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Review

Concepts for biocontrol in marine environments: is there a way forward?

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Abstract

The occurrence of problematic pest organisms is an increasing global phenomenon, adversely affecting a range of environments and associated values. In marine systems, the efficacy of pest control has to date been constrained by a lack of tools that are not only highly effective, but also applicable across broad spatial scales. Here we consider the extent to which biological control (biocontrol) has the potential to fulfil these needs. We describe different biocontrol approaches and potential ecological mechanisms (e.g. consumption, space competition, habitat modification) through which problematic species could be supressed. We also discuss the ideal traits of marine control agents within the context of the selection criteria commonly applied in terrestrial systems. Classical biocontrol based on the deliberate introduction of non-indigenous agents has a high risk of leading to adverse non-target effects in marine environments, and cannot be justified. By contrast, approaches that use indigenous species have a low risk of unacceptable non-target effects, and could be used as part of pest eradication, as a means of containing spread, or for the control of established pest populations to mitigate adverse effects. While biocontrol based on indigenous species can be highly effective for such purposes, it is unlikely that it could be feasibly applied at broad spatial scales, except in specific circumstances (e.g. in some types of aquaculture). There is clearly a need to develop new approaches to manage marine pests. Biocontrol when used in conjunction with traditional approaches can provide a valuable tool for pest eradication, containment and mitigation of adverse effects.

Key words: marine pests, biofouling, biological control, pest management, biosecurity

Introduction

The occurrence of problematic pest organisms is an increasing global phenomenon, adversely affecting a range of ecological and socio-economic values in terrestrial and aquatic environments (Ruiz et al. 1997). Examples of deleterious effects are numerous, including declines in native biodiversity (Byers 2000), decreases in productivity of economic activities (Bax et al. 2003) and impacts to social values (García-Llorente et al. 2008). The proliferation and spread of pests, including non-indigenous species, is exacerbated by climate change (Bellard et al. 2013), habitat change (Ruiz et al. 1999) and pollution (Gregory 2009). With respect to non-indigenous species, this situation is compounded through intensification of risk pathways and changing patterns of trade, which increase global connectedness (Mack et al. 2000).

In the marine realm, human activities such as vessel movements, aquaculture, and fishing represent significant pathways for the spread and introduction of pests into new areas, with invasion rates being recorded at unprecedented levels (Mack et al. 2000). Marine artificial structures, such as marinas, wharfs, ports and marine farms provide extensive novel habitats that enable many sessile organisms to proliferate, and provide stepping-stones for the spread of many pests (Ruiz et al. 2009). Currently, there is a lack of tools to eradicate or contain new marine pest introductions or to supress established populations. Most approaches to marine pest control rely on diver removal and physical or chemical treatments (Hewitt et al. 2005), which may have limited efficacy, or are labour-intensive and impractical to apply at broad spatial scales (Piola et al. 2009). Accordingly, there is a need for cost-efficient and acceptable alternatives.

Table 1. Types of biological control and key features for the corresponding agents. A: applied method; E: experimental

	Type of biological control	Principle	Agent's key features	Examples	
				Terrestrial	*Marine*
ORIGIN/SOURCE OF AGENT	Classical	Introduction of non-indigenous natural enemies to control of a pest	• non-indigenous • high specificity • high dispersal and establishment capacity	Introduction of lady bugs to control scale insects in the Galapagos Islands (Hoddle et al. 2013) (A)	A parasitic barnacle to control the European green shore crab (Goddard et al. 2005) (E)
ORIGIN/SOURCE OF AGENT	Conservation	Protection and enhancement of particular natural enemies to reduce the effect of a pest	• native • not released	Support alternative habitats to protect natural enemies in cereal crops (Landis et al. 2000) (A)	Protect grouper in marine reserves to supress invasive lionfish (*Pterios volitans*) (Mumby et al. 2011) (A)
ORIGIN/SOURCE OF AGENT	Augmentative	Release of indigenous natural enemies to control a pest	• high dispersal and native • easily available in large numbers	Use of *Trichogramma* (insect) to control crop pests (Kuhar et al. 2004) (A)	Periwinkles to reduce biofouling on oysters farms (Enright et al. 1984) (E)
MODE OF APPLICATION	Inoculation (classical or augmentative)	Small release of natural enemies; pest control increases with agent multiplication	• ability to multiply • low densities required	Release of microbial agents to control plant pathogens (Shoresh et al. 2010) (A)	Sea slugs to control the invasive alga *Caulerpa taxifolia* (Coquillard et al. 2000) (E)
MODE OF APPLICATION	Inundation (classical or augmentative)	Release of natural enemies in large numbers with proliferation not expected	• control by enhanced agents (not their progeny) • densities may decrease rapidly over time • large densities or frequency of release needed	Parasitoid insect to control the European corn borer in crops (Kuhar et al. 2004) (A)	Sea urchins to control the Asian kelp *Undaria pinnatifida* (Atalah et al. 2013b) (A)

Biological control (biocontrol) is one such alternative approach, which has a long history of use in terrestrial pest management, yet marine applications have not been comprehensively explored. One of the barriers to marine biocontrol is the perceived uncertainty regarding the nature and magnitude of adverse non-target impacts. This view appears to stem from classical biocontrol (i.e. using non-indigenous control agents), which in terrestrial systems has a legacy of creating greater problems than it has solved (Simberloff 2012). The limited knowledge of marine ecological dynamics makes it very difficult to evaluate the likely risks associated with classical control strategies (Secord 2003). As an alternative approach to classical biocontrol, strategies exist that rely on the enhancement of indigenous organisms (Bax et al. 2001; Secord 2003). Proof of concept for biocontrol using indigenous organisms in marine systems has been demonstrated in experimental applications involving suppression of pests on artificial habitats (Dumont et al. 2009; Lodeiros, García 2004; Ross et al. 2004) and in natural habitats (Atalah et al. 2013b). However, the use of such approaches in marine systems is still in its infancy. There are considerable knowledge gaps to be addressed to understand the potential for marine biocontrol in pest management, and for biocontrol to be widely accepted and effective at operational scales.

This paper describes different biocontrol approaches and potential ecological mechanisms through which biological agents could supress marine pest species. For this purpose we used the term marine pest to refer to an organism demonstrated to cause economic and ecological impacts, regardless of its origin (Falk-Petersen et al. 2006). With a focus on indigenous species as control agents, we characterise potential biocontrol applications and points of intervention through the invasion process, and discuss selection criteria for ideal biocontrol agents. The latter component does not provide a formal framework for the selection process, but rather addresses the utility of ideal biological traits that have been previously considered in other systems. Finally, we explore the issue of non-target impacts from indigenous control agents, and discuss the future research that is needed for the refinement and application of marine biocontrol at operational scales.

Types of biocontrol

A commonly accepted definition of biocontrol is the "use of living organisms to suppress the population density or impact of a specific pest organism, making it less abundant or less damaging than it would otherwise be" (Eilenberg et al. 2001). The types of biocontrol defined in the literature (Table 1) vary based on the origin of the agent (i.e. whether indigenous or non-indigenous), and the mode of release (i.e. inoculation and inundation). Classical biocontrol involving the deliberate introduction of exotic agents to control pests is common in terrestrial and freshwater systems and can be highly effective (e.g. Hoddle et al. 2013). The other strategies available capitalise on the potential of indigenous organisms to be used as control agents. Conservation biocontrol aims to protect populations of natural enemies to maintain and enhance their pest control action. For example, the protection of predatory grouper fish in marine protected areas of the Caribbean has been proposed as a strategy for the biocontrol of the invasive lionfish *Pterois volitans* (Mumby et al. 2011). This differs from augmentative biocontrol, where natural enemies are purposely released to increase their antagonistic effect on pests (Eilenberg et al. 2001). One approach is 'inoculation', whereby released agents are expected to multiply and spread, and exert sustained long-term pest control through successive generations (Eilenberg et al. 2001). The alternative 'inundation' approach relies on the action of the individuals released alone, often in high densities, with no need or expectation of further proliferation (Table 1).

Mechanisms of biocontrol using indigenous species

There are several ecological interactions through which indigenous biocontrol agents could suppress marine pests. The obvious is consumption, either through grazing or predation. This is a common terrestrial strategy (van Lenteren 2012), with a few marine examples in natural (Atalah et al. 2013b; Mumby et al. 2011; Thibaut and Meinesz 2000) and artificial habitats (Atalah et al. 2014; Enright et al. 1984; Ross et al. 2004). Stabili et al. (2010) provide an interesting example in which large numbers of the Mediterranean fanworm *Sabella spallanzanii* (itself considered a marine pest in some countries) were transferred to and cultured within the vicinity of a finfish aquaculture farm as a means of filtering out harmful bacteria.

Parasitism is also a common interaction exploited in biocontrol, with a long history in terrestrial systems (Clausen 1978). Parasites have also been proposed for controlling marine pests, for example castrator ciliates to supress Pacific seastar *Asteria amurensis* populations (Byrne et al. 1997). Parasitic castrator barnacles were also suggested as a classical biocontrol method for the invasive green shore crab *Carcinus maenas* (Lafferty and Kuris 1996). However, the main issue with the use of introduced parasitic agents relates to host specificity and potential non-target effects to native species (Goddard et al. 2005).

Competitive space pre-emption is a mechanism less explored in terrestrial system, but highly relevant in marine applications. A key factor that drives biofouling assemblage development is competition for space (Stachowicz and Byrnes 2006), thus by enhancing benign organisms that pre-empt space, one could prevent the colonisation by problem species. A recent study showed that high density inoculation of sea anemones prevented the settlement and accumulation of problematic biofouling (including non-indigenous species), with space pre-emption considered one of the key controlling mechanisms (Atalah et al. 2013a). A variant on the principle of conservation biocontrol (see above) is the idea that diverse indigenous communities are more resistant to non-indigenous species than species-poor ones (Stachowicz et al. 1999). As such, maintaining or enhancing indigenous biodiversity, for instance using marine reserves, may be an effective mechanism for decreasing the invasion success of certain pests. However, there is currently little evidence for the effectiveness of this biocontrol mechanism (but see Mumby et al. 2011), with high profile pests, such as *C. maenas*, being able to establish dense populations in relatively pristine habitats (Thresher et al. 2003).

More recent novel approaches include genetic biocontrol, which involves the intentional release of genetically modified organisms that are designed to reduce the survival or disrupt reproduction of target pest species. It involves manipulation of target species' chromosomes to skew sex ratios, recombinant DNA techniques to insert damaging genes into the target species' genome to disrupt reproductive cycle, or a combination of both techniques (Kapuscinski and Sharpe 2014; Thresher et al. 2014). However, these methods have not been tested at operational scales and their potential role as part of the integrated management of marine pests is still unknown. Genetic methods

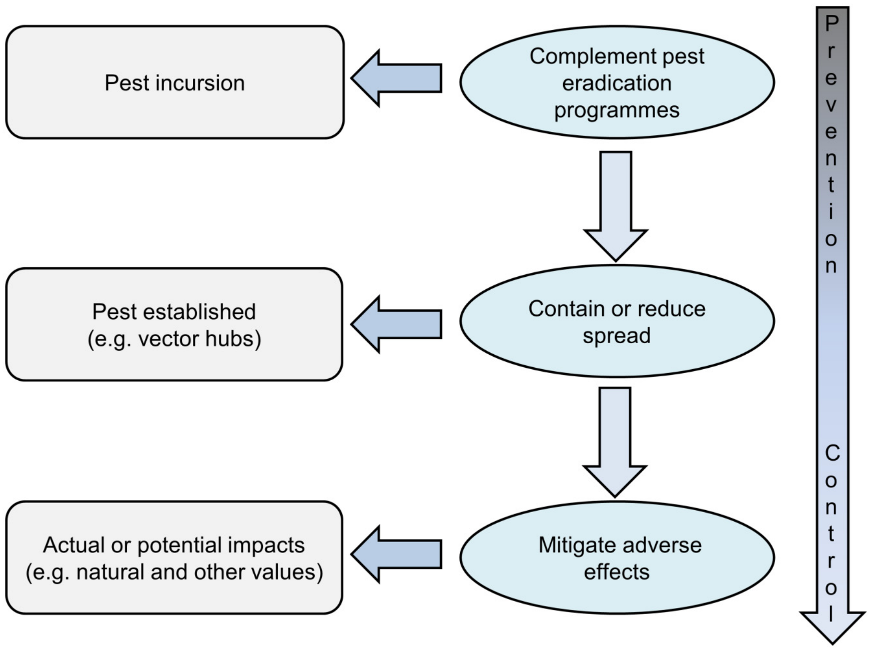

Figure 1. The range of potential augmentative biocontrol applications in marine systems. The diagram (left side) reflects the common events in the initial incursion, spread and widespread establishment of a marine pest. Each of these may lead to management responses (right side) where biocontrol can be applied. These include biocontrol as a complementary tool for pest eradication or containment, and the use of control agents to mitigate adverse effects on coastal ecosystems and associated values.

require prolonged interventions to be effective, and are possibly the least socially accepted mechanism of biocontrol (Thresher et al. 2014).

Potential biocontrol applications in marine systems

Overview

Terrestrial biocontrol programmes generally aim to suppress populations to low levels, thereby reducing density-dependent adverse effects (i.e. effects whose intensity increases with increasing pest density, Hoddle 2004). This approach has been applied to control a number of weed, arthropod and vertebrate pests. Insects are the most common biocontrol agent released against noxious weeds (e.g. Kuhar et al. 2004). These techniques are often applied in integrated pest management scenarios, whereby a range of control options are implemented simultaneously (Hajek 2004).

Population control using indigenous species to reduce the density-dependent adverse effects of problematic species (whether indigenous or non-indigenous) or assemblages (e.g. biofouling) is also a common goal of biocontrol in marine habitats. It is also conceivable that biocontrol, in particular augmentative biocontrol, could be included as part of early management interventions to restrict pest establishment (e.g. of a non-indigenous species) or to reduce spread. This range of marine biocontrol applications is conceptualised in Figure 1, and we elaborate on each below.

Biocontrol to complement pest eradication programmes

In terrestrial situations, rapid responses to invasive weeds and pests are predominantly based on mechanical or chemical methods (e.g. traps, baits and ground spraying) and do not traditionally incorporate a biocontrol component (Rejmánek and Pitcairn 2002). Terrestrial biocontrol is generally most effective for dense weed or pest infestations over large areas (Hajek 2004); as such, its application to isolated incursion events is unlikely. By contrast, the expansive and interconnected nature of marine environments, together with the unavailability of highly effective control tools, mean that pest eradication is often not feasible (Hewitt and Campbell 2007; Sambrook et al. 2014). Success usually depends on rapid detection and containment; and on timely implementation of available control measures (Lafferty and Kuris 1996; Mack et al. 2000; Piola et al. 2009). In this context, biocontrol could be used as an invaluable complementary management tool for eradicating pests in spatially-restricted areas, used in conjunction with traditional tools such as diver-based manual removal. Biocontrol has the potential to surmount the challenges that cryptic pests or life-stages pose to traditional methods (e.g. diver surveillance) for timely detection (Hewitt et al. 2005; Hunt et al. 2009). For example, in New Zealand an inundative approach with sea urchins is being used in conjunction with manual diver removal and chemical treatments to locally eradicate the invasive alga *Undaria pinnatifida* from an area of high conservation value (Atalah et al. 2013b). In that example, urchin biocontrol assists eradication both directly by supressing the target pest and indirectly by denuding the indigenous kelp canopy and aiding visual searches.

Biocontrol to contain or reduce spread

Decreases in population sizes of marine pests by biocontrol or other management methods are expected to translate to a reduction of spread (Forrest et al. 2009; Forrest and Hopkins 2013; Johnston et al. 2009). Reduction in spread can be through two means: reductions in mobile adults and reductions in propagule pressure. In the first instance, there is the potential for a direct biocontrol effect on mobile pest populations, leading to a reduced supply of adults for outward dispersal from the population boundary. This type of control is common in terrestrial systems (Cooper and Rieske 2007; Ryan 1990). Potential applications in marine environments are less obvious, although a pertinent example is use of wrasses to control parasitic sea lice in farmed salmon (Treasurer 2005). In that case the control effect was clearly of direct benefit to infected fish. Additionally, by reducing the overall parasite population in a given fish farm, it can be expected that the inoculation pressure for the infection of nearby farms will be reduced (Kristoffersen et al. 2013). Where the farmed species have wild conspecifics, it is also conceivable that a reduction in the farm parasite load will reduce exposure to wild stocks (Butler 2002; Chambers and Ernst 2005).

The second method by which biocontrol has the potential to reduce spread is by reducing the number of reproductive adults, hence the propagule supply. As many marine benthic species (especially sessile biofouling organisms) produce planktonic propagules that disperse with water currents, such a strategy may limit spread by natural dispersal, and also reduce the infection of human transport vectors. The latter application is of particular relevance to biofouling in marine transport hubs such as ports and marinas, whose extensive artificial habitats provided by structures such as piles and floating pontoons can be a significant reservoir for marine pests (Glasby et al. 2007; Ruiz et al. 2009). As the planktonic propagules of these organisms can readily colonise vessels and other transport vectors, infected transport hubs can greatly accelerate human-mediated spread (Floerl and Inglis 2005; Floerl et al. 2009). It has been shown that population control applied in such hubs can reduce the infection of vessels and other vectors (Sambrook et al. 2014), and consequently reduce human-mediated spread; however, this requires an intensive ongoing control effort which is seldom feasible with traditional tools (Forrest and Hopkins 2013). Biocontrol in vector hubs could therefore be valuable as a population management tool, and we are currently investigating potential approaches based on enhancement of benthic invertebrates on fixed and floating structures (J. Atalah, unpub. data). The terrestrial equivalent for this strategy would be treatment and containment practices in commercial shipping ports or airports (Magarey et al. 2009); however, such practices tend not to include a biocontrol component, probably reflecting the relative ease of local scale terrestrial control using traditional methods (e.g. sprays, baits).

Biocontrol to mitigate adverse effects

Biocontrol can theoretically be used to mitigate the adverse effects of pests in a range of marine environments. However, at present biocontrol for this purpose appears restricted to aquaculture, with previous studies illustrating applications in the control of pathogens (Stabili et al. 2010), parasites (Treasurer 2005), and biofouling (Enright et al. 1984; Lodeiros and García 2004; Ross et al. 2004; Switzer et al. 2011). Reducing biofouling on finfish or shellfish farms using biocontrol can mitigate direct impacts to production, and reduce operational problems and associated management costs (Fitridge et al. 2012). The most successful examples of biofouling biocontrol are found in shellfish aquaculture in situations where control agents can be contained, such as oyster grow-out cages (Enright et al. 1984; Lodeiros and García 2004). The use of biocontrol agents such as sea urchins in aquaculture provides an interesting perspective for polyculture, as they have a potential market value and low harvesting costs (Dumont et al. 2009; Ross et al. 2004). Another example of augmentative biocontrol in shellfish aquaculture is the use of a native rock shrimp (*Rhynchocinetes typus*) to control non-indigenous fouling pests on scallop pearl nets (Dumont et al. 2009). Here the shrimp's ability to remove fouling biomass resulted in decreased mortality and increased growth of the farmed bivalves (Dumont et al. 2009).

In finfish aquaculture, the example above describing the use of cleaning wrasses to control parasitic sea lice in farmed salmon constitutes a successful application of biocontrol in aquaculture (Treasurer 2005). In Norwegian farms, three different species of cleaning wrasse (Labridae) are co-cultured with salmon (up to 5% of the total pen density), to remove the ecto-parasitic sea lice (Skiftesvik et al. 2013). The role of this type of biocontrol has become increasingly important not only in terms of economic productivity and fish welfare, but also by reducing the spread of parasites into wild fish population (see previous section). Regional estimates for the economic cost of sea lice range between 4% and 10% of the total production value of the salmon industry (Costello 2009).

Selection of biocontrol agents

The process of selecting biocontrol agents is dictated mainly by the target pest, the ecological and management context, and the benefits expected from implementing the control programme. Although there is no formal framework to guide the selection of marine biocontrol agents, most traits that define a good control agent in a terrestrial context are relevant (Hajek 2004). These traits relate to a number of ecological factors, including feeding preferences, consumption rates, population dynamics, enhancement potential and risk of non-target effects (Table 2). Issues such as public perception and cost are also important in control agent selection (Table 2), but here we focus on ecological considerations.

A key matter to address is the ability to obtain biocontrol agents in sufficient quantities for effective control at the scales of interest. It may be possible to source marine agents from natural populations, in which case the agents should be widely distributed, abundant and ideally locally sourced to facilitate transplantation into target areas (e.g. Atalah et al. 2013b). It is often not practical to solely rely on natural populations that are constrained by seasonality, geography, or expensive collection methods. Where large numbers of individuals are required, and wild harvest is considered undesirable (e.g. due to negative ecosystem impacts), agents would ideally be mass-produced (Hajek 2004). The decision on sourcing or cultivating agents for augmentative biocontrol would be largely dictated by the scale and context of the application, as well as the amenability of the agent to cultivation.

When using consumers as agents, whether a species has specialist or generalist feeding preferences needs to be considered. In terrestrial systems, highly specialised controls agents are commonly used (Rosen 1990). However, most marine consumers are generalists, except for a few cases (e.g. nudibrachs, Thibaut and Meinesz 2000), which clearly limits choice. Generalists may pose a risk of non-target effects (see next section), but in some marine situations are beneficial. For example when used on marine artificial structures where the aim is to reduce the abundance of multispecies biofouling assemblages. Generalists also survive relatively well at low prey densities, whereas specialised predators may not (Burfeind et al. 2009). High consumption rates are desirable in order to minimise required densities. Ideal agents should be able to control pests at low densities. It is also desirable that agents are effective against cryptic life-stages that can thwart traditional control. For example, cryptic organisms or microscopic life-stages cannot be detected by visual diver-based searches. However, such organisms may be susceptible to predation (Osman and Whitlatch 1995), hence grazers or predators used as control agents have the potential to overcome this limitation. For example, gastropod grazing and disturbance activity on biofilms can prevent the accumulation of biofouling in artificial structures by removing early life-stages of pest organisms (Atalah et al. 2014).

Another important trait is the resilience to environmental change (Atalah et al. 2014). This is especially true in marine vector hubs, which are often located in highly-modified environments subjected to numerous sources of anthropogenic disturbance (Piola and Johnston 2008), and sometimes to large fluctuations in salinity, temperature and turbidity (Airoldi and Bulleri 2011). A high mortality rate would counteract an agent's utility; for example, because the agent would require ongoing replenishment. A related trait, which is critical in the use of mobile benthic invertebrate

Table 2. Summary of criteria to consider for the selection of indigenous marine biocontrol agents.

Key criteria	Description
Sources	Abundance in target areas
	Ability to mass-produce in captivity
Accessibility/Practicality	Availability year-round
	Ease of collection, transport and set up at target areas
	Amenability to caging or containment
	Retention on different types of substrata and orientation
Ecological traits	Feeding specificity (generalist vs. specialist)
	Dietary preference
	Feeding rates and methods
	Density or behaviour of agent population (gregarious/solitary)
	Longevity
	Population growth rates
	Larval dispersal and adult spread
	Resilience to environmental change
Cost-effectiveness	Cost of collection or cultivation
	Cost of transport and deployment in target area
	Cost of monitoring
	Added-value and harvest potential
Public perception	Perception of agent as risk to public health/environment
	Acceptability to enhance and release based on previous experiences

agents on artificial structures (on which vertical and horizontal under-surfaces are common), is their rate of retention. Retention in benthic species is function of body size and shape, substrate characteristic and attachment strength or tenacity of the foot system (Trussell 1997; Trussell et al. 1993). Agents such as gastropods, with high attachment strength relative to their body size, are advantageous.

For promising mobile benthic agents with poor retention rates, caging could be considered (Epelbaum et al. 2009; Lodeiros and García 2004). However, even where caging is technically feasible, cage structures themselves introduce new issues. For example, cages will be subject to biofouling, and mesh size will affect surface area for fouling colonisation, as well as the size of agents that can be retained. The ease of retention may also be affected by predator mobility, with highly mobile agents (e.g. sea stars) prone to escaping (Atalah et al. 2014). The use of sessile invertebrates would negate the need for caging. However, suitable candidates have not yet been fully evaluated for this purpose, apart from preliminary work with anemones (Atalah et al. 2013a) and colonial ascidians (Paetzold et al. 2012).

A control agent's mobility and dispersal mechanisms can also affect biocontrol efficacy. Biocontrol agents with low spread rates may necessitate the redistribution of individuals or a high density of release for effective control to be exerted. On the other hand, high spread rates may lead to a reduction in densities in target areas to a point where control is ineffective. Thus intermediate rates of spread are likely to maximize the success of biocontrol (Heimpel and Asplen 2011; Stimson et al. 2007). Likewise larval dispersal is an important trait to consider, but is often overlooked (Burfeind et al. 2009). Dispersal capacity can range from a few meters in direct developers to hundreds of kilometres for organisms with long larval durations (Shanks 2009). As such, recruitment is not necessarily a density-dependent process, as in open marine systems local recruitment is not always related to local reproductive output and is often influenced by factors at larger spatial scales (Kinlan et al. 2005). High larval dispersal and low local recruitment may be a significant limitation for inoculation-based biocontrol. For example, sea slugs were evaluated as control agents for the seaweed *Caulerpa taxifolia*, but their efficacy was hindered partly by poor larval retention in target areas (Thibaut and Meinesz 2000).

Non-target effects

There is a disparity between the amount of information available on non-target effects in terrestrial and freshwater biocontrol (Simberloff 2012) compared to marine systems, and the knowledge is not necessarily transferable (Bax et al. 2001). Unlike freshwater and terrestrial ecosystems, that are perceived as relatively closed, the marine environment is highly inter-connected and expansive. Population dynamics, life-histories, dispersal strategies, interactions and responses to change are generally different for marine taxa (Steele 1995). Furthermore, there is often limited technical information on the biology and ecology of marine species, which can make risk assessment of non-target effects difficult (Barratt et al. 2010). There is a perceived risk that non-target effects from biocontrol could be widespread, permanent and irreversible (Secord 2003), thus biocontrol may be less socially acceptable in marine systems (Selge et al. 2011). As noted earlier, these views arise from experiences with adverse impacts of classical biocontrol on ecological and socio-economic values in terrestrial environments (van Lenteren 2012).

Conservation or augmentative approaches that use native control agents seem the most acceptable option in marine habitats. We consider that native control agents are highly unlikely to cause negative non-target effects on a scale comparable to classical biocontrol. For example, if the biocontrol agent is widespread and abundant, the issue of its reproduction and spread from areas of enhancement is relatively trivial. In this respect, the greatest capacity for non-target effects occurs at the immediate scale of the control operation. Accordingly, non-target effects in early eradication applications are likely to be of limited concern, as the targeted areas are generally very restricted. The example described earlier that used sea urchins as part of an eradication programme for the invasive kelp *Undaria pinnatifida* (Atalah et al. 2013b) led to pronounced non-target effects on benthic native diversity. However, these effects were localised and temporary; over time the urchin densities were expected to decline to background levels, or could alternatively be reduced by deliberate removal. In that situation, the non-target effects arguably outweighed the irreversible and more profound impacts predicted to result from the establishment of *U. pinnatifida*.

Additionally, distinction needs to be made in terms of the species and habitats that are potentially affected by non-target effects of biocontrol. For example, special consideration may need to be given to non-target effects on endangered species or habitats, or species that provide crucial ecosystem services or are commercially important. By contrast, in artificial or highly-modified habitats where many high profile marine pests are first discovered, concerns around non-target effects are of minor relevance. The only exception would be the case of artificial habitats in an aquaculture situation, where the potential for non-target effects may need evaluation; for instance, a predatory biocontrol agent may have the capacity to consume cultured shellfish spat or crops. There is also potential for marine biocontrol agents to be intermediate hosts of parasites or diseases of aquaculture species. Thus, careful screening for the risk of parasite and disease transmission from biocontrol agents to farmed species is advised.

There is a clear need to improve the understanding and assessment of the risk of significant non-target impacts to increase social acceptability; and the economic and environmental benefits of biocontrol, while mitigating risk. Potential approaches for assessing and predicting non-target effects of marine biocontrol agents include laboratory and field manipulative experiments, ecological modelling and risk assessment (Babendreier et al. 2005).

Is there a way forward for marine biocontrol?

The efficacy of pest control in marine systems has to date been constrained by a lack of tools that are not only highly effective, but also applicable across broad spatial scales. Recent studies have demonstrated that many marine pests are highly amenable to augmentative biocontrol using indigenous agents; however, there remains a need to advance promising small-scale research or field applications to a point where they become more operationally feasible and routinely used. There is a need to tailor biocontrol approaches to specific-situations, consider the efficacy of combinations of different agents, better understand minimum control agent densities required to achieve effective control, and determine the influence of substratum type, surface orientation and environmental conditions in relation to retention.

We consider that feasible applications of routine biocontrol will typically be limited to small spatial scales, except perhaps in specific applications for aquaculture. In natural ecosystems, although augmentative biocontrol based on inundation strategies can be highly effective, this approach will conceivably be limited by cost and practicality at spatial scales beyond a few hectares. The high potential cost of biocontrol based on inundation reflects the need for repeated and ongoing efforts to maintain control agent populations at effective densities. For large-scale applications it would not be feasible to solely rely on natural populations (see 'Selection of biocontrol agents' section above). Thus, large-scale inundation strategies would require development and improvement of technologies to mass produce selected biocontrol agents. This process could be accompanied by selective breeding of agents to enhance desirable biocontrol traits.

For local-scale applications that target spatially restricted areas, augmentative biocontrol has considerable merit, especially when used in conjunction with 'traditional' approaches for local-scale management (e.g. physical or chemical treatments). Biocontrol as a complement to other management tools has the potential to increase the likelihood of success of early intervention and eradication efforts. This is especially true where biocontrol overcomes the typical limitations of diver-based approaches (e.g. depth restrictions, inability to detect cryptic life-stages). In the case of vector hubs (e.g. a port or marina), one of the benefits of local- scale population control (even if eradication has failed) is that it may prevent or reduce the human-mediated spread of pest organisms, hence protect coastal ecosystems and associated values at regional scales (Forrest and Hopkins 2013).

Despite such benefits, even local scale applications that require constant maintenance may lead to considerable cost, hence the merits and costs of inundation biocontrol would need to be weighed against the costs of applying traditional tools. Ongoing interventionist approaches are arguably likely to be most feasible in aquaculture situations, as aquaculture facilities get regularly maintained (e.g. for checks of stock or management of biofouling). Aquaculture applications also provide the possibility of co-culture approaches, whereby the control agent itself has value as an aquaculture product.

Inoculation strategies would clearly be more ideal than inundation approaches, given that an agent could be introduced, and subsequently reproduce, spread and exert an ongoing effect, at least at the local scale. However, most indigenous agents are unlikely to have this potential; it is more likely that their densities will subside over time to that which naturally occurs, as noted in the urchin example described in this paper (Atalah et al. 2013b). Although non-indigenous agents theoretically have a capacity to exert ongoing broad-scale effects via an inoculation strategy, the associated risk of non-target impacts in marine systems is likely to be unacceptable.

While inoculation strategies using indigenous control agents may not have the same efficacy in marine environments as is apparent in terrestrial systems, the principle of achieving a 'self-sustaining' control agent population is important, as it could greatly reduce intervention costs compared with an inundation approach. For this reason, we consider that investigation of approaches that aim to achieve self-sustaining agent populations is a particularly worthwhile focus in terms of a way forward. In relation to artificial habitats, the development of structures that have design features or properties that facilitate the establishment, colonisation or retention of native agents, would be a useful research focus (Airoldi and Bulleri 2011; Firth et al. 2014). Possible approaches for 'eco-engineering' of artificial structures include: incorporation of cages into the structure to retain biocontrol agents; provision of connections between structures and the seabed that facilitate access by mobile invertebrates; and development of materials with surface properties that serve as cues for the settlement of control agents. There is scope and need for fundamental and applied research to progress such ideas. There is clearly a need to develop new approaches to protect marine environments from the negative impact of marine pests, and biocontrol based on the use of indigenous species is a promising way forward, which is worthy of further investigation.

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