Introduced macroalgae – a growing concern

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Abstract

Introductions of non-indigenous species to new ecosystems are one of the major threats to biodiversity, ecosystem functions and services. Globally, species introductions may lead to biotic homogenisation, in synergy with other anthropogenic disturbances such as climate change and coastal pollution. Successful marine introductions depend on (1) presence of a transport vector, uptake of propagules and journey survival of the species; (2) suitable environmental conditions in the receiving habitat; and (3) biological traits of the invader to facilitate establishment. Knowledge has improved of the distribution, biology and ecology of high profile seaweed invaders, e.g. *Caulerpa taxifolia*, *Codium fragile* ssp. *tomentosoides*, *Sargassum muticum*, and *Undaria pinnatifida*. Limited, regional information is available for less conspicuous species. The mechanisms of seaweed introductions are little understood as research on introduced seaweeds has been mostly reactive, following discoveries of introductions. Sources of introductions mostly cannot be determined with certainty apart from those directly associated with aquaculture activities and few studies have addressed the sometimes serious ecological and economic impacts of seaweed introductions. Future research needs to elucidate the invasion process, interactions between invaders, and impacts of introductions to support prevention and management of seaweed introductions.

Introduction

Introduced species are considered to be one of the greatest threats to native marine biodiversity and resource values of the world's oceans (Norse, 1993; Vitousek et al., 1997; Carlton, 2000). Regional studies have identified hundreds of non-indigenous marine species (NIMS) introduced through human activities. These studies are, however, limited to a few countries or regions, i.e. Australia, Europe, New Zealand and the United States (e.g. Pollard & Hutchings, 1990; Cohen & Carlton, 1995; Cranfield et al., 1998; Coles et al., 1999; Ruiz et al., 2000; Hewitt et al., 2004). There is very little information on the status of NIMS in other regions (e.g. Williamson et al., 2002 for 20 member

economies of the Asia-Pacific Economic Cooperation, APEC). The rate of introductions of NIMS has increased in the last 20 years, reflecting increased global trade but also more survey effort (Ruiz et al., 2000; Ribera Siguan, 2002; Hewitt, 2003a). Some NIMS have had catastrophic effects on the recipient ecosystem, e.g. the Asian clam (*Potamocorbula amurensis*) in San Francisco Bay (Nichols et al., 1994) and the comb jelly (*Mnemiopsis leidyi*) in the Black Sea (Kideys, 2002). The combined effects of global change and species introductions are believed to result in biotic homogenization (e.g., Olden et al., 2004; Olden and Poff, 2004; Wilkinson, 2004). Widespread generalists and opportunistic species will dominate ecosystems, a pattern already observed in locations affected by environmental

Table 1. Number of non-indigenous marine species (NIMS) introduced to various regions.

Location	Total extant NIMS	Macroalgal NIMS (no.)	Macroalgal NIMS (%.)	Reference
French Atlantic Coast	104	21	20	Goulletquer et al. (2002)
Italy	110	32	29	Occhipinti Ambrogi (2002)
North Sea coast	82	20	24	Reise et al. (2002)
Chile	32	12	38	Castilla et al. (in press)
Hawaii	89	21	24	Coles et al. (1999), Godwin (2001) and Smith et al. (2002)
New Zealand	109	19	17	Cranfield et al. (1998)
Port Phillip Bay, Australia	99	16	16	Hewitt et al. (2004)
United States (continental)	298	24	8	Ruiz et al. (2000)

degradation, and likely to be amplified by species introductions (McKinney & Lockwood, 1999).

Marine macroalgae are a significant component of introduced NIMS (Table 1). These include several high profile species that have caused significant ecological and economic impacts (e.g. *Caulerpa taxifolia* (Vahl) C. Agardh, *Codium fragile* (Suringar) Hariot ssp. *tomentosoides* (Van Goor) Silva, *Sargassum muticum* (Yendo) Fensholt and *Undaria pinnatifida* (Harvey) Suringar; e.g. Trowbridge, 1998; Boudouresque & Verlaque, 2002; Ribera Siguan, 2002, 2003; Wallentinus, 2002; Occhipinti-Ambrogi & Savini, 2003). Macroalgae are considered to be especially worrying NIMS as they may alter both ecosystem structure and function by monopolizing space, developing into ecosystem engineers, changing foodwebs, and spreading beyond their initial point of introduction through efficient dispersal capacities (Thresher, 2000).

The majority (80%) of marine macroalgal orders contain introduced species: 7 out of 9 orders in the phylum Chlorophyta, 16 out of 19 orders in the Rhodophyta, 8 out of 12 orders in the Phaeophyceae. The numbers of introduced species per order are highly correlated with total species number (Figure 1, Pearson-Product moment correlation: $r^2 = 0.91$, $p < 0.05$). However, some orders contain more, others less, introduced species than expected by chance alone; for example the Ectocarpales, Laminariales and Bonnemaisoniales have more, while the Chaetophorales, Fucales and Corallinales have less introduced species than expected (Smith et al., unpublished data).

Recent reviews of the status of introduced marine plants, both with a regional and global scope, include current inventories of introduced species as well as assessments of introduction vectors and mechanism that may influence invasion success (Wallentinus, 1999a,

2002; Verlaque, 2001; Ribera Siguan, 2002, 2003; Smith et al., 2002). Despite recent research, especially in the Pacific region and the Mediterranean Sea, we still have a limited understanding of the invasion process, the distribution and ecology of less conspicuous introduced macroalgae, and the ecological and economic impacts of marine invasions. In this review we will update current knowledge of seaweed introductions using recent case studies to illustrate the three main phases of the invasion process: uptake and transport, release and establishment, and spread and impact.

Uptake and transport

The first stage in the invasion process depends on the presence of a transport vector and the availability of suitable macroalgal life stages for uptake by this vector. The most important pathways for the transport of NIMS are associated with shipping vectors (ballast water and fouling of hulls), aquaculture and the aquarium trade (Ruiz et al., 2000; Carlton, 2001; Hewitt et al., 2004). It is often difficult to pinpoint a pathway for a specific introduction; it may differ between regions or the introduction may have occurred through multiple pathways.

Fouling of ships' hulls, structures or other surfaces and living epibiotically (e.g., on mollusks) or as boring organisms (e.g., the conchocelis phase of Porphyra species boring into mollusk shells) are considered to be the most important pathways for the unintentional introduction of macroalgae (Ribera Siguan, 2003). All macroalgae have the potential to colonise ships' hulls and other maritime structures, especially species that occur either within or in close proximity to port environments. In Port Phillip Bay, Australia, fouling of ships' hulls is considered to be the most
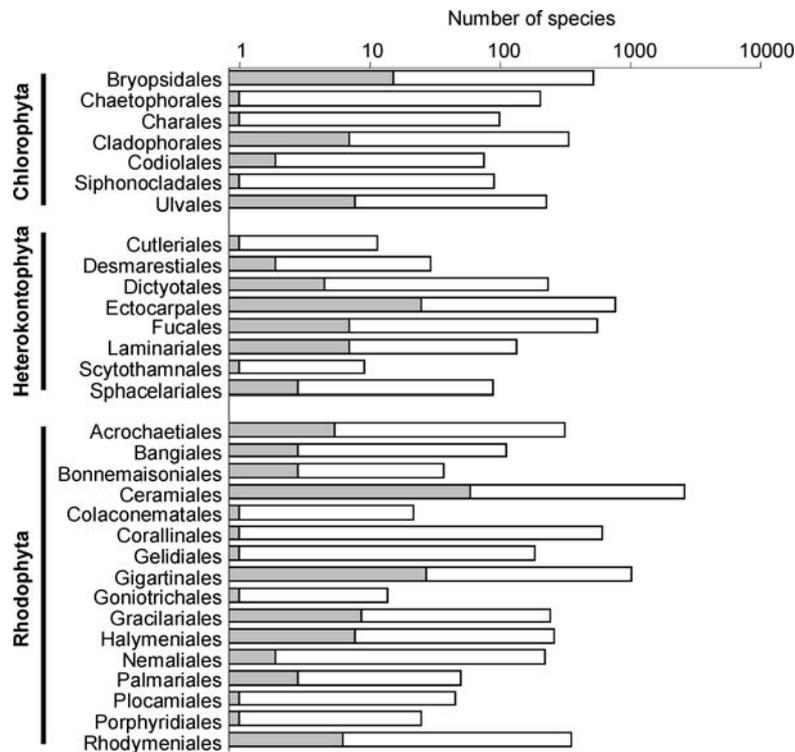
Figure 1. Proportion of number of introduced (grey bars) to total number of species (white bars) in macroalgal orders containing introduced species. Note logarithmic scale. Data are from a database with published records of introduced macroalgae (Smith et al., unpublished data) and AlgaeBase (http://www.algaebase.org, ©1996 – 2004 M.D. Guiry).

important vector for macroalgal introductions (Lewis, 1999; Hewitt et al., 2004). Availability of large numbers of propagules would facilitate colonisation of ships' hulls and other surfaces. For example, high-density populations of *U. pinnatifida* and *Laminaria japonica* J. E. Areschoug occur along the North West Pacific coasts, where the two species are widely cultivated. In these areas the probability is high for zoospores or gametophytes to settle on ships' hulls, aquaculture stock (e.g. oysters) and equipment. Introduced *Codium fragile* ssp. *tomentosoides* in Australia is also generally found in modified environments, often associated with shipping-related infrastructure such as marinas, wharfs, jetties, rip rap, and mooring sites.

In historical times, wooden ships carried vast amounts of fouling species, including macroalgae, on hulls and ballast rock (Carlton & Hodder, 1995; Carlton, 2003). This may explain the cosmopolitan distribution of many well-known fouling taxa such as members of the Ceramiaceae, Ectocarpaceae, Ulvaceae and Cladophoraceae. These are now considered to be 'cryptogenic' (of unknown origin, sensu Carlton,

1996a) in many locations, and include species that may have been introduced many centuries ago. The use of antifouling paint on modern vessels provides only partial protection. Even large vessels have areas on the hull and internal water intake structures (sea chests) that are not or incompletely antifouled and can be colonised by fouling species (Coutts et al., 2003). Smaller vessels, such as small commercial boats, private yachts and launches commonly used in coastal marine traffic may pose an even higher risk due to (i) their usual residence in coastal waters close to seaweed habitats, (ii) their frequently extensive mooring periods, (iii) their slow travel speed, and (iv) their highly variable hull maintenance patterns (Floerl & Inglis, in press; Floerl et al., in press). The incidence of hull fouling is likely to increase as the use of tributyltin (TBT), the main active ingredient in antifouling paints for commercial vessels, will be globally phased out by 2008 for environmental reasons (International Convention on the Control of Harmful Antifouling Systems on Ships 20012).[1]

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[1] Adopted 5 October 2001, http://www.imo.org accessed 18 May

Ballast water is the most important pathway for the introduction of plankton, species with planktonic life history stages and fish (Minchin & Gollasch, 2002). Ballast water is suggested as an important vector for *U. pinnatifida*, possibly transporting zoospores or suspended gametophytes (Hay & Luckens, 1987; Hay, 1990). However, an extensive international study of the species composition in ballast water tanks found only fragments of four macroalgal taxa within a total of 990 taxa (bacteria, fungi, protozoans, algae, invertebrates and fishes; Gollasch et al., 2002). We consider ballast water to be a less important pathway for macroalgal introductions. However, macroalgae may occur in the much less studied sediments deposited in ballast tanks.

The direct introduction of seaweed species for aquaculture is an important vector, especially in tropical regions (Smith et al., 2002). *Eucheuma and Kappaphycus* species have been introduced for production of carrageenan to 26 countries in the Pacific, east Africa and the Caribbean (Zemke-White, in press). Another well-known example is the translocation of introduced *U. pinnatifida* for aquaculture from the Mediterranean to Brittany where it established in the natural environment and spread along the Atlantic coast (reviewed in Wallentinus, 1999b).

The transport and cultivation of NIMS in the domestic and international aquarium trade, including public, private and research aquarium facilities, are potential pathways for the introduction of macroalgae. Whole thalli, fragments or propagules can be released to waterways through untreated effluent or disposal of biomass. The best-known example is the introduction of *Caulerpa taxifolia* into the Mediterranean, presumably by accidental release from a public aquarium (Meinesz & Boudouresque, 1996). Eleven species of marine macroalgae are available through the aquarium trade (Wallentinus 2002), as well as 'live rock', natural substratum cultivated for its variety of attached epibionts including macroalgae (Wallentinus, 2002; Frisch & Murray, 2002).

Macroalgal introductions to Europe are dominated by associations with aquaculture vectors (Maggs & Stegenga, 1999; Reise et al., 1999; Ribera Siguan, 2002; Wallentinus, 2002). The large-scale import of the Pacific Oyster to Europe in the 20th century, typically without any quarantine measures (Wolff & Reise, 2002), may explain the high proportion of Pacific macroalgae in European waters (data in Wallentinus, 2002).

Transport from the Red Sea through the Suez Canal into the Mediterranean ('Lessepsian migrations') was the most important vector for the introduction of macroalgae into the Mediterranean until the early 1990s (Ribera Siguan, 2003). Release of seaweed used for wrapping of fishing bait or seafood is a vector of local importance (Ribera Siguan, 2002; 2003; Wallentinus, 2002).

After uptake by the vector the species must survive the journey to a new location. To our knowledge, there have been no experimental studies on the trans-oceanic survival of hull-fouling species (but see Carlton & Hodder, 1995). We assume, however, species would survive if thalli are not physically dislocated and if the temperature and salinity regimes encountered during the journey were within their physiological tolerances (e.g., Hayes & Hewitt, 2000; Hewitt & Hayes, 2002). Physiological tolerance data are available for a large number of macroalgae. For example, *U. pinnatifida* gametophytes survive temperatures of –1 to 30 °C and salinities of above 15 ppt (Saito, 1975). *Caulerpa taxifolia* and *Codium fragile* ssp. *tomentosoides* survive emersion in high humidity for up to 10 and 90 days, respectively, potentially enabling them to survive shipboard transport for extended periods, for example entangled in fishing nets (Sant et al., 1996; Schaffelke & Deane, in press).

Release and establishment

Following release, a successful invader must survive and establish itself in the receiving environment. This phase in the invasion process is least well known for seaweeds. The definition of establishment has been ambiguous in the literature (Hewitt et al., unpublished). Here we use the definition of established as forming 'a reproductive and self-sustaining population' (e.g., Case, 1996; Williamson & Fitter, 1996; Duncan et al., 2001).

Establishment success is mainly determined by a combination of the following three factors:
- Inoculum pressure (vector frequency and rate of vector infection);
- Abiotic and biological characteristics of the receiving environment; and
- Eco-physiological characteristics of the arriving species.

Embayments and estuaries appear to more prone to introductions than open coast habitats (Carlton, 1996b). These environments, however, also have high

inoculum pressure, i.e. one or more significant vectors are generally present in port environments and urbanised embayments (Ruiz et al., 2000). International ports and harbours are both primary points of inoculation and initial establishment but may also be source populations for secondary spread (e.g., Ruiz et al., 2000; Hewitt, 2002; Ruiz & Hewitt, 2002; Hewitt et al., 2004). The accidental release of aquarium species is also significantly correlated with urban centers. Similarly, aquaculture facilities are typically located in embayments, often immediately adjacent to port environments. These locations represent 'hot spots' of species introduction (Ruiz & Hewitt, 2002; Hewitt, 2003a), even though invasions do occur in a wide variety of marine habitats (Carlton, 2002).

Successful establishment of species after arrival is dependent on matching environmental conditions in the source and recipient environments (e.g., Hewitt & Hayes, 2002). For example, low winter temperatures seem to have prevented the establishment of *Porphyra yezoensis* Ueda, introduced for aquaculture to the east coast of the United States (Watson et al., 2000) and of *Caulerpa taxifolia* in Japan, where it escaped from an aquarium facility (Komatsu et al., 2003). Risk assessments for bioinvasions use environmental conditions to predict, for example, whether the ballast water taken up by a vessel is of high risk to the environment at the destination, and species-specific physiological tolerance data to identify the risk of inoculation of a specific site (Hewitt & Hayes, 2002).

Some recipient environment characteristics are associated with increased introduction incidence: low native biodiversity and anthropogenic disturbance (e.g., water and sediment pollution, structures providing artificial substrates and altered temperature regime due to effluents; reviewed in Carlton, 1996b and Gollasch & Leppäkoski, 1999). For example, the establishment of *U. pinnatifida* in Australia was facilitated by reduced native macroalgal cover (Valentine & Johnson, 2003; 2004). Habitat 'invasibility' is also dependent on functional diversity of macroalgal habitats, e.g. less diverse algal turf assemblages and seagrass meadows can promote the establishment of introduced *Caulerpa* species (Cecherelli & Cinelli, 1998; Ceccherelli et al., 2002). *C. taxifolia* establishment and proliferation has been linked to enrichment of substrata by urban wastewater and organic matter (Chisholm et al., 1997). Extensive blooms of non-indigenous *C. brachypus* Harvey, recently discovered in Florida, may also be linked to local nutrient enrichment (Jacoby et al., 2004).

There is evidence that changes caused by numerous introductions into one region can synergistically operate as a biological disturbance agent and pave the way for new introductions, which has been called "invasional meltdown" (Simberloff & von Holle, 1999).

The successful establishment of *Codium fragile* ssp. *tomentosoides* in the North West Atlantic (Nova Scotia, Canada) versus presence at only low abundances in the North East Atlantic (England) has been explained by biological differences of the native community, despite similar abiotic environmental characteristics (Chapman, 1999). In the northeast Atlantic benthic biodiversity and grazing rates are high, whereas in the northwest Atlantic periodic disturbance of native kelp beds by sea urchin grazing has opened a window suitable for *C. fragile* ssp. *tomentosoides* establishment. This has been facilitated by factors that disrupt the natural sea urchin/kelp dynamics: spreading of the introduced bryozoan *Membranipora membranacea* that overgrows kelp blades and of several introduced red seaweeds colonising vacant space created by urchin grazing (Levin et al., 2002). In addition, grazing pressure is reduced by the decimation of the sea urchin *Strongylocentrus droebachiensis* from an amoebic disease, which presumably is also introduced (Harris & Tyrell, 2001; Chapman et al., 2002), and by avoidance of *C. fragile* ssp. *tomentosoides* by grazers (Scheibling & Anthony, 2001).

Species traits may facilitate the establishment of NIMS. Applying the properties of successful invaders after Lodge (1993), several *r*-selected traits have been identified for *Codium fragile* ssp. *Tomentosoides,* such as high growth rate and reproductive output, vegetative and parthenogenetic reproduction, and broad environmental tolerances (Chapman, 1999). However, most of these characteristics also apply to non-invasive subspecies of *C. fragile* (Trowbridge, 1998). In contrast, a quantitative ranking of European introduced and native seaweed species (using categories of species traits such as dispersal capabilities, environmental tolerances, reproductive mode, and size) indicated that introduced species indeed have species traits that increase the likelihood of successful invasion (Nyberg & Wallentinus, in press). Species most likely to be successful are: *C. fragile* ssp. *tomentosoides, Caulerpa taxifolia, U. pinnatifida, Asparagopsis armata* Harvey and *Grateloupia doryphora* (the currently accepted name for this species is *G. turuturu* Yamada (Gavio & Fredericq, 2002), however, the identity of records from Sicily has recently been disputed (Wilkes et al., unpublished data)).

Spread and impact

From the initial incursion sites, for example close to international ports or aquaculture facilities, NIMS spread to other areas by natural dispersal or by domestic translocation. Vectors for domestic translocation are similar to those of the initial introduction, such as aquaculture stock movements, coastal and recreational shipping (Kinloch et al., 2003).

Caulerpa taxifolia in the Mediterranean has spread steadily since its introduction in 1984, with an estimated colonised area of 131 km^2 (Meinesz et al., 2001). However, the current distribution and local abundance is disputed and remote sensing results suggest that *C. taxifolia* cover along the south coast of France may have been overestimated by a factor of ten (Jaubert et al., 2003). Since the early 1990s a second *Caulerpa* species has been spreading in the Mediterranean Sea, now identified as the proposed combination *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman *et* Boudouresque (Verlaque et al., 2003). The rate of spread of *C. racemosa* var. *cylindracea* and the co-occuring *Womersleyella setacea* (Hollenberg) R. Norris (see below) is dramatic compared to other introduced macroalgae in Europe (Verlaque et al., 2004). *C. racemosa* var. *cylindracea* is competitively superior to *C. taxifolia*, where the two species co-occur (Piazzi et al., 2001a; Piazzi & Ceccherelli, 2002).

The understanding of one introduction often cannot predict other introductions of the same species, as the factors determining success of establishment and further spread are site- or time-specific (Grosholz, 1996; see above for *Codium fragile* ssp. *tomentosoides*). While Boudouresque and Verlaque (2002) do not consider *U. pinnatifida* as an invasive species in the Mediterranean Sea (defined as NIMS that spread from the point of introduction and become abundant; Kolar and Lodge, 2001) the species is invasive, indicated by the continuously expanding range, along the European Atlantic coast (Wallentinus, 1999b), the west coast of the United States and Mexico (Silva et al., 2002; L. Aguilar Rosas, pers. comm.) and in the southern hemisphere (Sinner et al., 2000; Casas et al., in press).

Studies of impacts of NIMS are often hampered by the lack of ecological baseline studies. Typically, studies are only initiated after the incursion has already occurred and use comparisons of sites colonised and un-colonised by NIMS (Hewitt, 2003b). In such a study on *U. pinnatifida* Forrest and Taylor (2002) found no differences in native species richness and abundance, but suggest that the lack of benthic community data be-

fore establishment of *U. pinnatifida* limits inferences. *U. pinnatifida* has caused changes to the composition of native macroalgal communities (Battershill et al., 1999; Sinner et al., 2000, Valentine and Johnson, 2003), as well as decreases in cover (Curiel et al. 1998, 2001) and diversity (Casas et al., in press). Short-term studies indicated that the presence of *Caulerpa taxifolia* had a negative effect on seagrass shoot density, especially under nutrient enrichment (Ceccherelli and Cinelli, 1997). In contrast, long-term experiments suggest that *C. taxifolia* and seagrass are likely to co-exist and that high nutrient availability will not change competitive relations (Ceccherelli and Sechi, 2002). Overgrowth by *C. racemosa* changed macroalgal community composition and seagrass shoot density (Piazzi et al., 2001b; Ceccherelli and Campo, 2002).

Impacts of NIMS may also change through time. NIMS often persist at low levels and later start to increase in abundance and spread, which Stockwell et al. (2003) attributes to either an initial period of adaptation or a change to previously functional environmental controls such as competition or grazing. In contrast, adaptations to NIMS may also occur by herbivores changing preferences from native species to NIMS (Stimson et al., 2001). In other cases NIMS are not preferred (Schaffelke et al., 1995), preferred by only a few grazers (Trowbridge, 1998; Thornber et al., 2004) or no change of grazer populations and feeding habits was observed (Francour et al., 1995).

Apart from the handful of high profile species, rhodophytes are the most prevalent group of introduced macroalgae (Ribera Siguan, 2003). It is likely that consequences of these introductions are underestimated because the taxa involved are often inconspicuous and difficult to identify to species level. This is further complicated by separate introductions of morphologically dissimilar generations (e.g. gametophytes vs. tetrasoporophytes of *Asparagopsis armata*, Maggs and Stegenga, 1999) or cryptic invasions of sibling species that are morphologically indistinguishable from native species (e.g. McIvor et al., 2001). The detection of cryptic invasions is much aided by molecular techniques, which can also assist in the assignment of source regions of introductions (see below).

At least 21 seaweed species have been introduced to the Hawaiian Islands, both accidentally and intentionally for seaweed aquaculture (Godwin, 2001; Smith et al., 2002). The islands represent one of the most heavily invaded tropical systems in the world. Several species (*Acanthophora* spicifera (M. Vahl) Børgesen, *Avrainvillea amadelpha* (Montagne) A. Gepp and E.S.

Gepp, *Gracilaria salicornia* (C. Agardh) E.Y. Dawson, *Hypnea musciformis* (Wulfen) J.V. Lamouroux, *Kappaphycus* spp. and *Eucheuma* spp.), predominantly Rhodophytes, are now established in high abundance and spreading (Smith et al., 2002; Conklin and Smith, in press; G. Zucarello, pers. comm.). Four of these species are overgrowing live hard corals, sometimes leading to coral mortality (Smith et al., 2002). Costs associated with *H. musciformis* blooms are ∼US$55,000 per year for one town alone, for removal of rotting algal biomass washed up onto beaches (Van Beukering and Cesdar, 2004).

Womersleyella setacea is an Indo-Pacific species (e.g. Silva et al., 1996), recently introduced into the Mediterranean Sea (first report in Verlaque, 1989) where it is now widely distributed (Airoldi et al., 1995; Piazzi and Cinelli, 2001), and is also found in the Canary Islands (Haroun et al., 2002). The species has developed dense turf assemblages on rocky substratum and on seagrass rhizomes, with reduced biodiversity compared with unaffected sites (Piazzi et al., 2002; Piazzi and Cinelli, 2003).

Heterosiphonia japonica Yendo, a North Pacific species (e.g., Abbott and Hollenberg, 1976; Yoshida et al., 1990), was recently introduced to the East Atlantic and Mediterranean Sea, potentially by oyster imports, and has since spread along the Atlantic coasts of Spain, France, and Norway (Lein, 1999; Maggs and Stegenga, 1999; Verlaque, 2001). It is now the most common species in sheltered and semi-exposed subtidal locations along the south-west coast of Norway, overgrowing other benthos (Husa et al., 2004). Further north *H. japonica* is found mainly in or near harbours, indicating translocation by shipping and fishing activities (Husa et al., 2004).

Management options

Several steps have been identified as fundamental to the management of NIMS: prevention and monitoring; detection and rapid response; and long-term control. The development of awareness and understanding by public and political interests, appropriate research strategies, and information management and sharing, underpin these steps.

Prevention and monitoring

The most cost-effective management strategy in the marine environment will be to reduce the introduction risks through minimisation of inoculation frequency and propagule pressure. These options cannot be solely driven at a local or national level, but require significant international and regional cooperation (e.g., Bax et al., 2003; Hewitt, 2003a). Several international and multilateral regional actions have recently been enacted to reduce the rates of NIMS transfers from various vectors. Examples include: The International Convention for the Control and Management of Ship's Ballast Water and Sediments (http://www.imo.org; see also Hewitt, 2003a; McConnell, 2003) that now requires ratification. This convention will create a uniform standard for the regulation of ballast water management. The International Council for the Exploration of the Seas (ICES) developed a Code of Practice (CoP) for the Introductions and Transfers of Marine Organisms in 1994 (updated in 2003, available at http://www.ices.dk). This CoP aids the management of intentional introductions (e.g., mariculture and stocking) and accidental introductions associated with aquaculture species. However, most effective would be a preferential development of aquaculture of native species. APEC has undertaken an assessment of regulatory frameworks for NIMS management in member economies (Bax et al., 2003) to develop a common regional risk management framework for NIMS, primarily targeting ballast water and hull fouling. Altogether, these actions do not fully address the dominant pathways for macroalgal introductions, i.e., translocations for aquaculture and fouling of marine vessels and installations.

Detection, rapid response and long-term control

Most management plans for introduced species have elements of 'rapid response' for eradication action, identifying when and how to shift to long-term control (e.g., Wotton and Hewitt, 2004). Rapid response requires early detection, either through passive (e.g., public reporting) or active means (e.g., surveillance program) and an understanding of what is already present (e.g., baseline surveys). Australia and New Zealand have the established national systems of port baseline surveys using standardised collection methods (Hewitt and Martin, 2001; Ruiz and Hewitt, 2002).

The determination of source regions is fundamental to decisions on management action after discovery of an introduction. For example, *Caulerpa taxifolia* was discovered between 2000 and 2002 in both the USA (California) and in Australia (New South Wales

and South Australia). There are no native *Caulerpa* species in California, making the determination as an introduced species unequivocal. The two populations were identified as genetically identical with the 'aquarium-Mediterranean strain' (Jousson et al., 2000). A campaign to eradicate the alga commenced in the same year. In Australia, however, *C. taxifolia* is native to the tropical and subtropical regions (reviewed in Phillips and Price, 2002). Several populations of *C. taxifolia* were discovered in the region around Sydney, more than 800 km south of previous records, and even further away around Adelaide. Using molecular markers, Schaffelke et al. (2002) and Murphy and Schaffelke (2003) ruled out that *C. taxifolia* was introduced from overseas, i.e. from the Mediterranean or overseas aquaria, with high confidence for three of six new locations. It is most likely that the new records are the result of domestic translocation(s) from Australian (sub)tropical populations, assisted by human activities such as boat traffic and fishing or through the domestic aquarium trade (Schaffelke et al., 2002). A number of molecular markers are identical between the 'aquarium-Mediterranean strain' and certain Australian populations, indicating that the latter may be the origin of the introduction into the international aquarium market and thence to the Mediterranean (Meusnier et al., 2002, 2004; Fama et al., 2002). Recent molecular research indicates that *C. taxifolia* consists of at least two incipient species, of which only one is known to be invasive, and that there is evidence for a second, previously unrecognised, introduction event into the Mediterranean Sea (Meusnier et al., 2002, 2004).

Rapid response activities entail a variety of methods (e.g., physical or chemical control) with the intent of containing and eradicating introduced species as soon after detection as possible. Benefits and hazards of eradication/control efforts need to be balanced against the benefits and hazards of doing nothing, specific to each species and location (Hewitt et al., in press). While physical removal/control of introduced macroalgae (especially *Caulerpa taxifolia*) has shown some promising results, other methods such as chemical and biological control had limited effect (reviewed in McEnnulty et al., 2001). Recent efforts to eradicate or control *C. taxifolia* using chemical methods are more encouraging. In Australia, application of sea salt at 50 kg m^{-2} was successful in reducing abundance of the target species by up to 95% whereas native seagrass and infauna were less affected and had largely recov-

ered after 6 months (Glasby et al., unpub data). In California, chlorine was applied under black tarpaulins left in place for several months, after which no *C. taxifolia* was found in cores from the treated area (Anderson, 2002). Laboratory tests indicate that chlorine concentrations of 125 ppm for at least 30 min result in 100% mortality, and that treatment should preferably occur in winter when *C. taxifolia* grows slowly (Williams and Schroeder, 2004).

Manual removal of *U. pinnatifida* significantly reduces sporophyte numbers. However, in established populations, survival over more than 2.5 years occurs either through 'seed banks' of microscopic stages or selective gametophyte survival in microhabitats (Hewitt et al. in press). Zoospore release in *U. pinnatifida* in Australia is limited to larger sporophytes for most of the growing season, but late in the season small sporophytes form mature sporophylls within just one month (Schaffelke et al., in press). Hence, removal efforts need to be more frequent in the late season. Removal of *Kappaphycus* spp. in Hawai'i required ~2 h m^{-2} and regrowth was rapid (Conklin and Smith, in press). Manual removal of introduced macroalgae is a long-term commitment, and needs to be coupled with vector management and education to reduce the chances of re-inoculation and spread, and with monitoring (and response) on a larger spatial scale for the early detection of new incursion sites.

The eradication, or even control, of marine invasive species is both technically difficult and costly (Meyerson & Reaser, 2002). Globally, few marine incursions have resulted in response actions and, of those, a limited number have succeeded (e.g., Bax, 1999; Culver & Kuris, 2000; Wotton et al., in press). The recent successful eradication of *U. pinnatifida,* from the Chatham Islands near New Zealand was achievable because it only occurred on a single sunken vessel hull on sandy substrate, limiting the likelihood of spread (Wotton et al., in press). The total cost of this eradication was in excess of ~US$ 1.8 million (ibid.). The costs of the eradication campaign for *C. taxifolia* in California are to date ~US$ 4 million (R. Woodfield, pers. comm.).

Lastly, the crux to any long-term control or eradication effort will be sustained public and political will. Biosecurity must identify impacts of introductions in economic and social terms, create gains that can be readily identified, but also communicate losses and identify the causes, and link biosecurity to tangible examples that remain of current interest.

Conclusion

Macroalgal introductions are increasing. Despite sometimes being a new resource for harvest and aquaculture, there is a growing understanding of the often significant ecological and economic impacts of these introductions. Only sustained biosecurity management, based on better knowledge of invasion ecology, will prevent these impacts from changing ecosystems as we know them.

Acknowledgements

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