Management of Biological Invasions (2013) Volume 4, Issue 4: 317–326
doi: http://dx.doi.org/10.3391/mbi.2013.4.4.06

Open Access

Management in Practice

Population control to mitigate the spread of marine pests: insights from management of the Asian kelp *Undaria pinnatifida* and colonial ascidian *Didemnum vexillum*

Barrie M. Forrest* and Grant A. Hopkins
Cawthron Institute, Private Bag 2, Nelson 7010, New Zealand
E-mail: barrie.forrest@cawthron.org.nz (BMF), grant.hopkins@cawthron.org.nz (GAH)
**Corresponding author*

Received: 28 August 2013 / Accepted: 8 November 2013 / Published online: 26 November 2013

Handling editor: Marnie Campbell

Abstract

The control of marine pest populations in transport hubs has the potential to contain or limit spread by minimizing the infection of vessels and other vectors. We draw on New Zealand experiences with eradication or population control attempts on two marine pests, the Asian kelp *Undaria pinnatifida* Harvey Suringar and the colonial ascidian *Didemnum vexillum* Kott, to evaluate the extent to which vector infection was mitigated by management efforts. For both species we compare two levels of effort: sustained control involving intensive regional-scale eradication programs, and shorter-duration less intensive efforts that we refer to as partial control. The mean monthly proportion of vessels infected by *Undaria* was ~1% in two regions where sustained control reduced densities in marine habitats to 1–5% of the pre-treatment population. By contrast, 39% of vessels were infected during a partial control effort, which was comparable to the proportion of vessels infected in four ports where *Undaria* populations were not managed. For *Didemnum*, a reduction of the population to < 0.1% of the pre-treatment level almost completely negated vessel infection, to the extent that few vessels were implicated in the further spread of *Didemnum* while sustained control was in place. By contrast, partial population control led to limited benefit in terms of vector risk reduction. More importantly, a cessation or reduction in population control efforts resulted in relatively rapid vessel re-infection. Both case studies illustrate that intensive control of marine pest populations can greatly reduce the infection of susceptible vectors, but achieving such an outcome requires an indefinite commitment of resources, and may be impractical for multiple pest species or multiple infested locations. Although slowing the spread of marine pests can lead to demonstrable benefits, for population control to have greater practicality and stakeholder support, there is a need for socially acceptable and affordable control tools that are effective across relatively large spatial scales.

Key words: vector risk; pest management; eradication; biofouling; invasive species; biosecurity; New Zealand

Introduction

Pest management is common in terrestrial and freshwater environments, and adopts two primary approaches: (1) eradication to eliminate all individuals, or reduce densities to a point where populations become unsustainable; and (2) population control to contain or reduce the spread of target organisms, or to reduce density-dependent adverse effects (Moody and Mack 1988; Myers et al. 2000; Clout and Veitch 2002; Simberloff 2002; Liebhold and Bascompte 2003; Parkes 2006). In relatively interconnected marine environments, eradication of pest populations is considered difficult to achieve, although there have been a number of successes. These include programs that have: completely eliminated target species (Bax 1999); reduced pest populations below expected thresholds for reproductive success (Hopkins et al. 2011); or removed potential hosts for non-indigenous parasites, in order to prevent transmission and further spread (Culver and Kuris 2000).

The difficulties in achieving eradication in marine systems have led to a focus on reducing the anthropogenic spread of pests from transport hubs such as ports, marinas, and other localities highly connected by human vectors (Ruiz and Carlton 2003; Drake and Lodge 2004; Floerl et al. 2009; Hewitt et al. 2009a). This approach recognises the importance of anthropogenic activities in inadvertently transporting pest species across greater scales than can be achieved by natural dispersal mechanisms. An issue that arises when considering risk reduction measures for vessels and other vectors (e.g. marine farming gear) is that marine pests are often abundant in the extensive artificial habitats that characterise vector hubs (Glasby et al. 2007; Tyrrell and Byers 2007); hence their populations can provide an on-going source of planktonic propagules (e.g. larvae, spores) for vector infection (Floerl and Inglis 2003; Floerl and Inglis 2005; Lacoursière-Roussel et al. 2012). In such situations, stakeholders may resist adopting control measures for their activities where they perceive that re-infection from unmanaged pest populations undermines their efforts (Piola and Forrest 2009; Sinner et al. 2009).

To address such issues, population control in vector hubs has been conducted in parallel with direct vector management (e.g. removal of target pests from infected vectors) in New Zealand for two globally recognised invasive species; the Asian kelp *Undaria pinnatifida* Harvey Suringar (hereafter *Undaria*), and the colonial ascidian *Didemnum vexillum* Kott (hereafter *Didemnum*), in separate pest management operations. These programs provide a unique insight into the efficacy of population control, as there are sufficient records to enable comparisons of the outcomes of multi-year intensive control programs with scenarios where control efforts were short-term and greatly reduced in scope. In this paper, we refer to these scenarios as 'sustained control' and 'partial control', respectively. We compare success in terms of the population reductions achieved, and the concurrent incidence of vector (mainly vessel) infection, based on the hypothesis that population control will reduce vector infection by suppressing the propagule source pool (Floerl and Inglis 2005). To enable these comparisons, it was necessary to draw on disparate sources of information, namely published and unpublished reports, other unpublished records (e.g. monthly project reports), personal communications and observations from individuals involved in the management programs. Thus, this synthesis is primarily descriptive; although quantitative data (and metadata) are presented where possible, rigorous analyses (e.g. statistical hypothesis testing) were not deemed appropriate. Nonetheless, the general patterns evident from the available information, together with a broader discussion of related issues, provide valuable insights into the benefits and pitfalls of population control for marine pests.

Undaria management

Background

Undaria was first recorded in New Zealand in 1987 (Hay and Luckens 1987). It has an annual life-cycle that alternates between microscopic spores and gametophytes, and the visible kelp or sporophyte which can reach a length of > 1.5 m (Akiyama and Kurogi 1982; Hewitt et al. 2005). In southern regions of New Zealand (the case study area), populations of sporophytes are found in water depths up to 20 m on a range of natural habitats and on artificial structures for most of the year, although tend to be less abundant in autumn (Hunt et al. 2009). Reproductively mature sporophytes release asexual spores that settle and germinate into microscopic benthic gametophytes. Fusion of egg and sperm produced by the gametophytes gives rise to the next season's sporophytes, with sexual maturity potentially reached in 50–70 days (Stuart 2004). Spread by spore dispersal is generally limited to tens to hundreds of metres (Forrest et al. 2000), but can be substantially greater (e.g. kilometres) as a result of sporophyte drift (Sliwa et al. 2006).

Sustained regional-scale Undaria control (1997–2004)

A government-funded *Undaria* control program over 1997–2004 is one of the most comprehensive attempts anywhere in the world to eradicate a marine pest at a regional-scale, with a total budget of ~NZ$2.8 million over that period (Hunt et al. 2009). The program was primarily motivated by concerns regarding the potential impacts of *Undaria* on the outstanding biodiversity and conservation values associated with southern New Zealand and its remote offshore islands (Stuart 2004; Hunt et al. 2009). The two population control locations, Bluff Harbour and Big Glory Bay (Figure 1), were considered to be the key source regions for the further spread of *Undaria* to areas of high value. A dual approach was adopted (Table 1), involving sustained monthly *Undaria* population control on artificial structures and in natural habitats at both locations, together with monthly monitoring and removal of visible sporophytes from infected vessels (Hunt et al. 2009).

Population control was based on diver searches and hand removal of all visible *Undaria*, with additional methods (e.g. heat and chemical treatments) trialled later in the program to target the microscopic gametophyte life-stage. Monitoring and removal of sporophytes from infected vessels was simultaneously undertaken in four additional southern New Zealand ports (Oamaru, Timaru, Moeraki, and Otago Harbour), which were considered as important source hubs for *Undaria*-infected vessels (Figure 1). However, unlike Bluff and Big Glory Bay, population control was not concurrently undertaken in these four additional areas; hence we denote these areas as reference ports. Funding for the management program was discontinued in 2004 following further incursions into the region outside of the defined population control areas, and recognition that the continuing spread of *Undaria* at a national scale undermined the benefits of a regional response (Hunt et al. 2009).

Local-scale partial Undaria control (2007–2009)

The cessation of sustained control in 2004 led to renewed concerns among stakeholders regarding the threat from *Undaria* to Fiordland (see Figure 1), a region of southwest New Zealand with internationally significant conservation and biodiversity values. Hence, *Undaria* population management and vessel monitoring were again undertaken over 2007–09, but limited to Bluff Harbour, an important departure port for vessels travelling to the Fiordland area. The new program (see Table 1) aimed to remove *Undaria* from wharf piles and areas of seabed in the immediate vicinity (within tens of metres) of vessel berths in the port (Sinner et al. 2009), under the assumption that these adjacent populations were the most high-risk propagule sources for vessel infection.
Although removal by hand was used as a control method, the principle treatment adopted in Bluff Harbour involved encapsulating (i.e. 'wrapping') wharf piles and parts of the adjacent seabed in plastic, in order to contain and kill *Undaria* (e.g. by shading and anoxia, see Coutts and Forrest 2007). This method was expected to eliminate both the sporophyte and gametophyte life-stages, therefore be more effective than hand removal alone. The timing of treatments, and subsequent monthly monitoring and removal of *Undaria* from infected vessels, is described in Table 1. The program was discontinued in 2009 when it became evident that the partial control method was largely ineffective in achieving the management goals.

Results of Undaria population control programs

By the end of sustained control, *Undaria* densities and the incidence of vessel infection in the two managed areas were very low. In Big Glory Bay, the annual number of sporophytes removed in 1997 was ~17,000 and was steadily reduced to ~200 per year by the end of the program in 2004 (Hunt et al. 2009), representing ~1% of the initial infestation density. In Bluff Harbour, the annual number of sporophytes removed toward the end of the program was ~600–800, representing 4–5% of the baseline infestation in 1998. For three years during the management program (May 1998 to May 2001), mean incidences of vessel infection (n=11,531 vessel inspections in total) obtained from monthly surveys were reported by Stuart (2002) as 0.06% and 1.3% for Big Glory Bay and Bluff Harbour, respectively (Figure 2A). By comparison, the mean incidence of monthly vessel infection in reference ports not subjected to population control was 38% (range 31–56%) over the same period (Stuart 2002). As *Undaria* was regularly removed from vessels in all six locations, this spatial comparison suggests that simultaneous population

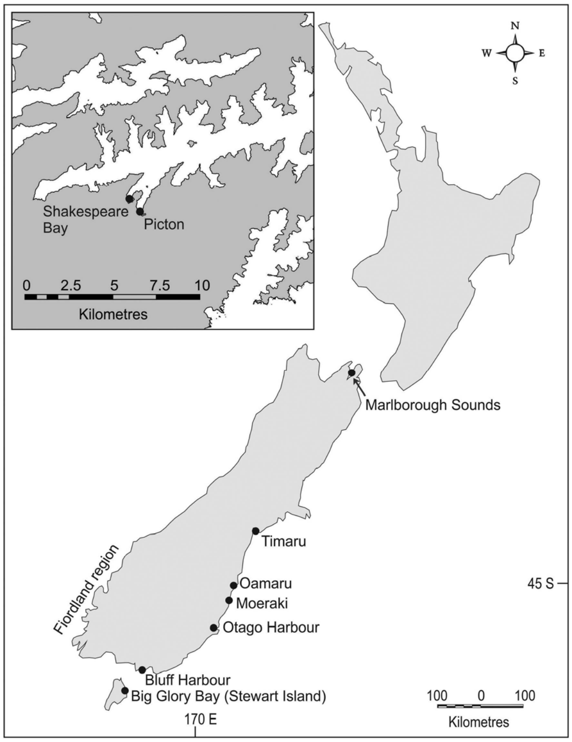

Figure 1. Main map shows locations in southern New Zealand subject to population control and/or vector management for the Asian kelp *Undaria pinnatifida*, and the Fiordland area whose high conservation values were a basis for continued vector management in Bluff Harbour. Inset shows Shakespeare Bay in the Marlborough Sounds region of central New Zealand, which was the focal area for management of the colonial ascidian *Didemnum vexillum*.

Table 1. Summary of population management programs for *Undaria* and *Didemnum*.

Management	*Undaria pinnatifida*	*Didemnum vexillum*
Partial control		
Management goals	Control *Undaria* population to minimise the infection of vessels travelling to areas of high conservation value.	Eradicate local *Didemnum* population, and trial different management tools at operational scale.
Main habitats infected	Wharf piles, artificial rock wall, moorings and vessels.	Wharf piles, artificial rock wall, moorings and vessels.
Spatial scale	Bluff port area (< 1 km^2).	Shakespeare Bay (~1 km^2).
Primary treatments	Encapsulated infected substrata in plastic, with hand removal of sporophytes from infected vessels and some seabed habitats.	Encapsulated infected substrata in plastic or semi-permeable fabric. Removed vessels to land for cleaning and antifouling.
Main treatment period	July–August 2007.	September–December 2003.
Efficacy monitoring and retreatment	March 2008–May 2009, monitored residual population and vessel infection rate, and maintained wharf piles wraps where feasible. Sporophytes removed from infected vessels.	May–June 2004, monitored residual population and assessed reinfection of vessels antifouled during the main treatment period.
Sustained control		
Management goals	Eradicate multiple *Undaria* populations and minimise the risk of reinvasion by anthropogenic vectors.	Contain and eventually eradicate multiple *Didemnum* populations, and minimise the risk of reinvasion by anthropogenic vectors.
Main habitats infected	Marine farms, moorings, shallow subtidal cobble habitats, artificial rock wall.	Marine farms, wharf piles, artificial rock wall, floating jetties, moorings and seabed debris.
Spatial scale	Regional scale within Big Glory Bay (~12 km^2) and Bluff Harbour (~10 km^2), with vector management in four additional ports.	Regional scale within the Marlborough Sounds (~750 km^2).
Primary treatments	Monthly hand removal of visible sporophytes from infected habitats and anthropogenic vectors. Trialled methods to treat microscopic gametophyte life-stage.	Encapsulated infected substrata in plastic, with monthly assessment and retreatment of residual populations.
Main treatment period	1997–2004.	2006–2008.
Efficacy monitoring and retreatment	1997–2004, monthly diver counts and removal of residual populations, and monthly assessment of rates of vessel infection. Intermittent regional delimitation outside main control areas.	2006–2008, monthly qualitative assessment of residual populations and intermittent assessment of vessels in same location as 2003. Intermittent regional delimitation.

control that sustained very low or near-zero population densities in two of the locations, almost completely eliminated the occurrence of *Undaria* on susceptible vessels.

In contrast, during the subsequent partial control efforts in Bluff Harbour, *Undaria* was recorded on an average of 39% of vessels (n=1,036 vessel inspections in total), with the range of monthly values being 27–45% (Figure 2A). These values are comparable to the reference port data from the sustained control program, suggesting that partial control did not measurably contribute to the goal of reducing vector infection and risk to Fiordland. A factor that could have contributed to the high level of vessel infection during partial control is continued emergence and growth of *Undaria* sporophytes from the gametophyte 'seed bank' (Hewitt et al. 2005), rather than new infection by spores. However, reports from the local dive contractor indicate that, simultaneous with observations of high vessel infection, there was considerable (but unquantified) infection of the plastic pile wraps by *Undaria* (i.e. representing new infection). Some spores may have arisen from *Undaria* that was not initially treated, but the most important source was probably the abundant *Undaria* remaining as a result of treatment failure. In particular, there was on-going dislodgement of plastic wraps by strong water currents in Bluff Harbour, with damaged wraps not replaced on 20% of piles, and monthly repair and maintenance needed for about half of the 450 wrapped piles remaining (Sinner et al. 2009).

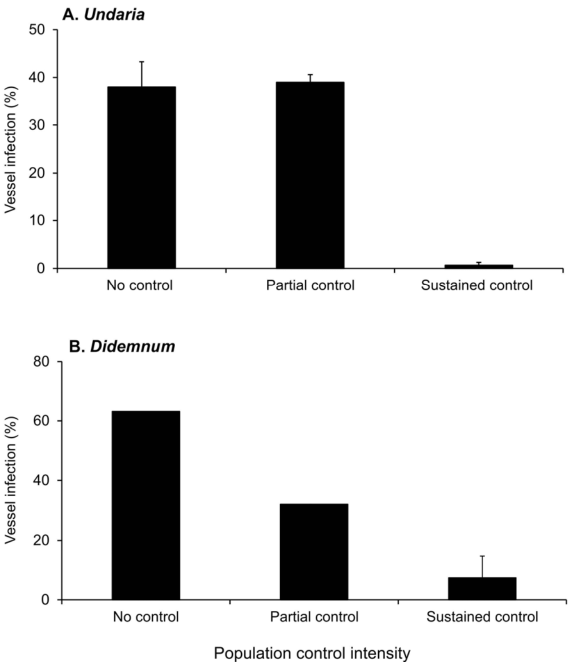

Figure 2. Incidence of vessel infection. A. Metadata on monthly vessel infection by *Undaria*, grouped according to population control strategy: no control (mean ±SE of monthly mean values from n=4 locations), partial control (mean ±SE of monthly values from a single location on n=12 occasions) and sustained controlled (mean ±SE of monthly mean values from n=2 locations). B. Vessel infection by *Didemnum* two years after the initial incursion (no control, one survey), in the year following partial population control and vessel antifouling (one survey), and during sustained control and on-going vessel treatment (mean ±SE of n=2 surveys).

Didemnum management

Background

Didemnum was first discovered in Shakespeare Bay in the inner Marlborough Sounds (the case study area, Figure 1) in December 2001. It is present year-round in this region, but is most prolific in summer when it can form extensive drooping colonies (Fletcher et al. 2013a). *Didemnum* populations occur almost exclusively on artificial structures (Forrest et al. 2013), and spread by larval dispersal typically occurs over scales of tens to hundreds of metres (Fletcher et al. 2013b). Efforts to manage the species were primarily funded by the aquaculture industry. Assistance from government agencies was limited, as they had been advised that *Didemnum* was likely to be a previously undescribed native species (Kott 2002), although subsequent studies suggest it originated from the northwest Pacific region (Stefaniak et al. 2009; Smith et al. 2012). The *Didemnum* management efforts provide parallels with *Undaria* in that there was a local-scale program that was only partly effective (detailed in Coutts and Forrest 2007), which we term partial control, followed by a multi-year regional-scale control effort that mirrors the sustained control program described for *Undaria* (see Table 1).

Local-scale partial Didemnum control (2003)

Over the two years following *Didemnum*'s discovery in 2001, the species became well established in Shakespeare Bay. Although regional delimitation surveys suggested that *Didemnum*'s distribution was confined to the bay, there was concern that infected vessels at the head of the bay would spread the species to aquaculture sites in the region. As such, an attempt to eradicate *Didemnum* from Shakespeare Bay was undertaken between September and December 2003. Treatment measures included the removal of infected vessels and barges to land where they were cleaned and antifouled, and encapsulation of the piles on an international shipping wharf, as well as the artificial rock wall beneath it (Table 1). As detailed in Coutts and Forrest (2007), these methods failed to completely eliminate *Didemnum*.

Sustained regional Didemnum control (2006–2008)

Following the unsuccessful eradication attempt in 2003, a substantial *Didemnum* biomass began to re-establish. In 2006 a more distant population was found on a mussel farm, which was linked to the earlier movement of an infected fish farm pontoon that had been temporarily moored in Shakespeare Bay. Due to concerns regarding impacts to shellfish aquaculture, an intensive surveillance and eradication program was initiated in July 2006 in Shakespeare Bay and the wider Marlborough Sounds, and continued for two years until eradication was no longer considered feasible with the limited funds available (Table 1). Infected vessels, wharf piles, floating pontoons, and moorings in the region were encapsulated, at times incorporating chemicals such as bleach and acetic acid (Pannell and Coutts 2007). Treatments on marine farms also included hand removal of colonies and water blasting. Initial treatments in 2006 were followed by monthly inspection and re-treatment as necessary. Periodic surveillance was undertaken across the Marlborough Sounds region, with knowledge of *Didemnum*'s distribution supplemented by stakeholder reports. Information on control success and population spread was extracted from records kept by a *Didemnum* Working Group (set up in 2006 to oversee the sustained control program) and contract divers involved in management operations.

Results of Didemnum population control programs

Reduction in population size and incidence of vector infection

Our ability to measure control success for the *Didemnum* programs is constrained by infrequent sampling, and single point-in-time assessments pre- and post-management. As the population size and incidence of vessel infection will be time-dependent, it is only the broad differences in the efficacy of the control scenarios that are considered here. The pre-mitigation level of *Didemnum* infection observed during July to September 2003 (immediately prior to partial control) is used here as the reference condition against which the efficacy of control efforts is compared. In that period, *Didemnum* had extensively colonised 99% of 178 piles of the shipping wharf in Shakespeare Bay and the artificial rock wall directly beneath. The baseline incidence of vessel infection in the bay was estimated at 63% (Figure 2B), reflecting the infection of five adjacent barges, and 7 of 14 moored recreational vessels (Coutts 2005; Coutts and Forrest 2007). At the completion of partial control in 2003, we estimated that the *Didemnum* population was suppressed to ~10% of the pre-treatment level (with only 7% of the 178 wharf piles infected), based on data provided in Coutts (2005). However, within 12 months post-treatment, 87% of the wharf piles were re-infected with *Didemnum*, and the concurrent incidence of vessel infection was 32%, which we define as illustrative of the success of partial control (Figure 2B).

In contrast with no control and partial control, sustained control from 2006–2008, led to a substantial reduction in multiple populations of *Didemnum* throughout the Marlborough Sounds, achieving local eradication from two locations. In Shakespeare Bay, the mean incidence of vessel infection over two surveys was 7% during the two year control period (Figure 2B), with no vessels infected at the time of a final survey in January 2008. The absence of vessel re-infection at that time was concomitant with a substantial reduction in *Didemnum* populations on treated structures. For example, from a visibly extensive cover on 178 wharf piles in Shakespeare Bay, only very small patches of *Didemnum* remained in 2008 (which we estimated to be less than 0.1% of the initial population, based on diver observations).

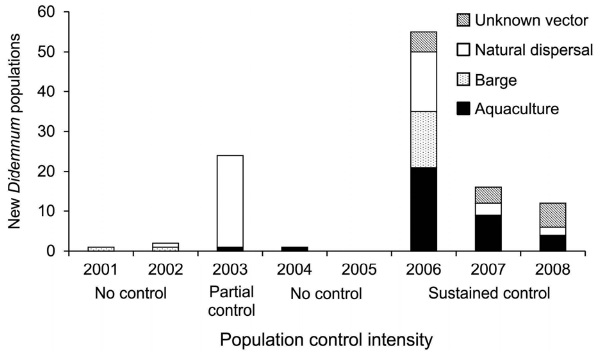

Figure 3. Records of new *Didemnum* populations throughout the Marlborough Sounds from first incursion in 2001 to the end of sustained population control in 2008. No population control was undertaken in 2004 and 2005. The relative importance of key anthropogenic pathways and natural dispersal in the occurrence of the new populations is indicated.

Regional spread of *Didemnum*

Treatment of vessels and other vectors by encapsulation, combined with population management to reduce further infection, was expected to negate or greatly reduce the regional-scale spread of *Didemnum*. Below we present data on the occurrence of new populations of *Didemnum* in the study region following its introduction in 2001, and discuss these findings in relation to the timing and levels of management intervention, and the known vectors of spread. As discoveries of new populations reflect different levels of surveillance over time, and include stakeholder sightings, it was not possible to normalise the data in relation to surveillance effort; nonetheless, a number of insights can be gained from the available information.

Regional delimitation revealed that *Didemnum* had a limited distribution over 2001–02 (Figure 3), with a substantial increase in new populations in Shakespeare Bay in 2003 almost certainly resulting from bay-scale natural dispersal from the shipping wharf (Coutts and Forrest 2007). In the subsequent year, only one new population was reported (although systematic surveillance was not being conducted), but the delimitation survey undertaken at the start of sustained control in 2006, revealed 55 new populations of *Didemnum* across the Marlborough Sounds. This is presumed to reflect cumulative spread over 2004–2006, and was exacerbated by specific known events (Figure 3). In particular, *Didemnum* Working Group records revealed that 38% of the new populations arose via intra-regional transfers of infected mussel seed-stock among marine farms; most of this stock had originated from a single marine farm. Additionally, a single barge from Shakespeare Bay was implicated in the establishment of a further 14 populations. Following regional anthropogenic spread to artificial structures, natural dispersal among adjacent structures was considered the key mechanism of local population spread in some bays, mirroring the 'stepping stone' process of spread described for other marine bioinvasions (Airoldi et al. 2005; Floerl and Inglis 2005; Bulleri and Chapman 2010).

A key observation from Figure 3 is the reduction in new *Didemnum* populations during sustained control in 2006–2008. Toward the end of this period, no vessel movements were implicated in the further spread of *Didemnum* within the Marlborough Sounds, which is consistent with the initial decrease and then absence of vessel infection. In contrast, aquaculture activities remained a significant means of transfer, arising from extensive infestations on 47 mussel farms across the region. While plastic encapsulation proved an effective treatment method for moorings and other structures (Pannell and Coutts 2007), mussel farms remained difficult to treat due to their size and structural complexity, and the unavailability of completely effective or affordable treatments for *Didemnum* that did not also adversely affect the cultured mussels (Denny 2008). Methods such as water blasting, and the colony fragmentation that resulted, may even have locally exacerbated the problem.

Discussion

We compared management efforts for two marine pests in New Zealand, for which population reduction was undertaken in concert with vector management to reduce the likelihood of spread to uninfected regions. Population control in transport hubs eliminated or substantially reduced vector infection, but required an intensive and sustained effort to almost completely eliminate propagule sources. By contrast, partial population control led to limited benefit in terms of vector risk reduction. More importantly, a cessation or reduction in population control efforts resulted in relatively rapid vessel re-infection. Such findings are consistent with marine pest control efforts internationally. Whereas many efforts have been ineffective in achieving long-term control of established populations (e.g. Critchley et al. 1986; Whitehead 2008), other examples exist where sustained and coordinated control of pests and risk vectors (e.g. using mandatory control measures) have been successful and even led to local eradication (Bax 1999; Hewitt et al. 2009b).

Our analyses re-emphasize the need for a long-term commitment to integrated population and vector control programs as part of the decision-making and management process. Simultaneously we recognize that such commitments are often difficult to obtain, therefore a focus on prevention and on development of improved control technologies remains a critical goal for the management of marine bioinvasions. The lack of commitment to the *Undaria* and *Didemnum* programs in part reflected a view by some stakeholders that the level of risk did not justify the expenditure required for effective management. In these programs as with others, it is evident that gaining stakeholder support can greatly depend on their perception of the level of risk, and also their belief in who should be responsible for management (Anderson 2005; Trenouth and Campbell 2013). The failure of the *Undaria* and *Didemnum* programs, combined with recognition that unmanaged risk pathways directly threatened the values that the programs aimed to protect (Dodgshun et al. 2007; Hayden et al. 2009; Sinner et al. 2009), led some stakeholders to question the value of managing established marine pests. This situation highlights the importance of aligning population management with effective controls on vectors, based on a systematic assessment of all risk pathways (e.g. Campbell and Hewitt 2013).

The characteristics of target pest species can have an important bearing on the efficacy and goals of population control (Vander Zanden et al. 2010; Pluess et al. 2012). Recognition that *Undaria* and *Didemnum* are slow to spread by natural processes, and may encounter barriers that restrict their range expansion (Forrest et al. 2009), provided a theoretical basis for controlling populations in the vicinity of anthropogenic vectors. As well as increasing the likely benefits of vector management, these biological attributes simultaneously made population delimitation and control a relatively tractable prospect. On the other hand, both species have features that made control more challenging than initially envisaged. For example, a single *Didemnum* larva has the potential to develop into a colony that can reproduce both sexually and by fragmentation (Fletcher and Forrest 2011; Morris and Carman 2012). Similarly, spores released from a single mature *Undaria* can seed a new generation of sporophytes (Hay and Luckens 1987). In both cases, any colonies or individuals missed during surveillance and control operations had the potential to reach maturity and inoculate susceptible habitats (including vectors).

Despite the availability of a range of potential management tools for marine population control (Piola et al. 2009; Bax 1999; Hewitt et al. 2009b), failings identified in our case studies reiterate the need for methods that are tailored to the species and environments for which they are used. In some instances, no suitable methods were available for *Undaria* and *Didemnum*; in particular the effective treatment of mussel farms, as techniques commonly employed to control mussel aquaculture biofouling in Canada (Locke et al. 2009) were not considered feasible or affordable in the context of the New Zealand industry. In some cases, a lack of treatment efficacy was attributable to the methods being in developmental stages (e.g. Coutts and Forrest 2007), or effectiveness was undermined by situation-specific factors. For example, plastic encapsulation of piles and other artificial structures was 93% effective in the first *Didemnum* program and almost 100% successful in the second (Pannell and Coutts 2007). By contrast, the same method was used by the same dive contractor in the subsequent Bluff Harbour *Undaria* program, but success in that location was comprised by the physical effects of strong water currents.

Conclusions and future directions

Sustained and intensive population control has the potential to greatly assist with the goal of reducing the human-mediated spread of marine pests, yet this management approach clearly poses challenges even for single species. Future scenarios will conceivably involve multiple risk species, or multiple infested locations, requiring managers to make decisions in the face of ever increasing complexity. Despite such challenges, it is becoming increasingly recognised that slowing the rate of marine pest spread (especially to high value areas) can be a worthwhile strategy, even in situations where incursion in the medium to long-term is inevitable. For example, recent analyses of the costs and benefits of managing the clubbed tunicate, *Styela clava*, in New Zealand, illustrated significant economic benefits for shellfish aquaculture by delaying spread from infected ports by a matter of a few years (Deloitte 2011; MPI 2013).

Although direct vector controls are clearly critical to any marine pest strategy based on spread reduction, a key benefit of simultaneous population control is that it provides insurance against ineffective vector management (e.g. because of non-compliance with management requirements, or unavailability of tools). Optimizing such approaches may benefit from advancement of existing frameworks proposed for management of pests and pathways (e.g. Bax et al. 2001; Forrest et al. 2006; Hewitt and Campbell 2007; Campbell 2009), and recognition of the key factors that influence management success (e.g. Myers et al. 2000; Pluess et al. 2012). However, it will be a significant challenge to progress beyond insights such as provided by our case study, to the provision of more quantitative guidance on the extent of population control needed to reduce or negate vector risk, as many situation-specific factors (e.g. propagule supply characteristics, hydrological conditions, vector susceptibility) will influence success. It will also be a challenge to convince stakeholders of the merits of marine pest management programs whose best outcome may be to slow the rate of marine pest spread. For population control to be perceived as having practicality in marine systems as a complementary means of reducing vector risk, there remains the need for socially acceptable and affordable control tools that are effective across relatively large spatial scales.

Acknowledgements

We thank Oli Floerl and Richard Piola for helpful comments on an early draft manuscript, anonymous referees for their critique of the first submission, and Lauren Fletcher for review of the final draft. We are grateful to Jennie Brunton (Ministry of Primary Industries) and Paul Young (dive contractor, Bluff) for providing information relating to the second *Undaria* management program in Bluff Harbour. Thanks also to Aaron Pannell, Bruce Lines and the *Didemnum* Working Group for providing access to data from the *Didemnum* management programs. This work was made possible through projects part-funded by NIWA under Coasts and Oceans Research Program 4 – Marine Biosecurity (2012/13 SCI) and the New Zealand Ministry of Business Innovation and Employment (Contract C01X0502, Effective Management of Marine Biodiversity and Biosecurity).

References

Airoldi L, Abbiati M, Beck MW, Hawkins SJ, Jonsson PR, Martin D, Moschella PS, Sundelöf A, Thompson PR, Åberg P (2005) An ecological perspective on the development and design of low-crested and other hard coastal defence structures. *Coastal Engineering* 52: 1073–1087, http://dx.doi.org/10.1016/j.coastaleng.2005.09.007

Akiyama K, Kurogi M (1982) Cultivation of *Undaria pinnatifida* (Harvey) Suringar: the decrease in crops from natural plants following crop increase from cultivation. *Bulletin of the Tohoku Regional Fisheries Research Laboratory* 44: 91–100

Anderson LW (2005) California's reaction to *Caulerpa taxifolia*: a model for invasive species rapid response. *Biological Invasions* 7: 1003–1016, http://dx.doi.org/10.1007/s10530-004-3123-z

Bax N, Carlton JT, Mathews-Amos A, Haedrich RL, Howarth FG, Purcell JE, Rieser A, Gray A (2001) The control of biological invasions in the world's oceans. *Conservation Biology* 15: 1234–1246, http://dx.doi.org/10.1046/j.1523-1739.2001.99487.x

Bax NJ (1999) Eradicating a dreissenid from Australia. *Dreissena!* 10(3): 1–5

Bulleri F, Chapman MG (2010) The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology* 47(1): 26–35, http://dx.doi.org/10.1111/j.1365-2664.2009.01751.x

Campbell ML (2009) An overview of risk assessment in a marine biosecurity context. In: Rilov G, Crooks JA (eds), Biological Invasions in Marine Ecosystems: Ecological, Management, and Geographic Perspectives. Springer-Verlag, pp 353–374, http://dx.doi.org/10.1007/978-3-540-79236-9_20

Campbell ML, Hewitt CL (2013) Protecting high-value areas from introduced marine species. *Management of Biological Invasions* 4: 171–189, http://dx.doi.org/10.3391/mbi.2013.4.3.01

Clout MN, Veitch CR (2002) Turning the tide of biological invasions: the potential for eradicating invasive species. In: Veitch CR, Clout MN (eds), Turning the tide: the eradication of invasive species. IUCN SSC Invasive Species Specialist Group, IUCN, Gland, Switzerland and Cambridge, UK, pp 1–3

Coutts ADM (2005) The detection, spread and management of *Didemnum vexillum* in Queen Charlotte Sounds, New Zealand. Cawthron Report 1092, Cawthron Institute, Nelson, New Zealand, 38 pp

Coutts ADM, Forrest BM (2007) Development and application of tools for incursion response: lessons learned from the management of the fouling pest *Didemnum vexillum*. *Journal of Experimental Marine Biology and Ecology* 342(1): 154–162, http://dx.doi.org/10.1016/j.jembe.2006.10.042

Critchley AT, Farnham WF, Morrell SL (1986) An account of the attempted control of an introduced marine alga, *Sargassum muticum*, in Southern England. *Biological Conservation* 35(4): 313–332, http://dx.doi.org/10.1016/0006-3207(86)90092-3

Culver KL, Kuris AM (2000) The apparent eradication of a locally established introduced marine pest. *Biological Invasions* 2(3): 245–253, http://dx.doi.org/10.1023/A:1010082407254

Deloitte (2011) MAF *Styela clava* economic impact assessment. August 2011, 26 pp

Denny CM (2008) Development of a method to reduce the spread of the ascidian *Didemnum vexillum* with aquaculture transfers. *ICES Journal of Marine Science* 65(5): 805–810, http://dx.doi.org/10.1093/icesjms/fsn039

Dodgshun TJ, Taylor MD, Forrest BM (2007) Human-mediated pathways of spread for nonindigenous marine species in New Zealand. DOC Research and Development Series 266, Department of Conservation, Wellington, New Zealand, 44 pp

Drake JM, Lodge DM (2004) Global hot spots of biological invasions: evaluating options for ballast-water management. *Proceedings of the Royal Society B* 271: 575–580, http://dx.doi.org/10.1098/rspb.2003.2629

Fletcher LM, Forrest BM (2011) Induced spawning and culture techniques for the invasive ascidian *Didemnum vexillum* (Kott, 2002). *Aquatic Invasions* 6: 457–464, http://dx.doi.org/10.3391/ai.2011.6.4.11

Fletcher LM, Forrest BM, Atalah J, Bell JJ (2013a) Reproductive seasonality of the invasive ascidian *Didemnum vexillum* in New Zealand and implications for shellfish aquaculture. *Aquaculture Environment Interactions* 3(3): 197–211, http://dx.doi.org/10.3354/aei00063

Fletcher LM, Forrest BM, Bell JJ (2013b) Natural dispersal mechanisms and dispersal potential of the invasive ascidian *Didemnum vexillum*. *Biological Invasions* 15: 627–643, http://dx.doi.org/10.1007/s10530-012-0314-x

Floerl O, Inglis GJ (2003) Boat harbour design can exacerbate hull fouling. *Austral Ecology* 28(2): 116–127, http://dx.doi.org/10.1046/j.1442-9993.2003.01254.x

Floerl O, Inglis GJ (2005) Starting the invasion pathway: the interaction between source populations and human transport vectors. *Biological Invasions* 7: 589–606, http://dx.doi.org/10.1007/s10530-004-0952-8

Floerl O, Inglis GJ, Dey K, Smith A (2009) The importance of transport hubs in stepping-stone invasions. *Journal of Applied Ecology* 46(1): 37–45, http://dx.doi.org/10.1111/j.1365-2664.2008.01540.x

Forrest BM, Fletcher LM, Atalah J, Piola RF, Hopkins GA (2013) Predation Limits Spread of *Didemnum vexillum* into Natural Habitats from Refuges on Anthropogenic Structures. *PLOS ONE* 8(12): e82229, http://dx.doi.org/10.1371/journal.pone.0082229

Forrest BM, Taylor MD, Sinner J (2006) Setting priorities for the management of marine pests using a risk-based decision support framework. In: Allen RB, Lee WG (eds), Biological invasions in New Zealand. Springer-Verlag, pp 299–405, http://dx.doi.org/10.1007/3-540-30023-6_25

Forrest BM, Gardner JPA, Taylor MD (2009) Internal borders for managing invasive marine species. *Journal of Applied Ecology* 46(1): 46–54, http://dx.doi.org/10.1111/j.1365-2664.2008.01544.x

Forrest BM, Brown SN, Taylor MD, Hurd CL, Hay CH (2000) The role of natural dispersal mechanisms in the spread of *Undaria pinnatifida* (Laminariales, Phaeophyta). *Phycologia* 39: 547–553, http://dx.doi.org/10.2216/i0031-8884-39-6-547.1

Glasby TM, Connell SD, Holloway MG, Hewitt CL (2007) Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? *Marine Biology* 151(3): 887–895, http://dx.doi.org/10.1007/s00227-006-0552-5

Hay CH, Luckens PA (1987) The Asian kelp *Undaria pinnatifida* (Phaeophyta: Laminariales) found in a New Zealand harbour. *New Zealand Journal of Botany* 25: 364–366, http://dx.doi.org/10.1080/0028825X.1987.10410079

Hayden BJ, Inglis GJ, Schiel DR (2009) Marine invasions in New Zealand: a history of complex supply-side dynamics. In: Rilov G, Crooks JA (eds), Biological Invasions in Marine Ecosystems: Ecological, Management, and Geographic Perspectives. Springer-Verlag, pp 409–423, http://dx.doi.org/10.1007/978-3-540-79236-9_24

Hewitt CL, Campbell ML (2007) Mechanisms for the prevention of marine bioinvasions for better biosecurity. *Marine Pollution Bulletin* 55(7–9): 395–401, http://dx.doi.org/10.1016/j.marpolbul.2007.01.005

Hewitt CL, Gollasch S, Minchin D (2009a) The vessel as a vector – biofouling, ballast water and sediments. In: Rilov G, Crooks JA (eds), Biological Invasions in Marine Ecosystems: Ecological, Management, and Geographic Perspective. Springer-Verlag, pp 117–131, http://dx.doi.org/10.1007/978-3-540-79236-9_6

Hewitt CL, Everett RA, Parker N (2009b) Examples of current international, regional and national regulatory frameworks for preventing and managing marine bioinvasions. In: Rilov G, Crooks JA (eds), Biological Invasions in Marine Ecosystems: Ecological, Management, and Geographic Perspectives. Springer-Verlag, pp 335–352, http://dx.doi.org/10.1007/978-3-540-79236-9_19

Hewitt CL, Campbell ML, McEnnulty F, Moore KM, Murfet NB, Robertson B, Schaffelke B (2005) Efficacy of physical removal of a marine pest: the introduced kelp *Undaria pinnatifida* in a Tasmanian Marine Reserve. *Biological Invasions* 7: 251–263, http://dx.doi.org/10.1007/s10530-004-0739-y

Hopkins GA, Forrest BM, Jiang W, Gardner JPA (2011) Successful eradication of a non-indigenous marine bivalve from a subtidal soft-sediment environment. *Journal of Applied Ecology* 48(2): 424–431, http://dx.doi.org/10.1111/j.1365-2664.2010.01941.x

Hunt L, Chadderton L, Stuart M, Cooper S, Carruthers M (2009) Results of an attempt to control and eradicate *Undaria pinnatifida* in Southland, New Zealand, April 1997 – November 2004. Department of Conservation, Invercargill, New Zealand, 48 pp

Kott P (2002) A complex didemnid ascidian from Whangamata, New Zealand. *Journal of the Marine Biological Association of the United Kingdom* 82(4): 625–628, http://dx.doi.org/10.1017/S0025315402005970

Lacoursière-Roussel A, Forrest B, Guichard F, Piola R, McKindsey C (2012) Modeling biofouling from boat and source characteristics: a comparative study between Canada and New Zealand. *Biological Invasions* 14: 2301–2314, http://dx.doi.org/10.1007/s10530-012-0230-0

Liebhold A, Bascompte J (2003) The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters* 6(2): 133–140, http://dx.doi.org/10.1046/j.1461-0248.2003.00405.x

Locke A, Doe KG, Fairchild WL, Jackman PM, Reese RJ (2009) Preliminary evaluation of effects of invasive tunicate management with acetic acid and calcium hydroxide on non-target marine organisms in Prince Edward Island, Canada. *Aquatic Invasions* 4(1): 221–236, http://dx.doi.org/10.3391/ai.2009.4.1.23

Moody ME, Mack RN (1988) Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* 25(3): 1009–1021, http://dx.doi.org/10.2307/2403762

Morris J, Jr., Carman M (2012) Fragment reattachment, reproductive status, and health indicators of the invasive colonial tunicate *Didemnum vexillum* with implications for dispersal. *Biological Invasions* 14(10): 2133–2140, http://dx.doi.org/10.1007/s10530-012-0219-8

MPI (2013) Cost benefit analysis: *Styela clava* in Picton. Ministry for Primary Industries, Wellington, New Zealand, 20 pp

Myers JH, Simberloff D, Kuris A, Carey J (2000) Eradication revisited: dealing with exotic species. *Trends in Ecology and Evolution* 15: 316–320, http://dx.doi.org/10.1016/S0169-5347(00)01914-5

Pannell A, Coutts ADM (2007) Treatment methods used to manage *Didemnum vexillum* in New Zealand. Report prepared for Biosecurity New Zealand. New Zealand Marine Farming Association, 29 pp

Parkes JP (2006) Does commercial harvesting of introduced wild mammals contribute to their management as conservation pests? In: Allen RB, Lee WG (eds), Biological invasions in New Zealand. Springer-Verlag, pp 407–420, http://dx.doi.org/10.1007/3-540-30023-6_26

Piola RF, Forrest BM (2009) Options for managing biosecurity risks from recreational vessel hubs. Cawthron Report 1591, Cawthron Institute Nelson, 45 pp

Piola RF, Denny CM, Forrest BM, Taylor MD (2009) Marine biosecurity: management options and response tools. In: Williams PA, Clout MN (eds), Invasive Species Management: A Handbook of Principles and Techniques. Oxford University Press, UK, pp 205–231

Pluess T, Jarošík V, Pyšek P, Cannon R, Pergl J, Breukers A, Bacher S (2012) Which factors affect the success or failure of eradication campaigns against alien species? *PLOS ONE* 7(10): 1–11, http://dx.doi.org/10.1371/journal.pone.0048157

Ruiz GM, Carlton JT (2003) Invasive Species: Vectors and Management Strategies. Island Press, Washington DC, 518 pp

Simberloff D (2002) Today Tititiri Matangi, tomorrow the world! Are we aiming too low in invasives control? In: Veitch CR, Clout MN (eds). Turning the tide: the eradication of invasive species. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK, pp 4–12

Sinner J, Forrest BM, O'Brien M, Piola RF, Roberts B (2009) Fiordland marine biosecurity risk management: operational plan recommendations 2009–2013. Prepared for MAF Biosecurity New Zealand and Fiordland Marine Guardians. Cawthron Report 1621, Cawthron Institute, Nelson, New Zealand, 32 pp plus appendices

Sliwa C, Johnson CR, Hewitt CL (2006) Mesoscale dispersal of the introduced kelp *Undaria pinnatifida* attached to unstable substrata. *Botanica Marina* 49: 396–405, http://dx.doi.org/10.1515/BOT.2006.051

Smith KF, Stefaniak L, Saito Y, Gemmill CEC, Cary SC, Fidler AE (2012) Increased Inter-Colony Fusion Rates Are Associated with Reduced COI Haplotype Diversity in an Invasive Colonial Ascidian *Didemnum vexillum*. *PLOS ONE* 7(1): e30473, http://dx.doi.org/10.1371/journal.pone.0030473

Stefaniak L, Lambert G, Gittenberger A, Zhang H, Lin S, Whitlatch RB (2009) Genetic conspecificity of the worldwide populations of *Didemnum vexillum* Kott, 2002. *Aquatic Invasions* 4(1): 29–44, http://dx.doi.org/10.3391/ai.2009.4.1.3

Stuart MD (2002) Translocation of *Undaria pinnatifida* by vessel fouling: analysis of the Department of Conservation vessel monitoring database, May 1999–May 2001, 55 pp

Stuart MD (2004) Review of research on *Undaria pinnatifida* in New Zealand and its potential impacts on the eastern coast of the South Island. DOC Science Internal Series 166. Department of Conservation, Wellington, New Zealand, 40 pp

Trenouth AL, Campbell ML (2013) Perceptions of ecological risk associated with introduced marine species in marine protected areas. *Management of Biological Invasions* 4(1): 7–24, http://dx.doi.org/10.3391/mbi.2013.4.1.03

Tyrrell MC, Byers JE (2007) Do artificial substrates favor nonindigenous fouling species over native species? *Journal of Experimental Marine Biology and Ecology* 342(1): 54–60, http://dx.doi.org/10.1016/j.jembe.2006.10.014

Vander Zanden MJ, Hansen GJA, Higgins SN, Kornis MS (2010) A pound of prevention, plus a pound of cure: early detection and eradication of invasive species in the Laurentian Great Lakes. *Journal of Great Lakes Research* 36(1): 199–205, http://dx.doi.org/10.1016/j.jglr.2009.11.002

Whitehead J (2008) Derwent Estuary introduced marine and intertidal species: review of distribution, issues, recent actions and management options. Derwent Estuary Program, Tasmania, Australia, October 2008, 48 pp