of observation number on the direction and strength of relationships in each data set.

Variable selection

Independent variables important in explaining lake whitefish early growth rates and condition were identified in each data set using three statistical approaches. First, the importance of biological versus environmental variables on each of our response variables was determined using partial linear regression (Legendre and Legendre 1998). This method allowed for the estimation of the partial independent contributions of matrices describing environmental (EV and GDD) and biological (CPUE and $\log_{10}$ *Diporeia*) factors towards the total explained variation in lake whitefish growth and condition among all independent variables (Legendre and Legendre 1998).

Second, path analysis (Legendre and Legendre 1998) was used to construct explanatory models and evaluate the direct and indirect components of predictor (independent) variables on our criterion (response) variables. Though related to multiple regression, this method differs from typical multiple regression in that it requires (user-defined) a priori hypotheses for the causal order of influence among variables (shown by directionality of arrows when presented graphically). Path coefficients describing relationships among variables are estimated from standardized multiple linear regression coefficients and correlation coefficients among predictor variables (Sokal and Rohlf 1995) and were determined in this study using the "sem" library in R (R Development Core Team 2006). Direct effects are defined as the independent influence of predictor variable X on Y, whereas indirect effects are defined as the influence of predictor X on Y via its association with any other predictor variable X_i. Direct and indirect effects of each predictor variable on criterion variables were estimated using path coefficients as described in Quinn and Keough (2002).

Third, hierarchical partitioning was employed to identify predictor variables with a significant degree of independent explanatory power in each of our response variables (Mac Nally 2000, 2002). This statistical approach considers all possible models in a multiple regression setting, where the independent influence of predictor variable X on Y (X_I) is estimated as the average increase in explanatory power in models possessing X compared with all submodels in which X does not appear (Mac Nally 2000). Hierarchical partitioning has an advantage over the previous methods in that the averaging of the added explanatory power of each variable over multiple model combinations is thought to reduce the influence of multiconlinearity among variables (Mac Nally 2000). Further, the statistical significance of X_I can be estimated by comparing the magnitude of the observed X_I against many iterations of the same data randomly shuffled. By expressing each X_I value as a Z score (considering all randomized estimates of X_I), those greater than or equal to 1.65 can be considered significant (based on upper 95% confidence limit; see Mac Nally 2002). Hierarchical partitioning was carried out using the "hier.part" library (Mac Nally and Walsh 2004) in R.

Evaluating association between variables with dreissenid effects

To determine the strength of association between dreissenids and our predictor variables of lake whitefish growth and condition, predictor variables (defined as those that

Table 1. Correlation matrix among all pairwise observations for variables examined in the study.

Variable	Growth	W_r	GDD	EV	CPUE	*Diporeia*
Growth	—	0.080	–0.322	0.330	0.167	0.605
W_r	0.157	—	–0.056	0.028	–0.326	0.126
GDD	–0.283	0.108	—	–0.395	0.139	–0.604
EV	0.453	0.064	–0.478	—	0.160	0.470
CPUE	0.059	–0.314	0.215	0.117	—	–0.344
Diporeia	0.541	0.105	–0.470	0.519	–0.517	—

Note: Lower triangular matrix contains Pearson's correlation coefficients, upper triangular matrix contains Spearman correlation coefficients. Growth, lake whitefish early growth rate (mm); CPUE, catch-per-unit-effort (geometric mean, $kg \cdot m^{-2} \cdot day^{-1}$); GDD, annual growing degree days (>5 °C); EV, percentage of volume of the inner basin in the epilimnion; W_r, relative weight (condition) of lake whitefish (%); *Diporeia*, $\log_{10}$ *Diporeia* density (m^{-2}).

were consistently identified as explaining a large independent proportion of variance in our response variables using the above methods) were used to standardize our measures of lake whitefish growth and condition using linear regression, and the residuals of these regressions were saved. Because our regressions assume that annual observations from the same population are statistically independent, residuals were evaluated for serial correlation using a Durbin–Watson test in the "car" package of R. Residual lake whitefish growth and condition were examined for differences before and after dreissenid establishment using *t* tests with a Welch correction.

Results

Examination of Pearson's correlation coefficients suggested that some of our variables might be subject to multicollinearity. Correlation coefficients among $\log_{10}$ *Diporeia* abundance (*Diporeia* hereafter) with CPUE, EV, and GDD and between EV and GDD were all greater than 0.4 (Table 1). Agreement between Pearson and Spearman correlation coefficients among all pairwise combinations suggested that relationships among variables were broadly linear (Table 1).

Associations among some variables were sensitive to the number of observations included in the analysis. Relationships among variables in the D– data set (Table 2, upper triangular matrix) were largely consistent with those observed among all pairwise combinations of variables (Table 1). Although other correlations in the D+ data set were consistent with pairwise correlations, those between CPUE and EV changed sign and became slightly stronger, and the relationship between CPUE and GDD was much stronger (Table 2, lower triangular matrix) compared with correlations among all pairwise observations (Table 1). This suggested that the strength of these particular correlations in the D+ data set might be somewhat artifactual and simply result from the particular combination of observations in that data set.

All variables showed temporal fluctuation and indicated that values observed after dreissenid establishment were either comparable with or beyond extreme values observed historically (Fig. 3). All variables differed significantly before and after invasion when considered independently (Table 3), indicating that any similar comparisons of mean growth or condition of lake whitefish over the period of dreissenid invasion could be easily confounded by covariation with other potential explanatory variables.

Table 2. Pearson correlation matrix among variables examined in the study considering only complete years of data (years with data missing from any of the variables deleted).

Variable	Growth	W_r	GDD	EV	CPUE
Growth	—	0.268	–0.369	0.544	–0.025
W_r	0.370	—	–0.082	0.027	–0.379
GDD	–0.387	–0.445	—	–0.455	0.150
EV	0.504	0.160	–0.595	—	0.403
CPUE	–0.131	–0.515	0.670	–0.229	—
Diporeia	0.543	0.150	–0.472	0.519	0.150

Note: Lower triangular matrix is from data set including *Diporeia* abundance (D+ data set, 18 years of observations), upper triangular matrix is the D– data set (excluding *Diporeia* abundance, 42 years of observations). Variables are as in Table 1.

Biological variables were identified as important predictors of lake whitefish growth and condition. Partial linear regressions on the D+ data set suggested that biological variables (CPUE, *Diporeia*) described a greater independent proportion of the total explained variance in lake whitefish growth than did environmental variables (EV, GDD). Biological variables described just over half of the total explained variation in the full model (Table 4). Similarly, biological variables explained the largest independent component of variation in whitefish condition. However, this component was smaller than the shared variation accounted for by both biological and environmental variables. Full-model regressions on the D– data set explained approximately one-third less total variation in growth and condition compared with those based on the D+ data (Table 4). Using the D– data, environmental (rather than biological) variation contributed the largest independent amount to the total variance explaining growth, whereas biological variables (CPUE) explained the greatest amount of variation in condition.

Path analysis revealed biological and environmental predictor variables with a significant direct effect on response variables. A number of path coefficients in the original structural equation models were nonsignificant ($p > 0.05$) using the D+ data set and were therefore eliminated (Figs. 4*a*, 4*c*). As a result, only *Diporeia* was retained in the model as a variable with direct influence on lake whitefish growth. The effect of EV on growth was indirect through *Diporeia*. GDD affected growth indirectly through both EV and *Diporeia*. CPUE was the only variable retained with direct influence on condition, whereas GDD affected lake whitefish condition indirectly through CPUE (Fig. 4*c*; Table 5). Using

Fig. 3. Independent comparisons of all variables considered in the study before (1947–1996, open symbols) and after (1997–2005, solid symbols) the invasion of dreissenids: (*a*) lake whitefish growth increment from age 2 to age 3 (mm); (*b*) lake whitefish condition (W_r, percent); (*c*) growing degree days (GDD, >5 °C); (*d*) epilimnetic volume (percentage of total volume of inner basin of South Bay); (*e*) *Diporeia* density (number (no.)·m^{-2}); and (*f*) geometric mean catch-per-unit-effort (CPUE, $\log_{10}$(kg·km^{-1}·day^{-1} + 1)). In (*b*), (*e*), and (*f*), error bars are ±1 standard error.

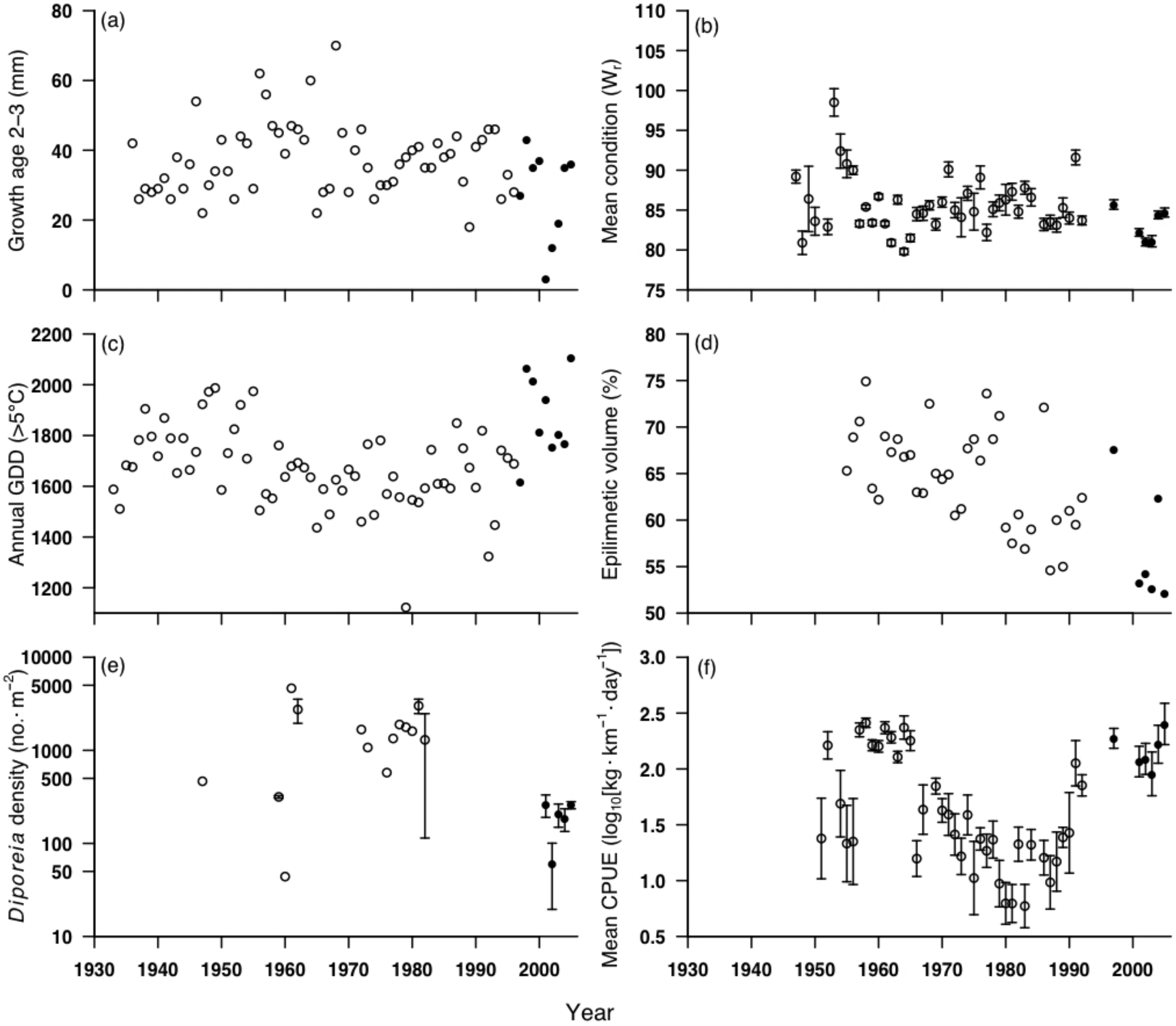


Table 3. Comparisons of means (± standard errors) for variables under investigation between before (<1997) and after (1997–2005) dreissenid establishment in South Bay, Lake Huron.

Variable	<1997	1997–2005	*t*	df	*p*
Growth (mm)	37.3±1.3 (61)	27.4±4.5 (9)	2.13	9.4	0.0302
Condition (W_r, %)	85.7±0.5 (44)	83.2±0.8 (6)	2.56	9.8	0.0144
Log_{10}(*Diporeia* abundance)	3.03±0.14 (14)	2.24±0.12 (5)	4.37	14.0	0.0003
CPUE ($\log_{10}$(kg·km^{-1}·day^{-1}+1))	1.6±0.1(39)	2.2±0.1 (6)	–5.66	23.6	0.0001
Epilimnetic volume (%)	64.7±0.9 (37)	57.0±2.6 (6)	2.78	6.1	0.0157
GDD (>5 °C)	1667.7±19.5 (64)	1876.3±54.7 (9)	–3.59	10.1	0.0024

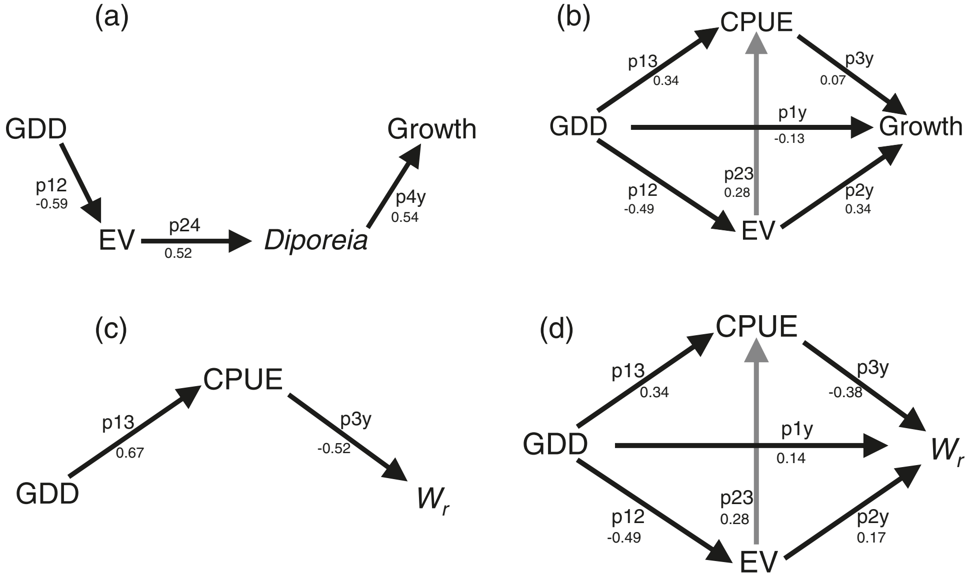
Note: Student's *t* value (*t*), degrees of freedom (df), and the *p* value associated with a test of the hypothesis of no difference are shown. Values in parentheses are numbers of observations in each group.

Table 4. Proportions of variation of growth or condition explained by either biological (CPUE, $\log_{10}$ *Diporeia*) or environmental (EV, GDD) variables obtained through partial linear regression.

	D+ (*Diporeia* included)		D– (*Diporeia* excluded)	
Fraction of variation	Growth	Condition	Growth	Condition
Biological	**0.213**	0.124	0.005	**0.129**
Environmental	0.145	0.039	**0.170**	0.025
Shared	0.065	**0.149**	0.001	–0.022
Total explained (R^2)	0.422	0.312	0.175	0.132
Unexplained	0.578	0.688	0.825	0.868
n	18	18	42	42

Note: Values in bold type indicate largest contribution to total explained variance.

Fig. 4. Path diagrams showing hypothesized directional relationships among variables and path coefficients (p*ij*) for analyses employed in the current study. Only statistically significant ($p \leq 0.05$) path coefficients are shown. (*a* and *c*) Growth and condition, respectively, based on D+ data set (including *Diporeia* abundance, 18 years of data); (*b* and *d*) growth and condition, respectively, based on D– data set (*Diporeia* abundance excluded, 42 years of data). CPUE, catch-per-unit-effort; GDD, growing degree days; EV, epilimnetic volume; W_r, relative weight (condition).



the D– data set, all path coefficients originally included in the model for growth and condition were significant (Figs. 4*b*, 4*d*). EV had the largest total and direct contributions to explained variance in growth, whereas GDD effects on growth were largely indirect (Table 5). CPUE had the largest total and direct contributions to variance in condition compared with either EV or GDD (Fig. 4*d*; Table 5).

Variables identified as contributing a large independent proportion of explained variance in our response variables using hierarchical partitioning were largely consistent with those variables identified as having large direct effects using path analysis. Hierarchical partitioning on the D+ data set indicated that *Diporeia* contributed the greatest total variation to explaining growth among independent models (Fig. 5*a*), as well as the largest proportion of independent variation in growth compared with other terms included in the full model (47%). *Diporeia* was also selected as the only variable to provide any significant independent contribution to explaining variation in lake whitefish growth (1000 iterations, Z = 2.0, Z_{crit} = 1.65). CPUE explained the largest total variation in condition (Fig. 5*c*) and contributed the largest proportion of independent variance relative to other variables in the full model (57%). No variables were selected to provide a significant independent contribution to condition, though CPUE was close to significant (1000 iterations, Z = 1.60; 10 000 iterations, Z = 1.61, Z_{crit} = 1.65). EV explained the largest total variance in growth using the D– data set (Fig. 5*b*), had the largest independent contribution towards growth (70%), and was the only variable to contribute a significant independent component towards lake whitefish growth (1000 iterations, Z = 2.75, Z_{crit} = 1.65). CPUE again explained the largest total variation in condition (Fig. 5*d*), had the largest independent contribution towards condition (89%), and was the only variable to contribute a significant independent contribution to explaining variation in condition (1000 iterations, Z = 2.95, Z_{crit} = 1.65).

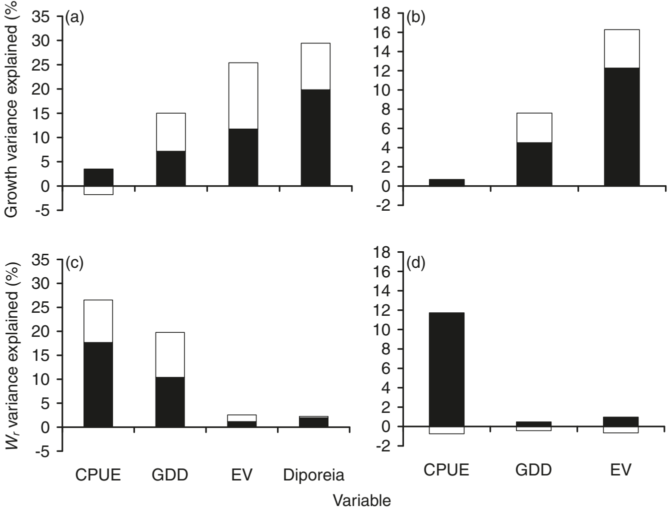
Lake whitefish growth and condition residuals from relationships with predictor variables were not related or only marginally related to dreissenid establishment. Using all available data, growth was fit as a function of *Diporeia*, and condition was fit as a function of CPUE. Smaller mean residual values from these fits after dreissenid establishment were not significant (growth: one-tailed *t* test, $t_{4.9}$ = 1.22, p = 0.14; condition: one-tailed *t* test, $t_{7.7}$ = 1.2, p = 0.14).

Table 5. Estimates of direct and indirect effects from path analysis.

Data set	Criterion variable	Path coefficients	Predictor variable	Direct effects	Indirect effects	Total
D+	Growth	p12, p24, p4y	GDD via EV, *Diporeia*		–0.168	–0.168
		p24, p4y	EV via *Diporeia*		0.282	0.282
		p4y	*Diporeia*	0.543		0.543
	Condition	p13, p3y	GDD via CPUE		–0.345	–0.345
		p3y	CPUE	–0.515		–0.515
D–	Growth	p1y	GDD	–0.126	–0.188	–0.314
		p12, p2y	via EV		–0.163	
		p13, p3y	via CPUE		–0.025	
		p3y	CPUE	0.066	0.039	0.106
		p23, p3y	via EV		0.039	
		p2y	EV	0.334	0.008	0.342
		p23, p2y	via CPUE		0.008	
	Condition	p1y	GDD	0.135	–0.054	0.081
		p12, p2y	via EV		–0.082	
		p13, p3y	via CPUE		0.027	
		p3y	CPUE	–0.378	0.020	–0.359
		p23, p3y	via EV		0.020	
		p2y	EV	0.167	–0.044	0.123
		p23, p2y	via CPUE		–0.044	

Note: D+, *Diporeia* included; D–, *Diporeia* excluded. Path coefficients (p*ij*) correspond to directional relationships among variables illustrated in Fig. 4. Direct and indirect effects estimated as described in Quinn and Keough (2002).

Fig. 5. Results of hierarchical partitioning on data sets included in the study. Bar plots show total variance explained by each variable in either lake whitefish growth or condition (W_r), decomposed into independent (solid bars) and joint (open bars) effects: (*a* and *c*) growth and condition, respectively, based on D+ data set (including *Diporeia* abundance, 18 years of data); (*b* and *d*) growth and condition, respectively, based on D– data set (*Diporeia* abundance excluded, 42 years of data). CPUE, catch-per-unit-effort; GDD, growing degree days; EV, epilimnetic volume.



Similarly, growth residuals from the relationship with EV were only marginally lower after dreissenid establishment (one-tailed *t* test, $t_{6.3}$ = 1.94, p = 0.049). Residuals from models used to generate growth and condition residuals did not display significant autocorrelation (Durbin–Watson test, $p > 0.05$) with the exception of growth residuals from the D+ data set (lag = 1, D–W = 0.86, p = 0.002).

Discussion

All three statistical approaches used in our study identified food (*Diporeia* abundance) and habitat availability (EV) as significant predictors of lake whitefish growth, and CPUE as a significant predictor of lake whitefish body condition. When residuals of these relationships were tested for differences before and after dreissenid establishment, all showed either no or only weak (EV) significance. This general lack of difference among residuals before and after dreissenid establishment suggests one of two possible scenarios: (*i*) the predictor variable used to generate residuals has changed largely as a function of dreissenid establishment, leaving little additional variance to be explained, or (*ii*) the response variable is controlled primarily by the predictor variable and differences in both the response and predictor variables observed before and after dreissenid establishment are merely coincidental. We believe that it is likely that each of these scenarios is at play in our data set for different variables. For instance, the timing of *Diporeia* declines with the establishment of dreissenids is well documented both within South Bay (McNickle et al. 2006) and in the main basins of Lakes Michigan, Huron, and Ontario (Nalepa et al. 2009). Given this strong and consistent pattern in *Diporeia* declines with dreissenid establishment throughout the Great Lakes, we interpret the lack of any significant difference in the residuals of growth adjusted for *Diporeia* abundance as strong evidence of the importance of *Diporeia* in supporting profundal fish species such as lake whitefish in the Great Lakes and of the negative relationship between dreissenid and *Diporeia* abundance.

On the other hand, it is unlikely that the establishment of dreissenids should negatively affect epilimnetic volume. Although dreissenids are ecosystem engineers and can act to increase water clarity (Hecky et al. 2004), this should lead to increased light penetration and thermocline depth

(Snucins and Gunn 2000). In contrast, we observed shallower thermocline depths after the establishment of dreissenids in South Bay (Rennie et al. 2009). Therefore, significant effects of environmental variables (EV) on lake whitefish growth are likely not related to dreissenid establishment, despite what we interpret as coincidental declines in EV in 1997–2005. The barely significant decline in lake whitefish growth residuals corrected for the influence of EV after dreissenid establishment does leave room for additional variation to be attributed to the negative influence of dreissenids on benthic food web energetics, but it also highlights the importance of environmental factors in shaping lake whitefish growth and condition.

Similarly, we believe it unlikely that dreissenids have directly contributed to increases in whitefish CPUE. If CPUE increases in South Bay lake whitefish are interpreted to directly reflect whitefish relative abundance (as has been the case elsewhere on the Great Lakes; DeBruyne et al. 2008), declines in whitefish condition after dreissenid establishment can be interpreted, in large part, as a response to density dependence as opposed to a direct response to dreissenids. The energetics of the prey field available to lake whitefish has declined since the establishment of dreissenids in South Bay (McNickle et al. 2006; Rennie et al. 2009), as has profundal invertebrate abundance (McNickle et al. 2006). An increase in CPUE seems an unlikely outcome of declines in both prey quality and availability. As such, we believe that the observed increase in CPUE is likely under the influence of other factors unaccounted for in the current study.

Though a significant serial correlation was detected among the residuals of lake whitefish growth with *Diporeia* density, we do not believe that this affects our conclusions regarding the weak effect of dreissenids on the growth residuals from this relationship. The presence of serial correlation suggests that our effective degrees of freedom for the effect of dreissenid establishment on growth residuals are inflated due to nonindependence between temporally related observations. In the current study, to reduce the degrees of freedom in this test would only act to make differences among pre- and post-invasion time periods even less significant. Further, *Diporeia* densities considered in this study are only continuous within each of five blocks of data consisting of one to seven consecutive years within each block, but blocks are separated by two to 18 years. Therefore, serial correlation detected in noncontinuous data such as these may be artifactual, resulting instead from spurious associations between discontinuous years.

Our study draws attention to the importance of environmental change in the Great Lakes during the past half-century and its effect on lake whitefish growth, both directly and indirectly. Though *Diporeia* density was the only variable to explain a significant independent proportion of variation in lake whitefish growth in the D+ data set, path analysis and correlation matrices revealed that *Diporeia* density was correlated with all other variables in the analysis, particularly so with environmental variables. Further, EV was the only variable to explain a significant independent component of variation in lake whitefish growth in the expanded data set (without *Diporeia*). This raises the possibility that changes in *Diporeia* density may be, in part, a response to a warming regional climate and that the positive relationship between EV and lake whitefish growth (in the absence of information on *Diporeia* abundance) reflects a strong positive influence of EV on *Diporeia* densities. Although declines of *Diporeia* have been observed throughout the Great Lakes, direct negative effects between dreissenids and *Diporeia* have thus far failed to emerge (Nalepa et al. 2006).

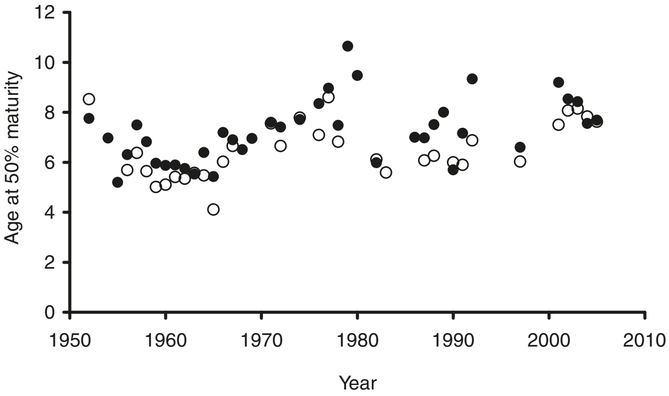
Decreasing epilimnetic volume may be related to declines in both lake whitefish growth and *Diporeia* density as a result of decreased epilimnetic primary productivity resulting from warmer regional climate. Epilimnetic photosynthesis has historically supported much of the production in the Great Lakes (Flint 1986). Productivity not used in the pelagic zone passes through the thermocline into the hypolimnion and settles into the sediments, directly linking profundal productivity with epilimnetic productivity. As the proportional epilimnetic volume of a water body declines, so too will its productive capacity because the thermal volume to support productivity is reduced. The most likely explanation for the observed reduction in epilimnetic volume over time in our study is a coincidental increase in GDD, which reflects increases in mean spring and summer temperatures in the Great Lakes basin. Other investigators have shown that within South Bay specifically (King et al. 1997) and elsewhere (King et al. 1999; Snucins and Gunn 2000; Keller 2007), thermocline depths are more shallow (and therefore epilimnetic volume declines) with increasing surface and air temperatures in the spring and summer. This appears to result from an earlier onset of stratification with a sharper density gradient at the thermocline in warmer years compared with more gradual and deeper thermoclines in cooler years (King et al. 1999).

As a cold-water species occupying the hypo- and metalimnion, declines in epilimnetic volume will provide lake whitefish with greater access to nearshore resources previously encompassed by epilimnetic waters. However, this is likely to have further negative impacts on whitefish growth and condition, as evidence shows that benthic nearshore resources provide less energy for lake whitefish compared with offshore resources (Rennie et al. 2009). Dreissenids may also contribute to declines in profundal productivity by sequestering pelagic nutrients into the nearshore through a process known as the nearshore phosphorous shunt (Hecky et al. 2004). This process has been proposed to play a significant role in lake whitefish growth and condition reductions in South Bay (Rennie et al. 2009). Spring phosphorous levels in South Bay have fallen from 7.0 $\mu g \cdot L^{-1}$ in 1998 to 3.5 $\mu g \cdot L^{-1}$ in 2005. However, this difference is small and falls within natural variation observed in the main basin of Lake Huron between 1983 and 2005 (Fernandez et al. 2009), calling into question whether the differences observed above are representative of a true decline that might be linked to the presence of dreissenids versus natural annual variation in spring phosphorous.

Our study represents the most conclusive attempt to date to evaluate the effects of multiple simultaneous factors on lake whitefish growth and condition declines in the Great Lakes. Previous studies have made comparisons of lake whitefish growth and condition among blocks of dates representing pre- and post-dreissenid establishment (Pothoven et al. 2001; Lumb et al. 2007), but failed to rigorously consider other contributing factors such as climate or density dependence. Wright and Ebener (2007) proposed that density dependence and reductions in food availability were largely responsible for declines in lipid concentrations (related to W_r; Rennie and Verdon 2008) in Lake Michigan lake whitefish. However, their proposal is based largely on the findings of previous studies; a multiple regression considering the effects of abundance of *Diporeia* and lake whitefish on lipid content in their study was nonsignificant, and patterns of growth with lake whitefish abundance were inconclusive (one positive, one negative significant relationship out of 15 age classes investigated over five populations). Lake whitefish lipid content is positively related to body size (Wright and Ebener 2007; Rennie and Verdon 2008). Therefore, a more parsimonious explanation for the observed decline in mean lipid levels of northern Lake Michigan whitefish is a decrease in mean fish size during the same time period (DeBruyne et al. 2008). In another study, Kratzer et al. (2007*a*) also relied heavily on the findings of previous studies to evaluate the effect of food web changes on lake whitefish growth rates. These authors found little evidence of density-dependent growth and only qualitative evidence of climate influences on growth, suggesting that early ice-on and warm springs may be related to better recruitment. Recently, DeBruyne et al. (2008) demonstrated that increased lake whitefish CPUE was associated with growth declines in Lake Michigan lake whitefish populations but failed to consider the potential influence of environmental variables. In comparison with these previous studies, we evaluate each of these parameters simultaneously in a single data set. Our study clearly demonstrates the relative importance of both biological factors (food availability, density dependence) and climate on lake whitefish growth and condition. Further, we illustrate the potentially spurious nature of conclusions that can be drawn when considering “before–after” type approaches to evaluating changes in fish growth and condition without carefully considering alternative hypotheses or potentially confounding variables.

CPUE in our study had a significant effect on condition, but not growth, of lake whitefish in South Bay. Other studies have also failed to find strong evidence for density-dependent growth in Great Lakes lake whitefish (Kratzer et al. 2007*a*; Wright and Ebener 2007, but see DeBruyne et al. 2008). This is perhaps surprising, as density-dependent changes in growth are commonly observed in exploited fish stocks (Healey 1980; Mills et al. 1995). We measured the early growth rates of lake whitefish where surplus energy is dedicated entirely to somatic growth (gonadal investment does not typically occur in this population until after age 3; Fig. 6). One might therefore expect density dependence (via resource limitation) to be more strongly expressed in young fish (Mills et al. 1995). We propose two possible mechanisms for the decoupling of individual growth rates of lake whitefish from density in our study. First, smaller, younger lake whitefish demonstrate more diverse diets indicative of the utilization of a broad range of habitats (i.e., both pelagic and benthic) compared with older, larger fish (Pothoven and Nalepa 2006). From an energetic standpoint, smaller fish can feed on zooplankton with greater efficiency than larger fish if benthic resources become scarce because of increasing costs of foraging activity and metabolism with increasing predator (i.e., whitefish) body size, relative to their prey (Pazzia et al. 2002; Sherwood et al. 2002). This is supported by isotopic evidence from this population; δ^{13}C signatures of small (<250 mm) fish collected in 2005 were highly variable, whereas variation in δ^{13}C for larger fish was more predictable (Rennie et al. 2009; mean size at age for age-2 and age-3 fish in 2005 were 208 mm and 258 mm, respectively). From a more mechanistic perspective, our measure of growth is an average increment in length achieved by a particular cohort exposed to a particular density of conspecifics. If investment in length is less plastic than investment in weight, effects on growth based on length may be less sensitive to subtle year-to-year variation in relative density (CPUE). Further, individual growth rates are likely more constrained by genotypic factors (Rogers and Bernatchez 2007) and life history constraints (Roff 1984; Jensen 1985) than is condition. Variation in condition over time is an easily measured trait that may respond to environmental variation more than growth, which is under a variety of selective forces. Population density has also been proposed as a mechanism to explain changes in Great Lakes lake whitefish fecundity over time (Kratzer et al. 2007*b*).

Fig. 6. Lake whitefish female (solid circles) and male (open circles) age at 50% maturity, 1950–2005. Values are estimated from inflection point of logistic regression fitting maturity against size-at-age data for each year. Average age at 50% maturity: females, 7.2 years; males, 6.5 years.



In conclusion, our results demonstrate the insight that can be gained by considering the influence of multiple stressors on changes in fish growth and condition, rather than considering the influence of only one factor in isolation of others (i.e., dreissenid establishment). These insights were gained only through the evaluation of an unusually rich collection of long-term data, highlighting the importance of such data-rich time series in interpreting ecosystem change. With particular reference to North American aquatic ecosystems, our study identifies a need to examine additional populations for which detailed long-term data exist. A comparison of such data-rich populations that differ in their invasion history may provide a broader understanding of the effect of dreissenids on lake whitefish growth and condition, so that invader effects can be better uncoupled from other potentially confounding variables.

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References

Atton, F.M. 1955. The relative effectiveness of nylon and cotton gill nets. Can. Fish. Cult. **17**: 18–26.

Barnes, M.A., and Power, G. 1984. A comparison of otolith and scale ages for western Labrador lake whitefish, *Coregonus clupeaformis*. Environ. Biol. Fishes, **10**(4): 297–299. doi:10.1007/BF00001482.

Beauchamp, K.C., Collins, N.C., and Henderson, B.A. 2004. Covariation of growth and maturation of lake whitefish (*Coregonus clupeaformis*). J. Gt. Lakes Res. **30**: 451–460.

Bryson, R.A., and Stearns, C.R. 1959. A mechanism for the mixing of the waters of Lake Huron and South Bay, Manitoulin Island. Limnol. Oceanogr. **4**: 246–251.

Casselman, J.M., Collins, J.J., Crossman, E.J., Ihssen, P.E., and Spangler, G.R. 1981. Lake whitefish (*Coregonus clupeaformis*) stocks of the Ontario waters of Lake Huron. Can. J. Fish. Aquat. Sci. **38**(12): 1772–1789. doi:10.1139/f81-225.

Collins, J.J. 1979. Relative efficiency of multifilament and monofilament nylon gill net towards lake whitefish (*Coregonus clupeaformis*) in Lake Huron. J. Fish. Res. Board Can. **36**: 1180–1185.

DeBruyne, R.L., Galarowicz, T.L., Claramunt, R.M., and Clapp, D.F. 2008. Lake whitefish relative abundance, length-at-age, and condition in Lake Michigan indicated by fishery-independent surveys. J. Gt. Lakes Res. **34**(2): 235–244. doi:10.3394/0380-1330(2008)34[235:LWRALA]2.0.CO;2.

Dermott, R. 2001. Sudden disappearance of the amphipod *Diporeia* from eastern Lake Ontario, 1993–1995. J. Gt. Lakes Res. **27**: 423–433.

Ebener, M.P. 1997. Recovery of lake whitefish populations in the Great Lakes — a story of successful management and just plain luck. Fisheries, **22**: 18–20.

Environment Canada. 2008. National Climate Data and Information Archive. Available at http://www.climate.weatheroffice.ec.gc.ca/Welcome_e.html [accessed 25 May 2008].

Fernandez, R.J., Rennie, M.D., and Sprules, W.G. 2009. Changes in nearshore zooplankton communities associated with species invasions and potential effects on larval lake whitefish (*Coregonus clupeaformis*). Int. Rev. Hydrobiol. **94**(2): 226–243. doi:10.1002/iroh.200811126.

Flint, R.W. 1986. Hypothesized carbon flow through the deepwater Lake Ontario food web. J. Gt. Lakes Res. **12**: 344–354.

Hart, J.L. 1931. The food of the whitefish (*Coregonus clupeaformis*) in Ontario waters, with a note on the parasites. Contrib. Can. Biol. Fish. **21**: 445–454.

Healey, M.C. 1975. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. J. Fish. Res. Board Can. **32**: 427–437.

Healey, M.C. 1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. Can. J. Fish. Aquat. Sci. **37**(2): 255–267. doi:10.1139/f80-033.

Hecky, R.E., Smith, R.E.H., Barton, D.R., Guildford, S.J., Taylor, W.D., Charlton, M.N., and Howell, T. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. **61**(7): 1285–1293. doi:10.1139/f04-065.

Henderson, B.A., and Fry, F.E.J. 1987. Interspecific relations among fish species in South Bay, Lake Huron, 1949–84. Can. J. Fish. Aquat. Sci. **44**(Suppl. 2): s10–s14. doi:10.1139/f87-304.

Hydrographic Service of Canada. 2008. Historical water level data. Available at http://www.waterlevels.gc.ca/C&A/historical_e.html [accessed 25 May 2008].

Ihssen, P.E., Evans, D.O., Christie, W.J., Reckahn, J.A., and Desjardine, R.L. 1981. Life-history, morphology, and electrophoretic characteristics of five allopatric stocks of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. **38**(12): 1790–1807. doi:10.1139/f81-226.

Jensen, A.L. 1985. Relations among net reproductive rate and life-history parameters for lake whitefish (*Coregonus clupeaformis*). Can. J. Fish. Aquat. Sci. **42**(1): 164–168. doi:10.1139/f85-020.

Keller, W. 2007. Implications of climate warming for Boreal Shield lakes: a review and synthesis. Environ. Rev. **15**: 99–112. doi:10.1139/A07-002.

King, J.R., Shuter, B.J., and Zimmerman, A.P. 1997. The response of the thermal stratification of South Bay (Lake Huron) to climatic variability. Can. J. Fish. Aquat. Sci. **54**(8): 1873–1882. doi:10.1139/cjfas-54-8-1873.

King, J.R., Shuter, B.J., and Zimmerman, A.P. 1999. Signals of climate trends and extreme events in the thermal stratification pattern of multibasin Lake Opeongo, Ontario. Can. J. Fish. Aquat. Sci. **56**(5): 847–852. doi:10.1139/cjfas-56-5-847.

Kinnunen, R.E. 2003. Great Lakes commercial fisheries. Available at http://www.miseagrant.umich.edu/downloads/fisheries/GLCommercialFinal.pdf [accessed 21 October 2009].

Kratzer, J.F., Taylor, W.W., Ferreri, C.P., and Ebener, M.P. 2007*a*. Factors affecting growth of lake whitefish in the upper Laurentian Great Lakes. Adv. Limnol. **60**: 459–470.

Kratzer, J.F., Taylor, W.W., and Turner, M. 2007*b*. Changes in fecundity and egg lipid content of lake whitefish (*Coregonus clupeaformis*) in the upper Laurentian Great Lakes between 1986–87 and 2003–05. J. Gt. Lakes Res. **33**(4): 922–929. doi:10.3394/0380-1330(2007)33[922:CIFAEL]2.0.CO;2.

Lawler, G.H. 1950. The use of nylon netting in the gill-net fishery of the Lake Erie whitefish. Can. Fish. Cult. **7**: 22–24.

Legendre, P., and Legendre, L. 1998. Numerical ecology. Elsevier Science B.V., Amsterdam, the Netherlands.

Lumb, C.E., Johnson, T.B., Cook, H.A., and Hoyle, J.A. 2007. Comparison of lake whitefish (*Coregonus clupeaformis*) growth, condition, and energy density between Lakes Erie and Ontario. J. Gt. Lakes Res. **33**(2): 314–325. doi:10.3394/0380-1330(2007)33[314:COLWCC]2.0.CO;2.

Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between and reconciliation of “predictive” and “explanatory” models. Biodivers. Conserv. **9**(5): 655–671. doi:10.1023/A:1008985925162.

Mac Nally, R. 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. Biodivers. Conserv. **11**(8): 1397–1401. doi:10.1023/A:1016250716679.

Mac Nally, R., and Walsh, C.J. 2004. Hierarchical partitioning public-domain software. Biodivers. Conserv. **13**(3): 659–660. doi:10.1023/B:BIOC.0000009515.11717.0b.

Madenjian, C.P., O'Connor, D.V., Pothoven, S.A., Schneeberger, P.J., Rediske, R.R., O'Keefe, J.P., Bergstedt, R.A., Argyle, R.L., and Brandt, S.B. 2006. Evaluation of a lake whitefish bioenergetics model. Trans. Am. Fish. Soc. **135**(1): 61–75. doi:10.1577/T04-215.1.

McCombie, A.M., and Fry, F.E.J. 1960. Selectivity of gill nets for lake whitefish, *Coregonus clupeaformis*. Trans. Am. Fish. Soc. **89**(2): 176–184. doi:10.1577/1548-8659(1960)89[176:SOGNFL]2.0.CO;2.

McNickle, G.G., Rennie, M.D., and Sprules, W.G. 2006. Changes in benthic invertebrate communities of South Bay, Lake Huron, following invasion by zebra mussels (*Dreissena polymorpha*), and potential effects on lake whitefish (*Coregonus clupeaformis*) diet and growth. J. Gt. Lakes Res. **32**(1): 180–193. doi:10.3394/0380-1330(2006)32[180:CIBICO]2.0.CO;2.

Mills, K.H. 1985. Responses of lake whitefish (*Coregonus clupeaformis*) to fertilization of Lake 226, the Experimental Lakes Area. Can. J. Fish. Aquat. Sci. **42**(1): 129–138. doi:10.1139/f85-016.

Mills, K.H., and Beamish, R.J. 1980. Comparison of fin-ray and scale age determinations for lake whitefish (*Coregonus clupeaformis*) and their implications for estimates of growth and annual survival. Can. J. Fish. Aquat. Sci. **37**(3): 534–544. doi:10.1139/f80-068.

Mills, K.H., and Chalanchuk, S.M. 1987. Population dynamics of lake whitefish (*Coregonus clupeaformis*) during and after the fertilization of Lake 226, the Experimental Lakes Area. Can. J. Fish. Aquat. Sci. **44**(Suppl. 1): s55–s63. doi:10.1139/f87-280.

Mills, K.H., and Chalanchuk, S.M. 2004. The fin-ray method of aging lake whitefish. Ann. Zool. Fenn. **41**: 215–223.

Mills, K.H., Chalanchuk, S.M., Allan, D.J., and Mohr, L.C. 1995. Responses of lake whitefish (*Coregonus clupeaformis*) to exploitation at the Experimental Lakes Area, Northwestern Ontario. Arch. Hydrobiol. **46**: 361–368.

Mills, K.H., Gyselman, E.C., Chalanchuk, S.M., and Allan, D.J. 2004. Growth, annual survival, age and length frequencies for unexploited lake whitefish populations. Ann. Zool. Fenn. **41**: 263–270.

Muir, A.M., Ebener, M.P., He, J.X., and Johnson, J.E. 2008. A comparison of the scale and otolith methods of age estimation for lake whitefish in Lake Huron. N. Am. J. Fish. Manage. **28**(3): 625–635. doi:10.1577/M06-160.1.

Nalepa, T.F., Hartson, D.J., Fanslow, D.L., Lang, G.A., and Lozano, S.J. 1998. Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980–1993. Can. J. Fish. Aquat. Sci. **55**(11): 2402–2413. doi:10.1139/cjfas-55-11-2402.

Nalepa, T.F., Fanslow, D.L., Foley, A.J.I., III, Lang, G.A., Eadie, B.J., and Quigley, M.A. 2006. Continued disappearance of the benthic amphipod *Diporeia* spp. in Lake Michigan: is there evidence for food limitation? Can. J. Fish. Aquat. Sci. **63**(4): 872–890. doi:10.1139/f05-262.

Nalepa, T.F., Fanslow, D.L., and Lang, G.A. 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. Freshw. Biol. **54**(3): 466–479. doi:10.1111/j.1365-2427.2008.02123.x.

Owens, R.W., and Dittman, D.E. 2003. Shifts in the diets of slimy sculpin (*Cottus cognatus*) and lake whitefish (*Coregonus clupeaformis*) in Lake Ontario following the collapse of the burrowing amphipod *Diporeia*. Aquat. Ecosyst. Health Manage. **6**(3): 311–323. doi:10.1080/14634980301487.

Pazzia, I., Trudel, M., Ridgway, M., and Rasmussen, J.B. 2002. Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. **59**(10): 1593–1605. doi:10.1139/f02-128.

Pothoven, S.A., and Nalepa, T.F. 2006. Feeding ecology of lake whitefish in Lake Huron. J. Gt. Lakes Res. **32**(3): 489–501. doi:10.3394/0380-1330(2006)32[489:FEOLWI]2.0.CO;2.

Pothoven, S.A., Nalepa, T.F., Schneeberger, P.J., and Brandt, S.B. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. N. Am. J. Fish. Manage. **21**(4): 876–883. doi:10.1577/1548-8675(2001)021<0876:CIDABC>2.0.CO;2.

Quinn, G.P., and Keough, M.J. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.

R Development Core Team. 2006. R: a language and environment for statistical computing. Available at http://www.R-project.org [accessed 1 January 2008].

Reckahn, J.A. 1986. Long-term cyclical trends in growth of lake whitefish in South Bay, Lake Huron. Trans. Am. Fish. Soc. **115**(6): 787–804. doi:10.1577/1548-8659(1986)115<787:LCTIGO>2.0.CO;2.

Rennie, M.D., and Verdon, R. 2008. Development and evaluation of condition indices for the lake whitefish. N. Am. J. Fish. Manage. **28**(4): 1270–1293. doi:10.1577/M06-258.1.

Rennie, M.D., Sprules, W.G., and Johnson, T.B. 2009. Resource switching in fish following a major food web disruption. Oecologia (Berl.), **159**(4): 789–802. doi:10.1007/s00442-008-1271-z.

Roff, D.A. 1984. The evolution of life history parameters in teleosts. Can. J. Fish. Aquat. Sci. **41**: 989–1000. doi:10.1139/f84-114.

Rogers, S.M., and Bernatchez, L. 2007. The genetic architecture of ecological speciation and the association with signatures of selection in natural lake whitefish (*Coregonus* sp. Salmonidae) species pairs. Mol. Biol. Evol. **24**(6): 1423–1438. doi:10.1093/molbev/msm066. PMID:17404398.

Sherwood, G.D., Pazzia, I., Moeser, A., Hontela, A., and Rasmussen, J.B. 2002. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish. Can. J. Fish. Aquat. Sci. **59**(2): 229–241. doi:10.1139/f02-001.

Smith, B.R., and Tibbles, J.J. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. **37**(11): 1780–1801. doi:10.1139/f80-222.

Snucins, E., and Gunn, J. 2000. Interannual variation in the thermal structure of clear and colored lakes. Limnol. Oceanogr. **45**: 1639–1646.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Company, New York.

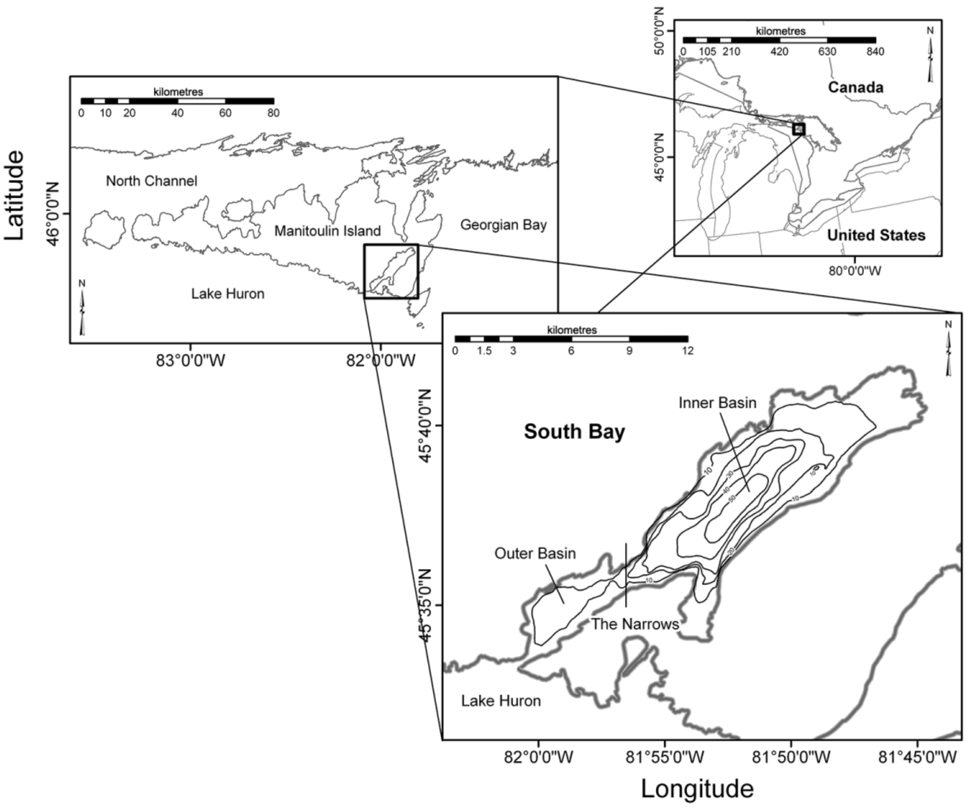
Wright, G.M., and Ebener, M.P. 2007. Potential effects of dietary lipid reduction on growth and reproduction of lake whitefish in northern Lake Michigan. Adv. Limnol. **60**: 311–330.

Zar, J.H. 1999. Biostatistical analysis. Prentice Hall, Inc., Toronto, Ontario.

Appendix A. Hypsographic curve used to estimate epilimnetic volume in the current study

The volume of a body of water in any particular year depends on both basin shape and water level. Water levels on Lake Huron have declined by nearly 1.5 m over the past 30 years (Hydrographic Service of Canada 2008). Because thermocline depth is measured from the water surface, the volume of water in the epilimnion will depend not only on thermocline depth, but also on the water level for a particu-

Fig. A1. Map of South Bay, Lake Huron.

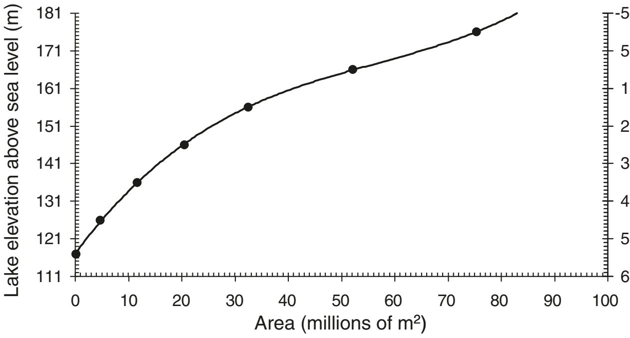


lar year. To generate a hypsographic curve for the inner basin of South Bay, Lake Huron, we scanned a bathymetric map of South Bay provided by the Ontario Ministry of Natural Resources. This image was saved and imported into the freely available image analysis software ImageJ (version 1.33u; http://rsbweb.nih.gov/ij/). The western boundary of the inner basin was chosen to correspond with the vertical line intersecting the narrows at 81°57′ (Fig. A1). Areas of 10 m contours and the perimeter of the inner basin were estimated from polygons manually traced to them using ImageJ. The maximum reported depth in the inner basin was 59 m (David Anderson, Ontario Ministry of Natural Resources, 1450 7th Ave. East, Owen Sound, ON N4K 2Z1, Canada, unpublished data). Areas of contours were then plotted against their respective depths to generate the hypsographic curve (Fig. A2). Lake depth = 0 was set at chart datum for Lake Huron (176 m; Hydrographic Service of Canada 2008).

To estimate the annual volume (millions of cubic metres) of the inner basin from the hypsographic curve (Fig. A2), we used reported mean annual water levels for Lakes Huron and Michigan (Hydrographic Service of Canada 2008). The maximum depth of the basin for a particular year was the elevation of mean annual water level minus the chart datum value for Lake Huron of 176 m, plus 59 m. This reflected the fixed nature of the bottom of the basin but took into account fluctuating annual water levels in the estimation of volume. The area under the curve bounded by the surface water level (in elevation) was then estimated using ImageJ and taken to equal the volume of the basin for that particular year.

To estimate the hypolimnetic volume, we subtracted the summer thermocline depth (King et al. 1997; this study) from the mean annual water level to determine the upper boundary of the hypolimnion. Hypolimnetic volume was estimated as the area under this level on the hypsographic curve. Epilimnetic volume was then estimated as the difference between total volume and hypolimnetic volume and expressed as a percentage of the total volume of the inner basin.

Fig. A2. Hypsographic curve used to estimate epilimnetic volume of the inner basin of South Bay, Lake Huron. Data points represent area of bathymetric contours.



References

Hydrographic Service of Canada. 2008. Historical water level data. Available at http://www.waterlevels.gc.ca/C&A/historical_e.html [accessed 25 May 2008].

King, J.R., Shuter, B.J., and Zimmerman, A.P. 1997. The response of the thermal stratification of South Bay (Lake Huron) to climatic variability. Can. J. Fish. Aquat. Sci. **54**(8): 1873–1882. doi:10.1139/cjfas-54-8-1873.