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The apparent eradication of a locally established introduced marine pest

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Abstract

Once a marine invader has become established, its subsequent control has rarely been attempted. We report the first apparently successful eradication of a locally well-established introduced marine pest. A previously unknown species of sabellid polychaete (now described as *Terebrasabella heterouncinata*) arrived as an epizoic contaminant on South African abalone imported to California for commercial aquaculture research. In 1996, we detected an established sabellid population at an intertidal site near Cayucos, California (35°45′ N, 120°95′ W). To mitigate the impact of this introduced marine pest at this site, and prevent or slow its geographic spread, we proposed an eradication program based on the epidemiological theory of the threshold of transmission. Specifically, we removed 1.6 million of the most highly susceptible and preferred host in the intertidal area; the black turban snail, *Tegula funebralis*. A screen was also installed at the associated abalone mariculture facility to eliminate release of additional infested material (the source of the established sabellid population) and all such material was removed from the intertidal area. Using transect surveys and mark and recapture studies, we monitored the success of the eradication effort. Transmission of the pest can no longer be detected. Hence, the established sabellid population has apparently been eradicated. This discovery demonstrates that some alien marine pests can be eradicated and supports development of new proactive approaches to the management of other exotic marine pests.

Introduction

The introduction and subsequent establishment of non-indigenous marine species continues globally (Carlton and Geller 1993; Cohen and Carlton 1998). As the detrimental impacts of such bioinvasions are realized, many nations are developing programs to prevent these introductions. However, for those marine pests already established, little is being done despite the availability of a variety of strategies to eradicate and control terrestrial (often agricultural) and freshwater exotics (Office of Technology Assessment 1993). While prevention of further marine introductions will generally be the most desirable option, it does not mitigate pests that are already here or are yet to come. Hence, the arrival and establishment of a new and serious alien marine species on the California coast led us to attempt its eradication.

In 1993 an unusual pest was discovered in California abalone mariculture facilities (AMFs) (Oakes and Fields 1996). It proved to be an undescribed species of sabellid polychaete, native to southern Africa (Culver et al. 1997; Kuris and Culver 1999); subsequently described as *Terebrasabella heterouncinata* (Fitzhugh and Rouse 1999). Its unique mechanism of settlement on the outer lip of the aperture altered shell deposition and often severely retarded the growth of infested individuals (Culver et al. 1997; Kuris and Culver 1999). Heavily infested abalone exhibited a characteristic domed teratology (Oakes and Fields 1996; Kuris and Culver 1999). These shells were brittle, being riddled with thousands of worm tubes. Ultimately all

AMFs in California became infested, economic losses to the industry were considerable and the California Department of Fish and Game (CDFG) established a policy to prevent further spread of the sabellid and ultimately to eradicate the worm from the AMFs (Culver et al. 1997; F. Wendell, pers. comm.). Fears concerning environmental contamination, by release of the worms from an infested facility, or from outplantings of infested stock for fisheries renewal, were realized when, in 1996, we discovered a substantial population of these sabellids in the rocky intertidal habitat below the water discharge outflow of a heavily infested AMF near Cayucos, California (35°45′ N, 120°95′ W).

We judged the potential impact of this worm to be considerable. Studies of host specificity indicated that, in addition to abalone, several species of abundant California native gastropods were highly susceptible to infestation by the sabellid (Kuris and Culver 1999; Culver 1999). In addition, in its native habitats in South Africa and Namibia, the sabellid infested many gastropod species (Ruck and Cook 1998; Culver 1999) and deformed the shells of some of these hosts (Kuris et al., in prep.). Further, its continuously produced benthic larval stage and rapid (within hours) competency for settlement suggested that the released sabellid would have only modest potential for long-distance dispersal, but great potential for local recruitment. This would enable establishment of locally dense pest populations with proportionate damage to susceptible host populations. Hence, we proposed actions to prevent further releases from the AMF and devised a plan to achieve eradication of the well-established intertidal sabellid population at Cayucos.

Our eradication strategy relied on the Kermack–McKendrick epidemiological theorem of the threshold host density for transmission (McKendrick 1940; Bailey 1957; Stiven 1964, 1968). There is a certain density of hosts required to maintain a rate of transmission sufficient for a parasite population to persist. We proposed to break this threshold by removing large numbers of the most susceptible host. Our host specificity and preference experiments indicated that the black turban snail, *Tegula funebralis*, was the most abundant highly susceptible and preferred host of the native mid- to upper-intertidal molluscs at Cayucos, and that large individuals ($>$ 10 mm) were much more susceptible than were small individuals (Culver 1999). By removing as many of these susceptible hosts as was feasible from the contaminated area, we intended to raise the threshold of transmission so high that the sabellid population could not attain replacement levels of recruitment. Here we report the effectiveness of this approach and the success of our sabellid eradication program.

Materials and methods

Our eradication program was conducted in cooperation with the associated AMF and CDFG and had 3 components. Firstly, a screening system was installed in the main discharge trough of the AMF. This system filtered the discharge water, flowing at a rate of 900 m^3/h, through a 46 cm diameter PVC pipe that contained approximately 12 mm holes. Screening prevented the further release of animals and shells harboring adult worms from the facility. However, since water flow from the facility was not finely filtered, it could have included benthic larvae of the sabellid.

Secondly, a clean-up effort was initiated in the intertidal zone near the discharge area. This included removal of all facility-associated animal and shell debris, including live and empty red abalone, *Haliotis rufescens*, and top shell snails, particularly *Tegula montereyi* (Monterey turban snail), *T. brunnea* (brown turban snail), and *Norrisia norrisii* (kelp snail) and shells of these species occupied by hermit crabs. These species typically occur in subtidal regions, often in association with kelp, and enter the culture tanks on kelp harvested and fed to the cultured abalone. *T. brunnea* is also common in the lower intertidal zone and *N. norrisii* is occasionally present in the lowest tidepools. Thus, their presence in the middle and upper intertidal zone was remarkable and undoubtedly due to their release from the aquaculture facility. Empty and hermit-occupied shells of these species were removed because although a live gastropod host is required for establishment, once the tube has been formed by the host, a living host is no longer required for worm survival (Culver et al. 1997; Kuris and Culver 1999), and even empty shells can harbor reproductively active sabellids. These materials were collected from a 1500 m^2 intertidal area directly below and to the south of the facility discharge (the eradication site). Observations indicated that the prevailing water movement at the shoreline was to the south of the outflow pipe, as was the majority of facility-associated animal and shell debris. In addition, most of the infested native snails were found in this area.

Thirdly, approximately 1.6 million *T. funebralis* over 10 mm in shell width were removed from the discharge site to decrease the number of susceptible hosts and thus the rate of sabellid transmission. Although transmission dynamics in the field had not been quantified, laboratory experiments and field observations indicated that transmission was affected by host susceptibility, host size and sabellid host preference. Taken together, the black turban snail was the most abundant, highly susceptible species at this intertidal site. In direct host choice experiments it was much preferred as a host for the larval sabellids compared to the other common snails in the middle to upper intertidal zone (C. Culver, unpublished data).

The eradication site was characterized by numerous tidepools formed by rock outcrops and surfgrass (*Phyllospadix* spp.) beds. The pools were 1–100 m^2 in size, and 15 cm to 3 m deep at low tide. The site was bound to the south by a pebble beach and a steep cliff. Rocky intertidal habitat extended to the north for approximately 50 m^2. However, this area was not included in the susceptible host removal area because sabellid-infested debris released from the facility and susceptible snails were rarely found there.

In September 1996, prior to the initiation of the eradication procedures, we conducted a mark and recapture sentinel host study to assess transmission of the sabellid infestation. These studies were conducted in the fall because this is when sabellid transmission is typically the highest. We collected 200 uninfested *T. funebralis* from Rincon Beach, Santa Barbara County, California. Rincon Beach had never been exposed to sabellid infestations and all snails were examined and confirmed to be uninfested prior to their release. These snails were marked with fingernail polish, released at the infested site and recaptured at 2 week intervals over the next 2 months. Search time was equalized for each recovery event, being limited to 2 h due to tidal incursions and light availability. Upon recapture, animals were examined for newly settled sabellids and released again. We repeated the sentinel host study in fall of 1998, releasing 300 snails. Additional snails were released to increase the likelihood of detecting the declining incidence of sabellid transmission anticipated if the control program was successful. The use of sentinel snails allowed identification of new infestations, and eliminated the possibility that detected infestations resulted from autoinfestation because reproduction to release competent larvae by newly settled sabellids takes longer than 2 months (C. Culver pers. obs.; Ruck and Cook 1998). Thus, we interpreted the data from the sentinel snail experiments as incidence, the number of new cases per unit time. Using incidence data, we can estimate changes in the infestation rate (Durfee 1978; Margolis et al. 1982).

In addition to the sentinel snail studies, surveys of wild *T. funebralis* were conducted prior to and throughout the eradication program. *T. funebralis* was a good indicator species for infestations occurring at the intertidal site because this species was rarely found in the AMF and it was highly susceptible to the sabellid. It was also the most abundant large gastropod in the middle to upper intertidal zones at this site. Further, we rarely detected new sabellid infestations in other gastropod species, including several mid- and upper-intertidal zone limpets (e.g., *Lottia gigantea*, *L. digitalis*, *L. pelta*) whelks (e.g., *Nucella emarginata*, *Acanthina punctulata*) and lower intertidal brown turban snails (*Tegula brunnea*). This indicated that *T. funebralis* was the primary host being utilized by the sabellid. In the first 2 surveys, samples of *T. funebralis* were collected from tidepools where we detected infested animal and shell debris released from the facility. Using this information, we conducted a series of transect surveys for this snail in the fall of 1997 and the spring and fall of 1998. Some of the early samples (September 1995 and July 1997) included locations along some of these transects, thus providing baseline data for our analyses.

During the transect surveys, we collected snails along 6 parallel transect lines, 10–15 m apart, with the first transect line beginning at the discharge pipe and extending perpendicular to the shoreline into the lower intertidal zone. Another 4 lines were located south of the discharge pipe and one was north of the discharge. This placement of the transects was based on observations of the prevailing water movement along the shoreline to the south. Up to 50 individuals were collected at 7 sample sites along each line (1, 5, 10, 15, 20, 30, and 50 m from the shore). Presence of newly settled (new) and established (old) sabellid infestations was recorded. New infestations are detected at the growing edge of the aperture, under the mantle, whereas old infestations are detected on the upper surface of the shell (Culver et al. 1997; Kuris and Culver 1999).

For each transect, the samples from 1 to 20 m from the shoreline were pooled. The outermost 2 samples (30 m and 50 m) were not included because on some transects few or no snails were collected. Where those samples were available, none were infested with sabellids. Prevalence (proportion of infested hosts; Margolis et al. 1982) of new infestations was calculated as the number of snails with new infestations divided by the total number of snails examined. Overall prevalence was calculated as the number of snails with new and/or old infestations divided by the number of snails examined.

Results

Our minimum estimate of the size of the sabellid population on native *T. funebralis* at Cayucos at the onset of the eradication program was 800,000 worms (1.6 million shells removed $\times$ 0.25 (prevalence) $\times$ 2 (mean worm intensity)). If worms on abalone released from the facility are included, the total rises to a minimum of 2.2 million sabellids (2000 (number of infested abalone shells removed) $\times$700 (mean worm intensity)). These estimates are very conservative because we did not include the many worms on the numerous kelp snails released from the facility (hundreds of worms per shell), our estimate of snail abundance was based only on removed snails (many remained in the habitat), and our mean intensity estimates are also low.

From our sentinel snail mark and recapture experiment we were able to confirm that the worms had become established in nature and estimate the rate of new infestations. On the first recapture date, 2 weeks after release of the sentinel snails, 8% were infested. This high incidence led to 32% of the sentinel snails becoming infested in just 6 weeks (Figure 1). After the eradication program was implemented, we repeated the sentinel snail experiment, releasing 50% more sentinel snails to increase the power to detect new infestations. As in the earlier sentinel snail study, the proportion of snails recovered was high, but more individual snails were examined during this latter study (Figure 2). Despite the increased sensitivity of detection and the good recovery rates, no new infestations were detected over the 8 weeks and 4 recapture events. If transmission was still occurring at the pre-eradication rate, the probability of recovering no infestations was extremely small, ranging from 2×10^{-5} to 2×10^{-9} (Table 1).

As indicated by the transect surveys, sabellid infestations were not evenly distributed below the Cayucos facility (Figure 3). The highest infestation rates were found directly below the discharge pipe and 10 m to the south of the pipe. No infested *T. funebralis* were recovered north of the discharge. In the earliest samples there was significant heterogeneity in prevalence among sites ($\chi^2 = 42.70$, $P = 0.001$). As eradication ensued, infestations declined to such low levels that no significant heterogeneity could be detected among sites.

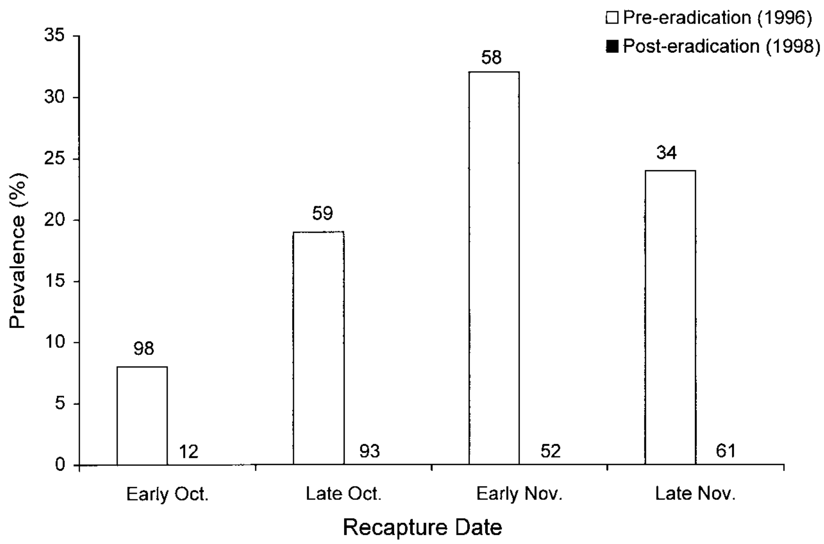

Figure 1. Prevalence of sabellid infestations in marked and recaptured sentinel snails. Number above bar denotes sample size. Number to right of bar denotes post-eradication sample size. Lack of black bars denotes zero infestations detected.

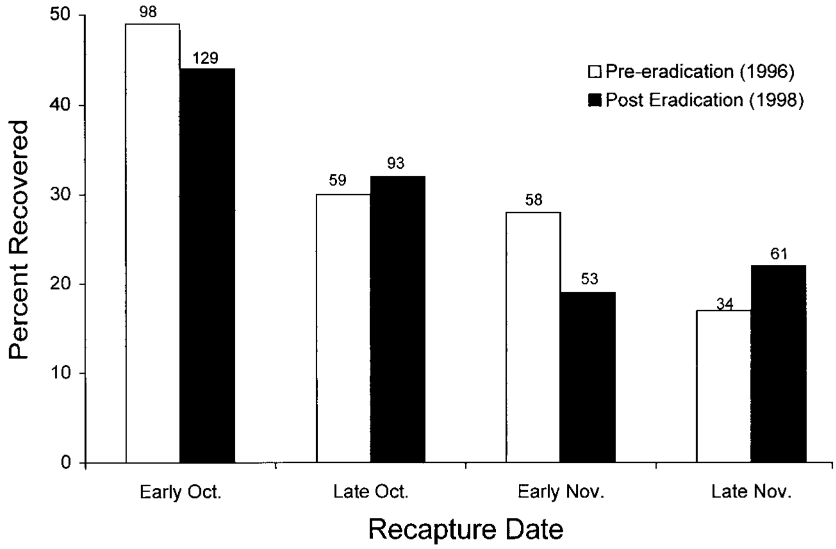

Figure 2. Recovery of marked sentinel snails. Number above bar denotes sample size.

Table 1 The probability of getting zero new infestations on marked sentinel snails (*Tegula funebralis*) recovered in 1998 at each sample date. Probability (*P*) is based on a prevalence of 8% (the lowest prevalence observed in the 1996 sentinel snail study).

Date	*N*	*P*
Early October	129	1.69E-05*
Late October	93	4.64E-09*
Early November	52	1.75E-09*
Late November	61	7.82E-08*

The impact of the initial eradication program at the most heavily infested site, 10 m south of the discharge pipe, is summarized in Figure 4. Upon detection of the sabellids in nature at Cayucos, about a quarter of the most susceptible (> 10 mm) *T. funebralis* at this site were infested and transmission, as indicated by new infestations, was similarly intense. Following initial removal of the facility-associated animals and shell debris, and installation of the screen at the outflow, the overall prevalence of sabellids remained high, but the rate of new infestations dropped to 10%. The removal of 1.6 million of the most susceptible potential host (*T. funebralis* > 10 mm) in July, 1997, greatly reduced the abundance of snails and the incidence of new infestations was barely detectable (< 0.5%). Over the next 14 months, no newly infested *T. funebralis* were recovered and the overall prevalence also declined to zero. The pattern of decline at the other sites was quite similar, although the decline of sabellid infestations was less dramatic because initial prevalence was much lower than at the large system of tidepools 10 m south of the discharge. Some old infestations were also detected.

Discussion

The high prevalence of adult sabellids on the abundant mid- to upper-intertidal host, *T. funebralis*, indicated that the sabellids had spread to native pests beyond the discharge of the AMF. Furthermore, the 8% rate of new infestations over a 2 week period suggests that the sabellid population had achieved epidemic status. The substantial decrease in new infestations following screening and removal of facility-associated animals and shell debris strongly suggests that the source of this population was the release of thousands of adult sabellids in the shells of the escaped gastropods and shell debris from the facility, rather than release of benthic sabellid larvae in the discharge water. In fact, this facility has two discharge sites. We found little to no debris at the other site, and no established sabellid population. Further, we found no, or only small quantities, of facility-associated infested animals and shells at discharge sites of other onshore facilities (C. Culver, unpublished data). Although a few of these farms contained hundreds of thousands to millions of infested abalone, no sabellid populations were detected in the intertidal areas adjacent to these sites.

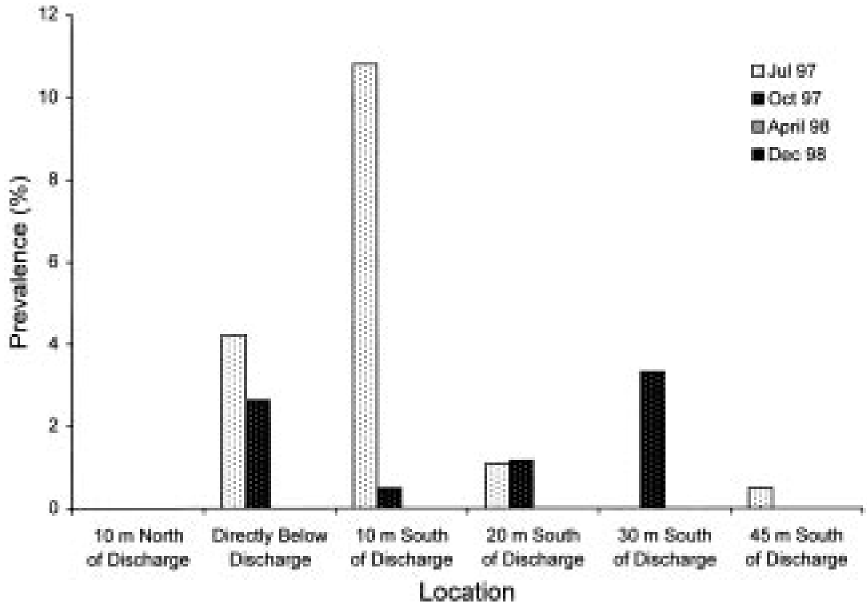

Figure 3. Prevalence of sabellid infestations of *Tegula funebralis* (new infestations only). Lack of bars denotes zero infestations detected.

The marked decrease (56%) in new infestations following clean-up of escaped animals and shell debris from the facility was consistent with the decrease in the sabellid population associated with this material (1.4 million of the 2.2 million sabellids; approximately 64% of the total sabellid population). Removal of this sabellid source, along with prevention of further introduction through screening of the outflow, greatly decreased the prevalence of new sabellid infestations. However, new infestations continued, indicating that the sabellid was well-established. We emphasize that, although prevalence of new infestations was low (10%), many parasite populations persist at prevalences even lower than this (Kuris and Lafferty 1994).

This apparently successful eradication of a locally well-established marine pest was theoretically grounded in the Kermack–McKendrick threshold theorem (McKendrick 1940; Bailey 1957; Stiven 1964, 1968). Importantly, it was clearly impossible to directly eradicate the worms by removing all infested specimens. This would have required examination of millions of large *T. funebralis* for the sabellids. The larval worms are small (< 1 mm in length) and the juveniles and adults (< 5 mm in length) are hidden within the host's shell. Thus, all stages are hard to detect without microscopy. Our indirect approach to eradication through removal of hosts was so successful that the population is apparently no longer self-sustaining. Of course, the removal of hundreds of thousands of infested hosts also contributed to decreased transmission rates. However, the continued presence of some previously infested *T. funebralis* after the host removals demonstrated that we did not remove all *in situ* sources of infestations (i.e., we did not remove every last sabellid worm). Further, although we removed an estimated 1.6 million snails from this locality, there were still many susceptible snails remaining. We had little difficulty recovering *T. funebralis* in the later surveys. Taken together, this indicates that if sufficient numbers of susceptible hosts had not been removed, a recovery of the sabellid population would probably have occurred. Although we have been unable to detect any new sabellid infestations at this location for a long time, and have no evidence to indicate that a self-sustaining population of the sabellid remains, we cautiously term this an 'apparent' eradication because it is theoretically possible that such a population remains at an undetectable level. The history of other 'eradications' and 'extinctions' demonstrates that sometimes populations survive below the level of detection.

The urgency imposed by the discovery of an established population of an exotic pest increasing with epidemic dynamics spurred our response and suggested the applicability of epidemic theory to this problem.

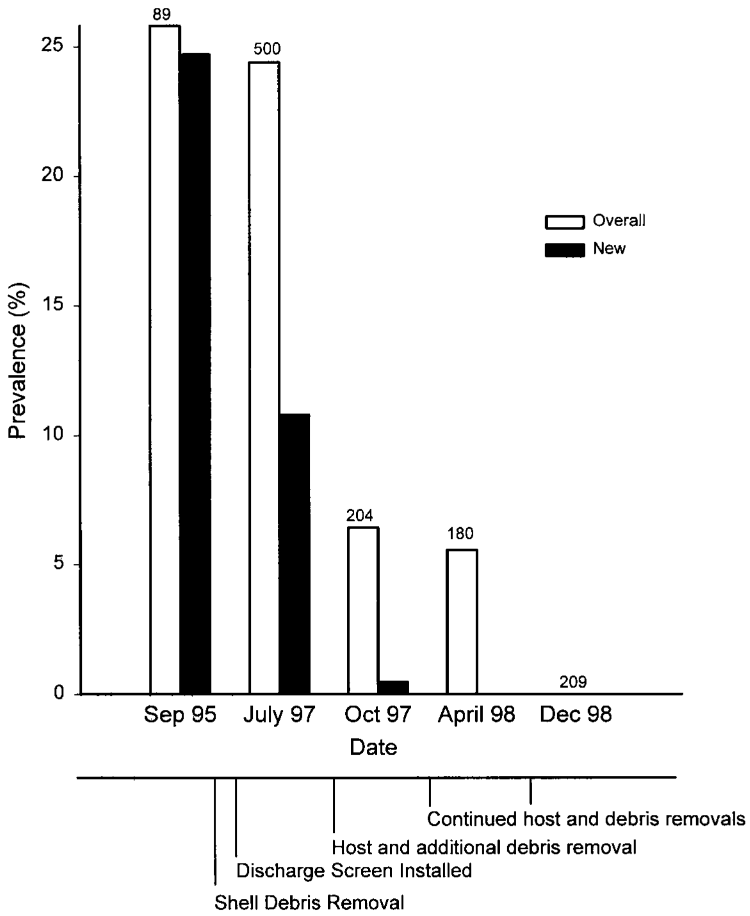

Figure 4. Prevalence of sabellid infestations of *Tegula funebralis* at 10 m south of the discharge. Number above bar denotes sample size. Time line below bar graph illustrates implementation of eradication components.

Although one might consider a parameterization of a host–parasite model to estimate the threshold density needed to sustain the epidemic this was neither needed nor practiced. The incidence estimates were so high that it was clear that the susceptible host population would have to be greatly reduced. Any estimate of the threshold would have involved at least a few parameters, each contributing their own additive error. To achieve an effective solution would have called for a great reduction in host density as practicable. So, we simply decided in the first phase to reduce the density of highly susceptible hosts to the lowest level we could achieve and measure its effectiveness, rather than conduct the parameterization exercise and then go and do the best we could anyway.

Biological characteristics of the sabellid contributed to the success of the eradication program. Limited dispersal due to the benthic larval stage kept the established population geographically isolated within a small, easily accessible area. In addition, its continual production of rapidly settling larvae allowed quick and indepth examination and experimentation of factors affecting transmission. As nothing was known about this species prior to its discovery in California aquaculture facilities, this information was critical for the development of a theoretically-based eradication strategy. The concentration of escaped gastropods and shell debris in the system of tidepools 10 m south of the discharge pipe, in a dense natural population of *T. funebralis*, likely aided the establishment and expansion of the sabellid population. However, it also probably aided the eradication effort by presenting an easily detectable target for removal. In addition, although the worm was microscopic, its dependency on a living gastropod for establishment enabled the eradication of this pest. Exploitation of such substrate-dependent characteristics, including settlement cues used by planktonic larvae, may provide a means to eradicate/control other introduced species.

Several other elements contributed to the success of this eradication effort. Firstly, eradication was feasible because the pest population was detected while it was still spatially restricted. In conjunction with early detection, a rapid response minimized the chance of spread of the pest population. Removal of facility-associated shells and animals from the intertidal site occurred within weeks of detecting the established sabellid population. At the same time, screening methods were developed by the AMF and an effective, efficient system was in operation within 2 months. We also conducted numerous experiments to better define factors affecting transmission that aided development of a theoretically-based eradication plan. Without this background biological information it is unlikely that an eradication plan would have been proposed and agreed to by the AMF or CDFG. Furthermore, additional ecological costs may have accrued if other potential hosts had been haphazardly removed, or if chemical treatments had been applied. Cooperation between private, public, regulatory and scientific communities also aided this eradication effort. This cooperation was particularly important to ensure that the eradication effort would persist past the point of its initial success. We emphasize that many pest populations persist at levels that are difficult to detect. Thus, it is extremely important that efforts, including monitoring of the program's efficacy, continue for many years. The success of this eradication will be strongly supported by sustained monitoring at this site.

The cost of this eradication program (approximately \$5100) was primarily the cost of labor (\$3800). The most expensive aspects were the cost of inspection of animals collected from the transect surveys and the follow-up removals. These labor costs were minimized because volunteer labor (from the University of California, Santa Barbara and Cuesta Community College, San Luis Obispo) was generously made available to this program. If the regulatory agency had formally conducted this program, costs would have been substantially greater due to their professional labor costs. Approximately 3750 person hours were contributed by personnel from the AMF, CDFG, U.C. Santa Barbara and Cuesta College. The remaining costs were related to travel expenses. Environmental costs were also apparently minimal, as our target host species, the black turban snail, remained in large numbers at the site.

Although the threshold theorem is a well accepted basis for the persistence of an infectious agent in a population, there have actually been few direct and well documented explicit field tests of its operation (Onstad et al. 1990). Usually, it is socially or economically undesirable to remove so many hosts that an epidemic process collapses to the point of elimination of the agent. The use of this approach against the sabellid is a direct test in support of the threshold theorem.

This study provides a model for the eradication of the sabellid should other populations be detected. The potential for establishment of other sabellid populations in natural environments remains, as several abalone culture facilities still contain sabellid-infested abalone. However, established sabellid populations have not been detected in any intertidal area adjacent to other onshore facilities. Further, sabellid populations have not been found in areas associated with nearshore culture operations or outplantings of infested abalone (C. Culver and F. Wendell, unpublished data), although examination of a few sites is still needed. Since the sabellid worm has also been transported in infested cultured abalone stock to AMFs in Mexico and Chile, with high infestations subsequently reported in a Mexican AMF, this pest and this protocol have international relevance.

Does this apparently successful eradication involving a localized population with a benthic larva have relevance to a more widespread invasion or to an invader with a pelagic larval phase? Initially it may seem 'easier' to eradicate a species such as *T. heterouncinata*, lacking a ready means of long-distance dispersal, because of its limited geographic spread. However, it is this same biological attribute that facilitated its ability to persist in a localized area and to rapidly reach a high density, with the Cayucos population estimated in the millions. Thus, it may be that species with limited dispersal are better able to maintain a local population from a few individuals. Further, we note that fisheries have often substantially reduced stocks, some to the point of near extinction. For example, the white abalone, *Haliotis sorenseni*, a once geographically widespread species with a pelagic larva, is believed to be on the brink of extinction following intense commercial and recreational fishing (Davis et al. 1998). This suggests that a widespread introduced pest population with a pelagic larva may be susceptible to an eradication effort because its population, especially if detected early, may not be able to sustain itself under the pressure of a concerted eradication regimen. If true, an eradication strategy similar to that used for the sabellid – a coordinated and monitored effort to achieve the greatest reduction feasible – may prove effective against more widespread pests, including those with pelagic larvae. Accumulating practical experience will guide future efforts.

Most broadly, as the first successful eradication of a well-established marine pest, this study supports a more pro-active response to introduced marine species. Early detection, aggressive action using a theoretically based program, and persistent efforts can lead to eradication of even locally well-established pests. Even for those pests not susceptible to eradication, these elements can contribute to the success of control programs. Failing prevention of introductions, this eradication program supports the need to reconfigure control strategies, designed for terrestrial and freshwater pests, towards the control of exotic marine pest species.

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