〈Review Paper〉

Biological and Ecological Considerations of the Freshwater Amphipod, *Diporeia* spp.

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Abstract - **Biological and ecological characteristics of *Diporeia* spp. are described including size, growth, life cycle, energy storage, temperature effect, bioturbation, feeding depth and sediment ingestion of *Diporeia*. Bioaccumulation and toxicity of organic contaminants and trace metals were reviewed in addition to an examination of the relationships among various condition indexes (i.e. wet weight, dry weight and body length) of *Diporeia*.**

Key words : biology, ecology, energy storage, *Diporeia*

INTRODUCTION

The amphipod *Diporeia* spp. (Figure 1) was formerly known as *Pontoporeia hoyi* (= *affinis*) (Smith 1972; Segerstrale 1977). Based on morphological and physiological differences, *Pontoporeia* was recently separated into three genera with the new genus *Diporeia* now considered the North American form (Bousfield 1989). This new genus has two natural groupings containing eight species. This genus is generally considered as one group because taxonomic differences have not been resolved (Landrum and Nalepa 1998).

The amphipod *Diporeia* is the most widespread and dominant benthic macroinvertebrate in the Great Lakes (Freitag *et al.* 1976) and can reach densities of 34,000 individuals m^{-2} (Nalepa *et al.* 1985). *Diporeia* is also found not only in North American freshwater, especially in the Great Lakes, arctic and subarctic lakes and rivers (Moore 1979; Nalepa *et al.* 1985) but also in brackish water in the Baltic Sea (Cederwell 1977). Unlike other freshwater amphipods including *Hyalella azteca* and several species of *Gammarus* which are usually found in the warmer and shallower regions of lakes (Hargrave 1970), *Diporeia* is more abundant in the deeper and colder regions of lakes, where the average temperature is less than 20°C (Smith 1972).

Diporeia biomass is up to 65% of total benthic biomass and their production is 70 to 90% of total benthic production in many regions (Nalepa 1989). *Diporeia* plays a major role in the movement of energy, nutrients, and contaminants through the food web (Landrum and Nalepa 1998). As a detritivore, *Diporeia* utilizes freshly settled algae as a primary food source and it is fed upon by many species of Great Lakes fish. Therefore, *Diporeia* is an important energy link between benthic and pelagic production and upper trophic levels.

In this study, particulate biological and ecological aspects of *Diporeia* spp. were described based on the various literature data and my own study results.

BIOLOGICAL CONSIDERATIONS FOR *DIPOREIA* SPP.

Growth and life cycle

Diporeia size and growth in natural populations may

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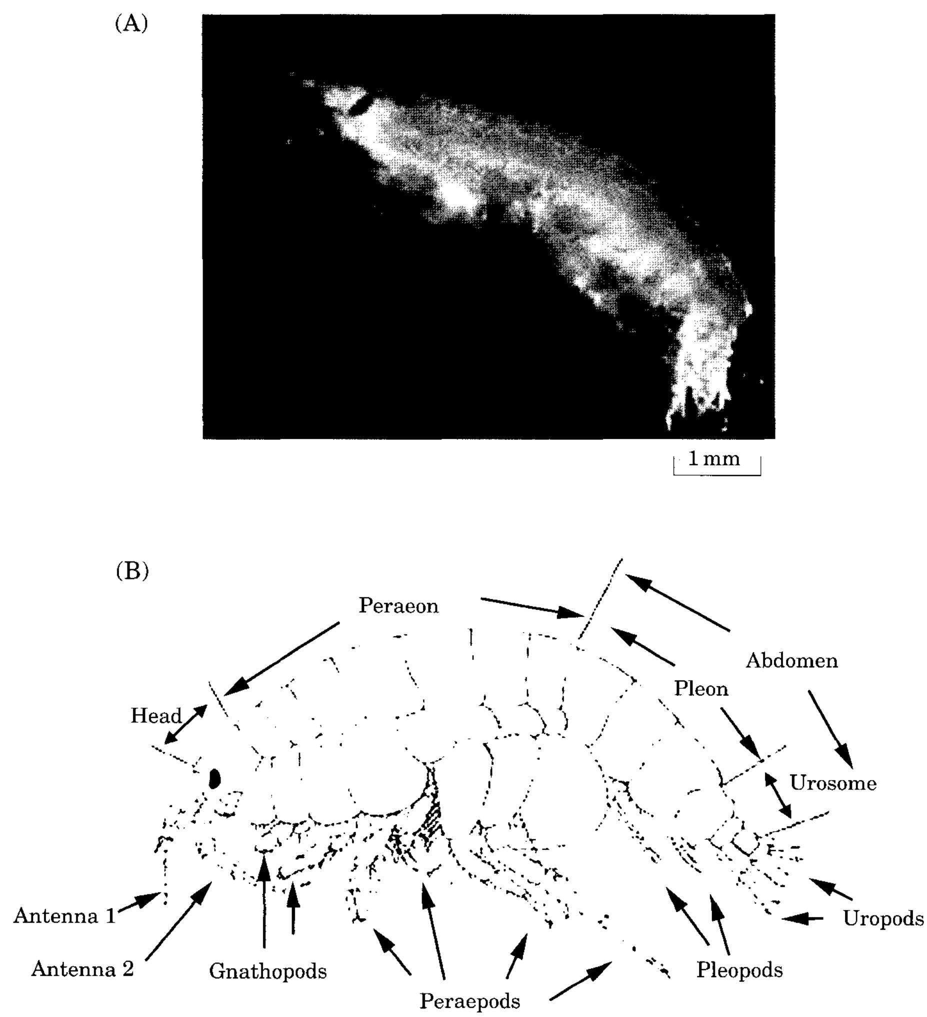

Fig. 1. A freshwater amphipod *Diporeia* spp. collected from Lake Michigan (A: female adult) and a female body outline (B: copied from Bousfield, 1989).

be related to temperature, life cycles, and maturation times. At shallow depths, *Diporeia* has a 1 year life cycle; small individuals are dominant in the spring, grow throughout the year, mature over winter, and then reproduce the following spring (Landrum and Nalepa 1998). *Diporeia* growth rates in a nearshore region (<30 m) of Lake Michigan were 0.59 mm month^{-1} from November through April (Winnell and White 1984). In deeper areas (>30 m), *Diporeia* life span is 2 to 3 years and reproduction tends to be more continuous, although greater numbers of small individuals are dominant in the spring and fall diatom blooms (Lubner 1979). Growth may be slower at these depths but production is higher because of higher *Diporeia* densities (Johnson 1988). Mean *Diporeia* size in the population is 4–6 mm in deeper areas (Winnell and White 1984; Evans *et al.* 1990).

Diporeia molt an estimated 8–12 times during their life span based on the assumption that *Diporeia* have the same number of instars as *Hyalella azteca* (Geisler 1944; Dermott and Corning 1988). However, I have not observed direct evidence of *Diporeia* molting during my laboratory microcosm experiments (Song 2000). Similarly, *Diporeia* molting has not been reported in other laboratory microcosm experiments (P. Landrum, personal communication).

Diporeia growth may impact lipid content and contaminant bioaccumulation. Small individuals are fast growing, and lipid content is low as energy is mostly used for somatic growth. Larger individuals accumulate lipids as growth slows and energy is stored for reproduction (Quigley 1988). Because larger individuals are more exposed to fish predation, most food-chain transfer of contaminants probably occurs through these larger individuals. At night, mature *Diporeia* move into the water column to reproduce making them even more susceptible to fish predation (Marzolf 1965b).

Energy storage

A high percentage of the organic matter assimilated in *Diporeia* is converted and stored as lipids. Because most organic contaminants are lipophilic by nature, lipid content relative to organism dry weight is important to contaminant body burdens and rates of elimination (Landrum and Nalepa 1998). The lipid contents are consistently higher in *Diporeia* compared to levels found in other common benthic macroinvertebrates in the Great Lakes (Gardner *et al.* 1985). This capacity to store energy as lipids is apparently a life-history strategy to survive and even to reproduce when food inputs are limited (Quigley 1988; Landrum and Nalepa 1998). Among the lipids, triacylglycerols play a role for energy storage during periods of limited food supply and for reproduction. Triacylglycerols are the dominant lipid (i.e. 84% of total lipids) in *Diporeia* taken from both Lakes Michigan and Ontario (Cavaletto *et al.* 1996).

In considering catabolic pathways of energy usage, an O : N ratio of 3 to 16 indicates a protein pathway, while ratios of 60 and above indicates a lipid-dominated pathway (Landrum and Nalepa 1998). The mean O : N ratio for *Diporeia* over several sampling dates in the spring and fall ranges from 56 to 230 in nearshore Lake Michigan (Landrum and Nalepa 1998). The mean lipid levels in *Diporeia* are 20-30% of its dry weight, but increase up to 50% when assimilation rates are high during the spring diatom bloom, and decrease to 7% in non-depositional, nearshore areas (Gardner *et al.* 1985; Cavaletto *et al.* 1996).

Diporeia can survive long periods without food (Landrum and Nalepa 1998). It may be due to their relatively low metabolic rate (i e. relatively low ammonium and phosphorus excretion rates) (Gauvin *et al.* 1989). In a 191 day laboratory experiment, the mean *Diporeia* ammonium release rate ranged between 0.5 and 1.8 nmole mg dry weight^{-1} h^{-1} (Gauvin *et al.* 1989). These excretion rates for *Diporeia* were lower than those values for *Diporeia* in Lake Michigan at either 4°C (3-5 nmole mg dry weight^{-1} h^{-1}) or 11°C (6 nmole mg dry weight^{-1} h^{-1}) (Gardner *et al.*, 1987). In similar, 191day laboratory experiment, phosphorous release rates were less than 0.15 nmole PO_4 mg dry weight^{-1} h^{-1} (Gauvin *et al.* 1989). This value resembled previously reported results for *Diporeia* from Lake Michigan (Nalepa *et al.* 1983).

Relationships among various condition indexes

Metabolic functions of small organisms are mostly defined on the basis of weight rather than length (Dermott and Corning 1988; Johnson 1988). To examine the relationships among the condition indexes (i.e. wet weight, dry weight and body length) I collected *Diporeia* spp. using a PONAR grab sampler from surficial sediment at a water depth of about 60 m in Lake Michigan in cooperation with P.F. Landrum (Great Lake Research Laboratory, NOAA). This site was previously sampled for *Diporeia* (Landrum and Faust 1994) for use in microcosm studies. The relationships among wet weight, dry weight and body length of *Diporeia* spp. were then determined using 150 randomly selected amphipods.

Results showed that dry weight-body length were significantly related ($r^2 = 0.92$, N = 150, $P < 0.01$) according to the power function $D = aL^b$, where D was dry weight (mg) and L = body length (mm). The parameters 'a' and 'b' for *Diporeia* in my experiments were determined to be 0.014 and 2.59, respectively (Figure 2A). These values were consistent with previously determined values of 'a' and 'b' ranging from 0.0011 to 0.014 and from 2.55 to 3.40, respectively in the Great Lakes (Johnson and Brinkhurst 1971; Winnell and White 1984; Johnson 1988; Landrum and Nalepa 1998). The range in values for these parameters may be due to the differences in the physiological and biological condition of *Diporeia* including season, location, reproductive state and sex (Personal communication with Dr. Robert Cerrato in SUNY at Stony Brook).

Results also showed that *Diporeia* wet weight-body length was significantly related ($r^2 = 0.96$, N = 150, $P < 0.01$) according to the power function $W = cL^d$, where W is wet weight. Parameters 'c' and 'd' in my experiments

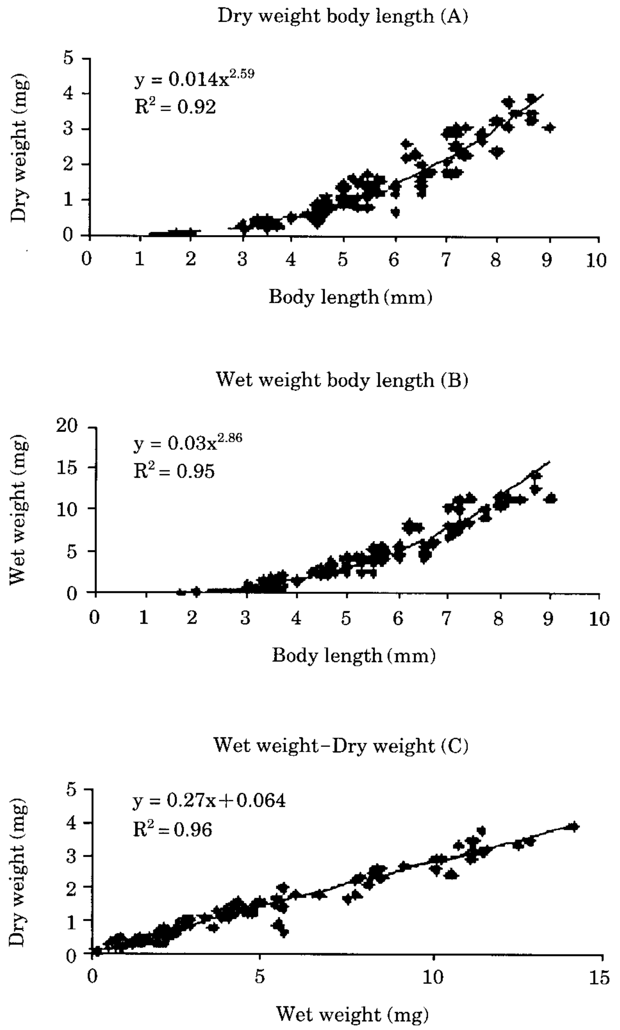

Fig. 2. Relationships among dry weight (A) wet weight (B) and body length (C) of *Diporeia* spp. collected from surficial sediments in Lake Michigan.

were determined to be 0.03 and 2.86, respectively (Figure 2B). These values may also vary with the physiological condition of *Diporeia* including season, location, reproductive state and sex.

Diporeia wet weight and dry weight were linearly related ($r^2 = 0.96$, $N = 150$, $P < 0.01$) according to $D = 0.27W + 0.064$ (Figure 2C). This value was also consistent with $D = 0.269W \pm 0.052$ determined using *Diporeia* collected from Lake Michigan (Landrum, 1988). The wet weight-dry weight relationships are particularly important when comparing measurements of contaminant accumulation expressed on a dry weight basis in field and laboratory experiments (Landrum and Nalepa, 1998).

ECOLOGICAL CONSIDERATIONS FOR *DIPOREIA* SPP.

Temperature effect

Temperature may play an important role in the distribution and metabolic rate functions of *Diporeia*. In general, *Diporeia* is most abundant in the colder and deeper areas of the Great Lakes below the summer thermocline, and is generally absent from warmer and shallower areas. Based on field distributions, *Diporeia* can tolerate temperatures as high as 23°C although abundance at these temperatures was low (Mozley and Howmiller 1977). In contrast, *Diporeia* in nearshore Lake Superior apparently had an upper thermal tolerance range of 10 to 14°C (Smith 1972).

There are strong negative relationships between *Diporeia* densities and bottom temperatures in Lake Huron and Lake Ontario (Johnson 1988; Sly and Christie 1992). *Diporeia* densities were higher in upwelling areas than downwelling areas in Lake Michigan (Alley and Mozley 1975). In general, maximal growth of *Diporeia* is observed from the optimum temperature (8 to 12°C) (Gordeev 1952; Bousfield 1958).

Bioturbation depth and sediment ingestion

As a detritivore, *Diporeia* burrows through the upper 2 cm of substrate to feed on the surficial layer of sediment (Nalepa and Robertson 1981; Hill and Elmgren 1987). Based on a radionuclide (^{137}Cs) and X-ray analysis, the bioturbation depth of *Diporeia* was determined to be about 1.5 cm (Robbins *et al.* 1979; Song 2000). Using either *Diporeia* that had filled their guts with sediment marked with fluorescent particles or surface-added fluorescent particles, Lopez and Elmgren (1989) similarly observed that most fluorescent fecal pellets were found within the upper 0-1 cm of the sediment core.

Sediment ingestion of *Diporeia* may not be significantly different on an annual basis over a range of conditions related with depth. Based on *Diporeia* populations (gram dry weight) in different depths in Lake Ontario (3.05 g m^{-2} at 35 m, 2.24 g m^{-2} at 70 m, and 0.99 g m^{-2} at 125 m), Dermott and Corning (1988) determined that mean sediment ingestion rates of *Diporeia* were 238, 213, and 211 mg dry sediment g dry *Diporeia*$^{-1}$ d^{-1}, respectively. These sediment ingestion rates corresponded with 23.8% (57 mg), 24.3% (52 mg), 24.4% (52 mg) organic matter ingestion per g dry *Diporeia* per day, respectively (Dermott and Corning 1988).

Organic matter ingestion by *Diporeia* may be different due to their selective feeding and the change of food supply in natural environments. Studies of feeding and food gut analysis suggest that *Diporeia* feeds primarily on bacteria-rich detritus and settled diatoms (Marzolf 1965a; Johnson 1987; Quigley and Vanderploeg 1991). In 20 day feeding experiments, Quigley and Vanderploeg (1991) observed that *Diporeia* ingested the filamentous diatom, *Melosira varians*. They suggested that *Diporeia* growth and production might be more closely linked to primary production than previously thought. The difficulty observing diatom cells in *Diporeia* gut analysis may be because cells are partially digested during passage through the gut, or that the cells are dead prior to ingestion (Evans *et al.* 1990; Quigley and Vanderploeg 1991).

Higher organic contents in the gut of *Diporeia* compared to the surrounding sediments may suggest that *Diporeia* selects for particle size and/or organic content (Dermott and Corning 1988). In the laboratory, *Diporeia* selected sediment particles smaller than ϕ1 (0.5 mm) and there was no apparent resolution of size differences in experiments utilizing sediments finer than ϕ1 (Marzolf 1965a). *Diporeia* abundance has been related to sediment organic content and/or associated bacteria in field studies (Sly and Christie 1992). This may affect contaminant metal uptake in *Diporeia* because organic carbon is an important phase which partitions metal contaminants in sediments, and thus influences bioavailability and toxicity (Landrum and Robbins 1990). In a laboratory study, Lopez and Elmgren (1989) abserved that about 40% of the sedimentary organic carbon was absorbed in *Diporeia* from surficial sediments. The detritus absorption by *Diporeia* was, however, not much different than that of other deposit feeders (Lopez and Levinton 1978).

Spring blooms may provide high quality food and maximal food abundance in the benthic regions. However, gut turnover times and ingestion rates may be lower in the spring bloom. Quigley and Vanerploeg (1991) observed that *Diporeia* feeding on the diatom *Melosira*, a common spring diatom in Lake Michigan, had a lower gut turnover time than animals feeding on regular sediment. Gut turnover time for *Diporeia* was estimated to be 1.6-2.4 h based on fecal pellet production in a 19 d experiment (Elmgren *et al.* 1986). The mean gut fullness over an annual period was relatively consistent ranging from 40-50% in Lake Michigan and 48% in Lake Ontario as a function of depth (Quigley 1988; Dermott and Corning 1988; Evans *et al.* 1990).

Accumulation of organic contaminants

Contaminant accumulation in *Diporeia* is an important area of study due to the transfer of contaminants to upper trophic levels through biomagnification. Lipid contents in *Diporeia* are a major factor in the accumulation of non-polar organic contaminants because most non-polar organic contaminants are lipophilic (Landrum and Nalepa 1998). The distribution of contaminants among classes of lipids in *Diporeia* suggests that the total lipid content is important because the lipid normalized contaminant concentration was similar for storage lipids (triglycerides) and for structural lipids (phospholipids) when the amphipods were exposed to benzo (a)pyrene (BaP) and hexachlorobiphenyl (HCBP) (Gardner *et al.* 1990).

Chlorinated hydrocarbon concentrations in *Diporeia* were higher in Lake Ontario by a factor of two or more than in Lake Erie (Whittle and Fitzsimons 1983). Differences in bioaccumulation of chlorinated hydrocarbon concentrations in *Diporeia* collected from different areas of Lake Michigan suggested that greater contaminant concentrations were in the southern part of Lake Michigan (Evans *et al.* 1991). Where chlorinated hydrocarbon bioaccumulation factors (BAF) can be calculated, these values are near the expected values, based on thermodynamic equilibrium, between the organic matrix of the sediment and the organism lipid content, assuming a 1% organic carbon content and a 25% lipid content for the two compartments (DiToro *et al.* 1991).

PAH concentrations in *Diporeia* ranged from about 40 ng g^{-1} wet weight to approximately 2000 ng g^{-1} wet weight for organisms from Lakes Erie, Huron, and Michigan (Eadie *et al.* 1985). Bioaccumulation factors (BAFs:

tissue PAH concentrations/sediment PAH concentrations) ranged from 1.2 to 3.3 for a range of PAHs with no definite pattern relative to the hydrophobicity of the compound. These values suggest that *Diporeia* is not near equilibrium between organic matter and organism lipid content for PAHs. Even attempting to account for the fraction that should provide a food source to *Diporeia* suggests that PAH bioaccumulation is kinetically limited, so that the thermodynamic potential is not reached (Eadie *et al.* 1985). This is consistent with the toxicokinetics and demonstrates greater availability of PCB congeners, compared to PAH congeners, in the laboratory studies (Landrum and Nalepa 1998).

A review of field data indicates that *Diporeia* were very sensitive to toxicants (Nalepa and Landrum 1988). In recent studies, *Diporeia* have been exposed to contaminants in the laboratory, both water and sediments, to verify these field observations and further evaluate toxicological responses in this organism. Toxic response studies of *Diporeia* have used concentration measures for both the environmental compartment and organism tissue to describe the mortality due to exposure to selected toxicants. The sensitivity of *Diporeia* to pentachlorophenol was similar to that of other amphipods and *Diporeia* were more sensitive to carbaryl (Sanders 1969; Kierstead and Barlocher 1989). However, in matched bioassays to field collected sediment, *Diporeia* was less sensitive to toxicants than *Hyalella azteca* (Burton *et al.* 1996).

Accumulation of trace metals

Trace metal accumulation in *Diporeia* has been not widely studied. In field studies, *Diporeia* body burden copper (Cu) concentrations were higher than Cu concentrations in other freshwater amphipods, including *Hyalella azteca* (79-89 μg g^{-1}: Borgmann *et al.* 1993), *Gammarus fasciatus* (76-82 μg g^{-1}: Amyot and Pinel-Alloul 1994) and *Gammarus* fossarum (59-78 μg g^{-1}: Plénet 1995). Copper concentrations in *Diporeia* collected from near Port Weller, outside Hamilton Harbor and Niagara River in 1996 were much higher (116-176 μg g^{-1}) than the Cu concentrations in *Diporeia* collected from western (99 μg g^{-1}) and eastern (86 μg g^{-1}) Lake Ontario (Song and Breslin 1998). For *Diporeia*, tissue Cu and Zn concentrations were correlated with Cu and Zn in easily extracted fractions (e.g. $MgCl_2$ and NaOAc) in the sediment. In addition, Cu and Zn concentrations in *Diporeia* tissue co-varied with those metal concentrations in the sediment (Song and Breslin 1998).

Laboratory studies examining trace metal toxicity to *Diporeia* were relatively few compared to other freshwater invertebrates (e.g. *Hyalella azteca*). Results of field studies showed that *Diporeia* densities decrease with increasing sediment Cu concentration. *Diporeia* in Cu tailing (395-1310 μg g^{-1}) areas were almost absent compared to the densities (470-4480 m^{-2}) of *Diporeia* in uncontaminated areas (14-298 μg g^{-1}) in Lake Superior (Kraft 1979). Results of long-term (460 days) laboratory soft-bottom microcosms, tissue cadmium (Cd) concentrations in *Diporeia* gradually increased up to about 3500 times compared to dissolved Cd concentrations (6.5 μg L^{-1}) in the overlying water and their mortality was about 70% for adults and 100% for juveniles (Sundelin 1983). In short-term (7 day) bioassay experiments using Hamilton Habor sediment, Jackson *et al.* (1995) found that *Diporeia* mortality exceeded 64% in the hypolimnion mud. In this study, they assumed that particularly high Zn, total PCBs and PAHs were the most likely candidates for the observed high mortality (Jackson *et al.* 1995).

CONCLUSIONS

Diporeia is widely spread in most North America freshwater environments including the Great Lakes, arctic and subarctic lakes and rivers. Especially, it has lots of lipids which play role as an energy storage for surviving few months without any food supply in harsh natural environments. It may be due to the use of stored lipid and to the low metabolic rates such as low excretion of ammonium and phosphorus in cold and limited conditions.

Due to the important food web role, many studies have examined the dynamics of contaminant accumulation in this species, including body burdens, bioaccumulation, and toxicokinetics. In particular, *Diporeia* is an excellent organism for examining the accumulation of contaminants from ingested sediment because it actively *feeds on sediment and it* exist both in aerobic and anaerobic (i.e. hypolimnion) sediment. *Diporeia*, therefore, may be useful benthic animal that can be used as a potential biomonitor for contaminants (i.e. trace metals) in freshwater environments.

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