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Biological Invasions in Aquatic Ecosystems: Impacts on Restoration and Potential for Control

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Biological invasions are increasingly recognized as a major threat to biological diversity and ecosystem integrity. Recent studies have found that invasions are a key factor contributing to the imperilment, endangerment or extinction of native plants and animals, ranking in most studies second only to habitat loss and alteration and well above pollution and over-harvesting (Cohen 2002). In the western United States, biologists consider invasion to be the most important threat to aquatic organisms (Richter *et al.* 1997).

The papers and abstracts that follow are based on presentations made at a session of the 1998 Annual Conference of the California-Nevada Chapter of the American Fisheries Society. They explore how the effects of invasions pose problems for the restoration of aquatic ecosystems in California, and how a variety of approaches may offer hope for preventing or controlling invasions in some cases. They cover habitats from freshwater to estuarine to marine, and address a broad range of exotic organisms from plants to invertebrates and fish. Three presentations discussed, from different perspectives, an exotic parasite that was accidentally imported into California, released into the environment, and became established at one site from which it was ultimately eradicated. More such success stories are needed.

Andrew Cohen
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Cohen, A. N. (2002) Success factors in the establishment of human-dispersed organisms. Pages 374-394 in: Bullock, J. M., R. E. Kenward and R. S. Hails (eds.) Dispersal Ecology, Blackwell Publishing, Oxford, for the British Ecological Society, London.

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Silversides, Smelt, and the Slough of Dreams: Who Will Come if We Restore It?

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Unlike many other species, Delta Smelt (*Hypomesus transpacificus*) abundance is not strongly associated with seasonal freshwater outflow or position of the low salinity zone, frustrating management and restoration planning in the San Francisco Bay-Delta estuary. One potential complicating factor is that exotic Inland Silversides (*Menidia beryllina*) may be important in regulating the abundance of Delta Smelt since this population crashed in 1981. Inland Silversides, though an unintentional and fairly innocuous addition to the Delta's food web, may have a substantial effect as intraguild predators of Delta Smelt, by consuming larvae and competing for resources with juvenile and adult Delta Smelt. Several lines of evidence are presented to support this hypothesis.

(1) The two species are ecologically very similar.
(2) Inland Silversides are notoriously efficient colonizers and competitors elsewhere in the United States.
(3) Inland Silversides are known to often occur in schools near the shoreline in Delta Smelt spawning habitat.
(4) Inland Silversides have been shown to be very efficient predators of Striped Bass (*Morone saxatilis*) larvae during experiments using large enclosures deployed in Suisun Marsh.
(5) Analyses of monitoring data indicates that abundances of Inland Silversides and Delta Smelt are negatively correlated during years of low freshwater outflow.

Seasonal freshwater outflow may influence the degree of co-occurrance between the species, such that the effects of Inland Silversides may be greatest when the low salinity zone is positioned landward. While such evidence indicates the potential benefit of maintaining adequate freshwater outflow to transport young Delta Smelt away from habitats occupied by Inland Silversides, it also suggests caution be used in the design and implementation of habitat restoration projects, because they may disproportionately benefit exotic species, including Inland Silversides.

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Management or Eradication? Strategies for Protecting Delta Fisheries from Non-native Aquatic Plants

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Economic and ecological impacts of non-native flowering aquatic plants have increased dramatically over the past 25 years in California. Demands on the state's water resources have exacerbated these impacts which include: (1) irrigation water delivery; (2) recreational and domestic (drinking) uses; and (3) fisheries and waterfowl habitats. Taken together, *Hydrilla verticillata* (Hydrilla), *Eichhornia crassipes* (Water Hyacinth), *Egeria densa* (Egeria), *Myriophyllum spicatum* (Eurasian Watermilfoil), *Potamogeton crispus* (Curlyleaf Pondweed) and *Myriophyllum aquaticum* (Parrotfeather) create nearly all of the negative impacts. Recent introductions and spread of *Lythrum salicaria* (Purple Loosestrife) also threaten the state's riparian systems. These agressive invaders utilize low light levels (in the case of submersed plants) and their rapid, prolific, and varied reproductive abilities to out-compete native vegetation. However, of these plants, only Hydrilla has a pest rating of "A" by the state, which requires it to be eradicated.

Costs for Hydrilla eradication have averaged about $1.2 million annually over the past 20 years, but this program has prevented the introduction of Hydrilla into the Sacramento-San Joaquin Delta. The long-term savings from Hydrilla eradication is enormous when one considers that without this program, Hydrilla would have become established in the Delta and a multitude of other large California waters. In contrast, two invaders from South America, Water Hyacinth and Egeria, now infest several thousand acres in the Delta. Water Hyacinth has been under management for 15 years, and a bill authorizing the management of Egeria was passed by the state legislature last year. Costs of these efforts to control Water Hyacinth and Egeria may equal or exceed the Hydrilla eradication expenditures within a few years. Management of Water Hyacinth and Egeria via biological control agents should be the long-term goal, yet effective herbicides and selective mechanical control need to be used now to prevent further spread of these weeds. Although there are strict statutory prohibitions against possessing, selling or transporting Hydrilla in California, these restrictions apply to neither Water Hyacinth nor Egeria, nor to other noxious members of the Hydrilla family. Thus, "management" of these species may have moderate success, but their continued spread cannot be contained without more stringent constraints on their movement and use. Ironically, Egeria should be more easily eradicated than Hydrilla since it does not produce seeds or tubers. Finally, the continued presence and movement of these species, particularly Egeria and other "submersed" types, increases the opportunities for introductions of the Zebra Mussel (*Dreissena polymorpha*). This non-native freshwater mussel is often attached to aquatic plants and may thereby become a "hitchhiker" on boats and trailers, or be transported via commercial shipments of these unregulated plants.

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The Introduction of the South African Worm: Biology, History, and Implications for Management

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ABSTRACT: In the early 1990's, California cultured abalone unknowingly became host to an undescribed polychaete pest. Several years later, it was determined that the worm was a non-indigenous species. By this time, the pest had been spread throughout the industry. Native to South Africa, it has been assigned to a new genus within the family Sabellidae. Initial research efforts were aimed at understanding the effect of the pest on abalone, as well as a means for controlling it within the facilities. However, with the determination that the worm was non-indigenous, research efforts shifted to the assessment of ecological issues. The primary concern was the release and establishment of the sabellid in California habitats. Biological and physiological characteristics of the pest are well suited for establishment in California. In fact, one established sabellid population has been found in an intertidal area near Cayucos, California. Eradication efforts are ongoing and appear to be effective. However, additional surveys of other potential release sites are badly needed. The events surrounding the introduction of this pest are complex. Understanding the biology, as well as the history of the introduction, is critical to assess appropriate management strategies. These features and their implications for management are discussed.

This paper has been developed as part of a panel discussion on controlling the release of the South African worm from California abalone aquaculture facilities. Recently, much attention has been focused on the evaluation of the management response to this introduction. For one to assess the adequacy of the response, certain information is needed. In this paper, we summarize general information on the biology of the exotic species and the history of the introduction. In addition, we provide basic management recommendations and we discuss implications of this introduction for future introductions. A more thorough description of these topics is covered in Culver *et al.* (1997).

BIOLOGY OF THE SABELLID

Prior to the introduction of the sabellid into California, this worm was unrecognized even in its native habitat. It has since been described and named by Dr. Kirk Fitzhugh of the Los Angeles County Museum of Natural History (Fitzhugh and Rouse 1999). It is a member of the family Sabellidae, a group collectively known as fan worms. It lives in a tube in a mollusc shell. A simultaneous hermaphrodite, sperm are broadcast out of the tube, while eggs are fertilized and brooded within the tube (Oakes and Fields 1996; Culver *et al.* 1997; Kuris and Culver 1999; Fitzhugh and Rouse 1999). Unlike the majority of marine organisms, this pest does not have a planktonic larval stage. Instead, a benthic larva develops directly within the parental tube. Transmission occurs when the larva crawls out of the tube and settles at the growing edge of either the parental host or a different host. Once settled it produces an elongate mucus sheath. The host then calcifies this transparent, fragile sheath. Thus, the worm obtains a tube as a result of the host's response. This process of establishment is unique among shell-inhabiting parasites, which normally bore directly into the host shell using mechanical or chemical methods (Haigler 1969; Blake and Evans 1973; Zottoli and Carriker 1974). In addition, although a living host is required for establishment of this pest, empty shells can retain live sabellids that became established while the host was alive.

Another important biological feature of this sabellid is that it has broad host specificity. This pest infests many different gastropods, not just abalone (Culver *et al.* 1997; Kuris and Culver 1999). Bivalves appear to be unsusceptible, although few species have been tested. Host specificity issues, including the role of habitat, host behavior, host size, host defense, and sabellid host preference, are currently being studied.

Infestations of this sabellid directly impact the growth of the host, altering both the rate and type of shell deposition. The impact is intensity dependent. For example, if only a few worms are present, the host may be virtually unaffected by the worm because growth is only temporarily interrupted. In contrast, high worm intensity causes prolonged impacts to shell deposition and structure. In the worst case, growth ceases and the shell becomes very brittle and abnormally shaped. Further, respiratory pores are often lacking. These direct impacts on growth can also have indirect affects on the host. Growers have reported increased mortality associated with heavy infestations (Oakes and Fields 1996). Given the lack of respiratory pores and the abnormal growth of heavily infested abalone, these mortalities are likely due to prolonged stress. In addition, preliminary laboratory experiments indicate that heavy infestations increase a host's susceptibility to predators (Culver and Kuris unpub. data). Further, as size is affected by sabellid infestations, fecundity is also presumably affected.

HISTORY OF THE INTRODUCTION: CALIFORNIA ABALONE AQUACULTURE FACILITIES

This pest appears to have arrived into California with a shipment of South African abalone being used for commercial research purposes. At this time, the existence of the worm was unknown to science. Initially, worm-infested abalone were simply characterized as having domed shells, often lacking respiratory pores. However, it was later learned that these abnormalities only occurred in animals with high worm intensities. In contrast, animals with low numbers of worms appeared normal. The failure to recognize low infestation levels allowed the continued spread of the pest throughout the industry. By 1995, all California abalone farms were infested with the sabellid. Although this pest did not affect the meat of the abalone, nor did it cause direct mortality, growers suffered because the animals were not reaching market size. Production levels plummeted.

Initially, control of this pest in the aquaculture facilities was a primary research focus. Thus, we attempted to identify potential sabellid predators for use as biological control agents (Kuris and Culver 1999). We were unsuccessful. Other control methods such as exposure to freshwater, to extreme temperatures, and to various chemicas were tried, but they too failed. The only treatment that provided some beneficial effect was coating the shell surface with wax or a non-toxic shellac. This technique effectively plugs the tubes and smothers the worms. Following this treatment growth resumes. However, this means of control is not currently used because it is extremely labor intensive and requires reapplication. Presently sabellid infestations in aquaculture facilities are controlled through isolation of infested stocks, use of antiseptic procedures and sale or destruction of infested stock.

The economic impacts have been devastating to the industry. Some companies have gone out of business, while those surviving have experienced production delays of up to two years. Currently, all growers are working toward eradication of the pest from their facilities. Some have already achieved this goal.

HISTORY OF THE INTRODUCTION: CALIFORNIA NATURAL ENVIRONMENT

Concern over the environment increased with the recognition that the sabellid is a non-indigenous species. Our research efforts evaluated the likelihood that the sabellid had been released into the environment. We identified several avenues of release including:

- Aquaculture facilities (both onshore and offshore);
- Enhancement projects (outplants);
- Live fish markets and distributors;
- Research and educational facilities (*e.g.* universities, aquariums, bioassay labs).

Our investigations of release of the sabellid began with onshore aquaculture facilities. These facilities had endured the heaviest infestations and contained the largest number of infested abalone. As onshore facilities discharge their effluent directly into the environment, we began by examining areas around discharge sites. At several sites, escaped animals and empty shells were being released from the facilities. Often these animals and shells contained reproductively active adult sabellids. In some areas, hundreds of adult sabellids were living in these shells.

It became obvious that the sabellid was being released into the environment through the discharge of infested animals and shell debris. Thus, we began taking samples of the native gastropods from around the discharge sites. Because we knew some animals were becoming infested in the facilities and then discharged, we targeted species that were not found in the facilities. At one site, the sabellid was found to occur frequently in a snail species, *Tegula funebralis*, that is rarely found in the facilities. However, the infestations were of low intensity. To further illustrate that infestations were occurring in nature at this site we conducted a mark and recapture study. New infestations were detected at the first recapture date, two weeks after release. Currently, eradication efforts are ongoing, infestation levels have sharply declined and eradication seems possible.[1]

Despite the swift action to eradicate the one known established sabellid population, additional surveys are critically needed. We have only been able to conduct intertidal surveys around onshore facilities. We have recommended that subtidal surveys also be conducted around these facilities. Further, we have recommended that the other avenues of release be assessed. Preliminary surveys around some offshore cage facilities have been conducted and no established sabellid populations have been detected. However, these surveys looked primarily at animals collected directly below or close to the cages. As it is likely that the larval worms are carried away from the cage areas by water currents, additional information on current patterns and broader surveys are needed. Similar surveys are also critically needed in areas where potentially infested abalone may have been outplanted.

MANAGEMENT OF THE SABELLID

Throughout the course of the sabellid introduction we have provided both the industry and CDFG with our research findings as they have become available. We have also provided recommendations about management of the problem (Culver *et al.* 1997). In general, we agree with some

1 NOTE ADDED IN PRESS: The eradication efforts were successful (Culver and Kuris 2000).

of the policies that have been developed. However, we also feel that some aspects of the introduction have been under-regulated, while others have been over-regulated.

When assessing sabellid management strategies, one should consider the history of the introduction, as well as the biology of the organism. Important dates surrounding the sabellid introduction include:

- 1981: Known importation of South African abalone to California.
- 1987: First observation of abnormal abalone in California.
- 1993: Identification of the pest as an undescribed sabellid.
- 1994: California research begins. Mechanism of shell deformation determined. Recognition that the pest is an introduced species from South African.
- 1995: Recognition that the pest is widespread in California aquaculture facilities. Broad host specificity demonstrated.
- 1996: Established wild population of the pest detected in California.
- 1998: Examination of the pest in South African habitats.

Given this timeline, it is likely that the sabellid has been in California for a minimum of 11 years. However, it has only been a few years since it has been recognized as an introduced species. In addition, only recently did we detect an established population in nature.

Because this sabellid was a completely unrecognized and undescribed species, its basic biological characteristics were unknown. The following biological characteristics of the sabellid have been identified:

- It is a simultaneous hermaphrodite.
- It has broad host specificity.
- It lives in habitats in South Africa similar to those available in California.
- It has a benthic crawling larval stage.
- It directly affects shell deposition and growth of host species (and indirectly affects survivorship and fecundity).

These features suggest that this pest has a strong potential to successfully invade Californian habitats. However, its benthic larval stage suggests that dispersal will be limited. Further, the impacts of the sabellid on its host are perceived by some as benign; this pest does not pose any human health risk and it does not kill any organisms outright. Development of a management scheme requires consideration of all of these factors, as well as the impact of such a strategy on affected entities (*e.g*. the abalone farming industry). Thus, depending on perception of the risks, different management strategies could be proposed.

IMPLICATIONS FOR FUTURE MANAGEMENT OF NON-INDIGENOUS SPECIES

Like all introductions, lessons can be learned from the introduction of the sabellid. In general, we must face the reality that importation, no matter how regulated, allows for the potential introduction of non-indigenous species. In the case of the one known importation of South African abalone, all animals were inspected and quarantined. However, the existence of the sabellid was unknown. The effectiveness of an inspection and quarantine system will be limited for organisms that have never been studied. The sabellid is not the first, and likely will not be the last, unknown species that is discovered after it has been introduced elsewhere.

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California Department of Fish and Game's Response to the Sabellid Worm Infestation

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The California Department of Fish and Game's (Department's) goal is the eradication of the sabellid worm infestation. The approach used to achieve the goal is guided by legislative mandate and has changed as research information became available. This presentation will describe the Department's response to the infestation in light of those changing conditions.

The Department became aware of the sabellid worm infestation in late 1994. Biological information was limited and the approach used by the Department took advantage of the cooperation that already existed between the abalone aquaculture industry and University researchers. Appreciable resources to address what appeared to be an aquaculture problem had already been marshaled, including obtaining Rapid Response funding for research from California Sea Grant. When that research determined in early 1995 that the worm was an exotic from South Africa, the Department sought recommendations from its Aquaculture Disease Committee.

Based on those recommendations, the Department's approach changed. While cooperative research was encouraged, the Department also committed its resources to addressing the problem and placed a prohibition on the planting of cultured abalone in the wild. Department resources were focused on determining the extent of the infestation and assisting in minimizing its spread through California's aquaculture industry.

When research subsequently showed that the worm was capable of infesting other mollusks, the Department required each facility to develop a plan for eradication and made its development a condition for renewal of aquaculture registration. Those plans, which include specific requirements imposed by the Department, have been implemented and are being evaluated further by the Department. Ongoing cooperative risk assessments are focusing on the control and eradication of the one known infestation in the wild. Surveys are also being conducted to determine whether other introductions to the wild have occurred as a result of past abalone enhancement efforts that used cultured abalone.

While these efforts are ongoing, the Department has also implemented a reorganization that effectively increases its ability to focus on aquaculture issues through the formation of an aquaculture team. This team is interested in expanding existing partnerships that are responding to this problem and in creating new partnerships to address a variety of related issues including the control and management of exotic introductions.

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The Release of Pest Species by Marine Aquaculture: Lessons from a South African Parasite Introduced into California Waters

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ABSTRACT: **A South African worm accidentally introduced into California abalone farms can infest, weaken and deform the shells of abalone and other native California marine snails, reduce growth and reproductive rates, and leave the host species more vulnerable to predation and environmental hazards. The worm was spread to all California abalone farms via stock transfers, has bankrupted some growers, and has infested native snails in the ocean in at least one site. Despite the potential for substantial harm to California's marine resources, the state continues to allow abalone farming practices that can release this parasite into the environment.**

Marine aquaculture in general is inadequately regulated to prevent the introduction of harmful exotic organisms. To avoid such impacts, aquaculture should be governed by the following principles:

- **Aquaculture facilities should be required to operate in a sustainable manner without causing harm to the marine environment, which includes not releasing exotic organisms.**
- **Aquaculture should be based on native, local stock whenever possible. Imports and transfers of stock should be minimized, thoroughly inspected, and quarantined for an appropriate observation period.**
- **Aquaculture stock infested by parasites should be isolated from the environment. If isolation is impossible, the stock should be destroyed.**
- **Proposals to import exotic stock should receive full public review, and advisory bodies should include all relevant stakeholders, not just the aquaculture industry.**

Aquaculture activities have a long history of introducing harmful parasites and diseases of fish and shellfish into various parts of the world (*e.g.* Farley 1992; Brock 1992; Mills *et al.* 1993; Barber 1996; Smolowitz 1996). Outbreaks of diseases and parasites are common in the crowded and often stressful conditions of aquaculture facilities (Huner and Brown 1985). In some regions, parasites or diseases accidentally imported by aquaculture have had devastating effect on native fish and shellfish populations (*e.g.* Mo 1994). Preventing such introductions in the future will require both better regulation of the initial importing of organisms, and better controls on the release into the environment of undesirable organisms that are cultured or that become established within aquaculture facilities. The recent importion and establishment of a harmful shell parasite in California abalone farms, and its subsequent release into the environment, suggests that there is substantial room for improvement in the regulation of marine aquaculture.

THE ABALONE PARASITE

In the early 1980s the exotic sabellid worm *Terebrasabella heterouncinata* (Fitzhugh and Rouse 1999), then unknown to science, was accidentally introduced into California abalone farms with imported South African abalone, *Haliotis midae*.[1] The worm established infestions in the shells of the California Red Abalone, *Haliotis rufescens*, the species cultured in California. Intense infestations produced

[1] It is unclear whether the abalone were imported with the knowledge of California agencies.

shells that were easily broken, disproportionately tall relative to the size of the aperture and foot, and frequently lacking respiratory holes. In addition the growth of soft tissue was slowed or halted. Overall, such infestations produced abalone with reduced reproductive potential and, were they to occur in the natural environment, greater vulnerability to predators and to dislodging or damage by waves or rock movement in the surf zone. Kuris and Culver (1999) found that these worms can infest not just Red Abalone but probably all species of California abalone (all of which are in decline and one of which, the White Abalone *Haliotis sorenseni*, is thought to be near extinction—Tegner *et al.* 1996) and a wide variety of native California marine snails.

As is common in some types of aquaculture, abalone stocks were frequently transferred between facilities, spreading the South African worm to all California abalone farms by the mid-1990s, with the resulting infestations bankrupting some growers. In 1994 researchers determined that the problem was caused by an exotic parasite, by 1995 they had demonstrated that it can infest a broad range of marine snails, and by 1996 the worm had been found in native snails in the ocean in at least one site (Kuris and Culver 1999).

THE GOVERNMENT RESPONSE

The California Department of Fish and Game (CDFG) is the state agency with the primary responsibility for managing and regulating aquaculture and for protecting the marine environment. However it also has a potentially conflicting mandate to promote and encourage the development of the California abalone farming industry.

CDFG took no action to prevent the release of the sabellid worm into California waters until December 1996, when CDFG notified abalone farmers that it would take the following steps (CDFG 1996):

(1) Stop the direct out-planting of abalone into California waters.[2]
(2) Require the installation of screens on the pipes that discharge water from on-shore abalone farms into the ocean; and require growers that rear abalone in cages and barrels in the ocean to stop dumping empty shells, kelp and other debris that could harbor sabellid worms into the ocean.
(3) Require abalone farmers to notify CDFG when abalone are being transferred between facilities, so that CDFG can inspect the shipments for sabellids.
(4) Not issue 1997 aquaculture registrations, which are needed in order to operate aquaculture facilities in California, to any abalone farms that do not have an approved plan for eradicating the sabellid worm.

While these are useful steps in concept, they did not go far enough, nor were many of them implemented effectively.

For example, screening the discharge pipes from on-shore facilities should help to prevent the release into the ocean of shell debris containing adult worms and of live gastropods infested with worms , but would still allow larval worms to be discharged into the ocean. The sabellid larvae are not planktonic, but rather disperse by crawling short distances on the shells of their host species or on other benthic substrates. However, they can be dislodged with aeration or when tanks are flushed, and float free in the water column (K. Ruck, pers. comm.; C. Culver pers.

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[2] Large numbers of cultured abalone, numbering at least in the tens of thousands and presumably including a significant number of sabellid-infested abalone, were planted in the ocean over several years to augment the declining abalone population. These plantings were made under Private Stocking Permits issued by CDFG, but in most cases the descriptions of the sites are too vague to enable them to be checked for sabellid infestations, and the records were retained for only three years (CDFG 1997).

comm.). A small number of sabellid larvae were collected in the discharge from an infested abalone farm (C. Culver pers. comm.) which, based on the relative volumes of water sampled and discharged, works out to over 70,000 larval worms per day carried in the discharge from this one farm (C. Friedman pers. comm.).[3] The screens installed on discharge pipes typically have a mesh size of 1 cm or larger, while the sabellid larvae are about 0.05 mm in diameter, so the screen openings need to be made about 200 times smaller if they are to catch sabellid larvae (K. Ruck pers. comm.). Furthermore, growers are allowed to rear infested abalone in cages or barrels in the ocean, with mesh or holes large enough to freely release larvae into the environment (C. Culver pers. comm.).

Effective inspection of all transfers of abalone stocks is essential to containing and ultimately eliminating the sabellid worm from California abalone farms, but unfortunately current procedures do not appear to be adequate for this job. For the inspections a number of abalone are randomly selected and shucked, and the shells are examined for sabellid worms. The more shells examined, the greater the chance of detecting an infestation, but CDFG's protocols only require the examination of 60 abalone per population unit (defined as a tank, barrel or year-class), which can include up to 9,000 abalone or more (P. Kalvass pers. comm.). Even if the individual examinations produce no false negatives (that is, if there is even a single sabellid worm in the shell of an examined abalone, it will be detected), then examining 60 shells per unit leaves about a 5% chance of missing a 5% infestation rate (meaning that one abalone out of 20 in the shipment has sabellids) and about a 55% chance of missing a 1% infestation rate (C. Gowan pers. comm.) In at least one recent case, a shipment that passed inspected did contain sabellids infested a previously "clean" abalone farm, which shortly thereafter shut down.

While requiring abalone farms to develop eradication and control plans is an important step, the content of those plans is also important. Several growers have proposed to eliminate the sabellid worm from their facilities by selling off their infested abalone. This would essentially transfer the problem out of CDFG's jurisdiction without eliminating the risk, since the sabellid worm could then be released into the ocean via unscreened discharges from the holding tanks of live seafood distributors or retailers, or by discarded shells. Furthermore, although CDFG said at the end of 1996 that it would not provide aquaculture registrations to abalone farms that did not have approved eradication plans, it has allowed abalone farms to continue operations even though no plans have yet (as of spring 1998) been approved.

CDFG is not the only government agency with the responsibility and authority to address this problem. The U. S. Environmental Protection Agency and California's Regional Water Quality Control Boards are responsible for regulating discharges of pollutants, including biological pollutants such as exotic species, under the Clean Water Act (Cohen and Foster 2000). Other agencies charged with protecting the coastal marine environment or marine organisms may have additional obligations and powers to

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3 It is unclear whether the larval worms collected came from the abalone farm itself, or from infested snails living in the discharge channel. However, in either case the data demonstrate that the discharge streams are capable of carrying large numbers of sabellid worms into the ocean, and may in fact be doing so. If the larvae did originate in the abalone farm, the number discharged may have been six times greater a year or two earlier, when the number of infested abalone was that much greater (R. Fields pers. comm.). Sabellid larvae have also been collected from abalone tank outflows in South Africa (K. Ruck pers. comm.).

prevent the introduction of this harmful parasite.[4] None have taken steps to do so.

PRINCIPLES FOR MANAGING MARINE AQUACULTURE

Such lapses are unfortunately not confined to the sabellid worm problem or to the abalone industry. Marine aquaculture in general is inadequately regulated to prevent the introduction of exotic organisms into the environment, and in many parts of the world aquaculture activities have imported and released parasites, diseases, predators or competitors of native fish and shellfish. To reduce the risk of impacts to important marine resources and the marine environment, the development and management of marine aquaculture should be based on the following principles:

- Aquaculture facilities should be legally required to operate in a sustainable manner, without causing harm to marine resources or ecosystems, which includes not releasing exotic organisms into the environment. Aquaculture operations that cannot meet this standard should not be encouraged or allowed.
- Whenever possible, aquaculture should be based on native, local stock. Imports of stock and transfers of stock between regions should be minimized, and whenever possible the stock should be transported in the egg or larval stage. All imported and transferred stock should be thoroughly inspected, and held in quarantine (in isolation from the environment and from other stock in the receiving facility) for an appropriate observation period.
- Any stock infested with exotic organisms should be immediately isolated from the environment. If isolating the stock is not feasible, the stock should be destroyed and properly disposed of. Any parasites or disease syndromes found in aquaculture stocks that are not known from the local environment should be managed as if they were exotic organisms until proven otherwise—that is, stock infested with such parasites or diseases should either be isolated from the environment or destroyed.
- Proposals to import exotic organisms for culturing should receive full public review. Participation on government advisory bodies or committees that address the management or regulation of aquaculture should include all relevant stakeholders, not just the representatives and consultants of the aquaculture industry.

[4] For example, the National Marine Fisheries Service is responsible for protecting marine species listed under the federal Endangered Species Act from harmful actions which can include "releasing non-indigenous...species into a listed species' habitat or where they may access the habitat of listed species;" and the California Coastal Commission is charged by the California Coastal Act with maintaining marine resources and ensuring that uses of the marine environment are carried out in a manner that will "maintain healthy populations of all species of marine organisms" (Cohen and Foster 2000).

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Biological Control of Marine Invasions

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ABSTRACT: Biological control, as used in terrestrial systems, may hold promise for application against exotic marine species. Marine systems, however, differ with respect to the types of control agents available, the degree of pest-population reduction needed for effective control, the spatial scale over which biological control must operate effectively, the practicality of implementation, and the nature and degree of concern over safety. As an example, Lafferty and Kuris (1996) proposed a strategy for developing a biological control program against the European green crab, *Carcinus maenas*, which has had substantial negative impacts where previously introduced (New England, Atlantic Canada, South Africa, South Australia) and which has recently been introduced to Central California and Tasmania. The green crab performs better in introduced regions, presumably because it has left its native parasites behind. This suggests that introducing native parasites may have some utility in controlling its numbers. Lafferty and Kuris (1996) suggest the evaluation of the safety and efficacy of a European rhizocephalan barnacle, *Sacculina carcini*, as a potential control candidate. The host specificity of this barnacle is presently being evaluated in the laboratory and mathematical models used are being used to assess the conditions under which the barnacle, a parasitic castrator, could lead to satisfactory levels of control.

Since the 1880s, biological control for terrestrial pests has involved the deployment of herbivores, predators, parasites or diseases. There now exists an extensive knowledge concerning biological control based on many successful applications and some notable failures. Natural enemies can find and track pest populations or locate new pest populations. They also evade the development of resistance by pests by coevolving. When successful, they provide either a long-term or a permanent low cost solution to a pest problem. Finally, when well chosen, they usually have sufficient specificity to be environmentally safe. Despite this, in the 40s and 50s, cheap and effective pesticides largely replaced biological control. The environmental damage caused by pesticides and the development of genetic resistance of pests has renewed interest in biological control today.

Before using natural enemies as a biological control, it is useful to survey introduced populations for parasites and predators and compare them with the types and abundance of such natural enemies where the pest is native. Most of the successfully introduced natural enemies that achieve good (economic) control in terrestrial systems without deleterious side effects are parasitoid wasps, flies and nematode worms.

In marine environments, damaging introductions are also common (Carlton 1987, 1989; Zibrowius 1991). Ballast water transport is the most important means disseminating exotic species (Carlton 1985, 1989). Since most such introductions arrive as larvae, they generally come free of natural enemies (parasitic castrators, specialized predators and pathogens of adults) that might normally control their abundance in their native regions. The resultant extremely high population densities attained by alien species is what usually leads to economic damage (Nichols *et al.* 1990). Clearly, one of the most efficient approaches to the control of marine pests is to carefully examine the use of biological control against terrestrial insect pests for appropriate analogous tactics (Lafferty and Kuris 1996). Marine systems have some important features that contrast with terrestrial biological control paradigms and require special consideration. The potential to use natural enemies against marine pests enjoys, in principle, a significant advantage compared to their use against terrestrial agricultural pests. In agriculture, farmers must cut pest populations to very low levels to minimize the cosmetic damage to their crops. In contrast, there is usually no reason to reduce marine pest populations to very low levels and modest reductions in pest abundance can provide a successful outcome.

Available control agents differ between marine and terrestrial systems. Parasitic castrators are more typical of marine systems than parasitoids and deserve special attention. Like the parasitoid-infected host, the parasitically castrated host has no reproductive potential. However, the castrated host continues to exert intraspecific competitive effects against unparasitized individuals (Lafferty 1993). It also continues to be a pest. Kuris (1974) postulated that, analogous to parasitoids, parasitic castrators may be able to control host populations.

Biological control using natural enemies is effective because control agents build up in local patches (Murdoch *et al.* 1985). Predictions about population dynamics in marine systems are sensitive to the assumptions implicit in global (large scale or closed recruitment) dynamics (Gaines and Lafferty 1995). In marine environments, planktonic larval stages disperse widely, offspring rarely settle and live near their parents, and natural enemies may not respond numerically to locally high pest density. At small scales, the apparent effect of parasitic castration should be reduced according to the amount of outside recruitment that occurs. This produces two relevant points. The first is that it may be difficult to assess the importance of parasitic castration at small spatial scales. The second is that the addition of a parasitic castrator may not provide control at a local scale in the same way that a predator, parasitoid or pathogen might. This does not mean that parasitic castrators are ineffective control agents, only that they might need to be employed on large scales for their effects to be observable. It also indicates, indirectly, that the benefits of control efforts at one location will be spread over a larger area. The most efficient use of a parasitic castrator would involve targeting source populations while ignoring sink populations of the host.

A potential disadvantage when using natural enemies in marine compared to terrestrial environments concerns safety. Though we may care little about impacts to native insects such as aphids or scale, most people would consider a natural enemy used against a marine pest, such as the green crab, to be unsafe if it were to significantly reduce commercially fished crab species. Thus, natural enemies used against marine pests must meet a high safety threshold to conserve our native fauna.

A TEST CASE

The European green crab makes an interesting test case because it is likely to prove to be a truly harmful introduction on the West Coast of the United States. Based on the history of *Carcinus maenas* after its introduction elsewhere (Ropes 1968; Le Roux *et al.* 1990; Cohen *et al.* 1995; Thresher 1997), the crab is likely to devastate intertidal and subtidal shellfish beds. So far, measures taken to reduce predation (mesh enclosures) seem to have been successful for shellfishery operations in Tomales Bay (Sawyer 1994 pers. comm.) and in Martha's Vineyard (Walton 1997). Although predicting the ultimate range of the green crab on the Pacific Coast is speculative, temperature regimes seem suitable from southern California north to Puget Sound, threatening the nation's largest oyster-rearing industry in Washington state. Lafferty and Kuris (1996) estimated that the crab could impact fisheries worth up to a conservative $44 million per year.

A global survey (Torchin *et al.* 2001) found that introduced green crabs were larger than native green crabs due to increased growth and/or survivorship, perhaps because they suffered less from predators and parasites. An exception is the introduction in Victoria, Australia where crabs were small, scarce and heavily infected with larval tapeworms. Such release from natural enemies may contribute to the success of invasions and supports the likelihood that classical biological control may be a feasible means to reduce the impacts of these introduced crabs. The only potential control agent known to infect green crabs in California is a nemertean egg predator, *Carcinonemertes epialti*, that normally infests the shore crab *Hemigrapsus oregonensis* (Torchin *et al.* 1996). At this point, it is unlikely that the nemertean alone will affect green crab abundance because infestation rates are apparently low.

The rhizocephalan barnacle, *Sacculina carcini*, presently seems the best candidate for biological control. The Rhizocephala are highly host-specific parasitic castrators that can theoretically control host populations. Determining the association between the prevalence of parasitism and the reduction of the host population by a parasitic castrator would help determine the degree to which the barnacles can depress host density in the field. Simple models indicate that on a global scale, for a host whose numbers are directly linked to reproductive output (*i.e.* a birth rate term is found in the solution for the host's equilibrium), there is a simple association between parasitic castration and host density. For the most simple model, this can be approximated as $N/K = 1 - p$, where N is the number of infected and uninfected hosts present in the population, K is the carrying capacity of the host in the absence of the parasitic castrator and p is the prevalence (proportion of hosts infected) of the parasitic castrator. In other words, if 60% of the crabs in a population are found to be parasitized, the total density of crabs (infected and uninfected crabs) is reduced to only 40% of the carrying capacity. This is an evaluation tool and does not indicate that parasitic castrators used in biological control should attain high prevalences and substantially reduce host populations. However, reports of high prevalences of rhizocephalan barnacles in the wild (Minchin 1997) suggest that, in Europe, the barnacle is substantially reducing green crab densities in some locations.

Inherent time lags can affect the stability of the host-parasite interaction in complex ways. Preliminary work indicates five possible outcomes. The first is straightforward, the host can go extinct if external sources of density independent mortality exceed per capita rates of reproduction. The second prediction is that the parasite might not be able to invade a host population that is too small. A third outcome is coexistence between the parasite and the host. A fourth outcome is that the parasite invades but goes extinct while the host persists. The fifth outcome is that the parasite may cause the host to go extinct (after which the parasite goes extinct as well). These outcomes are all of interest to a control program.

Experimental evidence from field studies (Blower and Roughgarden 1989; Lafferty 1993) supports a reduction of host populations by parasitic castrators. More importantly, a negative association between the prevalence of *S. carcini* and crab abundance in Europe (based on an analysis of Minchin's (1997) data ($R = -.38$, $N = 15$), and not representing his conclusions) suggests that barnacles reduce the abundance of native crab populations. In addition, infection by a barnacle substantially reduces the impact a crab has on shellfish (Minchin 1997).

TESTING HOST SPECIFICITY

Although the present information strongly suggests that *S. carcini* would be a safe control agent, the documentation of rhizocephalans with broader host specificity (*e.g. Loxothylacus panopaei* infects seven xanthid crabs (Grosholz and Ruiz 1995)) stresses the need for carefully controlled experiments to determine if native species are refractory to infections of the parasite. Høeg (1997) exposed a number of Australian crab species to *Sacculina carcini* cyprids under laboratory conditions and found that settlement occurred on most (including Australian *C. maenas*). Under natural conditions of exposure, cyprids settled on only 2 of 4 *C. maenas* and 2 of 4 *Paragrapsus gaimairdi* (an Australian species). However, no evidence of development of the parasite in a host species other than *C. maenas* has been demonstrated so far.

We (Lafferty, Torchin and Kuris) are presently investigating in the laboratory the susceptibility of crabs from the West Coast of the United States to infection by *S. carcini*. First, we built a culture facility that has several redundant filters to prevent the release of crab or barnacle larvae. We are presently developing our larval rearing techniques, and have been successful at getting barnacles to release nauplii larvae, which we can culture to the infective cyprid stage. These techniques were developed during the fall and winter when barnacles release male larvae, which are not infective to crabs. In the next several months we will be working with female larvae and can attempt to test for host specificity.

We will first assess the initial level of host specificity, the ability of larvae to settle on the host. If larvae do settle on the test crabs, we will subject newly metamorphosed and later stage juveniles (stages known to be more susceptible to infection) to infective cyprids according to the protocol of Ritchie and Høeg (1981). Following exposure, we will maintain the crabs for three months and dissect them to check for internal stages of the barnacle. If internal stages are found in the test crabs, we will also maintain a subsample of test crabs for a period of up to one year to determine if the parasites are able to mature.

We used five criteria to select native crab species to test: habitat overlap with the green crab, phylogenetic relatedness to the green crab, economic importance, ecological importance and known susceptibility to other distantly related rhizocephalan barnacles. For each of the three stages of the host specificity evaluation described above, we will expose individual crabs (or, for the larval settlement test, the limbs of individual crabs) to infective female cyprid stages of the parasite. As a control for our infection techniques, we will expose green crabs (or limbs) in an identical manner in separate containers (separate containers will prevent us from confusing host specificity with host preference). If the test crabs are susceptible, we expect to see signs of infection in them. If the test crabs are refractory, we expect to see signs of infection only in the green crabs.

Evaluating safety is different from typical hypothesis testing. It is not sufficient to determine that infection rates of test crabs are significantly less than infection rates of green crabs. The question is, can the parasite infect test crabs? If a test crab becomes infected, the answer is unquestionably yes. However, it is important to have sufficient power in the test so that the probability of a false negative result is low. Increasing two factors increases the power of the test: the proportion of green crabs that the parasite infects and the number of test crabs exposed. Probability theory allows a calculation of the minimum number of test crabs needed to expose to keep the probability of a false negative below 1/1000 (our chosen alpha). In this case, we set the criteria according to the model $(1 - p)^n < 0.001$, where p equals the proportion of green crabs infected in a given trial and n equals the minimum number of test crabs to expose. This relationship allows us to determine the number of test crabs needed for exposure depending on the success of the green crab infection rate. For each test, we will expose ten green crabs as controls and, based on the number of green crabs infected, expose the appropriate number of test crabs needed to meet the above standard. If the barnacle infects only one or no green crabs, we will consider the exposure technique flawed and start over.

FURTHER STEPS

Following a successful safety determination, techniques to raise the biocontrol agent would need development. Improved barnacle culture technology would be required for infecting large numbers of green crabs for release. Technological advancements in the early detection of infected crabs would increase the efficiency of the program and decrease delays. Implementation of biological control might comprise a sustained program of trapping and infecting crabs. This would also serve as a means to monitor the success of the control effort.

One safety advantage of this system is that an initial field trial could easily be designed to only release female barnacles which would remain sterile unless male barnacle larvae were intentionally released following the emergence of virgin externae in the infected green crab population. Such a trial release would allow an evaluation of host specificity under field conditions without having to introduce a breeding population of the parasite.

This approach might be applicable to other marine pests as well. One would assess the extent to which the pest is released from natural enemies, identify potential control agents and select the most promising candidates for safety testing and potential trial release. In some, perhaps many, cases, biological control will not be feasible and we will have to struggle with alternative approaches such as using pesticides, mechanical removal, subsidized fisheries or doing nothing. The lessons from terrestrial biological control indicate that host specific metazoan parasites are most likely to provide the level of control and safety most appropriate for marine systems.

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Controlling Invasive Cordgrass: A Tale of Two Estuaries

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ABSTRACT: **Open intertidal mud is a hallmark of Pacific estuaries. Shore birds, marine life, and the traditional fishing and oystering in these habitats depend upon openness. Alien cordgrasses of the genus *Spartina* threaten these estuaries. Growing further down the intertidal gradient than any other land plant, *Spartina alterniflora* (Smooth Cordgrass, introduced from the Atlantic coast) and *Spartina anglica* (English Cordgrass, introduced from the United Kingdom) form swards of dense stems and thick root-mats that exclude both wildlife and traditional human activities.**

San Francisco Bay has been invaded by Smooth Cordgrass brought from Maryland in the mid 1970s. This alien species competes and hybridizes with the closely-related native California cordgrass, *S. foliosa*. The native species produces mostly hybrid seed where it grows with the alien. Without control, the alien could cause the extinction of California cordgrass. Owing to concern for the native cordgrass, biological control is not an option for San Francisco Bay. Alien and hybrid cordgrass are vulnerable to the herbicide Rodeo, which is licensed for use in aquatic systems.

Willapa Bay and Puget Sound, Washington have been invaded by Smooth Cordgrass and English Cordgrass, respectively. Research has shown that both of these populations are unusually susceptible to a highly-specialized insect that feeds upon cordgrass in its native range; this insect does not occur in Washington, and no native cordgrasses occur there either. This circumstance suggests that biological control of the alien populations of cordgrass in the estuaries of Washington State is a sensible control option.

CORDGRASSES IN AMERICAN PACIFIC ESTUARIES

Open mud without vegetation is a hallmark of middle and lower intertidal zones in Pacific estuaries. The high intertidal region is occupied by low-growing species, with *Distichlis spicata* and *Salicornia virginica* often holding the lion's share of space; the remainder is shared by various combinations of such species as *Triglochin maritima*, *Jaumea carnosa*, and *Deschampsia caespitosa*. From 20 to 30 additional species complete the list of Pacific salt marsh plants (Chapman 1977). California Cordgrass, *Spartina foliosa*, frequently forms a modest lower boundary to the marsh vegetation, southward from Sonoma County, north of San Francisco Bay, through Baja California. No native cordgrasses are found north of Sonoma County on the Pacific coast. California Cordgrass is not an aggressive species, rarely invading stands of other plant species. It is a relatively short cordgrass; most plants are less than 0.75 m tall. With a culm density that is low for cordgrasses, *S. foliosa* does not cause appreciable accretion of sediment.

Smooth Cordgrass, *Spartina alterniflora*, native to Atlantic and Gulf coast marshes, occupies much lower intertidal habitats and is distinctly more aggressive than California Cordgrass. Smooth Cordgrass regularly invades patches of other saltmarsh species, grows to more than a meter tall, and forms dense monospecific swards (Adam 1990). English Cordgrass, *Spartina anglica*, is as aggressive as Smooth Cordgrass (Gray *et al.* 1991). Both species have spread widely in some of the Pacific estuaries to which they have been introduced. Both present substantial threats to Pacific saltmarsh species, including plants, fishes, marine invertebrates, and even marine mammals. A particularly conspicuous menace is to shorebirds, which forage upon open mud. Pacific estuaries have been greatly reduced by human activities over the past century (Macdonald 1977), and invasive Smooth and English cordgrasses threaten to accelerate this loss of habitat. Alien cordgrasses also threaten traditional human uses of Pacific estuaries, hindering access to the shore, interfering with mariculture and navigation, and blocking flood control channels (Daehler and Strong 1996).

Mindful of the uniqueness of the open mud vulnerable to invasion by *S. alterniflora* in Pacific estuaries, Adam (1990) remarked in his global overview of salt marshes that "...should [Smooth Cordgrass be introduced] it may cause profound change to western marshes." Little did he appreciate the degree to which his prediction has been realized. Smooth Cordgrass was introduced to Willapa Bay at least 60 years ago (Scheffer 1945; Sayce 1988) and has spread widely, reducing habitat for migratory birds, promoting siltation of mud and sand flats, and overgrowing oyster culture beds (Boyle 1991). English Cordgrass was introduced into Puget Sound in 1961 and has also spread widely, causing similar impacts to the environment (Parker and Aberle 1979). In the past few years the State of Washington has mounted a large-scale, expensive effort to control these cordgrasses with a combination of cutting and glyphosate herbicide treatments (J. Civille, pers. comm.).

Smooth Cordgrass was introduced to San Francisco Bay about twenty years ago (Daehler and Strong 1995) and has spread widely. It now competes (Callaway and Josselyn 1992) and hybridizes (Ayres *et al.* 1999) with California Cordgrass throughout the south portion of the Bay. San Francisco Bay supports the largest remaining stand of California Cordgrass in the United States. The habitat of the alien Smooth Cordgrass completely overlaps that of California Cordgrass, and the spread of the aggressive alien threatens the very existence of this important native species.

POSSIBILITIES FOR CONTROL

The complementary touchstones of safety in biological control are (a) choice of enemy species with very narrow diets and (b) target species with no close relatives. These reduce the chance of collateral damage to species other than the intended target. Therefore, classical biological control is not an option in San Francisco Bay because any introduced organism that would harm alien cordgrass would probably also harm the closely related native California Cordgrass. Thus, only chemical and physical controls are options in San Francisco Bay. Cutting the plant and applying the herbicide Rodeo™ have shown promise in preliminary trials in San Francisco Bay (Chamberlain 1995).

One complicating factor is the hybridization that occurs between the introduced Smooth Cordgrass and the native California Cordgrass in San Francisco Bay. The hybrids are not morphologically distinct from either parent, and RAPDs (randomly amplified polymorphic DNA) are used for determining hybrid status (Daehler and Strong 1997a). Current work (Ayres *et al.* 1999) shows that hybrids are widespread throughout the south end of the Bay, and that the hybrid swarm consists of backcrossed as well as F_1 individuals. These hybrids are fertile and are reproducing by seed. Morphologically, hybrids appear to be as fit as either parent, and they will probably become more common as seed disperses ever more widely in the Bay. Eradication efforts must be well informed about the distribution of these hybrids.

In contrast to the situation in San Francisco Bay, the alien cordgrasses in Washington State are prime candidates for biological control. No close relatives of cordgrass live in estuaries or near the coast north of the San Francisco Bay region, so Willapa Bay and Puget Sound are safe places to introduce highly specialized insect herbivores of cordgrass. These insects are restricted to areas where cordgrasses are native (Strong *et al.* 1984: Daehler and Strong 1997b) so the populations of alien cordgrasses in Willapa Bay and Puget Sound have not been exposed to these insects during their stay in the Pacific. Our experiments have concentrated upon the planthopper *Prokelisia marginata*, which is native to California where it feeds upon California Cordgrass, and to Atlantic and Gulf coast marshes where it feeds upon Smooth Cordgrass.

Smooth Cordgrass from Willapa Bay is quite vulnerable to the planthopper *Prokelisia marginata* (Daehler and Strong 1995). We discovered this in the greenhouse at the Bodega Marine Laboratory in Bodega Bay, California, where many Willapa Bay clones fed upon by *P. marginata* were severely harmed, and some were killed. High densities of the planthopper led to the deaths of about 1/3 of the Willapa Bay plants after the second summer of feeding by the planthopper. The control plants with very-low (but not zero) densities of the hopper grew normally and suffered very low mortality. This suggests that *Prokelisia marginata* could harm Smooth Cordgrass in Willapa Bay, were it introduced. Similarly, we have recently found in the greenhouse that both *Prokelisia marginata* and *Prokelisia dolus*, a sibling species to *P. marginata* that feeds upon Smooth Cordgrass on the Atlantic and Gulf coasts and upon California Cordgrass in Southern California (Denno *et al.* 1996), feeds upon and kills *Spartina anglica* clones from Puget Sound (Wu *et al.* 1999).

LOST RESISTANCE

The low resistance of the exiled cordgrass populations to feeding by *Prokelisia* species is unusual. In contrast, Smooth Cordgrass from both native areas and San Francisco Bay, and California Cordgrass are quite resistant to feeding by these insects (Daehler and Strong 1997b). These plants suffered little even at high densities of the planthopper.

While Smooth Cordgrass in San Francisco Bay was never exiled from specialist *Spartina*-feeding herbivores, the Washington populations of cordgrass have grown through a number of generations in the absence of specialist insect herbivores. Smooth Cordgrass has been in Willapa Bay for at least 60 years (Scheffer 1945; Sayce 1988). This species can set seed within three years, so this amounts to perhaps twenty or more generations of isolation from these insects in Willapa Bay. English Cordgrass has never been subjected to herbivory by *Prokelisia* spp. This plant species arose in England during the 19th century from a cross between European *Spartina maritima* and *S. alterniflora* from North America that was probably introduced with cast-off ships' ballast (Ferris *et al.*1997). This produced the sterile *Spartina* x *townsendii*, which subsequently gave rise to the fertile amphiploid *Spartina anglica*.

Why are these exiled cordgrass populations less resistant to *Prokelisia* than populations that have not been isolated from specialist herbivores? Three general ideas suggest themselves. Genes for herbivore resistance could have been absent by chance from the founding population resulting in a lack of resistance in contemporary populations. Second, the founding population could have gone through a deleterious genetic bottleneck in which inbreeding led to a loss of vigor resulting in erosion of herbivore defense and reduced competitive ability (Barrett 1982). However, sexual reproduction and rapid population growth can sometimes staunch such a loss of genetic diversity (Slatkin 1996), so it is not surprising that weed populations established by a few founders can be genetically diverse (Colosi and Schaal 1992).

The final hypothesis is based upon the premise that resistance or tolerance to herbivores represents a significant metabolic and developmental cost to a plant. The plant maintains resistance at a cost of slower growth or otherwise diminished capacities reducing its competitive ability, a major component of fitness in weeds (McEvoy 1993). Thus, resistance should be selected against in plant populations that have been exiled from their specialist herbivores where resistance has no value. For example, Blossey and Kamil (1996) have found such a correlation in purple loosestrife; lower resistance is coupled with greater competitive ability in weedy North America and Australian populations relative to native European populations of this plant. In a test of his trade-off hypothesis, Dino Garcia-Rossi (1998) of our laboratory performed a greenhouse experiment in which Smooth Cordgrass clones from Willapa Bay were placed in competition with clones from San Francisco Bay, in the presence of very low or very high densities of the planthopper. Confirming the susceptibility-resistance patterns found earlier (Daehler and Strong 1997b), the San Francisco Bay clones thrived while the clones from Willapa Bay were all killed in the treatment combinations that included high densities of the planthopper. However, the trade-off hypothesis was not confirmed as there was no difference in competitive ability between the two populations.

A practical question remaining is, will the planthoppers harm alien cordgrasses in the field? Questions for basic science are, what is (are) the mechanism(s) that cause these phloem-feeding insects to harm vulnerable cordgrass populations, and why are some populations vulnerable?

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