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Contamination of marine biogenic habitats and effects upon associated epifauna

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ABSTRACT

Habitat-forming organisms are frequently used as biomonitors in marine environments due to a widespread ability to accumulate toxic contaminants. Few studies, however, have considered the consequences of these accumulated contaminants on the abundant and diverse fauna associated with these habitats. In this review, we summarize research which has investigated the contamination of biogenic habitats (including seagrasses, macroalgae, ascidians, sponges and bivalve reefs) and the impact of this contamination on the habitat use, feeding behaviour and survival of associated epifauna. In many cases, ecological impacts upon epifauna are not simply predicted by levels of contamination in their habitat, but are determined by the foraging, feeding and reproductive behaviours of the inhabiting organisms. Thus, a thorough understanding of these ecological processes is essential in order to understand the effects of contaminants upon epifaunal communities. The scope of biomonitoring studies which assess the contamination of biogenic habitats should be expanded to include an assessment of potential effects upon associated epifauna. When combined with manipulative field experiments such an approach would greatly assist in our understanding of indirect effects of contaminants in these important benthic habitats.

1. Introduction

Marine pollution research has tended to focus on the direct effects of water-borne contaminants on organisms with fewer studies considering indirect pathways of contaminant exposure and effect. It is clear, however, that contaminants may have substantial impacts upon organisms mediated by their effects on co-occurring species (Fleeger et al., 2003; Johnston and Keough, 2003). Marine environments are often the final repositories of contaminants derived from industrial, urban and rural activities (Williams, 1996) and the build up of persistent contaminants in benthic habitats is often a lasting legacy of historical contaminant inputs (Morrisey et al., 2003). Biotic components of benthic systems are commonly studied as 'sentinels' of contaminant availability as many organisms can accumulate contaminants from surrounding waters, many of which persist within their tissues for long periods of time. Where these organisms also function as habitat, there is potential for accumulated contaminants to negatively affect associated epifauna.

Many marine habitats are created by the presence of benthic sessile organisms, termed biogenic habitats. These organisms provide physical structure in otherwise exposed environments and play a crucial role in many marine ecosystems (Bruno and Bertness, 2001). Biogenic habitats perform various functions including the provision of shelter, the alteration of abiotic conditions and the provision of food, all of which may alter the fitness and performance of associated faunal and floral communities (Bruno and Bertness, 2001; Sotka et al., 1999).

Many species that act as biogenic habitats are utilized as biomonitors because of their clear ecological importance. The marine literature is replete with examples of these habitats being contaminated by toxicants of anthropogenic origin. For example, macroalgae, seagrasses and sponges are all frequently used as biomonitors of trace metal availability (Rainbow and Phillips, 1993) and all are important biogenic habitats, supporting abundant and diverse epifaunal and infaunal communities (Heck et al., 2003; Hicks, 1986; Ribeiro et al., 2003). Whilst biogenic habitats may be utilized as 'sentinel species', providing opportunities to assess contaminant loads at specific locations, contamination of these habitats also poses potential indirect threats to organisms which rely upon them as habitat or as a source of food.

Here we review the evidence that contaminants are accumulated by biogenic habitats and the effects of such contamination upon associated fauna. Specifically, we have focused upon the accumulation of metals, hydrocarbons (PAHs) and chlorinated compounds in the biogenic habitats formed by macroalgae, seagrasses, ascidians, sponges and oysters. We have considered the ecological effects of this contamination upon both mobile and sessile fauna associated with these habitats.

2. Scope of review

From the literature we identified five biogenic habitats for which there is evidence of contamination by anthropogenically

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derived substances. These habitats included macroalgal beds, seagrass meadows, and the habitats formed by aggregations of sponges, ascidians and bivalves. In a structured search, we examined the available literature crossing the terms 'metal', 'PAH' and 'PCB' with 'sponge', 'ascidian', 'algae', 'seagrass', 'oyster' and 'bivalve' in the databases ScienceDirect, Biological Abstracts and ISI Web of Science. Papers were selected which dealt with marine species and which described contaminant concentrations from field collected samples, or manipulative field experiments and subsequent effects upon epifaunal organisms. The accumulation of naturally occurring substances to levels toxic to epifauna were also considered in so far as these studies may provide insights as to potential effects of contamination of biogenic habitats by substances of anthropogenic origin.

Organisms which form habitat and those that colonise these habitats are referred to by various terms in literature (e.g. biogenic habitats, habitat forming species and epifauna, epibiota, fouling organisms, respectively). For consistency, we use the term 'biogenic habitat' to indicate any plant, alga or animal which is colonised by any other organism. We use the term 'epifauna' globally for any sessile or mobile animal which inhabits a biogenic habitat. Parasites and their hosts are not considered to fall under these categories and interactions between organism contamination and susceptibility to infection are not reviewed here.

3. Contamination of marine biogenic habitats

The majority of studies that have examined the accumulation of chemical contaminants in biogenic habitats can be considered 'biomonitoring studies', whose major aim was to measure contaminant levels within a range of species in order to assess the bioavailability of toxic contaminants at sites of interest. The vast majority were concerned with the accumulation of metals, particularly by marine algae and seagrasses. Less information was available for biogenic habitats comprised of sessile invertebrates (ascidians, sponges and oysters).

3.1. Macroalgae and kelp

Macroalgal beds are one of the most productive habitats in the marine environment and frequently support high densities of mobile invertebrates including small crustaceans, gastropods, copepods and polychaetes (Edgar, 2001). Many of these are herbivorous (collectively termed "mesograzers"), living in close association with their algal hosts and consuming host tissues or algal epiphytes (Brawley, 1992). Macroalgal beds also support sessile epifauna such as bryozoans, ascidians, hydroids and sponges with some taxa rarely found growing on other substrata (Fletcher and Day, 1983; Pinter, 1969). The fauna associated with algal beds forms an important link to higher trophic level organisms such as juvenile fish (Andrew and Jones, 1990; Fletcher and Day, 1983; Powers et al., 2007).

Macroalgae accumulate trace metals from the surrounding water column and concentrate them within their tissues (Davis et al., 2003). Consequently, kelp and macroalgae are now amongst the most frequently used biomonitors around the world (Rainbow and Phillips, 1993) and they are routinely used to monitor trace metal availability in all regions from the poles (Farías et al., in press; Gasparon and Matschullat, 2006; Runcie and Riddle, 2004) to the tropics (Burdon-Jones et al., 1982; Denton and Burdon-Jones, 1986; Haynes and Johnson, 2000). In particular, species of brown (e.g. *Fucus vesiculosus* and *Ascophyllum nodosum*) and green algae (e.g. *Ulva lactuca*) have been widely used to estimate trace metal availability in Northern Hemisphere waters (Rainbow, 1995; Rainbow and Phillips, 1993). Brown macroalgae, which comprise most of the biomass of temperate algal beds, are particularly sensitive accumulators as they contain large amounts of sulphated polysaccharides within their cell walls for which metals display a high affinity (Davis et al., 2003). The concentrations of metals within algal tissue is generally considered to be a function of dissolved metals in the water column, rather than metals bound to organic matter (Phillips, 1990) although uptake from contaminated sediments may be possible (Luoma et al., 1982).

Many studies report trace metal concentrations in marine algae and it is not within the bounds of this review to summarize them extensively. It is clear however, that in some regions, metal accumulation by macroalgae is quite high and certainly indicative of anthropogenic contamination. Several studies from the United Kingdom have reported high concentrations of metals such as copper and cadmium in fucoids (Bryan and Hummerstone, 1973; Giusti, 2001; Romeril, 1977). Very high copper concentrations of up to 900 $\mu g\ g^{-1}$ have been measured in *Fucus gardneri* at the outflow of an acid mine drain (Marsden and DeWreede, 2000). More recently, we have reported high concentrations of copper (200 $\mu g\ g^{-1}$), lead (100 $\mu g\ g^{-1}$) and zinc (250 $\mu g\ g^{-1}$) in the brown alga *Padina crassa* from a major Australian estuary (Roberts et al., in press).

Macroalgal tissues may also accumulate a range of other contaminants such as PAHs and chlorinated compounds (Amico et al., 1979; Hashimoto and Morita, 1995; Micheli et al., 1995; Phaneuf et al., 1999) and macroalgal beds are believed to be a substantial reservoir of these anthropogenic contaminants in marine systems (Kirso and Irha, 1998; Moy and Walday, 1996; Parker and Wilson, 1975). Organochlorines tend to be hydrophobic and thus readily associate with lipids within biota and may persist in this form for long periods of time (Phillips, 1995).

The entry of polychlorinated biphenyls (PCBs) into benthic marine food webs frequently begins with the accumulation of PCBs by macroalgae which may then be transferred to grazing organisms (Hope et al., 1998; Hope et al., 1997; Okumura et al., 2004). Substantial amounts of organochlorines have been identified in various species of macroalgae in the Venice Lagoon (Maroli et al., 1993) and high concentrations may be found in macroalgae growing adjacent to untreated sewage outflows (Fytianos et al., 1997). Organochlorines are readily transported through the atmosphere and thus are found in regions considered to be pristine and removed from direct sources of these contaminants (Phillips, 1995). For example, PCB congeners have been measured in the brown alga *Desmarestia* sp. from the Antarctic Peninsula, far from any direct sources (Montone et al., 2001). Various macroalgal species have also been used successfully to monitor hydrocarbon contamination in marine waters around the world (Haynes and Johnson, 2000). In particular the brown algae *Fucus serratus*, *F. vesiculosus* and *Ascophyllum nodosum* have been used to monitor PAH availability in the Northern Hemisphere (Knutzen and Sortland, 1982). Extensive smothering of kelp blades by crude oil was also discovered in subtidal kelp forests following the *Exxon Valdez* oil spill (Pearson et al., 1995).

3.2. Seagrasses

Seagrass meadows are widely occurring biogenic habitats which support diverse communities including mobile invertebrates (such as crustaceans, gastropods and polychaetes), and sessile filter feeders (such as hydroids and ascidians) (Edgar, 2001). A persistent paradigm has been that seagrass tissues are less nutritious than macroalgae, and thus less heavily grazed upon (Heck and Valentine, 2006). The consumption of seagrass tissues, however, has been generally underestimated and many animals associated with seagrass beds graze directly on live plant tissues in addition to abundant algal epiphytes (Heck and Valentine, 2006). In addition to supporting communities of mobile and sessile invertebrates, seagrass beds are well known to act as nursery areas for some commercially important fish and invertebrates (Heck et al., 2003).

Seagrasses are able to accumulate heavy metals within their tissues and it has been suggested that the large surface area, widespread distribution and rapid metabolism of seagrasses makes them one of the most important sinks of water-borne contaminants in shallow and calm estuarine environments (Levine et al., 1990; Pergent and Pergent-Martini, 1999). Metals are generally concentrated within seagrass blades and can accumulate from both sediments (following accumulation through roots and translocation of metals) and directly from the water column (Lyngby and Brix, 1982; Malea, 1994; Pergent and Pergent-Martini, 1999; Schroeder and Thorhaug, 1980; Tiller et al., 1989).

Several species of seagrasses have been used to good effect in biomonitoring of metals around the world. In particular, the seagrass *Posidonia oceanica* has been a popular biomonitoring species in the Mediterranean (Lafabrie et al., in press; Malea and Haritonidis, 1989; Sanchiz et al., 2000; Schlacher-Hoenlinger and Schlacher, 1998). Seagrasses have also been used in more unusual biomonitoring studies to assess inputs of radionuclides following atmospheric nuclear testing and nuclear accidents (Calmet et al., 1988; Calmet et al., 1991). Furthermore, retrospective time-integrated analyses of trace metal availability are possible by analyzing the sheaths (or scales) left attached to the seagrass rhizomes following the detachment of leaves (Ancora et al., 2004; Roméo et al., 1995).

Seagrasses may also accumulate a variety of other contaminants such as tributyltin (TBT), PAHs and PCBs (Guilizzoni, 1991; Haynes et al., 2000; Lewis et al., 2007) although; they have been rarely used as biomonitors of these contaminants (Haynes and Johnson, 2000). TBT generally has a relatively short half-life in seawater (3–19 d) however, as with organochlorines; TBT is found to associate with lipids in marine biota and may persist for longer periods in this form (Francois et al., 1989). Seagrasses may play decontamination roles in marine systems by accumulating the highly toxic TBT and releasing the less toxic monobutyltin (Francois et al., 1989).

3.3. *Ascidians*

Ascidians are sessile invertebrates that inhabit subtidal and intertidal hard substrata worldwide. Solitary and colonial ascidians can form dense beds that are colonised by a diverse fauna of mobile and sessile invertebrates (Dalby, 1996; Voultsiadou et al., 2007). Mobile invertebrates live on the external surfaces of ascidians, with others living within the body cavity (Sepúlveda et al., 2003; Thiel, 2000). Some taxa are found only in these habitats (e.g., the ascidicolous copepods (Ho, 1994). Invertebrates found in habitats formed by ascidians may feed on epiphytes and detritus associated with the ascidians' surfaces (Sepúlveda et al., 2003) or use the feeding currents created by ascidians in their own feeding (Thiel, 2000).

The ability of ascidians to accumulate metals from the water column has been recognized since the early 1900s when high levels of vanadium were detected in tunicates (Henze, 1911). Since that time there has been much interest in the mechanisms underlying the selective accumulation of vanadium by ascidians, which may concentrate up to ten million times greater than in surrounding seawater (reviewed in Michibata, 1993 and Michibata et al., 2003). Ascidians appear to be the only organisms that exhibit this characteristic behaviour, however, not all species of ascidians selectively accumulate vanadium (Michibata, 1993). Vanadium appears to be largely incorporated within blood cells and the branchial basket, but may also be found in high concentrations in the tunic itself (Michibata, 1984; Michibata, 1993).

In addition to interest in vanadium uptake, ascidians have been investigated for use in biomonitoring studies and have been shown to accumulate a range of metals such as copper, lead and zinc (Denton et al., 2006; Philp et al., 2003) although it has been suggested that the ability to accumulate vanadium has evolved at the expense of other metals (Swineheart et al., 1974). Nevertheless, ascidians have been used in recent times to contrast availability of metals such as copper and lead in metal contaminated and natural harbours (de Caralt et al., 2002). Ascidians have also been shown to accumulate TBT following laboratory based exposures (Radford et al., 2000).

3.4. *Sponges*

Like ascidians, sponges are sessile habitat-forming invertebrates that are colonised by a wide variety of mobile invertebrates including echinoderms, polychaetes, molluscs and crustaceans (Henkel and Pawlik, 2005; Ribeiro et al., 2003; Sepúlveda et al., 2003). Some invertebrate taxa are found exclusively on sponges (e.g. sponge shrimps from Duffy, 1996) and many species display strong variation in abundance among potential sponge hosts (Poore et al., 2000; Ribeiro et al., 2003). Sponges are used primarily as habitats by herbivorous, suspension feeding and tube dwelling amphipods. However, direct consumption of sponge tissues and grazing upon sponge epiphytes has been noted in some species (Poore et al., 2000; Sepúlveda et al., 2003). Sponges may also support a range of sessile invertebrates including smaller sponges, cnidarians, ascidians and bryozoans (Ribeiro et al., 2003).

Sponges are known to accumulate metals from the water column and have been recommended for use as biomonitoring species (Hansen et al., 1995; Patel et al., 1985; Philp, 1999). The accumulation of metals is believed to occur both directly from dissolved metals as water is pumped through the sponge, and also from particulates as food particles are collected and ingested (Arnoux et al., 1992; Cebrian et al., 2003; Pérez et al., 2005). Several species have been used successfully to monitor the bioavailability of contaminants around the world (Cebrian et al., 2006; Denton et al., 2006; Johnston and Clark, 2007; Pérez et al., 2005; Rao et al., 2006).

Sponges may show species-specific affinities for metals, accumulating high concentrations of particular metals disproportionate to their availability in the surrounding environment (Patel et al., 1985). For example, Patel et al. (1985) recorded mean concentrations of chromium in the sponge *Spirastrella cuspidifera* of 1520 $\mu g\ g^{-1}$ yet in the sponge *Prostylyssa foetida* from the same sites, chromium could not be detected. Sponges may accumulate cadmium to much higher levels than non-sponge invertebrates from the same region (Philp et al., 2003) and high levels of acquired cadmium may reduce aggregation of sponge cells (Philp, 1999). Several studies have noted high concentrations of cadmium in sponges from the Antarctic coastline despite the region being removed from direct sources of anthropogenic contaminants (Bargagli et al., 1996; Negri et al., 2006). It is suggested the high accumulation of cadmium by Antarctic sponges is a result of both oceanographic features such as intense upwelling and physiological characteristics of sponges which limit their elimination of cadmium (Bargagli et al., 1996).

Sponges may also accumulate anthropogenic contaminants such as PAHs (Knutzen and Sortland, 1982; Pérez, 2000) and have been used to asses inputs of PCBs sourced from urban runoff and in deep water habitats (Arnoux et al., 1992; Pérez, 2000; Pérez et al., 2003). It has been argued that sponges may accumulate PCBs more efficiently than mussels which are more frequently used in monitoring studies (Pérez et al., 2003).

3.5. Bivalve reefs

Reefs of bivalve molluscs (oysters and mussels) often provide complex structure in otherwise exposed soft sediment habitats (Bruno and Bertness, 2001). These habitats are typically utilized by fish as well as epifaunal and infaunal invertebrates, present at abundances much higher than in or on surrounding sediments (Jacobi, 1987; Zimmerman et al., 1989). These reefs are primarily habitat for associated epifauna, but some mobile epifaunal species including carnivorous gastropods and flatworms feed directly upon the soft tissues of bivalves (Brown and Swearingen, 1998). As well as providing physical structure for many organisms, the shells of bivalves also provide hard substrata for sessile benthic invertebrates such as bryozoans, ascidians, sponges and hydroids (Wells, 1961). The epifauna associated with oyster reefs are believed to be an important source of food for many commercially important fish species (Zimmerman et al., 1989).

The ability of bivalves to accumulate metals, hydrocarbons and chlorinated compounds has long been recognized and bivalves are now used in global marine monitoring programs, including the well known 'Mussel Watch' program (Goldberg, 1975). Consequently there is an immense body of literature documenting contaminant concentrations within a variety of bivalve species which span virtually all classes of anthropogenic contaminants and all regions of the world from the tropics to the poles (Negri et al., 2006; Sericano et al., 1995; Tripp et al., 1992).

Contaminants typically accumulate more efficiently within soft tissues than shells (Brown and Depledge, 1998) however; bivalve shells have been used to monitor metal contamination (Cravo et al., 2007). Shells accumulate contaminants throughout the entire life of a bivalve and persist after the bivalve has died (Cravo et al., 2002), potentially providing a persistent pathway of contaminant exposure to epifaunal organisms. Contaminants may also be superficially deposited on bivalve reefs during smothering of oyster reef habitats following oil spills (Hulathduwa and Brown, 2006).

4. Effects upon associated epifauna

The diversity of epifaunal life histories, feeding modes and mobility is such that the contamination of biogenic habitats may affect epifauna via numerous pathways. Here we review the few studies which have considered these effects. Specifically, we review how contamination affects the colonisation of habitats by fauna (either by mobile species or settling larvae of sessile epifauna), the consumption of host organisms by herbivores or predators, and finally, the longer-term survival of associated epifauna (summarized in Table 1).

4.1. Colonisation by mobile epifauna

Abundant epifauna such as amphipods and gastropods are often highly mobile, and assemblages of these animals frequently demonstrate rapid turnover among available habitats (Edgar, 1992; Poore, 2005; Taylor, 1998). Thus, the effects of habitat-bound contaminants on the abundance of epifauna may be driven by the behavioural responses of dispersing organisms. For example, recruitment of epifaunal amphipods, copepods, ostracods and gastropods is reduced to macroalgae experimentally spiked with copper as a result of behavioural preferences for uncontaminated algal hosts (Roberts et al., 2006). Similarly, the contamination of oyster reefs by hydrocarbons reduces the recruitment of mobile crustaceans and molluscs to those habitats (Hulathduwa and Brown, 2006). Whilst such effects are now commonly predicted in contaminated soft sediment systems (Olsgard, 1999; Trannum et al., 2004), there has been remarkably little consideration of these same processes in biogenic habitats. Despite suggestions that the accumulation of metals, PCBs and PAHs within biogenic habitats pose potential threats to associated fauna, these threats are rarely considered (Kelly et al., 1990a; Moy and Walday, 1996).

Responses of dispersing fauna to habitat-bound contaminants will be influenced by spatial variation in the contamination of recipient environments (Hulathduwa and Brown, 2006). For example, macroalgal beds and seagrass meadows are typically comprised of a range of co-occurring species, each of which may vary greatly in their ability to accumulate contaminants (Brown et al., 1999; Roberts et al., in press, Sawidis et al., 2001; Schlacher-Hoenlinger and Schlacher, 1998). Consequently, dispersing organisms are faced with a landscape comprised of a mosaic of differentially contaminated habitats. An organism which is able to discern the most suitable host in a heterogeneously contaminated region may avoid much of the contaminant load in polluted systems. Such a scenario has been described in a contaminated Australian estuary (Roberts et al., in press) and in contaminated soft sediment habitats (Lefcort et al., 2004). Alternatively, if preferences for host species coincide with the tendency of that habitat to accumulate contaminants, habitat specialists may face higher exposures than habitat generalists, and higher exposures than predicted by average levels of contamination across alternate habitats.

Exposure to habitat-bound contaminants is thus likely to be spatially complex, with small-scale variation in contaminant concentrations interacting with variation among organisms in their ability to disperse among alternate habitats (Kelly et al., 1990a; Lefcort et al., 2004). Studies which contrast contaminant availability in benthic habitats across large spatial scales potentially provide little information regarding contaminant exposure for individual animals (especially those with limited small-scale dispersal). There is a need to measure contaminant distribution at the scales at which organisms perceive their environments (Kelly et al., 1990a).

4.2. Inhibition of larval settlement

Whilst mobile epifauna may disperse throughout available habitats, many epifaunal species are sessile or have relatively limited movement as adults. Their dispersal primarily occurs via free-swimming larval stages, with adult distributions being strongly determined by the habitat selection of settling larvae. Contamination of biogenic habitats onto which these larvae recruit is known to influence their settlement behaviour.

In experimental studies, Smith and Hackney (1989) applied petroleum to clam shells (*Mercenaria mercenaria*) which acted as substrate for recruiting American oysters (*Crassostrea virginicia*). The petroleum treatment reduced the abundance of oyster spat settling upon *M. mercenaria* shells (Smith and Hackney, 1989). In contrast, settling barnacles benefited from the reduced competition for space and responded by increased establishment on petroleum treated clam shells (Smith and Hackney, 1989). Similarly, Banks and Brown (2002) found substrates smothered with oil (using clay tiles as a settlement substrate) reduced the survival of settling bryozoan larvae, but barnacle and oyster larvae responded with enhanced colonisation. In this study, authors suggested hydrocarbons facilitated the development of a thick biofilm, which benefited barnacle and oyster larvae (Banks and Brown, 2002). Thus, the contamination of biogenic habitats may not only reduce the abundance of some epifauna, but may also alter the structure of epifaunal communities as more tolerant species are favored in contaminated habitats.

Some ascidians are known to produce a variety of secondary metabolites which specifically act against a range of recruiting epifauna, from sessile invertebrates, to algae and fungi (Wahl and Laf-

Table 1
Summary of studies considering the contamination of biogenic habitats and susbsequent impacts upon associated fauna

Habitat forming species	Contaminant	Research approach	Effects upon associated fauna	Reference
Macroalgae/Kelp forests				
Sargassum linearifolium	Cu	Manipulated contaminant levels	Reduced colonistaion and grazing, poor survival of herbivorous amphipod	Roberts et al., 2006
Laminaria digitata	Cu, Zn	Manipulated contaminant levels	Reduced grazing of intertidal talitrid amphipod upon contaminated diets	Weeks, 1993
Padina crassa	Cu	Correlative monitoring	Negative correlation between copper in algae and abundance of herbivorous amphipods	Roberts et al., in press
Ulva lactuca	Metals	Feeding assays with algae from contaminated and reference areas	Avoidance via retraction within shells, followed by mortality within 1 week	Weis and Weis, 1992
Enteromorpha intestinalis	Metals	Feeding assays with algae from contaminated and reference areas	Complete mortality within 4 weeks	Weis and Weis, 1992
Unspecified kelp	Petroleum	Collected exposed eggs, hatched in laboratory	Higher prevelance of malformed embryos in egg clusters oviposited onto highly contaminated kelp	Pearson et al., 1995
Seagrass beds				
Thalassia testudinum		Controlled mesocosms	Reduced survival of detritivorous amphipod feeding on contaminated tissues	Kelly et al. (1990a, b)
Cymodocea nodosa	Zn, Cd, Pb	Comparison of contaminated and reference beds	Epifaunal composition altered, probably due to reduced palatability of metal-contaminted diets	Marín-Guirao et al., 2005
Sponges				
Tedania charcoti	Cd	Tested sponge extracts	Antimicrobial activity, suggested anti-fouling properties	Capon et al., 1993
Prostylyssa foetida	Ni	Compared fouling on Ni-rich and Ni-poor sponges	Low Ni content, high levels of fouling epifauna	Patel et al., 1985
Spirastrella cuspidifera	Ni	Compared fouling on Ni-rich and Ni-poor sponges	High Ni content, fouling epifauna absent	Patel et al., 1985
Ascidians				
Ascidia nigra	V	Tested ascidian extracts	Vanadium killed recruiting hydroid and ascidian larvae	Stoecker, 1978
Various ascidians	V	Correlative monitoring	Vanadium content of ascidian could not predict level of fouling	Stoecker, 1980
Phallusia nigra	V	Tested ascidian extracts	No antimicrobial activity detected	Odate and Pawlik, 2007
Oyster reefs				
Crassostrea virginica	Metals	Feeding assays with oysters from contaminated and reference areas	Reduced feeding and poor growth of predatory snails	Weis and Weis, 1993
Crassostrea virginica	Crude oil	Manipulated contaminant levels	Reduced colonisation of mobile epifauna (crustaceans and molluscs)	Hulathduwa and Brown, 2006
Mercenaria mercenaria	Petroleum	Manipulated contaminant levels	Poor recruitement of oyster spat, enhanced settlement of barnacles	Smith and Hackney, 1989

argue, 1990). It has been suggested that the accumulation of metals (particularly vanadium) may also play defensive roles, by both deterring predatory fish and inhibiting the establishment of epifaunal species on the tunic (Odate and Pawlik, 2007; Stoecker, 1978). Stoecker (1978) found poor survival of recruiting ascidian (*Ecteinascidia turbinate*) and hydroid (*Pennaria tiarella*) larvae which settled on the tunic of *Ascidia nigra* which was suggested to be due to the presence of high concentrations of vanadium. These explanations have been recently queried, as potential effects of tunic acidity upon fouling species were not considered (Odate and Pawlik, 2007). Subsequent investigations have confirmed that surface acidity is an important defense against recruiting epifauna (Odate and Pawlik, 2007) and the role of metals in deterring fouling epifaunal settlement remains unclear (Odate and Pawlik, 2007; Stoecker, 1980).

Extracts from sponges such as *Tedania charcoti* exhibit strong antibacterial properties which are attributed to incredibly high cadmium and zinc concentrations within the sponge of up to 15,000 and 5100 $\mu g\,g^{-1}$ respectively (Capon et al., 1993). Whilst not tested directly, Capon et al. (1993) speculated that the high concentrations of metals may not only protect the sponge from bacterial growth, but also from colonisation by fouling epifauna and consumers (Capon et al., 1993). Indirect evidence of antifouling properties of metals is presented by Patel et al. (1985) who found the sponge *Spirastrella cuspidifera* contained very high nickel concentrations and was devoid of surface fouling, while the sponge *Prostylyssa foetida* from the same sites contained nickel contents below detection limits and was heavily infested by fouling epifauna.

4.3. Feeding by herbivores and predators

Considerably more research has focused upon the cycling of contaminants by organisms which consume host tissues. However, this research has largely focused upon seagrass habitats. Many studies assert that the accumulation of metals by macroalgae and seagrasses represent a potentially important pathway of contaminant exposure to grazing organisms (Camusso et al., 1998; Coelho et al., 2005; Pergent and Pergent-Martini, 1999; Prange and Dennison, 2000). Following accumulation by seagrasses, metals are available to herbivores and detrivores within seagrass beds and these grazing organisms may be responsible for much of the transference of metals to higher trophic levels (Barwick and Maher, 2003; Pergent and Pergent-Martini, 1999). Many studies have found consistent relationships between metal contents of seagrasses and grazing epifauna suggesting grazers accumulate contaminants directly from seagrass habitats (Nicolaidou and Nott, 1998; Schroeder and Thorhaug, 1980; Warnau et al., 1995). Marked alterations to the structure of epifaunal communities in metal contaminated seagrass meadows have been attributed to a reduction of seagrass epiphyte palatability due to the accumulation of metals (Marín-Guirao et al., 2005). The accumulation of contaminant from food source to consumer has also been demonstrated in bivalve reefs, where predators such as whelks may accumulate metals directly from contaminated bivalves on which they reside and feed (Blackmore and Wang, 2004).

Whilst metals within seagrass and bivalve tissues are known to be available to grazing and predatory organisms, the accumulation of contaminants by consumers does not in itself provide evidence of any impact upon those fauna (Marsden and Rainbow, 2004; Rainbow, 2002; Wilding and Maltby, 2006). In fact, very few studies have directly assessed the responses of epifauna to contaminants in their diets. Experimental manipulation of diets offers an excellent opportunity to examine how accumulation by host organisms affects their consumers. For example, both intertidal (Weeks, 1993) and subtidal (Roberts et al., 2006) amphipods are deterred from consuming algal diets that are experimentally spiked with metals. In some cases, feeding is inhibited at concentrations of metals known to occur in contaminated regions (Roberts et al., 2006).

4.4. Post-ingestive effects on epifauna

Biogenic habitats are frequently used a substrate on which epifaunal and other organisms raise juveniles. The quality of habitat on which a juvenile is raised may strongly influence its subsequent survival and fitness (Poore and Steinberg, 1999). For example, kelp beds are used by egg-laying organisms as a substrate to attach eggs. Pearson et al. (1995) found that poor selection of ovipositional habitat by adult herring (*Clupea pallasi*) may impair the development of their young. Adult herring deposit eggs onto kelp fronds where they are left to develop for up to 3 weeks before hatching (Pearson et al., 1995). Herring spawn deposited on kelp which was previously smothered by oil during the *Exxon Valdez* oil spill were less likely to develop into viable eggs at highly contaminated sites (Pearson et al., 1995). It was suggested that developmental effects could not have been derived from water-borne exposures to hydrocarbons, as concentrations in the water column were consistently below levels known to be toxic to herring eggs and larvae (Pearson et al., 1995).

For marine organisms with direct development, juvenile stages may have relatively limited mobility and be largely constrained to habitats selected for them by their mother. For example, juveniles of the herbivorous amphipod *Peramphithoe parmerong* begin feeding before they have left the maternal brood pouch, and habitat selection by brooding females strongly influences the survival and fitness of their juveniles (Poore and Steinberg, 1999). Juveniles raised on macroalgae contaminated by copper show poor survival at levels of contamination known to occur in their algal habitats in an urban estuary (Roberts et al., in press; Roberts et al., 2006).

Whilst juvenile stages often show greater sensitivity to contaminants than adult stages, the contamination of biogenic habitats may also impact upon the survival and fitness of adult epifauna. Weis and Weis (1992) found algal- and bivalve-bound metals to impact upon herbivorous and predatory epifauna at environmentally realistic concentrations. The algae *Ulva lactuca* and *Enteromorpha intestinalis* were collected from contaminated field sites and fed to herbivorous gastropods (Weis and Weis, 1992). Complete mortality occurred within 1–4 weeks of continuous dietary exposure (Weis and Weis, 1992). Similarly, the carnivorous gastropod *Thais haemastoma floridana* avoided metal contaminated oysters (*Crassostrea virginica*) and consequently suffered poor growth rates relative to those on control diets (Weis and Weis, 1993).

Kelly et al. (1990a,b) used seagrass microcosms to trace the fate and effects of experimental TBT pulses. The authors found strong accumulation within above sediment seagrass shoots and concluded that the accumulation of TBT within seagrass tissues may pose indirect threats to associated epifauna (Kelly et al., 1990a). This suggestion was supported by the finding that the macrophagous amphipod *Cymadusa compta* which feeds upon seagrass detritus showed amongst the highest accumulation of TBT of any organisms (Kelly et al., 1990a), resulting in substantial mortality when exposed to moderate to high concentrations (Kelly et al., 1990a; Kelly et al., 1990b). Mortality of organisms was linked to feeding habits, with detrivores that fed on decomposing seagrass tissues showing the greatest effects (Kelly et al., 1990a). Thus, it is clear that the contamination of biogenic habitats has the potential to impact directly upon epifaunal survival and fitness and this pathway of exposure must be more widely considered in marine ecosystems.

5. Discussion

Many chemical contaminants are known to accumulate within biogenic habitats. It is thus surprising given that the large sampling effort employed in biomonitoring studies have rarely considered the effects of that contamination upon associated epifauna. In the few instances where these ecological effects have been examined, effects upon associated epifauna have generally been identified. The contamination of biogenic habitats may influence their quality as both habitats and diets for epifauna and can directly influence survival, growth and reproduction of mobile epifauna and settling larvae. Thus it would appear that this is a potentially important pathway of exposure that has been largely overlooked in assessing the risks posed by contaminants in marine environments. Given the widespread use of biogenic habitats as biomonitors, an expansion of monitoring programs to incorporate an assessment of the effects of accumulated contaminants upon associated fauna would be useful. Very little increase in sampling effort would be required to expand the scope of these studies as habitat samples are already collected for chemical analyses. However, considerable taxonomic expertise is required to identify epifaunal species.

Given the range of factors that can influence the abundance and distribution of marine epifauna, demonstrating the effects of habitat contamination upon associated fauna is potentially difficult without the use of manipulative experiments. Many of the reviewed articles have taken manipulative approaches such as experimental spiking of habitats (Roberts et al., 2006; Smith and Hackney, 1989) and controlled mesocosms (Kelly et al., 1990a; Levine et al., 1990) to directly assess the effects of habitat contamination. Manipulative field experiments remain an essential but underutilized approach to the assessment of ecological effects of contaminants in marine systems (Underwood, 1995).

There are many instances in which the ecological consequences of biogenic habitat contamination have yet to be considered. The accumulation of naturally occurring substances as potential antifouling defenses provides insights into the possible effects of anthropogenic contaminants accumulated by biogenic habitats. Sponges and ascidians may benefit from the targeted accumulation of naturally occurring metals such as cadmium, zinc, vanadium and nickel in so far as these metals inhibit microbial growth and potentially settlement by fouling organisms or predation. In the same way that naturally available metals can be accumulated for these purposes, there is the potential for enhanced metal uptake due to anthropogenic activities to impact upon fouling species. In the terrestrial environment, plants which accumulate metals such as nickel and zinc from soils to high concentrations within leaves are known as ‘hyperaccumulators’ (Cobbett, 2003). Many studies have shown that these plants may benefit as accumulated metals deter grazing insects and in some cases, lead to direct mortality of herbivores (Hanson et al., 2003; Pollard and Baker, 1997). Plants growing in anthropogenically contaminated soils may similarly benefit from the passive accumulation of metals which deter herbivores. Further research is required to examine the complex interactive effects of contaminant accumulation upon biogenic habitats and associated fauna in contaminated marine systems.

Most of studies conducted to date have been concerned with the effects of accumulated metals upon associated epifauna and little information exists regarding the potential effects of other contaminants, such as organochlorines (see summary in Table 1). Chlorinated compounds are known to accumulate within biogenic habitats and show a tendency to be highly resistant to degradation in this form, thus persisting for long periods of time in recipient benthic environments (Okumura et al., 2004; Phillips, 1995). There is the potential for these contaminants to impact upon epifaunal communities over long time scales and hence much more research is required in this area.

6. Summary

In a recent discussion paper Rainbow (2002) challenged biologists to consider not only the 'why' of trace metal accumulation in aquatic invertebrates, but also the 'so what'. He challenged readers to consider the implications of trace metal accumulation in these organisms so commonly used as biomonitors (Rainbow, 2002). As a commonly used technique of environmental assessment, the use of biogenic habitats as biomonitors in marine systems also needs to be challenged by the 'so what' question. Biomonitoring studies need to move beyond simply documenting the concentrations of contaminants in benthic habitats (Goldberg and Bertine, 2000). The ecological effects of the contamination of biogenic habitats upon epifaunal communities which they support could be explicitly considered in biomonitoring studies in order to provide a more comprehensive picture of the ecological effects of anthropogenic contaminants.

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