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Introduction

The European shore, or green crab, *Carcinus maenas*, was first discovered in Australia in the late 1800s, in Port Phillip Bay, Victoria. How it got here from Europe is not known, but the most likely route was as a stow-away in the beach rocks used as semi-dry ballast in English ships bound for Australia. In the hundred years since, the species has spread from at least South Australia (there is one report from Western Australia) to New South Wales, including the north and east coasts of Tasmania.

The green crab is hardly unique as an introduced marine species in Australia. The CSIRO Centre for Research on Introduced Marine Pests (CRIMP) has documented over 170 such foreign species reported or known to be present in Australian waters, a list that grows steadily as more habitats and sites are investigated. Two observations make the green crab noteworthy, however. First, it is an exceptionally able invader. *C. maenas* has established large populations on both coasts of North America, in Japan, in South America and in South Africa. It has even been reported from Thailand (apparently an unsuccessful invasion). Second, it has all the hallmarks of a 'keystone' species. A large, tough and active sub-tidal crab, *C. maenas* can reach high densities in a range of inshore habitats and is a 'voracious' predator. Gut content studies indicate the crab typically consumes a wide variety of benthic invertebrates, though it clearly prefers bivalves such as clams and mussels. As an abundant, predatory species, *C. maenas* has considerable potential to alter the communities it invades.

The historical and current impacts of this invader in Australian waters are largely unknown, but may be substantial. Work overseas suggests (though does not prove) the species has 'wreaked havoc' on native bivalve populations, 'destroyed' local fisheries and even altered seabird migrations. Although hard data on most of these effects are sparse, the information available and the biology of the species are consistent with it being a high impact, introduced pest. Despite receiving much less publicity in Australia than, for example, the northern Pacific seastar (*Asterias amurensis*) or the European fan worm (*Sabellaria alveolata*), the green crab could very well be Australia's most environmentally destructive introduced marine pest. That it has not attracted the media attention of the seastar is likely due to its relative inconspicuousness and the length of time it has been here. While the seastar and fan worm form dense and very conspicuous aggregations, the green crab is not strikingly different in appearance from a number of native Australian crabs. As such, even where abundant it probably often passes un-remarked upon. And as an 'old' invader, in many areas the crab will have long since had its most dramatic impact, so that people accept the current situation as the norm. This may not be true in Tasmania, however, where available evidence suggests that *C. maenas* has only recently arrived in large numbers, and changes to the marine ecosystem may be in progress.

Currently, little is being done to manage or minimize impacts of the green crab, either in Australia or overseas. This is not due to lack of possibilities. Crabs lend themselves well to physical removal (via trapping) and the green crab can potentially be harvested in large numbers. In southern Europe, there is a commercial fishery for the species, suggesting a market-driven harvesting scheme could be established that might reduce its impact in invaded areas. As well, there appears to be considerable potential for biological control of the species. More is known about the biology of green crab parasites than those of almost any other introduced marine pest. Several of these parasites are known to castrate the crabs, suggesting that biological control via reducing population fecundity is a possibility.

In order to move the discussion on impacts and control beyond the realm of media-driven hype, the CSIRO CRIMP sponsored a two-day, international workshop on *Carcinus maenas*. The workshop was held at the CSIRO Marine Laboratory, Hobart, Tasmania, on 20-21 March, 1997. Its main objective was to review what was known about the demography and impacts of the species, both in Australia and overseas. The workshop had three ancillary objectives, as well. These were

1. to compare impacts of the crab in Australia with the broad criteria used by the Australian Commonwealth government to define 'key threatening processes', and to draw a preliminary conclusion as to whether or not *C. maenas* meets, or is likely to meet, those criteria;

2. to begin a comparison of the impacts of *C. maenas* in Australia with its impacts overseas, to determine what, if any, generalisations can be drawn regarding the invasion process; and

3. to determine what needs to be done next with regard to determining impacts and demographic processes.
control mechanisms that target adults might have a cosmetic effect (fewer obvious large crabs about), but little or no effect on impact reduction.

Two other approaches to biological control were also discussed briefly. First, the issue of specialist predators on mainland Australia holding down numbers of C. maenas there was re-visited. Two possibilities were noted: that the predators would also expand their ranges in response to the same features that resulted in C. maenas recently invading Tasmania (assuming that is the case), in which case the current situation of large, dense populations in Tasmania might be temporary, and the possibility of stocking fishing in the region. The latter was seen as a high effort approach, but one that might justify looking into current fishing practices, to determine if there might be local predatory fishes that would have a similar effect, but which are somehow limited by fishing pressure. If so, an education and management program to encourage re-building of the stocks might be a very effective way to minimise impacts of the crab.

The approach discussed briefly was the use of molecular engineering to control the invader, either by means of fertility reduction or by inducible mortality. Most participants felt that the approach had considerable merit and was well worth pursuing as an inherently safe approach to pest management (though most also noted they lacked the expertise to assess the merits of the specific ideas proposed). There was also some concern raised about the uncertainty of public response to the release of genetically modified organisms in the ocean.

Finally, some time was spent discussing the politics of releasing a parasitic control agent and the perceived risks associated with such a release. Aside from issues about the extent to which a particular minister or management agency might or might not be prepared to approve such a release, there were also concerns expressed about the perception of the 'clean, green ocean' and its apparent lack of boundaries (and hence natural limits to the dispersal of a biological control agent). This emphasised both the need for detailed ecological and oceanographic information on the basis of which risks could be determined as accurately as possible, and also the need both to inform the public and decision makers about the issues and to have them involved in the process leading to a biological control program as early as practical. However, it was also pointed out that a decision not to release an apparently effective and safe biological control agent - the 'do nothing' option - is also a decision, which is to accept indefinitely the impacts of an exotic species.

Research - the next steps

The research needed to develop further a management program against C. maenas was seen to be broad ranging. However, three priorities were recommended.

1. That the impacts of the species be determined as completely as possible, as it is against these impacts that the risks of any control program would be assessed. Hence, one priority is for a continuation or expansion of impact studies.

2. Detailed study of the biology of apparent biological control agents, as biological control is likely to be the only practical means of controlling the impacts of a species as widely spread as C. maenas. Critical next steps would be a modern evaluation of diseases and parasites in European populations of the crab, and an attempt at definitive specificity trials on what appear at this point to be the most promising (ie., safest) agents, e.g., Portunus maenadis and Sacculina carcini.

3. A detailed study of the demography and life history characteristics of the introduced populations, in order to assess population sources and sinks and to determine the most effective points of attack for a control program.

Priorities 1 and 3 would both be addressed by a targeted project of physical removal. Specifically, the crabs could be fished out of one or more embayments (paralleled by other unfished embayments, as controls) and the subsequent recovery of the native communities and crab populations monitored. Such an experimental fish down would provide detailed demographic information on the crab, assess its impacts on a large spatial scale, test the effectiveness of physical removal as a management tool and provide a risk-free trial of a control program, to assess its value relative to apparent impacts. It would also raise public awareness of the problem, and provide a good opportunity for community involvement in the research. Such a trial, combined with a program examining natural parasites of the crab in Europe, were seen as the logical next steps in any program to manage the crab.
They also differ markedly in the amount of background information available. Of the potential agents identified, by far the best known is the rhizocephalan *Sacculina carcini*. The life cycle of the species has been closed in the laboratory, its morphology and mode of action has been extensively studied over the last several decades, and it is currently the subject of several Ph.D. theses in progress. Information about other species, by comparison, is sparse and unfocussed.

Three central issues formed the basis for much of the discussion about prospects for biological control - safety, effectiveness and information needs to assess both.

The safety issue relates primarily to the degree to which potential agents are species specific. Two relevant approaches were discussed. First, the taxonomy of the parasites was seen to be often confused and subject to the bias of early investigators. Hence, all similar looking rhizocephalans on European portunids tended to be 'lumped' as *Sacculina carcini*, whereas researchers on entomiscids tended to assume that if a parasite was found on a different host, it must be a new species - hence *Portunion maenadis*. In neither case has there been a detailed morphological or genetic study of the nominal species either over its/their geographic range or over its/their nominal host range. Some preliminary information on genetics of *S. carcini* was reported at the meeting, which suggested parasites on *C. maenas* from Britain and Sweden were conspecific, but no data are yet available on parasites from other hosts. Such genetic studies were seen as almost essential in order to assess the potential for a particular control agent.

Second, even more critical than genetic or taxonomic studies of the parasites is the need for well-designed and well conducted specificity trials. To date, the only tests conducted are preliminary ones involving Australian native crabs exposed to Swedish *S. carcini*, reported on at the meeting. What would be considered by the group to be a convincing specificity test has not been done for any species. However, there was also considerable discussion over what exactly constitutes such a test. Although there is an extensive literature in the terrestrial (and particularly insect) biological control fields on protocols for such tests, the extent and the ways in which they need to be modified for marine species has not been thought through to date. The open life-cycle of most marine organisms, for example, mitigates against simple enclosure-based studies, in which potential hosts are exposed to infective stages of a parasite, in part because of difficulty in sourcing the infective (presumably in most cases, planktonic larval) stages of the parasite and in part because of risks associated with out-planting non-native hosts in the native range of the parasite. The complexity and, perhaps, sensitivity of planktonic larvae to artefacts in the laboratory could also cause difficulties in obtaining data that was biologically meaningful. Preliminary studies of *S. carcini*, for example, indicated that in a laboratory setting, a) infective-stage larvae (the nauplii) were largely, if not completely non-specific in host choice over a range of species, including one from a family never found infected in the field, but also b) relatively few larvae settled on a host at all. The latter observation suggests there was a 'problem' with the experiment, as the assumption would be that most competent larvae would choose to settle on a host rather than die; hence, the utility of the observed non-specificity is very much in doubt. The key requirement seems to be establishing an experimental protocol in which most, if not the ideal of all, competent larvae settle reliably on known hosts, against which standard other potential hosts can be assessed.

The effectiveness of a biological control program against marine pests was also discussed in some length, with particular regard to the actions of what appear to be the two major options for control - reducing fecundity (via the action of parasitic castrators and egg parasites) or reducing survival (perhaps by means of tapeworm or a scuticociliate). Considerable doubt was expressed that under anything but extremely high infection rates, parasitic castrators and egg parasites would have a significant impact on population densities or recruitment, due to the typical (but often just assumed) strong non-linearity of stock-recruitment relationships. The strongest evidence for an impact of fecundity reduction on a crab is the work by Kuris and Lafferty, which showed a very strong effect of Carcinonemertes infections on Alaskan king crab recruitment and population sizes. Counter-examples offered included the consistent observation that *C. maenas* populations heavily infected with *Sacculina* appear to be of 'typical' densities and that heavy infections by other rhizocephalans on crabs appear to have little, if any perceptible impact on their numbers. A number of hypotheses can be developed to account for such observed 'non-effects', all of which require data not yet available. It was also pointed out that it may be possible to augment infection rates of the parasite to the point where they did have an effect on recruitment; the issue under those conditions becomes one of cost-effectiveness, rather than biological effectiveness per se.

The issue of effectiveness was also discussed in the broader context of determining life history stages for attack that maximises the reduction of impacts. As an example, if field data demonstrated that the largest impact of the crab was the effects of juveniles on recruitment of bivalves (which was seen to be a strong possibility), then biological (or other)
The second day of the workshop reviewed possible management options, from physical removal to transgenic manipulations.

The workshop participants were from Australia, the United States, Denmark and Sweden. The intention, largely achieved, was to have present all of the biologists currently working on the species. This volume contains abstracts of their presentations, followed by bibliographies of relevant literature. Dr. Jonathon Geller (University of North Carolina) unfortunately had to cancel his participation at the last moment, but a brief overview of his work was presented by Ted Grosholz; Dr. Geller's abstract is included. As well, discussions after the workshop with Dr. Dan Minchin (Fisheries Research Centre, Ireland) indicated that his information on Carcinus-Sacculina interactions was very relevant to the workshop, and he graciously provided a summary of his recent work, which is enclosed in the workshop report.

I thank in particular Sue Spinks for her assistance in organising and staging this workshop, Craig Proctor and Dick Martin for their support throughout the project, and the participants, who in many cases travelled quite long distances to attend. I thank all for their willingness to provide up-to-the-minute research results to the group and for their enthusiasm in the discussions that followed.
Session 1. Ecology and Impacts

Part 1. Europe and North America
Summary of Discussions in Session 2.

The discussion on approaches to managing *C. maenas* divided itself naturally into three areas: prospects for control based on physical removal, prospects based on specific biological control agents, and the vulnerabilities in the life cycle that would be most suited for biological control. Thereafter, a brief series of research recommendations were made.

Physical removal

Physical removal as a means of controlling *C. maenas* has three very attractive features: the technology is available immediately, it can be very selective (hence minimal damage to native species), and it could even be profitable, assuming a market can be found for the crabs. Profitability could help mitigate what was seen as one of the main draw-backs of a physical control program, which is that it would be labour intensive and long-term.

The utility of physical removal as a means of controlling *C. maenas* largely depends on two points. First, what is the trade-off between effort and effectiveness? At this stage, we have seen little evidence of a fall-off in catch rates via trapping, the presence of which might indicate the beginning of a significant local effect on population density. On the other hand, sampling to date has not been undertaken with that objective in mind, and hence typically was not carried out long enough for a depletion, if any, to be evident. The effectiveness of a trapping program would need to be assessed on two time scales: impacts on immediate, adult catches, and longer term impacts on subsequent recruitment. In both instances, interactions with space scales are critical, and interpretation of the data generated by a trial fish-down project would be best against a reasonable back-ground of demographic information, and in particular information on juvenile and adult mobility and extent, direction and rates of larval dispersal. This information is currently lacking for all sites but California, where some adult tagging has been done.

Second, encouraging a fishery for the species was seen initially as a good idea, in the light of apparent markets (e.g., the European fishery and, perhaps, SE Asia). The prospect of developing a local 'soft-shell crab' industry, similar to that in the US for the related species, *Callinectes sapidus*, was also raised, as a potential high value fishery. Several weaknesses to the approach readily became evident, however. First, similar attempts to market *C. maenas* in the US were unsuccessful, in the absence of a ready market (exporting to Europe was apparently not tried, due to the cost involved). Hence, for such a scheme to work in Australia, a market would have to be developed and, for a while at least, the fishery might need to be subsidised (which could still be an inexpensive way to limit population size). Second, in the absence of information on sustainability of catch rates, it was thought unwise to encourage fisheries development, due to potential difficulties in expectation management. Third, the species does not 'signal' its intent to molt shortly (which apparently can be easily determined by visual inspection in *Callinectes sapidus*), so that the labour effort involved in a soft-shell crab industry might be substantial. And fourth, there was considerable unease at the idea of 'justifying' the continued existence of an apparently destructive exotic pest by using it as the basis for an industry. Although the decision to proceed down this route is clearly one that must be made by society as a whole, it was pointed out that once an industry, and jobs, are based on the species, efforts to eradicate it or bring its numbers down further might be strongly resisted by those with a financial interest in the continued viability of the stocks.

Biological Control

Unlike most other introduced marine species, there is no apparent shortage of candidate agents for biological control of the European crab, which most likely reflect the relative ease and long history of its study by European biologists. Agents potentially useful include an egg-predatory nemertean (*Carcinojemteres carcinophila*), two metazoan parasitic castrators (*Succulina carcini* and *Portunion maenadis*), several internal parasites (trypanorhynch tapeworms - *Dolphiella martini*, and *Trimacanthus acetobatidis*, and larval nematodes - cf. *Ascarophis*), and a variety of virus, dinoflagellate and ciliate diseases. The potential agents differ conspicuously in terms of features that make them attractive as controls, e.g., the life cycle of *Succulina carcini* seems to dis-positively effective management of the parasite itself; one or more of the Australian native tapeworms might be effectively encouraged with little impact on native crab species; and the scuticociliate, if species specific, appears to have the potential to rapidly reduce population sizes of the crab.

On the ecology of *Carcinus maenas* in European waters

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When Menge & Sutherland (1976) published a generalized food web of a protected rocky intertidal community in New England, they emphasized the muricid gastropod *Thais* as the most important epibenthic predator. They neglected other co-occurring species such as larvid fishes and crabs, among which was the European shore crab *Carcinus maenas*. However, Peterson (1979), in his study of epibenthic predators at the Barnegat Inlet, New Jersey, noted the importance of *C. maenas*, as had been reported earlier from European waters. As a consequence, Edwards et al. (1982) (Fig. 1) sparked a controversy entertaining the readers of "Ecology" for some time without answering the question: "What is the importance of the shore crab *C. maenas"? Surprisingly enough this question has not on a quantitative basis found its answer today, 15 years after. My purpose with this seminar therefore is to present some recently published data from European waters addressing this question.

Larvae of *C. maenas* are sensitive to salinity and temperature, requiring relatively low temperatures and high salinities for survival. Accordingly, high settlement occurs in European estuaries when these physical requirements are met (Nagaraj, 1993; Dawirs, 1985) (Fig. 2). The first seasonal settlement occurs during late June and early July. Juveniles crabs, on the other hand, tolerate both high temperatures and low salinities and survive estuarine conditions (Rasmussen 1973) (Fig. 3 & 4). During the summer, juvenile crabs feed in shallow water of estuaries and subsequently migrate to deeper waters, when the temperature drops during November. Adult crabs migrate from deeper waters, when the temperatures increase to about 8 degrees, which in Scandinavia usually occurs during the beginning of May (Rasmussen 1973) (Fig. 5).

The FAO (1994) reports that since 1985 a steady increase in catches in Europe of *C. maenas* has taken place, reaching a maximum of 900 metric tons in 1993 (Fig. 6). These catches are landed mainly in Portugal, Spain and France, where areas of the Ria Formosa estuary seem of particular importance. Nevertheless, available production data from Ria Formosa reveal that *C. maenas* constitutes less than 1% of the total biomass (Table 1). Detailed investigations of the quantitative importance of *C. maenas* (0 and 1 year-group) have been performed at many localities along the coast of Europe. A comparison reveals production figures of about double the values of other dominant epibenthic predators and in addition high P/B and consumption values (Table 1 & 2). Accordingly, the quantitative importance of *C. maenas* cannot be neglected.

Comparing the diet of *C. maenas* with other important epibenthic predators shows that *C. maenas* has a varied diet, especially the 0-group (Table 3). The 1-group gradually change to larger prey, mainly mussels and especially *Mytilus edulis*. At a small bay in Gullmarsfjorden, the total food consumption of *C. maenas* (0- and 1-gr) can be up to five times higher that other dominating epibenthic predators. The importance of *C. maenas* in intertidal sandflats is emphasized by Jensen & Jensen (1985) who reported that 26% of the crab production originates from elimination of the cockle *Cerastoderma edule* during the summer (Table 4).

*C. maenas* has originally been reported to be day active, correlating with an increase in temperature in shallow water (Rasmussen 1973) (Fig. 7). Recently, in a study of the activity of epibenthic predators in shallow waters in Scotland using video-recordings, *C. maenas* showed highest activity about two hours before sunrise, little activity during the day, and increased activity during and after sunset (Burrows et al. 1994) (Fig. 8). These results are in accordance with the observations by González-Gurriarán et. al. (1995) but migration in tidal areas may be independent of time of day (Hunter & Naylor 1993).

*C. maenas* has many predators, including other crabs and various fish species (predominantly the cod, flat- and larvid fishes) (Phil, 1985). Predation by herring gulls has also been shown to be important (Dumas & Witman 1993).
Fig. 1. Two views of community interactions. A. Menge and Sutherland’s (1976) generalized food web for protected rocky intertidal communities in New England treats only the *Thais-Mytilus-Balanus* triad as important in community structuring. Dashed lines = rare or little effect. B. As above, with the addition of highly mobile predators. References in text. Note: these food webs strictly apply only to northern New England (Gulf of Maine); extending them to southern New England would require further additions, e.g., *Tautogolabrus* co-occurs there with another labrid, *Tautoga onitis*; *Carcinus* with another portunid, *Callinectes sapidus*; *Thais* with additional muricids, *Urosalpinx cinerea* and *Eupleura caudata*; etc.
Transgenic manipulation

Genes which do not normally occur in a target species but which have specific effects can be inserted deliberately. Examples of this are the incorporation of rainbow trout growth hormone into coho salmon, and the inclusion of human sex determining gene into XX mice to produce functional male mice (Koopman et al., 1991).

According to a recent evaluation (Grewe 1996) of these four, only the inducible fatality gene (IFG) offers any real prospect of long-term control or even eradication of carp. In relation to the other methods, this report stated that:

“Chromosomal methodologies appear to offer only short term control of carp populations. Altering sex ratios can also produce short term benefits; however, population models indicate that using this approach XX females persist in the population, although at reduced absolute numbers, so that eradication is not possible. Consequently, neither chromosomal nor gender manipulation strategies appear to constitute a means of locally eradicating carp, though the techniques may still be useful as a means of augmenting other approaches.”

Reasons for considering IFG over other approaches were mainly related to its long-term application and its potential for 100% security, if correctly implemented (Grewe 1996) Species-specificity and the impossibility of developing immunity, which also are both positive reasons for using an IFG approach, are in fact common to all genetic manipulation approaches. Because technical aspects of the IFG approach are given already (Grewe 1996), this paper concentrates on general aspects of IFG as an approach.

Note that all forms of control relying on genetic manipulation are required to meet certain ethical and/or legal standards. However, these are not considered further here.

Overview of the Inducible Fatality Gene (IFG) Approach

The IFG approach has distinct stages or steps. These include: identification and selection of appropriate genetic material for transfer, which must include the fatality gene and a reporter gene (see below); incorporation of this genetic material into the individual genome; delivery of genetic material at a population scale; monitoring the spread of the IFG through natural populations via the reporter gene; pulling the trigger to activate the fatality gene once pre-determined levels of introgression have been met. Each of these presents its own technical, and logistical, challenges.

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Molecular approaches for the environmentally benign management of pest species

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Advances in molecular biology mean there are now a number of different molecular approaches for control, and possible eradication, of pest populations. This presentation discusses methods which were investigated for their potential to control carp Cyprinus carpio L. in Australia. However, while discussion is slanted toward carp control, the concepts are quite general and could be applied to other pest species. The variety of methods investigated include chromosomal manipulation, gender manipulation (via hormones and transgenic methods), immunocontraception, and the introduction of inducible fertility genes via transgenic techniques. The various methods are not restricted to carp and can be briefly summarized as follows:

Ploidy/Chromosome manipulation

Manipulation of ploidy levels, for example triploidy induction, can be achieved by blocking extrusion of the polar body. This method is primarily used to induce sterility in production line fish (Cassani and Caton 1995; Allen et al. 1996).

Controlling Sex composition of Populations

Single sex or homozygous populations can be achieved by treating gametes prior to fertilisation under controlled (laboratory) conditions. Gynogenesis is achieved by fertilising eggs with sperm that have been UV irradiated: it results in all female lines through blocking the polar body extrusion (heterozygous gynogen) or the first cell division (homozygous gynogen). Androgenesis is achieved by using gamma-irradiated eggs which results in blockage of first cell division and produces homozygous male and female lines. These manipulations are useful for rapid production of pure and inbred lines (Nagy et al., 1984; Nagy 1987; May and Grewe 1993). The advantages of producing monosex lines of fish include faster growth rates of female carp while male fish mature more quickly but at smaller sizes.

Hormonal Treatment

Treatment with the male hormone, testosterone, can produce all male fish, some of which are chromosomally female (XX) but function as fertile males. These functional males can be crossed with normal XX females to produce 100% female lines. Again if faster growth rates are required, production line fish which are 100% female would have an advantage over a mixed sex group of fish (for review of treatments see: Grewe, 1996).

Immunocontraception

This method is currently being developed by researchers at the CRC Vertebrate Biocontrol Centre, CSIRO Division of Wildlife and Ecology. The approach attempts to prevent population growth by reducing fertility. For the rabbit and mouse this involves delivery of a gene which expresses a particular species-specific reproductive protein using a species-specific virus as the delivery mechanism. Once the recombinant virus infects the host, the gene it delivers expresses the reproductive protein thereby invoking an immune response. The immune system of the host then produces antibodies for this vital reproductive protein thereby blocking reproduction. Thus if the animal does not die from the viral infection it should be rendered infertile (Tyndale-Biscoe, 1994, 1995). Clearly, the aim is to produce a species-specific effect which will have a significant impact on the pest species without any effects on non-target species. In terms of achieving a practical outcome, immunocontraception is high risk proposition and will require a multidisciplinary approach involving a team with expertise in molecular biology, immunology, virology, reproductive biology, field ecology, and population modeling.
Fig. 6. — *Carcinus maenas*: Predicted percent mortalities of zoeal stages from hatching to megalopa stage in different T-S combinations.

A. Zoea I  
B. Zoea II  
C. Zoea III  
D. Zoea IV

From Nagaraj (1993)
Fig. 4. Push-net catches of *Carcinus maenas* and *Crangon crangon* during 1982: total of two standard samples.

From Jensen & Jensen (1985)
white acanthocephalan - seals or water rats

orange acanthocephalan - shorebirds

The abundance of the tryps in green crabs, in *N. integrifrons*, and their lack of increased intensity in large crabs, suggest that fiddler rays are likely important predators of green crabs, at least in Swan Bay.

5. The entoniscid, *cf. Portunion*, is prevalent in common, hardy and convenient hosts. It could serve as a model research system awaiting importation for research of *P. maenadis* of the green crab. Similarly, the nemerteans of the nut crabs may prove a useful model. The rhizocephalan of *N. integrifrons* also has considerable potential as a research model, perhaps even as a control agent.

References


examined, nor have any juveniles been seen on the other non-ovigerous crabs. A nemertean has been reported from the nut crab, Philura laevis (Bell and Hickman 1985).

Parasites have been recovered from all locations where we have examined grapsid crabs; in numbers roughly proportional to search effort. No location can be termed a “hot spot”. The fiddler ray trypanorhynchs, however, are clearly very abundant at Swan Bay, Queenscliff, Victoria.

The lack of metacercariae from the substantial collections of C. maenas (and from N. integrifrons), from sites where they were abundant in grapsids, suggests that those parasites are restricted to the grapsids. This pattern may well reflect trophic links as these metacercariae are probably microphallids which use shorebirds as final hosts.

The two trypanorhynchs were sufficiently numerous to permit an ecological analysis in green crabs and N. integrifrons. Prevalence and intensity of the white tryp, D. martini, increased with size. This represented the lifetime accumulation of these worms since they cannot be lost from the hemocoel (and dead ones could be recognized). An intraspecific crowding effect was detected. At low intensities nearly all the white tryps were located in the pyloric region of the digestive gland. Hence this is inferred to be their preferred site. At higher intensities, an increasing proportion of these worms were found in other parts of the digestive gland.

The pink tryp, T. aestobotidis, is large, and for a larval trypanorhynch, highly site-specific. Except for a few individuals in high intensity infections, all specimens were recovered from the subcardiac region of the digestive gland, overlying the anterior nerves leading from the thoracic ganglion. It is remarkable that, above the smallest host size class available, intensity does not increase with host size. Several ecological hypotheses are available to account for such a phenomenon. Based on logic, general knowledge, and the available data, all can be rejected except one. It appears likely that high intensity infections are missing because the pink tryp induced increased susceptibility of the intermediate crab hosts to predation, presumably by fiddler rays (which are abundant at that site, G Parry, pers. commun.).

The examination of pie-crust crabs, Cancer novaezelandiae, recovered one species of metacercaria abundant in the thoracic ganglion and associated nerves, in the trowled specimens from off the Lyttleton Heads. The other crabs from both New Zealand and Tasmania were not parasitized.

Conclusions

1. So far, there are few sources of confusion likely for release of a biocontrol agent of the green crab. Rhizocephalans and egg predator nemerteaans do not occur in the hosts examined to date. The nemertean reported from the nut crab is likely easily recognizable, at least as an adult. The characteristics of the rhizocephalan reported from Western Port, and its presence in Tasmania must obviously be assessed.

2. Only a subset of the parasites using trophic transmission (two species of trypanorhynchs) have parasitized the introduced green crabs from a suite of at least six species. This is notable as such parasites are generally characterized by broad host specificity. The only parasitic castrator, an entoniscid isopod, is apparently limited to related species of grapsid crabs.

3. Prevalences and intensities of the two trypanorhynchs, and the nematode, that have crossed over to the green crab are lower than in the native host, N. integrifrons; even though that native crab is apparently less common than is the green crab.

4. Based on the life cycles of the several parasites with trophic transmission, several types of vertebrates may act as predators on green crabs, shallow water portunids and grapsids. These are:

   - white tryp - fiddler rays
   - pink tryp - fiddler rays
   - cf. Acanthoraphis - teleosts
   - metacercariae - shorebirds
Fig. 55. *Carcinus maenas*. Spring immigration in 1955 of shore crabs from the deeper to the quite shallow water in the Isfjord, Vollerup Vig, in relation to salinity and temperature, based on day-night maximum and minimum measurements. For further information see text, pp 212-213.

From Rasmussen (1973)
Fig. 58. Carcinus maenas. The presence in 1941-60 of newly metamorphosed bottom stages in the Isefjord in relation to temperature and salinity during the breeding period in the fjord, i.e., April-August. The curves show the average temperature and salinity values for these months while the numbers give the maximum and minimum monthly mean values for the same period. The thin horizontal line represents the salinity mean of the 20 years’ period. Calculated on the basis of the monthly mean values from Rørvig-Hundested (Naut. Meteorol. Ann.).

From Rasmussen (1973)
Survey of Tasmanian Crabs for Parasites: A Progress Report

Armand Kuris and Rob Gurney, University of California, Santa Barbara and Centre for Research on Introduced Marine Pests, CSIRO Marine Laboratory

We are surveying a selection of native Tasmanian crabs to 1) provide background data should a green crab parasite be ultimately released for biocontrol purposes, 2) to determine natural sources for native parasites that have involved the green crab as a host, 3) to compare the introduced green crab parasitofauna with that of taxonomically or ecologically similar crabs, 4) to obtain information, through trophic transmission, about probable crab host mortality sources, and 5) to discover possible model systems for research on life cycles and rearing techniques while use of green crab parasites awaits construction and AQIS approval of a quarantined research facility at CRIMP. We have also expanded the survey of Australian green crabs for parasites, including samples from Port Philip Bay, Victoria. As a subsidiary issue, we are also examining the introduced Cancer novaezelandiae to see how its parasitofauna compares with native New Zealand populations.

To this end we have dissected and examined 135 green crabs 206 native crabs 20 C. novaezelandiae from Tasmania and 23 from New Zealand. Native crabs were selected for examination either because they were portunids, or were from habitats appropriate to the green crab from geographic areas now, or soon expected to be, in the range of the green crab. Potential habitats of native crabs sought for comparison were mostly protected harbors; but some collections were taken from exposed rocky intertidal, sandy beach and exposed subtidal habitats.

For each crab examined, we recorded size (carapace width), sex, female abdomen width (for maturation), presence of eggs, egg development stage, ripeness of ovary and molt stage. For each crab, the external surfaces, especially limb axillae, abdominal furrow and gills were inspected. The hemocoeal was carefully examined and two squashes each were made of digestive gland and ovary. For the portunids, the entire digestive gland was examined; divided into three portions: pyloric, subcardiac and carapace. Voucher specimens were appropriately preserved and have either been sent for taxonomic evaluation (cestodes - Ian Beveridge, acanthocephalans - Sylvie Pichelin), or arrangements are still pending (nematodes, entoniscids). Metacercariae were not identified to species. They were examined under the compound microscope and their general features noted.

The green crabs were parasitized by larvae of two species of trypanorhynch tapeworms (Dolfusiella martini, Trimacanthus acrobatidis) and by larval nematodes (cf. Aescophysis). Adults of the tapeworms are commonly reported from fiddler rays, Trigonorhina guanarius, and some other elasmobranchs. The adult nematodes are probably in teleost fishes. Higher prevalences and intensities of all three worms were found in Nectocarcinus integrifrons. Both tapeworms were also occasionally found in 4 species of grapsids.

Rhzoecephalans were recently discovered by G Ruiz (pers. commun.) from N. integrifrons from Western Port, Victoria; apparently confirming the old record of Hale (1927). Determining their prevalence and making additional biological observations on them are high priorities.

The only other portunids examined were 27 Ovalipes australiensis from Oyster Bay; all were unparasitized.

Native grapsid crabs have a diverse parasitofauna including two tapeworms, two acanthocephalans, at least one species of trematode metacercaria, and an entoniscid isopod parasitic curator. The same two trypanorhynch tapeworms, D. martini and T. acrobatidis, were respectively present in four and one species of grapsid. Prevalences and intensities were always lower than in the two portunid crabs. Metacercariae were present in both species of Paragrupus. One species of larval acanthocephalan, Corynosoma sp., was rare; present in but two grapsid species. Pending further taxonomic resolution by S. Pichelin (South Australia Museum), its final host is either a seal or (interestingly) a water rat (Hydromys sp.). The other acanthocephalan, cf. Profilicollis sp., is sometimes locally abundant in all grapsid species so far examined. Its final hosts are likely shorebirds. The entoniscid isopod is likely referable to Portunion and is an undescribed species. Its prevalence ranges from 12-23% at three localities in Tasmania. Its hosts are Cyclogrupus granulosus and Paragrupus gaimardi. No adult nemertean egg predators have been collected from the 20 ovigerous grapsid crabs (4 crab species)
taxonomic affinities of the isolates from crabs, as well as their life histories to ascertain its ability to function as a control agent. If the ciliate was still considered a useful candidate for control, extensive transmission experiments would be necessary to ensure the ciliates could not infect native crab species: non target crabs in Australia include very valuable commercial species. More information on host population dynamics is also crucial to ascertain the ability of these parasites to control C. maenas populations. It is important to note that most biological agents will act synergistically to moderate populations of exotic species and their action may need to be supplemented by other strategies (e.g. selective harvesting) to control pest species.

Table 3. The characters of an effective biological control agent which are present (✓), absent (✗) or unknown (?) for several crab parasites

<table>
<thead>
<tr>
<th>CHARACTERS OF AN EFFECTIVE BIOLOGICAL CONTROL AGENT</th>
<th>DINOFLAGELLATE</th>
<th>CILIATE</th>
<th>Saccudina</th>
</tr>
</thead>
<tbody>
<tr>
<td>Efficient searching</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>High reproductive capacity of host</td>
<td></td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Transmission / life history known</td>
<td>✗</td>
<td>✗</td>
<td>✓</td>
</tr>
<tr>
<td>Host specific</td>
<td>?</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Effect host reproduction (? C. maenas)</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Causes host mortality (? C. maenas)</td>
<td>✓</td>
<td>✓</td>
<td>?</td>
</tr>
<tr>
<td>Effect host population (? C. maenas)</td>
<td>✓</td>
<td>✓</td>
<td>?</td>
</tr>
</tbody>
</table>

References


Annual commercial catches of the green crab *Carcinus maenas* (L.) in Europe

![Graph showing annual commercial catches of the green crab *Carcinus maenas* (L.) in Europe from 1982 to 1995. The graph indicates the trend in catches by France, Portugal, Spain, and the total catch combined.](image-url)
Fig. 56. *Carcinus maenas*. Day-night locomotory activity of immature shore crabs (♂ + ♀) in relation to maximum-minimum water temperatures. The crabs were collected with traps ("prawn pots") in shallow water off the Laboratory, Vellerup Vig, June 1955. The peaks of activity are in the daytime and are correlated with water temperature. For further information see text, pp 214-216.

From Rasmussen (1973)
Table 2. Prevalence and effect of ciliates which occur in crabs from various sites in the Atlantic and Pacific Oceans.

<table>
<thead>
<tr>
<th>COUNTRY</th>
<th>CRAB</th>
<th>CILIATE</th>
<th>PREVALENCE</th>
<th>EFFECT</th>
<th>REFERENCE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ATLANTIC OCEAN</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Venice, Italy</td>
<td><em>Carcinus aequuarii</em></td>
<td><em>Mesanophrys maggi</em></td>
<td>0.33% wild (n=300)</td>
<td>death</td>
<td>Cattaneo, 1888</td>
</tr>
<tr>
<td>Roscoff, France</td>
<td><em>Carcinus maenas</em></td>
<td><em>Mesanophrys maggi</em></td>
<td>0.2% wild (n=3000)</td>
<td>?</td>
<td>Poisson, 1929;</td>
</tr>
<tr>
<td>Maine, USA</td>
<td><em>C. maenas</em></td>
<td></td>
<td>0% wild (n=7)</td>
<td></td>
<td>1930</td>
</tr>
<tr>
<td>Roscoff, France</td>
<td><em>Maia squinado</em></td>
<td><em>M. maggi</em></td>
<td>6% infected</td>
<td>death</td>
<td>Bang, 1962</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>experimentally (n=36)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Roscoff, France</td>
<td><em>Cancer pegasus</em></td>
<td><em>Mesanophrys carinii</em></td>
<td>7-18% wild, wounded crabs (n=3000)</td>
<td></td>
<td>Grolière &amp;</td>
</tr>
<tr>
<td>France</td>
<td><em>C. pegasus</em></td>
<td><em>M. carinii</em></td>
<td>37% captive (n=295)</td>
<td>death</td>
<td>Leglise, 1977</td>
</tr>
<tr>
<td>England</td>
<td><em>C. pegasus</em></td>
<td></td>
<td>0% (n=37)</td>
<td></td>
<td>Bang et al., 1972</td>
</tr>
<tr>
<td>Maryland, USA</td>
<td><em>Callinectes sapidus</em></td>
<td><em>Mesanophrys chesapeakensis</em></td>
<td>0.3% wild (n=2500)</td>
<td>feeds on hemocytes</td>
<td>Messick &amp; Small, 1996</td>
</tr>
<tr>
<td>Maine, USA</td>
<td><em>Cancer irroratus</em></td>
<td><em>Anophryoides haemophilus</em></td>
<td>14% wild (n=14)</td>
<td></td>
<td>Sherburne &amp;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Bean, 1991</td>
</tr>
<tr>
<td><strong>PACIFIC OCEAN</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Washington, USA</td>
<td><em>Cancer magister</em></td>
<td><em>Mesanophrys pugettensis</em></td>
<td>&lt;0.4% wild (n=1916)</td>
<td></td>
<td>Morado &amp; Small, 1994</td>
</tr>
<tr>
<td>Washington, USA</td>
<td><em>C. magister</em></td>
<td><em>M. pugettensis</em></td>
<td>one wild, one captive</td>
<td>death</td>
<td>Sparks et al., 1982</td>
</tr>
<tr>
<td>Washington, USA</td>
<td><em>C. magister</em></td>
<td><em>M. pugettensis</em></td>
<td>Dipnet:15% wild (n=667) Trawl: 0.2% wild (n=1346)</td>
<td>death</td>
<td>Morado, 1993</td>
</tr>
<tr>
<td>Oregon, USA</td>
<td><em>C. magister</em></td>
<td><em>M. pugettensis</em></td>
<td>40% captive crabs</td>
<td></td>
<td>Armstrong et al., 1981</td>
</tr>
<tr>
<td>Washington, USA</td>
<td><em>Cancer productus</em></td>
<td><em>M. pugettensis</em></td>
<td>3% wild (n=87)</td>
<td></td>
<td>Morado &amp; Small, 1994</td>
</tr>
<tr>
<td>Washington, USA</td>
<td><em>Pugettia producta</em></td>
<td><em>M. pugettensis</em></td>
<td>29% wild (n=7)</td>
<td></td>
<td>Morado &amp; Small, 1994</td>
</tr>
</tbody>
</table>

Nemertean History

Nemerteans in the genus *Caricinonemertes* are obligate symbiotic egg predators of decapod crustaceans and are found on over ten species of crabs, including the Dungeness crab *Cancer magister* in Alaska. They feed on crab eggs and lay their egg masses within crab eggs. Their presence has been suggested as partially responsible for the crash of the Dungeness crab fishery in some areas of Alaska. However, recent mathematical modelling suggests that the nemertean egg-predator cannot, by itself, cause cycling of the Dungeness crab population, but probably contributes synergistically to it. In California, *Caricinonemertes* have transferred from the native shore crab *Hemigrapsus oregonensis* to the introduced European green crab *Carcinus maenas* (Torchin et al., 1996). The impact of the nemertean on population dynamics of *C. maenas* is unclear, however, its ability to switch hosts indicates that it may not be useful as a biological control agent.

Conclusions

For effective biological control, the prospective agent would need to be very efficient at finding a host even at low host density, have a high reproductive capacity (compared to the host), be host specific and finally, impact the fitness of the host and cause a decrease in host population density. Of the parasites investigated, the ciliate appears to satisfy most of these criteria and offer the best potential for biological control of *C. maenas*. However, it is necessary to determine the
Ciliates

Since 1985, Dungeness crab *Cancer magister* mortalities have been reported on the coast of north west America but their causes were not identified. In May 1987, there was a mass mortality of over 6000 Dungeness crabs in Washington. These crabs were infected by a scuticociliate *Mesanophrys pugettensis*.

Scuticociliates have been found in the blood of other crab species, including *Carcinus maenas* from Europe. Ciliates in the blood of *C. maenas* fed on the hemocytes of the crab. As the disease progressed, the numbers of crab hemocytes were reduced until they were replaced by a mass of ciliates and the blood appeared milky. Secondary bacterial infection usually followed which destroyed tissues. The ciliates also fed on bacteria in the moribund host.

Historical data suggests that histophagous ciliates are very rare in wild crab populations (0.1%, n=9150, total from various sources reported in Morado, 1993). However, recent work indicates that prevalence of histophagous ciliates in wild Dungeness crab populations can reach 15% (n=667) and vary between sites, depth, molt stage and sex of crabs (Morado, 1993). The number of species of ciliates which infect crabs, their host specificity and the mechanism of transfer between crabs is not clear. However, ciliates cause mortalities in several crab hosts which suggests they could impact host populations. The host specificity and pathogenicity of ciliates to non-target crab species will determine the utility of these organisms for biological control.
Mean numbers per hour [log$_{10}$(1 + n)] transformed) of six groups of animals observed passing beneath the subtidal camera in 1991 and 1992, and beneath the intertidal camera in 1992. Means are plotted relative to the times of sunrise (SR) for observations after midnight, and sunset (SS) for observations before midnight.

From Burrows et al. (1994)
Table 1. Macrobenthic production and mean biomass recorded from different localities. Values in brackets with the epibenthic predator *Carcinus maenas* included.

<table>
<thead>
<tr>
<th>Location</th>
<th>Production P (g AFDW m$^{-2}$)</th>
<th>Biomass B (g AFDW m$^{-2}$)</th>
<th>P/B</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tamar Estuary (GB)</td>
<td>13.3</td>
<td>13.2</td>
<td>1.01</td>
<td>Warwick &amp; Price (1975)</td>
</tr>
<tr>
<td>Grevelingen Estuary (NL)</td>
<td>50.3-57.4</td>
<td>0.1-119.9</td>
<td>0.7-8.7</td>
<td>Wolff &amp; de Wolf (1977)</td>
</tr>
<tr>
<td>Foz Estuary (E)</td>
<td>26.1-118.4</td>
<td>3.2-37.4</td>
<td>1.6-5.2</td>
<td>Anadón (1980)</td>
</tr>
<tr>
<td>Bay of Fundy (CA)</td>
<td>5.3</td>
<td>2.6</td>
<td>2.0</td>
<td>Schwinghamer <em>et al.</em> (1986)</td>
</tr>
<tr>
<td>Wadden Sea (D)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Arenicola</em> flat</td>
<td>50.2</td>
<td>27.6</td>
<td>1.83</td>
<td>Asmus (1987)</td>
</tr>
<tr>
<td><em>Nereis-Corophium</em> belt</td>
<td>17.5</td>
<td>16.5</td>
<td>1.05</td>
<td>Asmus (1987)</td>
</tr>
<tr>
<td><em>Zostera noltii</em> bed</td>
<td>48.2</td>
<td>30.2</td>
<td>1.6</td>
<td>Asmus (1987)</td>
</tr>
<tr>
<td>Ria Formosa (P)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sand flat</td>
<td>32.5 (34.4)</td>
<td>15.2 (15.4)</td>
<td>2.14 (2.23)</td>
<td>Sprung (1994)</td>
</tr>
<tr>
<td><em>Zostera noltii</em> bed</td>
<td>54.2 (57.6)</td>
<td>16.7 (17.2)</td>
<td>3.24 (3.35)</td>
<td>Sprung (1994)</td>
</tr>
<tr>
<td>Mud flat</td>
<td>54.7 (71.5)</td>
<td>22.4 (25.1)</td>
<td>2.44 (2.85)</td>
<td>Sprung (1994)</td>
</tr>
<tr>
<td>Gullmarsvik (S)</td>
<td>28.9 (30.7)</td>
<td>6.1 (6.4)</td>
<td>4.7 (4.8)</td>
<td>Möller <em>et al.</em> (1985)</td>
</tr>
</tbody>
</table>
Table 1. Prevalence of dinoflagellate parasites in crabs from various sites in the Atlantic and Pacific Oceans (REFERENCE as in Shields, 1994)

<table>
<thead>
<tr>
<th>PARASITE</th>
<th>HOST</th>
<th>PREVALENCE (%)</th>
<th>LOCATION</th>
<th>REFERENCE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ATLANTIC</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hematodinium perezi</em></td>
<td><em>Carcinus maenas</em></td>
<td></td>
<td>France</td>
<td>5, 25</td>
</tr>
<tr>
<td><em>Liocarcinus depurator</em></td>
<td></td>
<td></td>
<td>France</td>
<td>5, 25</td>
</tr>
<tr>
<td><em>Platyonychus laevis</em></td>
<td><em>Cancer pagurus</em></td>
<td></td>
<td>France</td>
<td>29</td>
</tr>
<tr>
<td><em>Necora puber</em></td>
<td>≤87</td>
<td></td>
<td>France</td>
<td>30</td>
</tr>
<tr>
<td><em>H. perezi</em></td>
<td>portunid hosts</td>
<td>&lt;0.1</td>
<td>France</td>
<td>5</td>
</tr>
<tr>
<td><em>H. cf. perezi</em></td>
<td><em>Cancer borealis</em></td>
<td>0.6</td>
<td>Delaware, USA</td>
<td>31</td>
</tr>
<tr>
<td><em>H. cf. perezi</em></td>
<td><em>Cancer irroratus</em></td>
<td>0.4</td>
<td>New York, USA</td>
<td>31</td>
</tr>
<tr>
<td><em>H. cf. perezi</em></td>
<td><em>Ovalipes ocellatus</em></td>
<td>0.6</td>
<td>New York, USA</td>
<td>31</td>
</tr>
<tr>
<td><em>H. cf. perezi</em></td>
<td><em>Ovalipes ocellatus</em></td>
<td>4</td>
<td>Delaware, USA</td>
<td>31</td>
</tr>
<tr>
<td><em>H. cf. perezi</em></td>
<td><em>Callinectes sapidus</em></td>
<td>≤30</td>
<td>SE USA</td>
<td>32</td>
</tr>
<tr>
<td><em>H. cf. perezi</em></td>
<td><em>Callinectes sapidus</em></td>
<td>≤100</td>
<td>SE USA</td>
<td>88</td>
</tr>
<tr>
<td><strong>PACIFIC</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hematodinium sp.</em></td>
<td><em>Chionoecetes bairdi</em></td>
<td>37 - 95</td>
<td>SE Alaska</td>
<td>11</td>
</tr>
<tr>
<td><em>Hematodinium sp.</em></td>
<td><em>Chionoecetes bairdi</em></td>
<td>2 - 95</td>
<td>SE Alaska</td>
<td>36</td>
</tr>
<tr>
<td><em>Hematodinium sp.</em></td>
<td><em>Chionoecetes opilio</em></td>
<td></td>
<td>SE Alaska</td>
<td>11, 36</td>
</tr>
<tr>
<td><em>H. australis</em></td>
<td><em>Portunus pelagicus</em></td>
<td>1 - 4</td>
<td>Qld, Australia</td>
<td>33</td>
</tr>
<tr>
<td><em>H. cf. australis</em></td>
<td><em>Scylla serrata</em></td>
<td>2</td>
<td>Qld, Australia</td>
<td>89</td>
</tr>
<tr>
<td><em>H. cf. australis</em></td>
<td><em>Trapezia arvelata</em></td>
<td>7</td>
<td>GBR, Australia</td>
<td>35</td>
</tr>
<tr>
<td><em>H. cf. australis</em></td>
<td><em>T. coerulae</em></td>
<td></td>
<td>Qld, Australia</td>
<td>35</td>
</tr>
</tbody>
</table>
Parasites (excluding *Sacculina*) which could regulate populations of the European green crab *Carcinus maenas*

Louise Goggin, Centre for Research on Introduced Marine Pests, CSIRO Marine Research

Several parasites are known to cause epizootics of wild crab populations and yet few of these diseases, or their long term impact on these populations, are well understood. Our understanding is hindered by our lack of knowledge of both host and parasite population dynamics. The numbers of both terrestrial and aquatic populations vary but the causes of these fluctuations have often not been determined: they are probably due to many factors which operate synergistically. The impact of disease on crab populations is often overlooked because crabs are a mobile, marine species and, according to Morado (1993), affected crabs are: unlikely to be observed with disease symptoms; more susceptible than healthy ones to predation and cannibalism; and less likely to be caught by non-selective fishing gear such as trawls. Infected crabs probably do not enter commercial pots or traps because they quickly become anorectic with the onset of disease. Therefore, the identification of a biological control agent for introduced crab populations requires research into the biology of both the host and parasite.

The following is not an exhaustive list of crab parasites but only those which, from the literature, could potentially regulate populations of the European green crab *Carcinus maenas* in Australian waters.

**Viruses**

Viruses have been found in the blood of many crabs including *Carcinus maenas*. A baculovirus in the hepatopancreas (B1), a hemocytic nuclear virus (RV-CM), a putative bunyavirus (CHV), a birnavirus and a rhabdovirus (Y-organ virus) have been reported from *C. maenas* (Brock & Lightner, 1990). The CHV virus isolated from *C. maenas* could be transmitted to uninfected crabs by inoculation and inhibited clotting of the blood in infected animals. The numbers of amoebocytes were reduced in infected *C. maenas*, although infected crabs could still heal wounds and some crabs could recover from infection. Experimentally infected crabs had higher mortalities than control animals. It is possible the CHV virus may be transmitted by *Sacculina carcini* which infects about 50% crabs at this site. The host specificity of these viruses and their effect on *C. maenas* populations have not been reported.

A virus could be used to deliver a genetically modified lethal gene to *C. maenas*. However, the use of viruses as biological control agents is not recommended at this stage due to the difficulties of containing marine viruses in the laboratory.

**Dinoflagellates**

Dinoflagellates include obligate parasites and photosynthetic organisms, some of which cause red tides. Parasites of the genus *Hematodinium* are primarily parasites of crustaceans. Epizootics of *Hematodinium* have been reported from southeastern Alaska, eastern USA, Scotland and France, where the parasite has impacted several fisheries (Shields, 1994). The dinoflagellate *Hematodinium* sp. occurs in the blood of the Tanner crab *Chionoecetes bairdii*, where it multiplies, reducing the number of hemocytes and the oxygen carrying capacity of the blood and inducing lethargy and finally death of the host. The infection causes Bitter Crab disease which produces a chalky texture and bitter taste in cooked Tanner crabs that is unacceptable to the market.

The type species *Hematodinium perezi* infects the hemolymph of *Carcinus maenas* in Europe, but has also been described from *Portunus depurator*. Many isolates of *Hematodinium* have been found from crabs around the world and their affinities are not clear. The impact of the parasite on *C. maenas* is also not known. Recent molecular work indicated several undescribed species exist within the *Hematodinium* complex. It is possible some isolates are not host specific which would limit the use of this parasite in biological control.
Table 2. Annual production (P), P/B-ratio, food consumption (C), and food conversion (P/C) of 4 mobile epibenthic species in Gullmarsvik (G) and Sandvik (S) in Gullmarsfjorden on the Swedish west coast during 1977 and 1978. The data are compared with other European sites. Data as g AFDW m⁻²

<table>
<thead>
<tr>
<th>Species</th>
<th>Area</th>
<th>P</th>
<th>P/B</th>
<th>C</th>
<th>P/C</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pomatoschistus microps</em> (0-gr)</td>
<td>G (1977)</td>
<td>0.56</td>
<td>4.1</td>
<td>1.8</td>
<td>0.31</td>
<td>Phil (1985)</td>
</tr>
<tr>
<td></td>
<td>G (1978)</td>
<td>0.42</td>
<td>3.0</td>
<td>1.6</td>
<td>2.6</td>
<td>Phil (1985)</td>
</tr>
<tr>
<td></td>
<td>S (1977)</td>
<td>0.27</td>
<td>2.8</td>
<td>1.3</td>
<td>0.21</td>
<td>Phil (1985)</td>
</tr>
<tr>
<td></td>
<td>S (1978)</td>
<td>0.43</td>
<td>4.2</td>
<td>1.3</td>
<td>0.33</td>
<td>Phil (1985)</td>
</tr>
<tr>
<td></td>
<td>Nivå Bay (DK)</td>
<td>2.0</td>
<td></td>
<td>0.26, 0.47</td>
<td></td>
<td>Andersen (1983)</td>
</tr>
<tr>
<td><em>Pomatoschistus minutus</em> (0-gr)</td>
<td>G (1978)</td>
<td>0.24</td>
<td>2.9</td>
<td>1.0</td>
<td>0.25</td>
<td>Phil (1985)</td>
</tr>
<tr>
<td></td>
<td>Gullmarsfjorden (1976)</td>
<td></td>
<td></td>
<td>0.4</td>
<td>0.24</td>
<td>Evans (1983)</td>
</tr>
<tr>
<td></td>
<td>Sweden (1977)</td>
<td>0.4</td>
<td></td>
<td>0.45</td>
<td></td>
<td>Evans (1983)</td>
</tr>
<tr>
<td><em>Pleuronectes platessa</em> (0-gr)</td>
<td>G (1977)</td>
<td>0.24</td>
<td>1.8</td>
<td>1.0</td>
<td>0.23</td>
<td>Phil (1985)</td>
</tr>
<tr>
<td></td>
<td>G (1978)</td>
<td>0.29</td>
<td>5.3</td>
<td>0.9</td>
<td>0.32</td>
<td>Phil (1985)</td>
</tr>
<tr>
<td></td>
<td>Naligian (NL)</td>
<td></td>
<td></td>
<td>0.03-0.3</td>
<td>0.45</td>
<td>Kuipers (1977)</td>
</tr>
<tr>
<td></td>
<td>Gullmarsfjorden (1976)</td>
<td></td>
<td></td>
<td>0.8</td>
<td></td>
<td>Evans (1983)</td>
</tr>
<tr>
<td></td>
<td>Sweden (1977)</td>
<td></td>
<td></td>
<td>1.4</td>
<td></td>
<td>Evans (1983)</td>
</tr>
<tr>
<td></td>
<td>Kysing Fjord (DK)</td>
<td></td>
<td></td>
<td>0.20</td>
<td></td>
<td>Bregnballe (1961)</td>
</tr>
<tr>
<td></td>
<td>Loch Ewe (Scotland)</td>
<td></td>
<td></td>
<td>0.36</td>
<td></td>
<td>Edwards et al. (1969)</td>
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<tr>
<td></td>
<td>Port Erin Bay, UK</td>
<td></td>
<td></td>
<td>0.20</td>
<td></td>
<td>Colman (1970)</td>
</tr>
<tr>
<td></td>
<td>Balgzand, (NL)</td>
<td></td>
<td></td>
<td>0.30-0.35</td>
<td></td>
<td>de Vlas (1979)</td>
</tr>
<tr>
<td><em>Carcinus maenas</em> (0-gr)</td>
<td>G (1978)</td>
<td>0.94</td>
<td>6.5</td>
<td>4.3</td>
<td>0.22</td>
<td>Phil (1985)</td>
</tr>
<tr>
<td></td>
<td>(1-gr)</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>(0-gr)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Balgzand (NL)</td>
<td>0.88</td>
<td>6.9</td>
<td>5.7</td>
<td>0.16</td>
<td>Phil (1985)</td>
</tr>
<tr>
<td></td>
<td>(1-gr)</td>
<td></td>
<td></td>
<td>0.7</td>
<td>0.16</td>
<td>Klein Breteler (1976)</td>
</tr>
<tr>
<td></td>
<td>(0-gr)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Klein Breteler (1976)</td>
</tr>
<tr>
<td></td>
<td>Island of Sylt (D)</td>
<td></td>
<td></td>
<td>3.6</td>
<td>0.30</td>
<td>Scherer &amp; Reise (1981)</td>
</tr>
<tr>
<td></td>
<td>adult</td>
<td></td>
<td></td>
<td>1.3</td>
<td>0.20</td>
<td>Scherer &amp; Reise (1981)</td>
</tr>
</tbody>
</table>
Table 3. Annual food consumption by *Pomatoschistus microps*, *Pomatoschistus minutus*, *Pleuronectes platessa* and *Carcinus maenas* of dominant meiofauna, macrofauna and epifauna groups, and detritus in Gullmarsvik, 1978. Data in mg AFDW m\(^{-2}\) and in brackets as % of total consumption. From Phil (1985).

<table>
<thead>
<tr>
<th>Food source</th>
<th><em>P. microps</em> 0-gr</th>
<th><em>P. minutus</em> 0-gr</th>
<th><em>P. platessa</em> 0-gr</th>
<th><em>C. maenas</em> 1-gr</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calanoida</td>
<td>279 (19)</td>
<td>45 (4)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MEIOFAUNA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Harpacticoida</td>
<td>453 (28)</td>
<td>44 (4)</td>
<td>91 (10)</td>
<td>66 (2)</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>407 (25)</td>
<td>105 (11)</td>
<td>19 (2)</td>
<td>20 (1)</td>
</tr>
<tr>
<td>MACROFAUNA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Corophium volutator</em></td>
<td>337 (21)</td>
<td>635 (66)</td>
<td>404 (45)</td>
<td>854 (20)</td>
</tr>
<tr>
<td>Nereis spp.</td>
<td>10 (1)</td>
<td>27 (3)</td>
<td>41 (5)</td>
<td>202 (5)</td>
</tr>
<tr>
<td>Mya arenaria</td>
<td>14 (1)</td>
<td>18 (2)</td>
<td>79 (9)</td>
<td>45 (1)</td>
</tr>
<tr>
<td>Cerastoderma edule</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spisula subtruncata</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mytilus edulis</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydrobia spp.</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>EPIFAUNA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crangon crangon</td>
<td>35 (2)</td>
<td>73 (8)</td>
<td>24 (3)</td>
<td>1794 (42)</td>
</tr>
<tr>
<td>Carcinus maenas</td>
<td></td>
<td></td>
<td>125 (14)</td>
<td></td>
</tr>
<tr>
<td>DETRITUS</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>47 (3)</td>
<td>10 (1)</td>
<td>89 (10)</td>
<td>384 (9)</td>
</tr>
<tr>
<td><strong>Total food consumption</strong></td>
<td><strong>1603 (12.0)</strong></td>
<td><strong>966 (7.2)</strong></td>
<td><strong>892 (6.7)</strong></td>
<td><strong>4271 (31.8)</strong></td>
</tr>
</tbody>
</table>
**Portunion moenadis in Carcinus maenas**  
from W. coast of Sweden 1996

<table>
<thead>
<tr>
<th>Crabs</th>
<th>Total</th>
<th>With Portunion</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>No <em>S. carcini</em> (dissection)</td>
<td>183</td>
<td>4</td>
<td>2.2%</td>
</tr>
<tr>
<td>With <em>S. carcini</em> (incl. scars)</td>
<td>165</td>
<td>4</td>
<td>2.4%</td>
</tr>
<tr>
<td>All crabs</td>
<td>348</td>
<td>8</td>
<td>2.3%</td>
</tr>
</tbody>
</table>

Pooled from two Carcinus maenas populations  
(Ellös, Malö)

Prevalence of *S.carcini* (all stages): 47%

53 "feminized" males without *S. carcini* (dissection) entered as uninfested!
The epicaridean parasite *Portunion moenadis* as a biological control agent on *Carcinus maenas*

Jens T. Hoeg (Univ. Copenhagen), Henrik Glenner (Univ. Copenhagen) and Malin Werner (Univ. Goteborg)

Among parasitic Crustacea, both the Cirripedia Rhizocephala and the Isopoda Epicaridea are parasitic castrators (O''Brien & van Wyk, 1985). Thus parasites from both taxa might candidate as biological control agents on their crustacean host species. But while the life cycle of the Rhizocephala is now well known in most aspects and can be cultured throughout in the laboratory, we remain ignorant on many key aspects of epicaridean biology and life cycles. The entoniscid epicaridean *Portunion moenadis* occurs in the body of the European green crab *Carcinus maenas*. The parasite is situated in the cephalothorax and can only be detected by dissection, except that male crabs are feminized in a way similar to those carrying the rhizocephalan *Sacculina carcini*. Veillet (1943, 1945) argues that *P. moenadis* always hyperparasitizes on the internal parts of *S. carcini*. If this is true, the sterilization of both host sexes and the feminization of males could be an effect of the rhizocephalan only, and *P. moenadis* would not be of use as a biocontrol agent of *C. maenas*.

We dissected 348 *Carcinus maenas* from the Swedish west coast. Among these we found eight *P. moenadis* (2.2%) and four of these occurred in crabs with no external or internal *Sacculina carcini*. The same population included 165 crabs hosting *S. carcini*, including 50 scarred crabs (total *S. carcini* prevalence 47%). These numbers indicates that *P. moenadis* is not, or not always, a hyperparasite on *S. carcini*. This would also agree with Kuris's (1974) observations that the *Hemigrapsus oregonensis* can sustain prevalences of *Portunion conformis* reaching 92%, although this graipsid crab is not known to host a rhizocephalan. Infestation by *P. moenadis* probably occurs by cryptoniscus larvae entering the branchial chamber, where they attach and develop into a parasite spreading through the cephalothorax of the crab. But all details remain obscure. The fully developed *P. moenadis* extend within the cephalothorax. But it always retains a connection with the branchial chamber and it is probably by this means that it releases entoniscus larvae to the exterior. Most Epicaridea have an intermediate crustacean host, which is infested by the pelagic entoniscus larvae. In *P. moenadis* this intermediate host seems to be a copepod, but that statement is not based on laboratory trials. The entoniscus molts into the cryptoniscus while on the intermediate host. We have observed release of entoniscus larvae from *P. moenadis* and are planning a SEM documentation. Many details remain unknown in the biology of *P. moenadis*, including key problems relevant for its use as biocontrol agent: The anatomy of the parasite; its morphological relation to both *C. maenas* and internal of possible coinfesting *S. carcini*; the biology and settlement of the pelagic stages; the nature of the intermediate host. We recommend initiation of a histological and biological study of these problems in *P. moenadis* before it is used actively in field trials as a biocontrol agent.

References


Table 4. Relation between production (P) of *Carcinus maenas* and elimination (E) of *Cerastoderma edule* on an intertidal sand flat in the Danish Wadden Sea. Elimination is estimated as \( E = \Delta N^{1/2} (w_{11} + w_{12}) \); production and weight given in mg AFDW m\(^{-2}\). GGE = gross growth efficiency. Data from Jensen & Jensen (1985).

<table>
<thead>
<tr>
<th></th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Carcinus maenas</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>84</td>
<td>1580</td>
</tr>
<tr>
<td>Production</td>
<td>1496</td>
<td></td>
</tr>
<tr>
<td><strong>Cerastoderma edule</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Numbers m(^{-2})</td>
<td>33055</td>
<td>7440</td>
</tr>
<tr>
<td>Mean weight</td>
<td>0.105</td>
<td>0.342</td>
</tr>
<tr>
<td>Elimination</td>
<td></td>
<td>5725</td>
</tr>
<tr>
<td>P/E x 100 (GGE)</td>
<td></td>
<td>26.1%</td>
</tr>
<tr>
<td>GGE Dutch Wadden Sea</td>
<td>≈30%</td>
<td>Klein Breteler (1975)</td>
</tr>
<tr>
<td>GGE Gullmarsfjorden</td>
<td>43%</td>
<td>Erikson &amp; Edlund (1977)</td>
</tr>
</tbody>
</table>
References


Carcinonemertes carcinophila Life Cycle on Blue Crab, Callinectes sapidus

**Ovigerous Female**
- Male and female worms eat crab eggs, grow, mature, mate, reproduce
- Worm eggs hatch
- Juvenile and regressed adult worms go to egg mass
- Crab oviposits

**Non-ovigerous Female**
- Juvenile and regressed adult worms encapsulated on exoskeleton

**Males and Female**
- Juvenile worms encapsulated on gills, lost at molt

**Fig. 2.** Life cycle of *Carcinonemertes carcinophila* on the blue crab, *Callinectes sapidus*. Heavy arrows represent movement of worms between crabs; light arrows movement on an individual crab; the broad open arrow denotes that a female crab has oviposited her eggs without an intervening molt.

**References**


Roe (1987) used sentinel crabs of three host species *in situ* in cages to measure and compare infestation rates of *Carcinonemertes epialti*. Settlement was very much higher on its natural hosts than on the other species of crab tested (which supported abundant populations of its own SEPN). However, it is clearly possible for some species to acquire a new host; as *C. epialti* from *Hemigrapsus oregonensis* has been shown to readily infest green crabs in nature in California and to respond to biological cues so that they move to the egg mass and feed on the eggs of the novel host (Torchin et al. 1996).

Life cycles are only partially understood for most SEPNs. Hence, for most species, the recruitment scales relative to that of their hosts can only be tentatively assessed. The greatest challenge for more effective research on SEPNs is to achieve successful larval settlement. It is unclear if this will be difficult as only the most informal and casual investigations have been made.

For some SEPN species, their recruitment appears closed relative to recruitment of their host. On the red king crab in Alaska, *C. regicida* appears to have a short life cycle and autoinfection causes high intensity infestations of hosts as the long breeding season advances. In some localized bays and fjords, crab populations consistently become heavily infested and lose all eggs to these predators. In contrast, larval development for *C. errans* of the Dungeness crab may be long and its recruitment relatively open.

Some species, most notably *C. errans*, have remarkably sophisticated abilities to track hosts through breeding and molting cycles such that a high proportion of the worm population funnels into the ovigerous fraction of the female host population (Wickham et al. 1984). Consequently, high intensities of these worms can be sustained even at low host population levels (Botsford & Wickham 1978).

To examine SEPNs as potential green crab natural enemies prior to construction and AQIS approval of *C. carcinophila* for the CRIMP containment facility, two model systems are available for research. An undescribed species of *Carcinonemertes* in Tasmania was reported from the common leucosid pebble (nut) crab, *Philyra laevis* (Bell & Hickman). Also, *C. mitsukurii* is available from Indo-Pacific portunids from Moreton Bay (Shields 1992). The latter appears to have a general morphology and life cycle similar to that of *C. carcinophila*. A new species of SEPN was observed on the deep water crab, *Pseudocarcinus gigas*, from Tasmania (C. Gardner pers. commun.) and is being described by Kuris and Gibson (in prep.). The unwieldy host makes this an unlikely model research system.

An asset to the further study of SEPNs is the ready ability to transfer these worms as juveniles and adults to experimental hosts (Torchin et al. 1996), to do direct contact transmission experiments (Kuris 1978) and to test feeding preferences and rates *in vitro* (Shields et al 1990). *Since in vitro* cultivation through worm egg oviposition and hatching is already available (worms actually grow more rapidly and mature earlier than *in vivo*), mass-rearing technology of SEPNs is probably more rapidly attainable than for other envisioned green crab natural enemies.

The single biggest research need is to induce larval settlement in the laboratory. Until that is achieved, convincing safety tests cannot be designed.


Genetic and systematic studies of *Carcinus maenas*

Jonathan Geller and Mark Bagley, University of North Carolina at Wilmington

A. Sibling species and source of invasions

1. ca 400 bp of 16S mitochondrial DNA sequences from Atlantic and Mediterranean populations of *Carcinus maenas* show a 2.5% difference. This is a greater difference than two morphologically distinct species of *Callinectes*, for example, and is indicative of separate species status for *C. maenas* and *C. aestuarii*.

2. Crabs from each area of invasion were assigned to Atlantic or Mediterranean haplotypes by comparison of sequences or by presence/absence of a diagnostic Alu I restriction site. [In Table 1: Total sample size(numbers of crabs sequenced)].

All crabs in California, New England, and Tasmania carried the Atlantic haplotype; further sampling may reveal a low frequency of Mediterranean crabs. Populations in Japan and South Africa were mixed (we now have additional samples from Japan with pleopods for comparison of morphological and genetic data).

Table 1

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<th>Mediterranean Haplotype</th>
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<td></td>
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<tr>
<td>Texel Isl. and Den Helder, Neth</td>
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<tr>
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<td></td>
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<td>Capetown, South Africa</td>
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</tr>
<tr>
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</tr>
<tr>
<td>Tokyo Bay, (Tokyo University of Fisheries)</td>
<td>8(3)</td>
<td>7(5)</td>
</tr>
</tbody>
</table>

B. Population genetics

3. Continuing studies target nuclear-encoded loci. We have begun to isolate microsatellite loci for:

a) higher resolution identification of source regions;

b) studies of patterns of secondary spread in sites of invasion;

c) demographic analyses of invading populations;

d) comparison of levels of genetic diversity in invading populations with regard to the role of genetic bottlenecks in invasions.

e) hybridization patterns between Atlantic and Mediterranean crabs in the native contact zone (possibly southern Spain) and in Japan and South Africa.

We currently have isolated 3 microsatellite loci, and have 25 positive clones yet to be sequenced.
Nemertean Egg Predators as Potential Biocontrol Agents for Carcinus maenas

Armand Kuris, University of California, Santa Barbara and Visiting Scientist, Centre for Research on Introduced Marine Pests

To provide a preliminary evaluation of the potential for symbiotic egg predator nemertans (SEPNs) to act as biocontrol agents for introduced populations of the green crab, Carcinus maenas, I will introduce the concept of an SEPN and then briefly review knowledge of the systematics and life cycle of Carcinonemertes carinophila. Since there has been little work on the biology of this nemertean on the green crab, I will briefly discuss its likely efficacy, safety and recruitment in the general context of studies of other SEPNs. Research needs and opportunities will also be presented.

The reason SEPNs are not called parasites is that they eat host embryos, genetic individuals (although still brooded by their mother). They are “symbiotic” in the original sense of the term (and still so used in Europe) meaning “intimate” (literally, “living together”), since they live on the host and their biology is closely attuned to that of their host. Adult worms migrate to the egg mass of ovigerous hosts and feed on the embryos. They can be modeled as parasitic castrators having a partial effect on host reproductive output (Kuris & Lafferty 1992).

The SEPN of the green crab, Carcinonemertes carinophila, is the first described such worm, first being recorded from Italy over 150 years ago. Actually the host was not explicitly Carcinus maenas, but merely a “small crab”. Thus, if it was a green crab, it would apparently be C. estuarii, based on its Mediterranean origin. The name, Carcinonemertes carinophila, has been applied to all SEPNs from a wide selection of crabs from Europe, and as a separate subspecies, imminuta, from all host crabs in the Western Atlantic as well (Humes 1942). Based on comparisons among the now better studied Eastern Pacific SEPN fauna (Wickham & Kuris), it seems likely that host specificity of C. carinophila is greater than indicated by its current usage. But, how much so has not even been tentatively examined. While there is information on its distribution and abundance, there are no direct studies of its impact as an egg predator. The few correlative studies suggest that this worm, as well as other SEPNs from portunid hosts, do not cause much egg mortality (Shields 1992, Comely & Ansell 1989, Lipcius pers. comm., reviewed by Kuris 1993). None of these studies were actually on Carcinus maenas.

The life cycle of Carcinonemertes carinophila has not been well studied, being presumed similar to the subspecies on the blue crab, Callinectes sapidus of the eastern USA (Figure 2 from Kuris 1993). It seems likely that larval worms are only successful when they recruit to adult female hosts. The are seemingly lost at ecdysis on males and juvenile females. On adult females, the juvenile worms are encapsulated on the gills. They exsheath, migrate to the eggs of the host following host oviposition, feed, mature, and lay their own egg sacs among the egg mass of the host. The egg eggs hatch as planktonic larva. Their duration in the plankton and time to settlement competency are unknown. After eclosion of the host embryos, the worms return to the gill lamellae, regress, and await the next host reproductive period to recrudesce and breed again. Regressed adults can be distinguished from juveniles by their color.

The impact of other species of SEPNs can be considerable. Species on the Dungeness crab and the red king crab have been shown to cause massive brood losses and these worms are implicated in both the collapse and the persistent non-recovery of these fisheries (Wickham 1986, Kuris et al 1991). Little effect on host reproductive output may be expected at low worm intensities. If the host has both a strongly seasonal brooding period and a brief embryogenic period (a few weeks), there is not enough time for worms to consume many eggs, nor for worm populations to build up to high intensities (Kuris & Wickham 1987).

The host specificity of SEPNs is unknown and arguments can be marshalled to support any position along the continuum from very broad to rather narrow host specificity. In support of the former, is the official taxonomy of the worms: few species reported from many hosts. Also, in vitro studies show that worms can feed on the eggs of a wide variety of hosts (Roe 1984). However, in regions where more than one species has been described, cross-over infestations have not been noted. More critical examination of worm morphology and host biology continues to distinguish further species and reveal complex life cycles closely coordinated with host biology. In the most critical experiment to date, Wickham and
Molecular Discrimination of *Sacculina carcini*

Nicole Murphy and Louise Goggin, Centre for Research on Introduced Marine Pests, CSIRO Marine Research

The parasitic rhizocephalan *Sacculina carcini* is being investigated as a potential biological control for the introduced European green crab *Carcinus maenas* in Australia. *Sacculina carcini* infects eleven crab species from three brachyuran families (Høeg, 1995). This has led to speculation that there is more than one species described within *S. carcini*.

We are using molecular data from the ribosomal RNA to compare isolates of *S. carcini* from Sweden and the United Kingdom. This region of the genome contains rapidly-evolving sections: the internal transcribed spacer regions (ITS1 and ITS2) which have been used to resolve affinities of morphologically similar species and isolates of protists, trematodes and insects (Goggin & Newman, 1996).

Externae of the parasite *Sacculina carcini* were collected from the European green crab *Carcinus maenas* from Elløsefjørd, Sweden and Plymouth, U.K. and preserved in ethanol. DNA was extracted from *S. carcini* externae from five crabs from Elløsefjørd and seven crabs from Plymouth and from *S. carcini* larvae from Sweden. The DNA was also extracted from muscle tissue of a single unparasitised *C. maenas* from Falmouth, Tasmania, Australia.

DNA was extracted using phenol/chloroform and precipitated from aqueous solution with ethanol (Sambrook *et al*., 1989). A region of ribosomal RNA (rRNA) was amplified by polymerase chain reaction (PCR) from all isolates. The region comprised the 3' end of the small subunit (SSU), the internal transcribed spacer 1 (ITS1), 5.8S and ITS2. DNA was purified using Qiagen spin columns (Qiagen Inc., Chatsworth), following the protocol recommended by the manufacturer. PCR products were sequenced using dye terminator sequencing reactions (Perkin-Elmer Co., California) and run on an acrylamide gel on an automated sequencer (ABI Prism 377 DNA Sequencer).

Nucleotide sequence data from the ITS1 (approximately 236 bp), 5.8S (approximately 122 bp) and ITS2 (approximately 140 bp) were collected from two isolates (two clones) of *S. carcini* from externae from Sweden, three isolates (two clones) from externae from Plymouth and one isolate (one clone) from larvae from Sweden. There were no differences in nucleotide sequence data between larvae and externae of parasites from Sweden, nor between externae from Sweden and the U.K.

Our preliminary results suggest that the parasite in *Carcinus maenas* from Sweden and Plymouth belong to the same species: *Sacculina carcini*. We will collect data from the rRNA from *Sacculina granifera* and *Heterosaccus lunatus* from Australia to assess the variation in this region between other species of rhizocephalans. These data could then be used to develop a diagnostic probe for *Sacculina carcini* in infected crabs prior to the development of the externa.

References


4. A preliminary analysis of three nuclear RAPD (random amplification of polymorphic DNA) products, one of which occurs only in Mediterranean crabs and two of which occur only in Atlantic crabs, indicates that all 8 Japanese specimens have the Mediterranean RAPD banding pattern, while the mtDNA assay indicated that 5 of these 8 have the Atlantic haplotype. This suggests a history, either pre or post invasion, of mitochondrial introgression.

C. Phylogenetic analyses.

5. Preliminary phylogenetic analysis of mitochondrial 16S rDNA including brachyurans from several families Portunidae (three species of Callinectes), Xanthidae (two species of Menippe, Panopeus), and Grapsidae (Sesarma) shows no strong support for inclusion of Carcinus in Portunidae.

A. Results from both neighbor-joining and maximum parsimony analyses show Carcinus joining closer to Xanthidae than to Portunidae (ie, three species of Callinectes).

B. With both methods, bootstrapping analyses, a method to evaluate confidence in a tree topology, show Carcinus clustering with Callinectes, but at very low levels of confidence (slightly above 50%).

C. These two observations can be interpreted to indicate that the single most likely or parsimonious tree retrieved by these methods do not place Carcinus in the Portunidae, but a slight majority of bootstrap replicates do. Typically, a bootstrap value of 95% or higher is taken as strong support.

D. Conclusion: Carcinus is at best distant from swimming crabs such as Callinectes. This clearly has implications for the likelihood of host-switching by biocontrol parasites to native swimming crabs. However, the 16S rDNA gene may be too variable to accurately assess relationships among genera.

E. Prospects: we are furthering phylogenetic analysis with more genera of brachyurans and exploring other genetic loci.

| Atlantic | Mediterranean | TAGCATAATC ATTAGTTCTT TAAATTGAGAA CTGCAGCATG AAAGTCGCCA | [50] |
| Atlantic | Mediterranean | AGAGAAAATC TGCTTCCATT GTAAAATTA AATTGACCT TTAAGTGAAA | [100] |
| Atlantic | Mediterranean | AGGCTTAATT ACTCAGCGG GACGATAAGA CCCTATAAAA CTITTATATC | [150] |
| Atlantic | Mediterranean | GCAAATAC AGTTGAATTA AACGATTTA ACCTATGAGA AAAAAATATAT | [200] |
| Atlantic | Mediterranean | TTAGTGAGG CGACTGAGT ATAATTTATA GTAACCTGT AAAAGCAAGA | [250] |
| Atlantic | Mediterranean | CAAAATATAT TTGATTACCT TTATGTCCCT CTTTTAAAAG ATTAAAGAT | [300] |
| Atlantic | Mediterranean | TAATGTTACCT TAGGGAATAC AGGCTTAATT TTTCTAAGAG TCCATATCGA | [350] |
| Atlantic | Mediterranean | AGAAAAAGAT TGCGACCTCG ATGTGAATT AAAATATCTT TATAG | [395] |
Invasive history of *Carcinus maenas* on the North American east coast and potential impacts upon a commercial shellfish, the hardshell clam *Mercenaria mercenaria*

William C. Walton Smithsonian Environmental Research Center

The European green crab, *Carcinus maenas*, is an abundant, widely distributed invader along the North American east coast, where it threatens shellfisheries and resident estuarine species. Despite a research focus on this crab's role as a predator in rocky shore communities (e.g., Menge 1983), green crabs can be extraordinarily abundant in New England soft-bottom habitats, and the numerically dominant predator. Due to the importance of soft-bottom habitats to many commercial molluscan fisheries (in addition to their more recent valuation as sources of biodiversity), serious concerns have been raised since the 1950s about the impact of green crab predation on many species: the soft-shell clam *Mya arenaria* (Smith et al. 1955); the bay scallop *Argopecten irradians* (Morgan et al. 1980); and the hardshell clam *Mercenaria mercenaria* (Walne & Dean 1972).

In the boreal summer of 1996 I began a multi-year investigation of the impacts of the green crab upon the hardshell clam fishery and mariculture (as well as the native community more broadly) within the shallow coastal ponds & bays of Martha’s Vineyard, MA, USA off the coast of Cape Cod. To test the hypothesis that green crab predation significantly impacts the abundance and survival of hardshell clams, I consider three related categories of green crab impacts: A) the relationship between green crab abundance and clam yield & survivorship among ponds; B) the relative importance of green crabs as hardshell clam predators via natural history observations and cage experiments; and C) the mechanisms and dynamics of green crab predation upon hardshell clams.

To evaluate the impacts of the green crab, I will test for a negative correlation between crab abundance and clam abundance (field surveys) and clam survivorship (experimental outplanting of clams to determine relative predation pressure). To determine the relative importance of green crab predation, I will assess the abundance of alternate predators (surveys), determine the importance of clams in each predator’s diet (gut content analysis) and perform short-term field enclosures to determine the effect of predominant predators. Finally, I will analyse the mechanisms of green crab predation upon this clam in an effort to identify the variables that regulate this interaction: for example, prey patch density, prey size structure, temporal patterns, and substrate types.

The rationale for establishing these impacts is to provide both a sound basis for investment of management time and resources as well as identify potential strategies to reduce such impacts (e.g., timing of clam seed release) upon maricultured hardshell clams.

**References**


### Data summary 1974-1996

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<th>% Infested</th>
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Table 1. Results of trap captures from fifteen populations about the Irish coast.

![Map showing regions](image)

Figure 1. Distribution of regions about the Irish coast where summer studies of crab populations took place.

![Graph showing data](image)

Figure 2. Upper predation capability trend lines *Pecten maximus* by normal and parasitized shore crabs based on Minchin (1990).
may also reduce predation pressure. It would appear that although there are behavioural differences of parasitised crabs the overall effect of this remains unclear, but it is likely that apparently normal crabs will be more frequent in shallow water, an area where aquaculture is likely to be more prevalent. Not all crabs in a population become infested and because of this crabs will still be capable of reproducing and their larvae will continue to be dispersed and so continue to allow the expansion of shore crabs where conditions permit. The study of crab larval stages by Queiroga (1996) off the Portuguese coast indicates that dispersal may take place over 100km from source. With present knowledge the potential host range of S. carcini remains unknown and should be elucidated in advance of any releases in new environments.

References


Fig. 1: Proportional abundance of trapped predators through the 1996 summer within Martha's Vineyard, MA, embayments (Watson, unpub. data)
of the externa and is similar to the behaviour of egg bearing female shore crabs. The findings in this study are consistent with Lutzen’s (1984) observations, with a reduced prevalence of S. carcinii and female crabs in shallower water. In this study there are clear differences between day and night-time captures demonstrating infested crabs are indeed more active during darkness over either sediment or rocky substrata.

There does not appear to be a relationship between the numbers of crabs captured per trap and parasite prevalence. This may be due to the wide ranging environmental conditions over which the study took place or perhaps due to other unstudied factors such as infestation by other parasites. Infestations of S. carcinii according to Høeg & Lützen (1995) are classified as random, which will mean that parasite densities in a population and hydrographic features must be of some importance in maintaining a high level of prevalence in populations.

Minchin (1991) examined the affects of parasitism on shore crab predation capabilities. This affliction results in a lower predation abilities, presumably due to the ramifying tissues of S. carcinii through the tissues, including the chelae, of its host. In his study the upper capability of shore crabs to feed on a range of scallop (Pecten maximus) sizes was determined. When parasitised crabs were used only smaller scallops for a crab of the same size could be crushed (Fig. 2). Trends lines were also obtained for oysters and mussels. These were similar to the pattern obtained for scallops; but clams showed a different trend.

The overall influence of this parasite on its host may be difficult to determine. However, some indication of the effect on overall size distributions may be obtained by examining the size distributions of all crabs, from all regions, either with or without an externa and according to their sex. Mean size reductions for parasitised crabs for males (2.2mm) and females (0.8mm) were obtained, equivalent to a reduction of body weight of 14g for males and 4g for females. In addition, the reduction in predation capacity for crabs due to infestation is equivalent to a reduction in carapace width of -4.5mm for males and -3.5mm for females. When combined the overall equivalent reductions due to reduced population size and reduced feeding capacity are -6.7mm for males and -4.3mm for females. In following this argument the overall reduced capability of a population of infested crabs on molluscs will amount to at best a 15-25% reduced predation on some molluscs, depending on their rate of growth. This assumes that the difference in the upper capabilities for feeding by parasitised crabs over normal crabs relates to the time difference between these levels of capability. It also assumes that mortality is constant for each vulnerable oyster size class, which is however, unlikely. The idea does however, enable some quantification of the overall effect this parasite may have in reducing predation on some molluscan resources.

During various Irish studies two crab species were found with Sacculina sp. externa in the south Irish Sea. These were Liocarcinus marmoratus (Portunidae) (Minchin, unpublished) and Atelocyclus sp (Atelocyclusidae) (Minchin, 1977). It is not clear whether the parasites present represent different species or whether S. carcinii has a broad host range as suggested by Viellet (1941) and Choy (1990). The morphological features of this group may be insufficient to reliably distinguish species, the use of DNA techniques, as suggested by Høeg & Lütken (1995) may do much to reveal whether there is host specificity or not.

In this study it has been found that S. carcinii:

1. Was present in all shore crab populations studied.
2. The prevalence of this parasite varied within and between bays and can vary with time.
3. Female crabs with a parasite externa did not carry eggs.
4. There was a smaller mean size for parasitised crabs.
5. Crabs once parasitised have a reduced ability to feed on molluscs.
6. May alter its hosts behaviour resulting in different foraging patterns and depth distributions.
7. Sacculina carcinii may not exclusively parasite C. maenas.

The overall benefits of introducing S. carcinii to control shore crab populations outside of their natural range would appear to be small. The reduced crab predation capabilities may result in less predation pressure within ecosystems for those organisms that are able to attain sufficiently robust shells to withstand predation. Estimated reductions in crab biomass
Results

Crabs were sampled from depths of 0-18m depth within fifteen Irish coastal areas (Fig. 1). The majority were sampled within shallow bays at 0-6m depth. The abundance of crabs within traps varied between bays (Table 1). The greatest number of crabs captured was from the shallow Back Channel of Cork Harbour with 60.4 per trap day. This is followed by 58.2 per trap day from one trapping site within a shallow tidal embayment, in Kingstown Bay, partly protected by a loose stone wall. Aughinish Lagoon which is connected to the sea for short periods had 43 per trap day. Only four bays had less than 5 crabs per trap day. Within bays crabs abundance was highly variable, in Cork Harbour for example this ranged from 1.2 to 60.4 per trap day over a distance of 5km.

The size of crabs also varied between and within bays. The largest at 90.5mm carapace width was from Valentia Harbour and is the largest known European specimen. Normally male crabs could attain ca 80mm. In some populations crabs >70mm were not found. Crab modal sizes for Irish populations ranged from ca 40-70mm and could vary within a bay system. In Cork Harbour there was gradual increase between the more remote and sheltered area of 25-50mm to the central part of the Harbour with modal sizes of 55-70mm.

Crabs with a S. carcinus externa demonstrated great variability between and within sites and even over time. Different trapping areas were studied within four bays. The prevalence in Lough Hyne ranged from 100% at 7-9m to 67% at 0-1m in 1985 but in other years levels of infestation in the shallows were lower (22%). In Carlingford Lough prevalence ranged from 15-51%, Cork Harbour 0-21% and the two closely associated Streamstown and Kingstown bays, 4-44%. The number of externa found on a crab was normally one, rarely were two found (nineteen occasions) and only four crabs were found with three externa.

Infested crabs varied in frequency according to capture method. In Cork Harbour trapping at 18m (the greatest depth examined in this region of the Harbour) provided a prevalence of 15% for both sexes whereas dredging obtained almost 70%. There was also a variation between crab sex abundance. Unparasitised males were less frequent than females in the same region yet the numbers of parasitized males were similar to the numbers of parasitized females when captured by dredge. Traps fished at progressively greater depths at this same locality in Cork Harbour demonstrated a trend of fewer males, more females and increased parasitism of females. In Carlingford Lough trawled crabs had a higher prevalence (39-51%) when compared with shallower trapping stations inshore (15-21%).

In Lough Hyne in shallows (0.5-3m) crabs captured on a scæmum expanse had a higher prevalence and abundance of parasitism (p<0.1) for night captures. Night captures for crabs without an externa were more frequent than during daytime. Over areas of nearby rock parasitised crabs also appeared in traps at a higher prevalence during nighttime (12.1 per trap - night; 2.68 per trap - day) but at a lower abundance than those captured without an externa.

Discussion

In Irish waters parasitised crabs were found in all areas studied, the prevalence was highly variable and appeared to be greatest in partly enclosed bays and lowest in shallow estuaries and in bays near areas of coastal upwelling. Low prevalence may relate to the distribution of cirripede nauplii for some reason being less available in estuarine regions perhaps due to less favourable conditions for the cirripede larva or kentrogon stage. In Cork Harbour the levels of infestation were 0-5% in estuarine areas (12 trapping sites) when compared with the more marine regions within the bay,10-4% (4 trapping sites). Levels were also low in the shallow Aughinish Lagoon, an area of <1ha which may be subject to abrupt changes in salinity. Larval stages may become well dispersed in regions where there is a replacement of ‘uncontaminated’ larval cirripede water. On the south-west Irish coast there is an area of upwelling which can result in exchanges of bay water from time to time (Edwards et al, 1996) these exchanges are also verified by studies on the biological effects of diffusion of organotins (Minchin & Minchin, 1997) (such approaches could be perhaps useful as a general predictive tracer from bay areas where crabs become established). Such areas are likely to become purged of cirripode larval stages and so result in the relatively low frequency of S. carcinus in shore crab populations in Valentia Harbour and Derrynane. In partly enclosed bays topographic features and concentrating vectors of the cirripede larval stages may result in increases of larval densities resulting in the higher levels of prevalence observed.

Crabs at depth have a greater level of infestation than those in shallow water. The parasite does influence crab behaviour (Høeg & Lützen, 1995). The movement to deeper water according to Lützen (1984) corresponds to the sexual maturation
The Impact of the Introduced European Green Crab on Benthic Invertebrates in Bodega Harbor, CA

Edwin Grosholz, Department of Zoology, University of New Hampshire

Introduced or exotic species represent a serious threat to the integrity of coastal marine systems, however, the magnitude of this threat is rarely quantified. In this study, we have quantified the impact of predation by the exotic European green crab, Carcinus maenas, on more than twenty species on benthic invertebrates in Bodega Harbor, CA. This has involved documenting the changes in the abundance of green crabs since their introduction in 1993, measuring the rapid declines of particular target species, conducting laboratory and field experiments to certify that green crabs are the cause of these declines, and measuring the indirect effects of green crab predation on other invertebrate taxa by means of path analysis.

Increasing abundance of Carcinus maenas in Bodega Harbor.
Several methods were employed to estimate both changes in the relative abundance of the Carcinus maenas population as well as the actual population size in Bodega Harbor. From 1983-1989, pitfall traps were used annually between late May and early June to estimate the relative abundances of newly recruited crabs in Bodega Harbor. At each of four tidal heights, we placed three, five-gallon pitfall traps at 50 m intervals and collected crabs daily for three days. No green crabs were ever reported during this period. From 1993-1996, these methods were employed similarly as from 1983-1989, but traps were also deployed at least quarterly. These data show that the number of green crabs increased exponentially from 1993-1996. Estimates of the actual density of green crabs were made using two methods. At least three times each year, counts of actively foraging crabs were made at high tide along the same four transects used for the pitfall traps (above). Along each transect, all crabs seen along a 50 m x 1 m area were counted by two persons using snorkel equipment. We found no differences in numbers of foraging green crabs in daytime vs. nighttime censuses. These data produce estimates of foraging crabs densities, but are likely minimum estimates of true densities because some crabs are missed. Estimates for each show a rapidly growing crab population, and suggest that present densities are in the range of 0.04-0.4 crabs per m².

We used several marking methods, together with mark-recapture estimation procedures, to estimate the size of the green crab population in Bodega Harbor. The first method involved subcuticular injection of pit tags, which are small (11 mm) glass-coated wires with unique bar-coded numbers that when used with a pit tag "reader," allow the nondestructive identification of individual crabs. These tags were injected into dorsal sinuses and laboratory trials demonstrated that these tags remained in place for one to two molts. We marked more than 250 crabs in 1994 at one site with relatively high densities and where crabs remained active during the winter. Although we were able to gather essential data on growth rates and molt increments from these marked crabs, we did not get a sufficiently high recapture rate with this method to estimate population sizes effectively.

We did get sufficient recapture rates using a second method involving subcuticular injection of micro-wire tags. These are very small (2-3 mm) uncoated tags allow large numbers of crabs to be marked more rapidly and inexpensively than with pit tags. However, this method does not allow individuals to be distinguished, but rather crabs are marked as a cohort. We marked approximately 1000 crabs collected from nine sites around Bodega Harbor, in which crabs were also given site-specific markings in addition to the wire-tags by clipping combinations of anterolateral spines. This additional site-specific information allowed us to estimate dispersal between the nine marking sites to further refine our population estimate.

These results of these estimation techniques suggest the actual population size of the green crabs ranges from 12,000 to 20,000.

Declining abundances of benthic invertebrates: Hemigrapsus oregonensis.

Data on the relative abundance of H. oregonensis extend for 13 years beginning in 1983. Estimates of the relative abundance of H. oregonensis are based on data from pitfall traps that were used to census up to six species of crabs foraging in this habitat during this period. At each of four tidal heights adjacent to the BML reserve, we placed three, 20 L. buckets along a 100 m transect and collected all crabs daily for three days. We found that during the period from 1985 through 1993, abundances are clearly variable but show no evidence of significant declines, with the exception of large declines in 1985-86 due to the Dungeness crab recruitment event. However, from 1994 to 1996, Hemigrapsus oregonensis
The influence of the parasitic cirripede *Sacculina carcini* on its brachyuran host *Carcinus maenas* within its home range.

Dan Minchin, The Marine Institute, Fisheries Research Centre Dublin

Introduction

Parasitic cirripedes infest a wide range of decapods and one genus *Sacculina* is principally associated with brachyuran crabs (Høeg & Lützen, 1995). *Sacculina carcini* is a common parasite of the shore crab *Carcinus maenas* in European waters. Earlier studies have demonstrated that young crabs first become infected by female nauplii whilst less than 30mm carapace width (Lützen, 1984). Those infested develop an *interna* over a number of moults. Eventually the *interna* moves through the abdominal wall to become an *externa*, the brood sac. The *externa* develops an open pore through which the male cirripede larva enters attaches to the brood chamber wall and soon after fertilises the female. The *externa* changes colour as it becomes older and may drop off after about a year to leave behind a black scar on the crabs abdomen. The parasite during its stage of infestation is capable of feminising infected male crabs, and eggs are not carried by infested females.

Shore crabs are significant predators of sessile organisms, in particular molluscs. The presence of shore crabs in some areas can result in significantly reduced profit margins where there are shellfish layings, and because these crabs may be common to several metres in depth their overall impact is of some consequence to naturally recruiting shellfish populations. The management of shore crabs within their home range has always been a consideration. In Ireland the most effective means of management has been the physical exclusion of crabs by overlaying molluscan stock with netting or by holding molluscs within frames or bags held off the sea floor.

This study of shore crabs is based on crab populations from different Irish coastal areas over a twenty year period. The review of the data has been prompted by the increasing interest in the use of *S. carcini* as a possible means for the control of green crab populations that have become established in areas beyond their natural range. The study of the influence of this parasite on its host within its home range may provide useful information on the effectiveness of using this species in managing shore crabs elsewhere.

Methods

In this account only the external features of the parasite have been considered. These include: virgin to mature *externa* as described by Lützen (1984) and crabs with *externa* scars. Scarred crabs are those that have lost the external features of the parasite but retain a dark plug indicative of the presence of a former *Sacculina carcini externa*. No other potential parasites of the shore crab were searched for. All crabs were sampled during the period 1974 to 1996 during June to September so as to reduce the influence of known seasonal frequency of the appearance of *externa* (Heath, 1971). In all a little over 8,000 crabs were sampled from fifteen Irish populations.

Black plastic barrel shaped traps 45cm in length and 31cm diameter with two slit funnel entrances of 55mm diameter were deployed to capture shore crabs. These traps are generally used by fishermen for the capture of the prawn, *Palaemon serratus*. Traps were set in trots of five to ten and spaced 5m apart, each was baited with mussels and replaced each day. Traps were set for a twenty-four hour period and the fishing effort recorded in trap days. All crabs were removed, sexed and measured for carapace width and those with a *S. carcini externa* were recorded separately.

Crabs were also trapped in 1986 during July over eight hour periods representing periods of night and daylight. Traps were placed over a sandy mud with shells for periods of either 0600-1400hrs, 1400-2200hrs and 2200-0600hrs BST. Cumulative numbers over similar periods were obtained for a rocky substrate nearby.

The relative frequency of infested crabs was obtained from dredge samples in an area of Cork Harbour that had previously been fished using traps. A scallop dredge with a tooth spacing of 11cm and mesh bar size of 6cm was used during daytime. In Carlingford Lough daytime trawled samples using a standard otter trawl were made in deeper water (8-14m) to the areas that were trapped (2-5m).
Settlement of *Sacculina carcini* larvae on different Swedish species, including *Carcinus maenas* of different moult stages.
showed a dramatic and significant tenfold decrease in abundance (Wilcoxon, $S_{(12,12)}=222.0$, $p<0.001$). During this time, mean numbers of *H. oregonensis* per trap declined to a mean level of $<1.0$ per trap in 1996 compared to a mean of 23 per trap in 1993. These declines show a significant negative association with the increasing abundances of green crabs (Spearman, $p<0.0005$).

**Declining abundances of benthic invertebrates: *Nutricula confusa* and *N. tantilla*.**

Estimates of the abundances of more than twenty benthic invertebrate taxa have been made annually for thirteen years from 1983-1996 years (Ruiz 1987, Grosholz and Ruiz, unpub. data). Estimates of total abundance are made directly from six replicate cores (10 cm dia. x 5 cm) taken along each of the same four tidal height transects as the pitfall samples and sieved through 1.0 and 0.5 mm sieves. These counts include estimates for bivalves molluscs, pericardian crustaceans, polychaetes, phoronsids, and others. Data have been analyzed completely for *Nutricula* spp. (pooled) from 1983 to 1993. From 1994 to 1996, both species of *Nutricula* showed significant tenfold declines at all four tidal heights relative to densities typical of the ten years preceding the invasion (Wilcoxon, $S_{(6,6)}=57.0$, $p<0.01$). These declines show a significant negative association with the increasing abundances of green crabs (Spearman, $p>0.01$). Significant, but short-term, declines were also witnessed in 1985-1986 due to the Dungeness crab recruitment event in 1985.

**Evidence supporting green crabs as the cause of invertebrate declines.**

**Laboratory experiments and analysis.**

Data were gathered to document the gut contents of green crabs by collecting actively foraging crabs with snorkeling methods at high tide. Crabs were collected crabs by hand, and placed on immediately (< 30 seconds) on ice until they could be fixed in 10% formalin (within one hour). These data are consistent with data from feeding experiments and analysis of changes in populations of prey species years (Grosholz and Ruiz 1995, 1996). Gut contents analysis confirmed the abundance of *Nutricula tantilla* and *N. confusa* shell fragments (>77% of feeding crabs). To estimate the potential consumption rate of crabs in the field, we performed feeding tests in the lab to estimate potential rates of consumption by green crabs. Individual crabs from six size classes ranging from 15 mm to 40 mm were enclosed in small (1 L.) containers with up to 75 intermediate (3-4 mm) individuals of *Nutricula* spp. Crabs were collected from the field and starved for 48 hours before experiments were begun and allowed to feed upon clams for either 12 or 24 hours. We found that the largest juveniles (40 mm) were able to consume up to 150 clams in a twelve hour period. Based on conservative estimates of consumption rates (100 clams per day), densities (0.1 crab/m$^2$), and non-conservative estimates of clam density (5,000/m$^2$), we estimate that the length of time needed for green crabs to consume the *Nutricula* spp. in Bodega Harbor is 500 days or 1.36 years.

To determine the relative feeding preferences of green crabs for *Hemigrapsus oregonensis*, we conducted experiments in which adult green crabs (maximum size 92 mm) were enclosed with equally sized juvenile green crabs (25 mm) and adult *H. oregonensis* (maximum size 25-30 mm). We found that rates of predation on native shore crabs (89%) was significantly higher than cannibalism rates of adult green crabs upon juvenile conspecifics (22%).

**Field enclosure/exclusion experiments.**

Large scale enclosure and enclosure experiments were conducted between May 1994 and May 1996. The design included six replicates of seven treatments arranged in six blocks. Each of the forty-two experimental areas measured 3 m x 3 m and was separated from other areas in a block by 3 m. Blocks were separated by 3-5 m. These experiments did not adequately measure the impact of green crabs because of the unexpected efficiency of predation by juvenile green crabs. The cage design was designed to exclude or include adult *Carcinus maenas*, and for this purpose worked as expected. However, the cages were not designed to exclude juvenile *C. maenas* and the results were not conclusive. The appropriate natural history data obviously could not be gathered in advance to anticipate this difficulty. This experiment will be repeated with an improved cage design and active removal of recruiting juvenile green crabs.

**Indirect effects of green crab predation.**

Data on the changing abundances of the more than twenty species taken from benthic cores (methods described above) allow the detection of indirect effects of green crab predation. In addition to Nutricula spp. mentioned above, the list of invertebrates includes seven species of bivalve molluscs (*Nutricula tantilla, N. confusa, Gemma gemma, Macoma nasuta, Macoma secta, Macoma balthica, Prototheca sp.*), five crustacean taxa including tanaids (*Leptocheilia dubia*), cumaceans
(Cumella vulgaris), amphipods (Eohaustorius sp., Paraphoxus sp., Corophium sp.), nine polychaete taxa (Lumbrineris sp., Exogene sp., Nephtys sp., Polydora sp., Orbinia sp., Ophelia sp., Capitella sp., Nereis sp., Eteone sp., Phyllococidae, Maldanidae, Opheliidae), Oligochaeta, Phoronida (Phoronopsis viridis), and occasional errant taxa such as harpacticoid copepods, and gastropod molluscs.

A preliminary investigation of the relative strength of direct and indirect effects has been conducted with path analysis in which these invertebrate taxa are grouped by phyla to determine the broadest patterns of response. The results indicate that the direct effects of green crab predation on molluscs and crustaceans are negative and significant. By contrast, there are positive and significant indirect effects on polychaetes. The mechanisms underlying these positive indirect effects will be addressed experimentally.

References


Settlement of *Sacculina carcini* on newly moulted and intermoult *Carcinus maenas*
Laboratory experiment on settlement on Australian species, with record of later moulting and death of the crabs.
Interactions between crab and shorebird populations in western North America: Patterns and predictions.

Gregory M. Ruiz, Smithsonian Environmental Research Center
Edwin D. Grosholz, Zoology Dept., University of New Hampshire

Bays and estuaries of western North America support relatively large winter populations of shorebirds (sandpipers and plovers), which rely almost exclusively on intertidal benthic invertebrates as their food resource. Most of these birds migrate to the north or interior of North America during the spring (April-May), remaining for the summer breeding season (May-July), and return to coastal marine and freshwater habitats for fall and winter (September-March). Although specific prey and habitat preferences in winter vary among species, most birds feed primarily on near-surface dwelling prey in soft-sediments and exhibit strong site-fidelity, returning year after year to the same bay or estuary. Thus, the abundance and availability of infaunal invertebrate populations can play a significant role in the condition, breeding performance, and survival of individual birds as well as the dynamics of bird populations (e.g., Goss-Custard 1981).

In these same bays and estuaries, some species of decapod crustaceans exhibit a high degree of overlap in prey selection and habitat utilization with shorebirds. In particular, the native dungeness crab Cancer magister and the European green crab Carcinus maenas both occur abundantly at sandflats and mudflats in the intertidal zone, where they feed intensively on the same species of infaunal invertebrates as shorebirds. The dungeness crab megalopae recruit primarily to bays and estuaries from Alaska to California in the late spring (April-June), utilizing shallow sandflats as a nursery habitat for up to a year, and move offshore into deeper water with age. The magnitude of recruitment for these crabs is highly variable both temporally (among years) and spatially (among bays). The green crab is a recent arrival (~1989) to western North America, where it is presently restricted to California, and recruits to the same habitats during the same season as the dungeness crab. Recruitment and postlarval population size are increasing through time at some sites, as the invasive population is still in its growth phase. However, green crabs do not migrate offshore with age but remain in the shallow subtidal and intertidal zone of these bays and estuaries.

Both species of crabs have strong effects on invertebrate prey populations which can impact shorebird populations through food-based competition. The best example of this comes from intensive study of invertebrate and bird populations in the harbor of Bodega Bay, California. Following a year of unusually high dungeness crab recruitment, the abundance of many common invertebrate species exhibited rapid and significant declines, approaching local extinction in some cases. Most spectacular was the decline of near-surface dwelling clams (Transmerella spp.), for which densities changed from 104-105 clams/m² to <1 clam/m² within a month and remained low for over two years. These invertebrates, and especially the clams, were the primary food resource for many of the 6,000 to 8,000 shorebirds that overwinter at Bodega Bay harbor. Following this decline in prey populations, the total number of shorebirds declined to the lowest year on record, and some species exhibited other signs of food-limitation: poor condition (weight and/or lipid stores), delayed molt, and shifts in age structure. Importantly, these patterns were not a regional phenomenon, as other bays in which dungeness crabs were rare did not exhibit similar changes (Ruiz 1987).

Coincident with the arrival and gradual increase of green crabs in Bodega Bay harbor, we have documented declines in the abundance of some invertebrate populations, including the same clam species that was impacted by dungeness crabs. Although the decline has been gradual, densities are now significantly lower than observed for years, excluding the dungeness crab event (see Grosholz, this volume). A numerical decline in shorebird abundance has not yet occurred. Compared to the dungeness crab event, changes to invertebrate prey populations following the green crab arrival have been gradual and much less severe. We hypothesize that the food resources have remained above some critical threshold for a numerical response, and that the gradual decline has provided more time for possible behavioral adjustments by birds to low food resources.

Although the green crab invasion has not yet had a measurable impact on shorebird populations in western North America, we predict this invader will continue to increase in abundance and distribution, causing both local and regional changes in shorebird populations. On a local scale, we predict further food resource decline that will result in both numerical and functional responses by birds. However, the predicted effects of green crabs on invertebrate prey differs in two significant
ways from that of dungeness crabs. First, the effect of green crabs will be persistent, instead of an episodic event like the
dungeness crab recruitment. Second, the impact of green crabs will become a regional instead of local scale phenomenon,
as the crab extends its range along the northwest coast to Alaska. The result of these two differences expands the scope of
impacts on food resources, limiting the opportunities for birds to exploit alternate sites within a region or for local food
resources to recover. Thus, we predict broadscale regional changes in the abundance, demography, and behavior of
shorebirds as the green crab invasion progresses.

References


University of California, Berkeley, CA, USA.
No. of settled Sacculina larvae/individual of Australian crabs, from the laboratory experiment.
Prevalence of *Sacculina carcini* on *Carcinus maenas* at some localities close to Kristineberg Marine Research station

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Session 1. Ecology and Impacts

Part 2. Australia
The invasive history, distribution and abundance of *C. maenas* in Australia.

Craig Proctor and Ron Thresher, Centre for Research on Introduced Marine Pests, CSIRO Marine Research

The first record of *C. maenas* in Australian waters is from Port Phillip Bay, Victoria, in 1902 (Fulton and Grant) and, given the lively shipping trade between ports in Europe and Port Phillip Bay in the 19th century, it is likely this is the point of first introduction. *C. maenas* is now an accepted part of the fauna in the bay and other areas of Victoria.

*C. maenas* were first reported in South Australia in 1976 (Zeidler 1978) and, at the time, appeared confined to isolated populations in the Outer Harbour-Port River region and at West Lakes. Since then additional populations have been found at Hallett Cove (Rosenzweig 1984), and in the Coorong (Zeidler, 1984).

A mature male *C. maenas* was found in the Swan River estuary in Western Australia in 1965, however, little information is available about its current distribution in that state. Trapping by CRIMP in two WA ports (Albany and Bunbury) resulted in no *C. maenas* being caught in either port.

*C. maenas* occur in southern NSW, hypothesised to be an extension of the Victorian distribution (Zeidler 1978). During 1996, CRIMP found *C. maenas* to be abundant in the Eden region. It is not known how far the species range extends northwards along the NSW coast.

The first report of *C. maenas* in Tasmanian waters appeared in 1993 (Gardner et al.), after several specimens were collected in Georges Bay. Between January and April 1996, CRIMP conducted a trapping survey to establish the distribution of *C. maenas* around Tasmania. The results of this initial survey showed *C. maenas* are abundant in estuaries and embayments along the north and east coasts, but absent from the west coast. It is assumed *C. maenas* are also absent from the south coast. At the completion of this first survey, the southern extent of the species distribution along the south east coast was thought to be Blackman Bay (due east of Hobart). However, in July 1996, a recreational fisherman found a juvenile *C. maenas* in Lindisfarne Bay in the Derwent estuary, and in September 1996, 2 mature *C. maenas* were found by oyster farmers in Great Bay on Bruni Island. However, from trap surveys done during the summer of 1996-1997, no embayments to the south of Blackman Bay, it appears this bay still marks the southern front of the east coast distribution.

The time of introduction of *C. maenas* into Tasmanian waters remains uncertain, although the observations and opinions of oyster farmers, marine naturalists, and long-term residents of areas where *C. maenas* is abundant lead us to believe the species has only been in the state for 5 to 10 years. The mode of introduction is also uncertain. The most likely vector of introduction is transport of larvae via ship ballast water or bilge water of smaller vessels, or the inadvertent transport of juvenile or mature crabs across Bass Strait. *C. maenas* do occur on at least some of the smaller islands (e.g. Flinders Is.) to the north of mainland Tasmania. Advection of larvae from mainland Australia to these islands and then, with time, advection of larvae from these satellite populations to the north and NE coasts of Tasmania cannot be discounted.

Trapping surveys during the recent summer have formed an integral part of the assessment of the occurrence and abundance of *C. maenas*. In addition to regular trapping at key sites, baseline trapping has been done at many other locations along the NE and SE coasts of Tasmania. Some sites in NE Tasmania (e.g. Georges Bay and Henderson Lagoon) have consistently yielded catches of 200-300 crabs per trap. The highest single-trap-catch to date was 428, taken from Lords Point in Georges Bay. The maximum size of *C. maenas* in Tasmanian waters surpasses that of most, if not all, other native and introduced populations of *C. maenas* worldwide, based on published figures. Some sites in Georges Bay consistently yield crabs of 80-90 mm carapace width or larger. The largest *C. maenas* caught was a male of 96 mm carapace width.
depurator, Macropodia sp., and Palaemon adspersus) and (iv) tested the preference of S. carcini cyprid against newly molted Carcinus maenas compared to internovut C. maenas with hard exoskeletons. As background information we (v) investigated the normal prevalence of S. carcini at two localities close to the Kristineberg Marine Research station. We finally ran a brief test of larval development time at different temperatures.

Preliminary results: In the flume experiment (i), Sacculina carcini cyprids settled on all of the Australian species, except Nectocarcinus. We presently keep the crabs from this experiment in captivity for long term observation and so far almost all of the crabs of all tested species have molted, irrespectively of whether they sustained settlement of S. carcini or not. Three exceptions are Charybdis callianassa that did not cope with the Scandinavian climate in the summer and all Portunus pelagicus which did not survive the water temperature in the winter. Besides these two species, only one other crab died, viz., one Australian Carcinus maenas that perished while trying to molt. In the field experiment (ii) two out of four Australian Carcinus maenas and two out of four Paragropsus gaimardi carried settled S. carcini larvae after exposure, but none of the other species. In the test with potential Swedish host species (iii) we only found Sacculina on Carcinus maenas. When we exposed newly molted Carcinus to Sacculina larvae (iv) we found significantly more settled larvae on them compared to the control crabs with older exoskeleton. Prevalence (including scarred and feminized crabs) of Sacculina carcini (v) in the two localities close to Kristineberg was 17.4 % and 29.5 %, which is very high compared to other data from the Swedish coast.

We conclude that Sacculina carcini, if introduced, will most likely infest populations of Australian Carcinus maenas. Attempts to employ Sacculina carcini as a biological control agent on C. maenas must await further trials and take into account a number of facts including: The longevity and ecological requirements of the parasite larvae. The specificity of the parasite in larval settlement and subsequent development, which should be further elucidated since native Australian crabs sustained settlement of larvae. The life cycle requires two separate settlement events of cyprids: female infection and acquisition of males, which provides avenues for managing a parasite population under control in the field. The effect of the parasite upon the reproduction of the host population.

References


The parasitic castrator *Sacculina carcini* as a possible biological control agent of *Carcinus maenas*: background and results of preliminary work

Jens Hoeg (Univ. Copenhagen), Malin Werner (Univ. Goteborg), and Henrik Glenner (Univ. Copenhagen)

*Sacculina carcini* (Cirripedia: Rhizocephala: Sacculinidae) is a common parasite of *Carcinus maenas*. Most aspects of the parasite’s life cycle are well known (Høeg & Lützen, 1995) and it can now be cultured in the laboratory. *S. carcini* has separate sexes (gonochorism). The actual parasite, situated in the abdominal brood chamber of the host, is female and releases a series of broods of nauplii. The nauplii develop lecithotrophically and moult into cypris larvae after about 5-6 days (at 15°C). The cyprids become morphologically competent to settle after another 3-4 days in the plankton. Male and female cyprids differ in size (males larger) and morphology (of antennular sense organs), whence sex frequency in broods can be easily assessed using a light microscope, a precondition to managing a laboratory culture.

Female cyprids settle on the exoskeleton of a host crab at the base of a plumose hair. Many cyprids attach on the limbs but attachment can occur virtually anywhere on the body (Høeg, 1984). The cyprid now metamorphoses into a kenotrogon, which penetrates the exoskeleton of the crab with a hollow stylet and inject the potential parasite into the hemocoelic fluid. There follows an endoparasitic phase where the parasite develop a ramifying root system. After an internal phase of a few months to 3 years (Lützen, 1984) the parasite emerge with a virginal reproductive body (externa) situated under the abdomen of the host. Its is a precondition to continued growth and development of the parasite that male cyprids settle on the externa, where they metamorphose into trichogons, and become implanted as dwarf males in the paired receptacles of the female externa. The males remain with the female externa for the duration of the latter’s life time and fertilize all its broods. Externa failing to receive males cannot mature and eventually perish.

*S. carcini* has severe and lasting effects on the growth, morphology, physiology, and behaviour of its host crab. It arrests the moult cycle of the host which in consequence will suffer from increasing amounts of fouling organism. The parasite castrate both male and female crabs. Situated in the abdominal brood chamber the externa furthermore manipulates the hosts of both sexes into accepting the parasite as its own brood: The externa is a morphological obstruction for the crabs to breed; infected males often becomes "feminized" in their secondary sexual characters, e.g. losing male characteristics and by acquiring a broader female-like abdomen; the behaviour of the crabs change so that both male and female crabs act as egg-bearing females, ventilating the "eggs" and migrate to deeper water. It is even possible that the host crab assist the virginal parasite in the vital step of acquiring male cyprids.

While rhizocephalan cirripedes usually infest more than a single host species, specificity is especially lax in *Sacculina carcini*. In Europe it occurs not only on *Carcinus maenas*, but also on *Carcinus aestuarius*, *Liocarcinus depurator* and some other Portunidae (Høeg & Lützen, 1985). It is even known from *Perimela denticulata* (Perimelidae), and there is no evidence that *S. carcini* comprise a complex of sibling species. The mechanism behind host specificity remains unknown. It might depend on larval choice at settlement, survival of the parasite on and inside the host (host grooming, parasite infection, internal development), or survival of the infected host. In another work studied rhizocephalan-crab system the cyprids actually settle also on closely related non-hosts.

We tested and are testing species specificity of *Sacculina carcini* by attempting settlement of cyprids on Australian and Scandinavian portunids and observing whether eventually settled larve developed an internal and external parasite? (i) We exposed the following crab species to settlement in the laboratory: *Portunus pelagicus*, *Paragrapsus gaimardii*, *Ovalipes australiensis*, *Charybdis callanassa* (1 specimen), *Nectocarcinus sp.* (1 specimen), and Australian *Carcinus maenas*, using Scandinavian *Carcinus maenas* as controls. (ii) We ran a field test (7 weeks) against natural densities of *S. carcini* cyprids using *Paragrapsus gaimardii*, *Ovalipes australiensis*, Australian *Carcinus maenas* and Scandinavian *Carcinus maenas*. In the laboratory trials we isolated the test crabs in individual small cages and placed them in a flume tank with *S. carcini* cyprids for 2-3 days. In the field test we packaged four individuals per species all in separate cages and put them in four larger cages suspended from a bridge (no tide on the Swedish west coast), checking twice a week for settled cyprids. (iii) We also exposed *S. carcini* cyprids to other Swedish decapod species (both natural hosts and non-hosts), viz., *Liocarcinus*
References


Figure 1. Results of a trapping survey for *Carcinus maenas* done in Jan - March 1996.

* = Confirmed findings of *C. maenas* at locations south of Blackman Bay; 1 juvenile in Derwent Estuary (July 1996), and 2 adults in Great Bay, South Bruny Is. (Sept. 1996).
References


8. Determine release strategy
9. Pilot release
10. Assess efficacy
11. Implementation

Some of the most important differences are requirements for efficacy, the different nature of recruitment, the availability and choice of control agents, knowledge of natural history, and, most critically, the safety (host specificity) of a potential control agent.

For natural enemies of insect pests, there has been traditionally little concern for the safety of the agent against other insects, even native species. Hence, the control agents can include relatively broad specificity parasitoids and some predators. Cultural values determine which species are desired. Few, if any, cultures place protection of herbivorous insects, such as scale, aphids and whitefly, on their environmental protection agenda. In the marine world, there are two important components to safety. One is common to probably all cultures; the other operates in at least some cultures. To use green crabs as an example, there is widespread concern that an introduced agent not impact commercially fished crabs. In agriculture, the species to be protected are plants; the pest is an insect; so insect natural enemies have virtually no potential to adversely affect desired species. In the marine world, it will often be the case that other desired species are taxonomically close to the pest, and thus potentially threatened by a pest natural enemy. Beyond economically important species, we also value our non-economic native marine organisms such as shore crabs. Most people would consider a biocontrol agent that spread to, and significantly impacted, a shore crab to have had an adverse and deleterious outcome. And, I hasten to add, so would I.

We may assume that neither Australia nor the USA, nor perhaps other nations, would approve the introduction of a potential control agent without careful review. Thus, safety tests, essentially assays of host specificity, must be designed with care to achieve a highly reliable prediction of the inability of a tested biocontrol agent to successfully infect a non-targeted native species. Firstly, it must be clear from the outset that "successfully infect" means ability to locate, infect, develop and successfully reproduce in a host. An agent that can only engage the host is still safe if it fails to completely develop. Secondly, the specificity assay must be statistically powerful. Reliability can be improved by raising the alpha level from the usual P<0.05 to, say, P<0.001. Experimental design can also generate power by using a highly sensitive probe to infect the pest (a low dosage exposure to the control agent) and compare that to a high dosage exposure of the native species to the control agent. (Other cells in the host species by dosage matrix could be included for symmetry and detection of interactions.) The objective of safety tests is the recognition of the potential susceptibility of the native species to the putative agent, and not the mere understanding of host specificity in its broad context. Hence, thirdly, to do this sort of work, a logistically reliable experimental procedure must be developed. This means that control green crabs must be readily infectable in large numbers over a long time periods. At present, it is generally considered that, for example, the rhizocephalan, Sacculina carcini, preferentially infects small, post-molt hosts and its infective cyprids are only seasonally available. In order to open the experimental window, it will be necessary to determine the maximum range of sizes and molt stages that are readily infectable. Then, the period of cyprid larval availability should be maximized by examining the roles of temperature, photoperiod and host feeding on S. carcini reproductive output and periodicity. Fourthly, to guard against false negatives, it will be most desirable to expose highly sensitive hosts (e.g., small, post-molt, native crabs). Finally, high standards should be set and clearly defined, so that, in the real world, a decline from these criteria can be readily recognized and evaluated.

The key biological issues that will determine whether biological control will be a theoretical option are its efficacy, the nature of marine recruitment and its host specificity for native non-target relatives of the pest. To evaluate safety we need to develop a powerful host specificity assay. For some suggested control agents, we need to complete their life cycles and reduce them to efficient laboratory research systems. To understand the consequences of a release of a control agent, we need to comprehend the recruitment scales of both host and control agent. Empirical studies of larval movement and recruitment dynamics should be coupled with host-parasite recruitment dynamics models (Kuris & Lafferty 1992). To reveal the needed level of control efficacy, we will gain by knowledge of the processes that limit the abundance of the control agent. Lastly, we will need to develop mass-rearing strategies to enable the control agent to become established in the marine environment (some of this technology will be acquired in the development of effective safety tests).
The European Shore Crab (Carcinus maenas) in South Australian waters

Wolfgang Zeidler, South Australian Museum

In 1978 I reported on the occurrence of C. maenas in Australian waters (Zeidler 1978) and recorded that the crab was now well established in South Australia. The first specimens were collected in 1976 from the Outer Harbour—Port River—West Lakes area. Although the species was relatively abundant it seemed to be restricted in its distribution suggesting a recent introduction. This was confirmed by subsequent surveys of the shallow water fauna from the Victoria border to just west of Ceduna.

Carcinus maenas does not seem to have spread beyond the Port River—Outer Harbour area except for two isolated records (Rosenzweig 1984, Zeidler 1988). Both of these records may represent strays rather than established populations. Surveys of the metropolitan coast are currently underway to determine the presence and abundance of the crab. There are no recent records of C. maenas outside the metropolitan area, but potential habitats like harbours, bays and aquaculture farms have not been surveyed for about five years.

In South Australia the crab seems to be restricted to relatively degraded areas. The record of a few specimens from Hallet Cove (Rosenzweig 1984) may have been due to a separate introduction via the nearby oil refinery and terminal at Port Stanvac. It is difficult to assess the impact of C. maenas on the native fauna as the natural habitat was degraded before its introduction. In South Australia, anyway, it would seem that the introduction of C. maenas is of little consequence providing it does not spread from its present habitat.

Casual observation suggests that the population of C. maenas in the Outer Harbour—Port River area has a tenuous hold as numbers seem to fluctuate gently. One year I could not find any specimens! A more detailed study of this population might be worthwhile to determine if factors exist that are limiting numbers.

It is interesting to note that C. maenas has become established in degraded habitats and seems to be restricted to these areas. The message is, keep the environment as pristine as possible and nasty introductions may be avoided.

References


Editor's Note: Discussion with students and staff at Flinders University (Adelaide, South Australia), after the workshop, indicated that they had carried out sub-tidal surveys in sand/mud/rock habitat around Adelaide. Their results, not yet published, indicate that C. maenas is moderately common throughout the region, and that it appears to be competively displaced by the heavily armored native crab, Ozias truncatus.
Interactions between native graspid crabs and *Carcinus maenas* in Victoria

Michael A. Sinclair, Monash University, Clayton

There exists at Coronet Bay, Victoria, an assemblage of native graspid crabs that interacts with the invasive European shore crab, *Carcinus maenas*. It is necessary to consider both temporal and spatial scales to appreciate the potential impact that *C. maenas* may have on graspid crabs. Two temporal scales need to be examined. First, that of a tidal cycle: *C. maenas* is a tidal migrator, so encounters between *C. maenas* and graspid crabs are most likely to occur during high tides and night low tides. Second, on a seasonal scale: *C. maenas* is rare in the intertidal zone from approximately June to September/October (i.e. the overwintering period), and thus, few encounters would occur between *C. maenas* and graspid crabs during this period; however, during the warmer months of the year when *C. maenas* is common in the intertidal zone, more encounters between introduced and native species would occur. During the warmer months of the year, graspid crabs are reproductive and interactions between *C. maenas* and reproductive graspid crabs may have negative effects on present and future populations of graspid crabs. Examination of the overlap in the distributions of *C. maenas* and graspid crabs can determine which species of graspid crabs are most likely to encounter, and thus, interact with *C. maenas*. The intertidal distribution of *C. maenas* (determined at night low tide), which occurs over the lower half of the shore, overlaps the distributions of four species of graspid crabs (*Brachyonotus spinosus*, *Paragrapalus goimardii*, *P. laevis* and *P. quadridentatus*), and thus, interactions between these native species and *C. maenas* are possible. Three species of graspid crabs (*Cyclograpsus audouini*, *C. granulosus* and *Helograpsus haswellianus*) that occur higher on the shore are less likely to encounter and interact with *C. maenas* because the overlap in their distributions and that of *C. maenas* is smaller. However, during high tides, *C. maenas* may move higher on the shore and also encounter *C. audouini*, *C. granulosus* and *H. haswellianus*. The distributions of some species of graspid crabs shift downshore during the warmer months of the year, thus increasing the area of overlap and the potential number of interactions between graspid crabs and *C. maenas*.

One type of interaction that may occur between *C. maenas* and graspid crabs is competition: algae was found in the gastric mills of both introduced and native species of crabs. However, competition for algae is not likely to be strong because the diet of *C. maenas* is comprised mainly of invertebrates. *C. maenas* consumes graspid crabs, and therefore, predation is a second type of interaction that may occur between *C. maenas* and graspid crabs. The predatory effects that *C. maenas* may have on communities that it has invaded have been discussed [e.g. le Roux et al. (1990) and Grosholz & Ruiz (1995)].

The effects of *C. maenas* on the distributions and abundances of graspid crabs were experimentally investigated at Coronet Bay. Two types of caging experiments were conducted in the field. In the first, cages with rocks placed in them were left in the mid-low intertidal zone for two days during which graspid crabs colonised the cages. After this period, one *C. maenas* was added to half of the cages. At the following low tide all crabs in the cages with and without *C. maenas* were recorded. In the second type of caging experiment, *C. maenas* was added to half of the cages at the start of the experiment and then left for approximately the same duration as the first experiment. During this period, graspid crabs colonised the cages; at the end of this experiment all crabs in the cages with and without *C. maenas* were recorded.

In the first experiment, where *C. maenas* was added after two days, more graspid crabs were found in cages with *C. maenas* than without. This positive effect was unexpected — fewer graspid crabs were expected in cages with *C. maenas* as a result of the predatory effects of the invader. The positive effect on the abundance of graspid crabs is probably due to the feeding behaviour of *C. maenas*. Laboratory observations showed that graspid crabs (*P. goimardii*) were attracted to and consumed crushed gastropod (*Austrocochlea constricta*), and that when *C. maenas* consumed *A. constricta*, parts of the gastropod were not consumed, remaining in the water column. Therefore, in the first of the field experiments, graspid crabs may have been attracted to the feeding behaviour of *C. maenas* in the cages, thereby accounting for the increased numbers of graspid crabs in cages with *C. maenas* compared with cages without *C. maenas*. In the second experiment, where *C. maenas* was added at the start, there was no difference in the numbers of graspid crabs in cages with or without *C. maenas*. Restricting the tidal migration of *C. maenas* may have negatively affected the behaviour and/or physiology of those crabs, and thus, may affect conclusions drawn from this experiment. *C. maenas* may not have behaved as a predator during the caging experiment, and therefore, not have indirectly attracted graspid crabs.
Conceptual Framework for Biocontrol of Introduced Marine Pests

Armand Kuris, University of California, Santa Barbara and Visiting Scientist, CRIMP

To continue the development of a conceptual framework for the control of introduced marine pests, I will briefly address the following topics: 1) Why are introduced species so often pests? 2) Is biocontrol feasible in marine environments? 3) I will present a general protocol for such a program. 4) I will discuss how issues arising compare with those in classical insect biocontrol. 5) I will address the issues of efficacy, recruitment, choice of potential control agent and safety. I will develop the safety issue in the context of the European green crab by discussing how to design powerful, effective and convincing safety tests. 6) Last y, I will summarize the research issues and propose needed studies.

Introduced animals are often pests because, in some sense, they experience ecological release. This term covers a variety of potentially improved circumstances for a species in its new world. These can be subsumed under two headings: improved environment/food or fewer natural enemies. The former may sometimes be important. However, it is the latter that may be intentionally rectified by biological or other forms of control. Experience with agricultural insect pests and our increasingly quantified observations on marine introductions, strongly suggest that they lack parasites upon their establishment outside their native range. Further, important host-specific potential control agents do not transfer to them in their new geographic area at a rate sufficient to make up for the loss of their native natural enemies. Our observations on green crabs (Carcinus maenas), pie-crust crabs (Cancer novaezelandiae), Hemigrapsus sanguineus and Asterias amurensis are all consistent with this pattern first seen for agricultural pests.

Biological control has scarcely been considered. Reasons for this lack of effort probably hinged on two perceptions: open recruitment via planktonic larvae prevented effective population regulation and no control agents were considered to be available.

Theory as well as work on crustacean fisheries have shown that parasites with a direct effect on reproduction (parasitic castrators and symbiotic egg predators) could have a strong impact on host population dynamics and, thus, on yield (Kuris 1974, Kuris et al 1991, Lafferty 1993). Also, their host-parasite dynamics could be (and often were) managed by the fishery, whether the fishery recognized it or not (Kuris and Lafferty 1992). In a pest management context, these sorts of natural enemies are available for consideration as introduced marine pest biocontrol agents. Fortunately, parasitic castrators are a common type of trophic interaction in marine systems (Kuris, 1974).

The 100 years of practical success with scientifically based classical biocontrol of agricultural insect pests provides a rich framework for the generation of a marine pest biocontrol schema. It should be noted, at the outset, that in its most modern form, biocontrol is developed and implemented in the context of Integrated Pest Management (IPM). In IPM, a coherent mix of technologies (chemical, cultivation techniques, etc.) is used in a coherent grand strategy. For marine pests, this would include consideration of fisheries, transgenic approaches and chemical control.

The following is an outline of a soup-to-nuts research protocol to develop and test a potential marine biocontrol agent. Where categories are denoted (*), there are very important differences in either theory or practice of marine versus agricultural insect biocontrol.

1. * Confirm impact
2. Assess geographic spread
3. Detect natural enemies
5. * Evaluate recruitment
6. * Evaluate safety
7. * Develop mass-rearing techniques
Figure 1. Changes in mean green crab abundance (± 1 SEM, n=3 traps/wk) at four sites over the course of the 1996 summer (week 1 = June 6 week 14 = September 5) on Martha’s Vineyard, MA (Walton and Ruiz, unpub. data) - note different scales.
At the scale of a cage, *C. maenas* has positive effects on the abundances and distributions of grapsid crabs. These effects should be considered in conjunction with the tidal and seasonal changes in abundance of *C. maenas* in the intertidal zone, the species of grapsid crabs that are likely to interact with *C. maenas*, the seasonal changes in the vertical distributions of grapsid crabs and the reproductive condition of grapsid crabs. It should be recognised that at the scale of a shore, *C. maenas* may have negative effects on the abundances and distributions of grapsid crabs directly and indirectly through its predatory abilities.

**References**


Colonisation of cages

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P. gaimardii
grapsid crabs

2 days = 4 days
no cage effects
Attempts at physical control of *Carcinus maenas* within coastal ponds of Martha’s Vineyard, MA (northeastern coast of North America)

William C. Walton, Smithsonian Environmental Research Center

In response to the threat to commercial shellfish (e.g., Tettelbach 1986) posed by the European green crab, *Carcinus maenas* (perhaps prompted by declining stocks) municipalities of Martha’s Vineyard, MA (USA) implemented green crab removal programs in 1992 to manage this predator in local salt ponds and bays. In 1995, for example, Edgartown, which pays a bounty for green crabs, destroyed ~22,000 lbs of crabs trapped out of local salt ponds. Although removal efforts are believed to improve survivorship of hatchery-reared scallops, *Argopecten irradians*, and hardshell clams, *Mercenaria mercenaria*, this approach remains to be demonstrated as a useful management tool.

To evaluate the removal program, I will test for a negative relationship between green crab abundance and removal effort (surveys and municipal data) over multiple years across coastal ponds on the island. Additionally, I will conduct long-term field enclosures of green crabs to mimic effective removal and evaluate resultant changes in clam and alternate predator abundance and size structure.

To test the effectiveness of the removal programs, I will examine the relationship between green crab abundance and removal effort among ponds (which are subject to different levels of removal effort). The number of crabs removed will be standardised by the number of traps deployed to assess removal effort. If removals are effective, increased removal effort would lead to decreases (or slower increases) in green crab populations.

To determine the consequences of successful reduction of green crabs for both hardshell clams and the benthic community more broadly, I will experimentally test the effects of complete removal of the green crab from the community (theoretically perfect control). I will conduct a long-term field experiment within a single pond (blocked by year) in which I will determine the effects of green crab exclusion upon clams, benthic fauna & other predators using two treatments: green crab-specific exclusion (unroofed enclosures to which other predators will be allowed access sensu Davies et al. 1980) and an enclosure control.

The first year’s data (boreal summer of 1996) did not suggest a dramatic reduction in the number of green crabs by trapping, as the abundance of green crabs increased at all sites through the season. Alternatively, however, the extent to which trapping deterred potentially larger increases in green crab abundance are not known and will be tested in subsequent years.

References


Session 2. Options for managing the impacts of *Carcinus maenas*
Abundance of *C. maenas* over time

Number of adult crabs

Month

1993

1994

1995


0  10  20  30  40  50  60  70
Reproductive cycles of grapsid crabs

Percentage of ovigerous females

Month

- B. spinosus
- C. granulosus
- H. haswellianus
- P. laevis
mainland is 'different' then effort should be expended into determining why this is the case. The information gained might be critical to predicting impacts of the species in other invaded areas.

5. In Tasmania, at least, populations of the crab are so dense and so pervasive that it may well threaten the existence of some endemic species. Unfortunately, the taxonomy of many temperate marine invertebrate groups is poorly known. It is critical that this work be encouraged, so that an accurate assessment of the impacts of the crab can be made.

6. At this stage, *C. maenas* does not appear to be having a large impact on Australian fisheries or mariculture. Whether or not there have been historical effects (such as marked declines in mussel populations) that have now been largely forgotten cannot yet be determined, though historical data could profitably be searched for such impacts. *C. maenas* would certainly have an effect on near-shore bivalve fisheries, such as for cockles, if the current small industry sought to expand. Impacts on mariculture are probably slight due to farming practices. However, seed oysters, in particular, seem vulnerable if and when other, perhaps preferred native food species decline in abundance.
Nonetheless, a number of qualitative observations are all consistent with large differences in the demography and behaviour of the species between Tasmania and the mainland. These include what appear to be large differences in mean crab size and population densities and indications that the species is more shelter-oriented on the mainland than in Tasmania.

Two suggestions were made regarding ‘constraining’ factors on the mainland. First, it was pointed out that there are large populations of a large-bodied and very aggressive portunid on the mainland - the blue swimmer, Portunus pelagicus, which is lacking in Tasmania. The hypothesis was raised that competition with the species, and perhaps predation by it on C. maenas, was significantly reducing its impacts. In discussion, it was pointed out that C. maenas may also compete poorly against a number of native ozid crab species, which are also common in some areas on the mainland. The specific hypothesis that P. pelagicus constrains populations of C. maenas was weakened by an observation that patterns of habitat occupancy of the two species are quite different, and they may rarely interact.

The second hypothesis generalised predation to include fishes. In particular, it was noted that skates and rays appeared to be much more common in Victorian waters than around Tasmania and that rays were well known predators of crabs (including C. maenas in Victoria). A more conspicuous relationship between crab numbers and apparent shelter (rocks, etc.) in Victoria would be consistent with the impacts of predation by skates and rays. In support of this hypothesis, it was noted that studies of parasites in Victorian and Tasmanian C. maenas indicated a number of internal parasites in Victoria, but not Tasmania, whose secondary hosts are well known to be skates and rays.

Finally, the issue of whether or not the impacts of C. maenas in Australian waters justified its inclusion as a ‘key threatening process’ was discussed in some detail. It was pointed out that as the legislation currently reads, key threatening process was defined almost entirely on evidence or likely impacts on threatened or endangered species or communities. Evidence of a broad impact of an invader on a community, even if the impact was very substantial, was not sufficient to define it as a key threatening process, unless those impacts affected a previously identified endangered or threatened native Australian species. Given a likely mosaic structure of habitat patches and populations, it seemed doubtful that any marine species, unless its impacts were overwhelming and pervasive, would ever easily fit the criteria for listing as a key threatening process. Several participants noted that this could indicate an inadequacy on the part of the legislation, but in response it was also noted that the listing of a species as a key threatening process was designed from the outset to relate to preventing species endangerment and extinction, rather than to minimize general impacts. Consequently, if C. maenas were to be proposed and successfully defended as a key threatening process, a critical first step would be to determine if there were any endemic Australian species being affected by its presence, to the extent that their continued existence as wild populations was threatened.

In that regard, it was also noted that there is a unique shallow water Tasmanian fauna in Port Davey, in the far southwest. This area appears to be within the tolerance range of the crab, and a strong case might be made for it as a key threatening process if its range expands to the southwest.

Several general recommendations emerged from these discussions:

1. A priority should be placed on getting before-and-after information on community function and structure in California and, potentially, Tasmania, as C. maenas' range expand polewards in both areas. Details would be left up to individual investigators, of course, but one essential element of any study was to be sites in front of the advancing distribution that were well studied for several years prior to the arrival of the crab, in order to provide a baseline against which impacts can be assessed.

2. In Australia, in particular, there was likely to be a large amount of information on coastal communities already available, such as results of fisheries surveys and bird counts, which could be usefully compared with what is known or suspected about the historical pattern of invasion by the crab.

3. Emphasis should also be directed as cascading effects of the crab, particularly with regard to flow-on effects of reduction in filter-feeding bivalves on, for example, water column nutrient dynamics and plankton communities and on seabird populations that might depend on those bivalves as food.

4. The pattern of impacts in Tasmania appears to be consistent with that reported in other parts of the world. The pattern of impacts on the Australian mainland seems to be very different, however. It is important that this hypothesis be tested with quantitative information on crab demography in both areas, and that if the Australian
Vertical distributions of grapsid crabs

- B. spinosus
- C. audouinii
- C. granulosus
- H. haswellianus
- P. gaimardii
- P. laevis
- P. quadridens
Vertical distributions of grapsid crabs and *C. maenas*

Mean number of crabs per quadrat (1 m²)

Distance (m)

- **C. maenas**
- **B. spinosus**
- **C. audouinii**
- **C. granulosus**
- **H. haswellianus**
- **P. gaimardii**
- **P. laevis**
- **P. quadridentatus**
Summary of Discussions in Session 1.

Several central points emerged from discussions following each of the presentations, and in the general discussion that followed.

First, surprisingly little seems to be known about the ecology of *C. maenas* in European waters. Although an abundant species, detailed community and ecosystem studies that would quantify both its own demographic features and its interactions with potential prey and predator species have not been done. Available information on impacts has been drawn mainly from general observations on the abundance of the species (including fisheries statistics for some areas) and general, energy-budget-type studies on coastal ecosystems. Consequently, the European ecological literature provides only a limited indication of the likely specific impacts of *Carcinus* as an introduced species. In contrast, qualitative information on its behaviour in Europe appear to be fully consistent with is observed behaviour elsewhere in the world, suggesting that broad demographic features, such as spawning periodicity, migrations and patterns of habitat occupancy, are likely to be conserved and be useful predictors of the animal in novel environments.

Second, even in areas where the species is perceived to have had a large impact, data supporting this conclusion are sparse. Inferences have consistently been drawn from correlations, unsupported by experimental data. A key observation is the limited data on the role of the species in causing the 'demise' of the northeast American bivalve fisheries. Although some fisheries did decline as *C. maenas* extended its range north along the coast, whether this was the proximate cause of population declines or a convenient alternative explanation to effects of, for example, over-fishing and environmental (eg., climate) change has not been explored. *C. maenas* is clearly common in areas where the bivalves are, or were present, but no experimental work has been done to distinguish among competing hypotheses. Bill Walton's thesis is directed, to a very large extent, at this problem.

Some such experimental work has been done on the west coast of the United States, where *C. maenas* is a recent invader. The implications of this work, most of which is still on relatively small spatial scales, have still to be worked through. The situation on the west coast appears to be an ideal one in which to ask questions about the invasion process and the specific impacts of this species. Recent information suggests that the range of *C. maenas* is still expanding to the north, providing an excellent opportunity for before and after comparisons of ecosystem function and structure.

The same may be true in Australia, where there are indications of a recent range expansion to Tasmania and south along the east coast. Aquaculturists and fishers report seeing more of the species in recent years than in the past, though it is difficult to disentangle the effects of increased awareness on sighting frequencies. Nonetheless, the strong consensus is that the species either arrived in Tasmania within the last ten years, or increased in abundance there over that same period. This raised quite a number of points about what was previously limiting its range, as temperatures, salinities and habitats along the east and south coasts of Tasmania appear to be well suited for the species. As *C. maenas* has clearly been in Victorian waters for about the last 100 years and given the planktonic larval duration of the species (nominally several months) and prevailing southward flowing coastal currents, there would seem to have been ample opportunity for it to spread south earlier. Why this did not occur cannot be answered, but it was pointed out that several other typically Australian mainland marine species (notably fishes) have also just recently been reported in northern Tasmania, which perhaps indicates a general response to an climate-induced shift in biogeographic provinces. Even if true, however, this does not explain why the crab is not already present in areas to the south that appear to be well within its tolerance ranges.

There was also considerable discussion about apparent regional differences in the impact of *C. maenas* in Australia. The evidence presented during the workshop for Tasmania is all consistent with a very large impact on coastal communities, with suggested effects on bivalve and native crab populations in particular. These preliminary conclusions are also consistent with data from California, and inferences drawn for the northeast US regarding likely impacts of the species. However, by comparison, impacts on the Australian mainland appear to be slight. Although not rare, the species in Victoria and South Australia, at least, does not appear to reach the densities it does in Tasmania, nor has it had a huge, perceived impact on local communities. It was acknowledged that conclusions regarding the mainland need to be very tentative in the absence of experimental data to distinguish current impacts (on communities already distorted by the presence of the crab) from ones in the past and that these studies need to be carefully thought through and carried out.


Worldwide distribution of *Carcinus maenas*
Spatial correlations between C. maenas abundance and elements of the Tasmanian marine benthic community.

Craig Proctor, Centre for Research on Introduced Marine Pests

One of the early objectives of CRIMP’s research on C. maenas was to examine links between C. maenas abundance and the physical and biological characteristics of the marine benthic community i.e. to characterise the preferred habitat of C. maenas in Tasmanian waters. In theory, knowing the preferred habitat would aid our predictions of where C. maenas could be expected to maintain its presence, but more importantly, to predict to where it is likely to extend its range in the future.

In March 1996 three sites on the NE coast of Tasmania, where C. maenas were known to be abundant, were chosen for the “habitat characterisation”: Georges Bay, the Scamander River estuary, and Henderson Lagoon at Falmouth. Within each of these locations, sampling stations were selected to provide a cross section of habitat types, differing in a range of characters including salinity, temperature, depth, turbidity, water movement, sediment type, amount of vegetation cover, and diversity and abundance of benthic infauna. Following measurements of all the physical parameters, and the taking of benthic grab sample, traps were set at each station and retrieved the next day.

Analysis of the samples and data from this study are incomplete and have now been supplemented by many more samples and observations from the 1996/1997 summer. However, there are some generalisations that can be made at this time, with regard to habitat preferences of C. maenas:

- Decades of literature on the biology and ecology of C. maenas, in other parts of the world, portray a species both extremely adaptable and hardy, apparently showing few limitations on where it can live and prosper in the marine inshore environment. The Tasmanian situation appears no different.
- We have found C. maenas in the full range of habitat types within embayments and estuaries that it has invaded. It occupies both heavily sea-grassed areas through to non-vegetated clean sandy bottom.
- It occurs in sediments from coarse gravel through to very fine, anoxic silt-mud
- During summer, it lives in water depths from shallow subtidal to no more than 3 - 4 metres.
- In contrast to its distribution on the shore in Europe (Crothers 1968, 1970), adult C. maenas in Tasmania are not found under rocks in the intertidal region.
- It does not occur on exposed, rocky or sandy open coast. Our trap catches have been low or zero in areas of strong current or heavy wave action.
- C. maenas can be found a long distance up river estuaries in water of low salinity (<10 ppt), although, within embayments, it appears to prefer more saline areas.
- At a site apparently homogenous in habitat characteristics within an embayment, the distribution of C. maenas can often appear very “patchy”, both in space and time.
- Benthic infauna is the likely key habitat parameter governing C. maenas distribution.

References


Possible impacts of *C. maenas* on Tasmanian mariculture and fisheries.

Craig Proctor, Centre for Research on Introduced Marine Pests, CSIRO Marine Research

The impact of *C. maenas* on mariculture in its native Europe and in other parts of the world where it has invaded are well documented (Cohen et al. 1995, Davies et al. 1980, Ropes 1968, Tettlebach 1986). The direct impacts have been exclusively to bivalve shellfish mariculture and shellfish fisheries.

In Tasmania, two species of shellfish are farmed; Pacific oysters (*Crassostrea gigas*), a species introduced to Tasmania in the late 1940’s, and the blue mussel (*Mytilus edulis planulatus*) which has been farmed in Tasmania since 1977. The oyster industry is worth approximately $14 million to the state, with 91 leases having a license to farm *C. gigas*, and the mussel industry has a value of $1.2 million, with 42 leases having mussels on the license (1995/96 figures). Many oyster farms have licenses that include the option of farming mussels as well, but they have yet to do so.

The distribution of *C. maenas* in Tasmanian waters overlaps significantly with the location of oyster and mussel leases. There are leases in some of the embayments (e.g. Georges Bay, Little Swanport, Blackman Bay) in which we have consistently observed and caught (via trapping) large numbers of mature and juvenile *C. maenas*. However, to date there has been little concern expressed by farmers about loss of shellfish that can be attributed to the crabs. If losses are occurring, they are not obvious, and given the voracious appetite of *C. maenas* for bivalves, this is surprising.

There are several possible, but as yet untested, reasons why *C. maenas* does not appear (to date) to be having an observable direct impact on either oyster or mussel industries:

- Both *C. gigas* and *M. edulis planulatus* are farmed "off the bottom" i.e. the oysters are grown in plastic mesh baskets on top of racks, approximately a metre above the substrate, and the mussels are grown on long-lines suspended vertically in mid-water which do not touch bottom. Shellfish mariculture that has been impacted by *C. maenas* in other areas of the world are species which are farmed or fished on, or very close to, the bottom.

- Benthic infauna, upon which *C. maenas* feeds, is rich in the sediment below and around oyster racks, and *C. maenas* have not reached the "hunger-level" which would cause them to climb up and forage among the racks. Also, the mesh-bags used to hold oysters on the racks are usually, but not always, fully enclosed — precluding entry by all but juvenile crabs.

- Birds may prey heavily on *C. maenas* which venture up into the oyster racks. Many farmers frequently report seeing obvious signs of birds having fed on crabs while perched on their racks.

The risk to the oyster industry is the possible, and largely unpredictable, dramatic increase in density of *C. maenas* at some future time and the subsequent depletion of food supply in and on the bottom, to the point where the crabs will venture upwards into the racks. The juvenile (seed) oysters are most at risk.

The southern scallop, *Pecten fumatus*, is fished, both commercially and recreationally in Tasmanian waters. This species may be impacted by *C. maenas*, if and when the crabs distribution extends to scallop rich areas such as the D’Entrecasteaux Channel, however, the preferred depth of the crabs (shallow subtidal - 3 metres) suggests impacts on this species would be minimal, as *P. fumatus* usually occurs in deeper waters. Seasonal movement of *C. maenas* into deeper water (as yet untested) would obviously increase the likelihood of impacts by the crab on scallops.

References

Nut Crab Interaction Experiment

Percentage of Nut crabs eaten

Control  Para  Sm. C.m.  Lg. C.m.
Preliminary evaluation of the impact of *Carcinus maenas* upon the native Tasmanian clam (*Katelysia scalarina*) fishery

William C. Walton, Smithsonian Environmental Research Center

The native clam, *Katelysia scalarina*, is the predominant of several *Katelysia* spp. that supports a modest shellfishery within Tasmania. The clam, a hard shelled intertidal bivalve which lives buried in shallow soft substrate, is harvested primarily from beds along the east coast of the state, but can be found along the entire coast. Based on the effects of the green crab upon bivalves in other invaded regions and particularly its apparent effect upon the North American hardshell clam, *Mercenaria mercenaria*, it was suspected that the green crab could have a potentially large impact upon the *Katelysia* fishery in Tasmania.

To test the hypothesis that green crabs are important predators of this native clam, I utilised several approaches. First, I conducted surveys of multiple *Katelysia* beds inside and outside of the known *Carcinus* range to evaluate differences in abundance, size structure and tidal distribution. Second, I planted out juvenile *K. scalarina* in the low mid-intertidal of the clam beds again inside and outside the range of *Carcinus* to determine relative predation pressure upon these individuals. Finally, I conducted a series of cage experiments to test the effect of green crab predation upon *K. scalarina* in more detail.

In these experiments, I tested for 1) the prey size preference of variously sized *Carcinus*, 2) the most damaging size-sex green crab type, and 3) differences between green crabs and native predators.

Although the survey samples are still being analysed, it is already apparent that one clam bed within the green crab range had a relatively dense population of *K. scalarina* juveniles, suggesting that green crabs did not control this species' abundance. The preliminary outplant results, however, suggest that relative predation rates are higher on beds inside the green crab range than on beds outside the range. Additionally, the cage experiments suggest that 1) juvenile *K. scalarina* (6-15 mm shell length) are preyed upon heavily by green crabs, 2) large (50-65 mm carapace width) *Carcinus* males are the most voracious type of green crab (relative to small [30-40 mm] crabs and large females), and 3) large *Carcinus* males are more important predators upon these juvenile clams than the native crab, *Paragrapsus* sp., and the native whelk, *Columinella* sp.

Thus, preliminary results suggest that *Carcinus* may have a very large impact upon the abundance and distribution of *K. scalarina*, and, subsequently, the fishery.
Comparison of Predation by *Carcinus* and Native Predators upon *Katelysia scalarina* juveniles
Effects of *Carcinus maenas* on Nut Crabs

Laura Rodriguez, Smithsonian Environmental Research Center

Nut crabs, also called pebble crabs, are members of the family Leucosiidae. They have very rounded bodies (max carapace width 30 mm), small eyes, long claws, and commonly inhabit sandy and muddy habitats, anywhere from 0 to 70 m depth (Edgar, 1997). Nut crabs are often seen in the intertidal foraging for small invertebrates. From personal observation they seem to forage mostly at low tide in shallow water.

There are three species of nut crabs in Tasmania, belonging to 2 genera: *Philyra laevis*, *Philyra undecimspinosa*, *Ebal intermedia*. Because nut crabs tend to live in habitats similar to those which *Carcinus maenas* also favours and there is good evidence that *C. maenas* preys heavily on grapsid crabs (G.Ruiz, these proceedings), questions were raised as to what effect *C. maenas* has on nut crabs. An initial hypothesis is that *C. maenas* will prey on nut crabs.

To determine if *C. maenas* prey on nut crabs, cage interaction experiments have been run. These experiments consisted of placing 5 nut crabs in a 0.5 m$^2$ cage with either a large *C. maenas* (60 mm), small *C. maenas* (40 mm) or large *Paragrapsus gaimardii* (40mm). This experiment showed that there was predation by *C. maenas* on nut crabs, although the difference between the treatments is not significant. The native grapsid, *P. gaimardii*, showed very low predation on the nut crabs. To further test the interaction between nut crabs and *C. maenas*, nut crabs were tethered. Nut crabs were tied with monofilament and outplanted for 24 hours at sites both inside and outside *C. maena* range. Both inside and outside the range there was no predation.

The preliminary results that have been obtained so far have only raised more questions. Further experiments will include more cage experiments with both *C. maenas* and the native grapsid. Since nut crabs seem to forage at low tide, this behaviour might provide a refuge from *Carcinus* predation. I am hoping to run more tethers at different intertidal heights and for different times to try to understand their behaviour better. Also, very little data has been obtained about the abundance and distribution of nut crabs. Trapping will be conducted to determine both their distribution intertidally and across sites.

References

Edgar, Graham J. *Australian Marine Life* Reed Books, Australia 1997: pg. 204-205
Decline in Predation Rate upon *Katelysia scalarina* Juveniles in Uncaged Plots
Differences in Relative Predation Rate upon
Katelysia scalarina juveniles

n = 3

Percent Predation

n = 2

Inside

Outside

Carcinus Range
SMALL ENCLOSURES

NO. PARAGONUS EATEN / 24 HRS.

1.0

1.5

2.0

2.5

3.0

+ CARCINUS

- CARCINUS

TREATMENT

1

2
Preliminary evaluation of impacts of *Carcinus maenas* on bivalve populations in Tasmania.

Craig Mackinnon, University of Tasmania

Both preliminary gut analysis and laboratory feeding experiments have been conducted to determine the crabs ability to affect bivalve species. Initial results from gut analysis confirm and suggest that a large portion of the green crabs diet in Tasmania consists of bivalves. This has been supported by preliminary laboratory feeding experiments which have shown that the crab is capable of consuming vast quantities of various bivalve species over short time durations. They also tend to indicate that size selection of bivalve prey is determined by the size and sex of the crab. Large males have shown greater feeding rates and ability to open larger prey items. Two native clam species (*Katelysia scalarina* and *K. rhytihora*) and two mussel species (*Mytilus edulis planulatus* and *Brachidontes rostratus*) have so far been used. Preliminary results suggest *Carcinus* has the ability to drastically reduce numbers of smaller sized mussels and clams, however have little impact on larger sized animals due mainly to their inability to open these larger animals. These results lead me to suggest that in areas with large green crab populations abundance of juvenile clams and mussels will be highly reduced compared to non green crab sites due to selective predation pressure by this crab. A benthic survey of bivalves from selected sites within and outside *Carcinus*’ range is currently being under taken to test for this correlation.

To further test the potential impact on native bivalves by the green crab a number of field experiments have, and are being conducted. Outplants of bivalves are being used to give an indication of predation pressure of *Carcinus*. *Mytilus edulis planulatus* and *Katelysia rhytihora* were outplanted within and outside the present *Carcinus* distribution. *Mytilus* less than 20 mm (greatest predation in lab. feeding trials) were collected and allowed to settle and reattach onto artificial rock substrates. The clams (< 16 mm) were placed in sieved sediment in plastic trays and allowed to bury before being placed within the substrate. Both species were layed out subtidally with five replicates for each species. They were collected after 24 hr and counted to determine mortality. *Mytilus* placed in sites with *Carcinus* present suffered 75% mortality of the 500 per site (100 per replicate) compared to 3.4% at sites outside it’s present range. This suggests, as no obvious other predator/s were evident within these sites, that *Carcinus maenas* could enforce significant predation pressure on mussel species. The clams outplanted gave no direct signal. One site within the green crab range, Falmouth had 50% mortality over a 24 hr period, while the other sites showed significantly reduced values (< 19%). Sites outside its distribution had varied values, however these were generally low.

A caging experiment was also conducted at a non *Carcinus* site to determine if the crab has an effect on native bivalve assemblages. 1m$^2$ enclosures which contained two densities of large male green crabs were used, with exclusion and uncaged plots as controls. These were set out randomly in three blocks just below the low tide mark. Benthic cores were taken from each plot at the start and at the completion of the experiment, while the top 5 cm of sediment from each plot was also taken and sieved (2.8 mm) after the five week period. Preliminary results of the final core (whole plot) suggest a significant decrease in bivalve abundance over the blocks over this time frame.

Preliminary results suggest so far that *Carcinus maenas* has the potential within Tasmania to drastically alter native bivalve assemblages. Laboratory and field trials have indicated that juvenile and smaller bivalves of numerous species are the most vulnerable to predation pressure. *Carcinus* may decrease abundance of select species by predation on new recruits, leaving reduced numbers available for later reproduction.
Preliminary evaluation and predictions of impacts of *Carcinus maenas* on native crabs in Tasmania.

Gregory M. Ruiz and Laura Rodriguez, Smithsonian Environmental Research Center

The European green crab *Carcinus maenas* is now abundant along the north and east coasts of Tasmania, where it appears to have a negative impact on some of the native crab populations. During the summer (January-March) of 1997, we implemented a research program to measure the impacts of the recent green crab invasion within its current range and as the crab invades new regions to the south and west. Herein, we summarize our preliminary results.

The green crab overlaps spatially with a variety of other crab species in Tasmania. Surveys, that utilize standard traps as a measure of abundance, demonstrate that green crabs occur in a broad range of soft-sediment habitats, where they overlap with at least two common native crabs: the grapsid *Paragrapsus gamardii* and the portunid *Nectocarcinus integrafrons*. Additional observations suggest habitat overlap also exists with the lycosid crab *Aplysia* and the soldier crab.

Our surveys demonstrate a strong negative relationship between the abundance of green crabs and grapsid crabs. This is largely confounded by geographic region. Along the northeast coast, where green crabs have been well established and abundant for many years, grapsid crabs are relatively rare to absent. At southeast sites, or the leading edge of this invasion, grapsids exhibit low to moderate abundances (10-60 crabs per survey). In sharp contrast, southwest of the green crab invasion, grapsid crabs are extremely abundant (>2,000 crabs for some surveys).

Preliminary field experiments and observations suggest that predation by green crabs on the grapsids is responsible for the observed abundance patterns. Specifically, green crabs feed on grapsids in field enclosures and when free-ranging. Tethered grapsid crabs also experience higher predation rates inside versus outside the green crab range. Interestingly, work by Sinclair (this volume) suggests that grapsids may actually be drawn to green crabs (perhaps attracted to their feeding activity) which may increase their risk of predation, although the mechanism and consequence of this attraction requires further experimental analysis. Nonetheless, our data to date support the hypothesis that predation is responsible for observed abundance patterns, and research by Grosholz and Ruiz (unpubl. data) demonstrate a decline in grapsids at Bodega Bay Harbor, California USA, coincident with the arrival of green crabs.

Surveys and observations of the other native crab species suggest some interactions with green crabs may variously influence these populations. First, there appears to be a negative association between *Nectocarcinus* and *Carcinus*, and between *Aplysia* and *Carcinus*. In the latter case, field experiments are now underway to evaluate the causal nature of this relationship, and we plan a similar evaluation for *Nectocarcinus*. Second, and in contrast, there is no apparent qualitative relationship between the abundance of green crabs and soldier crabs, perhaps due to a temporal refuge by burial that soldier crabs may experience during high tide exposure to green crab predators.

At this stage in our research, it appears that *Carcinus* predation is causing high mortality rates for each *Paragrapsus*, *Nectocarcinus*, and *Aplysia* and is causing significant declines in these native populations. We predict that the magnitude of declines will increase and low abundances will persist within the range of *Carcinus*, and that similar declines will occur outside of the current range of *Carcinus* in association with future invasion. Our current research program is designed to test these specific hypotheses and to characterize the nature of these interactions.
Effects of *Carcinus maenas* on the mud whelk *Batillaria australis*

Laura Rodriguez, Smithsonian Environmental Research Center

*Batillaria australis* is a common mud whelk of the family Potomidiidae. It inhabits mud flats and estuaries and is most common in the high intertidal. It is a conical shell with a high spire and its surface is brownish black and highly ribbed (Richmond, 1992). Initial observations by Greg Ruiz and Laura Rodriguez found that *Batillaria* shells are very common in the shell hash at several study sites, including Barilla Bay, Lord’s Point and Humbug Point, Tasmania. But, a live population of *Batillaria* had only been found at Barilla Bay, a site where green crabs are not yet established. This observation prompted questions about the distribution and abundance of *B. australis* across sites. An initial hypothesis was made that *Batillaria* populations would be different inside vs. outside of *Carcinus maenas* territory, and that this relationship might be due to predation by *maenas*.

Two experiments were conducted to determine if *Batillaria australis* is actually a prey item of *C. maenas*: outplants and a cage feeding experiment. The outplants consisted of tethering *Batillaria*, both large (30mm) and small (7mm), with monofilament. After being outplanted for 24 hours in a *C. maenas* area there was zero predation on the mud whelks. The cage experiments consisted of stocking 0.5 m² cages with 10 large *Batillaria* each, half of which received a large *C. maenas* (60 mm) and half which were left as *Batillaria* controls. After 24 hours there were no significant effects of predation.

Besides the experiments, gastropod surveys were conducted at several sites both inside and outside the range of *C. maenas*. While conducting these surveys a populations of *Batillaria* was found at Humbug Point, Georges Bay, a site with an established population of *C. maenas*.

We concluded that *Batillaria australis* is not a significant prey item of *C. maenas*. Although predation has been observed in a lab setting, no predation was observed in our field experiments. The initial results from our survey showed that our hypothesis is probably false, and that distribution of *Batillaria australis* is not significantly different inside vs. outside *C. maenas* areas.

**References**

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