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DISAPPEARANCE OF THE AMPHIPOD *DIPOREIA* SPP. IN THE GREAT LAKES: WORKSHOP SUMMARY, DISCUSSION, AND RECOMMENDATIONS

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Disappearance of the amphipod *Diporeia* spp. in the Great Lakes: Workshop Summary, Discussions, and Recommendations

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EXECUTIVE SUMMARY

A workshop was held in October, 2006 to discuss population status and causes of the disappearance of the benthic amphipod *Diporeia* spp. in the Great Lakes, and to provide recommendations for future research. Recent surveys indicate that *Diporeia* continues to decline in Lakes Michigan, Huron, and Ontario, but surveys in Lake Superior are conflicting. One data set shows that the population in Lake Superior is declining in offshore regions (> 90 m) but not in nearshore regions (< 90 m). Other data sets show that the population is stable throughout the lake. Reasons for this discrepancy were not resolved. In the other lakes, *Diporeia* are now rare or completely gone at depths < 90 m, and are declining at depths > 90 m. Declines at the latter depths are preceding the expansion of *Dreissena bugensis* (quagga mussel) from shallow to deeper regions. While there is a strong negative relationship between *Diporeia* and *Dreissena* in the Great Lakes, *Diporeia* remains abundant in the Finger Lakes, New York, despite the long-term presence of *Dreissena*. There are areas in the Great Lakes where *Diporeia* seemed to persist but are now declining, indicating that environmental conditions do play a mitigating role to some extent. While there was agreement that *Dreissena* was the cause of the disappearance of *Diporeia* in the Great Lakes, a survey of workshop participants indicated no clear consensus on potential mechanisms for the negative response. The most popular theories were food limitation directly or indirectly related to dreissenid filtering activities, a toxic by-product associated with dreissenid biodeposits, and an introduced pathogen/disease. Based on previous field surveys and laboratory experiments, there are inconsistencies in each of these theories, which may imply a multitude of causative factors whose relative importance may vary depending on specific environmental conditions. Given the potential for multi-stressors, techniques that provide genomic or protein profiles offer promise in defining a specific cause. Included among the recommendations for future research are continued monitoring of *Diporeia* in the Finger Lakes along with an assessment of conditions that allow it to persist, experiments to further define a dreissenid by-product that negatively impacts *Diporeia*, the development of genomic and proteonic approachesspecific for *Diporeia*, a better definition of taxonomic status, and further efforts to characterize/resolve conflicting trends in offshore populations in Lake Superior.

INTRODUCTION

Over the past few decades, one of the most dramatic and enigmatic changes in the biotic community of the Great Lakes has been the decline of the deep-water amphipod *Diporeia* spp. This organism was once the dominant benthic taxa in offshore waters (> 30 m) of all the lakes. Recently however, population declines have been documented in Lakes Michigan, Huron, Erie, and Ontario, and large areas in each of these lakes are now completely devoid of this organism (Dermott and Kerec 1997, Nalepa et al. 1998, 2003, Dermott 2001, Lozano et al. 2001) (Figure. 1).

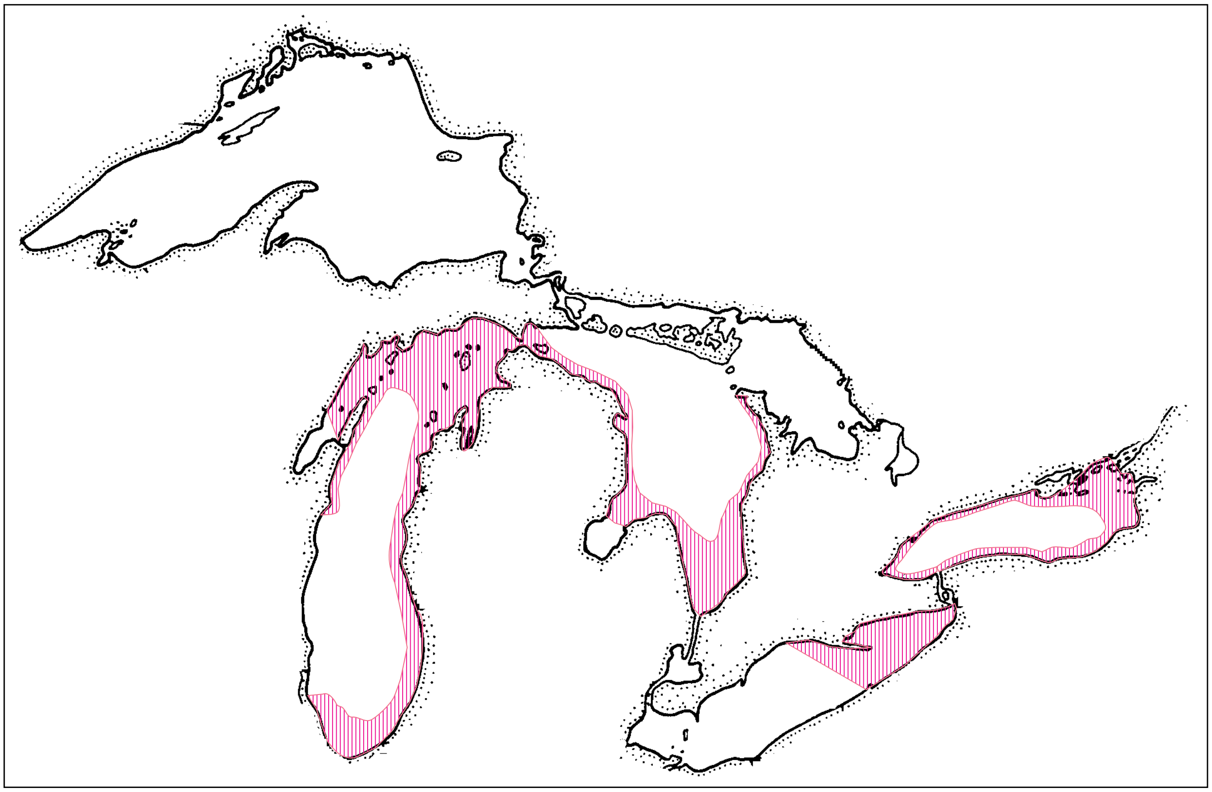

Figure 1. Area of the Great Lakes where *Diporeia* were once present but are now completely gone (hatched area). There is some evidence that *Diporeia* are now gone from portions of Georgian Bay and North Channel, Lake Huron, but the spatial extent of its disappearance is not known. Because of warm water temperatures, *Diporeia* are naturally not found in Green Bay, Saginaw Bay, Lake St. Clair, and in the western and central basins of Lake Erie.

Diporeia have long been considered a keystone species in the food web of offshore waters. It resides in the upper sediments and feeds on fresh organic material settled from the water column and, in turn, are fed upon by many fish species. Thus, it plays an important role in cycling energy from lower to upper trophic levels. *Diporeia* are high in lipids and therefore rich in calories, making it a valued food resource for fish. Recent changes in the condition, distribution, and abundances of several fish species have been attributed to the loss of this organism (Madenjian et al. 2003, Hondorp et al. 2005). A recent workshop explored the impact of declining *Diporeia* populations on the relative health of the commercially-important lake whitefish (*Coregonus clupeaformis*) (Mohr and Nalepa 2005).

While a number of studies have documented the disappearance of *Diporeia*, few have specifically examined reasons for its decline, and cause-and-effect mechanisms are currently unknown. Population declines were first noted in the early 1990s and, in all lake areas, these declines were coincident with the introduction and spread of the invading species *Dreissena polymorpha* (zebra mussel) and *Dreissena bugensis* (quagga mussel). On a broad scale, the decline of *Diporeia* is linked to the expansion of dreissenids, but on a more local scale inconsistencies are apparent. For instance, *Diporeia* has disappeared from lake areas that were far-removed from dreissenid colonies, yet it persists in other areas despite the long-term presence of dreissenids (Nalepa et al. 2006).

Because of growing concerns over ecological impacts, a workshop was held October 20-21, 2005 in Ann Arbor, MI to address the issue of *Diporeia* declines and potential causes. The objective of the workshop was to bring together researchers currently studying *Diporeia* to (1) assess the current status of populations; (2) discuss potential causes of the decline based on previous and ongoing studies, and (3) develop a list of research recommendations that may further our understanding of causes. By better understanding reasons for *Diporeia*'s decline relative to increased numbers of dreissenids, we may better predict the eventual extent and ultimate consequences of the population loss. Also, by better understanding the cause, we may better assess the potential for population recovery if and when driessenid populations stabilize or decline. The workshop was co-sponsored by the Great Lakes National Program Office, EPA, and the Great Lakes Environmental Research Laboratory, NOAA.

SUMMARY AND DISCUSSION OF WORKSHOP PRESENTATIONS

Initial presentations focused on population trends in Lake Superior. Ongoing yearly collections (1997-2005) by the Great Lakes National Program Office of EPA (GLNPO) indicated that populations at some offshore sites were in a downward trend (Balcer et al. Workshop Presentation; hereafter all workshop presentations will be abbreviated as WP). There was a statistically significant decline in densities at sites > 90 m (n = 9) between 1997 and 2005. Mean densities were 300 m^{-2} in 1997, but only about 40 m^{-2} in 2005. Nearshore sites (< 65 m; n = 2) did not show a similar downward trend. Since dreissenids are not abundant and mainly found in the far western end of the lake (Duluth Harbor), a decline in offshore waters of the main basin would indicate a cause potentially unrelated to *Dreissena*. In contrast, other surveys in Lake Superior have not shown population declines in either nearshore or offshore areas. In a survey of nearshore sites (n = 270) along the southern shoreline, densities did not decline but were actually higher in 2003 than in 1973 or 2000 (Scharold WP). Further, yearly densities at offshore sites in the western portion of the lake (n = 5) did not show a consistent trend between 1993 and 2001; however, densities were highly variable from year-to-year. In another Lake Superior study, densities at nearshore and offshore sites located off the Keweenaw Peninsula and sampled over the past several years did not show any consistent temporal trends (Urban et al. WP). Reasons for the discrepancy between the various studies were not clear. Naturally low numbers and substrate variability may contribute to some variation in yearly density estimates, but reasons for the statistically significant downward trend in densities at the offshore GLNPO sites could not be readily reconciled relative to the stable densities indicated by other studies.

A number of recent surveys confirmed the continued decline of *Diporeia* in Lakes Michigan, Huron, and Ontario (Nalepa WP, Watkins WP, Dittman WP). In each of these lakes, *Diporeia* are now completely gone or rare at depths < 90 m, and slowly declining at depths > 90 m. In contrast, quagga mussel populations are expanding in each of these three lakes. In Lake Ontario, the quagga mussel population has apparently stabilized at depths < 90 m, but is slowly increasing at deeper depths. In Lakes Michigan and Huron, where quagga mussels became established about 7 years later than in Lake Ontario, populations are presently increasing most rapidly at the 30-50 m interval. While presently not abundant at depths > 90 m in Lakes Michigan and Huron, quagga mussels are expected to gradually increase at these deeper depths in both lakes as they did in Lake Ontario. In all three lakes, the decline of *Diporeia* at depths > 90 m preceded the expansion of quagga mussels from shallow to deeper depths. Thus, mussels in shallow areas were remotely affecting *Diporeia* in deeper areas. Another example of remote effects was the pattern of *Diporeia* declines at a 45-m site in Lake Michigan (Nalepa WP). *Diporeia* densities at this site declined to near zero in just 6 months in 1992 and, although *Dreissena* was present at shallower depths, it was not present at the site itself. The site was located in an area with high rates of sediment deposition and strong nearshore-offshore sediment transport. Rapid declines have also been noted in depositional areas in northeast Lake Ontario (Dermott 2001) and in southern Lake Huron (Nalepa unpublished data).

Based on spatial distributions in earlier surveys, some lake areas were thought to be a "refugia" for *Diporeia*. For example, in Lake Ontario *Diporeia* persisted at a 130-m site despite disappearing at other sites of similar depth (Dittman WP). This site was located between depositional basins and is characterized by thin sand lags of postglacial sediment, an indication of winnowing and re-suspension of post glacial muds. Recent data, however, indicated that the *Diporeia* population at this site is now declining (Dittman WP). Lake areas subject to frequent upwelling were also thought to be a refugia for populations. In Lake Michigan, upwelling is far more frequent on the west side compared to the east side (Plattner et al. in press). Consequently, *Diporeia* persisted on the west side but declined rapidly on the east side (Nalepa WP). Lower temperatures and a greater abundance of food in upwelling areas likely provided a more favorable (or less stressful) habitat for *Diporeia*. Recent data collected in 2005 showed that *Diporeia* are now also disappearing from the west side of the lake (Nalepa WP). Declines on the west side appear to be temporally well-correlated to the recent expansion of quagga mussels throughout the lake. Although *Diporeia* have now declined in areas thought to be refugia for populations, some persistence in these areas would indicate that environmental conditions do play a mitigating role.

A number of deep lakes in North America outside the Great Lakes were re-sampled to assess long-term trends in *Diporeia* populations (Dermott et al. WP). Densities of *Diporeia* in lakes without *Dreissena* increased slightly over a 30-year period, indicating the decline in the Great Lakes was not part of a widespread regional problem associated with perhaps global warming or atmospheric inputs of contaminants. Also, densities did not decline in all lakes with *Dreissena* (i.e., some Finger Lakes), suggesting that other factors may be involved beyond the mere presence/absence of *Dreissena.* This finding further suggests that environmental conditions play a mitigating role.

A common theory for the decline is that dreissenids are outcompeting *Diporeia* for available food. Dreissenids filter feed near the sediment surface, and this theory assumes that settling organic material is intercepted by dreissenids before it reaches the upper sediments and becomes available to *Diporeia*. If true, then *Diporeia* should show some physiological signs of food limitation prior to and during population declines. Data collected at a 45-m site in Lake Michigan when the population was declining showed no corresponding decreases in length-weight, lipid content, and eggs per brood (Nalepa WP). Based on previous studies of cold-water amphipods, these three variables are directly linked to food availability and therefore should have declined if food was limiting. At this 45-m site, abundances gradually decreased over a 3-4 year period before the population totally disappeared. During this time, recruitment occurred, but the young-of-year (YOY) were not surviving to become juveniles (Nalepa WP). Adults did not decline until later in the 3-4 year period. This finding may indicate food was limiting since the young, because of higher metabolic rates, are more susceptible to declines in food availability compared to adults. Thus, at this Lake Michigan site, indicators of food limitation at the organism level and at the population level did not appear to be consistent.

As a component of the food-limitation theory, food quality as well as food quantity can be an important contributing factor. Previous studies have shown that *Diporeia* are heavily dependent upon the spring diatom bloom as a major source of nutrition (Gardner et al. 1985, Quigley 1988). Diatoms are rich in lipids and long-chain polyunsaturated fatty acids (PUFAs). Besides playing an important role in growth and reproduction, these fatty acids are needed by organisms such as *Diporeia* to maintain cell elasticity in cold-water environments. Because of *Dreissena*, diatom availability to *Diporeia* would likely be greatly diminished. One way to characterize shifts in the diet of *Diporeia* is through the use of phytoplankton pigments (Alben WP). Each of the major phytoplankton groups (including diatoms) have a unique carotenoid signature, and comparing signatures in populations from different locations within and between lakes (stable vs declining populations) may provide insights into the role of food composition on population trends.

Metabolic activities of dreissenids can affect algal composition and thus the availability of essential nutrients. Examples of direct effects include selection/rejection of specific phytoplankton groups during filtration, and shifts in nutrient availability through metabolic excretion. An indirect effect includes the change in light climate resulting from dreissenid particle removal. Increased light penetration in the water column can lead to biochemical and physiological changes in phytoplankton and lead to subsequent changes in the presence of essential nutrients (Arts and Rai 1997). An example of the effects of nutrient limitation promulgated through the food web is the connection between thiamine deficiency and early mortality syndrome (EMS) in juvenile salmonids (Fitzsimmons et al. WP). Thiamine deficiency is caused by thiaminase, which is found in varying amounts in alewife and other clupeids. When adult salmonids feed on alewife, thiamine is catabolized, creating a deficiency and leading ultimately to mortality in the young. Changes in phytoplankton composition could potentially lead to similar deficiencies in *Diporeia*.

In natural systems, food availability is one of the key factors in defining densities since it influences fecundity and survival. Sources and sinks of benthic food supplies (carbon) were examined along a depth gradient off the Keweenaw Peninsula in Lake Superior (Urban et al. WP). Pathways of carbon flow through components of the benthic system, including *Diporeia*, were quantified. The resulting model indicated a strong relationship between food inputs and standing stocks of *Diporeia*. The development of similar models in areas where populations are declining may provide insights into food availability relative to density trends.

To investigate whether *Diporeia* are responding to a toxic agent associated with *Dreissena*, individuals were exposed to dreissenid biodeposits (pseudofeces) in a 90-day laboratory experiment (Dermott et al. WP). The percent survival of *Diporeia* exposed to pseudofeces was only 75% compared to 100% in controls, which suggests that some unknown component associated with dreissenid biodeposits was having a negative impact on *Diporeia.* While these results may explain the loss of *Diporeia* in lakes with *Dreissena*, they are inconsistent with the persistence of *Diporeia* in other lakes also with *Dreissena* (i.e., Finger Lakes). The rapid loss of *Diporeia* in depositional areas of the Great Lakes does appear consistent with the toxic-agent theory. Biodeposits (and associated by-products) that are re-suspended from nearshore mussel beds would accumulate at high rates in these depositional areas. Also, the most severe population declines tend to occur after the spring period when deposition is at a seasonal maximum (Nalepa WP). Any toxicity associated with biodeposits is apparently short-lived. Sediments from depositional areas where *Diporeia* had disappeared were not acutely toxic to *Diporeia* in laboratory experiments (Landrum et al. 2000).

Another theory for the decline is that mortality rates have increased because of a pathogen or disease. To investigate this possibility, *Diporeia* were collected over a wide area in Lakes Michigan and Huron and incidence rates of parasites and pathogens were determined (Messick WP). Many different types of pathogens were found, including virus-like infections, rickettsia-like organisms, fungi, haplosporidian-like organisms, microsporidians, putative epibiont ciliates, gregarians, cestodes, and acanthacephalans. However, except for epibiont ciliates, incidence rates were uniformly low (< 5%) and not higher in populations that were declining compared to populations that were stable. This would indicate that these pathogens were not a likely cause of declines. For epibiont ciliates, incident rates were high, but were similar to rates in the 1980s prior to the introduction of dreissenids and population declines.

Studies have shown that *Diporeia* are sensitive to various contaminants. This taxa exhibited high mortality rates compared to other amphipod taxa when exposed to riverine sediments containing various organic and inorganic contaminants (Gannon and Beeton 1969). Also, densities were lower in lake areas subjected to anthropogenic inputs (Vander Wal 1977, Kraft 1979). One theory for current declines is that populations are responding negatively to persistent contaminants accumulating in the Great Lakes. An example is the herbicide athrazine and associated metabolites, which in Lake Michigan are now near concentrations shown to lower survival of *Diporeia* in the laboratory (Ralston-Hooper et al. WP). An argument against this theory is that *Diporeia* has disappeared in areas far-removed from major sources of contaminants, including atrazine.

Several developing technologies were put forth that may help define reasons for the decline. Genomic tools such as cDNA micro-arrays are useful in separating environmental factors that may influence organism health (Klapper et al. WP). An organism under stress will activate or deactivate suites of genes specific to the particular stress type. Thus, these gene “fingerprints” can be related to different environmental stressors such as food limitation, low oxygen, exposure to contaminants, etc. A similar approach involves the use of protein expression technologies (proteomics) (Ralston-Hooper et al. WP). Proteins serve as the functional effectors of cellular processes and the abundance, structure, and function of various protein complexes can be used as diagnostic tools to identify altered physiological processes at various levels of organization (molecular, tissue, and organism). Proteomics offers a method by which these stressors can be better characterized. Relevant to *Diporeia*, the functional protein complexes of most interest would be those associated with metabolic and nutritional pathways, protein destination and storage, metabolic transport, and disease-defense mechanisms (immune system). Both the genomic and proteomic approaches would compare profiles in individuals from declining and stable populations.

RESULTS OF WORKSHOP SURVEY

After all presentations, workshop participants were asked to consider the most common theories for the disappearance of *Diporeia* and then choose and prioritize the top three. The first choice was to be given 3 points, the second choice 2 points, and the third choice 1 point. Theories included:

Decrease in Food Availability –This theory assumes that there has been a decline in the quantity and/or quality of food available to *Diporeia* as a result of the filtering activity of dreissenids. The underlying assumption is that energetic requirements are no longer being met, and/or an essential nutrient is no longer available.

Toxic Excretions/Metabolic Wastes – This theory assumes that a metabolic by-product of dreissenid metabolism is having a severe negative impact on *Diporeia*. By-products can be directly or indirectly related to dreissenid excretion or biodeposition (feces/pseudofeces). For example, the proteinaceous mucous associated with dreissenid pseudofeces may be harmful to *Diporeia* when ingested, or it somehow interferes with *Diporeia*'s normal life habits.

Disease/Pathogen/Infection – This theory assumes that a pathogen was introduced coincident with *Dreissena* and is now affecting *Diporeia*. This theory also includes the possibility that a change in conditions caused by *Dreissena* is making *Diporeia* more susceptible to pathogens that were present prior to *Dreissena*, or that a change in conditions has led to an increase in harmful pathogens.

Contaminant Sensitivity – This theory assumes that a change in conditions caused by *Dreissena* is making *Diporeia* more sensitive to resident contaminants, or is making contaminant uptake more likely. This theory includes negative impacts of newer contaminants such as atrazine and /or old-use persistent organochlorines and heavy metals.

Fish Predation – This theory assumes that conditions have changed such that *Diporeia* are now more susceptible to fish predation. For instance, perhaps an increase in water clarity allow fish to more readily see *Diporeia,* or a decline in food availability has caused *Diporeia* to become more active at the sediment-water interface or in the water column.

Diminished Oxygen – *Diporeia* are sensitive to reduced oxygen, and this theory assumes that oxygen at the sediment-water interface has been diminished because of the deposition and accumulation of dreissenid biodeposits. Biodeposits are rich in nutrients and bacteria and would have a high oxygen demand during decomposition.

Results of the survey were: food limitation-29, toxic excretion-28, disease/pathogen-25, contaminants-9, diminished oxygen-6, and fish predation-3. Obviously, there was no clear consensus on a single, most probable cause. This may reflect perhaps the sometimes inconsistent results of previous studies, and/or the complexity of the issue. At least some aspect of all theories except "fish predation" and "diminished oxygen" were examined during workshop presentations. Some participants felt that several stressors were involved, and the relative importance of individual stressors varied depending on physical/chemical conditions associated with the particular lake environment. Regardless of exact cause(s), all participants agreed that the introduction and expansion of dreissenids was the event that initiated *Diporeia*'s decline.

GENERAL DISCUSSION

Many workshop participants thought it would be useful to review the chronology of initial *Diporeia* declines relative to the expansion of dreissenids in each of the lakes. In Lake Erie, *Diporeia* was historically found only in the eastern basin since it is the only basin deep enough to sustain a summer-cold hypolimnion, a condition critical for the existence of *Diporeia*. Both zebra and quagga mussels were first found in the eastern basin in 1989, and the first post-dreissenid survey of *Diporeia* occurred in 1992. Densities were lower in 1992 compared to 1979, and another survey in 1993 indicated densities continued to decline as dreissenid densities increased. A further survey in 1998 failed to find any *Diporeia*. In Lake Ontario, dreissenids were first found in the western end of the lake in 1990, and by 1991 had spread across the lake to the east end. Declines of *Diporeia* were first noted in nearshore areas off Olcott, New York (south shoreline) in 1992, and in the Bay of Quinte (northeast) in 1993. In Lake Michigan, zebra mussels were first reported along the southwestern portion of the lake off Chicago in 1989, and by 1991 had spread northward along the eastern shoreline. Initial declines of *Diporeia* were recorded in the southeastern portion of the lake in 1992. A detailed account of initial declines in the main basin of Lake Huron is lacking. However, in outer Saginaw Bay, Lake Huron, zebra mussels were first recorded in 1991, and subsequent declines in *Diporeia* were observed in 1992. For all four lakes the large-scale pattern is clear – initial declines in *Diporeia* populations occurred soon (< 3 years) after *Dreissena* first became established.

Given the strong negative relationship between *Diporeia* and *Dreissena* in Lakes Michigan, Huron, Erie, and Ontario, the persistence of *Diporeia* in some lakes with dreissenids outside the Great Lakes (i.e., Finger Lakes) is perplexing. In one of the Finger Lakes (Cayuga Lake) the density of *Diporeia* at a 45-m site was 3,750 m^{-2} in 2001 and 5,100 m^{-2} in 2002, even though *Dreissena* has been present at this site since 1994, and *Dreissena* density was 1,440 m^{-2} in 2001 (Dermott et al. 2006). In comparison, at a 45-m site in Lake Michigan a clear decline in *Diporeia* was evident when *Dreissena* density exceeded 14 m^{-2} (Nalepa et al. 2006). The Finger Lakes are deep and steeply sloped, and one theory is that coarse organic material from terrestrial sources (leaf debris) rapidly settles to the bottom and moves along the steep slopes to deeper regions. This material, along with associated bacteria, would not be filtered by *Dreissena* and would thus be available as a food source for *Diporeia.*

A topic of discussion was the uncertainty associated with *Diporeia* taxonomy. In the 1980s, the genus of freshwater pontoporeiid amphipods found in North America was changed from *Pontoporeia* to *Diporeia,* while the genus of its Eurasian counterpart was changed from *Pontoporeia* to *Monoporeia* (Bousfield 1989). Based on levels of genetic divergence using enzyme electrophoresis, the two organisms were more genetically diverse than previously believed, thus dismissing the theory of recent marine origins. In addition, the genus *Diporeia* was characterized as being a species complex, consisting of three, and possibly up to eight species (Bousfield 1989). Several of the species have yet to be described. Some researchers consider the distribution of genetic variation in the genus far too complex and too undefined at this point to even consider establishing how many species may be present (J. Witt, University of Waterloo, personal communication, post workshop). Because of the uncertainty regarding taxonomic status, field-collected specimens in North America are simply referred to as "*Diporeia* spp."

During subsequent discussions, it was argued that, if the different species have different distribution patterns and have different tolerance levels to an unknown toxic agent, observed differences in decline rates relative to *Dreissena* may simply be a function of species composition. Knowing the species present is therefore fundamental to understanding the cause of declines. There has been some preliminary work to define genetic variation in North American *Diporeia*. DNA analysis indicates that there are two distinct phylogroups of the genus that can be tentatively referred to as the western and eastern groups (J. Witt, University of Waterloo, personal communication, post workshop). The western group occurs in lakes in western North America and Lake Superior, and also occurs, but is rare, in Lake Huron. The eastern group is found in Lakes Michigan, Huron, Ontario, and in a number of deep lakes in the east, including the Finger Lakes, New York. Despite this differentiation, it is premature to assume that these phylogroups have unique adaptations that predispose them to different levels of success or failure relative to *Dreissena.* Genetic variation even in these phylogroups is substantial, and the only way to determine if there is a correlation between genetic variation and population declines is to analyze archived material from populations that have disappeared and compare it to material from populations that appear stable. Most likely, different rates of decline are a result of environmental conditions modifying responses, but it was agreed that more analysis is worthwhile to define genetic variation in *Diporeia*. Since preservation in formalin renders specimens useless for genetic analysis, participants were encouraged to preserve all specimens in alcohol rather than in formalin.

The two deepwater amphipods *Diporeia* and *Monoporeia* may be farther removed on the evolutionary scale than previously believed, but the two genera apparently share a common sensitivity to environmental change. *Monoporeia* occurs in deep, freshwater lakes in Eurasia and also in the brackish waters of the Baltic Sea. Like *Diporeia* in the Great Lakes, *Monoporeia* is declining in the Baltic Sea (Perus and Bonsdorff 2004). Declines were first observed in the late 1990s and, interestingly, circumstances associated with *Monoporeia*'s decline, as well as uncertainties of potential causes, closely parallel those for *Diporeia*. The decline of *Monoporeia* in most areas was temporally coincident with the invasion of the Baltic by the polychaete *Marenzellaria viridis*. This polychaete is a detritivore and believed to be competing directly with *Monoporeia* for available food resources. Yet the decline in *Monoporeia* was greater in offshore areas (>30 m) than in nearshore areas, even though densities of *Marenzellaria* were greater in the latter (Cederwall et al. 1999). Low oxygen levels have been suggested as the reason for the decline in offshore waters, but others suggest it is food limitation (Cederwall et al. 1999; Kotta and Olafsson 2003). Also, in some parts of the Baltic, the collapse of *Monoporeia* occurred prior to the establishment of *Marenzellaria.* Another theory suggests that recent run-off events have shifted the phytoplankton community from diatoms to dinoflagellates (B. Sundelin, Institute of Applied Environmental Research, Stockholm University, Stockholm, Sweden, personal communication). Dinoflagellates do not sink as readily as diatoms, and therefore food inputs to the benthic region would be greatly diminished.

Fish predation was the least likely cause of the decline as voted by participants, but some argued strongly it may be more important than many realize. Fish predation can greatly depress *Diporeia* abundances (Johnson and McNeil 1986, McDonald et al. 1990), and there are many examples in the literature of a prey becoming more susceptible to a predator because of a sudden shift in environmental conditions, resulting in the total elimination of the prey. Several *Dreissena*-related changes may have caused *Diporeia* to become more susceptible to fish predation. The filtering activities of dreissenids increases light penetration and thus would make *Diporeia* more visible to fish predators. *Dreissena* filtering also decreases food availability, perhaps causing *Diporeia* to become more active in search of food, thereby also increasing its exposure to predators. These interactions are complex, and while impacts of light climate and the presence/absence of dreissenids on predator-prey relationships have been studied in some amphipod taxa (Gonzalez and Downing 1999, Mayer et al. 2001), studies specifically with *Diporeia* are lacking. Thus, the relative role of fish predation on *Diporeia* declines is unknown. Some evidence suggests that the role of fish, at least initially, may be minimal. If fish were the cause of *Diporeia* declines because of increased susceptibility to predators, then relatively more *Diporeia* would be found in diets just prior to and during population declines. Unfortunately, few studies have assessed shifts in fish diet patterns prior to and during declines, and those that have show a decrease of *Diporeia* in diets in response to lower abundances (Pothoven et al. 2001, Hondorp et al. 2005). Further, as noted earlier, in Lake Michigan initial declines of *Diporeia* were characterized by a decrease in the number of juveniles while adults remained abundant. If fish were the cause, adults might be expected to decline prior to juveniles since fish tend to select for larger individuals (Evans et al. 1990, McDonald et al. 1990). Of course, selectivity could have changed given dreissenid-induced changes in the environment (i.e., increased light levels). Another consideration is the increased structural complexity of the bottom because of dreissenid clusters. Such complexity decreases susceptibility to predation for some amphipods (Mayer et al. 2001). Finally, *Diporeia* are declining at depths > 100 m in Lakes Michigan, Huron, and Ontario. Since fish abundances are minimal and light conditions would have changed little at these depths in the post-dreissenid period, declines in this deep, offshore region would not likely be a result of fish predation.

Profiles of genomic and protein expressions offer promise in characterizing the exact mode of negative physiological responses, yet much research is needed to realize the potential of these techniques. Individuals from stressed and unstressed populations may display different profiles, but the meaning (causes) of such differences need to be defined with carefully designed laboratory experiments. Individuals from unstressed populations need to be exposed to different kinds and levels of stress (low oxygen, starvation, etc.). The resulting profile would then be compared to profiles from stressed field populations. While stresses have been thus characterized for other biota, there has been no previous work on *Diporeia*. Given the apparent sensitivity of this genus to a variety of different environmental stressors, there are risks associated with this approach. Also, implications of dealing with an organism with high genetic variation are unknown.

KEY QUESTIONS AND RECOMMENDATIONS:

1) Why do Diporeia *populations within the Great Lakes appear to be more susceptible to* Dreissena *than populations in lakes outside the Great Lakes?*

Given that decline rates are highly variable in the Great Lakes, monitoring of populations in lakes outside the Great Lakes (i.e., Finger Lakes) is encouraged. Although populations in these lakes appear to be stable despite the presence of dreissenids, populations in areas thought to be "refugia" in the Great Lakes eventually declined to zero. Monitoring of dreissenids in these lakes is also recommended. The physiological health of *Diporeia* from these outside lakes should be assessed and compared to Great Lakes populations.

2) How are Diporeia *populations remotely affected by dreissenids?*

Evidence suggests an unknown toxic or inhibitory by-product associated with dreissenid biodeposits can be transported from nearshore to offshore areas, probably by normal currents or episodic storm events. This by-product does not accumulate or linger in the sediments since mortality cannot be induced when *Diporeia* are exposed to sediments from areas where the population has disappeared. Further laboratory studies are needed to verify and characterize a potential toxic agent(s) associated with fresh dreissenid biodeposits. Such studies should involve specimens of *Diporeia* and *Dreissena* collected inside and outside the Great Lakes.

3) Can new biochemical tools be used to determine a cause of declines?

Genomic and protein expression technologies offer great promise in providing insights into potential causes. To be useful, these techniques require studies that carefully coordinate field (comparison of stressed and unstressed populations) and laboratory studies (characterize stress responses).

4) Do we need to define genetic variation within the genus Diporeia *to fully understand the cause of declines?*

Knowing the extent of genetic variation would be useful and should proceed along with other decline-related research. While on a broad scale there are two genetically identifiable phylogroups, there is still substantial genetic variation within groups, and populations within a single Great Lake do not appear to be genetically uniform. Despite genetic variation, however, it remains that the entire population has disappeared in large areas of Lakes Michigan, Huron, Erie, and Ontario, and the one common feature in all these lakes is that declines were initiated by the introduction of *Dreissena*. If available, genetic composition of archived material from populations that have disappeared should be examined and compared to the composition of populations still present and seemingly unaffected by *Dreissena*.

5) Is the Diporeia *population in Lake Superior stable or declining?*

Data sets are conflicting, but the general consensus is that populations are generally not declining. Intensive monitoring should be continued and all Lake Superior data sets should be combined for further statistical analysis. For the GLNPO data set, which shows that densities in Lake Superior are trending lower at offshore sites while other Lake Superior data sets show no trend, the age structure of *Diporeia* in collected samples from the monitoring program in all the lakes should be determined. Populations at offshore sites in the other lakes (i.e., Lakes Michigan, Huron, Erie, and Ontario) are declining and, since shifts in age structure occur in declining populations, a comparison of age-structure trends between Lake Superior and the other lakes may provide further insights into density trends in Lake Superior.

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WORKSHOP PRESENTATIONS

Alben, K. "Case histories of using algal pigments as biomarkers of food web relationships."

Balcer, M., Schmude, K., Rockwell, D. C., and Barberio, R. "*Diporeia* are declining throughout the Great Lakes: does this include Lake Superior?"

Dermott, R., Bonnell, R., Carou, S., and Jarvis, P. "Negative association between *Diporeia* and presence of zebra mussels or their pseudofeces."

Dittman D. E. "*Diporeia* and *Dreissena bugensis* in southern Lake Ontario."

Fitzsimons, J., Brown, S., Brown, L., Vandenbyllaardt, L., Williston, B., Williston, G., Tillet, D., Zajicek, J., and Honeyfield, D. "Possible role of thiaminase in the food chain on declines in *Diporeia.*"

[1]Klaper, R., Goetz, R., and Janssen, J. "Use of micorarrays to assess sources of stress on *Diporeia*."

Messick, G. "Role of disease in the decline of *Diporeia.*"

Nalepa, T. F. "In search of a cause for declines of *Diporeia* populations in the Great Lakes."

Ralson-Hooper, K. J., Sepúlveda, M., Ochoa-Acuna, H., and Nalepa T. F. "New approaches for measuring the effects of multiple stressors on *Diporeia* survival."

Scharold, J. "Recent trends in abundance of *Diporeia* in Lake Superior."

Watkins, J. "Status of *Diporeia* in Lake Ontario: results from LOLA benthic survey 2003."

Urban, N. E., Auer, M. T., Auer, N. A., and Verhamme, E. "*Diporeia* distribution and carbon fluxes in Lake Superior."

[1]presented as a handout.

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