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Bioaccumulation of Marine Pollutants [and Discussion]

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Bioaccumulation of marine pollutants

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Bioaccumulation of pollutants can occur from sea water, from suspended particles, from sediments and through food chains. The rate at which accumulation occurs in an organism depends not only on the availability of the pollutant but also on a whole range of biological, chemical and environmental factors. The ultimate level which is reached is governed by the ability of the organism to excrete the pollutant or, alternatively, store it. This latter course often leads to the attainment of very high concentrations and sometimes no equilibrium level is ever reached. Two particular topics which are considered are the biological amplification of pollutants along food chains and the development of tolerance which sometimes occurs.

1. Introduction

Among the many substances regarded as environmental contaminants are some, such as zinc, which at natural concentrations are essential for life, others, such as mercury, which occur naturally at low levels but are not essential, and others, such as plutonium, which are largely man-made and foreign to the experience of organisms. Whether essential or not, inorganic or organic, many potentially toxic substances possess properties which make them readily available for accumulation by marine organisms, and this is the basis for much of our concern about pollution. This paper considers the different ways in which pollutants may be absorbed, stored and excreted by marine organisms, not only as processes controlling the ultimate levels of contamination, but also as processes providing a variable degree of protection against the toxic effects of pollutants.

2. Absorption from different sources

(*a*) *Absorption from solution*

Remarkably little is known about the processes by which pollutants cross the absorptive surfaces of marine organisms. Coombs & George (1978) have discussed the possibilities of carrier-mediated heavy-metal transport in larger organisms, but most of the evidence for this concerns unicellular organisms (cf. Bryan 1976*a*). It would not be surprising to find some affinity between heavy metals and systems for transporting calcium, and Wright (1977) has suggested that this may occur for cadmium in the crab *Carcinus maenas*, where active transport of calcium across the gills has been demonstrated at low salinities. Calcium transport systems almost certainly carry the fission product ^{90}Sr, although there is usually some discrimination against strontium in animals (cf. Mauchline & Templeton 1966). Similarly, Bryan (1963) showed that ^{137}Cs is almost certainly actively transported across the absorptive surfaces of the brackish-water isopod *Sphaeroma hookeri* by the potassium pump, which is activated at low salinities to maintain the potassium concentration of the haemolymph. Although caesium is exchanged much more slowly than potassium, it reaches a higher concentration factor and both factors increase as the salinity falls.

Most of the evidence for metals and their radionuclides points to uptake being passive, although this does not exclude some sort of carrier mediation. For example, Davies (1973) showed that the kinetics of zinc uptake by the diatom *Phaeodactylum tricornutum* were best explained by adsorption on to the cell membrane, diffusion which controls the rate of uptake, and binding to proteins within the cell. Similar conclusions were reached for other metals including mercury in the green flagellate *Dunaliella tertiolecta* (cf. Davies 1976, 1978) and evidence of a similar type for the passive uptake of metals by various seaweed and animal species has been discussed by Bryan (1976*a*, *b*). In some species there is direct proportionality between rates of absorption and external concentration, but in other species, possibly owing to the adsorption characteristics of the metal, the rate increases rather more slowly than the external concentration. The more acutely toxic metals are absorbed most rapidly and, in the polychaete *Nereis diversicolor*, uptake rates from 0.01 part/10^6 in 50 % sea water decreased in the order Hg > Cu > Ag > Zn > Mn > Cd > As.

Although the adsorptive phase of uptake is usually the most rapid, the amount involved may become relatively unimportant as internal accumulation proceeds. However, where penetration is limited, the adsorption phase may be very important and is related to the area of the organism. Thus, the uptake of ^{106}Ru by seaweeds such as *Laminaria digitata* has been shown to be an adsorption process (Jones 1960) and so also has the uptake of plutonium by the kelp *Macrocystis pyrifera* (Folsom, Hodge & Gurney 1975).

Although there is evidence for the carrier-mediated uptake of organic compounds such as amino acids from solution, there is little sign that uptake of the major organic pollutants occurs in this way. Rapid surface adsorption or partitioning to the lipoprotein cell membrane probably provides the momentum for diffusion into the organism, and molecules having a high degree of liposolubility are usually absorbed most readily (cf. Walker 1975). For example, Ernst (1977) showed that the rates of uptake of chlorinated pesticides by *Mytilus edulis* decreased in the order DDD > endrin > heptachlor epoxide > dieldrin > α-endosulfan > α-HCH > γ-HCH. Decreasing rate was closely related to increasing water solubility, presumably because there is a significant correlation between low water solubility and high lipid–water partitioning (Metcalf 1977).

(*b*) *Absorption from suspended particles*

In filter-feeding organisms, it is often quite difficult to determine experimentally the relative importance of uptake from solution or that from food, inorganic particles or oil droplets. One method is to follow radiotracer uptake from solution until equilibrium appears to have been reached and to compare this level with the concentration factor expected from stable element analyses. By using *Mytilus*, it was shown that metals such as zinc, manganese, cadmium and selenium must largely be absorbed from suspended particles (Pentreath 1973*a*· Fowler & Benayoun 1974, 1976). Schulz-Baldes (1974), who fed lead-contaminated phytoplankton to *Mytilus edulis*, also concluded that uptake from the food was important. Recent work on this species has shown that uptake of particulates is not confined to the digestive system, since George, Pirie & Coombs (1976) have shown that particles of hydrous ferric oxide can be taken up at a significant rate through the gills by pinocytosis and transferred to other tissues via circulating amoebocytes. This uptake process appears to be energy dependent and uptake of lead and the metalloprotein ferritin has also been observed (George, Pirie & Coombs 1975, 1977; Coombs & George 1978).

Although there is not much experimental evidence to show how important suspended particles are as a source of organic contaminants, they are probably very important. For example, Corner, Harris, Whittle & Mackie (1976) showed that in the copepod *Calanus helgolandicus* the dietary route was particularly important for the uptake of the petroleum-derived hydrocarbon naphthalene.

(*c*) *Absorption from sediments*

Simulating the natural uptake of contaminants from sediments by burrowing organisms in the laboratory seems to be particularly fraught with problems, since the ability of different artificial substrates to bind contaminants varies enormously and it is necessary to use particle sizes that the organism can accept. Thus it might be dangerous to draw too many conclusions from experiments carried out with single substrates. Luoma & Jenne (1976, 1977) studied the uptake of zinc, cobalt and silver by the deposit-feeding bivalve *Macoma balthica* from labelled artificial sediments such as precipitated oxides of iron and manganese. They corrected for the absorption of metals leached from the sediment by enclosing control animals in dialysis sacs and were able to show that availability of the metal to the animal was dependent on the type of sediment, zinc being absorbed far more readily from association with powdered clam shells than from iron oxide particles. A comparison was also made between the ability of the bivalve to absorb metals and the ability of chemical extractants to remove them from the sediments. This type of approach has been extended to the field, and Luoma & Bryan (1978) have found that the concentration of lead in the burrowing bivalve *Scrobicularia plana* is proportional to the concentration in the sediment as modified by the inhibitory effect of iron (see figure 1). In contrast, Luoma (1977*a*) concluded that levels of mercury in the deposit-feeding shrimp *Palaemon debilis* were related to availability from the water rather than from the sediment under field conditions. Experimental studies with the use of contaminated sediments in the laboratory have shown that uptake of plutonium is very limited in the polychaete *Nereis*

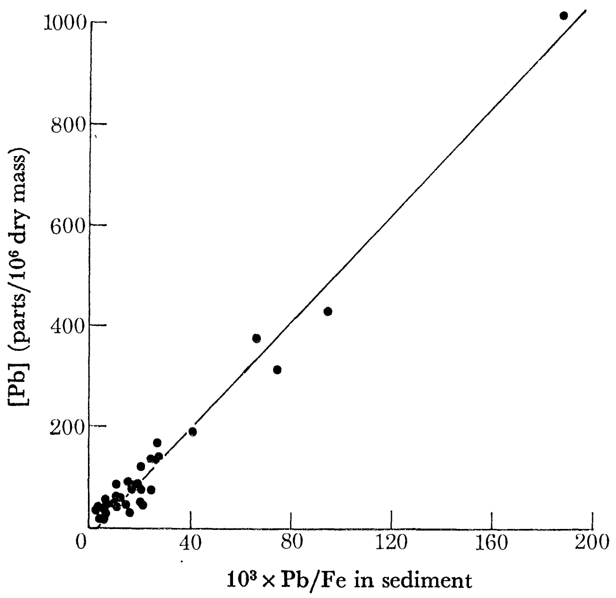

FIGURE 1. Relation between concentration of lead in whole soft parts of the bivalve *Scrobicularia plana* and Pb/Fe ratio in 1M HCl extract of less than 100 μm fraction of sediment from different estuaries. The direct relation to the Pb/Fe ratio rather than to lead in the sediment suggests that the availability of sediment-bound lead will be inhibited by higher levels of iron (after Luoma & Bryan 1978).

diversicolor (Beasley & Fowler 1976) and also in the bivalve *Lucina pectinata* (Mo & Lowman 1975). This latter species did not absorb plutonium leached from the sediment and contamination seemed to be confined to that transferred directly from the particles to external surfaces such as the gills, siphon and shell.

Contrasting results are also characteristic of studies on the availability of organic contaminants from sediments. Thus Roesijadi, Woodruff & Anderson (1978) concluded that when crude oil was strongly attached to sand by evaporation from solution in ether, its naphthalene content was not absorbed by the bivalve *Macoma inquinata*. On the other hand, Langston (1978) found that polychlorinated biphenyls dried on to particles of aluminium oxide were accumulated by *Macoma balthica*.

(*d*) *Absorption from food*

Experimental work on the plaice, *Pleuronectes platessa*, has shown that the food is the main source for most metallic contaminants and their radionuclides, including iron, cobalt, zinc, manganese, methyl mercury, cadmium and silver (Pentreath 1973*b*, *c*, 1976*a*, *b*, *c*, *d*, 1977*a*, *b*). Estimates of the retention of the radionuclides following a meal of labelled *Nereis diversicolor* gave values including 89 % for methyl mercury, 11 % for inorganic mercury and less than 5 % for silver and cadmium. Despite these low levels of retention it was calculated that, at natural levels of metals in the environment, only for inorganic mercury (Pentreath 1976*d*) and ^{137}Cs (Jefferies & Hewett 1971) does the contribution of the water approach that of the food. Although it might be expected that uptake of metals from the water would be more important in young fish, Pentreath (1976*a*) concluded that, even in the earliest stages, food is the major pathway for the uptake of zinc and manganese. Field observations on levels of plutonium in plaice showed that the gut contents usually contained concentrations orders of magnitude higher than the tissues, suggesting very inefficient absorption from the diet (Pentreath & Lovett 1976).

Among crustaceans, work on the euphausiid *Meganyctiphanes norvegica* has indicated that normally the diet is the main source of zinc and cadmium (Small, Fowler & Keckes 1973; Benayoun, Fowler & Oregioni 1974), whereas uptake from the water, particularly by adsorption, appears to be more important for ^{141}Ce and plutonium, which are assimilated only slightly from the food (Fowler, Heyraud, Small & Benayoun 1974; Fowler, Heyraud & Cherry 1976). Methyl mercury was absorbed much more efficiently than the inorganic form by *Meganyctiphanes* and it was suggested that uptake from the water may be more important than that from the food (Fowler, Heyraud & La Rosa 1976). Work on other crustaceans has shown that, unlike most organisms, *Carcinus maenas* has a considerable ability to absorb plutonium from its food and that food is the main source of selenium in the shrimp, *Lysmata seticaudata* (Fowler & Guary 1977; Fowler & Benayoun 1977). On the other hand, Bryan & Ward (1962) suggested that the water was rather more important than the food as a source of ^{137}Cs in the prawn, *Palaemon serratus*. For gastropod molluscs, Young (1975, 1977) has shown that in both *Littorina obtusata* and *Nucella lapillus* the food is the major source of zinc and iron.

Certainly in fish and crustaceans all the evidence points to food as being the main source of organochlorine residues such as DDT and polychlorinated biphenyls (cf. Odum, Woodwell & Wurster 1969; Addison 1976; Elder & Fowler 1976).

3. Factors affecting rates of absorption

Many of the factors that influence rates of absorption are those which have been recognized as having an important influence on the acute toxicity of pollutants (cf. Bryan 1976*b*). The chemical or sometimes the physical form of a contaminant in the water, sediment or food is a very important control on its rate of uptake. For example, for *Mytilus galloprovincialis*, Fowler & Benayoun (1976) showed that selenium in the form of selenite was absorbed from solution much more readily than selenate; and for *Mytilus edulis*, George & Coombs (1977) found that prior complexation of ionic cadmium with EDTA, humic acid, alginic acid or pectin doubled the rate of uptake. Studies on the uptake of mercury from food by *Pleuronectes platessa* showed that the retention of methyl mercury was 80–93 % with *Nereis* as food but only 4–42 % with *Mytilus* (Pentreath 1976*d*); this influence of the contaminated matrix has already been referred to with regard to sediments (cf. § 2*c*). Competition between chemically similar ions can influence rates of uptake and Bryan & Hummerstone (1973*a*) showed that the rate of uptake of cadmium by *Nereis diversicolor* was reduced by increasing the level of zinc.

Other important factors are those relating to the state of an organism such as its age, size, stage in life history and so on. For example, small organisms having a large surface area: volume ratio would be expected to absorb contaminants more rapidly than larger organisms, and this is generally true (cf. Morgan 1964). Rate of feeding is also related to size, and in the coho salmon, *Oncorhynchus tshawytscha*, it was shown that, because the smaller fish consumed proportionally more food, they received the highest dose of DDT (Buhler & Shanks 1970). In crustaceans the moulting phase is very important, since the permeability of the surface increases. Thus, in *Carcinus maenas*, the rate of absorption of ^{134}Cs increases during the moult and this is also the time when ^{90}Sr can be rapidly incorporated during the deposition of calcium in the new shell (Bryan 1961; Gibbs & Bryan 1972).

Environmental factors, including temperature, salinity, dissolved oxygen, pH and light, can influence both the form of the contaminant in the environment and the physiology of the exposed organisms. These factors have been extensively studied in toxicity experiments and often have a considerable influence (cf. Bryan 1976*b*). On the other hand, they may have a much smaller influence on the concentrations of contaminants ultimately accumulated, since rates of loss may equally be affected. For example, the rate of uptake of zinc by *Nereis diversicolor* and its toxicity are both increased when the salinity is reduced below 17.5 ‰ (Bryan & Hummerstone 1973*a*). However, analysis of zinc in animals from a wide range of salinities in the field has never revealed any influence of salinity on the concentration of zinc, which appears to be regulated.

4. Metabolism of pollutants

Basically there are two ways of handling contaminants to avoid their toxic effects: to store them in an inert form or excrete them. Both processes often involve chemical changes and are only gradually becoming understood.

(*a*) *Detoxification and storage*

For heavy metals, storage, at least of a temporary nature, is provided by the general binding capacity of compounds such as proteins. Recently, more specific storage proteins of the metallothionein type have been discovered in various marine groups. They may occur at low or undetectable levels in normal organisms, but their synthesis can be induced by contamination both in the field and in the laboratory. Cadmium metallothionein has been found in the liver and kidney of the sea lion, *Zalophus californianus* (Lee *et al.* 1977; see also table 1), in the liver of the plaice, *Pleuronectes platessa* (Overnell, Davidson & Coombs 1977), and, together with copper metallothionein, in the limpet, *Patella vulgata* (Howard & Nickless 1977). Induction does not appear to be a rapid process, and Noël-Lambot (1976) showed that although considerable induction of metallothionein followed the exposure of *Mytilus edulis* to 0.13 parts/10^6 cadmium for 36 days, little induction followed exposure to 13 parts/10^6 for 3 days.

Other methods of storage include deposition in skeletal material such as bone (table 1) and intracellular deposition. The green flagellate *Dunaliella tertiolecta* is very tolerant of mercury and, since it produces hydrogen sulphide during growth, Davies (1976) has suggested that the metal is precipitated within the cell as a sulphide. In *Nereis diversicolor* from a contaminated estuary we have observed copper deposits in membrane-bound vesicles within the epidermal cells (Bryan 1976*a*). Copper storage granules have also been observed in the parenchyma cells of the mid-gut of contaminated barnacles, *Balanus balanoides* (Walker 1977), and in amoebocytes from contaminated oysters, *Ostrea edulis* (George *et al.* 1978). In both cases copper was associated with sulphur, suggesting a combination with protein or sulphide. Other granules from the same species contained zinc, largely as zinc phosphate (Walker, Rainbow, Foster & Holland 1975; George *et al.* 1978).

In many fish, most of the mercury in the body occurs in the more toxic methyl form. Experiments, in which a pulse of ^{14}C- and ^{203}Hg-labelled methyl mercury was introduced into the fishes *Fundulus heteroclitus* and *Salmo gairdneri*, showed that the ratio of the two nuclides changed, thereby implying that slow demethylation can occur (Renfro *et al.* 1974; Olson, Squibb & Cousins 1978). Fish-eating marine mammals often contain high levels of mercury in the liver, largely in an inorganic form (table 1). Since the fish diet probably contains a high percentage of methyl mercury, this observation suggests that demethylation and storage is occurring in the liver. Koeman *et al.* (1973) showed that high mercury levels in the livers of marine mammals were equalled on a molar basis by those of selenium. A study of the whale *Ziphius cavirostris* has shown that the reason for this relation is the storage of demethylated mercury in the liver as granules of mercuric selenide (Martoja & Viale 1977). A similar explanation may account for the low proportion of organic mercury observed in both liver and muscle tissues of the Pacific blue marlin, *Makaira nigricans* (*ampla*), by Rivers, Pearson & Schultz (1972), since in the black marlin, *Makaira indica*, approximately equimolar concentrations of mercury and selenium were observed in both tissues by Mackay, Kazacos, Williams & Leedow (1975). A hint that metabolic processes may not always be advantageous has been given by the work of Matsumura, Doherty, Furukawa & Boush (1975) who found evidence *in vitro* for the methylation of mercury by liver tissue from tuna, a group of fish in which high levels of methyl mercury have sometimes been found. However, Pentreath (1976*b*) was unable to detect any methylation in the tissues of *Pleuronectes platessa* which had absorbed labelled inorganic mercury for 90 days.

Being generally lipophilic, organic contaminants such as organochlorines (Pearson & McConnell 1975; Addison 1976) and petroleum hydrocarbons (Varanasi & Malins 1977) are stored in the lipid reserves of an organism (see table 1). Their subsequent fate is likely to be linked with processes of fat metabolism and mobilization and, among birds especially, there are examples of organochlorine pesticides, rendered inert by storage in fat deposits, being lethally mobilized during periods of starvation (Stickel 1973).

As will be seen later, storage of pollutants can lead to a situation where the concentration in an organism never reaches equilibrium with the environment and increases continuously with age.

Table 1. Chlorinated hydrocarbons and heavy metals in sea lion, *Zalophus californianus*

		parts/10^6 (wet basis except Pb)					
tissue	lipid (%)	DDE	poly-chlorinated biphenyl	total Hg	methyl Hg	total Cd	total Pb†
liver	8.0	12.9	2.4	96	1.5	1.6	1.3
kidney	—	—	—	5.4	0.7	7.2	2.2
muscle	4.6	2.6	0.4	0.84	0.84	0.08	1.1
cerebrum	17.2	3.0	0.5	0.66	0.14	0.03	3.8
fat	64.7	342	21.2	0.19	—	0.04	0.3
humerus	—	—	—	—	—	—	34

From Buhler, Claeys & Mate (1975); †, from Braham (1973).

(*b*) *Detoxification and excretion*

There are a variety of mechanisms for removing contaminants, although their relative importance as a means of loss has rarely been measured. Clearly, some losses into the surrounding water will occur over the general body surface by diffusion or in association with secretions such as algal extracellular products or mucus. In decapod crustaceans, Bryan (1968) observed that losses of zinc occurred in the faeces, in the urine and through the gills, and that the importance of these routes varied with the level of zinc input and the species. In fish, these same routes appear to be important with losses to the faeces via the liver, gall bladder and bile being roughly equivalent to losses via the hepatopancreas and faeces of decapods. The periodic moult provides another potential method for removing contaminants in crustaceans and has been implicated in the loss of cadmium (Fowler & Benayoun 1974). Although not an excretory mechanism, egg production provides another method for removing contaminants from an organism (cf. Cunningham & Tripp 1973) and lactation in seals appears to be a route for organochlorine removal (Addison 1976).

There is now some information on the metabolic processes which often precede excretion. In the scallop *Chlamys opercularis*, Bryan (1971) showed that zinc is removed by incorporation into kidney granules which can be excreted; there may be some involvement with calcium metabolism, since recent analyses showed that they contained 12.5 % calcium, 7.1 % zinc, 11 % manganese, 2.2 % other metals and 5.7 % phosphorus. The kidney is a major site for the excretion of lead in *Mytilus edulis* and losses occur in the form of granules; losses of inorganic iron from the kidney also occur as granules, although excretion via the byssal gland appears to be more important (George, Pirie & Coombs 1976; Coombs & George 1978).

Concentrations of arsenic in marine organisms often exceed the limits laid down for most foodstuffs. This arsenic exists largely as organic compounds which, at least in mammals, are more readily excreted than more toxic inorganic forms such as arsenite. Most groups of marine organisms may be able to synthesize these organic compounds (Lunde 1973*a*, *b*), although in animals it is difficult to be certain whether or not this is being done by the intestinal flora (Penrose 1975). What forms the organic arsenic takes is still uncertain, although Andreae

(1978) showed that the diatom *Thalassiosira pseudonana* could produce dimethyl arsine and arseno-betaine has been identified in the rock lobster, *Panulirus longipes* (Edmonds *et al.* 1977).

In some marine organisms there are enzyme systems capable of metabolizing foreign organic compounds including organochlorines (Addison 1976) and petroleum hydrocarbons (Malins 1977; Corner 1978). In fish, for example, the polycyclic hydrocarbon benzo[a]pyrene is hydroxylated in the liver, concentrated in the bile in a partly conjugated form and released when the gall bladder empties in response to food. There is also some loss of metabolites in the urine (Lee, Sauerheber & Dobbs 1972; Corner *et al.* 1976). With the fish *Blennius pavo*, Kurelec *et al.* (1977) showed that the enzyme benzo[a]pyrene monooxygenase was induced by exposure to water saturated with diesel oil and that the activity was retained for at least a month. The ability to metabolize hydrocarbons is not confined to fish and has been found in crustaceans (Corner, Kilvington & O'Hara 1973; Corner 1978) but not, for example, in a bivalve, a ctenophore or a coelenterate (Lee, Sauerheber & Benson 1972; Lee 1975). Although the conversion of organic compounds to more water-soluble and excretable forms by processes such as hydroxylation can be regarded as a detoxification mechanism, there is also evidence for the production of metabolites which are less readily excreted than the original compound (cf. Sanborn & Malins 1977). In fact several workers have commented on the possibility that whereas some metabolic changes may facilitate the removal of hydrocarbons, others may increase their carcinogenic potential.

5. Relations between concentrations in organisms and the environment

Although rates of absorption may be almost directly proportional to levels of availability in the environment, there is no certainty that the concentrations finally achieved in an organism will be similarly related to the environment.

(*a*) *Types of relation*

Depending on the ability to excrete contaminants, at least three types of relation are possible.

(i) The rate of excretion from the organism is proportional to the body burden. Thus, if the input to the animal increases by a factor of two, the concentration in the body must double so that excretion can equal input. The concentration in the animal is therefore proportional to availability in the environment. Experimental work by Schulz-Baldes (1974) suggests that lead behaves in this manner in *Mytilus edulis*. It was observed that the kidneys contained much of the lead and were the tissues which gained and lost it most readily, that the rate of excretion was proportional to the body burden, and that the concentration in the animal after 40 days of exposure was directly proportional to that of the medium.

(ii) The organism stores the contaminant rather than excreting it, so that, unless the growth of new tissue is sufficiently rapid, the concentration in the body increases with age. The relation between the concentration of lead in *Scrobicularia plana* and its availability from the sediment when expressed as the Pb/Fe ratio, is almost one of direct proportionality (figure 1). However, unlike in *Mytilus*, it is doubtful whether this species can ever equilibrate with its environment, since it has been found that in the field the concentration of lead in the body increases with age at all levels of exposure. When animals were transferred from a contaminated to an uncontaminated estuary, losses of lead from the digestive gland, where about 85 % of the metal was stored, were very slow and much of an apparent fall in concentration over a period of a year could be explained by growth dilution (Bryan & Hummerstone 1978).

With cadmium, the concentration in *Scrobicularia* does not increase with size or age at low levels of exposure, but increases appreciably at higher levels (figure 2*a*). Whether the apparent equilibrium reached at low exposures is the result of being able to excrete the metal or is due mainly to growth dilution is not known, but there is clearly no tendency for equilibrium to be approached at higher levels of exposure. A similar type of observation was made by Boyden (1977) in the limpet, *Patella vulgata*, where cadmium is known to be stored as the metallothionein (Nöel-Lambot, Bouquegneau, Frankenne & Disteche 1978).

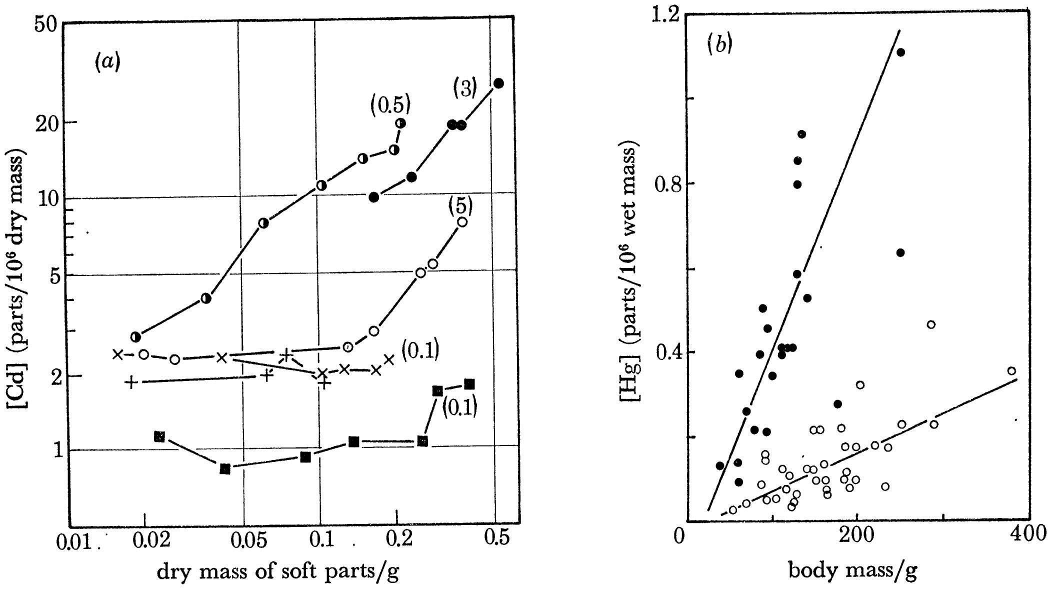

FIGURE 2. (*a*) Influence of mass of whole soft parts on cadmium concentration in the bivalve *Scrobicularia plana* from five estuaries. ●, Plym; ◑, Gannel; ○, Tamar; ×, +, East Looe; ■, West Looe. Numbers in parentheses are approximate concentrations of cadmium in sediments in parts/10^6. (*b*) Influence of body mass (wet) on concentration of mercury in muscle of cottid fish *Myoxocephalus quadricornis* from the Baltic Sea. ○, Uncontaminated area; ●, contaminated area (after Nuorteva & Häsänen 1975).

(iii) The organism excretes most of any additional input. Thus, it has been observed that in decapod crustaceans such as the crab, *Carcinus maenas*, the concentration of zinc remains comparatively independent of that in the environment, both in the laboratory and in the field (Bryan 1971, 1976*a*). Although some losses occur in the urine of crabs, losses via the faeces and gills are probably more important in high zinc concentrations. On the other hand, in the lobster, *Homarus gammarus*, losses in the urine are an important factor in regulating the concentration of zinc in the body (Bryan 1964). The urine:blood ratio has been found to vary from as low as 0.05 in starved animals from low-zinc sea water to more than 4 after injections into the blood.

(*b*) *Ability to regulate heavy metals*

There is little evidence for the regulation of metal levels in seaweeds, although Morris & Bale (1975) have suggested that it might occur for manganese in *Fucus vesiculosus*. In brown seaweeds, such as species of *Laminaria* and *Fucus*, absorption of zinc is a net uptake process since there is little excretion (Bryan 1969; Young 1975). Concentrations in the weed tend to reflect levels in the water and concentration factors of more than 10^4 (dry tissue) have commonly been observed. Because of the nature of the uptake process, older parts of the weed tend to contain the highest concentrations and seasonal variations depend on the relative rates of uptake and growth.

Among polychaete worms, regulation of zinc, iron and manganese has been observed in *Nereis diversicolor*, but concentrations of copper, silver, cadmium and lead appear to relate directly to concentrations in the sediments (Bryan 1976*a*).

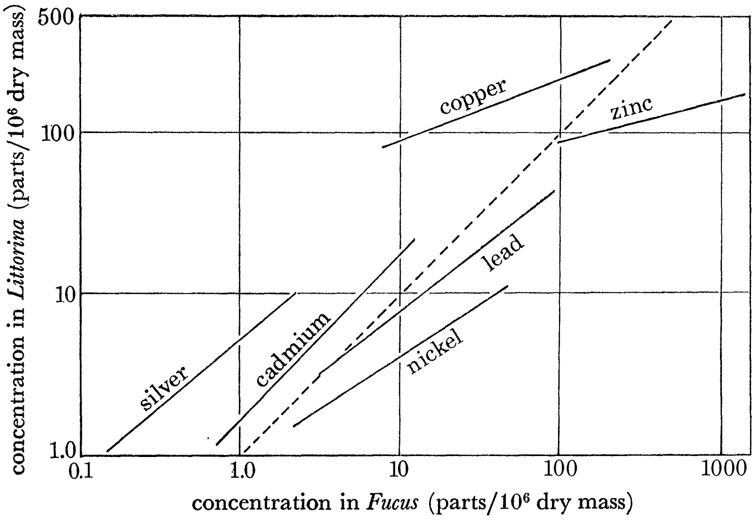

FIGURE 3. Relation between concentrations of metals in the seaweed *Fucus vesiculosus* and the herbivorous gastropod *Littorina littorea* from the same sites in various estuaries. Broken line shows direct proportionality.

Bivalve molluscs are not considered to be metal regulators, since concentrations have usually been found to reflect the availability of metals in the environment. We suspect that some regulation of zinc occurs in most bivalves and found some evidence for this in the adductor muscles of *Scrobicularia plana* (Bryan & Hummerstone 1978). In gastropod molluscs, evidence for the regulation of zinc has been given by Anderlini (1974) for *Haliotis rufescens* and by Young (1975) for *Littorina obtusata*. Figure 3 compares metal concentrations in *Littorina littorea* and *Fucus vesiculosus* from the same sites; although *Fucus* is not the primary diet of this herbivore, it should reflect the availability of metals in the various dietary components. The results suggest by their deviation from direct proportionality that, in addition to zinc, copper, which is involved in haemocyanin metabolism, is also to some extent regulated.

In decapod crustaceans, evidence for the regulation of zinc and copper has been given by Bryan (1968), but there is no evidence for the regulation of non-essential metals such as cadmium or mercury. Evidence for fish implies the ability to regulate levels of copper and zinc in muscle (cf. Saward, Stirling & Topping 1975; Pentreath 1976*a*). There is evidence for the regulation of cadmium in muscle from the trout, *Salvelinus fontinalis* (Benoit, Leonard, Christensen & Fiandt 1976) but methyl mercury is not regulated (McKim, Olson, Holcombe & Hunt 1976). In many species of fish a large proportion of the total mercury content occurs as methyl mercury. The ability to excrete this organic form is rather limited (cf. Pentreath 1976*c*), and in many species equilibrium with the environment is never achieved. Thus, concentrations of mercury in fish muscle frequently increase with size and the slope of the graph may increase with increasing levels of contamination (figure 2*b*). The demethylation and storage of mercury in the liver of marine mammals has already been described in §4*a*. As a result, mercury levels in the liver tend to increase with age, particularly in contaminated areas, whereas concentrations in muscle remain low. In the common seal, *Phoca vitulina*, concentrations of about 1 part/10^6 (wet) were found in muscle compared with more than 100 parts/10^6 in the liver of the oldest animals (Roberts, Heppleston & Roberts 1976). The same work showed that levels of cadmium in the kidneys increased with age, almost certainly due to storage as metallothionein, but levels of lead in all tissues were generally independent of age.

Generally speaking, therefore, the ability to regulate heavy metals, particularly in muscle, is greater in the more highly evolved species, and relatively abundant essential metals such as zinc and copper are usually better controlled than non-essential trace metals such as cadmium and mercury. Clearly, organisms which can regulate heavy metals are unsuitable for analysis as indicators of the availability of these metals in the environment.

(*c*) *Radionuclides*

Whether or not an element is regulated by a whole organism or a particular tissue is very relevant to contamination with radionuclides. If the concentration of stable zinc in an organism is proportional to that in the water then, assuming the chemical form is the same, the concentration factor for ^{65}Zn will remain the same irrespective of the level of stable zinc. If the stable zinc concentration is regulated, as in crustacean muscle, then the concentration factor for ^{65}Zn will be inversely proportional to the level of zinc in the water. The behaviour of ^{137}Cs and ^{90}Sr is dominated by that of potassium and calcium, which tend to be regulated by euryhaline organisms in estuaries. Concentration factors for the nuclides are independent of the stable levels of caesium and strontium, but increase as the salinity is reduced and are inversely related to the concentrations of potassium or calcium in the water (cf. Preston, Jefferies & Dutton 1967).

(*d*) *Organic contaminants*

Bivalve molluscs do not appear to be able to metabolize organic contaminants such as aromatic hydrocarbons with the same facility as some crustaceans and fish (Neff, Cox, Dixit & Anderson 1976). Therefore, the levels to which the more liposoluble compounds are accumulated depend on factors such as the lipid–water partition coefficient and the amount of lipid in the organism. For example, Ernst (1977) equilibrated *Mytilus edulis* with equal concentrations of different chlorinated pesticides and found concentration factors ranging from 100 for γ-HCH to 9120 for DDD (wet basis), which were inversely proportional to the water solubility of the compound (cf. §2*a*). In the oyster, *Crassostrea virginica*, Stegeman & Teal (1973) found that the short-term uptake of petroleum hydrocarbons was proportional to the external concentration up to 450 parts/10^9, and also that the lipid level of the animal was important. After 49 days of exposure, when equilibrium was still not reached, concentration factors were 1.72×10^3 and 3.15×10^3 (wet basis) in low- and high-lipid groups of animals, but were equal when calculated on a lipid basis at about 2×10^5. For the same species, Mason & Row (1976) showed that a concentration factor of about 2700 (wet basis) was reached for endrin after a week at external concentrations of 0.1 and 50 parts/10^9. The evidence, such as it is, suggests that in bivalves concentrations of organic contaminants are likely to be proportional to their availability in the environment.

Although crustaceans and fish are able to metabolize many organic compounds, there seems to be little information about relations between a range of external concentrations and those in the animals. In the copepod *Calanus helgolandicus*, uptake of the petroleum-derived hydrocarbon napthalene over 24 h was shown to be proportional to the external concentration over the range 0.1–1000 parts/10^9 (cf. Corner 1978). When experiments were continued to equilibrium, higher concentration factors were reached at 50 parts than at 1 part/10^9, suggesting that the higher levels of contamination are metabolized with less efficiency (Harris, Berdugo, O'Hara & Corner 1977). On the other hand, after exposure to 0.17–9.1 parts/10^9 of polychlorinated biphenyl for 7 days an approximately constant concentration factor of about 7000 (wet basis) was reached in the shrimp *Palaemonetes pugio* (Nimmo, Forester, Heitmuller & Cook 1974).

It is concluded that the relation between the concentration of a contaminant in an organism and that in the environment may deviate considerably from direct proportionality, depending on the ability to excrete or store the contaminant at different levels of input. In organisms where storage of a permanent or semi-permanent nature occurs, size and age are extremely important factors to consider when comparing levels of contamination in organisms from different areas. Some of the possible mathematical relations between body mass and concentration have been considered by Boyden (1977) and Fagerstrom (1977).

6. Effects of bioaccumulation

It is not proposed to describe the manifold effects which can be attributed to bioaccumulation, since this would include most of the literature on the toxic and sublethal effects of pollutants and their contamination of foodstuffs. Two aspects only will be considered; the development of tolerance to pollutants and the question of the biomagnification of pollutants along food chains.

(*a*) *Development of tolerance to pollutants*

It has been shown already that in some species the capacity for dealing with certain pollutants can be induced by exposure to sublethal levels, and this probably explains why it is sometimes possible to increase the tolerance of an organism to toxic levels of a pollutant by previous exposure to lower levels. For example, tolerance to mercury in the eel, *Anguilla anguilla*, can be increased by exposure to sublethal levels which induce the formation of mercury–metallothionein in the gills (Bouquegneau, Gerday & Disteche 1975). Provided they are given time to compensate, presumably all individuals of some species can adapt to higher levels of contamination and will gain advantage over other species.

After continuous exposure in the field, the selection of resistant strains has sometimes occurred, a classical example being the development of insecticide-resistant populations of the freshwater mosquito fish, *Gambusia affinis* (cf. Wells, Ludke & Yarborough 1973). In Restronguet Creek in Cornwall, where contamination with metals such as copper, zinc and arsenic from mining has occurred for more than 200 years, we have observed zinc-tolerant *Carcinus maenas*, copper-tolerant *Fucus vesiculosus* and tolerance to both metals in *Nereis diversicolor*. In this estuary, *Nereis* sometimes contain over 1000 parts/10^6 (dry basis) copper, much of it being deposited in membrane-bound vesicles in the epidermis. Results obtained by Bryan (1976*a*) suggested that although this type of detoxification mechanism is important, it is not the complete answer since animals with high levels of copper from other areas were not necessarily so tolerant to toxic solutions. In addition, tolerant animals in which the level of copper had been lowered to normal levels by growth dilution in the laboratory, retained much of their tolerance. Recent evidence from experiments with the use of ^{64}Cu indicates that at external concentrations exceeding 0.1 part/10^6, the copper-tolerant animals are less permeable to copper, a finding which agrees with earlier work on zinc tolerance in the same population (Bryan & Hummerstone 1973*a*).

The selection of tolerant strains indicates that a contaminant is exerting an effect which is greater than that to which a normal organism can adapt. Thus comparing the tolerance of different populations to various pollutants has been proposed as a method of assessing the pressures to which various ecosystems are being subjected (cf. Luoma 1977*b*). Even in normal organisms, the fact that enzymes for the metabolism of hydrocarbons, for example, may sometimes be induced and can persist after removal from the source of pollution, clearly forms a basis for assessing exposure to contamination in addition to residue analysis (cf. Kurelec *et al.* 1977).

The ability to adapt to pollutants is of considerable advantage to marine and especially estuarine organisms. However, adaptations involving special storage systems positively encourage the accumulation of high levels of contaminants which may be transmitted to unadapted predators.

(*b*) *The question of biomagnification of pollutants along food chains*

Although the absorption of pollutants from food is often the most important route for bioaccumulation and transfer along food chains certainly occurs, this does not automatically mean that predators at high trophic levels will contain the highest concentrations.

(i) *Organochlorine residues*

Certainly with pesticides such as DDT, there is evidence for increasing concentrations with trophic level in moving from, say, phytoplankton to seals. It has been pointed out, however, that much of this effect would still occur if these residues were not transferred along food chains, since pesticide levels tend to be related to the lipid pool of the organism and many of the top predators such as seals have large fat deposits (cf. Hamelink, Waybrant & Ball 1971; Portmann 1975). Portmann concluded that if DDT concentrations were calculated on a lipid rather than a wet mass basis, magnification of concentrations along the food chain phytoplankton-seals was reduced from several orders of magnitude to less than one order. Within invertebrate food chains, both Kerr & Vas (1973) and Rosenberg (1975) concluded that there was no clear evidence for accumulation with trophic level. Looking at the whole spectrum, Addison (1976) concluded that the trophic level effect and an age effect may apply in larger organisms and those not capable of direct uptake from the water, whereas the influence of partitioning from the water to body lipids is more likely to apply to small organisms where uptake from the water may be most significant.

Evidence from analyses of polychlorinated biphenyls has suggested that there may be no bioamplification from phytoplankton through the food chain to fish (cf. Elder & Fowler 1976; Cahn, Foehrenbach & Guggino 1977). In addition, Pearson & McConnell (1975) found that there was no evidence for the biomagnification of the C_1–C_2 aliphatic organochlorines such as perchloroethylene.

(ii) *Metals*

Preston, Jefferies & Pentreath (1972) have pointed out that it is the initial accumulation of metals (and organic compounds) from sea water by phytoplankton which provides much of the momentum for their transfer along food chains. Of 18 metals considered by Bryan (1976*b*), in various groups of marine organisms, mercury was one of the few where mean levels in fish exceeded those in phytoplankton or seaweed on a dry mass basis. Concentration factors observed for plutonium in the field, for example, fall markedly from values of the order of 1000 in seaweeds to 1–100 in fish (Hetherington, Jefferies & Lovett 1975; Guary & Frazier 1977).

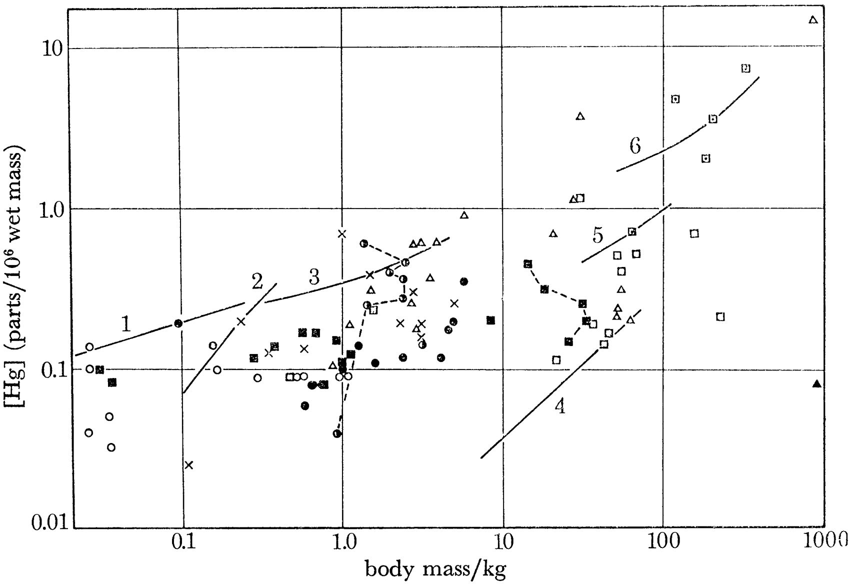

Figure 4. Relation between approximate mass of fish and muscle mercury concentration with the use of mean values for different species from literature. ○, Clupeids; ●, gadoids; ■, flatfish; ◑, sablefish; □, mackerel, tuna, swordfish; ⊡, marlin; △, sharks; ▲, basking shark; ×, others. Continuous lines, concentration–mass relation for (1) *Merlangus merlangus* (de Clerk, Vanderstappen & Vyncke 1974); (2) *Myoxocephalus quadricornis* (Nuorteva & Häsänen 1975); (3) *Potamus saltatrix* (Cross, Hardy, Jones & Barber 1973); (4) *Neothunnus albacora* (Menasveta & Siriyong 1977); (5) *Tetrapturus audax;* (6) *Makaira nigricans* (Shomura & Craig 1974). Broken lines show geographic variation in sablefish, *Anaplopoma fimbria*, and halibut, *Hippoglossus stenolepis* (Hall *et al.* 1976*a*, *b*). Other results are from Beckett & Freeman (1974), Childs & Gaffke (1973), Establier (1972), Freeman *et al.* (1974), Gilmartin & Revelante (1975), Greig *et al.* (1975, 1977), Knauer & Martin (1972), Peterson *et al.* (1973), Rivers *et al.* (1972), Robertson *et al.* (1975), Schultz *et al.* (1976) and Walker (1976).

Since mercury is one of the most important metallic contaminants, some of the evidence for and against its biomagnification along food chains has been considered. There is not much evidence for the amplification of mercury levels in moving from invertebrates to small fish (cf. Knauer & Martin 1972; Leatherland *et al.* 1973), but there is rather more evidence when larger fish are considered. Much of the mercury in fish is found in muscle and figure 4 compares concentrations in a wide range of species with the mass of the whole fish. There is a general increase in trophic level and mercury concentration in going from the plankton-feeding clupeids on the left to the large predaceous species on the right; this would support the conclusion of Ratkowsky, Dix & Wilson (1975) that mercury concentration is related to position in the food chain. However, leaving aside the problems of analytical and geographical variability, it is also clear from figure 4 that in some individual species concentrations of mercury increase markedly with size or age. Cross, Hardy, Jones & Barber (1973) have therefore proposed that the higher concentrations in large predacious fish may be as much a function of time as of trophic level, if it is assumed that the larger predacious fish are on average longer lived. Both factors are probably important since, although the high levels in some fish can be explained by old age, the very high levels in marlin and some sharks tend to support the trophic level idea, as also does the contrast in levels between the very large (although possibly quite young) plankton-feeding basking shark, *Cetorhinus maximus*, and the other sharks in figure 4. In marine mammals also both factors seem to be important. Nagakura *et al.* (1974) found only 0.02–0.03 part/10^6 (wet) of mercury in the muscle of baleen whales, which feed on krill, but more than 1 part/10^6 in muscle from the sperm whale. In seals, Sergeant & Armstrong (1973) recognized the influence of age on total mercury in the body, but also found more mercury in the grey seal, *Halichoerus grypus*, which has a diet of large fish and cephalopods, than in the harp seal, *Pagophilus groenlandicus*, which feeds on small fish and crustaceans.

TABLE 2. MEAN INORGANIC AND METHYL MERCURY CONCENTRATIONS IN ORGANISMS FROM A CONTAMINATED SALT MARSH (SUMMARIZED FROM GARDNER *ET AL.* 1978)

	inorganic mercury (parts/10^6 dry mass)	methyl mercury (parts/10^6 dry mass)
sediments (0–5 cm, 9 sites)	0.63	< 0.001
Spartina (leaf, 10 sites)	0.05	< 0.001–0.002
†annelids (3 species)	0.87	0.13
†bivalves (4 species)	1.45	0.15
(1 species, 2 sites)	1.49	0.26
gastropod (1 species, 10 sites)	3.25	0.25
crustacean (1 species, 5 sites)	0.24	0.28
†echinoderm (1 species)	0.10	0.01
†fish (11 species, muscle)	0.32	1.04
(6 species, liver)	0.96	1.57
mammals (4 species, muscle)	2.7	2.2
(terrestrial) (4 species, liver)	5.6	4.3
birds (12 species, muscle)	0.8	3.0
(12 species, liver)	5.5	8.2

† From river running through marsh.

Any tendency for total mercury levels to be amplified along food chains should be much more obvious for methyl mercury, since it generally accounts for an increasing proportion of the total in moving from some invertebrates with as little as 10 % to almost 100 % in some predaceous fish. In addition, the apparent ability of some species of marlin (figure 4) and marine mammals to demethylate methyl mercury (cf. § 4*a*) suggests that this mechanism may have developed in response to biomagnification. The biomagnification of methyl mercury is also strongly suggested by the results in table 2, although there is likely to be some age effect as well.

There is a certain amount of mystery surrounding the ultimate source of methyl mercury, although its production in sediments by microorganisms has been recognized (cf. Olson & Cooper 1976). In sea water the concentration is less than 0.005 part/10^9 (Egawa & Tajima 1977) compared with 0.011–0.033 for total mercury (Gardner 1975). Concentrations of about 200 parts/10^9 (dry mass) of which about 30 % was methyl mercury have been found in phytoplankton (Knauer & Martin 1972) and might be explained by a concentration factor for methyl mercury of perhaps 10^5 on a dry mass basis, which would not be unreasonable. It is possible that the formation of methyl mercury may occur at other points in the food chain, perhaps by intestinal microflora, but, as far as I am aware, there is no evidence for this in the field.

Although, for a number of contaminants, concentrations in individual predators sometimes exceed those of their prey, when the situation overall is considered only the more persistent organochlorine pesticides, such as DDT and its metabolites, and methyl mercury, show appreciable signs of being biologically magnified as a result of food-chain transfer.

7. LABORATORY *v.* FIELD STUDIES

Much of what is known about bioaccumulation and loss comes from laboratory experiments but there are numerous hazards in attempting to extrapolate these results to the field situation (cf. Patel 1975). For example, it is well known from experiments with radionuclides that rates of loss are dependent on the method of introduction into the organism. This is not surprising, since there is evidence that when a nuclide such as ^{65}Zn is absorbed from water it exchanges with a different pool of stable zinc from that involved in the exchange of ^{65}Zn from food and there may, in addition, be a pool of non-exchangeable zinc which would not be lost if it were labelled (cf. Young 1975, 1977). Young (1977) calculated that the rate constant governing the excretion of zinc from the dogwhelk, *Nucella lapillus*, under contaminated field conditions was only one-tenth of that obtained at relatively natural levels in the laboratory with the use of ^{65}Zn, again illustrating the problems of extrapolation. The same problems seem to exist in the field of organic pollution, and have been discussed by Boehm & Quinn (1977). They found that the clam *Mercenaria mercenaria* from a chronically contaminated area lost little of its accumulated hydrocarbons over a 120 day period in clean water, although a reasonably rapid loss would have been expected from laboratory studies with molluscs.

The contrasts observed between some field and experimental work form a strong argument for carrying out more experimental work under field conditions, especially in chronically contaminated areas (cf. Preston 1966; Stenner & Nickless 1974; Frazier 1975). Similar problems occur in the field of pollutant toxicity, since although it is clear that food is often the major source of contamination in marine animals, most experimental work has concerned pollutants in solution.

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Discussion

M. Waldichuk (*Pacific Environment Institute*, *West Vancouver*, *B.C.*, *Canada*). Is there evidence that metals other than cadmium (e.g. copper, zinc and lead) may get bound by proteins or some other biochemical components in marine organisms in the same way that cadmium is bound by metallothionein in sea lions, to make these animals more tolerant to the metals?

G. W. Bryan. Storage proteins of the metallothionein type have been observed in association with zinc, copper and mercury in organisms from various animal phyla, and in some plants. In addition, storage of metals has been observed in a wide range of intracellular granules. Usually, the abundance of the metallothionein or granules increases as the organism responds to contamination.

R. J. Pentreath (*Fisheries Radiobiological Laboratory*, *Hamilton Dock*, *Lowestoft NR*32 1*DA*, *U.K.*). With regard to the biological amplification of pollutants along food chains, one of the difficulties is that of making sensible comparisons. Thus those who argue for an increase in concentration along a food chain may compare the concentration in the liver of a vertebrate – an organ which usually has a high concentration relative to other organs – with the whole-body concentration of its food. Conversely, those who argue for a decrease in concentration along the food chain may compare the concentration in the muscle of a vertebrate – an organ which often has a relatively low concentration for many contaminants – with the whole-body concentration of its food. If both a vertebrate and its food organism, say a mollusc or crustacean, are compared on a whole-body basis the results will often reflect the greater percentage represented by muscle in the vertebrate. Would Dr Bryan care to comment?

G. W. Bryan. Since organisms are often consumed whole by predators, I would normally prefer to make analytical comparisons between whole organisms when considering biological amplification. For mercury in fish I have attempted to make comparisons by using analyses of muscle because there is comparatively little information on whole fish, especially large ones. As it happens, the concentration of mercury in fish muscle usually seems to be similar to that in the whole specimen, but this certainly does not apply to most other contaminants. My feeling is that comparisons should in the first place be made between whole organisms (preferably on a dry mass basis), although it is important to take account of concentrations in various tissues and of other factors before describing a particular predator–prey relation as an example of food chain amplification.

Ann Darracott (*Monitoring and Assessment Research Centre*, 459*A*, *Fulham Road*, *London SW*10 0*QX*, *U.K.*). I was interested in the factors affecting metal uptake which Dr Bryan listed. Pacific oysters, *Crassostrea gigas*, grown on in estuaries in the United Kingdom appear to exhibit baseline levels of zinc of *ca.* 2000 parts/10^6 dry mass whereas oysters obtained from the same U.K. hatchery grown on in South African estuaries show baseline levels of *ca.* 400 parts/10^6 dry mass. In the author's experience could a variation of this order of magnitude (5:1) be accounted for by the sort of factors that he described?

G. W. Bryan. Our work with deposit-feeding bivalves would suggest that although in two estuaries total concentrations of a specific metal in the surface sediments might be equal, chemical differences between the sediments may affect the biological availability of the metal to the extent of producing a difference of an order of magnitude between concentrations in animals from the two estuaries. The differences quoted for zinc in oysters may depend on such chemical factors, but biological factors, like rate of growth, or simply differences in zinc input to the estuaries, may also be important.