

BIOLOGICAL CONTROL OF THE EUROPEAN GREEN CRAB, *CARCINUS MAENAS*: NATURAL ENEMY EVALUATION AND ANALYSIS OF HOST SPECIFICITY

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ABSTRACT

Many introduced marine organisms are ecological and economic pests. Nevertheless, no management approach is available to mitigate their impacts. Now, a theoretical perspective borrows principles from classical biological control, as widely applied to terrestrial and fresh water systems, to control the abundance of introduced marine pests.

A banner example of a marine pest is the European green crab, *Carcinus maenas* (L.) (Brachyura: Cancridae). This crab invaded San Francisco Bay in the late 1980s and has expanded its geographic range at a record rate. Studies on the Pacific coast of the U.S.A. and elsewhere strongly indicate that it is a worst-case introduction, affecting native organisms and potentially harming fisheries and aquaculture. Extensive studies show that a significant element of its success, where introduced, has been release from its natural enemies, notably parasites.

Natural enemies are infectious agents with potential to contribute to green crab biological control include two parasitic castrators: *Sacculina carcini* Thompson (Rhizocephala: Sacculinidae) and, *Portunion maenadis* Giard (Isopoda: Entoniscidae), the parasitoid flatworm, *Fecampia erythrocephala* Giard (Fecampiida: Fecampiidae), and the symbiotic nemertean egg predator, *Carcinonemertes carcinophila* (Kolliker) (Hoplonemertea: Carcinonemertidae). Evidence for their potential efficacy derives from quantitative natural history studies and ecological modeling. Their safety with respect to non-target organisms is of great concern. Relevant information is available from qualitative field studies, host specificity experimentation, evolutionary theory, and the ability to detect and estimate the frequency of unsuccessful parasite attack rates in natural populations.

We interpret host specificity in the context of the double filter paradigm of Combes (2001). For a host to be suitable, two filters must be partially open. When the encounter filter is open, the infective stage can locate and enter the host because it shares the appropriate habitat and has suitable host location and attack behaviors. For the parasite to be successful, the compatibility filter must also be partially open. This occurs if the host provides appropriate nutrition and its defensive mechanisms cannot kill nor block reproduction of the infectious agent. For both rhizocephalan barnacles and entoniscid isopods in native (coevolved) regions, potential alternative hosts appear to be protected via inability to encounter the host, or due to incompatibility, or both filters are closed. Naïve hosts from an introduced area are located under permissive encounter experimental conditions, but the compatibility filter is closed.

INTRODUCTION

We now recognize the ubiquitous importance of introduced marine organisms as pests (Carlton 1989). Several international conferences have been organized in the past eight years and research funding has been substantially expanded. Studies of impacts of some of the most successful invaders such as the *Caulerpa taxifolia* alga in the Mediterranean (Meinesz 2004), *Musculista senhousia* mussels in southern California (Crooks and Khim 1999), and *Carcinus maenas* green crabs in Tasmania and on both coasts of North America (Grosholz *et al.* 2000) demonstrate that marine invaders can deplete native species through competition, predation, and alteration of habitat. Secondary facilitation of other exotics and other tri-trophic consequences also significantly and substantially alter natural communities in ways deemed undesirable. Most invasion problems are tackled at two levels: prevention and mitigation. For agricultural insect and weed pests both elements are actively developed. For marine pests, a major international effort has been mounted to prevent further introductions with increased regulation of major vectors such as ballast water, hull fouling and oyster mariculture (Cangelosi 2002). Some of these options are very costly (mid-ocean ballast exchange is estimated to add \$112-362 million per annum to the cost of shipping just to the U.S.A. (Hayes 2001). Amelioration of the impacts of the marine invaders that are already here receives little attention. The cause for this defeatist attitude is unclear. The vastness of the marine habitat and the pelagic larval dispersal strategies of many marine organisms do make it seem that an invader is unstoppable once it arrives (Kuris and Lafferty 2001). It could also relate to the training of most marine ecologists, which in accordance with the general ecological literature, extrapolates nonscientific biological control horror stories to an *a priori* suspicion of scientific classical biological control.

For marine exotics, Thresher and Kuris (2004) showed that for control options there is an inverse relationship between likelihood of success and the perceived willingness of the approach to be supported by investigators and regulators. One might conclude that, at present, the problems caused by marine exotics are not sufficiently severe to risk costs associated with mitigation. Of course, that begs the question: why then impose the substantial costs to prevent this problem?

Our perspective is that if costs imposed by introduced marine species are great, control strategies are worth developing. This has paid off with the first successful eradications of established marine pests (Culver and Kuris 2000; Kuris 2003a; Myers *et al.* 2000). For use of natural enemies, we showed that a theoretical window for biological control of marine pests was available (Kuris and Lafferty 1992). By extending models of the impact of parasitic castrators and symbiotic egg predators on crustacean fisheries, we proposed that at least these types of natural enemies could act as classical biological control agents against marine exotics and devised a general protocol for development of this approach. This was also extended for the use of marine parasitoids (Kuris *et al.* 2002). Efficacy models were generally related to those developed for insect pest control by parasitoid natural enemies (Lafferty and Kuris 1996) and modified by experiences controlling infectious diseases impacting crustacean fisheries (Kuris and Lafferty 1992). Safety concerns could be evaluated experimentally following protocols for weed pest biological control (Kuris and Lafferty 2001; Lafferty and Kuris 1996).

With the discovery of a population of the European green crab, *Carcinus maenas*, (L.) (Decapoda, Portunidae) in South San Francisco Bay in 1991 (Cohen *et al.* 1995), its rapid spread via larval dispersal to bays and estuaries as far north as Nootka Sound, British Columbia in less than 10 years (Behrens-Yamada 2001) was a record linear range expansion rate for a marine animal. Its eurytopic, euryhaline, and generalist feeding habits suggest European green crab is a worst case pestiferous invader. Experimental and empirical studies demonstrate its strong negative impact on other species of crabs, other invertebrates, and perhaps as a competitor with shorebirds for food (Cohen *et al.* 1995; Grosholz and Ruiz 1996; Grosholz *et al.* 2000). It has now also been shown to facilitate the adverse impact of an earlier introduction, the small clam, *Gemma gemma* (Totten) (Grosholz 2005). Hence, a control campaign against the introduced green crab appears warranted. These studies in California are supported by similar studies of other introduced green crab populations from the east coast of North America, South Africa, and Victoria and Tasmania in Australia (Glude 1955; Le Roux *et al.* 1990; MacPhail *et al.* 1955). Its sibling species, the Mediterranean *C. estuarii* Nardo has also been introduced in Japan.

Here, we will summarize the biology of the natural enemies of European green crab, evaluate their potential with respect to efficacy and safety, note technological difficulties impeding further work, and expand on the evaluation of the safety of parasitic castrators using experiments and field observations in the context of the host specificity encounter-compatibility paradigm of Combes (2001). This will focus on the potential safety of the most promising agent (in terms of efficacy), *Sacculina carcini* Thompson (Rhizocephala: Sacculinidae).

EVALUATION OF GREEN CRAB NATURAL ENEMIES

The green crab, *Carcinus maenas*, is the most common crab along the shores of Europe, and as an introduced species in New England and the Canadian Maritimes. Thus, it is the most studied crab with respect to its growth, reproduction, physiology, role in community ecology, and its parasitofauna. Based on the considerable available literature, and our extensive search for natural enemies in Europe, we provide an evaluation of natural enemies consistent in the context of scientific classical biological control. We briefly considered and re-

jected the use as predators as control agents. Although many species of birds and fishes eat green crabs, none are specialist green crab predators. The use of a generalist predator is unlikely to be an effective control agent and it is likely to have considerable unwanted consequences for non-target species.

MATERIALS AND METHODS

In Table 1, we summarize the published information of the infective agents of green crab. Although extensive and offering considerable detail for a few species of parasites, it does not include even a single study across a variety of taxa. Hence, our first task was to survey native populations of green crab over its entire range in Europe. We conducted several surveys of European green crab populations (20 sites, ~3000 crabs dissected) that extended from Tromsø, Norway to Gibraltar. These data were compared with our surveys of introduced green crab populations along the coasts of North America, in South Africa, Victoria and Tasmania, Australia, and of the closely related *C. estuarii* population in Japan (N=~2000) (Torchin *et al.* 2003). For metazoan parasites, we recovered all but one of the agents reported in the literature and discovered two that had not been previously reported. Table 1 summarizes our findings and provides a few details about their abundance and pathogenicity. Because certain types of host-parasite interactions have general implications for their use as natural enemies we have grouped these by trophic adaptive syndromes according to Lafferty and Kuris (2002).

RESULTS

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Crabs in introduced populations are infrequently parasitized and parasite species richness in all invaded regions falls well below the European total (California: one species, east coast of North America: 3 species, Victoria: four species, Tasmania: 2 species, South Africa and Japan: no parasites) (Kuris and Gurney 1997; Kuris *et al.* 2002; Torchin *et al.* 1996). Further, no parasitic castrators, nor parasitoids, have been recovered from any introduced green crab population.

EVALUATION OF NATURAL ENEMIES

The parasites listed in Table 1 vary with respect to their likely efficacy and safety as biological control agents for *C. maenas*.

Pathogens. Pathogens are intensity-independent infectious agents whose abundance increases in the host through reproduction. Their populations are generally limited by host defensive responses. They are suitable for modeling as microparasites (Anderson and May 1979). The microbial pathogens reported from the green crab are rarely seen in natural populations. These diseases, particularly the ciliates, appear to be associated with stressed, high density, captive host populations. We conclude that they are inefficiently transmitted, requiring high host densities and cofactors. Stressors including pollution, high temperature, low oxygen, or confinement are some of the needed cofactors to produce disease. Their host specificity has not been experimentally examined, but evidence from related agents in other crustaceans suggests that they may not be host specific (except perhaps *Microspora*) for non-target crabs.

Table 1. The abundance of infective agents of the green crab in Europe from the literature (Lit.) and our surveys (Surv.), + is reported, 0 is not found, – is not investigated. For Type of agent, Path is microbial pathogens (microparasite), TTPF is trophically transmitted parasite in its final (predator) host (macroparasite), TTPI is trophically transmitted parasite in its intermediate (prey) host, PC is parasitic castrator, Ptoid is parasitoid, SEP is symbiotic egg predator (terminology from Lafferty 2002); for references see (Provenzano 1983; Behrens-Yamada 2001; Torchin *et al.* 2001, Stentiford and Feist 2005).

Infective Agent	Type	Lit.	Surv.	Abundance	Remarks
<i>Viruses</i> (6 spp.)	Path	+	-	?	Sporadic, often in captive populations. Several species sometimes lethal.
<i>Bacteria</i> (3 spp.)	Path	+	+	?	Sporadic, sometimes lethal.
<i>Anophrys</i> (histophagic ciliates)	Path	+	0	rare	Only captive populations?
<i>Haematodinium perezii</i> (dinoflagellate)	Path	+	-	?	Can cause mortality in natural populations.
<i>Thelohania maenadis</i> , <i>Abelspora portulacensis</i> (microsporans)	Path	+	0	?	Sporadic, several species, sometimes lethal.
<i>Nematopsis</i> sp. (gregarine)	TTPF	+	+	common	Avirulent
<i>Fecampia erythrocephala</i> (Fecampiida)	Ptoid	+	+	to 20%	Lethal, geographically localized, habitat specialist.
<i>Microphallus lasmob</i> , <i>M. primas</i> , <i>Spelotrema excellens</i> (microphallid trematodes)	TTPI	+	+	often abundant (0-100%)	Metacercaria, birds are final hosts.
<i>Trypanorhynch</i> and <i>tetraphyllid cestodes</i>	TTPI	0	+	rare	Plerocercoid larvae, lasmobranchs are final hosts.
<i>Profillicolis botulus</i> (Acanthocephala)	TTPI	+	+	common	Acanthella and cystacanth larvae, geographically localized, birds are final hosts.
<i>Pararcuaria tridentata</i> , <i>Cosmocephalus obvelatus</i> (larval nematodes)	TTPI	+	0	rare	Found once, birds are final hosts.
<i>Carcinonemertes carcinophila</i> (Nemertean)	SEP	+	+	common (0-100%)	High intensities at some locations.
<i>Lecithomyzon maenadis</i> (nicothoid copepod)	SEP	+	-	common at one location	Sporadic and localized? eats eggs.
<i>Sacculina carcini</i> (rhizocephalan barnacle)	PC	+	+	common (0- 70%)	Stunts crab growth, feminizes males, blocks reproduction, varies with habitat.
<i>Portunion maenadis</i> (entoniscid isopod)	PC	+	+	Can be common (0- 15%)	Blocks reproduction.

Typical parasites and trophically transmitted parasites in final (predator) hosts. These infectious agents induce pathology in an intensity-dependent manner and are effectively modeled using the macroparasite models of May and Anderson (1979). The only such parasites in the green crab are gregarines. These appear to be avirulent and as such have no potential as biological control agents.

Parasitoids. Parasitoids are so closely associated with the study of insect natural enemies that some consider the term taxonomic (applying only to insects). “Parasitoid” is now applied to all intensity-independent infectious agents that require the death of their hosts to complete their life cycles. Examples include viruses (bacteriophage) mermitiids, monstilloid copepods and hyperiid amphipods (Kuris 1974; Kuris and Lafferty 2000; Lafferty and Kuris 2002). One of the most unusual parasitoids is the fecampiid flatworm, *Fecampia erythrocephala* Giard (Kuris *et al.* 2002). As with most parasitoids, it infects very early instars (crabs less than 12 mm carapace width [CW]). It is only known from the coasts of England, Ireland and Atlantic France (a related undescribed species may be present in the Mediterranean Sea [Brun 1967]). It is also a habitat specialist, occurring only in rocky or cobble habitats in the middle intertidal zone of semi-protected shores (Kuris *et al.* 2002). Estimates of its growth rate and its prevalence suggest that it is a major mortality factor of young green crabs in these habitats. It can infect other species of crabs (especially *Cancer pagurus* Linnaeus [Decapoda, Cancridae]), although, in its preferred habitat, only *C. maenas* is commonly encountered. As a habitat specialist, *F. erythrocephala* may be a useful biological control agent if those habitats are deemed worthy of protection, or serve as sources for green crab populations on a regional scale. Its host specificity remains to be experimentally investigated. In certain regions, presumably appropriate habitats are common and few other native crab species are found in the habitats of introduced green crabs (e.g., east coast of North America). It is likely that its life cycle can be maintained in the laboratory as the adults are free-living and its larvae are non-feeding.

Trophically transmitted parasites in their intermediate (prey) hosts (TTPIs). Several trophically transmitted parasites (TTPs) use *C. maenas* as their prey (intermediate) host. Predatory final hosts include birds for the nematodes, theacanthocephalan, *Profilicollis botulus*, in the northern range of the green crab in Europe, the trematodes throughout its range, and elasmobranchs for trypanorhynch and tetraphyllid larval tapeworms in the southern part of its range. Accumulating evidence suggests that these TTPIs may reduce host abundance through behavioral modifications leading to increased rates of predation by final hosts on infected intermediate hosts (Kuris 1997). There is some evidence that these parasites may play a role in green crab population control in Victoria, the only region where introduced green crabs are not considered pests. At sites sampled in Victoria, green crabs are frequently parasitized by large trypanorhynch plerocercoids (*Trimacanthus aetobatidis* [Robinson]: Trypanorhyncha: Eutetrarhynchidae). The site of infection of these large encysted parasites overlies the large nerves leading anteriorly from the thoracic ganglion. This site is likely to promote behavioral modifications contributing to higher rates of predation on infected hosts by the abundant final host, the fiddler ray, *Trigonorhinus fasciata* Muller and Henle (Rhinobatidae) (Kuris and Gurney 1997). While TTPIs may markedly reduce the fitness of their prey hosts, they generally have low pathogenicity in their vertebrate predator hosts (Kuris

2003b; Lafferty 1992), some (notably acanthocephalans) are certainly pathogenic in their final hosts. Since there are evident safety issues with respect to vertebrates and since the ability of these TTPIs to regulate prey populations may be modest and ephemeral (only when infected prey hosts are abundant – a condition only met for the microphallids), the available TTPIs do not seem to merit continued investigation. Native TTPIs that use exotic *C. maenas* may be suitable as augmentative natural enemies.

Symbiotic egg predators (SEPs). This distinctive type of natural enemy offers the infestation dynamics of a parasite, but its trophic impact is solely on the developing embryos brooded by the ovigerous crabs. These can have very strong effects on host populations. They have been associated with the collapse of a major fishery (red king crab in Alaska) and the non-recovery of others (Dungeness crab in Central California (Hobbs and Botsford 1989; Kuris and Lafferty 1992; Kuris et al. 1991). *Carcinonemertes carcinophila* (Kollicker) (Hoploneuridae, Carcinonemertidae) can occur at high infestation rates, causing catastrophic brood mortality (Plymouth, England, Mira River estuary, Portugal, our personal observations). There is strong circumstantial evidence for host specificity of nemertean SEPs. The introduced populations of the green crab in the Atlantic coast of North America have never acquired *C. carcinophila* (= *C. c. immunita*, a closely related undescribed species, Kuris and Sadeghian, unpublished information) found at high prevalences on two portunid crabs, *Callinectes sapidus* Rathbun and *Ovalipes ocellatus* (Herbst) despite their considerable habitat overlap with the confamilial green crab (Coe 1902; Torchin et al. 1996). However, there is incontrovertible evidence that other SEP nemerteans have transferred to the green crab (Torchin et al. 1996). Hence, nemertean SEP natural enemies merit further investigation because they may be efficacious control agents. No safety tests have been conducted but will obviously be required. Experimental studies of host specificity remain elusive for these nemerteans, as larval transfer to new hosts has not been achieved. Brood mortality remains to be quantified.

Nicothoid copepod SEPs have been reported from both native and introduced populations of green crabs. However, these have only twice been observed (Gallien and Bloch 1936; Johnson 1957). These natural enemies appear to be geographically patchy and sporadically abundant. The relatively brief brooding period for the green crab and trap aversion by ovigerous females impedes detection and evaluation of SEPs as potential control agents.

Parasitic castrators. There is considerable theoretical and empirical evidence that parasitic castrators can control host populations (Blower and Roughgarden 1987; Kuris and Lafferty 1992; Lafferty 1993). *Sacculina carcini* appears to have the most dramatic effects on green crab growth and abundance (Lafferty and Kuris 1996; Torchin et al. 2001; 2002), and thus on the ecological impact of *C. maenas* on native organisms. Our analysis of crab size and crab population biomass indicated that prevalence of the two parasitic castrators (*S. carcini*, and *P. maenadis*) are inversely correlated with mean and maximum crab size and crab biomass (trapped catch per unit effort). Parasitic castrator prevalence accounts for 60-65% of the variance in these indicators of crab performance. Green crabs in Europe rarely exceed 70 mm carapace width (CW), while in California and Tasmania crabs exceeding 90 mm CW are common. *Sacculina carcini* is the most studied parasite of the green crab. Its life cycle can be completed in the laboratory. Its effects on the host, and its host specificity have been investigated.

Parasitic castrator entoniscid isopods have been less studied. *Portunion maenadis* is not common on the Atlantic coast of Europe. However, it is often highly prevalent in Mediterranean populations of the closely related *C. estuarii* (Veillet 1945). This contrast may reflect differences in abundance or infection rates of the intermediate planktonic copepod host in the Mediterranean versus in the Atlantic.

HOST SPECIFICITY OF CRUSTACEAN PARASITIC CASTRATORS AND THE SAFETY OF *SACCOLINA CARCINI*

Evidence from host use patterns of *Saccolina carcini* and other rhizocephalans indicates that most species have narrow host specificity (one host or a few closely related hosts). We have been able to develop the life cycle of *S. carcini* as a reliable laboratory system, and have conducted host specificity experiments on green crabs and four native California crab species that were ecological analogs or economically important (*Cancer magister* Dana).

We interpret host specificity in the context of the double filter paradigm of Combes (2001). For a host to be suitable, two filters must be partially open. When the encounter filter is open, the infective stage can locate and enter the host because it shares the appropriate habitat and has suitable host location and attack behaviors. For the parasite to be successful, the compatibility filter must also be partially open. The host can provide appropriate nutrition and its defensive mechanisms cannot kill nor block reproduction of the infectious agent. Our experiments were designed to bypass the encounter filter (host location, behavior) and examine the compatibility filter (nutritional suitability, host defenses) (Goddard *et al.* in press). We readily infected all four native California species. However, in the naïve hosts, it never completed its development. Rather, pathology was markedly neurotropic and infected crabs became paralyzed and died. Hence, *S. carcini* can only pose a threat to these non-target species if it is well established in its natural host. In other words, its safety as a biological control agent is directly related to its efficacy. It would have to attain a high prevalence in green crab populations to provide sufficient excess larvae to be available to attack native crabs.

Additional experimental studies showed that infective *S. carcini* larvae could also attack a European crab, *Pachygrapsus marmoratus* (Kuris *et al.*, submitted). However, this crab mounted a fully successful defense by melanizing early internal stages in the thoracic ganglion. We were able to use the presence of these characteristic melanized lesions to estimate the effectiveness of the encounter filter for *S. carcini*. At the Mira River estuary, Portugal, green crabs are heavily infected with *S. carcini* (~ 50% prevalence), and *C. maenas* and *P. marmoratus* exhibit considerable habitat overlap. Here, we examined *P. marmoratus* for the melanized lesions in the thoracic ganglion and compared their presence with crabs from a site on the outer coast, remote from *C. maenas*. No lesions on *P. marmoratus* were associated with *S. carcini*. Consequently, for this species, both the encounter and the compatibility filters are closed. Processes governing the encounter filter have been difficult to investigate. Our use of melanized parasite early infective stages provides a demonstration of the importance of the encounter filter for the maintenance of host specificity in Rhizocephala and entoniscid isopods (Table 2).

Most recently, we were able to use the lesion-detection squash technique to evaluate encounter and compatibility for another parasitic castrator, the entoniscid isopod, *Portunion conformis* (Kuris et al. in prep.). This internal parasite is widespread and often highly prevalent (>90%) in *Hemigrapsus oregonensis* and *H. nudus* (where the latter co-occurs with *H. oregonensis*) (Kuris et al. 1980). At Elkhorn Slough in Central California, both *H. oregonensis* and *Pachygrapsus crassipes* are common and syntopic. The infective stage of the parasite is the cryptoniscus larva. In squashes of crab internal organs (gonads, digestive glands, thoracic ganglia), this stage is readily apparent because it retains its isopodan features as an exuvia even after it molts to the apodous juvenile. The latter becomes encased in a sheath of host blood cells and continues to grow and develop to the adult in a natural host (Kuris et al. 1980). By examining its host, *H. oregonensis*, and its potential host, *P. crassipes*, we were able to show that the encounter filter is as open for *P. crassipes* as it is for *H. oregonensis* (both crabs had similar prevalences and intensities of *Portunion conformis* larvae and juveniles, Kuris et al. in prep.). However, for *P. crassipes*, the compatibility filter was completely closed. All *P. conformis* larvae and juveniles were dead and had elicited a melanization defensive response. Most were still in the cryptoniscus stage; some had successfully molted. These were ensheathed by host blood cells, but had died and were thus melanized (Kuris et al. 1980). Thus, for this native parasite against a native non-host crab, the encounter filter was fully open while the compatibility filter was closed (Table 2); it could not evade the host's defensive response.

Table 2. Experiments and observations evaluating the encounter and compatibility filters for some parasitic castrators of crabs. Crabs categorized by their evolved relationship (E.R.) with the parasite and to whether encounter is possible (E.P.) and compatibility is possible (C.P.) *not evaluated, experimentally wedged open.

Parasite	Natural Host	Non-host	E.R.	E.P	C.P	Reason
<i>Sacculina carcini</i>	<i>Carcinus maenas</i>	<i>Cancer magister</i>	No	*	No	Parasite could not regulate its growth. A variable, partially successful cellular defensive response elicited
		<i>Hemigrapsus oregonensis</i>	No	*	No	same
		<i>H. nudus</i>	No	*	No	same
		<i>Pachygrapsus crassipes</i>	No	*	No	same
		<i>P. marmoratus</i>	Yes	No	No	Elicits a powerful and fully effective cellular defensive response
<i>Portunion conformis</i>	<i>H. oregonensis</i>	<i>H. nudus</i>	Yes	Yes	Yes	Lower prevalence suggests encounter filter may be less open (Kuris et al. 1980). Both hosts mount successful defensive responses against dead parasites.
		<i>P. crassipes</i>	Yes	Yes	No	Elicits powerful cellular defensive response.

FUTURE WORK

Further studies of host specificity of *Sacculina carcini* are needed to evaluate the encounter filter as a potential barrier to infection of non-target hosts. Models investigating the joint effect of *C. maenas* as a competitor/intraguild predator on native crabs, and the lethal parasitization of native crabs from larvae produced by infected green crabs, are needed to bound the costs and benefits of *S. carcini* as a control agent.

The technical ability to conduct experimental infections of both *Fecampia erythrocephala* and *Carcinonemertes carcinophila* should be developed. This will permit experimental investigations of the safety of these agents. A model for a parasitoid of a marine host with open recruitment should be developed to examine the potential of *F. erythrocephala* as a control agent in its specific habitat. Studies of dispersal and recruitment of *C. maenas* larvae to adult habitats will aid the recognition of the importance of different habitats as sources or sinks for larval production. Further field studies to detect Microspora and viruses will improve our understanding of the epidemiology of these potential natural enemies. For symbiotic egg predators (nemertean and nicothoid copepods), we need to estimate their impact on crab natality. The habitat use of *Portunion maenadis* Giard and Bonnier (Peracarida, Entoniscidae) should be evaluated to see if this parasite might be more common under environmental conditions available in regions where green crabs have been introduced. In addition, the regulatory potential of a parasitic castrator with a two-host life cycle (such as *P. maenadis*) should be modeled. Finally, continued investigations of the impact of green crabs on native species are needed to aid management agencies' decision-making processes. They must have a reliable estimation of costs of this pest, the predicted benefit of a control approach and the risk associated with control approaches. The public can then make a more rational decision to institute policies for mitigation of introduced marine pests such as the green crab.

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