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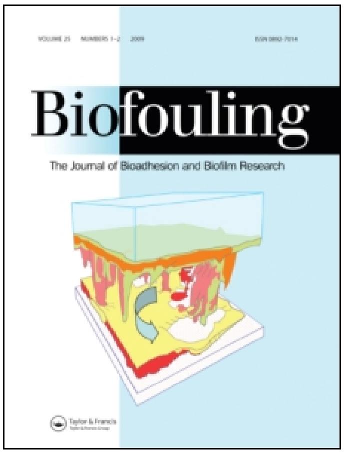

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MINI REVIEW

The influence of antifouling practices on marine invasions

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Vessel hull-fouling is increasingly recognised as one of the major vectors for the transfer of marine non-indigenous species. For hundreds of years, copper (Cu) has been used as a primary biocide to prevent the establishment of fouling assemblages on ships' hulls. Some non-indigenous fouling taxa continue to be transferred *via* hull-fouling despite the presence of Cu antifouling biocides. In addition, several of these species appear to enjoy a competitive advantage over similar native taxa within metal-polluted environments. This metal tolerance may further assist their establishment and spread in new habitats. This review synthesises existing research on the links between Cu and the invasion of fouling species, and shows that, with respect to the vector of hull-fouling, tolerance to Cu has the potential to play a role in the transfer of non-indigenous fouling organisms. Also highlighted are the future directions for research into this important nexus between industry, ecology and environmental management.

Keywords: copper (Cu); antifouling; non-indigenous species (NIS); hull-fouling; pollution; tolerance; invasion

Introduction

The introduction and establishment of non-indigenous species (NIS) can have profound effects on the economic potential, social values and environmental stability of affected regions (Vitousek et al. 1997; Mack et al. 2000; Pimentel et al. 2005; Colautti et al. 2006). Within the marine environment, ports and harbours are the primary 'hot-spots' for the increased occurrence and abundance of non-indigenous marine species (Cohen and Carlton 1998; Minchin and Gollasch 2003; Drake and Lodge 2004), with international shipping being one of the most important vectors responsible for their spread between regions (Otani et al. 2007; Hewitt et al. 2009; Yamaguchi et al. 2009). Furthermore, ports can act as stepping-stones for the intra-regional spread of unwanted species, *via* human-mediated pathways (eg domestic vessel traffic) or natural dispersal (Floerl et al. 2009b; Forrest et al. 2009).

Proliferation of NIS in ports and harbours occurs despite the fact these environments receive high levels of anthropogenic disturbance, such as chemical pollution (Hall Jr et al. 1998; Kennish 2002). Certain common marine pollutants such as copper (Cu) and zinc (Zn) are intrinsically associated with some modes of NIS transfer (eg vessel hull fouling) through their use as primary biocides in antifouling (AF) coatings. While the effects of toxicants in bays and estuaries have been of concern for a long time and have been discussed extensively (Hartman 1960; Phillips 1977; Preston and Shackelford 2002), concerted attention to the establishment and spread of invasive species in marine systems has occurred more recently (Carlton and Geller 1993; Ruiz et al. 2000). There is comparatively little understanding of the interactive and/or cumulative effects of pollution and invasion, especially given their regular co-occurrence at both the transport- and establishment-stages of the marine invasion process. As an ever increasing global population places more stress on coastal environments (eg poor water quality, habitat loss, decreased biodiversity, nutrient enrichment; Kennish 2002; Preston and Shackelford 2002; Goldman and Wasson 2008), and the reliance on shipping for the transport of goods and services worldwide increases, it becomes important to understand the links between toxicants and invasions in order to maintain the integrity of near-shore marine environments.

The application of AF coatings is a necessary and important maintenance requirement for all vessels. From an economic perspective, it is now recognised that even minor fouling, such as slime-film layers, can have significant impacts on the operating efficiency of affected vessels, resulting in increased fuel requirements to maintain desired operating speeds (Schultz 2007). From an environmental standpoint, AF biocides are vital to minimising the global spread of unwanted organisms *via* international vessel traffic

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(Evans et al. 2000). In spite of their importance and necessity, all biocidal AF paints are heavily scrutinised by regulatory authorities, due to environmental concerns arising from heavy metal pollution (Valkirs et al. 2003; Srinivasan and Swain 2007), bioaccumulation in marine organisms (Claisse and Alzieu 1993) and adverse effects on human health (Evans et al. 2000). These concerns have led to increased research into the development of non-biocidal coatings, such as silicone-based, fouling-release technology (eg Brady 2001; Candries et al. 2001; Kavanagh et al. 2005; Kim et al. 2007). However, as fouling-release coatings do not prevent the accumulation of fouling, but rather 'release' it as the vessel moves through the water, the potential for transmission of NIS appears to be high. As a result, AF formulations containing biocides such as Cu continue to be the most popular (and arguably most effective) broad-spectrum AF treatments in the market today (Srinivasan and Swain 2007).

AF biocides, such as Cu, exert strong selective pressures on both the target pests and non-target organisms, favouring individuals with increased resistance (Russell and Morris 1970, 1972; Reed and Moffat 1983; Floerl et al. 2004; Han et al. 2008; Piola and Johnston 2008a, Forthcoming 2009). As such, the use of Cu-based antifoulants on vessel hulls has the potential to select for the settlement and transport of non-indigenous organisms with a high tolerance to metal pollution. If these tolerant individuals are then transported to polluted recipient locations, a growing body of evidence suggests they may benefit from some degree of competitive advantage over native species (eg Dafforn et al. 2008; Han et al. 2008; Piola and Johnston 2008a; Dafforn et al. Forthcoming 2009; Piola and Johnston, Forthcoming 2009). Therefore, the question must be asked: could the presence of metal pollution at the transport- and establishment-stage of the invasion process facilitate the introduction and spread of NIS?

History of Cu as an AF agent

The toxic nature of Cu has been studied in detail. Early life history stages of marine invertebrates and algae are negatively affected by Cu concentrations in the 5–100 μg l^{-1} range, which is at least an order of magnitude lower than concentrations that may be toxic to humans (Hall Jr et al. 1998; Spencer 2003). Hence, Cu, in numerous forms, has a very long history of use as an antifoulant, and is still one of the most effective and practical means of preventing fouling on submerged aquatic structures. The first successful AF surface to receive widespread recognition was Cu sheathing, with the ancient Phoenicians and Carthaginians being credited with the first documented use of such sheathing on vessel hulls *c.* 700 BC (Almeida et al. 2007), though it did not become common practice until the 18th century (WHOI 1952). In the mid 1800s, the first widespread general-use AF coating (named 'McIness') was introduced in the Liverpool dockyards (in the UK), and used Cu sulphate as the toxicant (Yebra et al. 2004). A century later, the broad spectrum AF effectiveness of tributyltin (TBT) compounds became recognised (Huggett et al. 1992; Evans et al. 2000). TBT could be incorporated into a highly effective Self-Polishing Copolymer (SPC) paint matrix and as a result, TBT SPC coatings became the new standard for vessel AF for years to come (Yebra et al. 2004; Almeida et al. 2007). Towards the end of the 1970s however, the environmental impacts of TBT antifoulants raised concern, with links established between TBT and deformities in shellfish (Scammell et al. 1991), imposex in gastropods (Foale 1993; Wilson et al. 1993; Andersen 2004) and bioaccumulation in tissues of marine vertebrates (Harino et al. 2000). By the 1980s, many countries had banned the use of TBT paints on vessels <25 m in length (Evans et al. 2000), and by 2008 the International Maritime Organisation (IMO) had expanded this ban to include all non-government and non-navy vessels (IMO 2001; Lewis et al. 2004). As a result, Cu-based AF paints regained popularity, and are likely to remain the dominant AF method until more advanced technological solutions become widely available (eg Depree 2009). There exist several comprehensive reviews which discuss the range of AF technologies (past and present) used on maritime vessels (Yebra et al. 2004; Almeida et al. 2007).

Whilst TBT is not 100 percent effective at preventing all fouling growth on vessel hulls (Rainer 1995; Gollasch 2002; Minchin and Gollasch 2003), Cu is generally considered to be a less effective AF biocide against a broad range of taxa when compared to TBT. This can be attributed to both its reduced toxicity compared to organotin (Railkin 2004), and the fact that most Cu-based paints have reduced life-spans, and are less efficient and cost-effective compared to TBT-based self-polishing paints (Yebra et al. 2004; Almeida et al. 2007). From the perspective of marine invasions, this will invariably impact upon the numbers and types of organisms able to be transferred globally by fouling-related vectors such as vessel hull-fouling. Several groups of sessile marine organisms have shown significant tolerance to Cu, including calcareous tubeworms (Johnston and Keough 2003; Dafforn et al. 2008) barnacles (Weiss 1947), hydroids (Stebbing 2002), bryozoans (Floerl et al. 2004; Piola and Johnston 2006a), bivalves (Lee and Chown 2007) and algae (Russell and Morris 1970, 1972; Reed and Moffat 1983; Correa et al. 1996; Jelic-Mrcelic et al.

2006; Han et al. 2008). All these groups of taxa have similarly been associated with regional introductions and spread *via* vessel hull-fouling. A growing body of evidence suggests that these two factors may be related (eg Dafforn et al. 2008; Piola and Johnston 2008a, Forthcoming 2009; Dafforn et al. Forthcoming 2009).

Cu and marine invasions

In order to examine the links that exist between Cu and the transfer of NIS, it is necessary to first evaluate the invasion process as a whole. For an organism to become a successful NIS (or invader) it must survive and persist through a series of discrete events that transport it away from its natural range to a new recipient location (Miller and Ruiz 2009). A successful invasion can be conceptualised as a result of four stages: (1) the entrainment of an organism by a human vector; (2) the transport of that organism outside of its natural range; (3) establishment of viable population(s) of the organism in the new environment; and (4) population spread away from the initial point of incursion (Carlton 1985; Richardson et al. 2000; Floerl and Inglis 2005). These processes can exert very strong selective pressures on individuals involved, with large numbers of potential NIS present in source locations generally reduced to only a small few able to survive the stressors involved and become invasive. Williamson and Fitter (1996) attempted to characterise the probability of successful species introductions *via* this series of events, and proposed the 'tens rule', whereby: (1) 1 in 10 of all the species transported to a new region (*via* natural or human-mediated dispersal) will survive in the wild; (2) 1 in 10 of the species surviving will establish and form self-reproducing populations; and (3) 1 in 10 of the species establishing will proliferate and spread to become pest species. When considering that hull fouling is one of the most common vectors for the transport of marine NIS, on-going research indicates that Cu has the potential to play a role in the transfer of NIS at every stage of the invasion pathway (Figure 1).

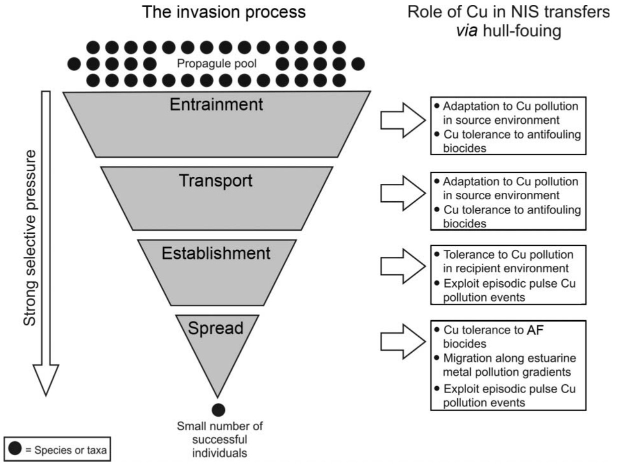

Figure 1. Diagram depicting the four stages involved in the invasion process and the influence that Cu may play in facilitating a successful species transfer *via* the common marine transport vector of hull-fouling.

Entrainment and transport

The first two stages of the invasion pathway involve the entrainment and transport of a species to a new region by means of a human-mediated vector. Along with ballast water discharge, hull-fouling (ie biofouling) is now one of the most important dispersal mechanisms for marine NIS (eg Hewitt 2002; Gollasch 2002; Godwin 2003; Hewitt et al. 2004), and one where NIS and Cu interact very closely. In regions such as Australia, North America and Hawaii, it is estimated that between 55 and 85% of recorded marine NIS are introduced *via* fouling on vessel hulls or other floating structures (Wasson et al. 2001; Eldredge and Carlton 2002; Hewitt 2002; Hewitt et al. 2004). This is particularly true for sessile invertebrate taxa such as bryozoans, ascidians, hydroids, serpulid polychaetes and barnacles (Hewitt et al. 2004). Species transfers *via* hull-fouling continue to occur despite the presence of AF biocides, such as Cu-based paints (Floerl et al. 2004; Piola and Johnston 2008b). While a proportion of these transferred species occur on hull areas that escape adequate AF coverage (eg dry-dock support strips, Coutts and Taylor 2004) or are prone to mechanical damage and/or high water turbulence (Otani et al. 2007), the indications are that at least some of these hull-fouling species have a tolerance to Cu biocides.

As early as the 1950s, scientists began noting marked Cu tolerance in some hull fouling organisms. When describing the proliferation of the previously unrecorded bryozoan species *Watersipora cucullata* (now known to be *Watersipora subtorquata*) in Australian waters, Allen (1953) noted '... it is exceedingly Cu-tolerant and can exist attached to fast ships for months ...'. He went on to state that based on the patterns of appearance and distribution of *W. cucullata* around Australia, '... the evidence suggests ship transport'. More recently, Floerl et al. (2004) found larvae of *W. subtorquata* and the arborescent non-indigenous bryozoan *Bugula neritina* were able to settle directly to surfaces coated with AF paints (including Cu-based coatings). Recruitment and growth on these surfaces was observed as little as 8 weeks post-submergence, with a percentage cover of

W. subtorquata similar to or greater than cover observed on non-toxic control panels. A similar study by Dafforn et al. (2008) compared the recruitment for native and NIS species to blank settlement panels with or without the nearby influence of Cu and TBT AF paints in boating harbours frequented by commercial and/or recreational vessels. After 10 months' submergence, the recruitment of native taxa was typically reduced by Cu, however, the total recruitment of NIS to Cu-influenced panels was 14–19% higher across all sites compared to control panels. Several NIS in particular showed considerable tolerance to Cu, with the early recruitment of the cosmopolitan encrusting bryozoan *W. subtorquata* and the calcareous tubeworm *Hydroides elegans* significantly enhanced by the presence of Cu. Given the primary dispersal mechanism for both these species has been closely linked to biofouling (Floerl et al. 2004; Pettengill et al. 2007), tolerance of Cu is a profound advantage. The recruitment of NIS to Cu-treated surfaces was generally greater in recreational boating harbours with a history of use by vessels treated with Cu-based antifoulants. The recreational boating harbours also had higher levels of Cu contamination in the water column than commercial sites (Dafforn et al. Forthcoming 2009). These studies support previous laboratory and field findings that detail substantial Cu tolerance in larvae and/or adults of NIS including *W. subtorquata* (Piola and Johnston 2006b, Forthcoming 2009) and *H. elegans* (Johnston and Keough 2003; Xie et al. 2005; Piola and Johnston 2008a). Studies examining marine algae have yielded similar findings to those seen for fouling invertebrate species. Ship-fouling populations of the marine algae *Ectocarpus siliculosus* and *Enteromorpha* (=*Ulva*) *compressa* have been found to exhibit greater Cu tolerance compared with populations sourced from an uncontaminated rocky shore location (Russell and Morris 1970,1972; Reed and Moffat 1983). Similarly, a study of two species of *Ulva* from Korea found the alien *Ulva armoricana* to exhibit less effect of Cu toxicity than the native *Ulva pertusa* (Han et al. 2008).

In another study, it was demonstrated that small-scale (cm^2) areas of unprotected settlement surface may be colonised by fouling taxa, even if these areas are surrounded by otherwise well maintained, newly applied Cu AF coatings (Piola and Johnston 2008b). Despite the likely exposure of unprotected ('scraped') areas to Cu from the adjacent painted surfaces, organisms were still found to recruit to scrapes as narrow as 0.5 cm wide. When scrape sizes were increased to widths of 1–2 cm, a much wider range of taxa recruited, including several well-known NIS, including the bryozoans *Aetea anguina, Bowerbankia gracilis* and *Bugula stolonifera*, the serpulid *H. elegans* and the colonial ascidian *Diplosoma listerianum*. This study has obvious implications when considering hull maintenance regimes and vessel care. On a recreational or commercial vessel hull, areas such as hull sides, keels, and propeller and rudder wells may be highly susceptible to this type of minor damage during everyday operations (Lewis et al. 2003; Coutts and Taylor 2004). Such damage can be easily overlooked, and may result in the translocation of Cu-tolerant NIS by well-maintained vessels with an otherwise effective AF treatment.

The transfer of specific Cu-tolerant species is not the only scenario for Cu/NIS interaction. Research has found that some Cu-tolerant species, such as *W. subtorquata*, that are able to recruit and grow directly on Cu-treated surfaces, in turn have the potential to facilitate the transfer of less tolerant NIS. Wisely (1958) observed '... colonisation of an antifouling paint surface by *Watersipora*, which in turn is being utilised as a settling surface by the less resistant tubeworm *Hydroides norvegica*'. Similarly, Floerl et al. (2004) found that *W. subtorquata* acted as a 'foundation species' for fouling assemblages on vessel hulls, recruiting to undesirable (ie Cu-treated) surfaces and in turn acting as refugia for other less tolerant NIS, such as algae, serpulids and bryozoans (Figure 2).

Establishment

Having survived the entrainment and transport stages of the invasion process, Cu tolerance can further aid in the establishment of NIS within recipient environments. Harbours and estuaries are the primary source and recipient locations of NIS in marine systems (Ruiz et al. 1997), and also rank amongst the most contaminated environments worldwide (Hall Jr et al. 1998), with metal pollution often a major contributor (Kennish 2002). Cu in particular, is one of the most commonly occurring metal pollutants, originating

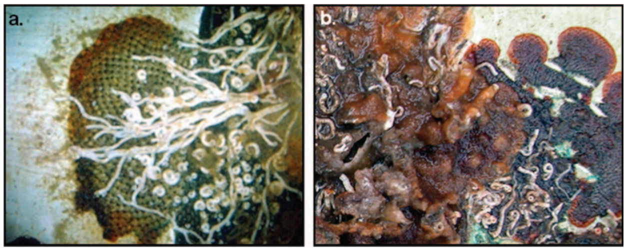

Figure 2. Images demonstrating how a Cu-tolerant foundation species can facilitate the establishment of less Cu-tolerant taxa. The cosmopolitan non-indigenous bryozoan *W. subtorquata* is shown growing directly onto a surface coated with Cu-based AF paint, in turn allowing the establishment of other taxa, including (a) the serpulid worm *S. australis* and spirorbid polychaetes, and (b) the encrusting bryozoan *S. errata* and serpulid worms. Photos: K. Dafforn.

from a wide range of sources including AF coatings (Warnken et al. 2004), industrial waste (Hall Jr et al. 1998), urban runoff (Pitt 2002), sewage discharge (Scanes 1996) and wood preservatives (Weis and Weis 2002). Since the banning of TBT there has been an increase in Cu levels around marinas and moorings associated with vessels using Cu AF paints (Claisse and Alzieu 1993). *In situ* studies have found that average passive flux rates of dissolved Cu for AF coatings on vessels may range between ~ 3 and 8 μg cm^{-2} day^{-1} (Valkirs et al. 2003; Schiff et al. 2004; Finnie 2006), with factors such as coating age, hull cleaning activities and the presence of microbial biofilms all acting to decrease or enhance the release rates of AF biocides (Schiff et al. 2004; Yebra et al. 2006).

Cu has been shown to have detrimental effects on the health and success of many species and concentrations that are protective of 90% of marine species within estuarine communities (ie affect the long-term viability of 10% of species) have been estimated at ~ 6 μg l^{-1} (Hall Jr et al. 1998). Cu concentrations directly next to a Cu antifouled surface can reach up to ~ 100 μg l^{-1}, whilst dissolved Cu concentrations in the range 60–85 μg l^{-1} have been recorded in polluted estuarine and open sea locations (Hall Jr et al. 1998; Stauber et al. 2000). The overall bioavailability and toxicity of Cu in marine aquatic environments is dependent on the presence and amounts of organic matter (eg detritus) and inorganic compounds such as iron and manganese oxides, which complex or adsorb metals (Stauber et al. 2000). Cu contamination can lead to fundamental changes in the structural composition of fouling communities (Weis and Weis 1996; Johnston et al. 2002). It is not difficult to imagine therefore, that the very same Cu-tolerance traits that allow some NIS to be transported to a new environment, for example by *via* hull-fouling, also serve to aid in their establishment within Cu-polluted habitats.

The marine alga *E.* (=*Ulva*) *compressa* exhibits differential Cu tolerance with populations from a Cu-enriched environment able to tolerate higher concentrations than populations from waters with reduced Cu contamination (Correa et al. 1996). When coupled with the higher Cu tolerance of ship fouling populations (Reed and Moffat 1983), this alga becomes a likely candidate for entrainment, transport and subsequent establishment *via* a Cu pathway.

A manipulative field study by Piola and Johnston (2008a) examined the effect of increasing Cu pollution loads on the diversity and distribution of fouling assemblages within two Australian harbours, concluding that NIS were competitively advantaged over native species in the presence of Cu. The spatial dominance of NIS increased significantly with increasing Cu pollution loads at three of the four sites examined. This increase was coupled with a corresponding decrease in the diversity of native taxa, often resulting in fundamental changes to community structure. The only site where this trend was not observed was the site that had the greatest levels of background pollution (including substantial Cu input) and the highest background levels of NIS cover.

Laboratory-based studies provided further evidence for differential Cu tolerance in some common non-indigenous hull-fouling species compared to similar native taxa. Piola and Johnston (Forthcoming 2009) examined the effects of exposure to a range of Cu concentrations on the health and growth of two cosmopolitan non-indigenous bryozoan species (*W. subtorquata* and *Schizoporella errata*) and two native bryozoan species (*Celleporaria nodulosa* and *Fenestrulina mutabilis*). They found that NIS were able to maintain biomass, feed and grow better under Cu-conditions relative to the co-occurring native species, which deteriorated rapidly. Further, the NIS displayed much faster post-Cu recovery compared to the natives, suggesting that this trend for greater Cu tolerance may hold true under both chronic and episodic pollution regimes.

Range expansion and spread

The role of Cu in the spread of NIS within new environments may in part be a repeat, or addition, of the steps that brought the individual there in the first place. For example, resistance to Cu AF paints and hull-fouling can just as easily facilitate intra-regional spread of an organism as it can inter-regional translocation between bioregions (eg Forrest et al. 2009). A study by Wasson et al. (2001) examining the macrofauna of Elkhorn Slough (California) revealed 56 known exotic species in the estuary, a large number considering the relatively natural setting of the estuary, the lack of international shipping, and its distance from other major shipping hubs (ie San Francisco Bay, 150 km to the north). They concluded that 70% of the exotics found were associated with hull fouling as a mode of introduction, and intra-regional spread *via* recreational yachts was an important factor in their arrival and spread. Similarly, following preliminary investigations into the abundance and distribution of NIS in the World Heritage Property of Shark Bay, Australia, Wyatt et al. (2005) suggested hull fouling of recreational craft to be the most important vector for NIS transfer in the region.

The impact of Cu pollution on native communities may be sufficient to reduce the resistance of these communities to biotic invasion regardless of the relative tolerance of NIS and native species (Clark and Johnston 2005). Biotic communities affected by pollutants can experience significant changes including the loss of rare/sensitive species, decreased species abundance, and changes to the size and age structures of populations (Schwinghamer 1988; Howells et al. 1990; Kennish 1997; Moran and Grant 1989). Such impacts invariably release valuable resources (eg space) that can be exploited by opportunistic species within the community (Johnston and Keough 2003). For example, Turner et al. (1997) used experimental epifaunal assemblages to investigate the effects of potential gradients of environmental stress arising from marina operations and boating activity. High levels of Cu and Zn were initially recorded in suspended sediments within marina sites, with levels decreasing along a gradient away from the marinas. Settlement panel arrays comprising established fouling communities were deployed along each pollution gradient and after 3–6 months, significant changes in epifaunal composition along the gradients were observed, with the most conspicuous change in assemblage structure being the loss of solitary ascidians at sites within marinas compared to sites furthest away. The non-indigenous bryozoan *W. subtorquata* was one of the most abundant species to occupy this newly created free space.

Cu tolerant NIS in harbours and estuaries may also take advantage of one-off episodic or ‘pulse’ pollution events to spread within a new environment. Cu pulses can enter coastal waters through a number of ways, including urban run-off, industrial, mining and metabolic wastes, AF paints and the corrosion of pipes (Mance 1987; Abel 1989; Paulson et al. 1989; Depledge et al. 1994; Pitt 1995; Fabris et al. 1999). As previously described in this review, numerous NIS across a range of taxonomic groups display superior Cu tolerance compared to similarly related native species (Piola and Johnston 2006b, 2008a, Forthcoming 2009; Dafforn et al. 2008). Further native taxa are often detrimentally affected by exposure to relatively low levels of Cu, often with prolonged recovery times post-exposure (Piola and Johnston 2006b, Forthcoming 2009). As such, short-term reductions in water quality from pulse Cu-pollution events may allow an opportunistic Cu-tolerant NIS to exploit temporary pollution-mediated impacts on native populations. This may provide a ‘foothold’ for expansion provided dependent factors such propagule availability and timing are also favourable (Clark and Johnston 2005). It should be noted, however, that the maintenance of Cu tolerance may be metabolically expensive and may not be essential to the persistence and spread of NIS that have established a foothold population (Piola and Johnston 2006a).

Management of AF and related practices with respect to NIS

Effective vessel AF practices remain the key to preventing NIS transfers. The age of an AF coating is often considered the most important factor governing the establishment of fouling assemblages on recreational vessels (Floerl and Inglis 2005; Floerl et al. 2005). TBT-based AF coatings had the potential to remain effective for up to 5 years between applications (Evans et al. 2000), and modern Cu-based SPC paints commonly used on deep-sea ocean-going vessels can achieve similar life-spans (Almeida et al. 2007). In contrast, however, conventional Cu-based coatings (ie soluble and insoluble matrix formulations) commonly used on many smaller coastal-going vessels (eg fishing vessels, tugs, and recreational craft) generally need to be applied every 9–18 months to ensure they are performing optimally (Lewis 2002; Almeida et al. 2007). In addition to regular maintenance, selecting the right paint for the type of vessel in question is crucial. Different types of Cu AF paints (such as self-polishing, soft ablative and hard non-ablative) all have advantages and disadvantages, with their suitability to provide adequate protection from fouling determined by such factors as the type of vessel, frequency of vessel use, season, geographic location, and the typical operating speed/profile of the vessel, as these affect polishing rate/ablation rate. The integrity of AF coatings on vessel hulls is highlighted as an important management priority for controlling species transfers (Piola and Johnston 2008b). Slight disruptions or minor damage in otherwise very effective AF coatings are sufficient to facilitate the recruitment and growth of fouling taxa. Such disruptions in AF coatings could easily occur through poor application of AF paints (eg uneven coverage, careless preparation, failure to follow manufacturer instructions), or as a result of everyday use (eg damage incurred from minor collisions, anchors, and groundings). Given that these areas of unprotected hull may occur on parts of the vessels that are not easily inspected (eg hulls, propeller wells, and keels) periodic haul-outs and dry docking may be necessary to ensure vessels that are new to a region are free of NIS, even if their AF maintenance histories records appear up to date.

One of the advancements in Cu AF technology since the banning of TBT coatings has been the use of organic booster biocides to supplement Cu oxide. However, these have their own suite of issues including the development of tolerant organisms within the target fouling community. Booster biocides such as Irgarol 1051, diuron, Sea-Nine^{TM} and Cu and Zn pyrithiones, were generally introduced to target algal slimes by inhibiting photosynthesis (Voulvoulis et al. 1999), but can also have a direct biocidal effect on invertebrates, as well as an indirect effect on invertebrate colonisation through biofilm modification and reduction (Keough and Raimondi 1996; Steinberg et al. 2002). Recent studies suggest that the use and accumulation of these biocides may also encourage the development of tolerance in marine communities and therefore reduce their effectiveness at preventing fouling and the transport of NIS. Petersen et al. (2004) found that high concentrations of Zn pyrithione resulted in increased growth of tolerant microbial species, and exposure to diuron (Molander and Blanck 1992) or Irgarol 1051 (Blanck et al. 2009) can induce tolerance in marine diatoms.

Alternatives to Cu-containing AF coatings are another option for preventing the transfer of Cu-tolerant NIS. For example, fouling-release coatings based on silicone (polydimethylsiloxane; PDMS) elastomers do not contain biocides. Such coatings are designed to 'release' accumulated organisms hydrodynamically, as the vessel moves through the water (eg Brady 2001; Candries et al. 2001; Kavanagh et al. 2005). However, such biocide-free fouling-release coatings will have a high potential for the introduction of alien species if used incorrectly. Watermann et al. (1999) found that removal of up to 90% of organisms on silicone coatings was directly dependent on the speed that the vessel was travelling. For some fouling-release coatings, voyage speeds of >20 knots may be required to remove growth (Brady 2001; Candries et al. 2001), making them better suited for use on relatively fast commercial vessels making regular voyages as opposed to intermittently used recreational vessels. While rigorous AF maintenance practices may not ensure that zero hull-fouling will accumulate on vessel hulls, when coupled with regular hull inspections they have the potential to reduce the number and frequency of Cu-tolerant species transferred *via* hull-fouling.

Traditionally, very little mention is made of water quality parameters as a means of controlling NIS. Current research however, highlights the importance of water quality as a management tool in the prevention or control of species introductions (eg Dafforn et al. Forthcoming 2009). In the past, it has been suggested that improvements to water quality in harbours and ports bearing high TBT burdens may promote the spread of exotic species, because reduced toxicity would allow a wider range of organisms to find port regions more suitable for colonisation (Minchin and Gollasch 2003). While this may have been true of TBT pollution, the comparatively less toxic nature of Cu presents a different scenario. Research suggests that rather than preventing the establishment of new species, increased levels of Cu pollution in port and harbours would instead alter established selection regimes within these areas, inhibiting the competitive success of sensitive native taxa while facilitating the establishment and spread of more tolerant-introduced species. For example, Piola and Johnston (2006a) found evidence for adaptive expression and loss of Cu tolerance among different populations of the same species of NIS. This raises the possibility that in environments where background Cu levels are already high, vessel hulls may be more readily/heavily colonised by tolerant hull-fouling species. Possible ways in which water quality may be improved to reduce this risk include the adoption of alternative non-toxic antifoulants (eg Stupak et al. 2003), better management of the paint application and hull-cleaning processes, and the remediation of contaminated sediments to avoid the risk of toxicant release during resuspension events (Beck 1996; Turner et al. 1997).

Changes to shipping and port practices (both commercial and recreational) may also provide benefits for managing species introductions. Ideally, the mooring and docking of vessels need to be conducted in areas of low metal pollution. Otherwise, non-indigenous fouling taxa present on the hulls of moored vessels may be competitively advantaged over native species in the area. This could not only be achieved by reducing metal pollution loads within ports and marinas (eg sediment remediation, improved port and marina design, and strict pollution regulations), but may also be achieved by mooring medium and long-stay commercial vessels in port areas that receive good flushing. Similar approaches may be employed for managing species introductions stemming from recreational vessels. Entrainment of water in low flow, semi-enclosed marinas and boat harbours has been demonstrated to exacerbate the prevalence of non-indigenous hull-fouling taxa by limiting the dispersal of propagules, effectively increasing propagule pressure in these areas (Floerl and Inglis 2003). In a similar way, increased water residence times in marinas and embayments can also lead to the build up of AF biocides such as Cu (Warnken et al. 2004; Dafforn et al. Forthcoming 2009). Mooring recreational vessels in areas of high water movement and flow would result in more efficient dispersal and removal of pollutants, with fewer pollution-mediated impacts on native assemblages. Some degree of caution may need to be adopted if considering such a strategy; however, because this approach may also have the effect of dispersing non-indigenous larvae over greater distances, encompassing a wider range of native habitats instead of retaining them within disturbed areas.

Determining the Cu tolerance of marine species that are susceptible to entrainment and transfer *via* vectors such as shipping (eg fouling assemblages in ports and harbours) may be a useful predictor of fouling species that have the potential to become invasive. Floerl et al. (2009a) measured the phylogenetic relatedness, ie similarity based on their evolutionary development or history, among marine bryozoans occurring in New Zealand ports and harbours, to determine whether the invasion process leads to higher or lower phylogenetic relatedness among NIS than that among native assemblages. They found phylogenetic relatedness among non-indigenous bryozoans was no different from that among natives in port environments, but instead native bryozoans occurring within ports had significantly reduced taxonomic distinctness relative to native New Zealand species occurring outside port environments, ie open coast. The authors suggest one possible explanation is that the distinct habitat characteristics associated with ports and harbours (eg high levels of pollution, dominance of artificial structures, and altered hydrodynamic regimes) have reduced the suite of native bryozoans present in New Zealand ports to a restricted subset of the entire native population, more tolerant of these conditions and hence more closely related to co-occurring NIS. Other studies within port environments support these findings, clearly demonstrating that some native taxa such as serpulids and barnacles exhibit some traits (eg Cu tolerance) that are commonly only associated with NIS (Dafforn et al. 2008, Forthcoming 2009; Piola and Johnston 2008a). If phylogenetic studies were to be combined with laboratory and field trials examining the Cu tolerance of native species, it may provide a useful toolkit for predicting future invaders or 'next-pests' amenable to transfer *via* hull fouling.

Future research directions

Recent progress in understanding the role of Cu pollution in species introductions and invasion biology has raised further questions and directions for research. One of the logical next-steps is the investigation of the evolution of metal tolerance in NIS. Detailed, multi-generational breeding experiments are required to determine the role of genotype and/or phenotypic plasticity in the development of metal resistance. Is metal tolerance in NIS induced during the organism's life, or is it a constant feature of certain genetic strains? Can this tolerance be passed on to offspring, thereby creating resistant propagule pools better adapted to colonise pollution disturbed environments? Can a vector such as hull-fouling, which has the potential to be highly selective for metal-tolerant species, be creating a growing body of 'super-invaders'? Knowledge of how rapidly metal tolerance can be acquired and lost amongst populations of NIS may help to predict some of the mechanisms behind successful invasions.

Preliminary research has demonstrated differential Cu tolerance among different populations of the same NIS, with costs associated with Cu tolerance manifested as reduced competitive success under non-polluted conditions (Piola and Johnston 2006a). Marshall (2008) found similar evidence of costs associated with Cu tolerance. He showed that maternal colonies of the non-indigenous bryozoan *B. neritina* exposed to a Cu toxicant produced larvae that were larger, more dispersive and more Cu tolerant than toxicant naive mothers. However, the 'trade-off' for this Cu tolerance among offspring manifested as a decrease in post-metamorphic survival in non-polluted conditions, especially in the presence of high intraspecific competition. These costs and benefits associated with pollution adaptation make it a highly context-dependent characteristic, and one that might usefully be 'switched off' when no longer needed. If metal-tolerance is a costly and inducible response, then organisms may evolve a high degree of phenotypic plasticity that increases their fitness under changing environmental conditions (de Jong 2005).

Knowledge about the characteristics of the invader and the abiotic conditions in both the source and recipient region are essential to predict where future invasions are likely to occur (Miller et al. 2007; Hayes and Barry 2008). Correlative studies that compare the distribution of NIS within harbours and estuaries with local patterns of pollution may provide valuable insights into relationships between these two factors. For example, within the Sydney region of Australia, extensive sampling has generated a large amount of data on the metal loadings in sediments within two of the major harbours, Sydney Harbour and Botany Bay (Birch 1996; Birch and Taylor 1999). Both these estuaries have also been the focus of large-scale NIS surveys (AMBS 2002; Pollard and Pethebridge 2002). By employing geographical information system technology, it may be possible to correlate both sets of data to determine if patterns exist, for example whether NIS and Cu-pollution 'hots-pots' correspond, or whether different sources of pollution correlate with specific types of invaders. Preliminary work by Dafforn et al. (Forthcoming 2009) has identified several non-indigenous and native Australian species that were more abundant in areas of high Cu contamination. These findings highlight the need for countries to identify which of their native species exhibit Cu tolerance that might enhance their potential for transport and establishment. This would allow targeted management efforts to minimise the export of such species to other countries.

Conclusion

The 'cost' of species loss through the use of efficient biocidal coatings (eg TBT SPC AF paints), *vs* the increased risk of species transmission by the use of less 'efficient' technologies (eg Cu; fouling-release coatings) to control fouling, needs to be assessed. In the case of TBT, this decision has already been made, with the detrimental environmental impacts resulting from its use deemed to be of greater importance than the question of whether cessation of its use may result in even greater ecological damage through the loss of native community composition and function in regions susceptible to invasion. In the absence of a readily available, effective alternative, Cu seems set to remain the most widespread commercial and recreational AF biocidal agent in use for the near future. Biocides such as Cu exert very strong selective pressures on both the target and non-target organisms, favouring individuals that have increased tolerance. When combined with a common transport vector for marine NIS, such as hull-fouling, the potential for such biocides to create competitively superior NIS (under polluted conditions) quickly becomes apparent. There is a growing body of evidence indicating that a repeating cycle of metal-polluted source environments, followed by metal-biocide influenced transport vectors, followed by equally polluted recipient locations, is leading to the evolution of a pool of highly metal-tolerant non-indigenous hull-fouling organisms that are successfully out competing less resilient native taxa worldwide. This transfer of metal-tolerant NIS is likely to continue into the near future, until: (1) alternative AF strategies, practices and regulations become more effective and widespread; (2) water quality issues (particularly concerning metal pollution) are addressed in ports, harbours and estuaries worldwide; and (3) a better understanding is gained of the nature and evolution of metal tolerance in marine fouling taxa, particularly with respect to differential tolerance among non-indigenous and native species.

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