698.34

Biological Control of Marine Invasions

Kevin D. Lafferty
Marine Science Institute
University of California
Santa Barbara, CA 93106

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.

ACKNOWLEDGMENTS

LITERATURE CITED

Blower, S. and J. Roughgarden (1987) Population dynamics and parasitic castration: a mathematical model. *American Naturalist* 129: 730-753.

Carlton, J. T. (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanography and Marine Biology Annual Review* 23: 313-371.

Carlton, J. T. (1987) Mechanisms and patterns of transoceanic marine biological invasions in the Pacific Ocean. *Bulletin of Marine Science* 41: 467-499.

Carlton, J. T. (1989) Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. *Conservation Biology* 3: 452-465.
Cohen, A. N., J. T. Carlton and M. C. Fountain (1995) Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. *Marine Biology* 122: 225-237.

Gaines, S. D. and K. D. Lafferty (1995) Modeling the dynamics of marine species: the importance of incorporating larval dispersal. Pages 389-412 in: McEdward, L. (ed.), Ecology of Marine Invertebrate Larvae, CRC Press, Boca Raton, Florida.

Grosholz, E. D. and G. M. Ruiz (1995) Does spatial heterogeneity and genetic variation in populations of

the xanthid crab *Rhithropanopeus harrisii* (Gould) influence the prevalence of an introduced parasitic castrator? *Journal of Experimental Marine Biology and Ecology* 187: 129-145.

Høeg, J. (1997) The parasitic castrator *Sacculina carcini* as a possible biological control agent of *Carcinus maenas*: background and results of preliminary work. Pages 69-75 in: Thresher, R. E. (ed.), Proceedings of the First International Workshop on the Demography, Impacts and Management of Introduced Populations of the European Crab, *Carcinus maenas*. Technical Report No. 11, Centre for Research on Introduced Marine Pests, Hobart, Tasmania.

Kuris, A. M. (1974) Trophic interactions: similarity of parasitic castrators to parasitoids. *Quarterly Review of Biology* 49: 129-148.

Lafferty, K. D. (1993) Effects of parasitic castration on growth, reproduction and population dynamics *Cerithidea californica*. *Marine Ecology Progress Series* 96: 229-237.

Lafferty, K. D. and A. M. Kuris (1996) Biological control of marine pests. *Ecology* 77: 1989-2000.

Le Roux, P. J., G. M. Branch and M. A. P. Joska (1990) On the distribution, diet and possible impact of the invasive European shore crab *Carcinus maenas* (L.) along the South African coast. *South African Journal of Marine Science* 9: 85-93.

Minchin, D. (1997) The influence of the parasitic cirripede *Sacculina carcini* on its brachyuran host *Carcinus maenas* within its home range. Pages 76-80 in: Thresher, R. E. (ed.), Proceedings of the First International Workshop on the Demography, Impacts and Management of Introduced Populations of the European Crab, *Carcinus maenas*. Technical Report No. 11, Centre for Research on Introduced Marine Pests, Hobart, Tasmania.

Murdoch, W. W., J. Chesson and P. L. Chesson (1985) Biological control in theory and practice. *American Naturalist* 125: 343-366.

Nichols, F. H., J. K. Thompson and L. E. Schemel (1990) Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. II. Displacement of a former community. *Marine Ecology Progress Series* 66: 95-101.

Ritchie, L. E. and J. T. Høeg (1981) The life history of *Lerneodiscus porcellanae* (Cirripedia: Rhizocephala) and co-evolution with its porcellanid host. *Journal of Crustacean Biology* 1: 334-347.

Ropes, J. W. (1968) The feeding habits of the green crab, *Carcinus maenas* (L). *Fisheries Bulletin* 67: 183-203.

Thresher, R. E. (ed.) (1997) Proceedings of the First International Workshop on the Demography, Impacts and Management of Introduced Populations of the European Crab, *Carcinus maenas*. Technical Report No. 11, Centre for Research on Introduced Marine Pests, Hobart, Tasmania.

Torchin, M. E., K. D. Lafferty and A. M. Kuris (1996) Infestation of an introduced host, the European green crab, *Carcinus maenas* by a native symbiotic nemertean egg predator, *Carcinonemertes epialti*. *Journal of Parasitology* 82: 449-453.

Torchin M. E., K. D. Lafferty and A. M. Kuris (2001) Release from parasites as natural enemies: increased performance in a globally introduced marine crab. *Biological Invasions* 3: 333-345.

Walton, W. C. (1997) Attempts at physical control of *Carcinus maenas* within coastal ponds of Martha's Vineyard, MA (northeastern coast of North America). Pages 64-65 in: Thresher, R. E. (ed.), Proceedings of the First International Workshop on the Demography, Impacts and Management of Introduced Populations of the European Crab, *Carcinus maenas*. Technical Report No. 11, Centre for Research on Introduced Marine Pests, Hobart, Tasmania.

Zibrowius, H. (1991) Ongoing modifications of the Mediterranean marine fauna and flora by the establishment of exotic species. *Mésogée* 51: 83-107.