Spatio-temporal dynamics of parasites infecting *Diporeia* spp. (Amphipoda, Gammaridae) in southern Lake Michigan (USA)

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**A R T I C L E  I N F O**

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**A B S T R A C T**

Since the 1990s, populations of the benthic amphipod *Diporeia* spp. (*Diporeia*) have sharply declined across much of the Laurentian Great Lakes. This study was undertaken to identify contemporary and historical community composition, structure, and dynamics of parasites infecting *Diporeia* collected from nine sites in the southern basin of Lake Michigan, where declines of the amphipod have been well documented over the past 20 years. An additional aim of this study was to assess whether infection dynamics and dreissenid densities could explain the declines in *Diporeia* densities that have occurred. We found that *Diporeia* were host to eight groups of uni- and multicellular pathogens. Of the 3082 amphipods analyzed, 1624 individuals (52.7%) were infected with at least one type of parasite. Ciliophora was the most prevalent parasite (50.08% prevalence of infection), followed by Gregarinina (2.79%), Microsporidia (0.68%), Cestoda (0.45%), Acanthocephala (0.36%), Haplosporidia (0.23%), Yeast (0.32%), and filamentous Fungi (0.10%). Considerable spatial and temporal variability were observed in parasite prevalences, with prevalences frequently appearing to cycle between low and high values. Parasite species belonging to Microsporidia and Haplosporidia were associated with tissue alteration and host inflammatory response; however, parasite prevalences explained very little in terms of *Diporeia* density declines at assessed sites. Despite these findings, we do not discount the possibility that parasitic infections may have played a role in declining *Diporeia* densities in the Great Lakes, as the cyclical prevalences that were observed are possibly suggestive of parasitic outbreaks that are followed by die-offs at affected sites. This study suggests that if parasites have affected *Diporeia* densities in the Laurentian Great Lakes, then the relationship may be a complicated one.

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1. Introduction

Amphipods of the genus *Diporeia* (hereafter referred to as *Diporeia*) occupy a central position in the foodweb of the Laurentian Great Lakes ecosystem (hereafter referred to as Great Lakes). As an infaunal detritivore that feeds on pelagic material that settles to the benthos, *Diporeia* are the foremost consumer of primary production in the Great Lakes (Gardner et al., 1990). Because *Diporeia* are important food resources for numerous Great Lakes fish species (Wells, 1980; Selgeby et al., 1994; Rand et al., 1995; Davis et al., 1997; Hondorp et al., 2005; Pothoven, 2005), they function as important conduits of nutrients and energy to higher trophic levels and serve as coupling mechanisms between pelagic and benthic zones of the Great Lakes (Fitzgerald and Gardner, 1993).

Historically, *Diporeia* have been the most widespread and dominant benthic macroinvertebrate in the Great Lakes, reaching densities in excess of 14,000/m² (Henson, 1966, 1970; Cook and Johnson, 1974). Over the last 20 years, *Diporeia* abundances have declined across much of the Great Lakes (Nalepa et al., 1998, 2007; Dermott and Kerec, 1997; Lozano et al., 2001; Barbiero et al., 2011). Due to the unique position of *Diporeia* in the foodweb and the fact that they once accounted for most of the benthic biomass in the lakes (Nalepa, 1989), it is believed that these large-scale declines have resulted in major foodweb restructuring in the Great Lakes (Nalepa et al., 1998).

Several hypotheses have been proposed to explain *Diporeia* declines in the Great Lakes, including (1) greater predation stemming from increases in certain fish populations, such as lake
whitefish Coregonus clupeaformis (Ebener et al., 2008), (2) decreased dissolved oxygen concentration (Nalepa et al., 2005), (3) decreased food availability due to increased abundance of invasive, filter-feeding dreissenid mussels (Nalepa et al., 2006), (4) the release of toxins by dreissenid mussels (Dermott et al., 2005), and (5) increased pollutants in sediments (Landrum et al., 2000). Although studies have been conducted exploring each of these hypotheses, the exact cause of the Diporeia declines remains unknown (Nalepa et al., 2009). In Lake Michigan, Diporeia abundances were declining in the late 1990s despite what was considered to be sufficient flux of organic matter reaching the benthos (Nalepa et al., 2006) suggesting that declining abundances were not simply a result of competition with dreissenid mussels. Similar questions have been raised as to whether predation, chemical contamination, and low dissolved oxygen were of a sufficient degree to be the sole cause of declining Diporeia abundances in Lake Michigan (Nalepa et al., 2005).

Previous studies have demonstrated that Diporeia can host an array of aquatic pathogens (Messick et al., 2004; Messick, 2009; Muzzall and Whelan, 2011), including a rickettsia-like bacterium, Ciliophora, gregarines, helminthes, Haplosporidia, and Microsporidia. It has been suggested that parasitic infection, perhaps exacerbated by other stressor events such as pollution or climate change, could have contributed to the population declines in Diporeia that have occurred in the Great Lakes (Messick et al., 2004). The most comprehensive study to date of parasitic infection in Great Lakes Diporeia was by Messick et al. (2004), who collected and assessed disease prevalence from Diporeia from multiple sites in lakes Huron and Michigan in 2000, and as far back as the mid–late-1980s for some southern Lake Michigan sites. Since the study of Messick et al. (2004) was completed, there have been no additional assays of parasitic infection in Diporeia. As well, we are not aware of any attempts to relate declines in Diporeia abundance to parasitic infection or to assess the importance of parasitism relative to other possible contributing factors, such as expansion of dreissenid mussels. Such studies are important because they can help identify why Diporeia populations have declined or why the declines have been particularly severe in some lakes and particular areas (Barbiero et al., 2011).

The aim of this study was to conduct an in-depth analysis of pathogen prevalences in Diporeia populations from the southern basin of Lake Michigan, a portion of the Great Lakes where the decline of the amphipod has been well documented (Nalepa et al., 1998). Archived Diporeia samples collected from several sites in southern Lake Michigan as far back as 1980 were examined to determine spatial and temporal variability in pathogen prevalences. Models were then fit in an effort to determine the relationship between Diporeia density and infection prevalence as well as to examine other possibly contributing factors, such as dreissenid density. Additionally, since multiple parasitic infections may synergistically affect Diporeia populations, diversity and richness of parasitic infections were also evaluated.

2. Materials and methods

2.1. Sample collection

For this study, a total of 3082 Diporeia were randomly subsampled from archived specimens collected between 1980 and 2007 at nine stations in southern Lake Michigan (Table 1). Diporeia that had been preserved in 5% buffered formalin were sorted by stage (juvenile < 5.0 mm, adult > 5.0 mm) (Nalepa et al., 2000) and transferred to 70% ethanol until further processing. For determining infection status, Diporeia samples were embedded in paraffin, sectioned (3–4 μm), mounted on glass slides, and stained with Mayer's hematoxylin and eosin (Luna, 1968). Additional diagnostic features of parasites were determined by examination of selected sections stained with Giemsa (MHE, Luna, 1968), Grocott's methenamine silver (GMS, Luna, 1968), and Feulgen picro-methyl blue (FPM, Farley, 1969) and Periodic acid Schiff (PAS, Lillie, 1965).

Sampling stations were chosen such that there was contrast in location, depth, and the rate in which Diporeia densities declined over time (Fig. 1). Since, Diporeia declined more rapidly on the east side of the lake (A-1, H-22, H-21, EG-14) compared to the west side (H-8, B-7, B-6, B-5) (Nalepa et al., 1998), samples were collected along an east-to-west gradient. Additionally, since populations generally declined progressively from shallow to deep regions (Nalepa et al., 2005), sites on the two sides of the lake were matched by depth with depths ranging from 18 m to 108 m. The 93-m site station (X-2) located on the far northeast side of the southern basin was also chosen for analysis because Diporeia density at this site was 10 per m² in 2005, while densities at B-6 and EG-14 were >1000 per m², and by 2010, populations were extirpated from X-2. We analyzed several amphipod samples collected in 1992 and after, representing pre- and post-invasion of dreissenids in the Great Lakes (Nalepa et al., 1998). Together these samples representing a span of 27 years were examined to provide an understanding of the diversity and prevalence of parasitic infections and determine if there was any variation in diversity or prevalence of parasitic infections associated with Diporeia populations from before or after the introduction of dreissenids.

2.2. Identification of organisms infecting Diporeia

Taxonomic systems for groups of organisms infecting Diporeia were based on the following sources: Ciliophora (Lom and Dyková, 1992; Corliss, 1979), Haplosporidia (Sprague, 1979), Microsporidia (Wittner and Weiss, 1999), Yeast (de Becze, 1956), filamentous Fungi (Dick, 1990), Gregarinasina (Levine, 1980), Cestoda (Wardle and Mcleod, 1952; Yamaguti, 1959), and Acanthocephala (Amin, 2002).

2.3. Analysis of Diporeia parasite community assemblages

Parasite-group richness and Shannon-Wiener diversity values were calculated for each examined Diporeia. The Shannon-Wiener diversity index was calculated as described in Shannon (1948). Generalized estimating equation (GEE) models assuming a Poisson distribution and a log link function were used to analyze parasite richness values in relation to site, year, and age of Diporeia. Year was centered to facilitate interpretation; thus intercept estimates for fitted models that included year as an explanatory variable corresponded to expected richness in the year 1994. Given that Diporeia for this study were collected by Ponar grabs, we felt it was likely that richness at each sampling occasion (i.e., sampling location and period combination) would be correlated, so individuals were assumed to have an exchangeable correlation structure. Fitted GEE models ranged in complexity from intercept-only models (i.e., richness equal across all sampling sites and period) to models that contained depth, year, and age of Diporeia as main effects and all possible first-order interactions. Fitted GEE models were compared using approximation quasi-likelihood information criterion (QICu) (Pan, 2001), which is an information-theoretic approach to model selection similar to Akaike information criterion (AIC). The model with the lowest QICu value was identified as the best models in terms of fit and parsimony. Although we originally were interested in doing so, we did not fit models to the Shannon-Wiener diversity values because parasite diversity was consistently low (see Results below). GEE models were fit in SAS using the PROC GENMOD procedure (SAS Institute Inc., 2010).
2.4. Analysis of infection parameters and Diporeia density

Kendall rank correlation analyses were initially conducted to assess associations among individual infection prevalences, depth of measurement, Diporeia densities, and dreissenid densities. Kendall rank correlation analyses were also used to assess associations among several composite infection prevalences that were identified (see Section 3.1) and depth of measurement, Diporeia densities, and dreissenid densities. Correlations were conducted in SAS using the PROC CORR procedure (SAS Institute Inc., 2010).

Multiple linear regression was used to relate Diporeia density for each sampling event and location to individual and composite infection prevalences, dreissenid density, and sampling depth. Diporeia and dreissenid mussel densities for each sampling event were obtained from National Oceanic and Atmospheric Administration Great Lakes Environmental Research Laboratory, Ann Arbor, MI (unpublished data). Diporeia and dreissenid densities were log + 1 transformed prior to analysis, whereas the prevalence variables were arcsine square root transformed. Our base model included dreissenid densities and sampling depth as explanatory variables. We then sequentially added individual and composite infection prevalences (i.e., forward selection) and used AIC to determine if improvements in model fit justified the increase in model complexity. We stopped once no additional variables resulted in lower AIC values. The multiple linear regression models were fit in SAS using the PROC GLMSELECT procedure (SAS Institute Inc., 2010).

3. Results

3.1. Identification of lesions associated with pathogens in stained Diporeia sections

Several parasites and fungi were identified in the examined Diporeia, including Microsporidia, Haplosporida, Ciliophora, Gregariniasina, filamentous Fungi, Yeast, Acanthocephala, and Cestoda. Altogether, 1624 amphipods (52.2%) exhibited at least one parasitic infection. The reaction to the pathogens varied greatly from differentiated and melanized hemocytic encapsulations in tissues adjacent to parasites to no obvious or negligible responses. Since all observed Ciliophora infections were external and all other observed infections were internal, three combinations of parasite groups were also analyzed: combined infections (CI), combined infections excluding Ciliophora (CIC), and more than one infection (MOI). MOI was defined as an amphipod being infected by more than one group of organisms.

Microsporidian infections were observed in 0.68% of amphipods. These infections were always associated with muscle tissues where infected tissues appeared to be replaced by the parasite. In a few amphipods, the microsporidian had apparently replaced the host tissue and melanized hemocytic encapsulations were observed engulfing masses of microsporidia (Appendix 1A–1C).

Haplosporian infections were observed in 0.23% of amphipods. Plasmodia in various stages of schizogony were observed in high densities throughout hemal sinus, muscle tissue, and connective tissue where infections commonly advanced to sporogonial sporocyst. Few host cells appeared to be replaced by parasites to no obvious or negligible responses. Since all observed Ciliophora infections were external and all other observed infections were internal, three combinations of parasite groups were also analyzed: combined infections (CI), combined infections excluding Ciliophora (CIC), and more than one infection (MOI). MOI was defined as an amphipod being infected by more than one group of organisms.

Ciliophora infections were by far the most prevalent (50.08%) compared to the other parasitic infections observed in Diporeia. Oval Ciliophora with a characteristic large macronucleus were observed in sections of Diporeia exhibiting haptosporidian infection (Appendix 2A).

Ciliophora infections were by far the most prevalent (50.08%) compared to the other parasitic infections observed in Diporeia. Oval Ciliophora with a characteristic large macronucleus were closely associated with the gills and periopods (Appendix 2B). All ciliophora infections appeared to be external. No obvious host response or tissue damage accompanying Ciliophora infections was observed.

Two types of mycoses (Yeast and filamentous Fungi) were observed in sections of Diporeia. Yeast were present in a single amphipod collected from sampling station A-1 in 1980. Filamentous Fungi appeared as coelozoic, branching, saprophytic-like Fungi (Appendix 2C). Yeast cells appeared as oval and hyaline and ranged between 2.5 to 5.5 μm in diameter and were often associated with melanized nodules (Appendix 2D). Filamentous Fungi were present in 0.10% of amphipods. One amphipod heavily infected with a filamentous, branching fungus had degenerated

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Fig. 1. Location of sampling stations for Diporeia in the southern basin of Lake Michigan from 1980 to 2007. Depth contours are 5 m.
tissues with many circulating hemocytes within the hemocoel (Appendix 2E).

Two groups of helminthes were present in the hemocoel of Diporeia. Acanthocephala (Fig. 4 panel F) was present in 0.36% of amphipods and Cestoda was present in 0.45% of amphipods. Although we were not able to determine the number of different acanthocephalan infections in the sections of Diporeia examined, it is likely that the observed species were Acanthocephalus dirus and Echinorhynchus salmonis (Amin, 1978; Messick et al., 2004; Muzzall and Whelan, 2011). While no host response accompanying helmhinct infection, each helmhinct filled the majority of the hemocoel and often displaced the intestine (Appendix 2F).

Gregarinasina infections were observed 2.79% of amphipods. In sections of Diporeia, trophozoites were present in both the intestine and the anterior caecum and were in close proximity to the outer epithelium of the mucosa. Histological manifestations of the Gregarinasina are displayed in Appendix 3. Groups of several trophozoites of various sizes were commonly found throughout the cecum. There was no evidence of tissue damage other than the occasional indentation associated with the presence of either an individual trophozoite or a group of trophozoites. In heavily infected amphipods both circulating basophilic granular hemocytes and basophilic/eosinophilic granular hemocyte were often in the hemal sinus. In one heavily infected female, a basophilic granular hemocyte was observed in the anterior caecum next to a group of trophozoites.

3.2. Community structure of Diporeia parasite community

Shannon-Wiener diversity index values ranged between 0.0 and 1.099, indicating that the diversity of parasite communities infecting Diporeia was low. In terms of richness of parasite communities infecting individual Diporeia, 95.2% of infected amphipods exhibited a single infection, 4.0% exhibited two infections, and a single amphipod exhibited three infections. Overall richness of parasites observed for each sampling occasion ranged between one and six. The overall richness was one on 14 occasions. In terms of richness for an entire year, the lowest richness (1) was observed in 2007 and the highest richness (6) was observed in 1980. In terms of overall richness for each sampling station over the duration of the study period, with the exception of station H-22 which was only sampled in two consecutive years and had a richness of 2, A-1 had the highest richness (6), followed by X-2 (5), and B-5, B-6, B-7, H-8, and H-21 (4).

For richness, the GEE model with the lowest QICu value included site and year as explanatory variable. Because the site × year interaction term did not show up in the best performing model, this suggests that sites responded similarly in terms of changes in richness over with time. The estimated coefficient for year (on a log, scale) equaled 0.002 (SE = 0.0057) suggesting that parasitic richness increased slightly over time for the sampling sites. In terms of individual sites, which again corresponded to estimated richness in 1994, sites EG14, H-21, and H-22, which were eastern sites with depths ranging from 45 to 73 m, had the highest richness, whereas sites B-6, H-8, and B-5, which were western sites with depths ranging from 18 to 105 m, had the lowest richness.

3.3. Spatial and temporal variability in parasite prevalence

Fluctuations in infection prevalences across sampling sites, years, and stage were observed for both combined and individual infections (Figs. 2–5). Adult Diporeia, on average, had higher infection prevalences than did juvenile Diporeia. The one exception was for Gregarinasina infections. The same trend was observed for the combined datasets: combined infections (CI), combined infections excluding Ciliophora (CIC), and more than one infection (MOI). The largest difference in infection prevalence between adult and juvenile Diporeia was observed for Microsporidia infections. As for differences in infection prevalences among sampling stations, Diporeia from EG14 had the highest prevalences of Gregarinasina and acanthocephalan infections compared to the other stations sampled. Similarly, Diporeia from this station had the highest CIC and MOI prevalences. In general, acanthocephalan infections prevalences increased with depth. As for differences in infection prevalences among sampling sites, the course of the study, on average, increases in prevalence of acanthocephalan, Gregarinasina, and microsporidian infections were observed for 1992 and 1993. The same trend was also observed for MOI prevalences while CI prevalences appeared to cycle between low and high values.

3.4. Investigation of infection prevalence, depth, and dreissenid density in relation to Diporeia density

Statistically significant positive correlations were observed between prevalences of acanthocephalan infections and microsporidian infections (τ = 0.355, P = 0.002), prevalences of hapolsporidian infection and Yeast infections (τ = 0.365, P = 0.004), prevalence of acanthocephalan infection and sampling depth (τ = 0.208, P = 0.049), prevalence of hapolsporidian infection and Diporeia density (τ = 0.226, P = 0.028), and prevalence of filamentous Fungi infection and dreissenid density (τ = 0.244, P = 0.035). Conversely, statistically significant negative correlations were observed between prevalence of Gregarinasina infections and dreissenid density (τ = −0.278, P = 0.007), Diporeia density and dreissenid density (τ = −0.478, P < 0.001), Diporeia density and sample depth (τ = −0.227, P = 0.012), and dreissenid density and sample depth (τ = −0.211, P = 0.036). In terms of the composite infections, statistically significant negative correlations were observed between prevalence of CIC infection and dreissenid density (τ = −0.231, P = 0.020) and prevalence of MOI infection and dreissenid density (τ = −0.291, P = 0.004).

The multiple linear regression model with the lowest AIC value included dreissenid density (log, + 1 transformed), sampling site depth, and microsporidian infection prevalence (arc sine square root transformed). This model explained approximately 66% of the observed variability in log, + 1 transformed dreissenid density among the sampling locations and times. The marginal contribution of microsporidian infection prevalence was only around 1%, suggesting an overall weak association between infection prevalence and Diporeia density after accounting for the effects of dreissenid density and sampling site depth. Parameter estimates for the best performing model were −0.495 (SE = 0.0476) for log, + 1 transformed dreissenid density, −0.021 (SE = 0.004) for sampling site depth, and 2.38 (SE = 1.63) for arc sine square root transformed microsporidian infection prevalence.

4. Discussion

In this study, histological examination revealed the presence of eight different pathogens infecting collected from the southern basin of Lake Michigan. Results of this study show that the relative diversity of parasite communities infecting Diporeia in southern Lake Michigan is low, with a maximum of six different parasite groups being present at a single sampling site over the study period and only two dominant parasitic infections. While all of the observed groups of parasites, such as Gregarinasina Microsporidia, Haplosporidia, Ciliophora, Yeast-like fungi, filamentous Fungi, Acanthocephala, and Cestoda have been previously reported to infect Diporeia in this region (Messick et al., 2004), rickettsia-like bacteria which have been reported by Messick et al. (2004) were not observed in the present study.
Acanthocephalan infections were positively correlated with depth while other infection prevalences differed mainly by sampling site suggesting that variations in limnological features at each sampling site have a stronger influence on particular infection prevalences in Diporeia. Unfortunately, limnological information available on each of the sampling sites of this study is not detailed enough to allow for drawing correlations between the site characteristics and infection parameters of each of the sites. Given the range in host specificity and the effect of depth on different acanthocephalan infection prevalences in amphipods (Zdzitowiecki and Presler, 2001), it is possible that multiple acanthocephalan species having varying infection characteristics are present in the specimens examined. Nonetheless, this study represents the first report of the spatial factors associated with infection prevalences of different helminthes in Diporeia. Since Messick et al. (2004), reported infection prevalences for combined helminth species in Diporeia for the total number of amphipods examined for both Lake Michigan and Huron, a direct comparison of the authors’ results to those of the current study cannot be made.

Acanthocephalans are known to both oophorectomize their intermediate hosts and modify the behavior of the hosts to increase the probability of predation of the intermediate host by the definitive host (Haine et al., 2005; Bethel and Holmes, 1977). Additionally, microsporidians are known to burden their hosts and are associated with a range of pathogenicity (Dunn and Smith, 2001). Interestingly, in the current study, microsporidian infection prevalence showed a significant positive correlation with acanthocephalan infection prevalence in Diporeia. While the reproductive and behavioral responses of Diporeia to acanthocephalan infection are currently unknown, the negative impact to Diporeia fitness as a result of muscle replacement by the observed microsporidian is obvious. It is therefore possible that these two parasites synergistically affect the fecundity, behavior, and fitness of Great Lakes Diporeia.

It has been shown that, in addition to competition and predation, parasitism is an important biological force that controls zooplankton community structure (Yan and Larsson, 1988). Some parasites of invertebrates are predicted to greatly reduce host survival and host fecundity despite having low infection prevalences in invertebrate hosts (Anderson and May, 1981; McCallum, 1994). In the current study, lower prevalences were observed for both haplosporidian and microsporidian infections compared to
infections for the other groups of parasites observed (e.g. Ciliophora and Gregarinasina). It is known, however, that haplosporidians and microsporidians may have more harmful effects on *Diporeia* despite their relatively low prevalence (Messick et al., 2004). It is therefore possible that even seemingly subtle increases in infection prevalences of these parasites (e.g. 0.01–0.1%) can significantly impact *Diporeia* populations. The fact that tissue alteration and host inflammatory response was associated with these infections further highlights the negative impacts these infections have on *Diporeia*.

Although the exact balance between virulence and transmission rates of the parasites infecting *Diporeia* is unknown, based on the host-parasite model of Anderson and May (1981), a number of biological conclusions about the persistence of parasitic infections of *Diporeia* in the southern basin of Lake Michigan can be drawn. For example, the finding that both microsporidian infection prevalence was a main effect in the selected *Diporeia* density model and microsporidian infection prevalence declined as *Diporeia* density declined and suggests that the transmission efficiencies of microsporidians is strongly dependent on *Diporeia* density.

Compared to the findings of Messick et al. (2004), similar infection prevalences were observed for Ciliophora infections relative to those of the other parasites detected (e.g. Haplosporidia and Microsporidia); however, different infection prevalences were observed for multiple groups of parasites. The observed differences in infections prevalences found in the two studies are likely due to differences in the distribution of parasites among different sites and years. This conclusion is supported by the occurrence of site and year as first-order interaction terms in the QICu-selected model for parasite richness.

Unfortunately, we were not able to identify a clear mechanistic link between parasitic infection and the decline of *Diporeia*. However, the observed increase in prevalence for a number of infections (both individual and MOI) in 1992 and 1993 coincides with the establishment of the zebra mussel (*Dreissena polymorpha*) in the southern basin of Lake Michigan (Nalepa et al., 1998). This finding provides evidence to suggest a mechanistic link exist between the presence of zebra mussels and increased infection prevalence in *Diporeia*. One explanation for this result may be that dreissenids are capable of harboring and spreading *Diporeia*-pathogenic

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**Fig. 3.** Prevalence of Acanthocephala, Cestoda, Ciliophora, Fungi, Gregarinasina, Haplosporidia, Microsporidia, and Yeast infections in adult *Diporeia* spp. collected from nine sampling sites in the southern basin of Lake Michigan between 1980 and 2007.
organisms; however the finding that infection prevalences did not continue to increase as dreissenid densities increased suggests the observed increase in infection prevalences may have been caused by a different mechanism. Another explanation may be that the ecological impact of the initial establishment of filter feeding zebra mussels stressed Diporeia populations to the point of being susceptible to infection. Furthermore, the observed cyclic nature of infection prevalence for multiple parasite groups might suggest increased declines of Diporeia occur when parasite load becomes high.

Predictions for Diporeia density based on the BIC-selected model appear to be inconsistent with the observed trends in Diporeia densities in that estimates show a negative correlation between depth and Diporeia density while research has shown that Diporeia populations in shallow regions in southern Lake Michigan are declining at a faster rate than those in deeper regions (Nalepa et al., 1998). We attribute this finding to the historically high relative Diporeia density at the shallow sites sampled, particularly A-1, B-7, and H-8. Additionally, since Diporeia have been extirpated from a number of regions in the study area, data for those sites were not included in the model further contributing to the observed inconsistency. Keeping in mind that the selected model for Diporeia density is based on data collected over 27 years, it is likely that similar models fit to data collected within the last decade would show a positive correlation between depth and Diporeia density.

5. Conclusion

In conclusion, through this work, we were able to determine the spatio-temporal patterns of a number of parasites infecting

Fig. 4. Prevalence of combined infections (CI), combined infections excluding Ciliophora (CIC), and more than one infection (MOI) in juvenile Diporeia spp. collected from nine sampling sites in the southern basin of Lake Michigan between 1980 and 2007.

Fig. 5. Prevalence of combined infections (CI), combined infections excluding Ciliophora (CIC), and more than one infection (MOI) in adult Diporeia spp. collected from nine sampling sites in the southern basin of Lake Michigan between 1980 and 2007.
Diporeia. Additionally, we were able to select a model that describes trends in Diporeia density in the southern basin of Lake Michigan over the past three decades in relation to physical and biological factors. Model testing showed a strong correlation between dreissenid density and Diporeia density, however, no distinct increase in a particular parasite infection(s) could be linked to increased dreissenid density or decreased Diporeia density. However, the finding that prevalences of co-infections by multiple parasites showed a significant negative correlation with Diporeia density suggests it is plausible that the interrelationship asites (MOI) showed a significant negative correlation with Diporeia density during the declines but also on the potential transmission of parasites that use Diporeia as an intermediate host. This new knowledge is needed to understand the potential causes of the decline in Diporeia and foster the development of efficacious management strategies for the restoration and conservation of Diporeia and other ecologically important organisms in the Great Lakes foodweb.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jip.2014.06.008.

References

Dreissenid density or decreased Diporeia density. How-
ever, the finding that prevalences of co-infections by multiple par-
asites (MOI) showed a significant negative correlation with Diporeia density suggests it is plausible that the interrelationship and dynamics of different parasitic infections may synergistically contribute to the decline in Diporeia populations in the southern basin of Lake Michigan. Additional research is required to elucidate the effect of parasitic co-infections in Diporeia. The findings of this study provide valuable insights not only on the dynamics of parasites infecting Diporeia during the declines but also on the potential transmission of parasites that use Diporeia as an intermediate host. This new knowledge is needed to understand the potential causes of the decline in Diporeia and foster the development of efficacious management strategies for the restoration and conservation of Diporeia and other ecologically important organisms in the Great Lakes foodweb.


