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Interaction and impacts of two introduced species on a soft-sediment marine assemblage in SE Tasmania

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Abstract Introduced species are having major impacts in terrestrial, freshwater and marine ecosystems worldwide. It is increasingly recognised that effects of multiple species often cannot be predicted from the effect of each species alone, due to complex interactions, but most investigations of invasion impacts have examined only one non-native species at a time and have not addressed the interactive effects of multiple species. We conducted a field experiment to compare the individual and combined effects of two introduced marine predators, the northern Pacific seastar *Asterias amurensis* and the European green crab *Carcinus maenas*, on a soft-sediment invertebrate assemblage in Tasmania. Spatial overlap in the distribution of these invaders is just beginning in Tasmania, and appears imminent as their

respective ranges expand, suggesting a strong overlap in food resources will result from the shared proclivity for bivalve prey. *A. amurensis* and *C. maenas* provide good models to test the interaction between multiple introduced predators, because they leave clear predator-specific traces of their predatory activity for a number of common prey taxa (bivalves and gastropods). Our experiments demonstrate that both predators had a major effect on the abundance of bivalves, reducing populations of the commercial bivalves *Fulvia tenuicostata* and *Katelysia rhytiphora*. The interaction between *C. maenas* and *A. amurensis* appears to be one of resource competition, resulting in partitioning of bivalves according to size between predators, with *A. amurensis* consuming the large and *C. maenas* the small bivalves. At a large spatial scale, we predict that the combined effect on bivalves may be greater than that due to each predator alone simply because their combined distribution is likely to cover a broader range of habitats. At a smaller scale, in the shallow subtidal, where spatial overlap is expected to be most extensive, our results indicate the individual effects of each predator are likely to be modified in the presence of the other as densities increase. These results further highlight the need to consider the interactive effects of introduced species, especially with continued increases in the number of established invasions.

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Introduction

Biological invasions, or the establishment of non-native species outside their historic range, have become a major force of ecological change throughout the world. Although invasions have occurred for millions of years, there has been a rapid increase in the rate of newly detected invasions over the last two centuries, driven by human-aided movement across and between continents and oceans (Carlton and Geller 1993; Vitousek 1994;

Cohen and Carlton 1998; Hewitt et al. 1999; Ruiz et al. 2000; Ruiz and Carlton 2003). The magnitude of ecological effects by invasions has become increasingly evident, resulting in fundamental changes to population, community and ecosystem processes (Cloern 1996; Vitousek et al. 1996; D'Antonio et al. 1998; Wilcove et al. 1998; Strayer 1999; Grosholz et al. 2000). Despite a growing amount of literature on invasion effects, the impacts of most invasions remain unstudied, and the interactive effects of multiple species have rarely been evaluated (Ruiz et al. 1999; Simberloff and von Holle 1999). The combined effects of several introduced species may not be strictly additive, and can result in many complex interactions, including accelerated impacts on native communities (Simberloff and von Holle 1999). Indeed, modification of interactions, whereby the direct interaction between two species is altered by the presence of a third, is thought to be commonplace (Kareiva 1994).

Hundreds of non-native marine species are now established in the coastal waters of Australia, despite the relative degree of geographic isolation (Pollard and Hutchings 1990a, 1990b; Jones 1991; Furlani 1996; Hewitt et al. 1999). Among the most conspicuous introductions are two large, predatory species found in sheltered, low-energy environments: the northern Pacific seastar *Asterias amurensis* and the European green crab *Carcinus maenas*. The green crab is known to have significant effects on infaunal communities in many parts of the world (Reise 1985; Grosholz et al. 2000; Walton 2003). Furthermore, both species are known to have significant effects on native populations in Tasmania (Ross et al. 2002, 2003a; Walton et al. 2002).

Both *A. amurensis* and *C. maenas* are now common in the coastal waters of Tasmania. *A. amurensis* was introduced to south-east Tasmania in the early 1980s, where it has become a dominant invertebrate predator in the Derwent Estuary (Grannum et al. 1996). *C. maenas* is thought to have been introduced to mainland Australia in the early 1900s (Fulton and Grant 1900), but it was not recorded in Tasmania until 1993, where its range has expanded rapidly (Gardner et al. 1994; Thresher et al. 2003). In their native ranges both species are important predators of a wide variety of epifaunal and infaunal species (e.g. Hatanaka and Kosaka 1959; Fukuyama and Oliver 1985; Jensen and Jensen 1985; Sanchez-Salazar et al. 1987; Fukuyama 1994). Bivalve populations in particular appear to be very susceptible to predation by *A. amurensis* (Hatanaka and Kosaka 1959; Kim 1969; Nojima et al. 1986) and *C. maenas* (Ropes 1968; Griffiths et al. 1992; Grosholz and Ruiz 1995; Walton 2003). Although the distributions of *C. maenas* and *A. amurensis* in Tasmania do not currently overlap, such sympatry appears imminent given the current rate of spread and apparent absence of any dispersal barriers for *C. maenas*. Since both species are major predators of bivalves in sheltered, low-energy environments, it appears that direct biological interaction between these species is

inevitable, and we predict the interaction between *A. amurensis* and *C. maenas* will modify the effects resulting from each species individually.

This seastar/crab/bivalve system is an excellent model to explore the interactive effects of multiple introduced species, because each predator leaves characteristic patterns on shells of their bivalve prey. Predation by seastars results in undamaged and empty shells, whereas bivalves eaten by crabs are broken by this crushing predator (i.e. usually hinges with only a fraction of the shell remaining). Using this physical evidence of predator type, we tested the separate and combined impacts of *A. amurensis* and *C. maenas* on a soft-sediment assemblage, focusing particular attention on bivalves. Because there was little information on the distribution and abundance of native species prior to the establishment of *A. amurensis* and *C. maenas*, the study focuses on experimental manipulations of the two species in a relatively unimpacted habitat at the interface of their current ranges.

Materials and methods

Collection and maintenance

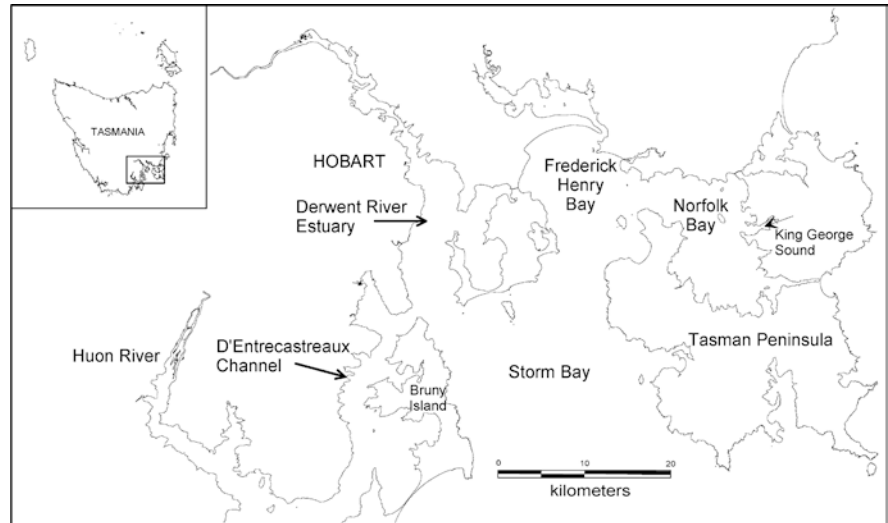
A manipulative experiment was undertaken in the sheltered upper reaches of King George Sound, south-east Tasmania at a depth of 2–3 m (Fig. 1). Sediment in the area is composed predominantly of sandy mud. The habitat type at this site is similar to that present in other bays and estuaries around Tasmania, in terms of depth profile, wave exposure and sediment quality. Because the area does not currently support populations of either *Asterias amurensis* or *Carcinus maenas*, the experiment was conducted in completely enclosed cages and only male specimens were used to reduce the risk of establishing these species.

The experiment consisted of five treatments, which included all possible combinations of presence (a single animal per cage) and absence of crabs and seastars in cages, and an unmanipulated 1 m² plot without either cages or added predators. The cages consisted of a rigid (1 m×1 m base×0.7 m high) steel frame with legs (0.5 m long) to securely anchor the cage in the sediment. The cage top and sides (except legs) were completely covered in plastic mesh (6 mm), and the cage legs were driven into the sediment so that 100–150 mm of the cage sides was buried to prevent passage in or out of large predators or prey by burrowing.

To control for patchiness of infauna in the analysis of treatment effects, we used a randomised complete-block design. In a pilot study, plots 3–5 m apart were similar in composition, while plots separated by 30–60 m were usually dissimilar. Thus, the experiment followed a randomised complete-block design, with one replicate of each of the five treatments applied randomly to separate experimental units (~5 m apart) in each of three blocks (~30 m apart). By accounting for the variation between blocks, we hoped to obtain a smaller experimental error and improve the power to detect treatment effects (see Newman et al. 1997).

The experiment was monitored weekly to check the condition of the enclosed predators and remove fouling organisms from the cage. Eight weeks after the commencement of the experiment, cages and predators were removed. Two different sampling techniques were employed. First, treatment plots were sampled with cores (150 mm diameter, 100 mm deep) to estimate the abundance of all infaunal and epifaunal organisms (>1 mm). Three replicate cores were taken at random positions in each plot. No samples were taken within ~0.1 m of the cage perimeter to avoid possible edge effects of the cages. Because it was not anticipated that core

Fig. 1 Map of south-east Tasmania showing study location, King George Sound



samples would provide precise estimates of the abundance of larger and/or rare species that may be important prey, the entire contents of the plots were subsequently sampled to a depth of 0.1 m, using a diver-operated, air-driven suction device. To do this, an open square frame (1 m×1 m) was inserted into the sediment to isolate the plot, and all contents vacuumed into a 1-mm-mesh bag. Sampling in both cores and air-lift samples was to a depth of 0.1 m, because the vast majority of macroinvertebrate infauna was found in this depth range in a pilot study.

Samples were sieved (1.0 mm mesh) prior to fixing in 5–10% buffered formalin with Rose Bengal stain, and then rinsed in freshwater before storing in 100% ethanol. For core samples, all infaunal and epifaunal organisms (>1 mm) were sorted and identified to the lowest possible taxon. Suction samples were sieved again (2.0 mm mesh), and all bivalves and the echinoid *Echinocardium cordatum* were sorted and identified to species.

Because both predators leave clear traces of their activities when consuming bivalves, the number of clams (*Fulvia tenuicostata* and *Katelysia rhytiphora*) eaten by each predator was counted in suction samples to examine the potential for interaction effects between predators in more detail. Undamaged, empty shells with gaping valves identified bivalves that were eaten by seastars. Bivalve hinges with only a fraction of the shell remaining were identified as prey eaten by crabs. To test for size selection by seastars and crabs and whether size selection is altered in the presence of the other predator, the lengths of live and undamaged empty bivalves were measured in all treatments.

Statistical analysis

The responses of dominant taxa to experimental treatments were determined using species abundance data obtained from suction samples of 1 m² plots, with the exception of polychaetes, which were counted in cores. For polychaetes we used the arithmetic mean of the three replicate cores taken from each plot. Tests for predation effects and cage effects were conducted separately. To test for the possibility of cage effects, a one-way randomised, complete-block ANOVA, with “treatment” (two levels: cage present and cage absent, both without added predators) as a fixed factor and “block” as a random factor were used. The effects of *A. amurensis* and *C. maenas* on prey species were analysed using a two-factor randomised, complete-block ANOVA, with “*A. amurensis*” (present or absent) and “*C. maenas*” (present or absent) as fixed factors and “block” as a random factor. Note, that, while there are no special assumptions required to conduct the tests, interpreting the significance of the predator effects requires no, or a relatively small, predator by block interaction. To assess treatment by block interactions, plots of dependent variables

versus block were examined. In cases where an interaction was clearly evident by visual inspection, the analysis was not conducted. Data were checked for normality and homoscedasticity, and transformed as necessary depending on the relationship between standard deviations and means of treatment groups (ignoring the blocking effect) (Draper and Smith 1981). Transformations are expressed in terms of the untransformed variate, *Y*. Where prey depletion occurred and multiplicative effects were likely, as was the case for *F. tenuicostata* and *K. rhytiphora*, we tested a multiplicative model by running the ANOVA on log abundances. The statistical package SAS was used for all univariate analyses.

In the absence of significant predation effects by the seastar and crab effects, or seastar×crab interactions, the minimum detectable effect size (MDES) for a power of 80% was calculated for predation effects. MDES values were calculated as the percentage change from the mean abundance in treatments in which the predator was absent using the $MS_{\text{block} \times \text{seastar}}$ and $MS_{\text{block} \times \text{crab}}$ interaction terms from the original ANOVA as the estimate of variation for seastar and crab MDES calculations, respectively. These power calculations were done using PiFace, a power analysis add-in for Microsoft Excel (available at: <http://www.stat.uiowa.edu/ftp/rleth/PiFace/>).

To test for size selection by seastars and crabs on the commercial bivalve *F. tenuicostata*, and whether size selection is altered in the presence of the other predator, we compared size-frequency distributions between treatment groups using the Kolmogorov–Smirnov (K–S) test. The specific comparisons of size-frequency distributions for:

1. seastar size selection: empty bivalves in the seastar treatment versus live bivalves in the cage control treatment;
2. crab size selection: live bivalves in the crab treatment versus live bivalves in the cage control treatment;
3. effects of crabs on seastar size selection: empty bivalves in the seastar treatment versus empty bivalves in the seastar+crab treatment; and
4. effects of seastars on crab size selection: live bivalves in the crab treatment versus empty bivalves in the crab+seastar treatment.

The sequential Bonferroni procedure for multiple testing was used to adjust significance levels (see Quinn and Keough 2003). Note that the size-frequency data were pooled across blocks for each treatment to ensure adequate sample sizes for construction of size-frequency distributions.

To depict the multivariate patterns among blocks and treatments, non-metric multi-dimensional scaling was done on Bray–Curtis distances calculated from fourth-root-transformed data, using the Primer computer program (Clarke 1993).

Results

The major groups found in the core samples were polychaetes, bivalves and heart urchins that represented 37%, 29% and 8%, respectively, of the total numerical abundance. The bivalves *Fulvia tenuicostata* and *Theora* spp.; the polychaetes *Simplisetia amphidonta*, *Lysilla jennacubinae* and *Glycera* spp.; and the echinoid *Echinocardium cordatum* represented 88%, 86% and 100% of the total abundance of bivalves, polychaetes and echinoids, respectively. The numerically dominant species from suction samples were the bivalves *F. tenuicostata*, *Theora* spp., *Kataleysia rhytiphora*, *Wallucina assimilis* and the echinoid *E. cordatum*.

Commercial bivalves: *F. tenuicostata* and *K. rhytiphora*

Effect of cages

There were no significant effects of cage controls on the abundance of *F. tenuicostata* or *K. rhytiphora* (Table 1).

Effect of predation by seastars

There was a major reduction in densities of *F. tenuicostata* and *K. rhytiphora* in all treatments containing *Asterias amurensis*; however, this difference was only significant for *F. tenuicostata* (Table 1; Fig. 2a). The abundance of recently opened shells (indicative of seastar predation) of both species was greater in treatments with seastars; however, this difference was only significant for *K. rhytiphora* (Table 1; Fig. 2a). Where there were changes in abundance but differences were not significant for live *K. rhytiphora* and open *F. tenuicostata*, only changes of >204% and 380%, respectively, of the mean abundance in treatments without seastars could have been detected with 80% confidence. Size selection by seastars was not apparent for *F. tenuicostata*, as the size-frequency distribution of this species eaten by *A. amurensis* was not significantly different from the size-frequency distribution of live bivalves in the cage control treatment (Fig. 3, K-S test $P > 0.05$).

Effect of predation by crabs

The abundance of *F. tenuicostata* was reduced in all treatments containing *Carcinus maenas* compared with the cage control; however, this difference was not significant (Table 1; Fig. 2a). Note that only a change of >212% could have been detected with 80% confidence for *F. tenuicostata*. Although there was a crab×seastar interaction, the abundance of *F. tenuicostata* hinges (indicative of crab predation) was greater in treatments containing crabs compared with treatments with no

added crabs (Table 1; Fig. 2a). Comparison of the size-frequency distributions of *F. tenuicostata* between the cage controls and treatments containing crabs shows that crab predation was largely on small (<25 mm) bivalves (Fig. 3a). The size-frequency distributions of *F. tenuicostata* remaining in treatments containing crabs and in the cage control were significantly different (Fig. 3a, K-S test $P > 0.05$). There was no evidence that predation by crabs influenced the abundance of the other commercial bivalve at this site, *K. rhytiphora*. It is noteworthy that the majority of *K. rhytiphora* in all experimental plots exceeded 25 mm in total length.

Interaction of crabs and seastars

The crab×seastar interaction was not significant for live bivalves or open bivalve shells for either *F. tenuicostata* or *K. rhytiphora*. In contrast, the crab×seastar interaction was significant for *F. tenuicostata* hinges (Table 1). The number of *F. tenuicostata* eaten by crabs (hinges) in the presence of seastars was reduced compared with when the crab was alone, but higher than when predators were absent (Fig. 2a). However, the size of bivalves eaten by the crab was not altered in the presence of the seastar; the size-frequency distribution of bivalves not eaten in the crab treatment was not significantly different from the size-frequency distribution of bivalves not eaten by the crab in the crab+seastar treatment (Fig. 3, K-S test $P > 0.05$). Although seastars consumed similar numbers of *F. tenuicostata* (open shells) in the presence of crabs (Fig. 2), there was a significant shift in the size-frequency distribution of bivalves consumed, with larger bivalves consumed in the presence of crabs (Fig. 3, K-S test $P < 0.05$).

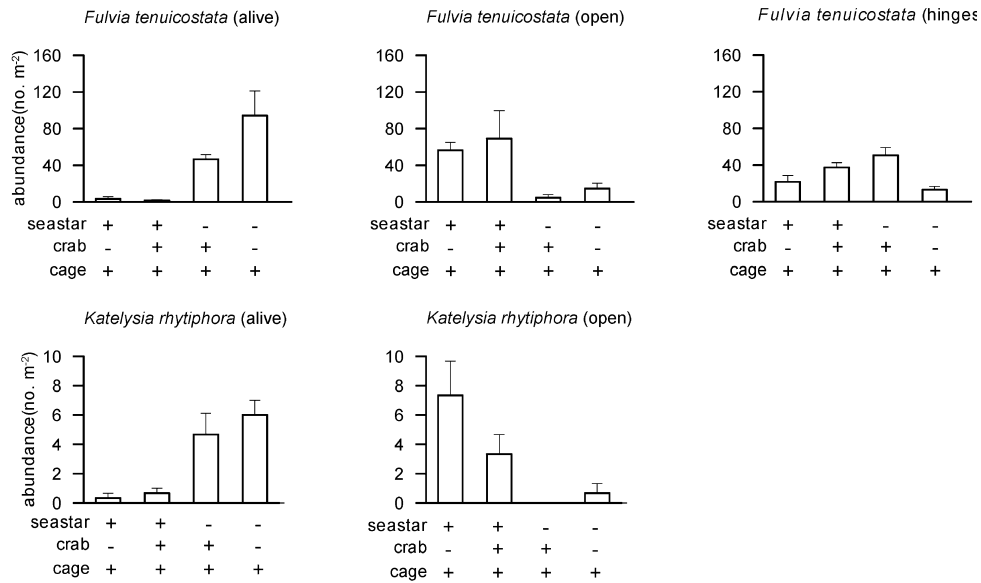
Other species

The general pattern described for commercial bivalves is evident in the ordination (MDS) of treatment plots based on abundances of bivalves and echinoids (Fig. 4a) and on those of the whole assemblage (Fig. 4b). However, on the basis of individual species, there were no significant effects of added predators or cages detected for *E. cordatum* and the bivalves *Theora* spp. and *W. assimilis* or for the polychaetes *S. amphidonta*, *L. jennacubinae* and *Glycera* spp. (Table 1; Fig. 2b, c). Of the species for which there were no apparent changes in abundance in the presence of either predator, changes of between 9% and 97% in the presence of either predator could have been detected with 80% confidence for the polychaetes and *Theora* spp. For the remaining species for which there were no apparent changes in abundance in the presence of either predator, only changes of >100% could have been detected in the presence of either predator with 80% confidence.

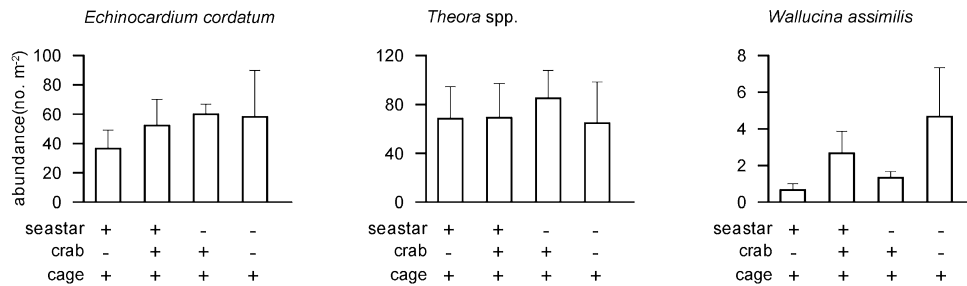
Table 1 Analysis of effects of predation and caging on the abundance of numerically abundant taxa. The table shows results of the ANOVA test of predation comparing among treatments of *Asterias amurensis* (present or absent) and *Carcinus maenas* (present or absent) and the ANOVA test of caging comparing among treatments (cage present and cage absent) with no predators added. Significant *P*-values (<0.05) are shown in *boldface*. Note *K. rhytiphora* hinges were not present in samples. Minimum detectable effect sizes (*MDES*) for a power of 0.8 have been calculated for predation effects in the absence of significant predator or predator \times predator interactions and are expressed as percent change from the mean abundance in treatments in which the predator was absent

	Predation effects										Cage effects		
	Transformation	MS _{resid}	MS _{seastar} \times block	MS _{crab} \times block	<i>P</i> _{seastar} \times crab	<i>P</i> _{seastar}	MDES (%)	<i>P</i> _{crab}	MDES (%)	MS _{resid}	<i>P</i> _{cage}	MS _{resid}	<i>P</i> _{cage}
Degrees of freedom		2	2	2	2	2							
Denominator used in each <i>F</i> -test													
Commercial bivalves													
<i>Fulvia tenuicostata</i>													
Alive	log($x+0.01$)	4.350	1.464	5.504	0.711	0.026	250	0.495	247.167	0.611			
Empty shell	log($x+0.01$)	4.006	1.968	5.370	0.336	0.067	204	0.404	112.500	0.408			
Hinge	log($x+0.01$)	0.012	0.003	0.595	0.026	0.102		0.144	66.500	0.792			
<i>Kateleyhia rhytiphora</i>													
Alive	log($x+0.01$)	1.578	4.463	2.385	0.323	0.086	380	0.573	3.500	0.580			
Empty shell	log($x+0.01$)	1.330	2.139	3.844	0.558	0.025	751	0.369	1.167	0.742			
Other bivalves and echinoids													
<i>Echinocardium cordatum</i>	x	1160.359	382.443	648.328	0.756	0.324	102	0.612	211.211	0.406			
<i>Theora</i> spp.	$x^{0.5}$	16.083	21.583	3.083	0.707	0.812	70	0.665	390.167	0.524			
<i>Wallucina assimilis</i>	x	8.911	3.862	6.742	0.219	0.449	690	0.415	4.167	0.251			
Polychaetes													
<i>Simplisetia amphidonta</i>	x	1.590	0.174	1.507	0.507	0.136	9	0.155	0.233	0.075			
<i>Lysilla jennacubmae</i>	x	0.750	0.287	0.731	0.574	0.547	35	0.843	1.167	0.529			
<i>Glycera</i> spp.	x	1.766	0.488	0.424	0.493	0.126	33	0.845	0.056	0.074			

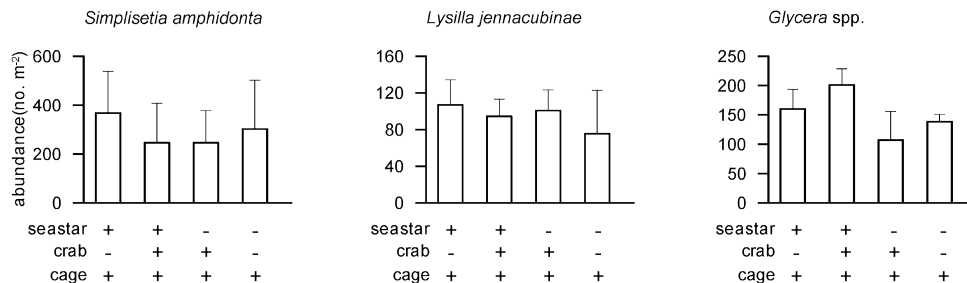
a) Commercial bivalves



b) Other bivalves and echinoids



c) Polychaetes



TREATMENT

Fig. 2a–c Densities of the most abundant species in each treatment. Densities of commercial bivalves (**a**) and other bivalves and echinoids (**b**) are means per square meter (+SE) taken from suction samples to a depth of 100 mm ($n=3$ plots). Polychaete densities (**c**) are means per square meter (+SE) scaled from counts in cores ($n=3$ cores pooled, each 150 mm diameter, 100 mm deep) in each plot ($n=3$ plots)

Discussion

The main effect of both predators was on the commercial bivalves, *Fulvia tenuicostata* and *Katelaysia rhytiphora*.

There was no evidence that either predator influenced abundances of the echinoid *Echinocardium cordatum*, the bivalves *Theora* spp. and *Wallucina assimilis*, or the polychaetes *Simplisetia amphidonta*, *Lysilla jennacubinae* and *Glycera* spp. However, the tests on unaffected species varied in power. For species in which variation between blocks was high (e.g. *E. cordatum*), or densities were very low (e.g. *W. assimilis*), the power to test for treatment effects was low and little weight is given to these non-significant results. Power analysis indicated that only very large changes in abundance (> 592% and 165%) could have been detected with 80% confidence

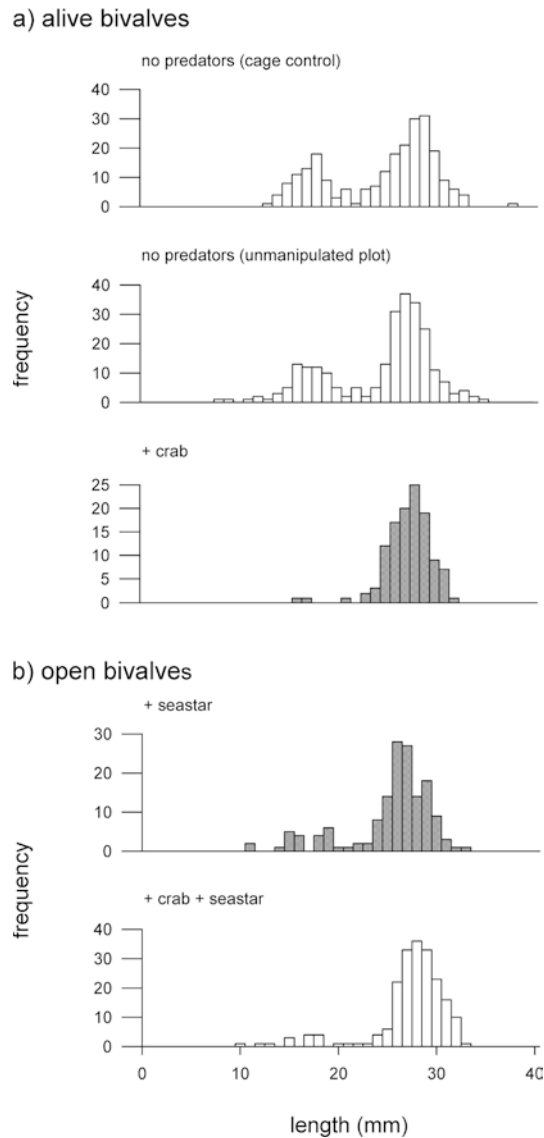


Fig. 3 Length-frequency histograms of *Fulvia tenuicostata* remaining at the end of the experiment in: **a** live treatments (uncaged control, cage control and treatments with crabs) and **b** open treatments (with seastar + crab and seastar). *Unshaded* and *shaded* histograms were significantly different in paired Kolmogorov–Smirnov tests

when testing for crab effects on *W. assimilis* and *E. cordatum*, respectively. In contrast, for polychaetes, there was sufficient power to detect much smaller changes in abundance (between 9% and 54%) with 80% confidence, which is smaller than changes detected for seastar and crab effects in other experiments (Ross et al. 2002, 2003a; Walton et al. 2002). Thus, for polychaetes we are confident that they were unaffected by predators in this experiment. Importantly, it is also possible that not all direct and indirect effects had occurred before the termination of the experiment given its relatively short duration (2 months). It is noteworthy that in a short-term study carried out in the Derwent Estuary, *Asterias* fed predominately on *F. tenuicostata* after its massive settlement, but shifted to feed on

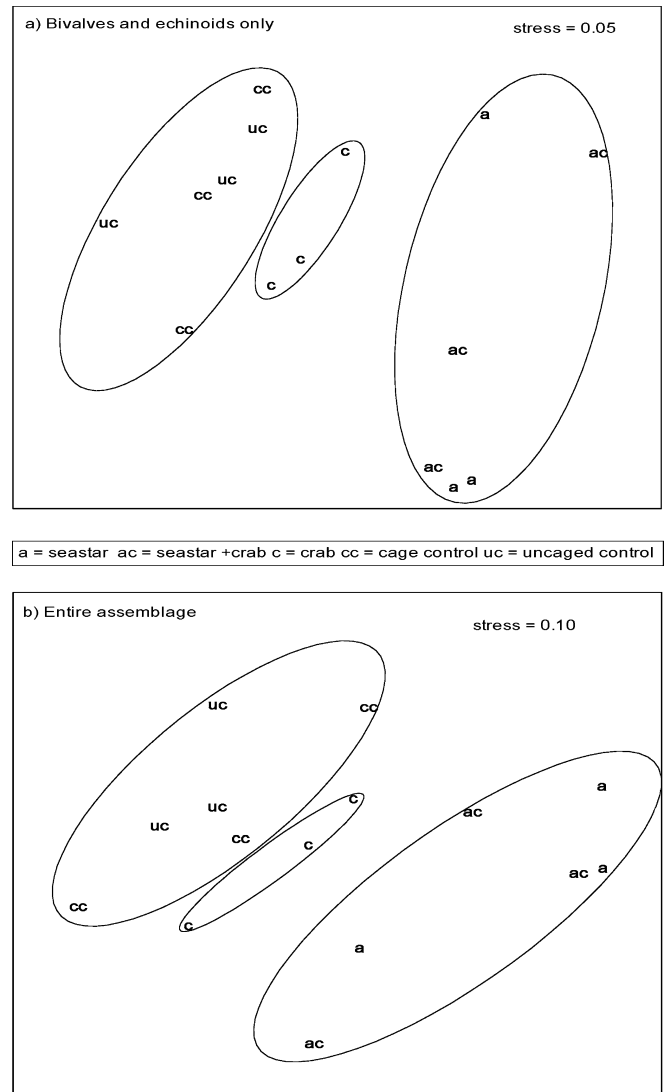


Fig. 4 Ordination (MDS) of treatment plots based: **a** on abundances of bivalves and echinoids and **b** on the entire assemblage. For both ordinations, plots with added seastars separate clearly from plots with only added crabs, and both are distinct to plots without added predators. These groupings have been *outlined with ellipses* for clarity. The grouping is consistent with the general pattern described for the commercial bivalves in the univariate analysis. Note that the mean number per core in each treatment plot was used to estimate the number per square meter for taxa found in cores for this comparison

other species including polychaetes when the bivalve became rare. While the commercial bivalves were clearly preferred over polychaetes in our short-term experiment, had the experiment run longer *A. amurensis* may have switched to polychaetes when the bivalves were exhausted.

Caging effects

Caging experiments are recognised as a valuable tool in examining the effect of predators on marine communities

(see Peterson 1979; Thrush 1999); however, the potential for cage artefacts to confound true treatment effects is well recognised (e.g. Hulberg and Oliver 1980; Underwood 1986). By undertaking the experiment immediately beyond the current range of the seastar in a similar but unimpacted area, the contrast of open plots with empty cages provides a straightforward test for most cage artefacts. In our experiments, there were no significant effects detected in making this comparison. However, it was not possible to control for cage effects on predator behaviour, and so we must assume that the cage has not greatly affected the behaviour of the predators. In this context an important point to emphasise is that both seastar (Nojima et al. 1986; Grannum et al. 1996; Ling 2000) and crab (Crothers 1968; Jensen and Jensen 1985; McKinnon 1997) densities similar to and substantially higher than those we used in the cages have been recorded in Tasmania and in their native ranges, and that these high densities have persisted for periods much longer than our experimental period. Thus, we suggest it is reasonable to expect similar effects on native species should the predators attain the densities used in this experiment.

Impacts of *Asterias amurensis*

In this study, densities of the commercial bivalves were ~ 80 individuals m^{-2} lower for *Fulvia tenuicostata* and ~ 5 individuals m^{-2} lower for *Katelysia rhytiphora* in the presence of seastars at a density of 1 individual m^{-2} compared with the cage control. Recently opened shells were far more abundant in the presence of seastars compared with the cage control for both bivalve species, indicating that seastar predation was largely responsible for the differences in densities between treatments. These results have been supported from feeding observations in non-experimental areas both in the Derwent Estuary and in a recently invaded area outside the estuary, where aggregations of seastars consumed virtually all the *F. tenuicostata*, as anticipated from this and other experiments (Ross et al. 2002, 2003a, 2003b).

The results of the present study are consistent with observations in the native habitat of the seastar, where it is a major predator of bivalves, including cockles, oysters, scallops and other clams (Hatanaka and Kosaka 1959; Kim 1969; Nojima et al. 1986). In the Derwent Estuary, Grannum et al. (1996) calculated electivity indices based on field data; they found that *A. amurensis* was highly selective for bivalves and concluded that predation by *A. amurensis* posed a serious threat to many bivalve species, particularly the populations of *Chioneryx striatissima* and *Venerupis* spp., within the estuary. For many bivalve species such as *F. tenuicostata* and *K. rhytiphora* live large adults are rare in the Derwent Estuary, despite the presence in the sediments of numerous remains (intact shells) of large individuals. This is disturbing given the high prevalence of juveniles in the sediments and the diet of *A. amurensis* (Lockhart

1995; Morrice 1995; L. Turner, personal communication). The results of the present experiment are consistent with the hypothesis that predation by *A. amurensis* is responsible for the rarity of adult *F. tenuicostata* and *K. rhytiphora* in the Derwent Estuary. Moreover, in a recent study, the seastar was shown to have a major impact on the survivorship of juvenile *F. tenuicostata* in the Derwent Estuary, effectively arresting a massive settlement event (Ross et al. 2002).

Impacts of *Carcinus maenas*

Although there was no significant effect of *C. maenas* on *F. tenuicostata* in the experiment, the pattern of abundance of live *F. tenuicostata* and hinges remaining after predation events are consistent with predation by the crab. The abundance of *F. tenuicostata* in the presence of the crab was $\sim 50\%$ lower than in the control treatments. Hinges were far more abundant in the presence of crabs compared with treatments in which the crab was absent, indicating that crab predation was largely responsible for the differences in densities between treatments. Furthermore, a comparison of the size frequency of *F. tenuicostata* in the cage control and crab treatment indicates that *C. maenas* consumed the majority of small bivalves (> 25 mm). It is likely that *C. maenas* is unable to prey on larger bivalves. Comparable size constraints have been recorded for similar-sized *C. maenas* feeding on other cockles, such as *Mercenaria mercenaria* (Walne and Dean 1972), *Katelysia rhytiphora* (McKinnon 1997; Walton et al. 2002) and *Cerastoderma edule* (Mascaró and Seed 2000). Similarly, size constraints in handling prey explain the absence of a detectable effect on *K. rhytiphora*, given that the majority of *K. rhytiphora* in this experiment were large (> 25 mm).

In similar short-term experiments in intertidal soft-sediment habitats, *C. maenas* predation was shown to significantly reduce the abundance of the bivalves *Paphies erycinaea*, *K. rhytiphora* and *K. scalarina* in Tasmania (McKinnon 1997; Walton et al. 2002), and the bivalves *Nutricola confusa* and *N. tantilla* in California (Grosholz and Ruiz 1995). These earlier studies indicate that predation by *C. maenas* is likely to impact populations of small bivalves in both intertidal and subtidal soft-sediment habitats where it becomes abundant, including Tasmania. Although our results did not demonstrate a significant effect of *C. maenas* predation, despite a large decline in bivalve density, we interpret this as a lack of statistical power due to the relatively high variation among plots compared to the previous studies.

Interactions of *A. amurensis* and *C. maenas*

The presence of *C. maenas* appeared to have no effect on *K. rhytiphora* predation by *A. amurensis*. This likely resulted from an absence of small individuals of this bivalve and the inability of *C. maenas* to consume large

ones. In contrast, the individual effects of each predator on *F. tenuicostata* were influenced by the presence of the other species. Fewer *F. tenuicostata* were consumed by *C. maenas* in the presence of the seastar compared with when it was alone. Although similar numbers of *F. tenuicostata* were consumed by *A. amurensis* in the presence of *C. maenas* compared with when it was alone, the seastar consumed larger bivalves when the crab was present. Thus, the interaction between *C. maenas* and *A. amurensis* appears to be direct competition for resources, resulting in the partitioning of bivalves according to size. *C. maenas* consumes only small bivalves. The seastar eats all sizes of *F. tenuicostata* in the absence of crabs, but predominately eats larger bivalves when the crab is present.

Conclusions

The results of this short-term manipulative experiment are consistent with other recent studies conducted in Tasmania, which collectively suggest that predation by *A. amurensis* and *C. maenas* may have a large impact on bivalve populations in sheltered soft-sediment habitats in Tasmania where they become abundant (e.g. Ross et al. 2002, 2003a, 2003b; Walton et al. 2002; Ruiz et al., unpublished data). Should the distribution of these two predators overlap, the combined effect on bivalve populations may be greater than that due to each predator alone, simply because their combined distribution covers a broader range of habitats: *C. maenas* occurs predominately in the intertidal through to the shallow subtidal, while *A. amurensis* occurs predominately in the shallow through to depths > 30 m. Furthermore, in the shallow subtidal, where spatial overlap is most likely, the results of this study indicate that the effect of each predator is likely to be modified in the presence of the other should they attain the densities used in this experiment.

We expect the interactive effects of these two predators to vary due to changes in the composition of assemblages and predator behaviour. Recent work has demonstrated that the nature of seastar effects is likely to be site and time specific given the inherent natural variability in soft-sediment assemblages and the seastar's responses to them (Ross et al. 2003a). The current experiments provide a first test of interactive effects under those conditions, and the biological prey community, present for one place and time. Overall, the results of this study further highlight the need to examine the combined effects of multiple introduced species when sympatry is likely.

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