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The role of feeding behaviour in bioaccumulation of organic chemicals in benthic organisms

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Hydrophobic organic chemicals tend to sorb to suspended organic material and to accumulate in the sediments. Due to their strong affinity to sediment particles, the most probable bioaccumulation route to benthic animals is through the ingested food. The feeding behaviour of benthic organisms significantly affects the bioaccumulation of hydrophobic organic chemicals. This behaviour includes processes like food selection, manipulation, ingestion, digestion and assimilation. Especially selective feeding and the ingestion rate of deposit feeders are involved in bioaccumulation. According to theories on foraging models, deposit feeders adjust their ingestion and digestion rates to a level where net energy gain is highest. If the uptake of organic chemicals is dependent on gut turnover time, the feeding behaviour of benthic animals should be taken into account in bioaccumulation studies.

1. Introduction

Organic chemicals include a variety of different compounds which can be very hydrophobic. In water ecosystems, these chemicals tend to bind with suspended particulate matter and to accumulate in the bottom sediments of lakes and seas. This results in sediment contamination which threatens biological systems. Besides their hydrophobic nature, organic chemicals are often metabolically stable. Benthic organisms are able to accumulate chemicals from their environment via different routes (e.g. overlying water, interstitial water and sediment particles). Probable particle pathways are sediment ingestion (organic and inorganic) and direct contact with sediment particles (e.g. Knezovich et al. 1987). Bottom-dwelling animals have a greater risk of accumulating toxic compounds than open water animals because they are exposed to all probable accumulation routes. Contaminated sediments, however, are a potential risk for all living systems. Sediment-sorbed chemicals can spread through food webs to pelagic organisms and predatory birds. Contaminants can also be transferred from sediments directly to the terrestrial environment via emerging insect adults (Larsson 1984).

The role of bioaccumulation is heavily influenced by the characteristics of chemicals. For example, the uptake of sediment-associated polycyclic aromatic hydrocarbons (PAH) is claimed to happen only after the chemical has desorbed into interstitial or overlying water (Andersson et al. 1977, Rossi 1977, Roesijadi et al. 1978a), but certain PAH compounds have been shown to also accumulate through ingested sediment particles (Landrum & Scavia 1983, Landrum 1989). Further, direct uptake from the sediment-associated fraction is generally reported to be important in bioaccumulation of polychlorinated biphenyls (Fowler et al. 1978, Klump et al. 1987, Boese et al. 1990). Knowledge of bioaccumulation pathways for organic compounds is still limited but the processes of assimilation from ingestion and desorption from sediments contribute significantly when formulating a framework for bioaccumulation of nonionic organic compounds (Landrum & Robbins 1990).

In this review, the focus is on the role of the feeding behaviour of benthic organisms in the bioaccumulation of organic chemicals. A short description of factors that affect the sorption and bioavailability of toxic compounds is also presented because these processes are closely linked to bioaccumulation. For clarity, the terms bioavailability and bioaccumulation are defined here according to Landrum and Robbins (1990): Bioavailability is the fraction of the total contaminant in the interstitial water and on the sediment particles that is available for bioaccumulation, whereas bioaccumulation is the accumulation of a contaminant via all routes available to the organism.

2. Factors affecting chemical sorption and bioavailability

The hydrophobicity of chemicals is one of the most important factors determining the affinity of a compound to sediment particles and bioavailability. Hydrophobicity can be represented by the octanol-water partition coefficient (Kow) (Miller et al. 1985). Chemicals with low log Kow values (less hydrophobic chemicals) are less strongly sorbed and hence are more bioavailable than chemicals with high log Kow values that tend to sorb strongly and are less bioavailable. The relationship between chemical characteristics and bioavailability is not so simple. Other characteristics of compounds like hydrogen-bonding capacity, ionization or chemical reactivity, may also affect the partitioning of sediment particles and thus the bioavailability (Neff 1984, Adams 1987, Rodgers et al. 1987). The bioaccumulation of organic chemicals of different log Kow values from sediments is reported to be affected by a combination of uptake and elimination rates, and the sorption properties of compounds (Landrum & Robbins 1990).

Besides the chemical characteristics of toxicants, sediment properties, that have a great impact on sorption and bioavailability, comprise organic carbon content, particle size distribution, clay type and content, cation exchange capacity and pH (Neff 1984, Adams 1987, Knezovich et al. 1987, Raynoldson 1987, Rodgers et al. 1987). The sorption of neutral organic chemicals to sediments is assumed to be directly related to the sediment organic carbon content (Karickhoff et al. 1979, Chiou et al. 1983). Organic carbon in sediments tends to sorb toxic chemicals and hence reduces bioavailability and bioaccumulation. This relationship has been used to advantage for assessing sediment toxicity in sediment-quality criteria (SQC) by the U.S. Environmental Protection Agency (EPA). The equilibrium partitioning (EqP) approach has been proposed as one method to estimate the hazard of contaminated sediments (Chapman 1989, Di Toro et al. 1991). The EqP approach normalizes bioavailability using organic carbon (OC) content. The theory assumes that bioavailability is directly proportional to the contaminant concentration in interstitial water and is inversely proportional to the organic carbon content of the sediment. According to the theory, as the OC content of the sediment increases, the bioavailability of the compound from the contaminated sediments concomitantly decreases. The EqP approach has been supported by some experiments (Swartz et al. 1990). In a test using more variable test sediments, with the same OC content, the sorption of a contaminant and its bioavailability were affected by different forms of organic carbon as well as the total amount (Suedel et al. 1993).

The relationship between organic carbon content and bioavailability of toxic compounds is further complicated by uneven distribution patterns of chemicals between different particle size classes. In recent studies with non-polar organic compounds, pyrene, benzo(a)pyrene and hexachlorobiphenyl distribution differed from the organic carbon distribution in fine particles (< 63 μm in diameter) (Harkey et al. 1994, Kukkonen & Landrum 1994). There were also different distributions for different compounds (Harkey et al. 1994). These relative differences in distribution directly affected the bioavailability of these sediment-associated contaminants to *Diporeia* spp. and *Lumbriculus variegatus* (Harkey et al. 1994, Kukkonen & Landrum 1994, 1995, Landrum et al. 1994a).

Other factors controlling the distribution of organic chemicals are dissolved organic matter (DOM) that can bind chemicals (Landrum et al. 1985, McCarthy et al. 1985), and contact time between sediment particles and the contaminant that can cause changes in bioavailability (Landrum et al. 1992). Partitioning of the contaminants between sediment particles and porewater is a function of adsorption and desorption processes. It may even taken years to achieve an equilibrium (Karickhoff 1980, Di Toro et al. 1982, Witkowski et al. 1988). During this equilibrium phase, contaminant bioavailability can also be expected to change with time. This can be especially important when examining data from bioassays which use a spiked sediment (Landrum et al. 1992).

The significance of biological factors should also be taken into account when considering the fate of contaminants in bottom sediments. The behaviour of benthic organisms may significantly effect the establishment of an equilibrium between the contaminant and sediment. For instance, burrowing oligochaetes ingest sediment from deeper sediment layers and egest to the sediment-water interface. These animals mix bottom sediments constantly and, at high animal densities, reworking can be significant (Davis 1974, McCall & Fischer 1980). Laboratory studies have also shown that more than 90% of organic contaminants sorbed to sediments in freshwater may be rapidly transported and concentrated at the surface of the sediment by the selective feeding activities of tubificids (Karickhoff & Morris 1985).

There are other elements in the behaviour and physiology of benthic animals which influence the bioaccumulation of contaminants. Among them are production of tubes and burrows, sediment avoidance, changes in the physiology, organism age, sex, lipid content and reproductive stage (Landrum et al. 1995). Last but not least, the feeding behaviour of organisms, which is reviewed below, will also influence exposure.

3. The feeding behaviour and bioaccumulation

Feeding habits, for example, food source and feeding rate, are potentially important factors controlling bioaccumulation in benthic invertebrates. These animals have a vast array of different feeding and life habits (Adams 1987). Pure deposit feeders are quite scarse among the freshwater benthic assembly. Oligochaetes and certain chironomids are exeptions. Particulate organic matter of various forms and inorganic sediment particles form a combination which is the typical source of food for benthic animals. Contrary to the freshwater environment, marine benthic species, particularly burrowing ones, frequently ingest sediment (Adams 1987). So using intertidal and subtidal fauna in feeding and bioaccumulation experiments is quite common (e.g. Cammen 1980a, Brown 1986, Swartz et al. 1990, Weston 1990, Meador et al. 1993).

The bioaccumulation of contaminants through food/sediment ingestion is a process that is modified by the ingestion rate, the pollutant concentration in the food/sediment and gut uptake efficiency of the pollutant in the organism. The prediction of ingestion rates and ingested doses for sediment-ingesting invertebrates is complicated by the type of feeding, selective ingestion of particles based on size or composition and the wide range of food quality (Landrum et al. 1994b). Several models have been created to describe sediment ingestion in deposit feeders. The background of these theories is mainly based on studies using marine deposit feeders (Self & Jumars 1978, Taghon et al. 1978, Doyle 1979, Phillips 1984, Taghon & Jumars 1984) but can be used in freshwater organisms also (see Cammen 1980b).

3.1. Foraging models

Taghon et al. (1978) have developed an optimal foraging model that is the basis for most of the discussions. The model examines particle selection behaviour in relation to optimal foraging considerations and suggests that deposit feeders should select smaller particles in order to maximize their rate of energy gain. The particle selection model is based on the assumption that the nutritional value of a particle is proportional to its surface area, smaller particles being more nutritious. However, if the cost of sorting through particles and rejecting the less desirable larger particles becomes too high, no selection should occur (Taghon et al. 1978).

A complementary model of the optimal foraging theory uses a more mechanistic approach of particle selection (Self & Jumars 1978, Jumars et al. 1982, Taghon 1982). According to Jumars et al. (1982), selection can occur during the process of particle pickup as well, after a feeding appendage has contacted a particle. Whether a particle is accepted, depends on the adhesive strength of the mucus on the feeding apparatus which favors the retention/selection of smaller and less dense particles, or larger and denser particles. The model was shown to be true with spionid polychaetes (Taghon 1982).

The optimal foraging theory has also been extended to cover non-selective deposit feeders (Taghon 1981). This model predicts that ingestion rate should increase as food quality increases, in order to maximize the net rate of energy gain. The increase in ingestion rate should continue until some maximum ingestion rate is reached, and then that maximum rate should be maintained, even if the quality is still improving. The model has received support by some studies (Doyle 1979, de Wilde & Berghuis 1979, Taghon & Jumars 1984) but also been contradicted in others (Gordon 1966, Cammen 1980b, Kudenov 1982).

A more realistic model for explaining optimal foraging has been proposed by Phillips (1984). In Taghon's (1981) model all other physiological processes were expected to be unbounded while assuming maximum ingestion rate. It is unlikely that any physiological rate process can increase indefinitely. Phillips' (1984) model assumes an additional physiological limitation for the organism (e.g. maximum rate of transport across gut wall, and maximum metabolism rate of assimilated material). When the physiological limit is reached, the optimal response of an animal to variation in food quality changes abruptly, since increasing of ingestion rate is no longer advantageous. The ingestion rate of an organism increases with increasing food quality until some threshold value is reached, at which point, the ingestion rate should begin to decrease. The study of Guidi (1986), with an amphipod *Siphonoecetes dellavallei*, supported this theory. Below incipient-limiting concentration, the ingestion rate of an amphipod is controlled by food concentration, and above it, by gut capacity.

3.2. Feeding rate

In view of these foraging models, the feeding rate of benthic animals should be far from stable. Deposited sediments are very heterogenous where food/energy resources are unevenly distributed between different particle types (Lopez & Levinton 1987). An organism has to adjust its ingestion rate in a given sediment to fulfill the energy demands for reproductive and somatic growth. Ingestion rate, therefore, is assumed to vary with changing sediment characteristics, as is shown by Hargrave (1970), Taghon and Jumars (1984), Guidi (1986) and Cammen (1987).

The feeding behaviour of an animal is an essential feature governing the bioaccumulation because one possible pathway for accumulation of organic chemicals is through food/ingested sediment. Bioaccumulation is also affected by characteristics of the chemical. More hydrophobic chemicals, with log Kow values varying between 5 and 7, are suggested to accumulate significantly via diet (Adams 1987). For example, the individuals of polychaete *Abarenicola pasifica* tended to accumulate greater benzo(a)pyrene residues in their tissues with higher feeding rates (Weston 1993). Increased feeding rates resulted in a greater accumulation of hexachlorobiphenyl and benzo(a)pyrene also with an amphipod, *Diporeia* spp. (Harkey et al. 1994, Kukkonen & Landrum 1995). In sediments with low organic carbon content, increased bioavailability of contaminants, together with increased feeding rates, can cause greater accumulation rates. On the other hand, it is proposed that in high sediment contaminant concentrations the ingestion rate can decrease as a response to a chemical, and cause lower accumulation rates (Kukkonen & Landrum 1994). The process of bioaccumulation is, without a doubt, species dependent. As the feeding mode (deposit versus filter feeding) and rate of sediment-ingesting benthic animals is very variable, universal predictions about accumulation/uptake rates are difficult to formulate.

3.3. Assimilation efficiency

Feeding rate has a direct effect on digestive processes. The absorption of food/contaminant from the gut is a time-dependent process that is controlled by ingestion rate (Kofoed et al. 1987). One of the few studies to examine the absorption of contaminants (Klump et al. 1987) found that there is an inverse relationship between assimilation efficiencies and defecation rates. In this study, the feeding rate of an oligochaete was measured via defecation rate. The slower the passage of material through the gut, the greater the relative transfer of hexachlorobiphenyl from the sediments across the gut wall and into the organism. The relationship between the average gut-clearing times and the average assimilation efficiencies of the toxicant was linear. The kinetics of uptake might, therefore, be expected to be controlled primarily by the concentration of the PCB in the sediment and feeding rate of the worm.

Models have been constructed to explain digestion and optimization of food resources (Kofoed et al. 1987, Penry & Jumars 1987). The principles behind the feeding models (or conclusions drawn from the results) might help to explain also the assimilation of contaminants. The assimilation efficiency of food does not increase continuously. Saturation of absorption occurs rapidly with certain food types that are digested and absorbed easily, like bacteria (Kofoed et al. 1987). The nutritional content of sediment controls absorption efficiency. An increase in ingestion rate and, at the same time, decreasing efficiency of food absorption, due to a shorter passage-time in the gut, leads to greater energetic costs. For this reason, net absorption rate is expected to show a maximum at intermediate levels of gut turnover (Kofoed et al. 1987). It is still unknown if the uptake of organic chemicals follows this general rule of food assimilation kinetics.

3.4. Selective feeding

The selective feeding on particles is a very common feature in benthic organisms. Both filter (Fenchel et al. 1975, Hylleberg & Galucci 1975, Lopez & Levinton 1978, Lopez & Kofoed 1980) and deposit feeders (Brinkhurst et al. 1972, Fenchel et al. 1975, Hylleberg 1975, Moore 1977, Brinkhurst & Austin 1979, Tevesz et al. 1980, Nielsen & Kofoed 1982, Krezoski & Robbins 1985, Landrum & Faust 1991, Harkey et al. 1994) are able to select particles of a certain size. There is also evidence that some organisms selectively ingest particles on the basis of specific gravity and/or surface texture (Self & Jumars 1978), as well as on the basis of organic content (Taghon 1982). The selection of particles can change with time; Miller (1984) found that an amphipod, *Corophium volutator*, becomes more selective, favoring small particles the longer it feeds.

In the case of selective feeding, the concentration of a contaminant in bulk sediment does not indicate the actual chemical concentration on the particles an animal is ingesting, which makes accumulation/assimilation-efficiency experiments more problematic. As previously mentioned, the chemicals are not always distributed evenly among particle size classes. Different compounds can sorb to particles of different sizes (Harkey et al. 1994, Kukkonen & Landrum 1994) or particles with different chemical characteristics (Lydy & Landrum 1993). Differential partitioning of a compound, together with selective feeding, have a distinct effect on bioaccumulation. The selectively-feeding amphipod, *Diporeia* spp., ingests particles of certain size (20–63 μm), which exposes the species to contaminants sorbed to that fraction (Harkey et al. 1994). The same study showed that the accumulation of hexachlorobiphenyl was consistently greater than the accumulation of benzo(a)pyrene in dual-labelled sediment assays, suggesting that the chlorinated compound was more bioavailable to *Diporeia* spp. than BaP. Selectivity of food particles can also affect bioaccumulation in oligochaetes (Klump et al. 1987).

3.5. Feeding habit

The highly heterogenous nature of sediments is exploited by benthic invertebrates with different feeding modes. Animals may forage on different particle types, or vertically in different sediment layers. Infaunal and epifaunal species, with different feeding habits, may be exposed to different chemical concentrations, especially if contaminants are not uniformly distributed within the sediment horizons. The surface deposit-feeding clam *Macoma nasuta* accumulated sediment-associated hexachlorobenzene (HCB) almost completely from sediment particle ingestion (Boese et al. 1990). This clam favors fine particles with high OC content, which can have greater contaminant concentrations than the bulk sediment. Also, Foster et al. (1987) showed that *Macoma balthica* accumulates xenobiotics either by particle ingestion or through direct absorption from interstitial water. In the same experiment, a filter-feeding clam *Mya arenaria* did not accumulate pollutants from the sediment. In the case of benthic filter-feeding animals, exposure to the contaminants may happen when chemicals are found dissolved in the water column or sorbed to suspended sediment. The difference in accumulation between deposit and suspension feeders has also been reported by Roesijadi et al. (1978b). Contrary to the surface-foraging animals, oligochaetes may ingest sediment even 8–10 cm below the sediment-water interface (Davis 1974, Robbins et al. 1979, McCall & Fisher 1980). Differences in the feeding depths of the oligochaeta species can result in different bioaccumulation factors for endrin (Keilty et al. 1988): *Stylodrilus heringianus* feeds closer to the sediment surface, and is exposed to higher chemical concentrations than *Limnodrilus hoffmeisteri*, which forage in deeper zones of sediment layers. Feeding mode is one possible reason explaining different accumulation rates of HCBP between omnivorous deposit-feeding polychaete *Nephtys incisa* and the deposit-feeding bivalve *Yoldia limatula* (McElroy & Means 1988). Accumulation differences between the amphipods *Rhepxynius abronius* and *Euhaustorius washingtonianus,* and the clam *Macoma nasuta* may also be partly explained by feeding strategies for polycyclic aromatic hydrocarbons (Varanasi et al. 1985).

Basic ecological knowledge of the test species used in bioassays helps to explain organism behaviour in the laboratory and use to an advantage. It also helps to evaluate the bioaccumulation of contaminants in nature more accurately. A freshwater amphipod *Diporeia* spp. is a good example of a species whose feeding behaviour can be described in more detail than just by classifying the organism as either a filter or a deposit feeder. It differs from other continous-feeding amphipods regarding its gut fullness (Quigley 1988). *Diporeia* feeds intermittently and there can be members of the population with empty or partially-full guts. Variation in their feeding rate also exists in a wider time scale; an increased feeding rate during spring and autumn reflects feeding strategy that exploits newly-deposited detritus from phytoplankton blooms (Dermott & Corning 1988, Quigley 1988). There are also regional differences in *Diporeia* populations. Profundal populations in Lake Michigan feed more continuously, but less intensively than slope populations. Regional differences in feeding behaviour may be related to differences in food regime and to predation avoidance strategies (Evans et al. 1990). Increased feeding in spring and autumn causes a peak in lipid content of *Diporeia* which, in turn, increases its capacity to accumulate lipophilic compounds. On the other hand, discontinuous feeding decreases elimination of compounds because the movement of food through the intestine of an animal is apparently important for the elimination of xenobiotics (Abedi & Brown 1961, Landrum & Scavia 1983, Frank et al. 1986).

4. Conclusions

It has been known for a long time that selective feeding is common among deposit feeders (e.g. Brinkhurst et al. 1972, Fenchel et al. 1975). For this reason, the bulk sediment concentration is not an accurate estimate of the concentration in the food they ingest, which complicates the evaluation of sediment toxicity. The feeding biology of benthic animals can not be totally described by any single parameter. The term includes processes like food selection, manipulation, ingestion, digestion and assimilation, all of which have a great effect on the bioaccumulation of organic xenobiotics. In the case of foraging models, the integrated effect of these processes will determine the optimal feeding behaviour of an animal. So far, the relationship between feeding and the accumulation of organic hydrophobic contaminants has not been thoroughly investigated.

Another subject which needs to be studied in more detail is the effect of feeding rate on bioaccumulation. If benthic animals are able to change their feeding rate according to the nutritional value of a sediment, in order to maintain optimal energy gain, it is important to test whether the optimal foraging behaviour affects the bioaccumulation of organic compounds. These studies need estimates of sediment nutritional value, which might be difficult to obtain. For example, sediments with a high algae concentration have a high energy value, but if the rest of the sediment is sand, the measurements of organic carbon on a dry weight basis might underestimate their energy content. Another extreme along the axis of organic matter is lignin, which needs longer gut residence time and is probably not fully absorbed (Lopez & Levinton 1987). Although the organic carbon content of sediments is an important parameter describing the capacity of sediments to sorb hydrophobic organic chemicals, it's contribution in explaining bioaccumulation is far more complex. The basic ecology of test species, and their feeding behaviour in different sediment types, are vital for understanding the processes of bioaccumulation.

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