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► To cite this version:

G T Banta, O Andersen. BIOTURBATION AND THE FATE OF SEDIMENT POLLUTANTS Experimental case studies of selected infauna species. Vie et Milieu / Life & Environment, 2003, pp.233-248. hal-03205288

HAL Id: hal-03205288
https://hal.sorbonne-universite.fr/hal-03205288v1

Submitted on 22 Apr 2021

VIE MILIEU, 2003, 53 (4) : 233-248

BIOTURBATION AND THE FATE OF SEDIMENT POLLUTANTS

Experimental case studies of selected infauna species

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BIOTURBATION
SEDIMENT POLLUTION
ARENICOLA MARINA
NEREIS DIVERSICOLOR
INFAUNA
PAH

ABSTRACT. – In this review we examine the interactions between bioturbating infauna and sediment pollutants with emphasis on what determines the fate of contaminants in bioturbated sediments. Our review is based on experimental case studies, especially of the polychaetes *Arenicola marina* and *Nereis diversicolor*. Bioturbation by infauna affects pollutants via a number of mechanisms such as particle mixing and irrigation which lead to the transport and redistribution of pollutants, through the stimulation of microbial degradation of organic contaminants by enhancing the availability of molecular O_2 in bioturbated sediments, and via their own metabolism of contaminants. *A. marina* is an example of an infauna species that mostly affects pollutant fate via transport, both particle mixing and especially its effective flushing of porewaters via irrigation. It also stimulates microbial processes in sediments, including the degradation of organic pollutants. *N. diversicolor* is an example of an infauna species that actively metabolizes organic pollutants and plays an important role on pollutant fate in that way. It also flushes dissolved components from sediments and stimulates microbial degradation, but to a lesser extent than *A. marina*. *N. diversicolor* affects the particle-associated fraction of contaminants to an even lesser extent via its biodiffusive mixing. By examining the effects of these two and other species on the fate of sediment pollutants we demonstrate that the many different mechanisms by which infauna affect pollutants interact in complicated and, at times, contradictory ways, also depending on physicochemical characteristics and the localization of sediment pollutants. This makes the overall effects on pollutant fate variable and dependent on the specific situation. We suggest that mechanistically correct models which link the fates and effects of pollutants to bioturbation transport processes provide promising tools for the prediction of the outcome of these complicated interactions. Such models are therefore of interest to both scientists studying these phenomena and to managers who need to predict the fate and effects of pollution events in bioturbated habitats.

BIOTURBATION
POLLUTION DES SÉDIMENTS
ARENICOLA MARINA
NEREIS DIVERSICOLOR
FAUNE DES SÉDIMENTS
HYDROCARBURES AROMATIQUES

RÉSUMÉ. – Dans cette revue de synthèse nous examinons les interactions entre la faune des sédiments causant de la bioturbation et les polluants des sédiments, en mettant l'accent sur le devenir des contaminants dans les sédiments soumis à la bioturbation. La synthèse se base sur des études de cas expérimentaux, à propos des Polychètes *Arenicola marina* et *Nereis diversicolor* principalement. La bioturbation engendrée par la faune intrasédimentaire affecte les polluants via un certain nombre de mécanismes tels que le remaniement des particules sédimentaires et l'irrigation, qui entraînent le transport et la redistribution des polluants, avec la stimulation de la dégradation microbienne des contaminants organiques par l'augmentation de la disponibilité en O_2 moléculaire dans les sédiments subissant la bioturbation, et via le métabolisme propre des contaminants. *A. marina* est un exemple d'espèce de sédiments qui agit sur le devenir des polluants par leur transport de manière importante, à la fois par le remaniement des particules sédimentaires et spécialement par l'évacuation de l'eau interstitielle par irrigation. Elle stimule aussi les processus microbiens dans les sédiments, y compris la dégradation des polluants organiques. *N. diversicolor* est un exemple de représentant intra-sédimentaire qui métabolise activement les polluants organiques et joue ainsi un rôle important sur le devenir des polluants. Elle élimine aussi les composés dissous des sédiments et stimule également la dégradation microbienne, mais à un degré moindre que dans le cas de *A. marina. N. diversicolor* agit sur la fraction des contaminants associée aux particules sédimentaires encore plus faiblement en les mélangeant par biodiffusion. L'examen des effets de ces deux espèces, et d'autres espèces sur le devenir des polluants des sédiments nous permet de montrer que les nombreux mécanismes différents par lesquels la faune des sédiments intervient sur les polluants inter-agissent selon des voies complexes et parfois contradictoires, qui dépendent en outre des caractéristiques physicochimiques et de la localisation des polluants dans le sédiment. Ceci rend l'effet global sur le devenir des polluants variable et dépendant de la situation donnée. Nous suggérons que des modèles théoriquement corrects liant le devenir et les effets des polluants aux processus de transport induit par la bioturbation fournissent des outils prometteurs dans la prédiction du bilan de ces interactions complexes. De tels modèles sont intéressants pour les scientifiques étudiant ces phénomènes, comme pour les décideurs qui ont besoin de prévoir le devenir des polluants et l'impact des pollutions dans les habitats soumis à la bioturbation.

INTRODUCTION

Infauna, animals that live buried in sediments, have evolved to live in a difficult and physiologically challenging environment. These animals have developed a number of physiological adaptations to deal with living in sediment. They must be able to burrow readily through the sediment medium and in this way are capable of moving significant quantities of sediment over short time periods. Furthermore, deposit-feeders must process large amounts of sediments to obtain their nutrition (Lopez & Levinton 1987). Infauna must also rapidly ventilate their burrows or obtain oxygen from the overlying waters in other ways in this otherwise anoxic environment. These physiological adaptations and processes can have profound effects on physical and biogeochemical characteristics of the sediment environment.

BIOTURBATION

The effects of burrowing, feeding and ventilation activities of infauna, collectively referred to as bioturbation, on sediment physical properties and biogeochemical processes have been the focus of much research and have been the subject of several thorough reviews (e.g., Aller 1980, Andersen & Kristensen 1991, Krantzberg 1985, Kristensen 2000, Rhoads 1974). Most research has been focused on the effects of infauna on organic matter and nutrient cycling. Particle bioturbation by infauna leads to redistribution of organic matter within the sediment. Especially relevant is the mixing of labile organic matter to deeper layers within the sediment and thus fuelling anaerobic decomposition processes. Similarly, particle bioturbation returns refractory organic matter buried at depth within the sediment to the oxic sediment surface which enhances its decomposition. In fact, oscillating between oxic and anoxic zones may stimulate the decomposition of organic matter to a greater extent than constant exposure to either aerobic and anaerobic conditions alone (Aller 1994a, Sun *et al.* 2002). Particle bioturbation is also import for driving metal cycling within sediments by providing a means by which insoluble forms of oxidized metals (Fe and Mn oxides and hydroxides) are mixed into reduced zones supplying these electron acceptors to deeper sediment layers (Aller 1994b). More importantly, bioturbation returns insoluble forms of reduced metal complexes (e.g., FeS and FeS_2) to oxidized zones within the sediments allowing them to be reoxidized and thus replenishing the supply of oxidized metals as electron acceptors for organic matter decomposition and other oxidation reactions via metal reduction (Thamdrup *et al.* 1994)

Irrigation by infauna leads to an increased exchange of solutes between the porewaters and overlying water. One of the major effects of infaunal irrigation is to extend the oxidized zone to depth within the sediments (Fenchel 1996) which stimulates aerobic and suboxic (i.e., metal reduction) decomposition processes (Banta *et al.* 1999, Hansen & Kristensen 1998, Thamdrup *et al.* 1994). Irrigation also favors the oxidation of NH_4^+ to NO_3 in the bioturbated zone and thus stimulates both nitrification and denitrification (Kristensen *et al.* 1991, Pelegri & Blackburn 1995). Both particle mixing and irrigation lead to increases in sediment porosity within the bioturbated zone (Jones & Jago 1993) and to the oxidation of reduced sulfur compounds (Banta *et al.* 1999). These are only a few examples of the many documented effects that bioturbation by infauna has on sediment characteristics and processes.

SEDIMENT ASSOCIATED POLLUTANTS

The fate of persistent organic or inorganic pollutants in marine ecosystems depends to a great extent on their physicochemical characteristics. Due to their hydrophobicity and particle reactivity, concentrations of many pollutants are often several orders of magnitude higher in sediments compared to concentrations in the overlying waters. As such, sediments are often a sink for pollutants in aquatic environments. Pollutants associated with sediments represent a potential hazard to the environment as they can be remobilized to the overlying water and re-released to the environment under certain circumstances, e.g., changed hydrodynamic conditions leading to resuspension and erosion. Such chemical depots can thus be coined “chemical time bombs”. The ultimate fate of sediment associated pollutants in a given environment is determined by the physicochemical properties of the pollutants, diagenetic processes within the sediments and the physical stability of that particular environment. Thus, areas where sediments are resuspended due to, e.g., storm events or severe wave action can episodically be sources of pollutants previously stored in sediment (e.g., Mitra *et al.* 1999, Petersen *et al.* 1997).

Bioturbation, given its profound effect on the physical and biogeochemical characteristics of sediments, also affects the fate of particle reactive pollutants. Both particle and solute mixing caused by infauna lead to constant alterations of sediments and associated pollutants. The net effects of bioturbation on the fate of pollutants are not always straightforward, however, and vary greatly, depending on the circumstances. The number and size of infauna species, the mode and intensity of bioturbation, the compositions, concentrations and the physicochemical characteristics of often complex mixtures of pollutants as well as sediment geochemistry are factors that affect the ultimate outcome of these complex interactions.

When considering the effects of bioturbation on sediment pollutants it is important to keep in mind that there are two related, though separate components of bioturbation – particle mixing and solute transport, and that these will have different effects on the fate of sediment pollutants. While particle bioturbation transports sediment-associated pollutants through different zones within sediments (as well as through gut environments of deposit-feeders), irrigation transports water borne (freely dissolved or bound to dissolved organic matter, DOM) pollutant components, often leading to enhanced fluxes across the sediment-water interface and affecting adsorption-desorption kinetics. In addition to effects mediated by bioturbation, infauna can play a role via their direct, metabolic transformation of pollutants or indirectly by stimulating bacterial degradation of pollutants.

The purpose of this review is to provide an overview of the variety of effects that bioturbating infauna have on the fate of particle-reactive pollutants in marine sediments and to discuss the contributing mechanisms. There are many studies examining the effects of pollutants on infauna species and benthic communities (e.g., Bryan & Langston 1992 and many more, Gray *et al.* 1990). There is much less work examining the effects of infauna species on the fate of sediment pollutants, however. Krantzberg (1985) examined the ways in which infauna affected the fate of metals in freshwater sediments in particular, but there has been a great deal of research, especially on the interactions between marine infauna and organic pollutants, since her review which we include here. Our review is based on the examination of experimental case studies of selected infauna species and their interactions with sediment-associated pollutants, some of which originate from our research group. Interactions between both organic and inorganic pollutants, sediments and selected estuarine infauna species, in particular the lugworm *Arenicola marina* and the polychaete *Nereis diversicolor* have been our major research focus in recent years.

CASE STUDIES OF SELECTED INFAUNA SPECIES

Arenicola marina

The lugworm *Arenicola marina* is a common member of the benthic community in coastal areas of Europe. It is a head-down deposit feeder living in J-shaped tubes in sandy sediments with a relatively low organic content, typically at depths of 15-40 cm (Riisgård & Banta 1998, Riisgård *et al.* 1996). Their densities are often between 20 and 50 animals per m^2. *A. marina* irrigates its burrow with oxygenated water, pumping 10-60 ml per hour through the feeding funnel at the terminal of the tube (Riisgård *et al.* 1996). Despite relatively low ventilation rates compared to other infauna species, solutes are transported rapidly and over great distances in sediments bioturbated by *A. marina* due to advective flow resulting from the injection of water into the sediment at the feeding gallery (Timmermann *et al.* 2002). The lugworm eats 10-30 g of sediment per day from the bottom of the feeding funnel and defecates digested material on top of the sediment surface (Riisgård & Banta 1998). The uppermost sediment material is thereby gradually buried and brought down at a rate of 1-2 cm per month (Riisgård & Banta 1998). In heavily populated areas the sediment is turned over at least one time per year down to depths of approximately 30 cm. Thus, *A. marina* has major effects on both particle and solute transport in the sediments and would be expected to dramatically alter the distribution and ultimate fate of sediment-associated pollutants in polluted environments it inhabits.

Rasmussen *et al.* (1998, 2000) investigated the effects of bioturbation by the lugworm on sediment-water exchanges and distribution of Cd within sediments in a series of experiments. Cd was chosen as an example of a heavy metal that actively cycles both in the water and sediment phases and that is bioavailable to infauna (Bryan & Langston 1992). Using trace levels of ^{109}Cd, Rasmussen *et al.* observed that bioturbation by the lugworm either increased the net transport of Cd from the overlying water to the sediment (in the case of a water source) (Rasmussen *et al.* 1998) or greatly reduced the rate of release of Cd from contaminated sediments (Rasmussen *et al.* 2000). In both cases, this was likely due to the fact that particle mixing by the lugworm led to a continuous exposure of new sediment binding sites for Cd while irrigation assured that any dissolved Cd relatively quickly came into contact with these sites. Cd was incorporated both at the sediment surface and at the feeding depth due to *A. marina* bioturbation (Fig. 1). The increased binding of Cd in bioturbated sediments occurred despite the fact that *Arenicola marina* oxidizes sediments, reducing the concentrations of reduced sulfides (Banta *et al.* 1999) which are known to bind metals such as Cd (Di Toro *et al.* 1992, Di Toro *et al.* 1990). Thus the enhanced Cd uptake in bioturbated sediments is likely to be due to increased availability of other binding sites such as metal oxides and mineral and organic matter surfaces. Similar increases in sediment uptake and binding of Cd from the water column in the presence of *A. marina* has been seen by Everaarts & SaralaDevi (1996) and Petersen *et al.* (1998). It is worth noting that all of these experiments had a duration of 2-6 weeks. It is possible that over a longer time frame (months-years) this stimulatory effect of lugworm bioturbation on sediment Cd uptake would attenuate as available binding sites within the bioturbated zone became occupied and the system approached steady-state in terms of Cd partitioning between dissolved and adsorbed phases. No studies are available that experimentally test this hypothesis, however, and attainment of equilibrium would require quite high concentrations of Cd in the water, and thus would only likely occur in very polluted settings. In any case, it is clear that bioturbation by the lugworm increases the capacity of sediment to take up, bind and retain Cd and presumably other inorganic pollutants and it increases the rates of the exchange and adsorption processes.

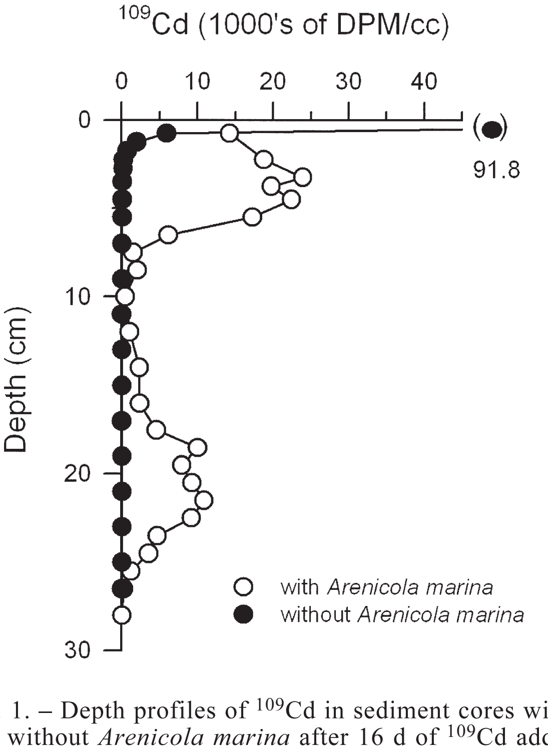

Fig. 1. – Depth profiles of ^{109}Cd in sediment cores with and without *Arenicola marina* after 16 d of ^{109}Cd addition to the overlying water. Data were previously published in Rasmussen *et al.* (1998).

Much of the work in our research group the past years has been focused on studying the dynamics between infauna and organic contaminants associated with oil and polycyclic aromatic hydrocarbon (PAH) pollution. Christensen *et al.* (2002b) investigated the effects of lugworm bioturbation on the fate of sediment-associated pyrene homogeneously distributed in sediment microcosms. Pyrene is a polycyclic aromatic hydrocarbon (PAH) associated with petrogenic but mainly pyrogenic pollution sources and is one of the PAH's often found at the highest concentrations in sediments (Kaag *et al.* 1998). Pyrene has a log K_{ow} of approximately 5 meaning that while it strongly binds to sediment, it is also present in solute phases, both freely solubilized and associated with dissolved organic matter in porewater and overlying water (Timmermann & Andersen 2003). Furthermore, pyrene is readily bioavailable to infauna species (Kaag *et al.* 1998, Timmermann & Andersen 2003). *Arenicola marina* bioturbation greatly enhanced the release rates (i.e., flux rates) of pyrene and its metabolites from sediments compared to rates observed in sediments without infauna (Christensen *et al.* 2002b). It was especially evident that the presence of *A. marina* led to rapid flushing of unmetabolized pyrene from the sediments due to its advective irrigation (Fig. 2, left). Over time, *A. marina* also significantly stimulated the release of pyrene metabolites, both microbial and those produced by the lugworm itself (Christensen *et al.* 2002a), but the greatest effect was an enhanced release of pyrene itself from sediments inhabited by *A. marina*. Similar enhanced removal due to lugworm bioturbation was observed by Kure (1997) with fluoranthene, a slightly larger PAH than pyrene. Furthermore, she observed that the greatest fluoranthene removal occurred in the deeper sediment layers associated with the feeding depth for *A. marina*. This is the area subjected to significant advective flow due to lugworm irrigation (Timmermann *et al.* 2002).

In contrast, Kure & Forbes (1997) saw that bioturbation by the lugworm reduced the rate of fluoranthene removal and mineralization from sediments where the contamination occurred at the sediment surface. In that study, lugworm bioturbation buried the contaminated layer, moving it away from the sediment surface increasing the transport distance to the overlying water. Mineralization was also reduced as fluoranthene was buried below the sediment surface thus reducing the availability of

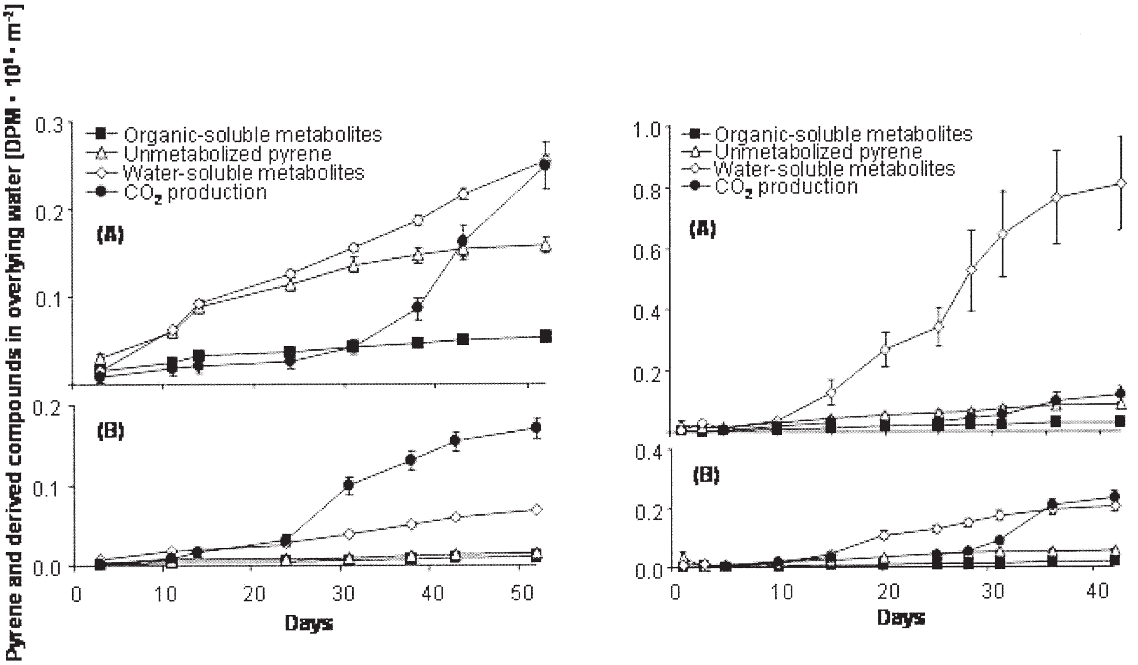

Fig. 2. – Sediment water fluxes of ^{14}C-pyrene, metabolites and $^{14}CO_2$ in sediment cores uniformly contaminated with ^{14}C-pyrene with (A) and without (B) *Arenicola marina* (left) or with (A) and without (B) *Nereis diversicolor* (right). Data were previously published in Christensen *et al* (2002b)

molecular O_2 which facilitates the microbial degradation of lipophilic and especially aromatic sediment pollutants such as PAH's (e.g., Cerniglia & Heitkamp 1989).

These results indicate that bioturbation by the lugworm *Arenicola marina* can lead to varied effects on the fate of PAH's in sediment environments, depending on where the contaminants are found. In the case where PAH's are found at or near the sediment water interface (or in the water presumably), the effect is one of enhancing burial and incorporation within the sediment which reduces the rate of release and mineralization of PAH's. In contrast, if PAH's already are distributed throughout the sediment, then lugworm bioturbation will enhance their removal from the sediment, both as untransformed compounds and as metabolic products.

Nereis diversicolor

Nereis diversicolor is another common polychaete often found at densities up to 5000 m^{-2} in a wide range of sediment types in shallow estuarine and marine habitats (Muus 1967). *N. diversicolor* is an omnivore that can feed on detritus, sediment or as a filter feeder on phytoplankton (Fauchald & Jumars 1979, Vedel & Riisgård 1993). It lives in U-shaped burrows with two or more openings and pumps intensively at rates up to 350-600 ml h^{-1} with the highest ventilation rates obtained while filter-feeding (Kristensen 1983, Riisgård 1991). Irrigation by *N. diversicolor* occurs within its burrows leading to enhanced transport of dissolved components out of sediments. This form of non-local transport is quite effective at altering solute distributions in the upper 5-10 cm of the sediment where *N. diversicolor* burrows are present (Kristensen & Hansen 1999) and significantly influences the biogeochemistry of at least the upper 10 cm of sediment (Banta *et al.* 1999).

We investigated the effects of *Nereis diversicolor* on the fate of pyrene in sediments. *N. diversicolor* significantly enhanced the removal of pyrene from sediments, but in a different manner than *Arenicola marina* did (Christensen *et al.* 2002b). Although flushing of unmetabolized pyrene from bioturbated sediments did occur, the main mode of removal with *N. diversicolor* was in the form of metabolites, both putative phase I metabolites of low water solubility and phase II metabolites of higher water solubility (Fig. 2, right). This observation and investigations of pyrene uptake into and metabolism in *N. diversicolor* tissues (Christensen *et al.* 2002a) indicate that *N. diversicolor* actively biotransforms sediment-associated pyrene and that this mechanism is important for the fate of pyrene and other PAH's in sediments inhabited by *N. diversicolor*. This is consistent with the results of McElroy (1985) who previously demonstrated that *Nereis virens*, a closely related species, was apt at metabolizing benz(a)athracene. McElroy *et* *al.* (1990) also showed that bioturbation by *N. virens* enhanced flushing of benz(a)athracene and metabolites from sediments in a manner similar to what we observed for *N. diversicolor* (Christensen *et al.* 2002b). It is clear from these studies that *Nereis* spp. affect PAH's via their own metabolism, but unfortunately, we know very little about the fate and effects in the environment of the metabolites they or other infauna produce. Primary metabolites of organic compounds are sometimes more toxic or carcinogenic than parent compounds, especially for the PAH's forming highly reactive epoxides; also, in some cases, phase 2 metabolites spontaneously disintegrate forming free radicals or carbonium ions, and thus they are highly toxic (Parkinson 2001). Giessing & Lund (2002) recently identified 1-hydroxypyrene as the sole phase 1 metabolite and several phase 2 metabolites of pyrene in nereids. Both types of metabolites are likely to be short-lived in oxic environments, where they presumably are degraded further by microorganisms. We know almost nothing about the fate of such metabolites in marine benthic environments, especially in anoxic sediments. Clearly more work is needed on the topic to fully understand the effects of *N. diversicolor* and other infauna capable of metabolizing PAH's (Forbes *et al.* 2001).

In Christensen *et al*'s (2002b) study, *Nereis diversicolor* stimulated microbial mineralization of pyrene as was evident with the increased rates of $^{14}CO_2$ production originating from the ^{14}C-labelled pyrene added to the microcosms. This effect was again likely due to *N. diversicolor*'s stimulation of aerobic processes in sediments, although the extent of stimulation was less than for *Arenicola marina*, which fits well with the impacts of these two species on sediment metabolism in general (Banta *et al.* 1999). In addition, the burrow environment may provide good conditions for PAH degrading bacteria, both because it is aerobic and because of the increased availability of labile organic matter. Granberg *et al.* (pers comm) demonstrated that bacteria from *N. diversicolor* burrows were as good as or better than bacteria from the aerobic sediment surface at degrading pyrene in their experiments. Chung & King (1999) observed a similar enhancement of bacterial degradation of several 2-3 ringed PAH's for burrow sediments from *Nereis virens*.

Whatever the mechanism involved, the effects of *Nereis diversicolor* on sediment-associated pollutants is likely limited to the upper, bioturbated layers (5-10 cm) of the sediment, in contrast with *Arenicola marina*, due to its mode of bioturbation (i.e., enhanced solute transport via non-local mixing). It is in this bioturbated zone that we would expect to observe remediating effects due to the enhanced transport and microbial degradation of pollutants. We found evidence of such effects in sediment microcosms contaminated with a heavy bunker oil where we observed more than twice as much loss and degradation of oil components, especially alkanes, after 2 1/2 months in sediments associated with *N. diversicolor* burrows compared to the surrounding anoxic bulk sediment (Pécseli *et al.* 2002). Extensive changes in diagnostic ratios for microbial alkane degradation (C17/pristane, C18/ phytane) indicated enhanced biodegradation. Similarly, Gilbert *et al.* (1994) observed that bioturbation by *N. diversicolor* led to both lower concentrations of hydrocarbons in the upper sediment and greater loss of hydrocarbons from the sediment in experimental sediment cores contaminated with a light crude oil at the sediment surface. Some of the oil was, however, mixed deeper within the cores, away from the sediment surface. The net effect of *N. diversicolor* in that study was to enhance the loss and degradation of oil by 44% relative to defaunated sediments. In an *in situ* experiment using the same design, Gilbert *et al.* (1996) observed both effects again, although the burial of hydrocarbons from the surface was greater than the enhanced loss from the sediment surface due to bioturbation, leading to a greater incorporation and retention of pollutants in sediments with *N. diversicolor* compared to defaunated sediments over the 6 month experiment. There were indications that this buried oil was still undergoing biodegradation, however, so the ultimate fate of the added oil in these bioturbated sediments is unclear.

These two studies by Gilbert *et al.* (1994, 1996) are good examples of that the complex interactions between bioturbating infauna and sediment pollutants can lead to different net effects, depending on the specifics of each situation. The results of Petersen *et al.* (1998), where rates of sediment uptake of Cd was enhanced with infauna, is another example that bioturbation by *Nereis diversicolor* doesn't always remediate pollution. In their study the source of pollution was the overlying water and the presence of *N. diversicolor* led to a more rapid and deeper sediment contamination than if there were no fauna present, although not to the same extent as with *Arenicola marina*. Reidel *et al.* (1997) observed that *Nereis succinea*, a species closely related to *N. diversicolor*, increased the sediment uptake of arsenic while it enhanced the release of manganese and copper.

To sum and compare the two species considered so far, we can conclude that both species affect the fate of sediment pollutants through a variety of mechanisms but to different extents. Some of the differences in their effects can be seen in their depth, intensity and mode of bioturbation. *Arenicola marina* affects contaminant fate throughout a deep sediment column (15-30 cm) due to its active particle mixing and advective flushing of the sediment. It stimulates aerobic microbial activity throughout much of the sediment column which also has an effect on pollutant fate. On the other hand, it is itself a relatively poor metabolizer of organic pollutants

(Christensen *et al.* 2002a), so it only plays a minor role in the direct biotransformation of these compounds. In contrast, *Nereis diversicolor* is a good metabolizer and is effective at biotransforming organic pollutants (Christensen *et al*. 2002a). The resulting effect of high densities ($\geq 5000\ m^{-2}$) on pollutant levels could conceivably be very important. Quantitative estimates of population level effects via metabolism are lacking and should be a topic of future research. The effects of *N. diversicolor* bioturbation on pollutant fate via physical processes and indirect stimulation of microbial degradation are lesser and limited to a shallower bioturbated zone (5-10 cm). Bioturbation by *N. diversicolor* leads to enhanced transport of soluble components via enhanced diffusion, which is slower than the advective transport seen with *A. marina*, however. Particle mixing is limited with *N. diversicolor*, although particle associated pollutants would be incorporated into the burrows due to feeding activities. Finally, *N. diversicolor* also stimulates aerobic microbial activity, although this is limited to the sediments surrounding its burrows. Still, this leads to a greater bacterial degradation of organic pollutants at depth within the sediment than would be the case without infauna.

Other species

In addition to the studies of *Arenicola marina* and *Nereis spp.* presented above, there has also been some focus on pollutant interactions with the small, opportunistic polychaete *Capitella* spp. The *Capitella capitata* species complex is a group of sibling species that often are found in organically rich and polluted sediments. The most studied and known species is *Capitella* species I (Grassle & Grassle 1974), although in recent years a number of other sibling species have been investigated (e.g., Gamenick *et al.* 1998, Mendez *et al.* 2000). Given *Capitella* spp.' association with polluted sediments, they have been the focus of much ecotoxicological research mostly focusing on the effects of pollutants on *Capitella* spp. (e.g., Grassle & Grassle 1984, Hansen *et al.* 1999a, Linke-Gamenick *et al.* 2000, Selck *et al.* 1998). A few studies have, however, shed light on the effects of *Capitella* spp. on the fate of sediment pollutants. In one of the first studies of its kind, Gardner *et al.* (1979) demonstrated that *Capitella* spp. enhanced the loss rate of PAH's from sediments, presumably by enhancing microbial degradation. Later studies have provided more direct evidence for the stimulation of the microbial degradation of organic pollutants by *Capitella* spp, by measuring $^{14}CO_2$ production from added labelled pollutant compounds (Bauer *et al.* 1988, Hansen *et al.* 1999b).

The effects of *Capitella* spp. on organic pollutants in sediments appear to be intermediate between those of *Arenicola marina* and *Nereis diversicolor* (Selck *et al.* 2003). Similar to *A. marina*, *Capitella* spp. redistributes sediment-associated pollutants via its conveyor-belt feeding, often leading to the burial of surface contamination (Forbes *et al.* 1996, Grassle & Grassle 1984, Hansen *et al.* 1999a, Holmer *et al.* 1997, Linke-Gamenick *et al.* 2000, Selck *et al.* 1998) although only in the top 5 cm or less. Similar to *N. diversicolor*, *Capitella* spp. actively metabolizes and biotransforms organic pollutants (Forbes *et al.* 2001, Hansen *et al.* 1999b, Selck *et al.* 2003). Enhanced transport of dissolved contaminants does occur with *Capitella* spp, but it appears to be less important than biotransformation and occurs to much lesser extent than for, e.g., *A. marina* (Selck *et al*. 2003). The net effect of *Capitella* spp. is that it facilitates a reduction in the concentrations of organic pollutants in sediments it inhabits in most cases through a variety of mechanisms.

The effects of other species on the fate of sediment pollutants have been studied less intensively than those of the polychaete species reviewed above. There have also been a few studies of other deposit feeders and their effects on sediment pollutants, however. Bioturbation by *Clymenella torquata*, a common maladanid polychaete which is a head-down deposit feeder in fine sediments, was shown to significantly reduce fuel oil concentrations in sediments, especially surrounding its burrows (Koerting-Walker & Buck 1989). This effect was mostly attributed to particle reworking, i.e., the deposition of fecal pellets on the sediment surface, which enhanced the loss of oil components to the overlying water, although irrigation within the worm burrows was also likely important, especially with the large effects observed over a short time scale (10 d). On the other hand, stimulation of the microbial metabolism of oil components due the bioturbation was less likely for the same reason. In the case where oil was added only to the sediment surface, bioturbation by *C. torquata* led to the transport of oil to depth within the sediment, most likely due to the "hoeing" behavior of this species where surface sediment is scraped down into its burrows (Dobbs & Whitlatch 1982). *C. torquata* accumulated high concentrations of oil components, so Koerting-Walker & Buck (1989) concluded that it is a relatively poor metabolizer of organic pollutants, although this was not directly studied.

A similar effect of particle reworking by tubificid worms increasing PAH release in freshwater sediment has also been seen (Reible *et al.* 1996). Here again it was proposed that the deposition of fecal pellets on the sediment surface was the main mechanism leading to the greater flux of PAH's from bioturbated sediments compared to defaunated sediments. While this transport of pollutants in fecal pellets to the sediment surface enhanced loss rates to the water, a large fraction of organic pollutants remained in or was readsorbed to fecal pellets reducing the potential rate of loss due to bioturbation (Karickhoff & Morris 1985). Bioturbation by tubificids and by worm-like insect larvae (chironomids and chaoborids) also altered sediment redox and metal pools favoring the release of metals to the overlying water (Krantzberg & Stokes 1985).

Most of the studies on bioturbation and the fate of sediment pollutants have focused on deposit-feeding polychaetes due to their intense bioturbation, but there are a few studies of the effects of other bioturbating infauna. Irrigation by the sediment-dwelling amphipod *Corophium volutator* was shown to increase the flux of dissolved Cd from the overlying water (the source of contamination) into the upper layers of the sediment in a similar fashion as the polychaetes studied (Petersen *et al.* 1998). The depth of sediment contaminated in this manner was much less, however, than with the larger polychaetes. Also, it is not clear from this study what effect *C. volutator* would have on the net transfer of contaminants out of the sediments in the case the latter was the source of pollution. Sundelin & Eriksson (2001) observed a surprisingly little effect on metal mobility with bioturbation by another estuarine amphipod, *Monoporia affinis*, despite the fact that it greatly reduced the concentrations of sulfides in the sediment. It may be that irrigation alone is not as an effective mode of mobilizing sediment-bound metals as particle mixing, although this is likely dependent on the specific system considered.

There has been remarkable little research focused on the effects of infaunal bivalves on the fate of sediment pollution. In one of the few published studies on the topic Chung & King (1999) observed enhanced degradation potential for some small PAH's in burrow sediments of the soft shell clam *Mya arenaria* although not to the same extent as observed for *Nereis diversicolor* or *Clymenella torquata* burrows. Riedel *et al.* (1997) observed that bioturbation by the deposit feeding mussel, *Macoma balthica* slightly affected net metal fluxes from sediments, but nearly to the same extent as the polychaete *Nereis succinea.* Recent work within our research group confirms that infaunal bivalves have much smaller effects on the fates of pollutants than e.g., polychaetes. While both suspension feeding (*Mya arenaria* and *Cardium lamarcki*) and deposit feeding species (*Macoma balthica* and *Scrobicularia plana*) readily take up, eliminate and presumably metabolize oil components (L Frederikson pers com), bioturbation by some of these species had only slight effects on the fate of oil components (Fig. 3). Surprisingly it was the two smaller and shallow burrowing species, *C. lamarcki* and *M. balthica* that led to noticeable removal and degradation of oil components, but only in the upper few cm. These two species are quite mobile and thus actively mix the sediment surface. The deeply burrowing, but stationary, *M. arenaria* had no observable effect on the fate of oil components compared to defaunated sediments. *S. plana* has a similar mode and depth of living as *M. balthica*, but must be less active as it too had little influence on the fate of oil in these experiments.

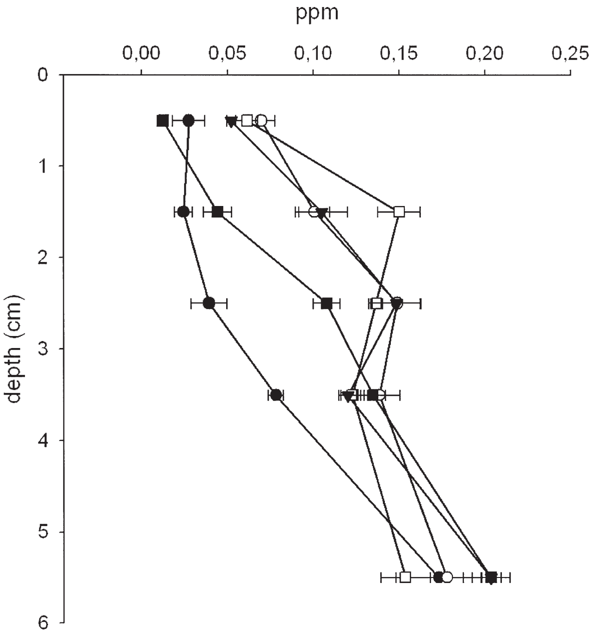

Fig. 3. – Depth profiles of methylphenanthrene (a 3-ringed PAH in the oil added uniformly to sediments) in microcosms after 5 months of bioturbation by the infauna bivalves *Cerastoderma lamarcki* (●), *Macoma balthica* (■), *Mya arenaria* (○), *Scrobicularia plana* (□), or no bioturbation (▼). Data are presented as avg. ± s.e. (L. Frederiksen, unpubl data).

Natural infauna communities

All of the studies cited until now have focused on the effects of single species. This is experimentally more tractable and makes interpretations more straight forward. On the other hand, it does not reflect the situation in nature where whole communities of infauna interact to affect the fates of pollutants. There are very few experimental studies examining the effects of entire communities of infauna on pollutant fate. In one of the few studies of this type Schaffner *et al.* (1997) demonstrated that the fate of sediment associated pollutants depends both on season, physicochemical pollutant characteristics and the presence of infauna communities. They added sediment with hydrophobic organic contaminants with log K_{ow} varying about two orders of magnitude to the top of Chesapeake Bay sediment microcosms either defaunated or containing a benthic community dominated by polychaetes, hemicordates, bivalves and crustaceans.

During winter conditions, the retention of contaminants in sediment was positively related to log K_{ow} both with and without fauna in sediment, while during summer conditions, the retention only depended on log K_{ow} in defaunated sediment, being positively related to log K_{ow}. During winter, the rates of loss of organic pollutants were greater in defaunated sediment than in sediment with fauna while during summer, with more intensive bioturbation, the rates of loss were much higher in sediment with fauna than in defaunated sediment, especially for the compounds with high log K_{ow}. Comparing winter and summer rates shows a higher rate of loss during winter in defaunated sediment, while the rates of loss from sediment with fauna were higher during summer than during winter. Furthermore, contaminants were buried to a greater depth at the same time when infauna were present. The depth of contaminant burial with bioturbation was inversely related to log K_{ow}. The authors speculate that the main effects of infauna on pollutant fate were via resuspension and biodiffusion, enhancing contaminant loss on the one hand and burial, leading to preservation, on the other hand. The balance between those processes and thus the net effects are likely to depend both on pollutant physicochemical characteristics, especially diffusivity, and season as temperature affects both diffusive processes and bioturbation, but not necessarily to the same extent.

A similar series of *in situ* experiments in the Mediterranean (Gilbert *et al.* 1996, Grossi *et al.* 2002) demonstrated the role of the infauna community both for burial, with the potential for contaminant preservation, and for enhancing biodegradation of aliphatic components of oil. In both experiments there was measurable degradation of aliphatic compounds despite burial but losses to the overlying water decreased as burial moved the surface contamination away from the sediment-water interface. That degradation still occurred despite burial is likely due to both stimulatory effects of the infauna, especially polychaetes, and the fact that aliphatic compounds can be degraded anaerobically (Grossi *et al.* 2002). Burial by bioturbation likely enhanced the preservation of aromatic components as these are much less subject to degradation in anaerobic conditions. Results from these *in situ* experiments supported results from laboratory experiments with *Nereis diversicolor* alone, although loss and degradation rates were greater *in situ.*

Box microcosms have also been used to experimentally investigate the effects of natural communities on the fate of pollutants at a more appropriate scale than in smaller cores, but in a way that is more controlled than *in situ* experiments. Biodiffusive bioturbation driven by the large infaunal urchin Echinocardium cordatum led to the burial of the organic contaminant di(2-ethylhexyl)phthalate (DEHP) added to the sediment surface of box microcosms collected from Olsofjord (Sandnes *et al.* 2000). There was no measurable degradation of DEHP during this 48 d experiment so it is difficult to conclude what the ultimate consequence of this burial would be for the fate of DEHP, although there was some evidence that bioturbation enhanced degradation processes. Results from this experiment demonstrate that the effect of a community on the fate of a pollutant can be controlled by the effects of one or a few dominant, "keystone" species (Lawton & Jones 1995).

Similarly, a tetrabrominated diphenyl ether (BDE-47) was buried by biodiffusive bioturbation in box microcosms collected from the Gullmar Fjord in Sweden where the infauna community was dominated by brittle stars (*Amphiura spp.*), ampharetid polychaetes (*Melinna cristata*) and tellenid bivalves (*Abra nitida*) (Magnusson *et al.* 2003). More than half of the added BDE was lost to the overlying water, however, in this experiment in contrast to Sandnes *et al.*'s (2000) experiment. The exact role of infauna on the fate of BDE-47 is difficult to interpret as there were no defaunated control microcosms to compare, but it is clear that bioturbation leads to a predictable burial occurred of BDE-47 into the sediment. A similar burial of benz(a)athrazene added to the water of a large MERL mesocosm (1.8 m diameter with approximately 5 m water column overlying a 30 cm sediment column) due to bioturbation by a benthic community dominated by small polychaetes (*Mediomastus ambesita*) and bivalves (*Nucula anulata*) (Hinga *et al.* 1980). Again, precise interpretations of the effects of the infauna were difficult as this experiment was unreplicated. Having a large number of replicates and controls is of course one of the major trade-offs of conducting such large scale experiments. Still, the results from such experiments provide insights into more realistic interactions between entire infauna communities and sediment pollutants.

DISCUSSION

In this review of the effects of various infauna species and communities on the fate of sediment contaminants, there are a number of general patterns and mechanisms that emerge. Infauna affect pollutants directly via the transport processes associated with their bioturbation and through their own uptake and metabolism of specific pollutant components. Infauna also affects pollutants indirectly through their effects on the sediment environment, especially the conditions for sediment microorganisms. Many of the mechanisms by which infauna affects pollutant fate result in both "positive" and "negative" effects, depending on the specific situation and the interpretation of those ef-

Table I. – Summary of positive and negative effects of infauna and their bioturbation on the fate of particle-reactive pollutants.

Mechanism	Effect	
	Positive	**Negative**
Irrigation/solute transport:		
Biodiffusion	Can lead to an enhanced flux of contaminant out of the sediment	A pollutant source in the overlying water will be drawn more rapidly and deeper within the sediment.
Irrigation of burrows (i.e., non-local mixing)	Flushing of pollutants from porewater near burrows	A pollutant source in the overlying water will be incorporated into sediments surrounding burrows
Advective irrigation (in porous sediments)	Flushing of pollutants from large regions of sediment	A pollutant source in the overlying water will be drawn down to contaminate a large zone of the sediment
Transport of O_2 into sediment	Stimulates the aerobic degradation of organic pollutants (especially important for aromatic compounds). Inhibits sulfate reduction which may reduce the methylation of mercury	Oxidizes sediments which can lead to increased mobility of metals bound to sulfides.
Particle mixing:		
Deposition of sediments on the sediment surface (often in the form of fecal pellets) Resuspension (due to infauna)	Increased release of pollutants due to transfer to an aerobic environment, a shorter diffusion distance to the overlying water, and possibly, microbial stimulation	Continual exposure of "clean" sediments and binding sites to water-born contaminants
Mixing of surface sediments to depth	May eventually transfer pollutants from an aerobic to an anaerobic zone where they may be more stable and less bioavailable.	Can lead to a greater depth of contamination.
Metabolism:		
Phase I (P_{450}) and II metabolism	Actively metabolize organic pollutants, removing them from the sediment	The metabolites may be more toxic and mobile than the parent compound
metallothionin	May detoxify metals by making them less bioavailable	Leads to the accumulation of metals in infauna which may enhance bioaccumulation in the food chain.

fects in a given case. We summarize the different mechanisms by which infauna affects the fate of pollutants in Table I and have given a few examples of how this might lead to positive and negative effects on the environment. It is clear that these interpretations are subjective and will depend on specific conditions of the case to be considered.

On the positive side, bioturbation stimulates the conditions for the microbial degradation of persistent organic pollutants in many situations by the same mechanisms that stimulate the decomposition of refractory organic matter in general, especially by increasing the availability of O_2, NO_3^- and metal oxides in otherwise anoxic sediments that would be dominated by sulfate reduction. Bacteria using O_2 and these other favored terminal electron acceptors are better able to carry out the catabolic processes associated with the degradation of organic pollutants than sulfate reducing bacteria (e.g., Rockne & Strand 1998). Furthermore, many infauna species actively metabolize pollutants themselves. Both of these effects lead to the removal of organic pollutants from the sediment, thus remediating sediment pollution. The environmental fate of metabolites produced by both microorganisms and infauna is poorly understood, however, and should be the focus of study in the future, especially in relation to possible accumulation in anoxic sediments. We speculate on the other hand that metabolites produced in oxic zones of bioturbated sediment, while they may have increased toxicity, will be short-lived and thus the stimulation of the microbial production of metabolites by infaunal bioturbation and the production of metabolites by the infauna themselves lead to a real and positive effect in the case of sediments contaminated by organic pollutants in the bioturbated zones.

On the other hand, bioturbation, especially irrigation, leads to a greater mobility of pollutants in sediments. This can lead to a greater release of pollutants from sediments than otherwise would be the case without bioturbation. Thus, the expected transition from azoic sediments after a catastrophic pollution event to sediments recolonized by first pioneer and afterwards later successional stages of infauna as the benthic community recovers can have a detrimental effect in the form of greater mobilization of previously quiescent sediment pollutants.

Irrigation also leads to a greater oxidation of sediments. This enhances aerobic metabolism as discussed on the one hand, but it can alter the mobility of metals on the other hand. Metals, such as Cd and Hg, are tightly bound by sulfides and thus a reoxidation of sulfides can lead to an increased mobility of these metals which may have detrimental effects in some circumstances. The methylation of Hg, which greatly increases Hg's mobility and bioavailability, is thought to be related to the process of sulfate reduction (King *et al.* 2000). Thus, an inhibition of sulfate reduction due to bioturbation should lead to a reduction of Hg methylation and thus the toxicity of Hg in the environment. The very complex series of interactions between bioturbation and metal cycling, both abundant metals such as Fe and Mn and heavy metals, and S cycling in sediments is poorly understood and should be the focus of further study if we are to fully understand the effects of infaunal bioturbation on the fate of heavy metals in sediment environments.

Particle mixing by bioturbation results in the redistribution of particle associated pollutants according to the manner and mode of bioturbation. The consequences of this redistribution can vary, however. In the case of head-down deposit feeding or resuspension, where sediments are deposited on the sediment surface, sediment-associated pollutants may be released to the overlying water more rapidly or dissolved pollutants may be taken up from the water column by these newly exposed sediments.

Particle mixing in the other direction leads to the transport and burial of particles to deeper layers within the sediment which may increase their retention and preservation, both by increasing the distance for diffusive transport to the overlying water and by exposing the pollutants to anaerobic conditions. On the other hand, burrow sediments can be "hot spots" for microbial activity including the degradation of organic pollutants.

Comparing the relative importance of irrigation and particle mixing for the fate of pollutants, we can conclude that irrigation is important for the rapid transport and removal of dissolved pollutants to the overlying water (assuming lower concentrations there). These dissolved components will be replaced by desorption of particle-associated fractions via adsorption-desorption kinetics. Repeating this process over time, irrigation should be capable of "flushing" the irrigated zones of sediments if the pollutants have a dissolved fraction of any measurable size. Irrigation also supports the microbial degradation of organic pollutants leading to their removal as well. Thus irrigation should be quite important for removing organic pollutants in particular from sediments. *A priori*, irrigation would be expected to have greater effects on the fate of compounds with a low log K_{ow} as they are more soluble. There are very few studies that have included compounds ranging in solubilities where this hypothesis can be directly tested, however. Schaffner *et al.* (1997) found that in bioturbated sediment, burial rates increased with decreasing log K_{ow} while loss rates to the overlying water was independent or even positively related to log K_{ow} which is at variance with a general expectation of a greater diffusive loss due to bioturbation for compounds with low log K_{ow}. Only in non-bioturbated sediment or sediment bioturbated at low intensity (i.e., during winter), were the rates of loss from the sediment inversely related to log K_{ow} as expected. The surprising result of relatively greater retention of more soluble compounds in bioturbated sediments during summer suggests that biodiffusive transport of contaminants via irrigation deeper into the sediment became important during periods of intense infauna activity, compensating to some extent the tendency for greater diffusive loss of contaminants with lower log K_{ow} to the overlying water.

Particle mixing is important for determining the depth and distribution of particle-associated pollutants within bioturbated sediments. Particle mixing also ensures that pollutants actively cycle within sediments via their transport between various layers and biogeochemical zones within the bioturbated layer. This may lead to both a continued metabolism and degradation of pollutants on the one hand and a greater potential for periodic release to the overlying water on the other hand. We do not expect particle bioturbation to have as great an effect on the release or removal of pollutants from sediments as irrigation, however.

When considering interactions between infauna, bioturbation and sediment pollutants, size matters. It is the large, dominating bioturbators that determine the fate of pollutants in sediments. This was clearly seen in the studies of macrofaunal communities dominated by a large bioturbator such as a burrowing urchin. This means that one can focus on understanding the role of these "keystone" species as a first step to understanding the effects of infaunal communities on sediment pollutants. It also means that pollution events which lead to dramatic shifts in macroinfauna community size and structure have important implications for the interactions between infauna and pollutants and, as such, for pollutant fate. Recovery of benthic communities over time (e.g., Pearson & Rosenberg 1978), with the associated increases in size of infaunal organisms and their mode of bioturbation, will have important consequences for the subsequent fate of the pollutants in the impacted environment.

Bioaccumulation

Bioaccumulation has not been the focus of this review, but if coupled to further trophic transfer it can lead to the removal of pollutants from the sediment. There is a great body of literature examining bioaccumulation of pollutants (e.g., Bernds *et al.* 1998, Bryan & Langston 1992, Christensen *et al.* 2002a, Kukkonen & Landrum 1994, Lee *et al.* 1998, Timmermann & Andersen 2003) and its role in the trophic transfer of contaminants (e.g., McElroy

& Sisson 1989, Wallace *et al.* 1998, Wallace & Luoma 2003). While very important for toxicity of sediment pollutants, it is unlikely that bioaccumulation and trophic transfer of pollutants is a quantitatively important route of removal of pollutants from sediments.

The environment within the gut of deposit feeders is very different from the sediment environment. Surprisingly deposit feeder digestive systems are characterized by relatively neutral or even slightly alkaline pH's and the presence of surfactants (Mayer *et al.* 1997), both of which enhance the release of organic matter bound to mineral particles. Recently the role of the gut environment for the uptake, transformation and mobility of sediment pollutants has been the focus of research and it is clear that it plays an important role in the bioavailability of pollutants (Ahrens *et al.* 2001, Weston & Mayer 1998). It is less clear, however, what role transformations within the gut environment may have on the fate of pollutant that is not taken up, but excreted again. It can be speculated that particle associated pollutants may be made more bioavailable to microbial transformation due to changes during gut passage, but little direct evidence is available. This is another area of active research that we have chosen to leave out of this review. There is currently much focus on the role of the gut environment for the uptake and bioavailability of sediment-associated pollutants for deposit feeders. Little focus has been on the fate of the pollutants that pass through the gut environment and reemerge in the sediment, however.

Is bioturbation good or bad for sediment pollution?

As shown in the discussion above, the various mechanisms involved in bioturbation and metabolism by infauna can have both positive and negative consequences for the fate of pollutants in the marine benthic environment.

The net results of the opposing effects of bioturbation on a pollutant will depend on a number of initial, case-specific conditions:

1. What are the physicochemical characteristics of the pollutant (high vs. low Kow, for example)?

2. What is the concentration and distribution of the pollutant within the environment? Is the source of pollutant the overlying water, a surface deposit or a more uniformly contaminated sediment? How strong is the binding to sediment, which is known to depend on sediment-pollutant "aging"?

3. Which infauna are present and what is their major mode of bioturbation?

4. How are these infauna affected by the pollution? Are there major changes in the infauna community? Are physiological processes such as feeding or ventilation affected? Community changes and physiological effects are well documented (and treated elsewhere), and both types of changes affect rates and mode of bioturbation and thus will have important implications for pollutant fate.

Furthermore, whether a greater mobilization and transfer of a pollutant from the sediment to the overlying water or *vice versa* is a "good thing" is also dependent on the specific pollution situation under consideration.

Modeling as a tool

We end our review of the interactions between infauna and sediment pollutants by suggesting that modeling provides a useful tool for unraveling the many, sometimes contradictory, effects of bioturbation infauna, and environmental conditions that lead to differing fates and effects of pollutants in bioturbated sediments. The requirements to such models are that they adequately describe, preferably in a mechanistically correct fashion, the transport processes associated with bioturbation and couple them to physical chemical, microbial and other metabolic processes that affect pollutant fate. These models will be even better and more useful if the models include feedbacks of pollutant effects on infauna and their rates and modes of bioturbation. Forbes & Kure (1997) presented a simple example of how one can model the effects of bioturbation on the fate of pollutants. With their model they demonstrated that increased bioturbation by the lugworm *Arenicola marina* leads to a greater pollutant inventory in sediments with surface contaminations. This effect is clearly a result of the initial conditions interacting with the infauna organism considered. Different initial conditions lead to differing results as is clearly indicated by the modelling results presented in Figure 4 where three different outcomes of interactions between the lugworm and pyrene are shown. This model demonstrates that the effects of bioturbation by the same species (*A. marina*) can range widely – from enhanced sediment remediation (Fig. 4, left) to retarded sediment remediation (Fig. 4, middle) to greatly enhanced incorporation of pyrene into the sediment (Fig. 4, right). Models such as this one provide useful tools for predicting the net effects of the complicated interactions between infauna and pollutant fate.

Finally, modeling allows the important feedback of pollutant effects on bioturbating organisms to be considered. It is quite common that pollutants affect the physiology of infauna including there rates of bioturbation (e.g., Fig. 5, Mulsow & Landrum 1995, Stromgren *et al.*, Timmermann & Andersen 2003). Timmermann *et al.* (this issue) present a good example of such a model where pollutant effects are included as a feedback link to the infauna. To fully understand and be able to predict the results of the complicated interactions between bioturbating infauna and sediment pollutants we will ultimately need to link these fate and effects

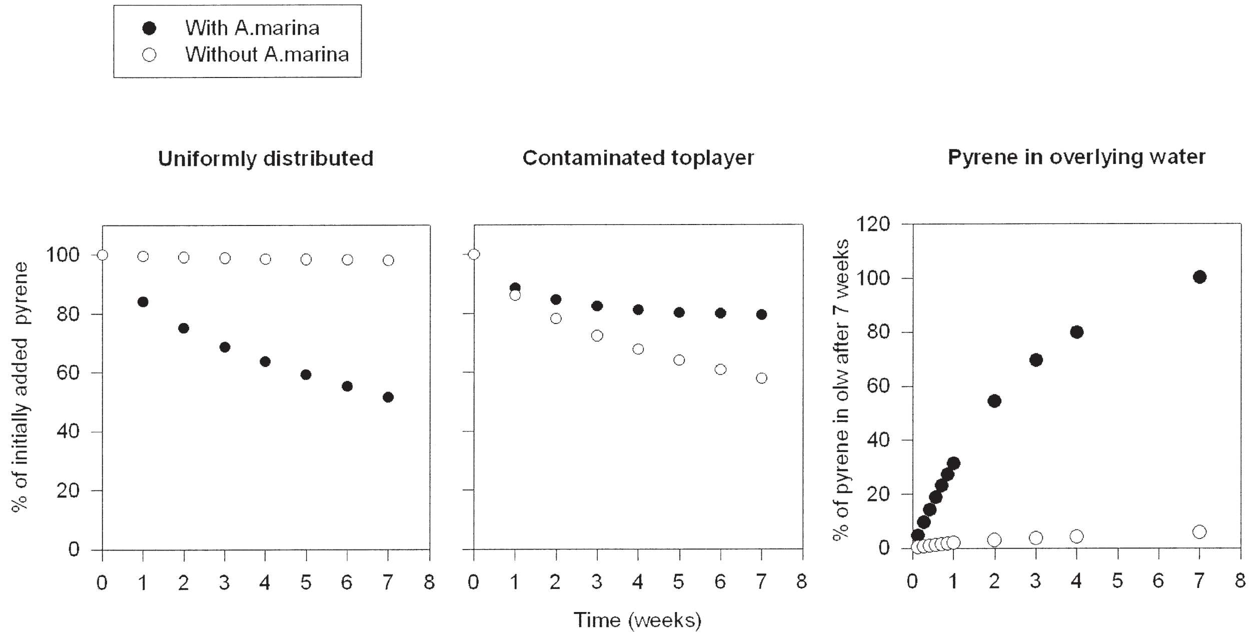

Fig. 4. – Predicted sedimentary inventories of pyrene (expressed as % of the pyrene added to the system) over time in systems with and without *Arenicola marina* when pyrene is added uniformly throughout the sediment (left), as a surface contamination (middle) or to the overlying water (right). These predictions are the results of a particle and solute bioturbation model for *A. marina* linked to a pyrene adsorption-desorption and degradation model (Timmermann 2001). The validity of the model has been tested with experimental data in the same study.

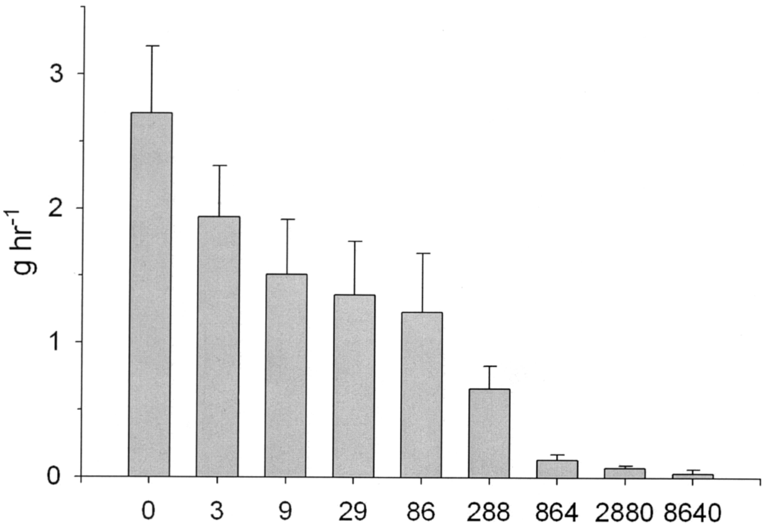

Fig. 5. – Feeding rates of the lugworm *Arenicola marina* as a function of concentrations of heavy bunker oil homogeneously mixed in sediments. Data were previously published in Pécseli *et al.* (2002).

models to generate a more holistic, but mechanically correct, model that describes and predicts these interactions. This is no easy task, however, as it requires a great deal of insight into the relevant mechanisms and processes involved with the pollutants and infauna communities being considered. Still, it is a goal worth pursuing as it will provide both scientists and managers with better understanding of and insights in the processes involved and with powerful scientific and management tools.

Acknowledgments. – Thanks to K Timmermann for constructive discussions and feedback during the preparation of this review and for loaning us her modeling results. Thanks also to A Rasmussen, M Christensen, and L Frederiksen for allowing some of their data to be used in this review. This manuscript was improved by the constructive comments of two anonymous reviewers. This work is supported by the Danish Natural Sciences Research Council and the Danish Environmental Research Programme via the BIOPRO Centre.

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Reçu le 21 novembre 2003; received November 21, 2003
Accepté le 17 décembre 2003; accepted December 17, 2003