

Mapping the Condition of *Diporeia*: Insights into Mechanisms of Declines

Primary Investigator: Tom Nalepa - NOAA GLERL (Emeritus)

Co-Investigators: Dave Fanslow, Steve Pothoven - NOAA GLERL, Tom Johengen, Mike Wiley, David Jude, Wendy Stott - CILER, University of Michigan, Tomas Hook, Marisol Sepulveda, Krista Nichols, Jiri Adamec - Purdue University, Jacques Rinchar - SUNY Brockport

Overview

We will evaluate the general hypothesis that physiological condition and genetic diversity of *Diporeia* varies throughout the Great Lakes region, and specifically that individual organisms inhabiting pockets of persistence within lakes Michigan, Huron, and Ontario and throughout Lake Superior and the Finger Lakes, are in better condition than individuals from decimated areas. While coarse measures of condition may not detect subtle impacts of changes in food quality or unknown stressors, we suggest that sensitive measures of individual condition will respond not only to low food conditions, but also to poor food quality, contaminants, and disease. To evaluate this hypothesis, we will: 1) Undertake a large scale field survey to collect *Diporeia* from throughout the Great Lakes region and map their physiological condition and genetic variation; 2) In the laboratory, use metabolomic techniques to characterize the metabolite profiles expressed by individual *Diporeia* when exposed to various environmental stressors; and 3) Integrate field survey and experimental results to conduct a focused assessment of metabolite profiles of natural populations to elucidate potential causes of population declines.

Proposed Work

1. Undertake a large scale field survey to collect *Diporeia* from throughout the Great Lakes region and quantify their physiological condition and genetic variation.
2. In the laboratory, use metabolomic techniques to characterize the metabolite profiles expressed by individual *Diporeia* when exposed to various environmental stressors.



Sample processing and analysis at the Great Lakes Environmental Research Laboratory

Scientific Rationale

The holo-arctic amphipod, *Diporeia* spp., historically constituted a large component of benthic invertebrate communities throughout the Great Lakes region. However, since the early 1990's, this species-group has experienced a precipitous decline in abundance in not only lake Michigan (Nalepa et al. 1998), but also lakes Huron (Nalepa et al. in press), Erie (Dermot and Kerec 1997), and Ontario (Dermott 2001; Lozano et al. 2001). Despite intense research efforts, mechanisms of these declines remain enigmatic (Nalepa et al. 2006a; 2006b). However, declines have occurred coincident with establishment of invasive dreissenid mussels, suggesting that dreissenid-induced changes to lower trophic levels or alteration of lake physical properties may be contributing mechanisms. Interestingly, *Diporeia* declines have not progressed in a spatially uniform manner, and there are areas within the aforementioned lakes (especially offshore sites) and Lake Superior (Scharold et al. 2004; Dermott et al. 2005; Nalepa et al. 2006b) where *Diporeia* persist. Further, *Diporeia* remains abundant in other systems (e.g., New York's Finger Lakes) despite invasion by dreissenids (Dermott et al. 2005). This suggests that *Diporeia* population characteristics and/or environmental conditions critical for persistence vary across and within systems.

While the mechanisms of the *Diporeia* decline remain unclear, the negative consequences for certain Great Lakes fish populations are unequivocal. *Diporeia* historically constituted an important source of energy for many Great Lakes fish populations (e.g., Lake Whitefish *Coregonus clupeaformis*, Yellow Perch *Perca flavescens*, Alewife *Alosa pseudoharengus*, Slimy Sculpin *Cottus cognatus*, Deepwater Sculpin *Myoxocephalus thompsonii*, Bloater *Coregonus hoyi*, and Rainbow Smelt *Osmerus mordax*; Wells and Beeton 1963; Wells 1980). Many of these species have now shifted their diets in response to the declines of *Diporeia* (e.g., Pothoven et al. 2001; Owens and Dittman 2003; Hondorp et al. 2005) and experience reduced growth rates and condition (e.g., Pothoven et al. 2001; Madenjian et al. 2003 and 2006; Hondorp et al. 2005). In particular, condition of lake whitefish stocks (an ecologically and commercially important species) have declined in lakes Michigan (Pothoven et al. 2001 and 2006), Huron (Pothoven et al. 2006), and Ontario (Hoyle et al. 1999; also see workshop

proceedings Mohr and Nalepa 2005). Previously, Lake Whitefish derived a substantial proportion of annual energy from *Diporeia*, but now whitefish rely on an altered diet, including a significant amount of dreissenid mussels (a low energy prey item, which is difficult to digest; Pothoven et al. 2001; Pothoven 2005; Pothoven and Nalepa 2006). In short, the proliferation of dreissenid mussels and the decline of *Diporeia* may not only threaten the ecological integrity of Great Lakes ecosystems, but also may compromise the sustainability of economically important fisheries (e.g., both commercial and subsistence lake whitefish fisheries and recreational salmonine fisheries). Thus, it is imperative to elucidate the underlying mechanisms of *Diporeia* declines so that we can better predict if these declines are likely to spread to other areas, or if declines are likely to reverse themselves. Further, such elucidation could reveal if other taxa (e.g., *Mysis*) are in imminent risk of experiencing similar declines.

Mean lipid content (% dry weight) of *Diporeia* in each water body sampled in 2008. Values with the same letter are not significantly different (ANOVA, P = 0.05). We hypothesized that lipid levels would be lower in lakes where *Diporeia* is declining, but there does not appear to be a correlation. That is, *Diporeia* is not declining in Lakes Superior and Cayuga, yet *Diporeia* in these two lakes have the lowest (Superior) and highest (Cayuga) mean lipid content of all the lakes measured.

Water Body	Lipid Content (%)	Station Range	n
Superior	20.89 ± 0.71 ^a	18.17 – 21.99	78
Huron	22.57 ± 2.96 ^{ab}	21.75 – 24.44	53
Michigan	23.17 ± 0.86 ^{ab}	13.88 – 32.43	160
Batchawana Bay	27.44 ± 0.79 ^{bc}		70
Ontario	30.57 ± 1.27 ^c	22.24 – 35.46	78
Cayuga	31.15 ± 1.05 ^c		60

While several studies have documented both spatio-temporal patterns of Great Lakes *Diporeia* declines and subsequent consequences for various fish populations, relatively few studies have evaluated potential underlying mechanisms of declines (see Nalepa et al. 2006b). Further, most studies have individually evaluated a single potential causative factors of *Diporeia* declines and have generated equivocal conclusions. For instance, there is both supportive and refutative evidence relating to the most obvious hypothesis, i.e., that dreissenid mussels have out-competed *Diporeia* for limited food resources (Nalepa et al. 2006a). *Diporeia* burrow and feed on material deposited onto sediments (Nalepa et al. 2006a) while dreissenid mussels filter water above the sediments. Therefore, dreissenids could potentially intercept settling algae before they reach *Diporeia*. During the initial decline of *Diporeia* at a Lake Michigan site these organisms experienced a drastic drop in lipid levels (Nalepa 2006a). However, physiological condition appeared to quickly rebound and while *Diporeia* abundances remained low, lipid levels increased to levels comparable to those observed prior to the arrival of dreissenids (Gardner et al. 1985; Nalepa et al. 2006a). In addition, one might expect that under resource limitation *Diporeia* populations would decline to abundances found in less productive systems (e.g., L. Superior) and not become locally extinct (Dermott et al. 2005).

Studies evaluating other potential causes of the *Diporeia* decline have similarly yielded inconsistent results. 1) Dreissenid toxins: It is possible that the decline of *Diporeia* is related to

some unknown toxic agents associated with dreissenid mussels. Dermott et al. (2005) showed that *Diporeia* fed a diet of zebra mussel pseudo-feces survived at a lower rate than *Diporeia* fed normal diets. However, observations that *Diporeia* persist in several areas with large dreissenid mussel colonies (e.g., Finger Lakes, some areas of Lake Michigan) would seem to indicate that *Diporeia* survival is possible in the presence of dreissenids. 2) Contaminants: Another hypothesis is that the bio-availability of anthropogenic sediment contaminants or natural toxins has increased through dreissenid activities. *Diporeia* are sensitive to certain anthropogenic-related contaminants (Gossiaux et al. 1993) and are largely absent in areas with persistent contaminants. However, Landrum et al. (2000) found no increased mortality for *Diporeia* reared in sediments from areas recently devoid of the species group. On the other hand, Landrum et al. (2000) observed that *Diporeia* tended to avoid such sediments and Dermott et al. (2005) found that survival of *Diporeia* in the laboratory differed depending upon sediment source. 3) Food quality: Historically, *Diporeia* have relied upon diatoms as a key source of energy. Phytoplankton such as diatoms contain high levels of polyunsaturated fatty acids which are key molecules for growth, reproduction, and survival. If dreissenids reduce diatom concentrations (Makarewicz et al. 1999), then they may be unavailable to *Diporeia*. Consistent with this hypothesis, recruitment of *Diporeia* has failed in some areas of Lake Michigan (Nalepa 2006a). However, this hypothesis has not been thoroughly evaluated. 4) Disease/Parasites: Another hypothesis is that declines of Great Lakes *Diporeia* are attributable to a disease or parasite epidemic. While several parasites have been found on Great Lakes *Diporeia*, there is no indication that parasite burdens are higher than pre-decline levels, and there are no clear spatial differences in parasite burdens between decimated and seemingly-healthy *Diporeia* populations (Messick et al. 2004; Foley et al. 2006; Nalepa et al. 2006b). On the other hand, Dermott et al. (2005) found that the addition of dying *Diporeia* to otherwise normal *Diporeia* cultures dramatically reduced survival, suggesting the possibility of a disease agent. 5) Genetics: Finally, *Diporeia* taxonomy is not well understood (but see Bousfield 1989) and it is likely that different species are present throughout the Great Lakes. Therefore, it is possible that spatial differences in relative survival of *Diporeia* may simply arise from population or species-level differences in susceptibility to some causative agents (Nalepa et al. 2006b). Preliminary mitochondrial DNA analysis indicates that there are two distinct *Diporeia* lineages in North America: a 'western' group, observed in Lake Superior and, rarely, in Lake Huron, and an 'eastern' group found in lakes Huron, Michigan, Ontario, and the Finger Lakes in New York (Nalepa et al. 2006b).

Hypotheses

We will evaluate the general hypothesis that physiological condition and genetic diversity of *Diporeia* varies throughout the Great Lakes region, and specifically that individual organisms inhabiting pockets of persistence within lakes Michigan, Huron, and Ontario and throughout Lake Superior and the Finger Lakes, are in better condition than individuals from decimated areas. While coarse measures of condition may not detect subtle impacts of changes in food quality or unknown stressors, we suggest that sensitive measures of individual condition will respond not only to low food conditions, but also to poor food quality, contaminants, and disease.

To evaluate this hypothesis, we will: 1) Undertake a large scale field survey to collect *Diporeia* from throughout the Great Lakes region and map their physiological condition and genetic variation; 2) In the laboratory, use metabolomic techniques to characterize the metabolite profiles expressed by individual *Diporeia* when exposed to various environmental stressors; and 3) Integrate field survey and experimental results to conduct a focused assessment of metabolite profiles of natural populations to elucidate potential causes of population declines.

Research Design/Methods

Our specific research objectives for this project are three-fold:

1. Undertake a large scale field survey to collect *Diporeia* from throughout the Great Lakes region and map their physiological condition and genetic variation.
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Governmental/Societal Relevance

The ramifications of the *Diporeia* decline in Lake Michigan have been far reaching, affecting a series of ecologically and economically important fish and fisheries. Understanding the mechanistic causes of this decline is necessary before any potential management actions can be put forth. It should be noted, however, that for many potential causes of the *Diporeia* decline, necessary management actions to reverse the decline may be infeasible. For instance, if *Diporeia* are now limited by the quantity or quality of their food (due to decreased system-wide nutrient loading and dreissenid filtering activities), then potential reactive management actions (i.e., undoing nutrient abatement measures and actively controlling dreissenids) are both politically and technically intractable. Nonetheless, understanding the mechanisms of the decline is necessary to prevent inappropriate management actions. Further, such understanding can facilitate predictions of whether other taxa (e.g., *Mysis*) are at risk of similar decline. Finally, documenting potential invasive species effects (i.e., dreissenid-induced *Diporeia* decline) may provide fodder to advocate for more stringent future controls of potential invaders.

Relevance to Ecosystem Forecasting

Hindcasting and forecasting how dreissenid mussels have and will impact important native taxa, such as *Diporeia*, is confounded by a poor mechanistic understanding of the effects of dreissenids. This project should contribute towards improving such mechanistic understanding and hopefully facilitate future hindcasting/forecasting.