A Review of the Factors Affecting the Ecotoxicology of *Diporeia* spp.

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ABSTRACT. Based on its biomass, Diporeia spp. represent the major benthic invertebrate in offshore waters of the Great Lakes. This work reviews the recent findings of factors influencing the organism with particular focus on interpreting the potential for contaminant stress, with an emphasis on organic contaminants, and the benthic pelagic link for contaminant food web transfer. The review includes examination of the environmental features that limit the distribution and population density. The physiology of Diporeia spp., including energy storage, respiration, and nutrient elimination, are discussed. The toxicokinetics from both aqueous and sediment exposures are reviewed, as well as both the environmental factors that influence the kinetics and the limitations to our knowledge. The interactions of the physiology and toxicokinetics are presented for interpretation of toxic responses and the sensitivity of the organism to selected contaminants. Finally, this review suggests areas where increased information is needed to improve our understanding of Diporeia toxicokinetics and toxicity in the Great Lakes environment.

INDEX WORDS: Diporeia, amphipod, review, toxics, toxicokinetics.

INTRODUCTION

The amphipod *Diporeia* is the most widespread and dominant benthic macroinvertebrate in the offshore waters of the Great Lakes (Cook and Johnson 1974). This species can account for up to 65% of total benthic biomass (Nalepa 1989), and 70 to 90 % of total benthic production in many regions (Johnson and Brinkhurst 1971). In areas where it is found, *Diporeia* plays a major role in the movement of energy, nutrients, and contaminants through the food web. As a surface-feeding detritivore, this organism utilizes freshly-settled algae as a major source of food (Gardner *et al.* 1990a) and, in turn, is fed upon by many species of Great Lakes fish in at least some season or life stage (Scott and Crossman 1973). Thus, this species is a major energy link between benthic and pelagic production and upper trophic levels.

Because of this important food web role, a number of studies have examined the dynamics of contaminant accumulation in this species, including body burdens, bioconcentration, and toxicokinetics (for review, see Landrum 1988). This paper summarizes the most recent findings regarding the up-

take and elimination of contaminants in this organism and places these findings in perspective with respect to earlier works. In addition, a summary is provided of environmental factors unique to this organism's habitat and life mode that most influence contaminant dynamics. This review is provided with the realization that *Diporeia* is declining in many areas of the Great Lakes probably as a result of food competition with *Dreissena* (Dermott and Kerec 1997, Nalepa *et al.* In Press). The cycling of contaminants in these areas will be dramatically changed, and this review provides a basis for future investigations.

In North America, the genus *Diporeia* was formerly known as the species *Pontoporeia hoyi*. Based on recognized morphological and physiological differences, the genus *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 that may contain as many as eight species. Because taxonomic differences have not been resolved, this genus is considered herein as one group with the realization that future studies may define taxonomic distinctions and differences in ecological and physiological characteristics.

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Ecological Considerations Relevant to Contaminant Dynamics

Temperature

Temperature plays a major role in the distribution and metabolic rate functions of *Diporeia,* which is a glacial-marine relic. In this regard, the upper thermal tolerance limit and the temperature for maximal growth and reproduction are important considerations. In general, *Diporeia* is most abundant in the colder, offshore areas of the Great Lakes in areas below the summer thermocline, and is generally absent from warm, shallow bays and basins. Based on field distributions in nearshore Lake Michigan (12 m), *Diporeia* is able to tolerate temperatures as high as 23°C, although abundances at these temperatures were quite low (Mozley and Howmiller 1977). These rather high upper thermal limits were confirmed in laboratory experiments; *Diporeia* from Lake Michigan exhibited essentially no mortality at temperatures up to 26°C, but mortality exceeded 80% at 28°C when the temperature was gradually increased (Gossiaux *et al.* 1992). In contrast, *Diporeia* from nearshore Lake Superior apparently had an upper thermal tolerance limit of only 10 to 14°C (Smith 1972). Other studies of field distributions have shown tolerance limits of 14 to 20°C (Segerstråle 1977). These differences in tolerance limits are great, and are probably related to either differential thermal adaptations, development of thermally-modified strains, or the presence of different species complexes. The latter theory is a distinct possibility. For example in Lake Mazinaw, Ontario, Canada, the cold-stenothermal *Diporeia filicornis*-group was found only at temperatures below 15°C (below summer thermocline), whereas the more eurythermal *Diporeia brevicornis*-group was found above the thermocline in warmer waters (Vainola and Varvio 1989). Both taxonomic groups are found in the Great Lakes (Bousfield 1989). However, regardless of taxonomic group, higher densities are always associated with colder temperatures. In Lake Ontario, there was a strong negative relationship between *Diporeia* densities and bottom temperatures exceeding 15°C (Sly and Christie 1992), and areas in Lake Michigan which are prone to upwelling events, and thus to colder mean temperatures, had higher densities than areas with downwellings (Alley and Mozley 1975). The strong relationship between *Diporeia* and water temperatures was apparent when distributions were examined relative to various physicochemical parameters in individual lakes (Dadswell 1974). Of a number

of glacial-marine relics, *Diporeia* displayed the strongest negative relationship between occurrence and maximum bottom temperatures.

Probably more important in terms of population dynamics and toxicokinetics is the optimum temperature for maximal growth, which is apparently 8 to12°C (Gordeev 1952, Bousfield 1958). This is within the general temperature range in which reproduction occurs and where maximal densities are found (Alley 1968). In Lake Huron, distributions of various size classes were strongly related to water temperature, with older individuals preferring cooler temperatures (< 11°C, Johnson 1988). As a result, most production occurred in the cooler, deeper regions of the study area.

Feeding, Ingestion, and Energy Storage

As a detritivore, *Diporeia* burrows through the upper 2 cm of substrate to feed on the surficial layer of sediment. Studies of food selection and gut analysis indicate that this organism feeds primarily on bacteria-rich detritus and settled algae (Marzolf 1965a, Johnson 1987). It appears to be highly selective of the particles ingested; organic content of gut material is higher than in corresponding sediments, indicating selection on the basis of particle size or organic content (Dermott and Corning 1988). In field studies, abundances have been related to sediment organic content and/or associated bacteria (Marzolf 1965a, Sly and Christie 1992). This, of course, is relevant to contaminant uptake, since organic carbon is the primary phase which partitions non-polar contaminants to sediments, and thus influences bioavailability and toxicity (Landrum and Robbins 1990).

Rates of ingestion of organic material, and hence, ingestion of sediment-associated contaminants, are a function of a number of different factors, but probably the most important is the quality of food that is settling from the pelagic region. Based on estimates of gut fullness, feeding in *Diporeia* is intermittent and very adaptable, with maximal feeding (gut fullness) during and just after the spring diatom bloom (Dermott and Corning 1988, Quigley 1988). This time period is when food inputs to the benthic region are of high quality and maximal abundance. In the spring, the dominance of large diatoms and the lack of thermal gradients allows pelagic material to settle rapidly; also, a greater percentage of pelagic production reaches the bottom because losses in the water column resulting from bacterial decomposition and zooplankton

grazing are at a minimum (Scavia *et al.* 1986). However, while gut fullness is greatest in the spring, gut turnover times, or ingestion rates, may be lower. Animals feeding on the diatom *Melosira*, a common spring diatom in Lake Michigan, had a lower gut turnover time than animals feeding on regular sediment (Quigley and Vanderploeg 1991). It was hypothesized that the slower gut passage time of animals feeding on *Melosira* allowed more time for the full assimilation of this high-quality food source. Spatial feeding patterns are also related to food inputs; gut fullness was greatest in regions of the lake where pelagic inputs were the highest (Evans *et al.* 1990).

During non-bloom periods, the percentage of food material in the gut declines. However, in regions where benthic inputs are not as seasonal, such as in the profundal, there is less temporal variation in the amount of food in the gut because feeding is more continuous (Evans *et al.* 1990). The net result is that, despite regional and seasonal differences in feeding, mean gut fullness over an annual period (May to October) is fairly consistent regardless of depth, and ranges from 40% to 50% at several depths in Lake Michigan (Quigley 1988, Evans *et al.* 1990). These values are quite similar to the mean of 48% reported in Lake Ontario (Dermott and Corning 1988).

Given the consistency of food intake on an annual basis, yearly ingestion rates may also be considered fairly uniform over a range of conditions related to depth. Ingestion rates determined for populations at three different depths in Lake Ontario (35 m, 70 m, and 125 m) appear to confirm this assumption. Mean annual ingestion rates were 238, 213, and 211 mg DW sediment/g DW *Diporeia*/d, respectively (Dermott and Corning 1988). Corresponding ingestion of organic matter was 57, 52, 52 mg organic matter/g DW *Diporeia*/d, based on sediment organic content of 10.5, 9.7, and 6.0%, respectively. These ingestion rates are higher than the 3 to 17 mg DW sediment/g DW *Diporeia*/d determined in laboratory experiments of contaminant uptake which used a soil composite (silt-loam) with 1% organic matter (Harkey *et al.* 1994a).

Because not all ingested material is assimilated, a critical value in determining contaminant uptake is the assimilation efficiency. Although direct estimates of assimilation efficiency in *Diporeia* are lacking, estimates based on the amount of organic material assimilated (measured directly or calculated via production) relative to the amount of freshly-settled material can provide some indica-

tion. Such estimates assume that *Diporeia* feeds mostly on organic matter that is freshly settled from the water column, and that time constants of horizontal transport rates are long compared to vertical settling rates. At a 45-m site in Lake Michigan, the amount of organic material required to support *Diporeia* production was determined to be 11 to 23% of all organic material settling on an annual basis (Gardner *et al.* 1985). More direct studies at the same site found that *Diporeia* assimilated 61% of all material settling to the bottom during the spring bloom (Fitzgerald and Gardner 1993). Similarly, yearly assimilation of settled material by *Diporeia* in Lake Ontario was calculated to be 15%, but can be as high as 65% when feeding on fresh algae (Dermott and Corning 1988). The assimilation efficiency of a related amphipod species feeding on settled material from the spring bloom in the Baltic Sea was 40% (Lopez and Elmgren 1989). Clearly, assimilation efficiency can be highly variable and strongly dependent on the quality of food. Intermittent feeding and relatively low ingestion rates (6% of body weight per day based on organic matter; Dermott and Corning 1988) on an annual basis would suggest the need to feed on a high-quality food source such as diatoms. Thus, while it has been shown that *Diporeia* may select organic material rich in bacteria (Marzolf 1965a), bacteria alone probably do not meet its energy demands. A study on a related amphipod species indicated that bacterial carbon only accounted for 2 to 5% of the total carbon demand of the population (Goedkoop and Johnson 1994).

Since most contaminants are lipophilic by nature, lipid content relative to organism dry weight is important to contaminant body burdens and rates of elimination. Of the material that is assimilated by *Diporeia*, a relatively high percentage is converted and stored as lipids. When compared to levels found in other common benthic macroinvertebrates in the Great Lakes, lipid/energy content is consistently highest in *Diporeia* (Johnson and Brinkhurst 1971, 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, Gauvin *et al.* 1989). Of the six lipid classes, triacylglycerols are chemical stores of energy used for periods of limited food supplies and for reproduction. Triacylglycerols were the dominant lipid class found in *Diporeia* taken from both Lakes Michigan and Ontario and comprised up to 84% of total lipids (Cavaletto *et al.* 1996). The predominance of lipids in the metabolic

functions of *Diporeia* was apparent when O:N ratios were examined (ratio of moles of oxygen consumed to moles of nitrogen excreted as ammonia). When considering catabolic pathways of energy usage, an O: N ratio of 3 to 16 indicates a protein pathway, while ratios of 60 and above indicate a lipid-dominated pathway. In nearshore Lake Michigan, mean ratios for *Diporeia* over several sampling dates in spring and fall ranged from 56 to 230 (unpublished data, Quigley, M. A., Great Lakes Enviornmental Research Lab, Ann Arbor, MI).

On the average, lipid levels in *Diporeia* are 20 to 30% of dry weight, but can reach as high as 50% when assimilation rates are high as during the spring diatom bloom, and as low as 7 % in non-depositional, nearshore areas (Whittle and Fitzsimons 1983, Gardner *et al.* 1985, Cavaletto *et al.* 1996, Nalepa unpublished data). While temporal changes in lipid content are clearly a function of the spring bloom, other variables besides benthic inputs of lipid-rich diatoms must be considered when examining spatial or between-lake differences. For instance, lipid levels of *Diporeia* taken at similar depths were significantly higher in Lake Ontario than in Lake Michigan (Cavaletto *et al.* 1996), despite the fact that diatoms are more prevalent in the latter lake (Sly and Christie 1992). It has been suggested that a lower proportion of diatoms may actually be reaching the bottom in Lake Michigan because of grazing by the greater number of hypolimnetic copepods (Cavaletto *et al.* 1996). At any rate, higher body burdens of contaminants found in *Diporeia* from Lake Ontario than in those from Lake Michigan (Nalepa and Landrum 1988) may be partly related to these differences in lipid levels.

Size, Growth, and Life Cycle

The size distribution of individuals in natural populations is related to temperature, growth cycles, and maturation times. In warm nearshore waters (above summer thermocline), *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. Growth rates in a nearshore region (< 30 m) of Lake Michigan were 0.59 mm/mo from April through November, and 0.33 mm/mo from November through April (Winnell and White 1984). In deeper waters (> 30 m), the life span is 2 to 3 years and reproduction tends to be more continuous, although greater numbers of small individuals are apparent in the spring and fall, at the times of diatom blooms (Lubner 1979). Growth is slower at these depths but production is higher because of higher densities (Winnell and White 1984, Johnson 1988). At these greater depths, mean size of individuals in the population is 4 to 5 mm (Alley 1968, Winnell and White 1984, Evans *et al.* 1990). *Diporeia* becomes mature at about 6 mm in Lake Michigan (Winnell and White 1984).

As might be expected, size and growth have a great impact on lipid content and, subsequently, on contaminant bioaccumulation. Small individuals are fast-growing, and lipid content is low as energy is mostly used for somatic growth. In contrast, larger individuals accumulate lipids as growth slows and energy is stored for reproduction (Quigley 1988). Because larger individuals are more prone to fish predation (McDonald *et al.* 1990), most food-chain transfer of contaminants probably occurs through these larger individuals. Also, large, mature individuals migrate into the water column at night for reproductive purposes, making them even more susceptible to fish predation (Marzolf 1965b).

Because metabolic functions are mostly defined on basis of weight rather than length, the relationship between mass and size has been determined in several Great Lakes studies. The relationship fits the power equation $W = aL^b$, where W = dry weight (mg) and L = body length (mm). The constants a and b range 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, Dermott and Corning 1988, Johnson 1988, Quigley, M.A. Personal Communication, Great Lakes Environmental Research Laboratory, Ann Arbor, MI). The constants relating ash-free dry weight and length were found to be a = 0.0033 and b = 3.306 for individuals from Lake Michigan (Nalepa *et al.* 1985). Dry weight was 0.269 ± 0.052 of wet weight, whereas ash-free dry weight was 0.231 ± 0.046 of wet weight (Landrum 1988). These last relationships are particularly important when comparing field measurements of contaminant accumulation that are expressed on a dry weight basis to laboratory-derived measures of bioaccumulation, which are generally reported on a wet-weight basis.

Toxicokinetics

The rates of accumulation and loss of contaminants by *Diporeia* define the extent of exposure and the ability of *Diporeia* to biotransform contaminants which could measurably affect the toxicokinetics and ultimate toxicity of contaminants.

However, no measurable contaminant biotransformation has been found (Landrum 1982, 1988). Thus, the accumulation from either water or sediment and the toxicity of contaminants can be investigated without consideration of this complicating factor. Contaminant accumulation reflects the physiological and behavioral response of *Diporeia* to selected environmental variables that alter the overall volume or mass of the source compartment carrying the contaminant into contact with the amphipod. Thus, factors such as exposure temperature and organism size have significant affects on contaminant accumulation and loss rates (Landrum 1988, Landrum and Stubblefield 1991, Landrum 1995). The effects of these two variables on exposure to sediment-associated contaminants has yet to be reported. However, sediment composition and equilibrium conditions between the contaminant and the sediment on accumulation of sediment-associated contaminants have been examined (Landrum 1989; Landrum and Faust 1991,1994; Landrum *et al.* 1992, 1994, 1997).

The toxicokinetics of two compound classes are generally well studied in *Diporeia*: polycyclic aromatic hydrocarbons (PAH) and polychlorinated biphenyls (PCB), although some data also exists on other compounds (Landrum 1995). These findings will be presented in four major sections: The first will discuss accumulation from water-only exposures, the second will focus on elimination, the third on sediment exposures, and the fourth on the relationship between ingestion and accumulation.

Aqueous Exposures

Aqueous exposures have been studied under both static and flow-through conditions and accumulation rate determined as uptake clearance. The uptake clearance is defined as the amount of source compartment scavenged of contaminant per unit mass of organism per time. Aqueous exposures have been used to develop most of the information on the effects of environmental temperature and organism physiology on the accumulation process. However, in many cases, the relationships and variables were not sufficiently segregated to obtain completely controlled studies, e.g., not all the studies on the role of temperature controlled for organism size. However, a sufficient quantity of investigations involving organism size have been conducted so that both characteristics can be evaluated.

At 4°C, and for compounds with large log oc-

tanol:water partition coefficients (log $K_{ow} > 5.2$) such as benzo(a)pyrene (BaP) and 2,4,5,2',4,5',-hexachlorobiphenyl (HCBP), the uptake clearance declines exponentially with increasing organism size (mass) (Figs. 1 and 2). However, size has little influence on more water soluble compounds with log K_{ow} values below 4.5 (Landrum 1988, Landrum 1995). The decline in uptake clearance with increasing size is consistent with the hypothesized kinetic resistances that influence the accumulation of relatively insoluble compounds. The uptake of compounds such as BaP and HCBP are likely kinetically limited both by membrane diffusion and the distribution (movement) through the organism to the final storage site (Landrum and Stubblefield 1991). However, for 2,2',5,5'-tetrachlorobiphenyl (TCBP, Log $K_{ow} = 5.98$), the relationship between uptake clearance and mass showed a linear decline with increasing mass (Landrum 1988), perhaps due to the limited amount of data to define the relationship. For compounds with log K_{ow} values between 4.5 and 5.2, specifically pyrene, anthracene, and phenanthrene, there was apparently no relationship between uptake clearance and organism mass (Landrum 1988, Landrum 1995). This was somewhat surprising because in a smaller study there was a linear relationship between organism surface area and phenanthrene uptake (Landrum and Stubblefield 1991).

Before a relationship between contaminant hydrophobicity, as described by log K_{ow}, and the rate of uptake can be established, the effect of organism
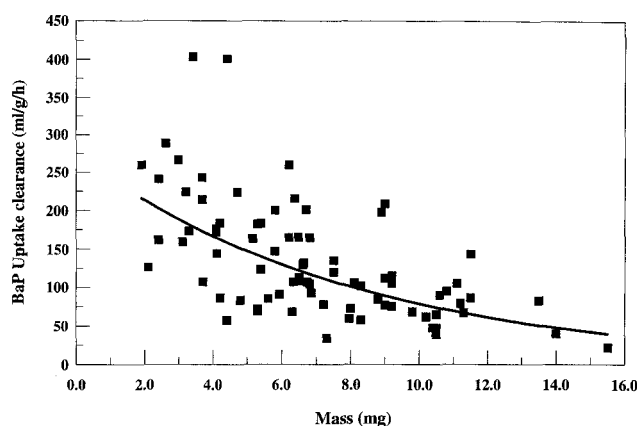
FIG. 1. Uptake clearance (ml/g/h) for the accumulation of benzo(a)pyrene from water by **Diporeia** *spp. as a function of mass (mg, $k_u = 272.2$ $e^{-0.125(mass)}$); data from Landrum 1995.*
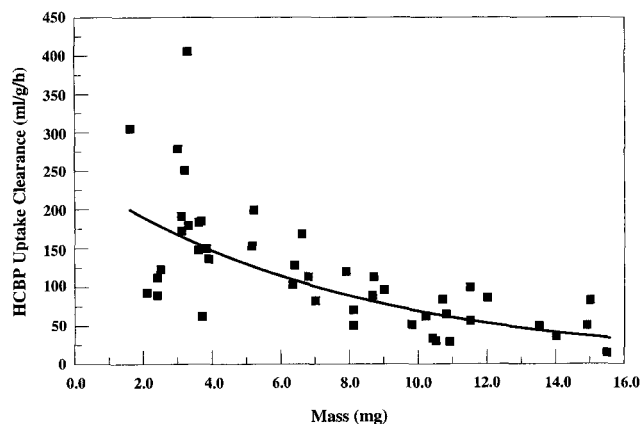
FIG. 2. *Uptake clearance (ml/g/h) for the accumulation of 2,4,5,2',4',5'-hexachlorobiphenyl from water by* **Diporeia** *spp. as a function of mass (mg, $k_u = 244.1e^{-0.127(mass)}$); data from Landrum 1995.*

size must be removed. A relationship between log K_{ow} and uptake clearance (k_u) at 4°C can be determined at the limit where mass equals zero for compounds that show size dependence or for those compounds that do not exhibit a dependence upon organism mass, by using the average value:

$$k_u \text{ (mL/g/h)} = -90.5 \ (\pm 70.8) + 52.8 \ (\pm 13.6) \log K_{ow},$$
$$r^2 = 0.702, n = 7. \tag{1}$$

This equation is not statistically different either for the intercept or the slope from a previously determined relationship (Landrum 1988). This log-linear relationship is expected to be limited at very high log K_{ow} values (> 7) where the size of molecules becomes a significant barrier to membrane penetration (Zitko 1980, Opperhuizen *et al.* 1985, Saito *et al.* 1990).

Attempts to examine the relationship between k_u and log K_{ow} by minimizing the influence of size using specific size classes of amphipods adds some information on the uptake process. For large (9 to 10 mg wet weight) and medium (6 to 7 mg wet weight) amphipods, there was no relationship between k_u and log K_{ow} suggesting that internal rates of distribution may dominate the rate determining step since contaminant characteristics appear to be unimportant. For small amphipods (1.6 to 4 mg wet weight), a statistically significant linear relationship

between k_u and log K_{ow} was observed with the data from Landrum (1995).

$$k_u = -8.1(163.3) + 28.3 \ (2.6) \log K_{ow}, n = 31,$$
$$r^2 = 0.12, p < 0.05 \tag{2}$$

This relationship was similar to that found for the limit where size equals zero but has significantly more variability due in part to size effect on k_u and variability between experimental determinations. Thus, for small organisms, where the internal distribution processes would be expected to be minimal, the rate of membrane transfer may dominate the rate determining step and would result in a positive relationship between k_u and log K_{ow}.

The uptake from water apparently occurs across both the gills and the carapace (Landrum and Stubblefield 1991) and is proportional to the rate of oxygen consumption, but apparently occurs with much greater efficiency than oxygen uptake. The uptake clearance for oxygen ranges from 20 to 60 mL/g/h, while that for contaminants ranges from about 100 to 300 mL/g/h (Landrum and Stubblefield 1991). Thus, either the efficiency for oxygen uptake is about 1/3rd to 1/10th that for contaminants or the oxygen in *Diporeia* is near saturation and is only replaced as consumed.

The thermal response for contaminant accumulation is not as well characterized as the response with respect to mass. There is an abundance of data for 4°C, but little data for elevated temperatures (Landrum 1995). To evaluate thermal response, the potential impact of mass was removed from the analysis. For 5 to 7-mg wet weight amphipods and at temperatures between 4 and 15°C, there is a linear relationship between temperature and uptake clearance with a slope of 9.9 ± 2.9 mL/g/h/°C for anthracene, 12.9 ± 4.9 for BaP, and 10.4 ± 2.1 for TCBP (Landrum 1995). However, the analysis for phenanthrene yielded a somewhat gentler slope than for the other compounds, 5.6 ± 2.9 mL/g/h/°C. All of these slopes suggest a doubling of uptake clearance for approximately each 10°C elevation in temperature, an expected response for a physiologically driven process. Further, the activation energy estimated for the uptake from plots of log k_u versus 1/T (°K) ranged from 7.1 to 12.9 kcal/mol. This suggests that membrane diffusion limits the uptake (Smulders and Wright 1971, Garrick *et al.* 1982).

Lipid content can also affect the rate of accumulation in some organisms (Bruner *et al.* 1994). For *Diporeia*, the lipid content of the organisms does not appear to affect the accumulation rate from

water (Landrum 1988). However, as shown below, elimination is strongly affected by the lipid content.

Elimination

Early efforts to examine the elimination of anthracene under water-only conditions showed no measurable loss (Landrum 1982). Thus, the elimination was determined in the presence of a substrate on which *Diporeia* could feed (Landrum 1988). Elimination was also found to vary with both temperature and organism size, as did the uptake clearance. In addition, with increasing percent lipid content of the organism there was a decrease in the rate of elimination for non-polar lipophilic compounds. The influence of lipid content was greater for the more hydrophobic BaP, log K_{ow} 5.9, and less for phenanthrene, log K_{ow} 4.5 (Landrum 1988). At 4°C, phenanthrene and BaP exhibited strong linear relationships between k_e (the elimination rate constant,1/h) and lipid content (for BaP, k_e = −5.0 (±2.0) × 10^{-5} × (% lipid) + 0.003 (±0.001); r^2 = 0.55, n = 73 and for Phe, k_e = −2.2(±0.5) × 10^{-4} × (% lipid) + 0.012(±0.001), r^2 = 0.71, n = 12) (Landrum 1988). While elimination depends on the lipid content of *Diporeia*, there are insufficient data to establish a broad relationship between lipid content and elimination rate. Because of the importance of lipid content on the elimination of these compounds, the higher lipid content of amphipods in Lake Ontario compared to Lake Michigan (Cavaletto *et al.* 1996) leads to greater accumulation. As noted, this supports a greater contaminant accumulation in Lake Ontario amphipods (Nalepa and Landrum 1988) and would afford greater food web transfer from *Diporeia* to its predators in Lake Ontario compared to Lake Michigan.

Strong relationships were found between organism mass and k_e for anthracene and BaP at 4°C with decreased elimination rates in larger organisms. The best relationship to describe the elimination rate constant at 4°C was log $(1/k_e)$ = 0.30(±0.024) log K_{ow} + 0.06(±0.02) Mass (mg) + 0.691(±0.18), r^2 = 0.60, n = 102 (Landrum 1995). Insufficient data are available to relate size and lipid together with the kinetics, although, as discussed above, larger animals generally have greater lipid contents.

The thermal response of the elimination rate constant apparently varies with season (Landrum 1988). Overall, the elimination rate constant appears to increase with increasing temperature over the range of 4 to 15°C at 0.0016/h/°C in the spring and 0.0003/h/°C in the summer for compounds cov-

ering a range of log K_{ow} as represented by BaP and phenanthrene (Landrum 1988). This effect of changing thermal response may reflect the seasonal variation in lipid content of *Diporeia,* as discussed earlier.

Sediment Exposures

Variables such as temperature, organism mass, and compound hydrophobicity are expected to influence the accumulation of contaminants from sediment. In addition, the interaction between the compound and sediment is expected to have a major influence on bioavailability, with reduced bioavailability occurring with increasing organic carbon content (Landrum and Faust 1991, 1994; Landrum *et al.* 1997). Other factors, including the concentration of the contaminants and the contact time between the contaminant and the sediment particles, can also influence accumulation, generally reducing the bioavailability with increasing contact time (Landrum 1989, Landrum *et al.* 1992). Because of the potentially overriding influence of these other factors, experimental designs have not as yet separated the potential influence of mass or temperature.

Organic carbon is thought to be the primary phase influencing the partitioning of non-polar organic contaminants to sediments. Increasing contaminant hydrophobicity and sediment organic carbon content increases the partition coefficient. This binding regulates the bioavailability and toxicity of non-polar organic contaminants in sediments (Di-Toro *et al.* 1991). When examining the bioavailability, as measured by uptake clearance for sediment-associated contaminants from the same sediment source, the relationship with hydrophobicity is consistent only within a single compound class (Landrum 1989, Landrum *et al.* 1989, Landrum and Faust 1991, Landrum 1995). The uptake clearance for sediment-associated PAH congeners declines with increasing log K_{ow}, e.g., for PAH accumulation from Lake Michigan sediment, log k_s (g dry sed./g/h) = 3.14 (±0.55) − 0.98 (±0.10) log K_{ow}, r^2 = 0.737, n = 33 (Fig. 3). While there are insufficient data at this time to generate a similar relationship for PCBs, PCB congeners are more bioavailable to *Diporeia* than the PAH congeners for a given log K_{ow} (Landrum 1989; Landrum *et al.* 1989; Landrum and Faust 1991, 1994).

When comparing accumulation across a range of sediments of differing characteristics, particularly organic carbon contents, uptake clearance is not a
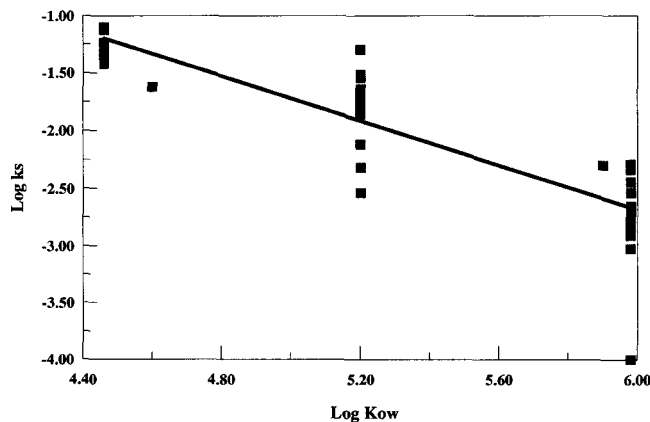
FIG. 3. Uptake clearance (g dry sediment/g/h) for the accumulation of polycyclic aromatic hydrocarbons from sediment by **Diporeia** *spp. as a function of log* K_{ow}*; data from Landrum 1995.*

FIG. 4. Uptake clearance (g dry sediment/g/h) for the accumulation of Benzo(a)pyrene from sediment by **Diporeia** *spp. as a function of organic carbon content of the sediment; data from Landrum 1995.*

clear function of the organic carbon concentration (Landrum and Faust 1994, Landrum 1995, Landrum *et al.* 1997). Thus, normalizing the bioavailability across sediments by normalizing to the amount of organic carbon leaves substantial unexplained variability as shown in Figures 4 and 5 for BaP and HCBP, respectively (Landrum 1995). The reasons for the remaining variability for *Diporeia* appear to result from both selective feeding by this amphipod and selective partitioning of the contaminants among the sediment organic matter (Harkey *et al.* 1994a, Kukkonen and Landrum 1996). While carbon normalization does not account for all the bioavailability differences, it can reduce the variability by about a factor of two (Landrum and Faust 1994, Landrum *et al.* 1997). Still it does not correct for differences observed between compound classes, as noted above. When sediments were taken from diverse environments, carbon normalization worked best in explaining the bioavailability of PCB congeners to *Diporeia* (Landrum *et al.* 1997). However, for PAH congeners, the polarity of the carbon was most important and greater bioavailability was found with more non-polar carbon. This finding may reflect the feeding preference of *Diporeia* combined with selective partitioning within the sediment.

When *Diporeia* was exposed to higher concentrations of compounds, in ranges that produced overt toxicity, the uptake clearance increased with increasing contaminant concentration; but at the highest doses, some decrease was observed (Landrum *et*
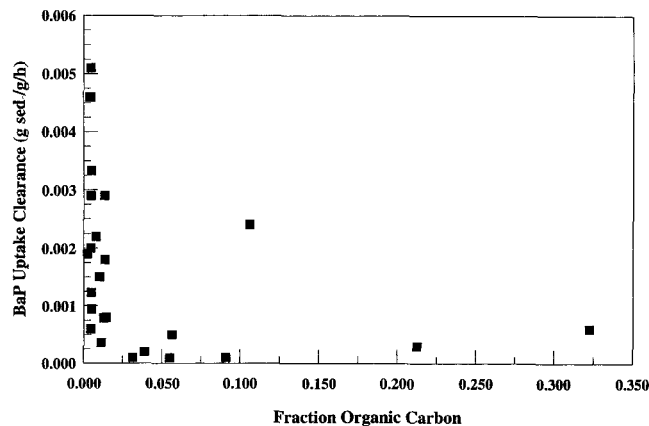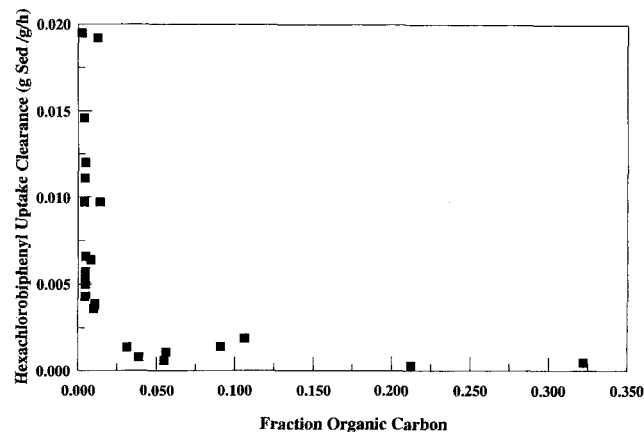

FIG. 5. Uptake clearance (g dry sediment/g/h) for the accumulation of 2,4,5,2',4',5'-hexachlorobiphenyl from sediment by **Diporeia** *spp. as a function of organic carbon content of the sediment; data from Landrum 1995.*

al. 1989, 1991; Kane Driscoll and Landrum 1997; Kane Driscoll *et al.* 1997). It is hypothesized that non-polar narcotics, such as PAH, initially enhance uptake by increasing organism activity, but as the organisms become narcotized, the activity, and therefore the uptake clearance, declined. This is currently thought to reflect changes in feeding behavior, because increased feeding increases the rate of accumulation of sediment-associated contami-
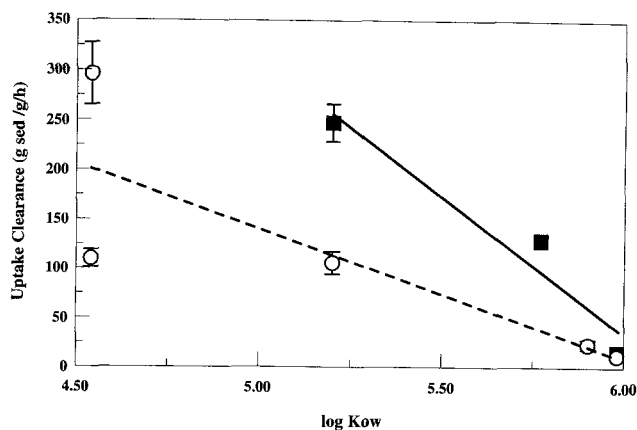
FIG. 6. Uptake clearance (µg organic carbon/g/h) for the accumulation of polycyclic aromatic hydrocarbons from sediment by Diporeia spp. as a function of Log K_{ow} for 4°C(○) and 10°C(■); data from Landrum 1995.

nants (Harkey *et al.* 1994b, Kukkonen and Landrum 1995). This mechanism may account for the reduced accumulation observed at doses above which initial stimulation occurs, where organisms exposed to a range of concentrations exhibit the greatest accumulation at intermediate exposure doses (Landrum *et al.* 1991, 1994; Kane Driscoll and Landrum 1997; Kane Driscoll *et al.* 1997).

When comparing the bioavailability of sediment-associated contaminants (PAH congeners) between 4 and 10°C, and using a single sediment source (Fig. 6), the uptake was faster at 10°C, but the difference in rates between the temperatures decreases with increasing log K_{ow} (Landrum 1995). The larger difference in uptake clearance at lower log K_{ow} values may result from increased desorption kinetics at higher temperatures, or from increased feeding rates resulting in a greater exposure. However, the data set is limited and insufficient for truly defining the role of temperature on the bioavailability and accumulation of sediment-associated contaminants.

Assimilation Efficiencies from Ingested Material

The routes for accumulation of sediment-associated contaminants include uptake from interstitial water and uptake from ingestion of contaminated material. To determine the importance of the ingestion route, the rate of ingestion, the contaminant concentration on the particles, and the assimilation efficiency of ingested contaminants must first be

determined. For *Diporeia*, attempts to measure assimilation efficiency have proved difficult due to an inability to exactly determine the ingestion rate or the contaminant concentration on the ingested particles. Three methods were used to evaluate the assimilation efficiency by *Diporeia* for BaP (Lydy and Landrum 1993, Harkey *et al.* 1994a, Kukkonen and Landrum 1995). The first, a dual-label approach, uses a non-assimilated tracer; both ^{51}Cr and ^{14}C-polydimethyl siloxane (PDMS) have been used in conjunction with a radiolabeled compound having a different label than the unassimilated tracer. For this method to work, the unassimilated tracer must be distributed in the sediment in the same manner as the contaminant, and the two tracers must be ingested in the same ratio as in the bulk sediment. A difference between the ratio of the radiolabels in the food and in the feces would be attributable to assimilation. For the ^{51}Cr, instead of the unassimilated tracer increasing from food to feces relative to the assimilated tracer, the relative concentration decreased; thus, assimilation of the contaminant could not be determined with this tracer (Lydy and Landrum 1993). This result was attributed to differences in the distribution of the tracers among particles and to differential feeding on particles by *Diporeia*. With PDMS as the unassimilated tracer, the assimilation efficiency for BaP was 56% (Kukkonen and Landrum 1995).

A second method for estimating assimilation efficiencies involves measuring the concentrations in sediment and fecal matter relative to organic carbon. In this method, the organic carbon becomes the tracer through the organism. However, unlike ^{51}Cr and PDMS which were not assimilated, carbon is expected to be assimilated. Thus, the efficiency of the carbon assimilation from sediment must be quantified before the contaminant assimilation efficiency can be determined. Carbon assimilation efficiency for *Diporeia* ingesting the diatom *Melosira italica* was found to be 61% (Fitzgerald and Gardner 1993). However, the assimilation efficiency for carbon from algae was considered to be large, compared to that expected for organic detrital matter from sediments. Thus, the fractional reduction in carbon through the gut was estimated from literature values for other benthic organisms to range from 0 to 22%. While zero is the extreme limit, this range is similar to the range of settling organic material required to support production of *Diporeia*. Using 0 to 22% as estimates for carbon absorption gave BaP assimilation efficiencies of 46 to 60% (Lydy and Landrum 1993).

The third method for estimating assimilation efficiencies required measurement of the amount of fecal material produced as a measure of feeding rate. A regression between total accumulation and fecal production would produce a y-intercept value that could be used to estimate the contribution of other processes, i.e., accumulation from water. Thus, the amount of contaminant assimilated from sediment could be determined, and in turn, the assimilation efficiency, based on the ingestion rate and sediment contamination after correcting for feeding selectivity. Using this method, the assimilation efficiency for BaP was 17.6 ± 10.5%; but for HCBP, the estimated value was unrealistically high, 140.9 ± 92.4%. The difficulty in determining an assimilation efficiency for HCBP was thought to result from both selective feeding and differential partitioning of the contaminant among sediment particles (Harkey *et al.* 1994a). This was confirmed by exposing *Diporeia* to two sub-fractions of the sediment with particles in the 20–63 μm and < 20 μm size ranges. Exposure to particles in the 20–63 μm range resulted in enhanced accumulation, compared to exposures to the whole sediment or to the < 20-μm particles. There was also a larger difference between feeding and non-feeding organisms when exposed to the 20–63-μm subfraction. Further, exposure to the < 20-μm subfraction resulted in lower exposure than when exposed to the whole sediment. No difference was observed between feeding and non-feeding organisms (Harkey *et al.* 1994a). Using Lake Michigan sediment with this third approach resulted in assimilation efficiencies of 11 to 15% and 36 to 56% for BaP and HCBP, respectively. Thus, the problems of determining the actual material ingested and the contaminant concentration on those particles remains an obstacle to accurate measurement of assimilation efficiency, particularly for a selective-feeding invertebrate.

Bioaccumulation of Contaminants from the Field

Bioaccumulation is the net result of the kinetic processes discussed above. Because lipid content, due to its influence on elimination, is a major contributor to the accumulation of non-polar organic contaminants, current approaches suggest normalizing organism contaminant concentrations to lipid content. This is particularly important for comparison to sediment concentrations which should be normalized to organic carbon (DiToro *et al.* 1991). Together, both normalizations facilitate calculation

of a biota-sediment accumulation factor (BSAF), which is the concentration in the organism per amount of lipid divided by the concentration in the sediment per amount of organic carbon.

The technique used to determine organism lipid content can alter the normalizing factor applied to organisms and can, in turn, affect the resultant biota-sediment accumulation factor (Randall *et al.* 1991). The distribution of contaminants found among classes of lipids in *Diporeia* suggests that a total lipid measure is required, because the lipid normalized contaminant concentration was similar for storage lipids (triglycerides) and for structural lipids (phospholipids) when the amphipods and mysids were exposed to BaP and HCBP (Gardner *et al.* 1990b).

Chlorinated hydrocarbon concentrations in *Diporeia* have only been measured for a few compounds for Lakes Ontario and Erie (Table 1). The concentrations in *Diporeia* were higher in Lake Ontario by a factor of two or more than in Lake Erie (Whittle and Fitzsimons 1983). This may reflect different exposures, differences in lipid content, or both for *Diporeia* between the two lakes. Differences in bioaccumulation were also observed between 1981 and 1982 within Lake Michigan, but these likely reflect the differences in study site rather than a decline in contamination (Evans *et al.* 1982, 1991) and clearly demonstrates the greater contaminant concentration in the southern part of Lake Michigan.

Where chlorinated hydrocarbon bioaccumulation factors (BAF) can be calculated (Table 1), these values are near the expected values, based on thermodynamic equilibrium between the organic matrix of the sediment and the organism lipid, assuming a 1% organic carbon content and a 25% lipid content for the two compartments. Thus, predictions of the extent of contaminant accumulation for the chlorinated hydrocarbons would seem to match simple equilibrium calculations (DiToro *et al.* 1991).

PAH concentrations in *Diporeia* ranged from about 40 ng /g wet weight to approximately 2,000 ng/g wet weight for organisms from Lakes Erie, Huron, and Michigan (Eadie *et al.* 1985). Bioaccumulation factors (wet weight organism to the dry weight of sediment) ranged from 1.2 to 3.3 for a range of PAH with no definite pattern relative to the hydrophobicity of the compound. These values suggest that *Diporeia* are not near equilibrium between organic matter and organism lipid for PAH. Further, the BAF, calculated using the dry weight concentra-

TABLE 1. *Concentrations (µg/g) of chlorinated hydrocarbons* Diporeia *from Lakes Michigan, Erie, and Ontario. Numbers in parentheses represent BAF values.*

Contaminant	Lake Michigan	Lake Erie	Lake Ontario
PCB	0.79[1], 1.12[2] (12.2)[2]	0.56[3]	1.38[3](16[3,4]) WB 1.85[3] (21.7[3,4]) EB
Dieldrin	0.14[1]	0.06[3]	0.23[3] WB 0.38[3] EB
DDE	0.15[1], 0.53[2]	0.06[3]	0.29[3] WB 0.73[3] EB
DDD	0.10[1]	NR[3]	NR[3]
DDT	ND[1], NR[2]	NR[3]	NR[3]
Total DDT	0.71(21)[2]	0.11[3]	0.44[3](7.1[3,4]) WB 1.1[3] (17.7[3,4]) EB
Chlordane	0.25[1]	0.035[3]	0.06[3]
Toxaphene	0.47[2]		
Mirex			0.23[3] WB 0.04[3] EB

1. Evans *et al.* 1982, ND = Not Detected.
2. Evans *et al.* 1991, NR = Not Reported.
3. Whittle and Fitzsimons 1983, EB = Eastern Basin, WB = Western Basin, NR = Not Reported.
4. Sediment concentrations for BAF calculation from Borgmann and Whittle 1983.

tion of small particles, the expected food source for *Diporeia* (< 60-µ dia), ranged from 0.6 to 1.5 and did not appreciably change the inference that PAH bioaccumulation was not near the thermodynamic potential (Eadie *et al.* 1985). Thus, 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. This is consistent with the toxicokinetics that demonstrate greater availability of PCB congeners, compared to PAH congeners, in the laboratory studies discussed above.

PAH concentrations in *Diporeia* do not exhibit strong seasonal variation, typically within a factor of about two for BaP, fluoranthene, and pyrene. However, over the course of a season significant unexplained variability was observed that was not apparently related to organism lipid content. Only phenanthrene exhibited a strong seasonal signal that corresponded to the lipid content of the amphipods (Eadie *et al.* 1988). The limited bioaccumulation, failure to reach thermodynamic potential, and decoupling of *Diporeia* PAH concentrations from the lipid content for pyrene, fluoranthene, and BaP are all probably due to slow desorption kinetics off ingested particles rather than to biotransformation of PAH.

Sensitivity of *Diporeia* to Toxicants

Toxicity can be expressed in terms of exposure concentration in water or sediment, or in terms of residue found in the organism. The latter measure has recently been recognized as important for assessment of hazard or risk, since environmental exposures can be complicated by the many factors discussed above in the toxicokinetics section. In addition, understanding the residue concentrations associated with toxic responses can improve the interpretation of bioaccumulation data (Bridges *et al.* 1996).

A previous review of field data indicated that *Diporeia* were very sensitive to toxicants (Nalepa and Landrum 1988). In more recent studies, *Diporeia* have been exposed to contaminants in the laboratory, via both water and sediments, to verify these field observations and further evaluate toxicological responses in this organism (Table 2). Toxic response studies in *Diporeia* have used concentration measures for both the environmental compartment and organism residue, to describe the mortality to selected toxicants. The sensitivity of *Diporeia* to pentachlorophenol was similar to that of other amphipods (Spehar *et al.* 1985, Kierstead and Barlocher 1989) and it was more sensitive to carbaryl (Sanders 1969, 1972; Bluzat and Seuge 1979). However, in matched bioassays to field collected sediment, *Diporeia* was less sensitive to toxicants

TABLE 2. Response of** Diporeia **to selected organic toxicants.

Compound	Exposure Medium	LC_{50}[1]	LR_{50}[1] (μmol/g)	Reference
Pentachlorophenol	Water (pH 8)	4.8 (24h)[2] 2.3 (96h)[2]	0.34 (24 h) 0.92 (96h)	Landrum and Dupuis 1990
Carbaryl	Water (pH 8)	2.3 (24 h)[2] 1.2 (96 h)[2]	0.21 (24 h) 0.24 (96 h)	Landrum and Dupuis 1990
Fluoranthene	Sediment	NC[3]	2.35 (28d)	Kane Driscoll *et al. 1997*
Pyrene	Sediment	NC[3]	7.85 (28d)	Landrum *et al.* 1994
Mixture of PAH	Sediment	0.6 (28 d)[4]	6.1 (28 d)	Landrum *et al.* 1991
Lindane and Dieldrin	Sediment	0.005 (72 h)[4] 0.0005 (144 h)[4]	0.006 (72 h)	Landrum *et al.* 1989
Lindane and Dieldrin	Sediment	0.0008[4,5] (119 h)	0.004 (119 h)[5]	Landrum *et al.* 1989
Chlorinated Hydrocarbon Mixture	Sediment	0.0015 (144 h)[4]		Landrum *et al.* 1989

1. LC_{50} is lethal concentration in water or sediment, LR_{50} is lethal body residue.
2. LC_{50} in units of μmol/L.
3. NC indicates that an LC_{50} value could not be calculated because intermediate sediment concentrations gave greater response than the highest doses.
4. LC_{50} in units of umol/g dry sediment.
5. LT_{50} is the time to mortality at a given exposure or dose.

than *Hyalella azteca* (Burton *et al.* 1996). In fact, it is the slow toxicokinetics that limit the response of *Diporeia* in short-term tests and create the illusion of reduced sensitivity. For instance, a two fold greater external concentration of pentachlorophenol or carbaryl is required to produce mortality at 24 h than at 96 h, but the internal residue concentration responsible for the toxic response is the same (Landrum and Dupuis 1990). Also, the amount of PAH required to produce mortality (Landrum *et al.* 1991) was in the range of body residues required for 50% mortality in other organisms (McCarty and Mackay 1993). Thus, *Diporeia* is apparently as sensitive as most other amphipods if the exposures are sustained for a sufficient period of time to attain the appropriate body residues for this high-lipid-content species.

Cadmium is the only heavy metal against which *Diporeia* has been tested in the laboratory. *Diporeia* was exposed to cadmium in both fresh water and at 20‰ salinity over a temperature range of 4 to 15°C. Two linear relationships between LC_{50} (mg/L at 96 h) and temperature (°C) were found for *Diporeia's* response (Gossiaux *et al.* 1992):

$$\text{Log } LC_{50} = 0.291\ (\pm 0.147) - 0.093\ (\pm 0.014)\ T$$
$$\text{(Fresh water)} \tag{3}$$

$$\text{Log } LC_{50} = 2.036\ (\pm 0.133) - 0.078\ (\pm 0.012)\ T$$
$$\text{(Salt water)} \tag{4}$$

Diporeia sensitivity appeared to be comparable to that of other amphipods, but large variations in experimental conditions made direct comparisons difficult.

Because residue-effect concentrations are known for several compounds, some speculative hazard evaluations can be made based on observed residues measured as part of field monitoring studies. For instance, the concentrations observed for dieldrin in *Diporeia,* after accounting for the differences between the monitoring study which used a dry-weight basis (Table 1) and the laboratory toxicity tests which used a wet-weight basis are within a factor of eight with the observed LR_{50} after 119 h exposure (residue concentration required to produce 50% mortality, measured as the molar sum of lindane and dieldrin 4.0 nmol/g, Landrum *et al.* 1989). While population declines have not been reported, this important benthic organism could be consid-

ered to have been under some toxic stress considering the expected difference in the exposure duration which was only 119 h in the laboratory setting compared to chronic exposures from the field samples. This assumes that chronic exposures require lower concentrations to produce toxic effects as have been observed in fish for several mechanisms of action (McCarty and Mackay 1993). There were several other neurotoxic pesticides at similar levels which could also contribute to the potential toxic stress. However, the other compounds, PCBs and PAHs, that operate primarily by narcosis should not be significant contributors to toxic stress due to their different mechanisms of action and low concentrations relative to that required for narcotic effects. Laboratory studies have demonstrated that, when *Diporeia* are exposed to mixtures, such independence of action between compounds exerting different mechanisms of action does occur (Landrum *et al.* 1989). Thus, not only can the risk or hazard of specific compounds be interpreted but with *Diporeia*, the beginnings of interpretation on the impact of mixtures are possible.

Research Needs

Diporeia is an important Great Lakes benthic invertebrate that has a high bioaccumulation potential for organic contaminants due to its high lipid content and absence of biotransformation capability. This amphipod inhabits large areas of the Great Lakes and is sensitive to the presence of contaminants. Because of its place in the Great Lakes food chain and its bioaccumulation characteristics, *Diporeia* will be important for the reintroduction of sediment-associated contaminants to the food chain. Therefore, further development of our knowledge of the basic biology, e.g., improved culturing techniques, feeding behavior, including identification of food preferences, lipid dynamics, and respiration dynamics, along with the routes, kinetics, sensitivity to toxicants, and factors affecting bioaccumulation, will be important for interpreting and predicting the role of *Diporeia* in contaminant cycling in the Great Lakes. Improved methods are required to better interpret the extent of exposure through the food route and for measuring assimilation efficiency. There is a paucity of data on the bioaccumulation and effects of heavy metals in *Diporeia*. Data on the residue concentrations, particularly for chronic responses, e.g., reproduction and growth, will help with interpretation of contaminant monitoring studies and contaminant risk assessment

for this species, as well as with interpretation of the impact of mixtures. In addition, improved methods for interpretation of exposures to contaminated sediments are required to properly interpret the impact of in-place pollutants on *Diporeia*.

REFERENCES

Alley, W.P. 1968. Ecology of the burrowing amphipod *Pontoporeia affinis* in Lake Michigan. University of Michigan, Great Lakes Research Division, Ann Arbor, MI, Report 36.

————, and Mozley, S.C.. 1975. Seasonal abundance and spatial distribution of Lake Michigan macrobenthos, 1964–67. Great Lakes Research Division, University of Michigan, Ann Arbor, MI, Special Report No. 54.

Bluzat, R., and Seuge, J. 1979. Effects de trois insecticides (lindanen, fention et carbaryl): Toxicite aigue sur quatre sepeces d'invertebres limniques; toxicite chronique chez le mollusgue pulmone *Lymena. Environ. Pollut.* 18:51–70.

Borgmann, U., and Whittle, D.M.. 1983. Particle size conversion efficiency and contaminant concentrations in Lake Ontario biota. *Can. J. Fish. Aquat. Sci.* 40:328–336.

Bousfield, E.L. 1958. Freshwater amphipod crustaceans of glaciated North America. *Can. Field. Nat.* 72:55–113.

————. 1989. Revised morphological relationship within the amphipod genera *Pontoporeia* and *Gammaracanthus* and the glacial relict significance of their postglacial distributions. *Can. J. Fish. Aquat. Sci.* 46:1714–1725.

Bridges, T.S., Moore, D.W., Landrum, P.F., Neff, J., and Cura, J. 1996. *Summary of a workshop on interpreting bioaccumulation data collected during regulatory evaluations of dredged material.* U. S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, MS, Miscellaneous Paper D-96-1.

Bruner, K.A., Fisher, S.W., and Landrum, P.F. 1994. The role of the zebra mussel, *Dreissena polymorpha*, in contaminant cycling: I. The effect of body size and lipid content on the bioconcentration of PCBs and PAHs. *J. Great Lakes. Res.* 20:725–734.

Burton, G.A., Ingersoll, C.G., Burnett, L.C., Henry, M., Hinman, M.L., Klanie, S.J., Landrum, P.F., Ross, P., and Tuchman, M. 1996. A comparison of sediment toxicity test methods at three Great Lakes Areas of Concern. *J. Great Lakes Res.* 22:495–511.

Cavaletto, J.F., Nalepa, T.F., Dermott, R., Gardner, W.S., Quigley, M.A., and Lang, G.A. 1996. Seasonal variation of lipid composition, weight, and length in juvenile *Diporeia* spp. (Amphipoda) from Lakes Michigan and Ontario. *Can. J. Fish. Aquat. Sci.* 53:2044–2051.

Cook, D.G., and Johnson, M.G.. 1974. Benthic Macroin-

vertebrtaes of the St. Lawrence Great Lakes. *J. Fish. Res. Board Can.* 31:763–782.

Dadswell, M.J. 1974. Distribution ecology and postglacial dispersal of certain crustaceans and fishes in eastern North America. *Natl. Mus. Nat. Sci. Publ. Zool.* No. 11.

Dermott, R., and Corning, K. 1988. Seasonal ingestion rates of *Pontoporeia hoyi* (Amphipoda) in Lake Ontario. *Can. J. Fish. Aquat. Sci.* 45:1886–1895.

———, and Kerec, D. 1997. Changes in the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. *Can. J. Fish. Aquat. Sci.* 54:922–930.

DiToro, D.M., Zarba, C.S., Hansen, D.J., Berry, W.J., Swartz, R.C., Cowan, C.E., Pavlou, S.P., Allen, H.E., Thomas, N.A., and Paquin, P.R. 1991. Technical basis for establishing sediment quality criteria for nonionic organic chemicals by using equilibrium partitioning. *Environ. Toxicol. Chem.* 10:1541–1583.

Eadie, B. J., Faust, W.R., Landrum, P.F., and Morehead, N.R. 1985. Factors affecting bioconcentration of PAH by the dominant benthic organisms of the Great Lakes. In *Polynuclear Aromatic Hydrocarbons: Mechanisms, Methods and Metabolism.* eds. M. Cooke and A. J. Dennis, pp. 363–378. Battelle Press, Columbus, OH.

———, Landrum, P.F., and Faust, W.R. 1988. Existence of a seasonal cycle of PAH concentration in the amphipod, *Pontoporeia hoyi.* In *Polynuclear Aromatic Hydrocarbons: A Decade of Research,* eds. M. Cooke and A.J. Dennis, pp. 195–209. Battelle Press, Columbus, OH.

Evans, M.S., Bathelt, R.W., and Rice, C.P. 1982. PCBs and other toxicants in *Mysis relicta. Hydrobiologia* 93:205–215.

———, Quigley, M.A., and Wojcik, J.A. 1990. Comparative ecology of *Pontoporeia hoyi* populations in southern Lake Michigan: the profundal region versus the slope and shelf regions. *J. Great Lakes Res.* 16:27–40.

———, Noguchi, G.E., and Rice, C.P. 1991. The biomagnification of polychlorinated biphenyls, toxaphene, and DDT compounds in a Lake Michigan USA offshore food web. *Arch. Environ. Contam. Toxicol.* 20:87–93.

Fitzgerald, S.A., and Gardner, W.S. 1993. An algal carbon budget for pelagic-benthic coupling in Lake Michigan. *Limnol. Oceanogr.* 38:547–560.

Gardner, W.S., Nalepa, T.F., Frez, W.A., Cichocki, E.A., and Landrum, P.F. 1985. Seasonal patterns of lipid content of Lake Michigan macroinvertebrates. *Can. J. Fish Aquat. Sci* 42:1827–1832.

———, Quigley, M.A., Fahnenstiel, G.L., Scavia, D., and Frez, W.A. 1990a. *Pontoporeia hoyi*—A direct trophic link between spring diatoms and fish in Lake Michigan. In *Large Lakes: Ecological Structure and Function,* eds. M. M. Tilzer and C. Serruya, pp. 632–644. Springer-Verlag, NewYork, NY.

———, Landrum, P.F., and Chandler, J.F. 1990b. Lipid-partitioning and disposition of benzo(a)pyrene and hexachlorobiphenyl in Lake Michigan *Pontoporeia hoyi. Environ. Toxicol. Chem.* 9:1269–1278.

Garrick, R.A., Patel, B.C., and Chinard, F.P. 1982. Erythrocyte permeability to lipophilic solutes changes with temperature. *Am. J. Physiol.* 242:C74–C80.

Gauvin, J.M., Gardner, W.S., and Quigley, M.A. 1989. Effects of food-removal on nutrient-release rates, lipid content and survival time of Lake Michigan *Pontoporeia hoyi. Can. J. Fish. Aquat. Sci.* 46:1125–1130.

Goedkoop, W., and Johnson, R.K. 1994. Exploitation of sediment bacterial carbon by juveniles of the amphipod *Monoporeia affinis. Freshwater Biology.* 32:553–563.

Gordeev, O. N. 1952. Biology and ecology of the relict crustacean Pontoporeia affinis Lindstrom in the Lakes of Karelia. *Biol. Nauk.* 4:98–109.

Gossiaux, D. C., Landrum, P.F., and Tsymbal, V.N. 1992. Response of the amphipod *Diporeia* sp. to various stressors: Cadmium, salinity and temperature. *J. Great Lakes Res.* 18:364–37.

Harkey, G.A., Lydy, M.J., Kukkonen, J., and Landrum, P.F. 1994a. Feeding selectivity and assimilation of PAH and PCB in *Diporeia* spp. *Environ. Toxicol. Chem.* 13:1445–1455.

———, Landrum, P.F., and Klaine, S.J. 1994b. Comparison of whole-sediment, elutriate and porewater exposures for use in assessing sediment-associated organic contaminants in bioassays. *Environ. Toxicol. Chem.* 13:1315–1329.

Johnson, M.G. 1988. Production by the amphipod *Pontoporeia hoyi* in South Bay, Lake Huron, Canada. *Can. J. Fish. Aquat. Sci.* 45:617–624.

———, and Brinkhurst, R.O. 1971. Benthic community metabolism in Bay of Quinte and Lake Ontario. *J. Fish Res. Board Can.* 28:1715–1725.

Johnson, R. K. 1987. The life history, production and food habits of *Pontoporeia affinis* Linstrom (Crustacea:Amphipoda) in mesotrophic Lake Erken. *Hydrobiologia* 144:277–283.

Kane Driscoll, S., and Landrum, P.F. 1997. A comparison of equilibrium partitioning and critical body residue approaches for predicting toxicity of sediment-associated fluoranthene to freshwater amphipods. *Environ. Toxicol. Chem.* 16:2179–2186.

———, Landrum, P.F., and Tigue, E. 1997. Accumulation and toxicokinetics of fluoranthene in sediment bioassays with freshwater amphipods. *Environ. Toxicol. Chem.* 16:742–753.

Kierstead, W.D., and Barlocher, F. 1989. Ecological effects of pentachlorophenol on the brackish-water amphipod *Gammarus tigrinus. Arch. Hydrobiol.* 111:149–156.

Kukkonen, J., and Landrum, P.F. 1995. Measuring

assimilation efficiencies for sediment-bound PAH and PCB congeners by benthic organisms. *Aquat. Toxicol.* 32:75–92.

———, and Landrum, P.F. 1996. Distribution of organic carbon and organic xenobiotics among different particle-size fractions in sediments. *Chemosphere* 32:1063–1076.

Landrum, P. F. 1982. Uptake, depuration, and biotransformation of anthracene by *Pontoporeia hoyi*. *Chemosphere* 11:1040–1057.

———. 1988. Toxicokinetics of Polycyclic Aromatic Hydrocarbons in the amphipod, *Pontoporeia hoyi*: Role of Season and Temperature. *Aquatic Toxicol.* 12:245–271.

———. 1989. Bioavailability and toxicokinetics of polycyclic aromatic hydrocarbons sorbed to sediments for the amphipod, *Pontoporeia hoyi*. *Environ. Sci. Technol.* 23:588–595.

———. 1995. Toxicokinetics from aqueous and sediment exposures for *Diporeia* spp. Great Lakes Environmental Research Laboratory, Ann Arbor, MI, NOAA Technical Memorandum ERL GLERL-87.

———, and Dupuis, W.S. 1990. Toxicity and toxicokinetics of pentachlorophenol and carbaryl to *Pontoporeia hoyi* and *Mysis Relicta*. In *Aquatic Toxicology and Risk Assessment: Thirteenth Volume*, ASTM STP 1096, eds. W. G. Landis and W. H. van der Schalie, American Society for Testing and Materials, Philadelphia, PA, pp. 278–289.

———, and Faust, W.R. 1991. Effect of variation in sediment composition on the uptake clearance of selected PCB and PAH congeners by the amphipod, *Diporeia* sp. In *Aquatic Toxicology and Risk Assessment: Fourteenth*, ASTM STP 1124, eds., M.A. Mayes and M. G. Barron, American Society for Testing and Materials, Philadelphia, pp. 263–279.

———, and Faust, W.R. 1994. The role of sediment composition on the bioavailability of laboratory-dosed sediment-associated organic contaminants to the amphipod, *Diporeia* (spp.). *Chem. Speciat. Bioavail.* 6:85–92.

———, and Robbins, J.A. 1990. Bioavailability of sediment associated contaminants: A review and simulation model. In *Sediments: Chemistry and Toxicity of In-Place Pollutants*. eds. R. Baudo, J. P. Giesy and H. Muntau, Lewis Publishers, Chelsea, MI. pp. 237–263.

———, and Stubblefield, C.R.. 1991. Role of respiration in the accumulation of organic xenobiotics by the amphipod, *Pontoporeia hoyi*. *Environ. Toxicol. Chem.* 10:1019–1028.

———, Faust, W.R., and Eadie, B.J. 1989. Bioavailability and toxicity of a mixture of sediment associated chlorinated hydrocarbons to the amphipod, In *Pontoporeia hoyi*. *Aquatic Toxicology and Hazard Assessment: 12th Volume*, ASTM STP 1027. eds. U. M. Cowgill and L. R. Williams, American Society for Testing and Materials, Philadelphia, PA pp. 315–329.

———, Eadie, B.J., and Faust, W.R. 1991. Toxicity and toxicokinetics of a mixture of sediment-associated polycyclic aromatic hydrocarbons to the amphipod, *Pontoporeia hoyi*. *Environ. Toxicol. Chem.* 10:35–46.

———, Eadie, B.J., and Faust, W.R. 1992. Variation in the bioavailability of polycyclic aromatic hydrocarbons to the amphipod, *Diporeia* sp, with sediment aging. *Environ. Toxicol. Chem.* 11:1197–1208.

———, Dupuis, W.S., and Kukkonen, J. 1994. Toxicokinetics and toxicity of sediment-associated pyrene and phenanthrene in *Diporeia* spp.: Examination of equilibrium partitioning theory and residue based effects for assessing hazard. *Environ. Toxicol. Chem.* 13:1769–1780.

———, Gossiaux, D.C., and Kukkonen, J. 1997. Sediment characteristics influencing the bioavailability of nonpolar organic contaminants to *Diporeia* spp. *Chem. Speciat. Bioavail.* 9:43–55.

Lopez, G., and Elmgren, R. 1989. Feeding depths and organic absorption for the deposit-feeding benthic amphipods *Pontoporeia affinis and Pontoporeia femorata*. *Limnol. Oceanogr.* 34:982–991.

Lydy, M.J., and Landrum, P.F. 1993. Assimilation efficiency for sediment sorbed benzo(a)pyrene by *Diporeia* spp. *Aquat. Toxicol.* 26:209–224.

Lubner, J.F. 1979. Population dynamics and production of the relict amphipod *Pontoporeia hoyi* at several Lake Michigan stations. Ph.D. dissertation, University of Wisconsin, Milwaukee, WI.

Marzolf, G.R. 1965a. Substrate relations of the burrowing amphipod *Pontoporeia affinis* in Lake Michigan. *Ecology* 46:579–592.

———. 1965b. Vertical migration of *Pontoporeia affinis* (Amphipoda) in Lake Michigan. Great Lakes Research Division, The University of Michigan, Publication No. 13, pp. 133–140.

McCarty, L.S., and Mackay, D. 1993. Enhancing ecotoxicological modeling and assessment. *Environ. Sci. Technol.* 27:1719–1728.

McDonald, M.E., Crowder, L.B., and Brandt, S.B. 1990. Changes in *Mysis* and *Pontoporeia* populations in southeastern Lake Michigan: a response to shifts in the fish community. *Limnol. Oceanogr.* 35: 220–227.

Mozley, S.C., and Howmiller, R.P. 1977. Environmental Status of the Lake Michigan region. Volume 6, ANL/ES-40, Argonne National Laboratory, Argonne, IL.

Nalepa, T.F. 1989. Estimates of macroinvertebrate biomass in Lake Michigan. *J. Great Lakes Res.* 15:437–443.

———, and Landrum, P.F. 1988. Benthic invertebrates and contaminant levels in the Great Lakes: Effect, fates, and role in cycling. In *Toxic Contaminants and Ecosystem Health: A Great Lakes Focus*. ed. M.S. Evans, pp. 77–102. John Wiley & Sons, New York, NY.

_____, Quigley, M.A., Childs, K.F., Gauvin, J.M., Heatlie, T.S., Parker, M.P., and Vanover, L. 1985. Macrobenthos of Southern Lake Michigan, 1980–81. National Oceanic and Atmospheric Administration, U.S. Department of Commerce, Ann Arbor, MI, NOAA Data Report ERL GLERL-28.

_____, Hartson, D.J., Fanslow, D.L., Lang, G.A., and Lazano, S.J. 1998. Decline of benthic macroinvertebrate populations in southern Lake Michigan, 1980–1993. *Can. J. Fish. Aquat. Sci.* (In Press).

Opperhuizen, A., Velde, E.W., Gobas, F.A.P.C., Liem, D.A.K., Van der Steen, J.M.D., and Hutzinger, O. 1985. Relationship between bioconcentration in fish and steric factors of hydrophobic chemicals. *Chemosphere* 14:1871–1896.

Quigley, M.A. 1988. Gut fullness of the deposit-feeding amphipod *Pontoporeia hoyi* in Southeastern Lake Michigan USA. *J. Great Lakes Res.* 14:178–187.

_____, and Vanderploeg, H.A. 1991. Ingestion of live filamentous diatoms by the Great Lakes amphipod, *Diporeia* sp.: a case study of the limited value of gut contents. *Hydrobiologia* 223:141–148.

Randall, R.C., Lee II, H., Ozretich, R.J., Lake, J.L., and Purell, R.J. 1991. Evaluation of selected lipid methods for normalizing pollutant bioaccumulation. *Environ. Toxicol. Chem.* 11:1431–1436.

Saito, S., Tateno, C., Tanoue, A., and Matsuda, T. 1990. Electron microscope autoradiographic examinaion of uptake behavior of lipophilic chemicals into fish gill. *Ecotoxicol. Environ. Safety* 19:184–191

Sanders, H.O. 1969. *Toxicity of pesticides to the crustacean* Gammarus lacustris. Bureau of Sport Fisheries and Wildlife, U.S. Department of Interior, Washingron, D.C., Technical Paper No. 25.

_____. 1972. *Toxicity of some insecticides to four species of malaostran crustaceans.* Bureau of Sport Fisheries and Wildlife, U.S. Department of Interior, Washingron, D.C., Technical Paper No. 66

Scavia, D., Fahnenstiel, G.L., Evans, M.S., Jude, D.J., and Lehman, J.T. 1986. Influence of salmonid predation and weather on long-term water quality trends in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 43:435–443.

Scott, W.B., and Crossman, E.J. 1973. Freshwater Fishes of Canada. *Bull. Fish. Res. Board Can.* 184.

Segerstråle, S.G. 1977. The taxonomic status and prehistory of the glacial relict *Pontoporeia* (Crustacea Amphipoda) living in North American lakes. *Commentat. Biol.* 89:1–18.

Sly, P.G., and Christie, W.J. 1992. Factors influencing densities and distributions of *Pontoporeia hoyi* in Lake Ontario. *Hydrobiologia* 235–236:321–352.

Smith, W.E. 1972. Culture, reproduction and temperature tolerance of *Pontoporeia affinis* in the laboratory. *Trans. Amer. Fish. Soc.* 101:253–256.

Smulders, A.P., and Wright, E.M. 1971. The magnitude of nonelectrolyte selectivity in the gall bladder epithelium. *J. Membrane Biol.* 5:297–318.

Spehar, R.L., Nelson, H.P., Swanson, M.J., and Renoos, J.W. 1985. Pentachlorophenol toxicity to amphipods and fathead minnows at different test pH values. *Environ. Toxicol. Chem.* 4:389–397.

Vainola, R., and Varvio, S.L. 1989. Molecular divergence and evolutionary relationships in *Pontoporeia.* (Crustacea:Amphipoda). *Can. J. Fish. Aquat. Sci.* 46:1705–1713.

Whittle, D.M., and Fitzsimons, J.D. 1983. The influence of the Niagara River on contaminant burdens of Lake Ontario biota. *J. Great Lakes Res.* 9:295–302.

Winnell, M.H., and White, D.S. 1984. Ecology of shallow and deep water populations of *Pontoporeia hoyi* amphipodia in Lake Michigan. *Freshwater Invertebr. Biol.* 3:118–138.

Zitko, V. 1980. Metabolism and distribution by aquatic animals. In *The Handbook of Environmental chemistry*, O. Hutzinger, ed., pp. 221–229. Volume 2 Part A, Springer, Berlin.