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# BIOLOGICAL CONTROL OF MARINE PESTS[1]

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*Abstract.* Biological control, as used in terrestrial systems, may hold promise for use against exotic marine species. We first review some marine pests, displaying their diversity, the damage they cause, and possible controls. We then contrast approaches for marine and terrestrial pest control, providing guidelines for adapting terrestrial controls to the marine environment. Although several of the same principles apply in terrestrial and marine environments, marine systems 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, we propose 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 to Tasmania. We conclude that biological control may be possible for some marine pests, but that existing strategies and expectations will require modification.

*Key words: biological control; biocontrol agents, safety testing of;* Carcinus maenas*; green crab; host specificity; introduced species; marine pests, biological control of; natural enemies; parasitic castrator; recruitment, importance of; Rhizocephala.*

## INTRODUCTION

Some species, often those that are introduced from elsewhere, are "pests" to the extent that efforts have been made to control them in terrestrial and freshwater environments. Prior to the advent of chemical pesticides, use of natural enemies of these pests was an important area of applied research, particularly in agriculture. We now recognize the unfortunate environmental damage caused by some of these pesticides and we have repeatedly witnessed the development of genetic resistance of pests. Hence, interest in biological control has been renewed. We now have an extensive body of practical and theoretical knowledge concerning biological control, and a track record that includes many successful applications interspersed with some notable failures. Biological control for these pest problems has involved the deployment of herbivores, predators, parasites, or diseases.

In marine environments, introductions are also common and damaging (Carlton 1987, 1989, Zibrowius 1991), but efforts at pest control have been limited to conventional pesticides. Recent studies on mechanisms of transport and establishment indicate that ballast water, as a larval conveyance, is the most important means of dissemination (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 (Lafferty and Kuris 1994). The resultant, extremely high population densities attained by alien species is what usually leads to economic damage (Nichols et al. 1990).

There have been several recent calls for research on biological control of marine pests (Miller 1985, Moyle 1991, Buttermore et al. 1994, Lafferty and Kuris 1994). Australia's CSIRO (Commonwealth Scientific and Industrial Research Organization) Division of Fisheries has recently taken the lead in marine pest problems by establishing the Centre for Research on Introduced Marine Pests (CRIMP) in Hobart, Tasmania. CRIMP plans a pro-active approach to marine pests in the style of Australia's historically aggressive and innovative use of terrestrial biological control. To stimulate further dialogue on control of marine pests, particularly introduced species, we first briefly consider some marine pests in U.S. waters. We illustrate the highly diverse nature of these pests and focus on the type of damage they cause and on considerations for their control. The heart of our paper contrasts the general nature of marine vs. terrestrial pest control, and we provide some guidelines for the adaptation of existing biological control strategies to the unique challenges of the marine environment. Finally, we present a case study of the introduced European green crab, *Carcinus maenas.* Since

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[1] For reprints of this Special Feature, see Footnote 1, p. 1963.

this has been recognized as a serious pest and is a well-studied animal, we outline a general approach to its control.

## SOME MARINE PESTS

The introduction of marine pests to new habitats is as old as nautical experience. Recall that Sir Francis Drake had to rebuild the Golden Hind in California in 1579, probably because it was riddled with (mostly) Atlantic shipworms. It is quite possible that this first ship served to introduce a marine pest to California. So it is not surprising that introduced species such as *Mytilus galloprovincialis* and the western Atlantic populations of the European green crab have planted themselves so firmly on our shores that most ecologists accept them, without concern, as a naturalized part of the biota. Many other introductions, particularly polychaetes and amphipods, are cryptic and have been considered species with natural cosmopolitan distributions (Chapman 1988). The following subsections describe and discuss a series of well-known marine pests.

*Red and brown tides.*—Red tides result from blooms of marine dinoflagellates. For many years, these dinoflagellates have been considered cosmopolitan, and the increasing frequency of blooms a result of coastal eutrophication. Now it appears that some species have been transported by ballast water (Hallegraeff 1993) or with shellfish for mariculture (Shumway 1989). Red tides can cause massive fish mortality, with consequent pollution of beaches and losses to fisheries. When algal toxins build up in edible shellfish, humans can die of paralytic shellfish poisoning. Massive brown-tide blooms caused by chrysophytes have also caused heavy mortalities of invertebrates and eel grass beds and have severely impacted scallop fisheries. Algal consumers, such as planktonic ciliates and heterotrophic dinoflagellates, might act as control agents (Jeong and Latz 1994). Viral outbreaks have been implicated as important controls for algal blooms and offer potential for prevention or attenuation of such blooms (Sieburth et al. 1988, Suttle et al. 1990, Milligan and Cosper 1994).

*Red algae.*—Two species of introduced red algae affect community structure of Hawaiian coral reefs. *Acanthophora spicifera* came to Hawaii in the 1950s (Doty 1961), possibly attached to ships or with aquarium fishes. A highly adaptable alga, it became well established and is currently the most widespread exotic alga in Hawaii (Russell 1992). *Hypnea musciformis* invaded Hawaii in 1974 (Abbott 1987) and became a dominant species at several reefs on Oahu by 1977. Both exotic algae have rapid growth rates, high reproductive capacities, and compete with the native *Hypnea cervicornis* (*A. spicifera* also competes with the native *Laurencia nidifica*). Both species resist herbivory, which may complicate the use of grazers as natural enemies. The high productivity of these introduced species on some reefs raises drag and causes the eventual loss of reef material (Russell 1992). On a positive note, both species are now significant food sources for globally endangered green sea turtles, *Chelonia mydas* (Russell and Balazs 1994).

*Jellyfish.*—Although it is apparently native, the summer jellyfish, *Chrysaora quinquecirrha,* becomes periodically abundant in the Chesapeake Bay region, reaching pest proportions. Its relatively powerful stinging nematocysts are responsible for intense burning reactions among swimmers and those who must work around the water. Its presence has a negative but unmeasured impact on tourism in that area, as swimming is often avoided. Jellyfish have sometimes become so abundant that they clog nets and block water-intake pipes (Ruppert and Fox 1988). Hyperiid amphipods might be possible control agents. These generally host-specific amphipods act as parasitoids, parasites, or parasitic castrators on gelatinous zooplankton (Kuris 1974). However, biological control in this case may have risks. In Chesapeake Bay, *C. quinquecirrha* preys on, and may control, the ctenophore *Mnemiopsis leidyi* (Feigenbaum and Kelly 1984). The cascading release of *M. leidyi* from predation could lead to the sorts of problems that occur now in the Black Sea, where *M. leidyi* was introduced in 1982 (Vinogradov et al. 1989). Achieving incredible densities there, it has altered the food chain and led to the collapse of fisheries by consuming a large proportion of the zooplankton (Harbison and Volovik 1994). Ironically, two jellyfish from the Black Sea have recently invaded San Francisco Bay (Mills and Sommer 1995).

*Nemerteans.*—Egg predators in the genera *Carcinonemertes* and *Pseudocarcinonemertes* can cause very substantial mortality of eggs in the clutches of Dungeness crabs (*Cancer magister*), red king crabs (*Paralithodes camtschatica*), and American lobsters (*Homarus americanus*) (reviewed in Kuris [1991]). This mortality is sometimes so substantial that it has been implicated as the cause of the non-recovery of the Central California Dungeness crab fishery and the collapse of some red king crab stocks (Hobbs and Botsford 1988), Kuris et al. 1991). Models of brood mortality and parasitic castration in crustacean fisheries suggest that adaptive management strategies, such as intensive fishing of both sexes in heavily infected localities, may be able to break the threshold of nemertean transmission without reducing yield to the fishery (Kuris and Lafferty 1992). This represents an instance where the ability to fish a pest (in this case, along with its host) might lead to its removal.

*Snails.*—Snails introduced with oyster culture have been quite successful in bays and estuaries. The oyster drill, *Urosalpinx cinerea,* has sometimes become an established pest even where introduced oyster culture has failed (Carlton 1975). In San Francisco Bay, *Ilynassa obsoleta* (from the East Coast) is able to outcompete the native mud snail, *Cerithidea californica,* by preying on its egg masses (Race 1982). The Japanese snail *Battilaria attramentaria* may also be competitively superior to *C. californica* (Whitlatch and Obrebski 1980; S. McDermott, *unpublished manuscript*). Interestingly, the latter two introduced species are castrated by native larval trematodes (K. D. Lafferty, *personal observation*). Unlike the oyster drill, the primary consequence of these grazers is the replacement of a functionally similar competitor. Thus, alterations to the ecosystem are likely to be relatively subtle.

*Bivalves.*—The oyster industry has paid a price for its frequent and inadequately monitored spread of new species for culture. Introduced oyster diseases have caused severe mortality in several new culture areas (Farley 1992). The Asian clam, *Potamocorbula amurensis,* invaded San Francisco Bay and became abundant in the late 1980s, reaching phenomenal densities (>10 000 individuals/m$^2$) (Carlton et al. 1990). It may cause major alterations in this estuarine system, including displacing other suspension and filter feeders, altering diets of fish and birds, reducing phytoplankton, and altering substrate stabilization. Another bivalve, the brown mussel (*Perna perna*) from South Africa, has appeared in large numbers on the Texas coast where it has crowded out other organisms, becoming the dominant organism on pier pilings (Hicks and Tunnell 1993). As most of the hard-substrate habitat (piers, breakwaters, jetties) in Texas is not natural, it might not seriously affect native fauna. Mussels, in general, may increase the drag on subsurface pilings to the extent that they must be removed (the same is true of a wide range of fouling organisms on ships).

*Sea urchins.*—The destructive impact of sea urchins, *Strongylocentrotus* spp., on kelp forests was a major, inshore, marine environmental concern from the 1950s to the 1970s. Dense aggregations of urchins (>100 individuals/m$^2$), termed "barrens," prevented the recolonization of kelp (Ebeling et al. 1985). A protozoan parasite, *Paramoeba invadens,* was recommended and tested in the laboratory as a biological control agent because natural outbreaks of this ameba greatly reduced sea urchin abundance (Jones 1985, Jones and Scheibling 1985, Miller 1985). Fatal to this control scheme was the emergence of sea urchins as a major U.S. fishery in the 1980s (with the highest landings value among California fisheries, Parker and Kalvass 1992). Not surprisingly, there are now no control efforts against sea urchins. Instead, research efforts aim to protect dwindling stocks.

*Polychaetes.*—Spionid polychaete worms in the genus *Polydora* are shell borers, inhabiting many commercially important marine molluscs (Lauckner 1983). High infestations inhibit normal growth of the host, weaken the shell, and can kill the animal. Classification as a "pest" dates back to 1940, following large mortalities of east coast oysters due to *Polydora websteri* (Lunz 1940, 1941, Loosanoff and Engle 1943). The worm is likely native and is found naturally at low densities, but mariculture apparently provides host densities conducive for high worm densities (Wargo and Ford 1993). In addition, substantial damage to mussels (Kent 1979, 1981) and scallops (Evans 1969, Bergman et al. 1981, Mori et al. 1985) has been attributed to *P. websteri* and *P. ligni.* Infestations of abalone (Blake and Evans 1973, Hahn 1989) and other intertidal gastropods (Blake 1971, Blake and Evans 1973) also occur. Because worms are prevalent in mariculture operations, some control methods exist (reviewed by Lauckner [1983]). Most control is chemical, killing many existing individuals but allowing rapid re-infestation. In 1993 an undescribed species of sabellid polychaete was recognized as the causative agent of marked shell deformations and cessation of growth in cultured abalone in California. The worm is a South African species (K. Fitzhugh and G. Rouse, *unpublished manuscript*). Outflow from culture facilities and release of infested abalone in outplanting programs threaten to introduce this pest into California waters (A. Kuris, C. Culver, and K. Fitzhugh, *unpublished manuscript*).

*Burrowing shrimps.*—The native ghost shrimp (*Callianassa californiensis*) and mud shrimp (*Upogebia pugettensis*) disturb and suspend sediments in bays and estuaries, negatively affecting some filter-feeding organisms. The oyster industry in Washington State initiated chemical control with carbaryl to reduce bioturbation by shrimps. Since 1990 the Burrowing Shrimp Committee has been developing an integrated pest management plan. The Committee ranked biological control agents second among research priority areas and specifically recommended the use of oyster shell as refuge for juvenile Dungeness crab that prey on the shrimps (B. Dumbauld, *personal communication*). Although, as yet, there has been no search for potential parasites and pathogens of the shrimps, research on natural enemies continues while Washington and Oregon try to develop non-chemical means of control. Cooperation with the mudshrimp bait fishery might also help reduce densities.

*Crabs.*—Several species of crab are pests or potential pests. The European green crab, *Carcinus maenas,* became established in California around 1990 and has received much attention. We will discuss it at length below (see *A case study: the green crab*). McDermott (1991) noticed a shore crab from the western Pacific, *Hemigrapsus sanguineus,* in New Jersey in 1988. It presently ranges from at least Chesapeake Bay to Cape Cod. Its widely dispersing larval stages may help expand its range further. It is difficult to predict what impact *H. sanguineus* will have. It lives higher up in the intertidal than other east coast crabs and, therefore, may not compete much with the native fauna. An even more recently observed introduction (1994) is the Chinese mitten crab (*Eriocheir japonicus*) into San Francisco Bay and the Sacramento–San Joaquin Delta region. This species has clear potential for damage. It burrows into banks and could further weaken levees in the Delta. Mitten crabs invaded Germany in the 1920s where they caused substantial erosion in the Lower Rhine Valley. The Germans eventually extirpated them with an intensive trapping program. An additional concern surrounding the introduction of the Chinese mitten crab in California is that it is an important second intermediate host for Oriental lung fluke (*Paragonimus westermani*), a trematode that causes substantial pathology in Asia. Since many infected people from Asia have already immigrated to California (Burton et al. 1982), the arrival of *E. japonicus* closes a further link in the life cycle of the lung fluke. If the mitten crab becomes abundant, it may also serve as a suitable host for native North American lung flukes *P. kellicotti* and *P. mexicanus* (Pachucki et al. 1984, Markell et al. 1992: 216), increasing the potential for zoonoses (infection of humans by normally sylvatic parasites).

*Tunicates.*—Following the regrettable release of the compound tunicate, *Botrylloides sandiegensis,* by a developmental biologist in the vicinity of Woods Hole, Massachusetts, this orange tunicate, known now as Freeman's blight, has spread along the southern New England coast, coating rocks, piers, and other hard substrates with a layer of orange gelatinous slime. It has replaced other encrusting organisms and is a nuisance in harbors. No attempt to control this species has been made and it is likely to continue its rapid spread to the south.

*Fishes.*—The yellowfin goby, *Acanthogobius flavimanus,* is an estuarine fish that turned up in the lower Sacramento Delta region of California around 1963 (Brittan et al. 1970). Although it probably invaded as a result of the transport of oysters from Japan, it could also have arrived in ballast water or as a discard from live shipments meant for food (McGinnis 1984). The goby has successfully dispersed from estuary to estuary in a southward expansion along the coast. It grows to large sizes for a goby (>25 cm) and feeds on invertebrates and small fish. This is of concern in areas where it overlaps with the federally endangered tidewater goby (Lafferty et al. 1996). Yellowfin gobies are considered a delicacy in Japan and, although difficult to seine, are relatively easy to trap (McGinnis 1984). Encouraging a trap fishery for Asian American markets or export might be one method for control.

## CAN BIOLOGICAL CONTROL BE APPLIED TO MARINE PESTS?

The absence of studies on the control of introduced marine and estuarine pests approaches fatalism. Occasional forlorn cries for solutions (e.g., MacPhail et al. 1955) have yielded little response from researchers and management agencies. This is odd, considering that the use of natural enemies in classical biological control is a robust approach with a long track record of remarkable successes in agriculture. Since the successful scientific application of biological control to an insect pest in the 1880s (the cottony cushion scale in California by the Vidalia beetle and parasitoid wasps), its use against many insect pests has become well established and analyzed. 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. A 100-yr head start provides a vast source of insight. With similarities and differences more clearly in view, we can then use the terrestrial experience as an ample source of guidance for the control of marine pests (see Fig. 1 for a proposed general strategy).

Certain biological and economic features made the use of natural enemies highly desirable in terrestrial systems. Firstly, successful natural enemies are able to either track pest populations or to locate new pest populations as they eradicate others. Secondly, because natural enemies can evolve, they largely evade development of resistance on the part of the pests (by coevolving). Thirdly, when well chosen, and carefully tested on native hosts, they usually have sufficient specificity to be environmentally safe. When successful, they provide either a long-term or a permanent solution to a pest problem. Thus, use of natural enemies will generally produce a low-cost solution to pest problems.

The underlying question for the biological control of an introduced species is, "What controlled its abundance in its native region and why is it a problem in its introduced locale if it is not a problem where it is native?" The extensive practical success of the insect pest biological-control approach demonstrates how to answer these questions. Natural enemies generally control insect populations and these enemies are more likely to be available in the native regions of the pests (Huffaker 1971, DeBach 1974, Kuris and Norton, 1985). In essence, biological control strategies are seemingly paradoxical: seek the solution where there may be no apparent problem. Therefore, to use natural enemies as a biological control, it is clearly necessary 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

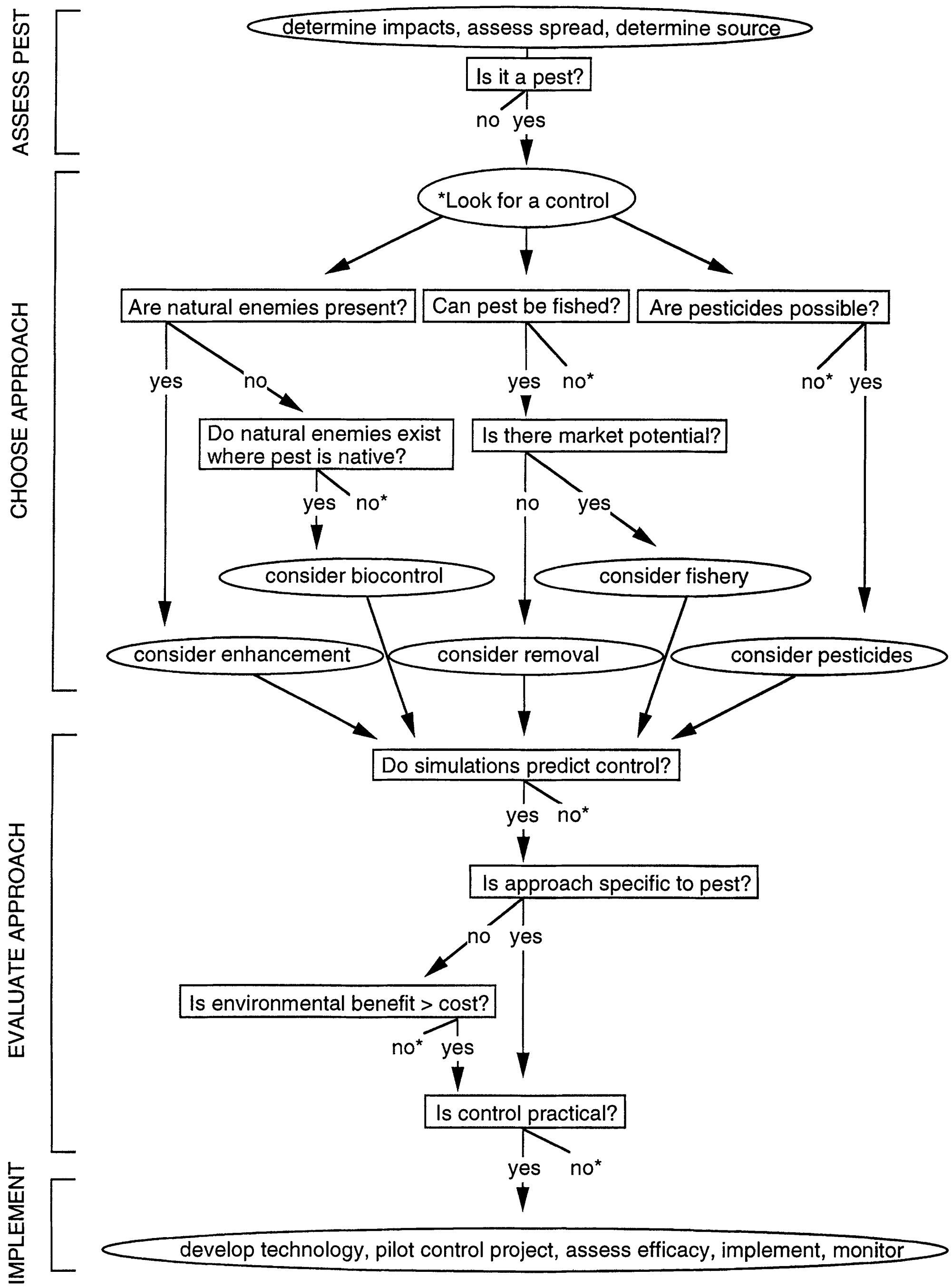

FIG. 1. A flow diagram for controlling marine pests. This approach emphasizes the ability to consider and use a variety of approaches (our figure is not meant to be all-encompassing). Although all decisions in the chart could be made based on extensive research, in some cases the choices will be obvious. The value of rigorous evaluations needs to be weighed against the advantage of a rapid response. The "no*" choice means return to "*Look for a control."

good (economic) control in terrestrial systems without deleterious side effects are parasitoids. Parasitoids are like parasites in that they permanently feed on a single host, but they are like predators in that a single parasitoid will always ultimately kill its host. Pathology is not intensity dependent; more parasitoids do not cause more damage than does a sole parasitoid (Kuris 1974).

Several criteria define a good biological control agent (Kuris 1973, DeBach 1974). The agent should respond numerically to host outbreaks. At low host densities it should either be able to find the host and persist so that pest outbreaks do not occur after pest density drops, or be able to rapidly and efficiently locate pest patches so that outbreaks do not occur (although some have argued that this overemphasizes the importance of stabilizing factors at local scales [Murdoch et al. 1985, Waage 1990]). The agent should also have the physiological capacity to survive in the target area. The ability to culture the biological control agent is important for implementing a control strategy. Most importantly, biological control agents should be host specific so that they do not damage valued native organisms.

### *Special considerations in marine environments*

Marine systems have some important features that contrast with terrestrial biological control paradigms and require special consideration. To develop a protocol for the biological control of a marine pest, it is first necessary to precisely consider what qualifies as "control." Eradication is certainly not possible once a pest has become well established. 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 maximize the economic yield of their crops. For many crops, merely maximizing tonnage is insufficient; the cosmetic condition of the produce is also important. In contrast, for marine pests, it seems probable that it will not be economically nor culturally necessary to achieve such an exquisite degree of control. Damage due to marine pests occurs at outbreak densities. There is usually no reason to reduce pest populations to very low levels, and relatively modest reductions in pest abundance will usually provide a successful outcome.

Another important difference between terrestrial and marine systems is the general nature of recruitment (Gaines and Lafferty 1995). In terrestrial habitats, recruitment of most species is relatively closed; offspring mostly live in the vicinity of the parents. Recruitment to a distant suitable patch is a rarity, and biological control using natural enemies is effective because control agents either reduce and persist in local patches or can disperse and efficiently locate more distant pest patches (Murdoch et al. 1985). In marine environments recruitment is generally open; planktonic larval stages disperse widely, and offspring rarely settle and live near their parents. Oceanic and local abiotic factors drive recruitment, and numerical responses to a locally high pest density may not occur. Biological control may not have been sought because actions taken against adults at a particular location are intuitively deemed to have no impact on future recruitment. Approaches aimed at reducing the reproductive output of a pest population with parasitic castrators or egg predators might appear even more futile. In this case, efforts would neither reduce pest densities nor prevent subsequent recruitment. However, these limitations are scale-dependent phenomena that require a new frame of reference. In other words, the perspective of terrestrial crop damage or disease transmission with localized impacts has traditionally dominated pest control, in both theory and practice. To devise and implement biological control in marine systems requires a vision of a much broader spatial scale. Therefore, large-scale institutional efforts may be needed for success.

Control agents for marine systems include parasitic castrators as well as predators, competitors, and diseases. Parasitic castrators are more typical of marine systems than parasitoids and deserve special attention. Unfortunately, in comparison with insect parasitoids (see Murdoch and Briggs 1996), there has been little attention paid to the ability of parasitic castrators to control host populations. Like parasitoids, parasitic castrators do not cause intensity-dependent pathology (Kuris 1974); a single parasitic castrator blocks the reproductive capability of its host. Also, like the parasitoid-infected host, the reproductive potential of the parasitically castrated host is nil. However, the castrated host continues to exert intraspecific competitive effects against unparasitized individuals (Lafferty 1993). It also continues to be a pest. Other differences of parasitic castrators include an inability to attack more than one host and limited abilities to search out dense host patches. Kuris (1974) postulated that, analogous to parasitoids, parasitic castrators may be able to control host populations. Analytical models (Blower and Roughgarden 1987, Lafferty 1991, Kuris and Lafferty 1992, Gaines and Lafferty 1995) and experimental evidence from field studies (Blower and Roughgarden 1989, Lafferty 1993) support this. Other effective control agents include some predators (Van den Bosch et al. 1982, Hofkin et al. 1991) and, for control of freshwater snails, competitors (Jobin et al. 1977, Nassi et al. 1979, Pointier 1983, Pointier et al. 1991).

A potential disadvantage when using natural enemies in marine environments compared to their use in terrestrial counterparts concerns safety. It would seem that our society cares little about native insects such as aphids or scale. In contrast, 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 Dungeness crab populations, even if the natural enemy was effective against the targeted pest. Thus, environmental safety of natural enemies used against marine pests must meet a high safety threshold to conserve our native fauna.

In addition to biological control in its classic mode (introducing an exotic natural enemy to control an exotic pest), we also consider aspects of control suitable for an integrated pest management approach. These may include: pesticides, mechanical removal, fisheries, and the enhancement of native natural enemies (Fig. 1). Chemical controls (in the form the anti-fouling agent tributyltin or penta-impregnated pressure-treated pilings) are effective but, like many pesticides used on terrestrial pests, have collateral effects on non-target species. Mechanical removal of pests has been used to clear fouling organisms from offshore oil platforms. In recent years, it was realized that the fouling community was dominated by mussels, an increasingly valuable seafood commodity. A substantial fishery has replaced mechanical removal (R. Meek, *personal communication*). Enhancing native predators, such as increasing the abundance of Dungeness crabs to control burrowing shrimps, is a relatively safe form of biological control because it does not involve introducing exotic control agents. We next provide a case study that recommends a combination of introducing a parasite and initiating a fishery.

## A CASE STUDY: THE GREEN CRAB

The European green crab makes an interesting test case because it is likely to prove to be a truly bad introduction. Establishing in San Francisco Bay in 1990 (Cohen et al. 1995), it is euryhaline and extends up estuaries to low-salinity conditions (1.4%) (Williams 1984). On the West Coast the green crab lives in protected bays, on soft bottoms, from the intertidal zone to 6 m deep. On the Atlantic coast, and where native in Europe, it also occurs on semi-protected rocky outer coasts. Since its discovery, *Carcinus maenas* has spread north to Bolinas Lagoon, Drake's Estero, Tomales Bay, Bodega Harbor, and Humboldt Bay and south to Elkhorn Slough (T. Carlton, A. Cohen, E. Grosholz, *personal communications*). It now encompasses a latitudinal range of over 500 km in California. As it has also invaded South Africa and Australia (mainland and Tasmania) international cooperation is likely to aid the development of control over the next several years.

The green crab is a well-studied species. The literature of the past 25 yr has emphasized the feeding habits of the green crab as this provides the most direct evidence of its economic impact on shellfish prey (Glude 1955, Moulton and Gustafson 1956, Ropes 1968, Elner 1981, Le Roux et al. 1990). In their native range, green crabs are voracious predators of many benthic invertebrates (Scherer and Reise 1981, Klein Breteler 1983, Sanchez-Salazar et al. 1987). For example, in Britain they each consume up to forty 15-mm-long cockles per day. After its introduction to the western Atlantic, the green crab had a devastating impact on shellfish fisheries. The demise of the softshell clam fishery in northern New England and Nova Scotia is associated with *Carcinus maenas* (Glude 1955, Moulton and Gustafson 1956, Ropes 1968). They have destroyed artificial shellfish beds and consumed large numbers of young oysters and *Cancer* crabs (MacPhail et al. 1955, Ropes 1968, Elner 1981).

Virtually all groups listed by Nichols and Thompson (1985) as the predominant macrobenthic species (introduced and native) of South San Francisco Bay are known prey types for the green crab (Ropes 1968). It is unlikely that native shellfish will exhibit useful defensive preadaptations to this voracious generalist, eurytopic, euryhaline predator. The green crab is likely to alter the distribution, abundance, and species interactions of intertidal and subtidal faunas, both native and non-native, wild and cultured (Cohen et al. 1995, Grosholz and Ruiz 1995).

Based on the history of *Carcinus maenas* after its introduction elsewhere (Ropes 1968, Le Roux et al. 1990), the crab is likely to devastate the intertidal and subtidal beds of the softshell clam, *Mya arenaria,* the Japanese cockle, *Tapes japonica,* several *Macoma* species, and the marsh mussel *Geukensia demissa* in San Francisco. If population densities increase in the substantial shellfish mariculture industry of nearby Tomales Bay and Drakes Estero, it may heavily impact young shellfish. So far, measures taken to reduce predation (mesh enclosures) seem to have been successful for clam and oyster seeding operations in Tomales Bay (T. Sawyer, *personal communication*).

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. The spread is mostly likely to come in spurts (Grosholz 1996). The large volume of commercial shipping along the Pacific Coast is very likely to introduce green crabs in ballast water to most of its major harbors. This would threaten the nation's largest oyster-rearing industry in Washington state. Green crabs could also reduce commercial stocks of Dungeness crab in Washington and Oregon and of rock crabs to the south. Since Dungeness crabs use bays for nursery areas, juveniles would be exposed to both competition for a similar food base of small epibenthic

TABLE 1. Preliminary assessment of the economic value of the existing fishery harvest (landings) that are potentially threatened by the introduction of green crabs on the west coast of the United States. Landing estimates are conservative, based on information in Leet et al. (1992) and from S. Berry (*personal communication*); net value estimates† are also conservative. Other fisheries may be at risk if crabs extend their range to Washington State.

| Landings |  | Threatened annual value ($10^6$ U.S.$) |  |  |
|---|---|---|---|---|
| Type | Year | Northern and central California | Additional if crabs reach southern California | Additional if crabs reach Puget Sound |
| Dungeness crab | 1990–1991 | 17.0 | ··· | 16.4 |
| Rock crabs | 1990 | ··· | 2.5 | ··· |
| Mussels | 1990 | 0.5 | 0.5 | ··· |
| Oysters | 1990–1991 | 1.0 | ··· | 20.0 |
| Bait | 1990–1991 | 0.5 | ··· | ··· |
| Total |  | 19.0 | 3.0 | 36.0 |
| Net value† |  | 15.2 | 2.4 | 29.1 |
| Net value including secondary and tertiary values† |  | 22.8 | 3.6 | 43.7 |

† Net value is the gross value of the landings less a liberal 20% estimate for the fishermen's expenses. Secondary values are processing and wholesaling; and tertiary value is in retailing; these are accounted for by multiplying the simple net value by 1.5.

invertebrates, and direct predation by green crabs (Grosholz and Ruiz 1995).

Although the impact of the green crab on West Coast fisheries is potentially very considerable, there is, as yet, no damage assessment. Potentially, the green crab introduction could cause direct losses of all or part of the oyster, mussel, and clam mariculture industries in Tomales Bay and Drakes Estero, a 1993 harvest value of about U.S.$2.5 × $10^6$, as well as losses to the Dungeness fishery, and impact on bait fisheries and sports fisheries (Table 1). Beyond this direct economic impact, the ability of *C. maenas* to burrow extensively in marshes (Berill and Berill 1981) suggests that bioerosion and destabilization of marsh channel banks, levees, and dikes may occur.

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 predators and parasites of the green crab in Europe are relatively well known (Crothers 1968, Williams 1984). In particular, in-depth studies of two parasitic castrators, *Sacculina carcini* and *Portunion maenadis,* are available. These document their life cycles and effects on host growth, reproduction, and behavior, and provide some information on their prevalence in different populations (Day 1935, Veillet 1945, Rasmussen 1959, Crothers 1968, Heath 1971, Lützen 1984, Høeg and Lützen 1985).

The parasitic barnacle *Sacculina carcini* presently seems the best candidate for biological control as the Rhizocephala are highly host-specific parasitic castrators that can theoretically control host populations. Høeg and Lützen (1985) recently reviewed the host range of *S. carcini.* All valid records are for portunid crabs (including *Carcinus maenas*) or for the related Pirimelidae. Fortunately, the native crab fauna of central California lacks representatives of these families (Schmitt 1921, Carlton and Kuris 1980, Garth and Abbott 1980). Further, the family Cancridae seems to be remarkably unsusceptible to rhizocephalans. Only the European *Cancer pagurus* is parasitized by the distinctive host-specific species, *S. triangularis* (Høeg and Lützen 1985). It is likely that host specificity is even stronger than currently recognized. Karyological analyses of morphologically similar sacculinids from different species of crabs demonstrate species-level differences in chromosome number and organization (Fratello 1968). 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]) underscores the need for carefully controlled experiments to determine if native species are refractory to infections of the parasite.

Following 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. Determination of the geographic origin of the introduced crabs using genetic techniques would allow better selection of an appropriate source of parasites. 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.

In addition to this rather classical biological control program, it might be useful to integrate a subsidized fishery for green crabs. After all, fisheries are a proven way to eradicate a species. Although the green crab is too small for traditional seafood markets, it is a tasty crab (A. M. Kuris, *personal observation*) and should be acceptable to several ethnic groups with sizable communities around San Francisco Bay. In the Tokyo Bay area of Japan, the introduced Mediterranean green crab is split in two and adds flavor to miso soup (M. Takeda, *personal communication*). So far, it is not a pest in Japan.

## CONCLUSIONS

It is absolutely certain that more deleterious invasions are yet to come (we predict, for example, that the Asiatic seastar, *Asterias amurensis,* will invade the West Coast just as it has invaded Tasmania). Shipping will continue to expand as our national economy inexorably integrates into the global economy. This will intensify the rate of ballast-water introductions. Management of ballast water continues to be a minimally regulated, controversial issue. Mariculture of imported species has always included unwanted hitchhikers that accompany the shipments of commercial species. This second major source of new pests is also expanding as we struggle to replace declining fisheries. Beyond the obvious need to protect our waters from unwanted introductions, ecologists can help predict new arrivals, study the basic biology of these probable new arrivals, and work on biological controls. We cannot overemphasize that, as has been long evident in the management of agricultural pests, early detection and a rapid response afford the greatest opportunity to control pest invasions.

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