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CHAPTER 42

Context-Dependent Changes in Lake Whitefish Populations Associated with Dreissenid Invasion

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ABSTRACT

The manner in which an organism responds to a change in its environment can depend greatly on previous conditions. In this regard, lake whitefish (*Coregonus clupeaformis*) populations from a wide range of aquatic environments have demonstrated a variety of responses to the establishment of dreissenid mussels. A review of the literature indicated that individual growth rates and condition of lake whitefish have typically declined after dreissenid establishment where *Diporeia*—a key prey item of lake whitefish—have also

declined in abundance. Temporal declines in lake whitefish growth and condition occurred following dreissenid establishment despite reported increases in lake whitefish consumption rates. A review of lake whitefish populations from noninvaded systems revealed declines in lake whitefish growth and condition as a common response to resource limitation, supporting the hypothesis that typical lake whitefish responses to dreissenid establishment are a function of resource limitation. In contrast, lake whitefish populations from shallow, nutrient-enriched lakes with dreissenids (Lake Erie where *Diporeia* has declined, and Lake Simcoe where *Diporeia* was absent

prior to dreissenid establishment) show no evidence of declines in lake whitefish growth and/or condition after dreissenid establishment. Age at maturity was delayed in all but one population of 18 surveyed, regardless of whether dreissenids were established or *Diporeia* had declined in abundance. Body condition of lake whitefish appeared to closely track resource declines in most populations. However, growth declines sometimes appeared to be independent of trends in resource abundance, which suggests effects of other stressors besides dreissenids on lake whitefish growth rates. These stressors may include density dependence, climate warming, and changes in ecosystem community structure that may lead to increased interspecific competition.

INTRODUCTION

Lake whitefish (*Coregonus clupeaformis*) are one of the most economically important species of fish to commercial, recreational, and sustenance fisheries in North America. They are distributed throughout Canada and the northern United States, ranging from the Great Lakes in the south to anadromous populations in the Arctic (Scott and Crossman 1998). In the Great Lakes, lake whitefish accounted for the majority of the commercial catch during the past decade. In 2000, they accounted for 45% (nearly 10,000 metric tons) of the Great Lakes commercial fishery with a dockside value of \$40 million (year 2000 Canadian dollars, Kinnunen 2003). Beyond the Great Lakes, lake whitefish are the most heavily exploited species of fish from inland fisheries and second economically only to walleye (Freshwater Fish Marketing Corporation 2010). Lake whitefish are a highly sought after species in recreational winter fisheries on both the Great Lakes and surrounding inland lakes (Evans et al. 1988) and are an important staple fish for many North American First Nations communities (Hopper and Power 1991).

Invasive species have in the past threatened this key economic resource and may be doing so once again. In the Great Lakes, lake whitefish suffered dramatic declines in abundance in the 1950s coincident with the invasion of sea lamprey, *Petromyzon marinus* (Smith and Tibbles 1980), and lamprey control efforts are largely thought to be responsible for the dramatic recovery that followed (Ebener 1997). Sudden and unexpected declines in lake whitefish growth rates and body condition were then observed in the mid-1990s, coincident with the establishment of dreissenid mussels (zebra mussel *Dreissena polymorpha* and quagga mussel *D. rostriformis bugensis*). Simultaneously, abundance of the deepwater amphipod, *Diporeia*—a major prey item for lake whitefish—declined. Following dreissenid establishment in Lake Ontario, declines in *Diporeia* abundance and lake whitefish growth and condition were followed by a substantial and sudden decline in lake whitefish abundance (Hoyle et al. 1999, Dermott 2001). Similar declines in *Diporeia* abundance and lake whitefish growth and condition were

subsequently documented following dreissenid establishment in Lake Michigan (Pothoven et al. 2001) and Lake Huron (Dobiesz et al. 2005, Rennie et al. 2009a).

Declines in *Diporeia* abundance and lake whitefish growth and condition following dreissenid establishment have led to hypotheses in the literature that negative impacts of dreissenids on *Diporeia* populations are the cause, under the assumption that *Diporeia* contributed substantially to historical lake whitefish diets (Pothoven et al. 2001). However, these patterns have not been consistent. For example, lake whitefish populations in Lake Erie were relatively stable during dreissenid establishment and a collapse of *Diporeia* (Lumb et al. 2007). Though a number of studies over the past decade have investigated links between dreissenid establishment, *Diporeia* declines, and lake whitefish populations, both within and outside of the Great Lakes basin, these studies have to date not been reviewed and considered together.

This chapter provides a review of existing literature and available unpublished data for the purpose of synthesizing current knowledge of the impacts of dreissenid establishment on North American lake whitefish populations. The potential roles of other factors (climate change, density dependence) that have been shown in the literature as affecting lake whitefish populations are also considered.

DIPOREIA AND DREISSENID MUSSELS

The observed timing between the spread of dreissenids and loss of *Diporeia* among many sites throughout the Great Lakes has been virtually simultaneous (Dermott and Kerec 1997, Nalepa et al. 1998, Dermott 2001). Despite this coordination of events, the exact mechanism behind dreissenid-*Diporeia* interactions remains unknown. While not the focus of the current chapter, some discussion regarding the mechanisms proposed is warranted, given the consequences this interaction is thought to have had for lake whitefish. In a recent survey of expert researchers attending a workshop on Great Lakes *Diporeia* declines (Nalepa et al. 2006a), the top two mechanisms supported by participants were (1) food limitation due to filtration activity by dreissenids and (2) harmful agents affecting *Diporeia*, including yet-to-be-identified metabolic by-products produced by dreissenids that are harmful to *Diporeia*, or pathogenic introductions coincident with or facilitated by dreissenids.

The food-limitation hypothesis seems to be supported by recent work implicating dreissenid filtration in reductions of pelagic primary productivity in Lake Michigan (Fahnenstiel et al. 2010). This is also consistent with the conceptual near-shore phosphorous shunt model (Hecky et al. 2004), which posits a concentration and redirection of productivity from offshore and profundal regions of lakes to the nearshore where dreissenids (particularly zebra mussels) can exist at high densities, and may also act to intercept land-based deposition of

nutrients from offshore transport. However, other work examining this hypothesis explicitly in a declining population of *Diporeia* in Lake Michigan found no evidence that *Diporeia* declines were a result of food limitation (Nalepa et al. 2006b). Further, primary productivity does not appear to be driving *Diporeia* declines in Lake Ontario (Watkins et al. 2007).

Research into potential harmful agents that might be affecting *Diporeia* has similarly been inconclusive. Experimental *Diporeia* did not avoid or experience differential mortality when exposed to sediments from locations where the species had previously been extirpated (Nalepa et al. 2006b). Other work found that the exposure of *Diporeia* to sediments where dreissenids were abundant resulted in a minor reduction in *Diporeia* survival (mean survival across all treatments was between 70% and 80%; Dermott et al. 2006). A number of pathogens of *Diporeia* have also been identified (Messick et al. 2004); however, there is currently no clear indication as to how these pathogens might be related to dreissenids or how they may have played a role in the decline of *Diporeia*.

Observations in the New York Finger Lakes further complicate the matter. In these lakes, *Diporeia* abundance appears stable despite dreissenid establishment (largely quagga mussels, Dermott et al. 2006, J. Watkins personal communication). This coexistence in the Finger Lakes suggests an interaction between dreissenids and other stressors may have contributed to different patterns observed in the Great Lakes (Dermott et al. 2006, Rennie et al. 2009a).

Despite the aforementioned difficulties in identifying clear and direct links between dreissenid distributions and *Diporeia* declines, the timing between arrival of dreissenids and loss of *Diporeia* in the Great Lakes makes it difficult to imagine that these changes in benthic communities are totally independent of one another. However, it is clear that more work is needed to better establish the mechanistic relationship between *Diporeia* declines and dreissenids.

CHANGES IN LAKE WHITEFISH POPULATIONS WITH DREISSENIDS

In this chapter, temporal trends in lake whitefish populations that have been exposed to ecosystem changes associated with dreissenids are primarily from the North American Great Lakes (Table 42.1). Where available, additional data were also compiled for lake whitefish populations exposed to dreissenids outside the Great Lakes. In addition, data for uninvaded populations of lake whitefish not subject to dreissenid influences are included to contrast temporal trends with invaded ecosystems.

Great Lakes Populations: Consistencies

Impacts of dreissenids on lake whitefish growth and condition have been nearly ubiquitous following their establishment in the Great Lakes (Table 42.1). Lake whitefish growth

rates declined following dreissenid establishment in all but two cases, and all but one population showed declines in condition (Table 42.1). In many cases, the response of lake whitefish to dreissenid establishment has been almost immediate. In Lake Ontario (Hoyle et al. 1999) and in Lake Michigan (Pothoven et al. 2001), declines in lake whitefish growth and condition (and *Diporeia* abundance) were observed to occur within 1–2 years of dreissenid establishment. Of three populations where size-at-age data were available in Lake Huron, one (Southampton) demonstrated a response in growth rates within 1–2 years of reported dreissenid establishment (in 1993; Figure 42.1). Similarly, weight-at-age in northern Lake Michigan stocks appeared to display a change in slope in the early- to mid-1990s (Figure 42.2). For example, lake whitefish growth in Big Bay de Noc began to decline in 1992 shortly after dreissenid establishment and prior to the collapse of *Diporeia* in and around the bay (Nalepa et al. 2006b). While data available to estimate condition from this stock was limited and thus the onset of declines was impossible to pinpoint, relative weight (calculated using Equation 5 in Rennie and Verdon 2008) estimated in 2000–2006 was lower by 30% compared to 1980 values (Figure 42.3). Relative weight in the Southampton stock declined by 5.7% between 1992 and 1994 (Figure 42.3).

Other lake whitefish populations exhibited a lag between dreissenid establishment and declines in growth and condition (Figures 42.1 and 42.2). In these cases, lake whitefish appear to be responding to a decline in *Diporeia* following dreissenid establishment. For instance, dreissenids were established in Georgian Bay, Lake Huron, in 1996 (Rennie 2009), but declines of lake whitefish growth in the Cape Rich stock (located in southern Georgian Bay) were not observed until after 2001 (Figure 42.1). This coincided almost directly with reported declines of *Diporeia* abundance in transects off Cape Rich (Nalepa et al. 2007). Similarly, lake whitefish from Naubinway (northern Lake Michigan) appeared to show major declines in size-at-age in 1997 (Figure 42.2) and marked declines in condition in 1994 and 1997 (Figure 42.3). The timing of these declines coincided with dramatic declines in *Diporeia* abundance in northern Lake Michigan between 1995 and 2000 (Nalepa et al. 2006b) and not with the earlier establishment of dreissenids in the region (Nalepa et al. 2009).

Elsewhere, declines in condition of lake whitefish from near Cheboygan (northwestern Lake Huron) were coincident with dreissenid establishment (Figure 42.3), but declines in growth were delayed until 2000 (Figure 42.2). These responses were similar to those in Georgian Bay (northeastern Lake Huron) where declines in many invertebrate species (including *Diporeia*) occurred in 2000–2003 (Nalepa et al. 2007). In regions of the Great Lakes where the decline of *Diporeia* was less pronounced (e.g., Detour Village, northwestern Lake Huron), declines in lake whitefish growth were similarly delayed (Figure 42.2), and declines in lake whitefish condition were more gradual (Figure 42.3).

Table 42.1 Changes in Measured Parameters of Lake Whitefish Populations during Dreissenid Establishment. Up Arrow (↗) Represents an Increase, Down Arrow (↘) Represents a Decrease, and Equal Sign (=) Represents No Change. Numbers in Parentheses Correspond to References in Table Footnotes.

Location	Parameter								
	Growth	Body Condition	Reproductive Investment	Age-at-Maturity	Size-at-Maturity	Energy Density (Fish)	Energy Density (Diet)	δ ¹³ C (Energy Source)	δ ¹⁵ N (Trophic Position)
Dreissenid Invaded									
Lake Ontario									
Northeastern	↘ (1)	↘ (1)		↗ (2)				= (3)	↘ (3)
Kingston Basin		↘ (3)							
Bay of Quinte		↘ (3)							
Lake Huron									
South Bay	↘ (6)	↘ (6)		↗ (6)	= (28)		↘ (7, 8)	↗ (8)	↘ (8)
Main Basin				↗ (9)	↘ (9)				
Northern	↘ (10)	↘ (11, 27)	↘ (12)		↘ (9)				
Central	↘ (25)	↘ (27)		↗ (28)	= (28)				
South	↘ (11)	↘ (11)		↗ (11)					
Lake Huron									
Georgian Bay	↘ (11, 25)			↗ (9, 28)	= (28); ↗ (9)				
No Dreissenids									
Lake Michigan									
Basin-wide				↗ (9)	↘ (9)	↘ (13)			
Northern: Big Bay de Noc, Naubinway	↘ (26)	↘ (27)	↘ (12)						
Northern: Grand Traverse Bay	↘ (14)	↘ (14)	↘ (12)						
Midlatitude	↘ (14)	↘ (14)							
Southern	↘ (14, 15)	↘ (14, 15)							
Lake Erie	= (1); ↘ (3)	= (1)						↘ (3)	↘ (3)
Lake Simcoe	↗ (25)	↗ (16)		↘ (28)	↗ (28)			↗ (17)	= (17)
Lake Superior									
Whitefish Bay	↘ (29)	↘ (29, 16)	↗ (12)	↗ (30); = (9)	= (30); ↗ (9)				
Apostle Islands	↘ (29)	↘ (29)		↗ (30)	↘ (30)				
Lake Nipigon	= (29)	↘ (16)		↗ (30)	↗ (30)				

^a Densities based on trawling (active sampling method); all other estimates based on catch from gillnetting (passive sampling method).
1 (Lumb et al. 2007); 2 (Hoyle 2005); 3 (Lumb and Johnson 2012); 4 (Hoyle et al. 1999); 5 (Hoyle et al. 2008); 6 (Rennie et al. 2009a); 7 (McNickle et al. 2006); 8 (Rennie et al. 2009b); 9 (Wang et al. 2008); 10 (Rennie et al. 2012b); 11 (Mohr et al. 2005); 12 (Kratzer et al. 2007); 13 (Pothoven et al. 2006); 14 (DeBruyne et al. 2008); 15 (Pothoven et al. 2001); 16 (Rennie et al. 2010); 17 (M.D. Rennie, D. O. Evans and J. L. LaRose, unpublished data); 18 (Rennie et al. 2012a); 19 (Fernandez et al. 2009); 20 (Riley and Adams 2010); 21 (Pothoven and Madenjian 2008); 22 (Gewurtz et al. 2011); 23 (Gorman et al. 2010); 24 (Nalepa et al. 2005); 25 (Figure 42.1); 26 (Figure 42.2); 27 (Figure 42.3); 28 (Figure 42.5); 29 (Figure 42.6); 30 (Figure 42.7).

Table 42.1 (continued) Changes in Measured Parameters of Lake Whitefish Populations during Dreissenid Establishment. Up Arrow (↗) Represents an Increase, Down Arrow (↘) Represents a Decrease, and Equal Sign (=) Represents No Change. Numbers in Parentheses Correspond to References in Table Footnotes

Location	Parameter								
	Depth Distribution	Relative Abundance	Contaminants	Juvenile Growth	Energy Density (Juvenile Diet)	Total Consumption	Feeding Rate	Activity Rate	Conversion Efficiency
Dreissenid Invaded									
Lake Ontario									
Northeastern Kingston Basin		↘ (5)							
Bay of Quinte			↘ Hg (16)						
Lake Huron									
South Bay	↗ (8)	↗ (6)	= Hg (18)		= (19)		↗ (18)	↗ (18)	↘ (18)
Main Basin	↘ (20)	↗ (11)				= (21)			= (21)
Northern		↗ (11, 12)					↗ (21)		
Central		↘ (20) ^a	= Hg (16)				↗ (21)		
South		↘ (20) ^a					↗ (21)		
Lake Huron									
Georgian Bay			↘ Hg (16)						
Lake Michigan									
Basin-wide									
No Dreissenids									
Northern: Big Bay de Noc, Naubinway		↗ (12)							
Northern: Grand Traverse Bay		↘ (12, 14)				↗ (21)	↗ (21)		= (21)
Midlatitude		↗ (12, 14)				↘ (21)	↗ (21)		= (21)
Southern		↗ (14)				= (21)	↗ (21)		= (21)
Lake Erie		= (1)							
Lake Simcoe		↗ (17)	↗ Hg; ↘ PCB; ↘ DDT (16, 22)						
Lake Superior									
Whitefish Bay		↘ (12, 23 ^a)	↘ Hg (16)						
Apostle Islands		↘ (23 ^a)							
Lake Nipigon		= (24)	↘ Hg (16)						

^a Densities based on trawling (active sampling method); all other estimates based on catch from gillnetting (passive sampling method).
1 (Lumb et al. 2007); 2 (Hoyle 2005); 3 (Lumb and Johnson 2012); 4 (Hoyle et al. 1999); 5 (Hoyle et al. 2008); 6 (Rennie et al. 2009a); 7 (McNickle et al. 2006); 8 (Rennie et al. 2009b); 9 (Wang et al. 2008); 10 (Rennie et al. 2012b); 11 (Mohr et al. 2005); 12 (Kratzer et al. 2007); 13 (Pothoven et al. 2006); 14 (DeBruyne et al. 2008); 15 (Pothoven et al. 2001); 16 (Rennie et al. 2010); 17 (M.D. Rennie, D. O. Evans and J. L. LaRose, unpublished data); 18 (Rennie et al. 2012a); 19 (Fernandez et al. 2009); 20 (Riley and Adams 2010); 21 (Pothoven and Madenjian 2008); 22 (Gewurtz et al. 2011); 23 (Gorman et al. 2010); 24 (Nalepa et al. 2005); 25 (Figure 42.1); 26 (Figure 42.2); 27 (Figure 42.3); 28 (Figure 42.5); 29 (Figure 42.6); 30 (Figure 42.7).

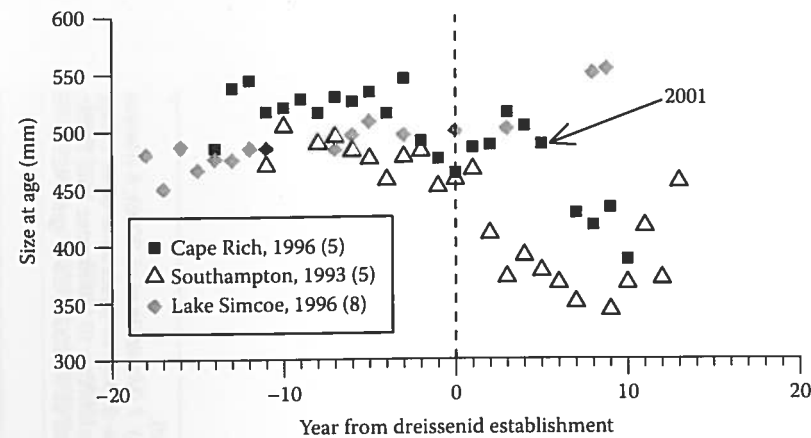


Figure 42.1 Mean size-at-age of lake whitefish in Lake Huron (Cape Rich and Southampton) and in Lake Simcoe in relation to the establishment of dreissenids (year 0 = establishment). Year of dreissenid establishment shown in the legend. (From Rennie, M.D., Influence of invasive species, climate change and population density on life histories and mercury dynamics of *Coregonus* spp., PhD thesis, University of Toronto, Toronto, Ontario, Canada, 2009.) Numbers in parentheses indicate age of lake whitefish examined. Year of major *Diporeia* declines in Cape Rich (2001) is noted. Lake whitefish data taken from Ontario government indexing records.

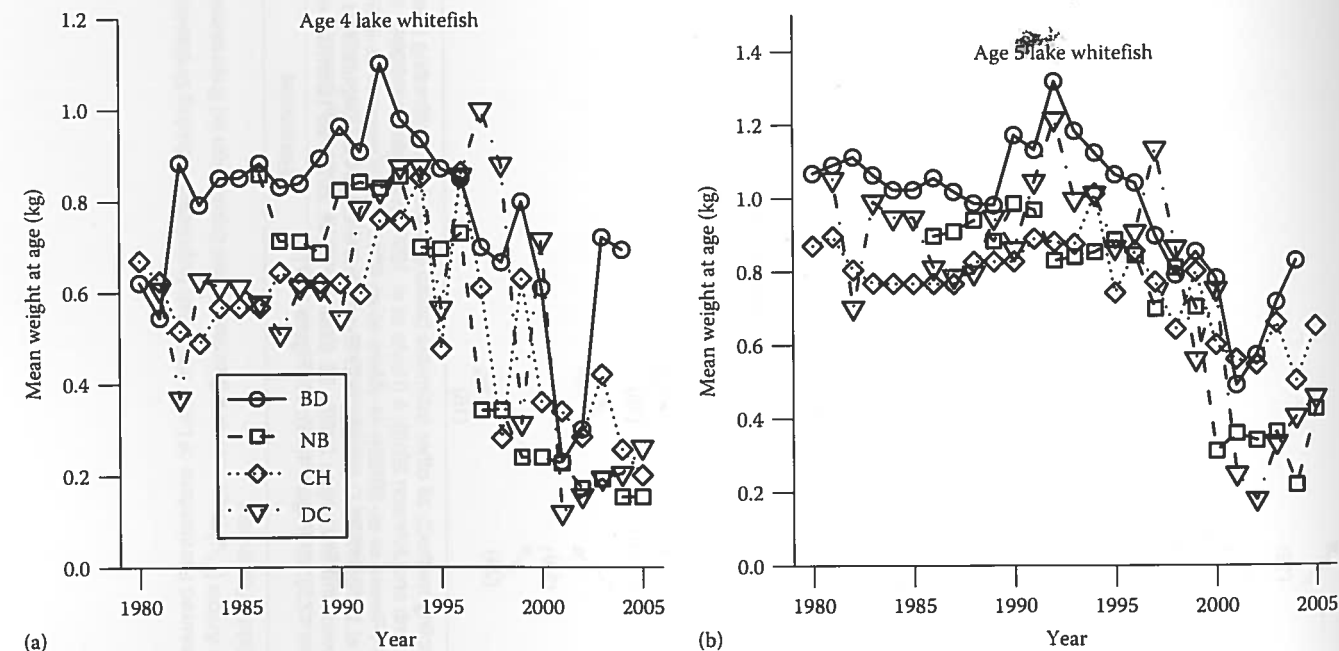


Figure 42.2 Mean weight-at-age for age-4 (panel a) and age-5 (panel b) lake whitefish in northern Lake Michigan (BD = Big Bay de Noc; NB = Naubinway) and northeastern Lake Huron (CH = Cheboygan, DC = Detour-Cedarville). (Reproduced from Rennie, M.D. et al., *Adv. Limnol.*, 63, 455, 2012b. With permission, available at <http://www.schweizerbart.de>)

Growth, and to some extent condition (Bajer and Hayward 2006), is ultimately related to bioenergetics processes (i.e., the relative rates of energy intake and expenditure) of an organism (Weatherley 1966). Two independent studies have reported an increase in mass-specific consumption rates of lake whitefish following dreissenid establishment (Pothoven and Madenjian 2008, Rennie et al. 2012a). The latter study also estimated higher consumption rates among lake whitefish populations where dreissenids were established compared with populations where dreissenids were not present (Figure 42.4a). Both studies showed that lake whitefish

growth rates declined in the presence of dreissenids despite higher rates of food intake, suggesting forage declined in quality. This evidence supports previous work showing a decline in lake whitefish prey quality following dreissenid invasion (McNickle et al. 2006, Rennie et al. 2009b).

While age-at-maturity increased significantly in all but one population exposed to dreissenids, these changes were gradual compared to the abrupt changes in growth and condition more frequently observed (Table 42.1, Figure 42.5a). Further, this pattern was observed over a wide geographic range and in populations without dreissenids (Table 42.1),

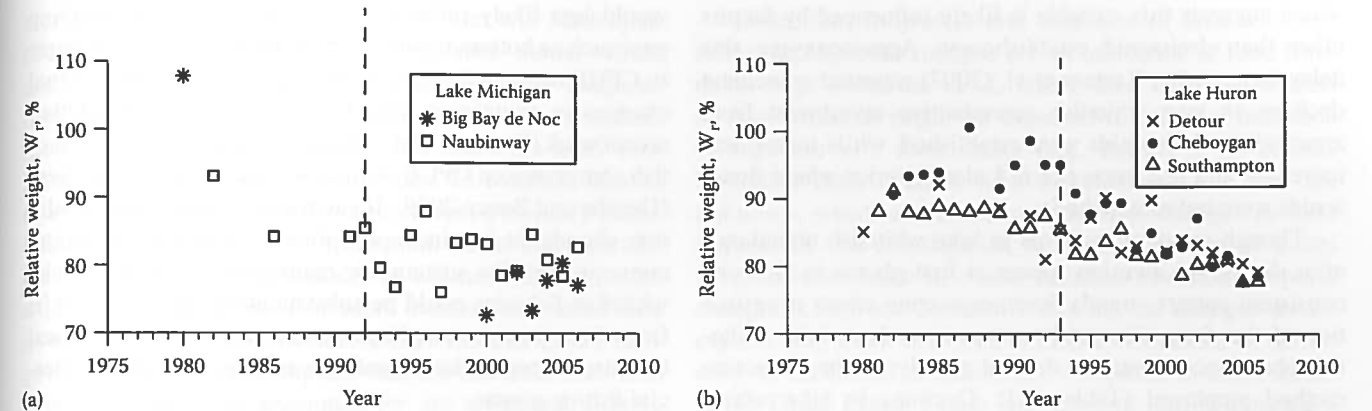


Figure 42.3 Lake whitefish condition (relative weight, W_r , expressed as a percentage of standard weight estimated from Equation 5 in Rennie and Verdon 2008) in northern Lake Michigan (panel a) and Lake Huron (panel b). Dashed line represents year of reported dreissenid establishment in these lakes.

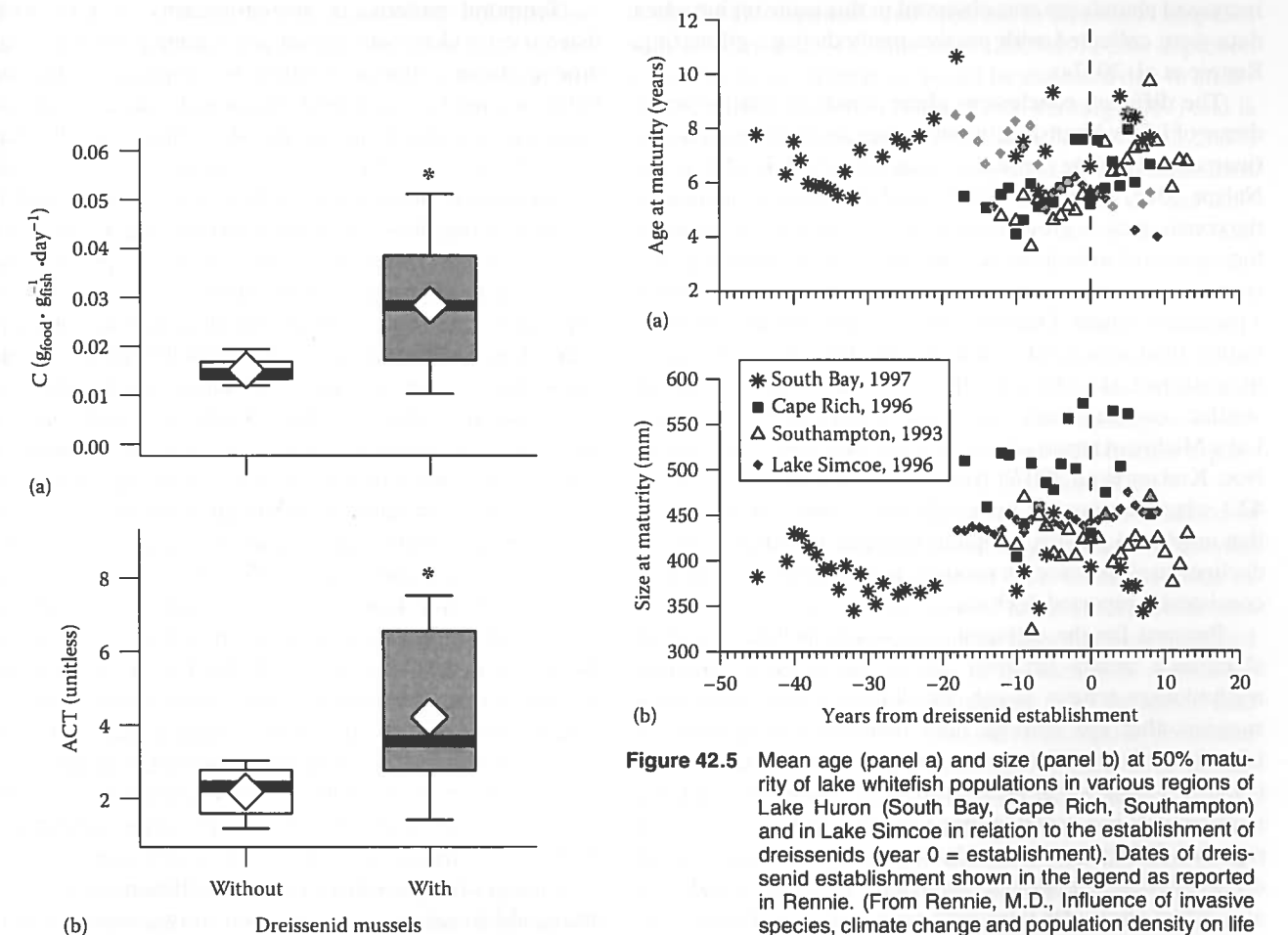


Figure 42.4 Boxplots of relative consumption (C) (panel a) and activity multipliers (ACT, expressed as a multiple of standard metabolism, panel b) obtained from bioenergetics models of lake whitefish populations without (open) and with dreissenids (shaded). Upper and lower bounds of boxes represent the first and third quartiles of the data, whiskers represent 95% confidence intervals, thick bars are medians, and diamonds are mean values. (Reproduced from Rennie, M.D. et al., *Can. J. Fish. Aquat. Sci.*, 69, 41, 2012a. With permission.)

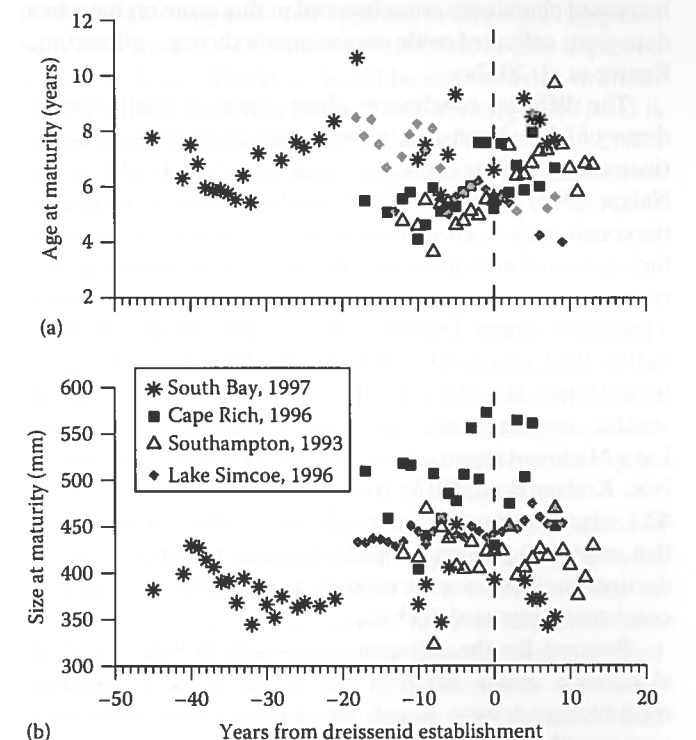


Figure 42.5 Mean age (panel a) and size (panel b) at 50% maturity of lake whitefish populations in various regions of Lake Huron (South Bay, Cape Rich, Southampton) and in Lake Simcoe in relation to the establishment of dreissenids (year 0 = establishment). Dates of dreissenid establishment shown in the legend as reported in Rennie. (From Rennie, M.D., Influence of invasive species, climate change and population density on life histories and mercury dynamics of *Coregonus* spp., PhD thesis, University of Toronto, Toronto, Ontario, Canada, 2008.) Lake Simcoe estimates (from trap nets on spawning shoals that likely underrepresent immature individuals) are estimated as the mean age and size of the youngest and smallest 5% of individuals captured each year, respectively. Linear trends in age-at-maturity are significant and positive for South Bay ($p = 0.08$), Cape Rich ($p = 0.04$), and Southampton ($p < 0.0001$) and negative for Lake Simcoe ($p = 0.0002$). Linear trends in size-at-maturity are significant (positive) for Lake Simcoe only ($p < 0.0001$).

which suggests this variable is likely influenced by factors other than dreissenid establishment. Accompanying this delay in maturity, Kratzer et al. (2007) reported coincident declines in lake whitefish reproductive investment from areas where dreissenids were established, while investment increased at a reference site in Lake Superior where dreissenids were not established.

Though temporal patterns in lake whitefish abundance after dreissenid invasion appear at first glance to lack any consistent pattern, trends do emerge upon closer examination of the data. Observed temporal trends in lake whitefish abundance appear to depend greatly on the collection method employed (Table 42.1). Declines in lake whitefish abundance in central and southern Lake Huron were observed only when data were collected with active sampling methods (bottom trawls, Riley et al. 2008). In contrast, increased abundance was observed in this same region when data were collected with passive methods (e.g., gillnetting, Rennie et al. 2012a).

The different conclusions about trends in relative abundance of lake whitefish between active (decrease) and passive (increase) sampling methods within the same lake (Mohr and Nalepa 2005, Riley et al. 2008) are difficult to reconcile with the consistency in growth and condition declines observed in the same stocks (Mohr et al. 2005, this study). Further, differences exist even when using the same collection methods in a particular region. DeBruyne et al. (2008) reported declines (rather than increases) in lake whitefish relative abundance in northern Lake Michigan from passive sampling gear, but similar sampling from other studies elsewhere in northern Lake Michigan report increases (e.g., Naubinway, Big Bay de Noc, Kratzer et al. 2007). Among sites summarized in Table 42.1 where dreissenids are established, only 2 of 10 regions that employed passive sampling methods report evidence of declines in abundance. In contrast, active sampling programs consistently reported declines.

Reasons for the different conclusions in lake whitefish abundance trends between active and passive sampling methodology remain largely unaddressed, but recent work suggests that the activity (and therefore catchability) of lake whitefish increases in the presence of dreissenids (Figure 42.4b) as a consequence of increased foraging requirements in a depleted-prey field. While it is possible that reported differences in abundance genuinely reflect regional differences among stocks, behavioral changes in fish can also affect encounter rates with sampling gear. Passive collection methods rely on the movements of organisms for capture (Rudstam et al. 1984). As such, a substantial component of catch-per-unit-effort (CPUE) estimates is related to gear encounter, or "catchability" (Spangler and Collins 1992, Biro and Post 2008, Biro and Dingemanse 2009, Rennie et al. 2012a). A hypothesis of increased swimming activity in lake whitefish or increased range dispersal (Rennie et al. 2012b) could manifest itself as increased rates of encounter with passive gear, whereas changes in activity or range distribution

would less likely influence catch rates of active sampling gear such as bottom trawls. If this hypothesis is true, changes in CPUE estimated from passive gear may not reflect actual changes in abundance (e.g., Henderson et al. 1983). Other recent work illustrated the influence of factors independent of fish abundance on CPUE estimates of passive collection gear (Deroba and Bence 2009). If catchability rather than population abundance has increased after dreissenid colonization, consequences for sustainable management efforts of lake whitefish fisheries could be substantial because it is CPUE from these passive sampling methods that is frequently used to estimate population abundance and, in turn, set commercial fishing quotas.

Great Lakes Populations: Inconsistencies

Temporal patterns in size-at-maturity of lake whitefish varied widely both within and among populations, and among studies. Size-at-maturity for populations typically either declined or remained unchanged, while it increased in only a minority of cases (Table 42.1, Figure 42.5b). Wang et al. (2008) reported a significant increase in lake whitefish size-at-maturity among cohorts born after 1990, though the increase among these cohorts was on the order of 2.0–2.5 cm, only 3%–4% of typical asymptotic size in this species (50–70 cm; Scott and Crossman 1998). However, increases of this magnitude may relate to delays in age-at-maturation of 1–2 years, based on reported relationships between size- and age-at-maturity for this species (Beauchamp et al. 2004).

Trends in depth-of-capture of lake whitefish following dreissenid colonization were also variable. Commercial fishing habits and a recent analysis of trawling surveys suggest that lake whitefish in the main basin of Lake Huron moved deeper following dreissenid establishment (Mohr et al. 2005, Riley and Adams 2010). In contrast, lake whitefish in South Bay, Lake Huron, exhibited evidence of more shallow distributions following dreissenid establishment (Rennie et al. 2009b). It is possible that fish in the main basin of Lake Huron pursued remnant *Diporeia* populations in deeper waters of the main basin (Nalepa et al. 2007). While a remnant *Diporeia* population did persist in South Bay, it may have been insufficient to keep whitefish offshore compared to increased abundance of invertebrates nearshore in the bay after dreissenid invasion (McNickle et al. 2006).

Changes in lake whitefish growth efficiencies following dreissenid invasion were examined in two studies and the results were not consistent (Table 42.1). In one study, lake whitefish conversion efficiency (or growth efficiency; the proportion of food consumed that is converted into growth) decreased in South Bay lake whitefish following dreissenid invasion and tended to be highest in areas with low *Diporeia* abundance (Rennie et al. 2012a). In another study, conversion efficiencies in Lake Huron and Lake Michigan populations were similar before and after dreissenid invasion (Pothoven and Madenjian 2008). This discrepancy between

studies is likely methodological. Pothoven and Madenjian (2008) used a bioenergetics mass-balance model where activity costs are estimated as functions of water temperature and body mass. Therefore, all energetic losses in their model were the result of sub-models and were used with growth rates to estimate consumption. In contrast, Rennie et al. (2012a) estimated consumption from a mercury mass-balance model and used consumption as an input parameter in the bioenergetics model to estimate activity costs expressed as a multiple of standard metabolism (rather than as a sub-model of total metabolism). In the latter case, energetic losses from consumption that are not translated into growth or otherwise accounted for are estimated directly in the mass balance. If lake whitefish activity (associated with increased foraging) increased as a result of dreissenid colonization, the activity sub-model used by Pothoven and Madenjian (2008) in their post-dreissenid colonization models would not reflect this change, resulting in an underestimate of losses to activity. This would then translate into an underestimate of consumption rate and overestimate of growth efficiency in their post-dreissenid bioenergetics models.

Historical studies of isotopic variation and contaminants in whitefish have also been inconsistent between populations. Isotopic signatures of carbon ($\delta^{13}\text{C}$) in lake whitefish scales have been observed to increase in at least two populations of lake whitefish where dreissenids colonized (Table 42.1). In South Bay, Lake Huron, this increase was sudden and of substantial magnitude (approx. 4‰ increase), which is consistent with an increased reliance on nearshore carbon following dreissenid establishment. Increases in Lake Simcoe $\delta^{13}\text{C}$ were in the same direction as South Bay, but smaller in magnitude (M. D. Rennie, D. O. Evans and J. L. LaRose, unpublished data). Based on a more coarse temporal comparison, $\delta^{13}\text{C}$ signatures of scales from Lake Erie and Ontario stocks appear to have declined after dreissenid invasion (Table 42.1). Tissue concentrations of contaminants (primarily mercury) have declined or remained stable regardless of dreissenid establishment, though there is evidence for increased mercury tissue concentrations in lake whitefish from Lake Simcoe (Table 42.1).

Lake Erie

For all regions of the Great Lakes except Lake Erie, the temporal sequence of events was consistent: dreissenids establish, *Diporeia* decline in abundance, and lake whitefish growth and condition decline shortly thereafter. While *Diporeia* was extirpated from Lake Erie after dreissenid establishment (Dermott and Kerec 1997, Barbiero et al. 2011), lake whitefish growth, condition, and abundance generally appear to have been unaffected (Table 42.1). However, a more recent assessment of growth in Lake Erie whitefish suggests slight growth declines (Lumb and Johnson 2012).

If declines in growth and condition of lake whitefish following *Diporeia* collapse are an indication of food limitation (e.g., Pothoven et al. 2001), then changes in diets of lake whitefish might be expected to reflect a reduction of *Diporeia* as a food source (e.g., Rennie et al. 2009b). Historical diets of adult lake whitefish in Lake Erie are unknown, which makes an evaluation of changes in diets impossible. An investigation of isotopic values of scales from archived Lake Erie lake whitefish revealed temporal changes (Lumb and Johnson 2012), but the changes do not explain why Lake Erie lake whitefish responded so differently to dreissenid establishment compared to other stocks in the Great Lakes. Lumb and Johnson (2012) reported a depletion in $\delta^{13}\text{C}$ values (approximately 2‰) after dreissenid invasion was observed, which suggests an increased reliance on pelagic or offshore-derived resources. This pattern is smaller in magnitude and opposite in direction compared with another study (Rennie et al. 2009b). A 2‰ depletion is roughly twice as large as would be expected due to atmospheric carbon depletion (Suess 1955, Verburg 2007) and is consistent with contemporary diet data (Lumb et al. 2007) that is dominated by pelagic zooplankton and organisms common in offshore habitats such as sphaeriids and chironomids. Dreissenids were also a major component of lake whitefish diets in Lake Erie (Lumb et al. 2007), and dreissenids are $\delta^{13}\text{C}$ depleted relative to other organisms found at similar depths (Rennie et al. 2009b). All of these prey organisms are typically thought to be lower in caloric content than *Diporeia* (Madenjian et al. 2006, Rennie et al. 2011a), and dreissenids likely require a great deal more energy for lake whitefish to process compared to more soft-bodied organisms such as *Diporeia* (Owens and Dittman 2003).

Relative stability of lake whitefish growth and condition in Lake Erie during *Diporeia* declines suggests that: (1) *Diporeia* were never a major component of lake whitefish diets; or (2) the switch to alternative prey of lower caloric value was accompanied by higher consumption rates that were mediated by higher densities and/or rates of production of alternative prey following dreissenid establishment or by increased lake whitefish foraging activity. Increased consumption (Pothoven and Madenjian 2008) and activity rates (Rennie et al. 2012a) have been reported in other lake whitefish populations after dreissenid establishment. The isotopic pattern in lake whitefish in Lake Erie suggests they did not utilize increased abundance and biomass of benthic invertebrates in the nearshore region following dreissenid establishment (Dermott and Kerec 1997). Rather, isotopic patterns suggest that alternative prey would likely consist of offshore zooplankton that are reported to have declined in biomass in the eastern basin but increased in biomass in the central and western basins (Conroy et al. 2005). Lake Erie whitefish undergo seasonal migrations from the eastern basin into the central and western basins (Lumb et al. 2007), and by doing so could gain access to more dense zooplankton communities. Finally, conclusions about changes in lake whitefish growth in Lake Erie may partially depend

on how data were analyzed. Previously, temporal trends in growth (size-at-age) in Lake Erie were considered to be more stable than trends observed in Lake Ontario. However, recent work based on growth curves of Lake Erie lake whitefish collected in 1991–2003 suggested growth rates declined relative to those estimated prior to 1986, which was the earliest time period considered in previous assessments (Lumb et al. 2007, Lumb and Johnson 2012).

Lake Simcoe

Like lake whitefish in Lake Erie, the pattern observed in lake whitefish in Lake Simcoe is largely inconsistent with the general pattern observed in the rest of the Great Lakes. Unlike other lake whitefish populations investigated, growth rates, condition, size-at-maturity, and abundance all *increased* in Lake Simcoe after dreissenid invasion, while age-at-maturity *declined*. Also, unlike other lakes discussed in this chapter, *Diporeia* has never been reported in Lake Simcoe (Rawson 1930). Like many lake whitefish populations in the Great Lakes, fish in Lake Simcoe were subject to many simultaneous stressors, including nutrient abatement and urbanization (Evans et al. 1996, Winter et al. 2007). However, differences in response of lake whitefish in Lake Simcoe compared to most in the Great Lakes suggest some additional studies may be warranted.

Total abundance of the benthic invertebrate community in the offshore region of Lake Simcoe declined between 1983 and 2008 (Jimenez et al. 2011). However, biomass over the same time period increased for certain taxa due to a shift in size distributions. Additionally, certain nearshore taxa extended their distribution to deeper waters. Thus, subtle changes in benthic invertebrate communities may be responsible for a sustained lake whitefish population in Lake Simcoe. Ongoing research into ecosystem-level changes in the absence of *Diporeia* may help to better explain trends in Lake Simcoe whitefish populations after dreissenid establishment. In particular, comparisons between lake whitefish populations in Lake Simcoe and Lake Erie may prove to be useful to determine why neither has responded like so many other populations in the Great Lakes to dreissenid establishment.

CHANGES IN LAKE WHITEFISH POPULATIONS WITHOUT DREISSENIDS

Lake Superior: *Diporeia* Declines

Long-term patterns in lake whitefish populations in areas where dreissenids are absent further support the hypothesis that some aspects of lake whitefish life histories are more closely linked to resource abundance (e.g., densities of *Diporeia*), whereas other aspects may be indicative of stressors not yet identified. Declines in *Diporeia* populations in Lake Superior between 1994 and 2000 were observed in

regions near Whitefish Bay and the Apostle Islands where dreissenids had not colonized (Scharold et al. 2004). While these declines were not nearly as large or sudden as in the lower Great Lakes where dreissenids were established, lake whitefish from both regions displayed declines in condition (Figure 42.6a) and growth (Figure 42.6b) between the early 1990s and 2000. However, trends over this period may just reflect a general pattern of declines over the longer term (Figure 42.6). Relative and overall abundance of *Diporeia* between the 1970s and early 2000s (Scharold et al. 2004) suggest that other factors besides intraspecific resource limitation influence these more long-term patterns in lake whitefish.

Though data prior to 1990 are sparse, a pattern of gradual increase in age-at-maturity in Lake Superior populations seems evident (Figure 42.7a). This suggests the influence of some unidentified stressor(s) not yet considered. Discrepancies between results presented here for Whitefish Bay, Lake Superior (Table 42.1), and those of Wang et al. (2008) are likely due to differences in methodologies. Although the statistical approach used was identical (Beauchamp et al. 2004), the manner in which data were grouped for estimating age-at-maturity was different. Wang et al. (2008) estimated age- and length-at-maturity for a group of cohorts during two different time periods (before and after 1990; Wang et al. 2008), whereas results

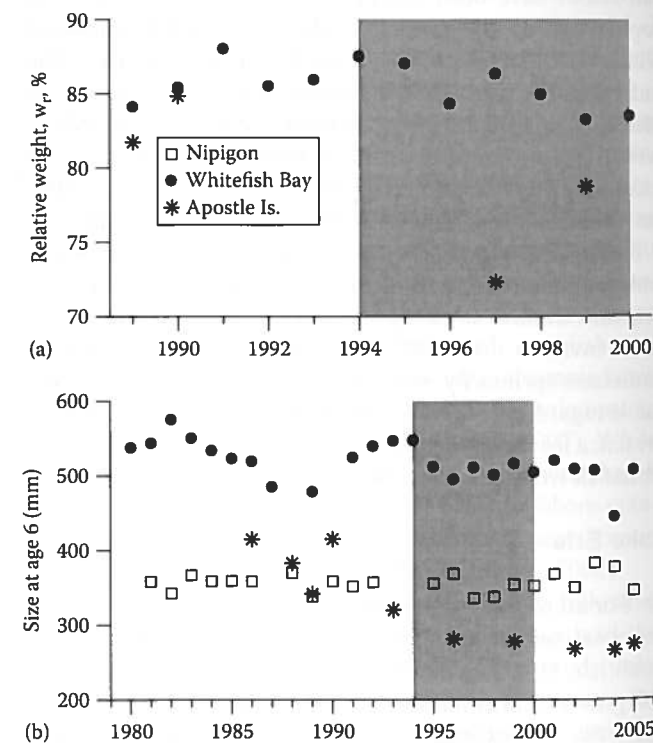


Figure 42.6 Lake whitefish condition (relative weight, W_t , Rennie and Verdon 2008, panel a) and size at age 6 (panel b) from Lake Superior (Whitefish Bay, Apostle Islands) and Lake Nipigon. Gray shaded area represents period of reported *Diporeia* declines in Lake Superior. (From Scharold, J.V. et al., *J. Great Lakes Res.*, 30, 360, 2004.)

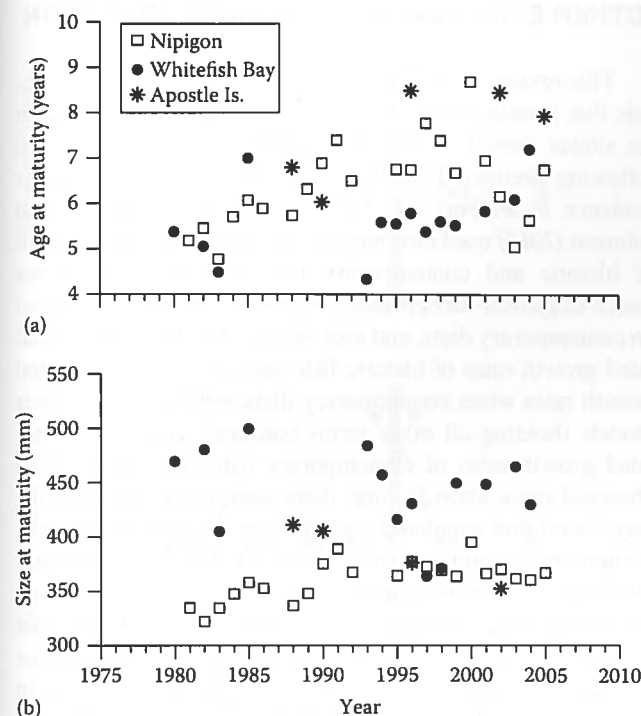


Figure 42.7 Mean age (panel a) and size (panel b) at 50% maturity of lake whitefish populations from Lake Superior (Whitefish Bay, Apostle Islands) and Lake Nipigon as estimated using the method of Beauchamp et al. (From Beauchamp, K.C. et al., *J. Great Lakes Res.*, 30, 451, 2004). Linear trends in age-at-maturity are significant (positive) for Lake Nipigon only ($p = 0.04$). Linear trends in size-at-maturity are significant (positive) for Lake Nipigon ($p = 0.001$) and Apostle Islands (negative, $p = 0.002$).

presented here were based on age-at-maturity estimated for a given year, fitting the statistical model to all cohorts captured within a particular year. Both methods integrate data from many cohorts over time, but the method adopted here permits age-at-maturity estimates for each year in series, for the group of fish spawning in that particular year, rather than limiting estimates for comparison across two time periods only.

Lake Nipigon: *Diporeia* Stable

Like Lake Superior, Lake Nipigon is another large-lake system that has *Diporeia* but few dreissenids; indeed, dreissenids have not been reported from Lake Nipigon. Lake whitefish in Lake Nipigon show no significant detectable trends in growth and no reported changes in abundance (Figure 42.6; Table 42.1); however, recent analysis suggests a decline in condition (Rennie et al. 2010). While historic data are sparse, there is no indication that *Diporeia* in Lake Nipigon has declined. Abundance in the 1920s was about 1000/m² (Adamstone 1924), while a recent survey reported that mean amphipod abundance density at 20 m depth was 2300/m² (Bentz et al. 2002). Amphipods at this depth were likely *Diporeia*

(McNickle et al. 2006). Lake whitefish length- and age-at-maturity in Lake Nipigon increased, though there was some evidence of earlier maturation in recent years (Figure 42.7).

DREISSENID EFFECTS VIA DECLINES IN RESOURCE ABUNDANCE

The most common and consistent pattern that emerges from this chapter of available information on interactions between dreissenid mussels, lake whitefish populations, and *Diporeia* is that, with one notable exception, lake whitefish growth and condition appear to respond negatively to *Diporeia* declines, even in the absence of dreissenids. Fish condition appears to track temporal declines in *Diporeia* more closely than growth. The correspondence between declines in *Diporeia* abundance and declines in lake whitefish growth and condition suggests the processes that control growth and condition (e.g., food intake, activity) may also be affected by *Diporeia* abundance. Recent work has shown this appears to be true (Rennie et al. 2012a). Rates of lake whitefish consumption, activity, and conversion efficiency were correlated to *Diporeia* abundance (Figure 42.8).

There are some interesting commonalities in the two lakes that were invaded by dreissenids but where growth rates of lake whitefish increased or did not change (Lake Erie and Lake Simcoe). Both lakes are relatively shallow; mean depth of Lake Simcoe is 15 m (Rawson 1930), and mean depth of Lake Erie is 18 m (Rawson 1952). These depths are only 20%–23% of mean depths in the other Great Lakes or in Lake Nipigon (Rawson 1952). Total abundance and biomass of benthos has generally increased in shallow nearshore regions but declined in offshore regions following dreissenid establishment (Higgins and Vander Zanden 2010). Thus, increased food availability in nearshore benthos could mitigate declines in offshore regions, but evidence for such an offset of resources is inconsistent between lakes. In Lake Erie, lake whitefish did not show evidence of increased reliance on nearshore resources (Lumb and Johnson 2012). However, in South Bay (Lake Huron), which is also a relatively shallow system (mean depth 16 m, King et al. 1997), lake whitefish demonstrated an increased reliance on nearshore resources (Rennie et al. 2009b), but growth and condition declined nonetheless (Rennie et al. 2009a). In Lake Champlain, another relatively shallow system, growth and condition of lake whitefish actually appears to have recovered after the establishment of dreissenids (S. Herbst and J. E. Marsden, personal communication). Like Lake Erie, *Diporeia* in Lake Champlain disappeared after dreissenid invasion (Dermott et al. 2006). Unique responses of lake whitefish after dreissenid establishment in these systems (Lake Erie, Lake Champlain, Lake Simcoe) may be associated with differences in nutrient inputs. Although nutrient abatement programs reduced total phosphorus loading

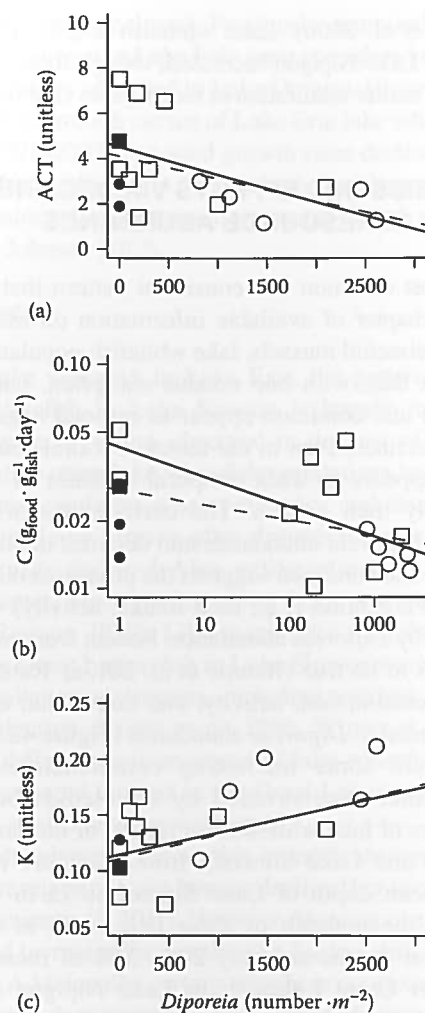


Figure 42.8 Relationships among activity (ACT) (panel a), consumption (C) (panel b), and conversion efficiency (K) (panel c) of lake whitefish with *Diporeia* density. Squares are populations with dreissenids established, and circles are those without. Filled symbols are populations in which *Diporeia* were historically absent or where their absence preceded the appearance of dreissenids. Dashed lines are relationships over all populations; solid lines are relationships excluding filled symbols. (Reproduced from Rennie, M.D. et al., *Can. J. Fish. Aquat. Sci.*, 69, 41, 2012a. With permission.)

in Lake Simcoe (Winter et al. 2007), Lake Erie (Dolan 1993, Dolan and McGunagle 2005), and Lake Champlain (Medalie et al. 2012), current nutrient inputs to all three systems are almost certainly higher compared to South Bay, Lake Huron, where nutrient levels are low and comparable to levels in the main lake basin (Fernandez et al. 2009). Further work that looks in detail at comparisons among populations from lakes of different basin morphology and/or nutrient inputs may provide a clearer explanation for the unique responses of lake whitefish to dreissenid invasion and/or *Diporeia* loss in these lakes versus most others.

OTHER EVIDENCE FOR RESOURCE LIMITATION

This review of observational studies supports the hypothesis that resource limitation is at least a partial explanation for slower growth and reduced condition in lake whitefish following dreissenid establishment. Models provide further evidence to support this hypothesis. Recently, Lumb and Johnson (2012) used bioenergetics models to simulate growth of historic and contemporary lake whitefish populations under reciprocal diet crosses (i.e., historic fish growth based on contemporary diets, and vice versa). They found that simulated growth rates of historic fish were slower than reported growth rates when contemporary diets were applied to their models (holding all other terms constant). Likewise, simulated growth rates of contemporary fish were greater than observed rates when historic diets were used. Additionally, they found that simulated growth rates declined as the proportion of dreissenids in diets increased. This work elegantly illustrated (1) the substantial impact that changes in diet (e.g., loss of *Diporeia*) can have on lake whitefish growth rates and (2) increased proportions of dreissenids in diets that are not also accompanied by increased consumption will result in decreased growth rates. Similarly, Pothoven and Madenjian (2008) estimated contemporary consumption rates of lake whitefish from Lakes Huron and Michigan would need to be up to 122% higher based on contemporary diets in order to achieve growth rates comparable to those observed prior to dreissenid establishment.

Experimental evidence also supports resource limitation as an explanation of declines in lake whitefish growth and condition following dreissenid establishment. Reductions of nutrient inputs to small boreal lakes generated dramatic declines in lake whitefish growth, condition, and abundance (Mills et al. 2002) that were similar to those observed in Lake Ontario after the disappearance of *Diporeia*. Fertilization of an acidified lake caused a pulse in recruitment and survival that resulted in a near order of magnitude increase in lake whitefish abundance (Mills et al. 2002). After nutrient additions were ceased in this lake, lake whitefish growth, condition, survival, and abundance declined dramatically, well beyond pre-manipulation levels (Figure 42.9). Because zooplankton make up a large portion of lake whitefish diets in inland lakes (Carl and McGuinness 2006), it is likely this pattern was the result of food limitation in the system. Zooplankton biomass declined dramatically after cessation of nutrient addition (M. Patterson, personal communication), which likely resulted in intense competition among lake whitefish. In another manipulation, fertilization of a lake resulted in faster growth and improved condition of lake whitefish (Mills 1985). A rapid and dramatic decline in lake whitefish condition (Mills and Chalanchuk 1987) and growth (Mills et al. 1998) in response to cessation of fertilization in the same lake was also documented, though changes in lake whitefish biomass were slower to respond (Mills and Chalanchuk 1987).

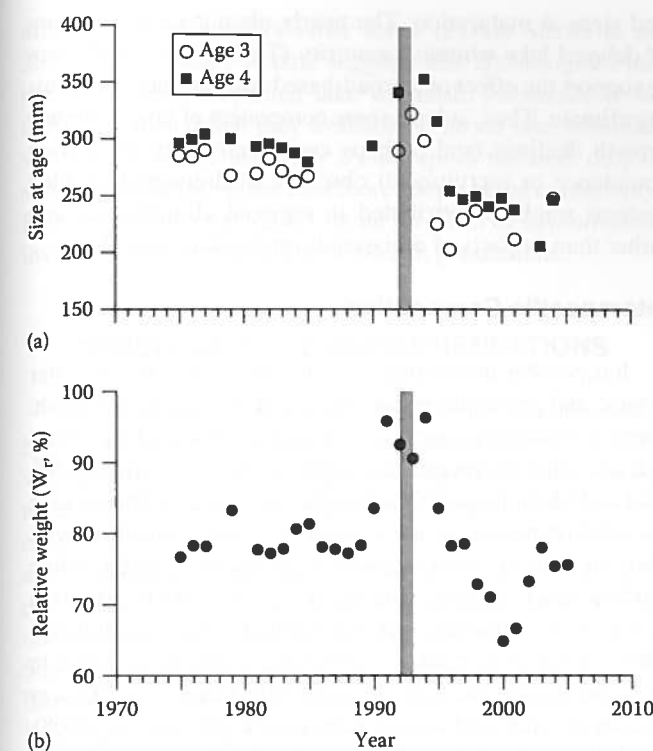


Figure 42.9 Mean size-at-age for age 3 and age 4 lake whitefish only (a) and (b) condition (relative weight, Rennie and Verdon 2008) of all lake whitefish encountered in an experimentally manipulated lake (Lake 302 North, Experimental Lakes Area, Ontario). Shaded region indicates period of nutrient (phosphorus) additions.

Both nutrient manipulation experiments suggested that declines in lake whitefish growth, condition, and abundance may be universal responses to reductions in system productivity and/or prey availability. Dreissenids appear to have negatively impacted primary productivity in the Great Lakes (e.g., Fahnenstiel et al. 2010) and hence deposition of primary production in profundal zones would also be reduced. Declines in growth and condition in lake whitefish may therefore reflect a general reduction in profundal resources. This appears to have been the case in South Bay, Lake Huron, where whitefish shifted their foraging habitat and behavior toward shallower regions (Rennie et al. 2009b). Perhaps shallow systems with higher nutrient inputs (e.g., Lakes Simcoe, Erie, and Champlain) may be enriched enough to maintain lake whitefish growth and production, despite the redirection of a substantial proportion of production to nearshore habitats at the expense of offshore habitats.

ALTERNATIVE HYPOTHESES/ CONTRIBUTING FACTORS

In addition to dreissenid colonization/*Diporeia* loss, there are several other stressors that may affect life-history traits of lake whitefish. Age-at-maturity increased in

every population except one (Table 42.1). Growth declines in many populations appeared to be more gradual than punctuated declines observed for other life-history traits. In many cases, changes in population abundance appeared to be more gradual (e.g., DeBruyne et al. 2008, Rennie et al. 2009a) than the establishment of dreissenids or loss of *Diporeia* could explain (e.g., Hoyle et al. 1999). A number of possible explanations for these broader, more long-term changes hypothesized in the literature include density dependence, fishery-dependent evolution, climate change, interspecific competition, and other invasive species.

Density Dependence

There is strong evidence for density-dependent growth in lake whitefish (Jensen 1981). In independent studies, experimentally controlled exploitation has resulted in increased lake whitefish growth and recruitment after a proportion of the lake whitefish population was removed, presumably as a result of decreased intraspecific competition (Healey 1975, Healey 1980, Mills and Chalanchuk 1988). Recruitment, juvenile survival, and growth of lake whitefish were all shown to be density dependent in Lake Huron (Henderson et al. 1983). Lake whitefish body condition may also vary with density (Rennie et al. 2009a).

Given the historical tendency for lake whitefish populations to be density dependent, it is perhaps surprising that it is not as clear and apparent among contemporary lake whitefish stocks in the Great Lakes. Abundance in many populations actually declined as growth rates declined (Table 42.1, see Lake Ontario, central and southern Lake Huron, northern Lake Michigan, and southern Lake Superior). Density dependence has been invoked as an explanation for growth declines in central and southern Lake Michigan (DeBruyne et al. 2008). However, the same study also shows declines in growth and condition in northern Lake Michigan where CPUE had also declined. Another study compared temporal changes in lake whitefish growth and density and found that CPUE was less important than other biological (e.g., *Diporeia* abundance) or environmental variables (growing degree days >5°C, epilimnetic volume) in explaining growth declines (Rennie et al. 2009a). Both studies relied on passive sampling gear to estimate CPUE, which is subject to changes in fish activity and catchability as previously noted (Rudstam et al. 1984). Potential behavioral changes in lake whitefish following dreissenid invasion may bias gillnet catch data and influence conclusions regarding density-dependent growth of lake whitefish in the Great Lakes in the period of dreissenid establishment. A study by Stapanian and Kocovsky (2013) also provided evidence of behavioral changes in other fish species in response to dreissenid-induced ecosystem changes in Lake Erie that have potential to influence CPUE and density estimates. Formal studies that examine relationships between annual density estimates from multiple methods (e.g., capture-recapture, active sampling gear) with growth rates and

with biologically relevant time lags in response considered may provide a more robust evaluation of density dependence among contemporary Great Lakes stocks.

Climate Change

Authors have speculated about the effects of climate change on lake whitefish populations occurring both in the Great Lakes (Lynch et al. 2010) and in inland lakes (Rennie et al. 2010). The entire Great Lakes region, but especially regions in the upper Great Lakes, has experienced substantial increases in air temperature over the past 30–40 years, particularly since the early 1990s (Jensen et al. 2007, Rennie et al. 2010). Duration of ice cover over the past 30 years has also declined (Jensen et al. 2007), and thermocline depth (and therefore epilimnetic volume) in many lakes appears to have decreased (King et al. 1997, 1999, Snucins and Gunn 2000, Coats et al. 2006, Keller et al. 2006, Keller 2007), as supported by climate model predictions (McCormick 1990, Hondzo and Stefan 1993). Rennie et al. (2010) implicated warmer air temperatures and shallower thermoclines in contributing to reduced rates of primary productivity, which could negatively affect profundal deposition of pelagic algae and abundance of *Diporeia*. Variables associated with climate have been shown to be correlated with *Diporeia* abundance (Rennie et al. 2009a).

In lake whitefish, impacts of warmer air temperatures appear to be stage dependent. In their first year, growth rates of lake whitefish have been shown to be positively related to annual growing degree days (GDD, number of days above a critical temperature) $>0^{\circ}\text{C}$ (Henderson et al. 1983). For older lake whitefish that are capable of behavioral thermoregulation, the opposite was true; that is, third-year growth of fish from south Bay, Lake Huron, was negatively related to annual GDD $>5^{\circ}\text{C}$ but positively related to the percent volume of the epilimnion within the bay (i.e., increasing thermocline depth, Rennie et al. 2009a). Body condition was found to decline in populations in northwest Ontario where climate has warmed dramatically over the past 40 years, whereas body condition was more stable in southern Ontario where climate warming has been less dramatic (Rennie et al. 2010). Taylor et al. (1987) found colder, more severe winters were associated with higher recruitment events and egg survival. Henderson et al. (1983) found that environmental conditions at spawning (November) and hatching (April) did not influence year-class strength, suggesting that at this stage, larval competition for resources can influence juvenile survival rates, independent of environmental conditions (Freeberg et al. 1990).

The sum of evidence suggests that warmer temperatures over the past 40 years would negatively affect lake whitefish. While growth rates in the first year may be more rapid in warmer climates, egg survival and recruitment might be expected to decline (due to milder winters), as would growth rates and body condition of older year classes approaching sexual maturity. This might in turn cause delays in maturity

and sizes at maturation. The nearly ubiquitous observation of delayed lake whitefish maturity (Table 42.1) would seem to support the effect of a broad-based stressor such as warming climate. Thus, at least some component of lake whitefish growth declines (and perhaps even declines in population abundance or recruitment) observed in dreissenid-invaded systems might be attributed to regional climate warming rather than impacts of dreissenids on resource abundance.

Interspecific Competition

It is possible that changes in fish communities in coldwater pelagic and profundal regions have influenced lake whitefish. There is evidence of negative interactions between lake whitefish and other deepwater coregonines (Davis and Todd 1998, Carl and McGuinness 2006). In Lake Superior, declines in lake whitefish densities in the mid-1990s were coincident with sharp increases in bloaters densities (Bronte et al. 2003). While rainbow smelt (*Osmerus mordax*) have also been suggested to negatively influence lake whitefish (Loftus and Hulsman 1986), densities of rainbow smelt have gradually declined in the upper Great Lakes (Bronte et al. 2003, Riley et al. 2008), as have most other coldwater demersal fishes (Riley et al. 2008). While lake whitefish and round whitefish have considerable dietary overlap, spatiotemporal differences in habitat preferences were concluded to mitigate any substantial competition between these fishes (Macpherson et al. 2010).

Fishery-Dependent Evolution

A number of studies have shown clear relationships between lake whitefish mortality rates and life-history strategies, based on a theoretical foundation of life-history invariants (Jensen 1985, Jensen 1996). Evolutionary models have demonstrated how relationships among life-history traits can lead to fishery-induced evolution through various harvest strategies (Wang and Hook 2009). Typically, evolutionary consequences of fisheries-induced mortality (via selection of the largest individuals following maturity) include more rapid growth and earlier and smaller sizes at maturity as harvest rates increase. Where commercial harvest does appear to have increased in Lakes Michigan and Huron over the past 30 years (Mohr et al. 2005, DeBruyne et al. 2008), patterns of lake whitefish growth and maturity in Great Lakes stocks are opposite those predicted by fishery-dependent evolution (Table 42.1).

Other Invasive Species

It is possible that other invasive species have contributed to patterns observed in lake whitefish after dreissenid establishment. An obvious candidate might be the spiny water flea, *Bythotrephes longimanus*, which invaded the Great Lakes only 5 years before dreissenids (Sprules et al. 1990). *Bythotrephes* can make up a substantial component of lake whitefish diets (Macpherson et al. 2010) and has negatively

affected growth rates of other fishes (Parker Stetter et al. 2005). Yet evidence to date suggests that *Bythotrephes* has not significantly impacted lake whitefish. Fernandez et al. (2009) estimated that prey available to larval lake whitefish was similar before and after *Bythotrephes* invaded, despite significant changes in the nearshore zooplankton community. Further, Rennie et al. (2010) found no effect of *Bythotrephes* invasion on condition of lake whitefish populations.

CONCLUSION AND RECOMMENDATIONS

An examination of available data seems to support the hypothesis that effects of dreissenid establishment on lake whitefish have been largely negative in oligotrophic systems but appear to have been less pronounced in more shallow, nutrient-rich systems. Observed declines in lake whitefish growth and condition associated with dreissenid invasion appear to be due to food limitation, consistent with evidence from populations without widespread dreissenid establishment (e.g., Lake Superior), or from populations in experimentally manipulated lakes where a decrease in resources resulted in similar patterns. While more research is needed to help clarify the context dependence of dreissenid establishment on lake whitefish populations and the underlying mechanisms involved, a broader investigation that considers systems both in and outside the Great Lakes basin may ultimately provide the most fruitful approach.

Directed future research may help to fill what appear to be major knowledge gaps in understanding effects of dreissenid establishment on lake whitefish. Quantitative comparisons of contemporary data on larval lake whitefish to historic data prior to dreissenid establishment are lacking. Though Fernandez et al. (2009) estimated little effect of dreissenid establishment on the energy available to larval prey, their conclusions were based on changes observed in the nearshore zooplankton community. With one notable exception (Hoyle et al. 2008), data on changes in lake whitefish recruitment during dreissenid establishment are also sparse. Further investigation into both of these topics would substantially improve our understanding of why differences in abundance patterns exist among stocks where dreissenids have established.

Additionally, focused laboratory studies that investigate assimilation and growth of lake whitefish fed various prey items, including dreissenids, would substantially contribute to our understanding of the role of diet changes (vs. behavioral or environmental changes associated with dreissenid invasion) on lake whitefish life histories. While it is generally assumed that dreissenids are energy poor and difficult to handle relative to other diet items (Owens and Dittman 2003, Pothoven and Madenjian 2008, Rennie et al. 2009b), there have been no laboratory studies to date that attempt to verify this empirically. Indeed, lake whitefish in the Great Lakes are persisting on diets consisting largely of dreissenids and may even exert enough predation pressure so as to influence dreissenid abundance and distribution (Madenjian et al. 2010).

Uncertainty regarding effects of dreissenid establishment on lake whitefish swimming behavior and dispersal—and therefore the potential to affect catchability of passive gear—also deserves investigation (Rennie et al. 2012a). The ability of government agencies to set sustainable harvest quotas is highly dependent on the ability to accurately estimate population abundance. Direct comparisons of active and passive sampling methods between populations in invaded and noninvaded lakes, or among populations known to vary in swimming behavior or resource availability, could provide estimates of the potential magnitude that intraspecific variation in behavior can have on gear encounter and, in turn, population abundance estimates.

Finally, these are not simple systems, and many stressors are likely impacting whitefish populations simultaneously (Rennie et al. 2009a). As such, observational data must be subjected to analytical approaches that consider multiple stressors and partition variance of many potential stressors on response variables of interest (e.g., Deroba and Bence 2009).

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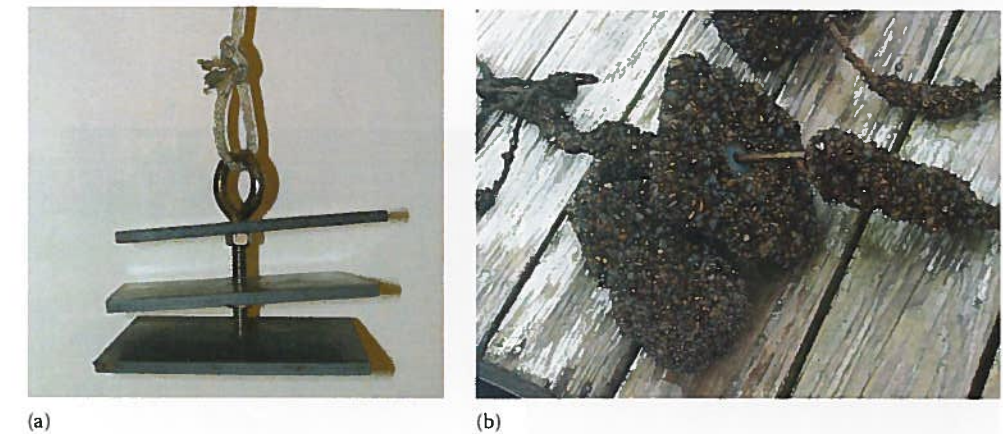


Figure 2.3 Settling plate array used to monitor seasonal recruitment of juvenile zebra mussels. (a) Plate prior to deployment and (b) plate after 24 weeks deployment at station CHIP in 2003.

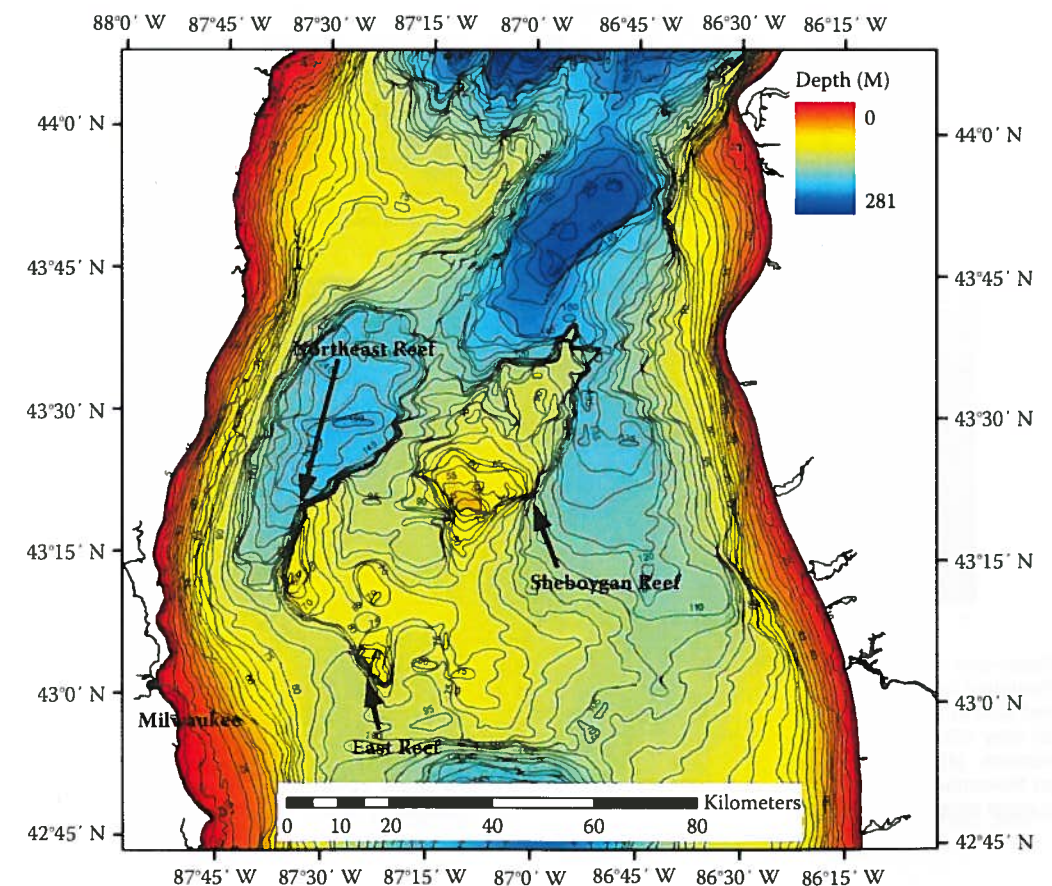


Figure 4.1 Bathymetry of central Lake Michigan's MLRC indicating positions of the three major summits, East Reef, Northeast Reef, and Sheboygan Reef. (Modified from NOAA: Great Lakes Data Rescue Project—Lake Michigan Bathymetry, Area III, 2010.)