

Variability in the impact of an introduced predator (*Asterias amurens*: Asteroidea) on soft-sediment assemblages

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Abstract

The introduction and establishment of the predatory asteroid *Asterias amurens* in coastal waters of southern Australia is considered a major threat to benthic marine assemblages and commercial bivalve species. We compare the impact of the seastar in experiments on three soft-sediment assemblages. The experiments were carried out immediately beyond the current range of the seastar in southeast Tasmania. This allows us to assess the repeatability, and hence predictability, of the type and magnitude of the impact of *A. amurens* on soft-sediment assemblages. Responses to manipulations at the species level were dissimilar across the three experiments, reflecting marked initial differences in the three assemblages at both the species and functional group levels. However, at the functional group level, there were notable similarities in the impact of the seastar on the different assemblages. When potential prey taxa were separated into functional groups reflecting ecological availability (e.g. surface dwelling vs. deep burrowing bivalves), seastar effects were largely restricted to the surface bivalves. While the effect of seastar predation on surface bivalves was common in all three assemblages, the magnitude of the impact varied both among and within assemblages. Variability in the impact of *A. amurens* at both levels appeared to be largely due to differences in relative availability of prey species. Overall, the results of these experiments indicate that while the impact of the seastar is broadly predictable at the functional group level, the exact

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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.

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1. Introduction

Globalisation of the marine environment has become a major concern as the number of human-mediated introductions of exotic species continues to accumulate (Carlton, 1992; Carlton and Geller, 1993; Lafferty and Kuris, 1994; Cohen and Carlton, 1998; Ruiz et al., 2000). Most often, species are already widely established before they are first discovered with the result that eradication attempts are often not feasible. Management priorities for established exotic species are largely based on immediate, and in particular on the anticipated, impacts on native assemblages and/or commercial species. However, if the nature and/or magnitude of impact is variable, then assessing current and predicting future impacts of exotic species may be difficult (see Elton, 1958; Thompson et al., 1987; Andow et al., 1990). While it is increasingly evident that invasions can trigger fundamental changes to population, community and ecosystem processes (Nichols et al., 1990; Cloern, 1996; Grosholz et al., 2000), quantitative data on the impacts of most introduced species in the marine environment are limited, and the amount of variability (spatial and temporal) of the direct and indirect effects remains uncertain.

Relatively few studies of introduced marine species have investigated variability in impacts (but see Allmon and Sebens, 1988; Nichols et al., 1990; Grosholz and Ruiz, 1996). Ruiz et al. (1999) suggested that spatio-temporal variability in impacts of introduced species in Chesapeake Bay stems primarily from space–time patterns of density of the exotic species. However, they also noted the potential for variation in impact independent of density. Studies of impacts of native species have revealed several factors that may influence the nature and magnitude of effects of introduced species. These include the density of the impacting species and its potential prey, water temperature, current velocity, turbidity, the nature of functional responses and sediment characteristics (e.g. Lipcius and Hines, 1986; Woodin, 1978; Everett and Ruiz, 1993; Skilleter, 1994; Thrush, 1999).

The introduction and establishment of the asteroid *Asterias amurensis*, a voracious generalist predator, is considered a major threat to benthic marine communities and commercial species in Tasmania (Grannum et al., 1996; Lockhart and Ritz, 1998; Ross et al., 2002). In its native range, the seastar causes considerable damage to commercial shellfishes (e.g. oysters, cockles, scallops, other clams; Hatanaka and Kosaka, 1959; Kim, 1969; Nojima et al., 1986) and feeds opportunistically on a variety of other epifaunal and infaunal species including other molluscs, ascidians, bryzoans, sponges, crustaceans, polychaetes, fish and echinoderms (Hatanaka and Kosaka, 1959; Fukuyama and Oliver, 1985; Fukuyama, 1994).

Despite the strong rhetoric and publicity surrounding the establishment of *A. amurensis* in Tasmania (e.g. McLoughlin and Thresher, 1994), the impact of the seastar on native assemblages had not been examined directly or quantitatively until recently (Ross et al., in

press). Feeding observations suggest that the impact of the seastar may vary depending on the composition and relative availability of prey taxa, both of which are spatially and temporally variable (Ross et al., 2002). In this study we assess variability (incorporating elements of both spatial and temporal variation) in the impact of *A. amurensis* in experiments on three soft-sediment assemblages in southeast Tasmania.

2. Methods

2.1. Experimental sites and protocol

Manipulative experiments were conducted on soft-sediment assemblages in three sheltered bays in southeast Tasmania at a depth of 3–5 m (Fig. 1). The sediment at these sites is composed predominantly of fine sands (Ross, unpublished data). The habitat type at each site is common in other areas of the Derwent Estuary and adjoining bays and estuaries. The experiments ran for ≈ 2 months, commencing in April 1997, May 1998 and July 1999 at Murdunna, Conningham and Saltwater River, respectively. Because the experiments were necessarily carried out at different times, it is not our intention to distinguish either spatial or temporal components of variability in impacts, but simply to assess the variability in impacts among experiments on three soft-sediment assemblages. Because these areas do not currently support populations of *A. amurensis*, to reduce the risk of establishing the seastar, the experiments were conducted in completely enclosed cages and only male seastars were used. All seastars used in experiments had a mean radii length of 110–120 mm.

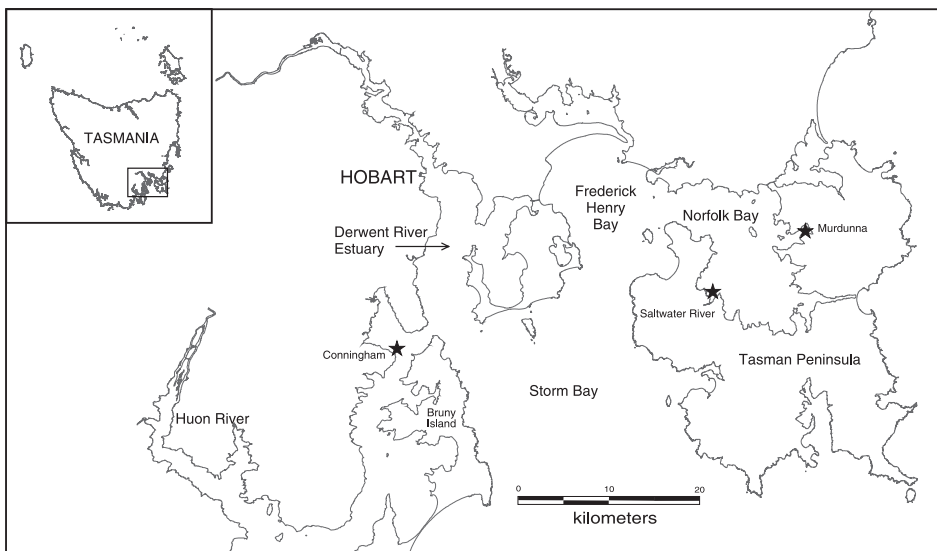


Fig. 1. Map of southeast Tasmania showing study sites at Conningham, Saltwater River and Murdunna.

Cages consisted of a rigid (1×1 m base \times 0.7 m high) steel frame with protruding legs (0.5 m long) to securely anchor the cage in the sediment. The cage top and sides were covered in stiff plastic mesh (6 mm), and the cage legs driven into the sediment so that 100–150 mm of the cage sides was buried to prevent passage of large predators or prey by burrowing. The three treatments used to investigate seastar effects and to test for potential cage effects were follows: I, caged inclusion of a single seastar (thus at a density of 1 m^{-2}); C, cage control without seastars; and P, unmanipulated plots with neither cages nor seastars.

Because of the spatial scale of infauna patchiness indicated in pilot studies, a randomised complete block design was used in which each of the three treatments were represented once (each treatment ≈ 5 m apart) in each of three blocks (≈ 30 m apart). Experiments were monitored weekly to check the condition of the enclosed predators and remove fouling organisms from the cages.

Two months after the commencement of the experiment, cages and seastars were removed, and three replicate cores (150-mm diameter, 100-mm deep) 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. After coring, the entire contents of each plot were sampled to a depth of 0.1 m using a diver operated air-driven suction device. To do this, an open square frame ($1 \text{ m} \times 1 \text{ m} \times 0.1$ m depth) was inserted into the sediment to isolate the plot, and all contents were then vacuumed into a 1-mm mesh bag.

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. Suction samples were sieved a second time through a nested series of sieves (2-, 4- and 8-mm mesh). Bivalves, crabs and the echinoid *Echinocardium cordatum* retained on each sieve size were identified to species and counted. For core samples, all infaunal and epifaunal organisms (>1 mm) were sorted and identified to the lowest taxon that was possible. This entailed identification to class (ostracods, copepods, nemerteans and sipunculids), order (amphipods, isopods, leptostracans, cumaceans and tanaids), family (most polychaetes) or species (bivalves, echinoderms, gastropods and common polychaetes).

2.2. Statistical analysis

2.2.1. Multivariate analysis

To depict and test for differences in the structure of soft-sediment assemblages among the three experiments and between treatments in each experiment, nonmetric MDS and nonparametric MANOVA (Anderson, 2001) were undertaken (on Bray–Curtis distances calculated from 4th root transformed data) using the PRIMER v4.0 (Clarke, 1993) and npMANOVA (Anderson, 2001) programs, respectively. The comparison of assemblages among the experiments used data from the three unmanipulated plots in each experiment. Because the macrofaunal assemblages in each experiment were distinctly different, comparisons among treatments were carried out for each experiment separately. Data for all taxa are densities of individuals (per 1 m^2). For all bivalves, crabs and the echinoid *E. cordatum*, abundance was determined from suction samples. For the remaining taxa abundance was scaled from counts in the three cores in each plot.

A principal components analysis (PCA) and associated biplot was also used to compare assemblages among the experiments at the functional group level. This was conducted on

a covariance matrix after pooling taxa into broad functional groups, viz. surface bivalves (bivalves with short or nonexistent siphons that live on, or just under the sediment surface), deep bivalves (bivalves with long siphons that normally occur deep in the sediments), errant polychaetes, sedentary polychaetes, gastropods, crustaceans and infaunal echinoderms. After pooling in this way, the structure of data was suitable for PCA.

2.2.2. Univariate analyses

For each experiment, univariate statistics were used to examine the effects of treatments on dominant taxa, functional groups (groupings as above), number of species and individuals, and species diversity (Shannon–Weiner).

Responses of bivalves, crabs and the echinoid *E. cordatum* were determined from suction samples. Responses of all remaining taxa were determined from core samples, in which case the arithmetic mean of the three replicate cores taken from each plot was used. To test for seastar and caging effects in each experiment, a randomised complete block ANOVA was conducted, with ‘treatment’ (three levels = I, C and P) as a fixed factor, and ‘block’ as a random factor. 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). The statistical package SAS® was used for analysis.

Two planned comparisons were carried out following the initial analysis for treatment effects. For planned comparisons, we adjusted the significance level using the conservative method of Todd and Keough (1994), i.e. α was reduced to $\alpha/(1 + \text{the number of non-orthogonal contrasts})$. With two non-orthogonal comparisons, the adjusted significance level was 0.016. Following Todd and Keough (1994), the exact probabilities are presented in recognition of the lack of consensus about the appropriate adjustment of the significance level. The contrasts were C vs. I, which assesses the effect of seastars on invertebrate abundances, contrasting treatments with and without seastars in the presence of cages, and C vs. P, which assesses the effect of cages on invertebrate abundances, contrasting treatments with and without cages in the absence of seastars.

3. Results

3.1. Comparison of assemblages between sites

The soft-sediment assemblages in each experiment were significantly different (npMA-NOVA, $F_{2,8} = 10.44$, $P = 0.0002$; Fig. 2). The number of taxa recorded was much higher at Conningham (63) compared with Saltwater River (43) and Murdunna (38). The average density of macro-invertebrates was also highest at Conningham ($2766 \text{ m}^{-2} \pm 362 \text{ S.E.}$), followed by Murdunna ($1778 \text{ m}^{-2} \pm 351 \text{ S.E.}$) and Saltwater River ($973 \text{ m}^{-2} \pm 222 \text{ S.E.}$). The separation of assemblages among experiments was also distinct at the functional group level (Fig. 3a). The biplot analysis (Fig. 3b) shows that Conningham and Murdunna had higher densities of sedentary polychaetes than did Saltwater River. The assemblage at Conningham was also characterised by much higher densities of crustaceans compared with the other two assemblages, whereas Murdunna had much higher densities of errant

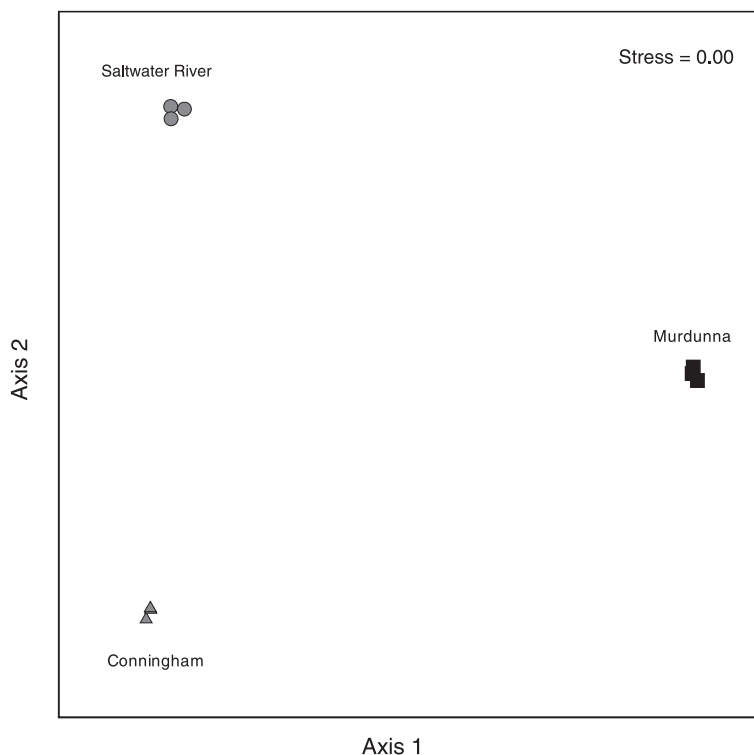


Fig. 2. Ordination (MDS) of unmanipulated plots at each site based on Bray–Curtis matrix of 4th root transformed data of densities of macro-benthic species. The macro-benthic assemblages are distinctly different at each site.

polychaetes compared with the two other assemblages. At Murdunna, one of the plots (no. 3) supported three times the density of polychaetes observed in other plots in this experiment. Given vastly different assemblages in each experiment, it was not sensible to include effects of ‘experiment’ in the analysis of treatment effects. Thus, responses to treatments were analysed separately for each experiment.

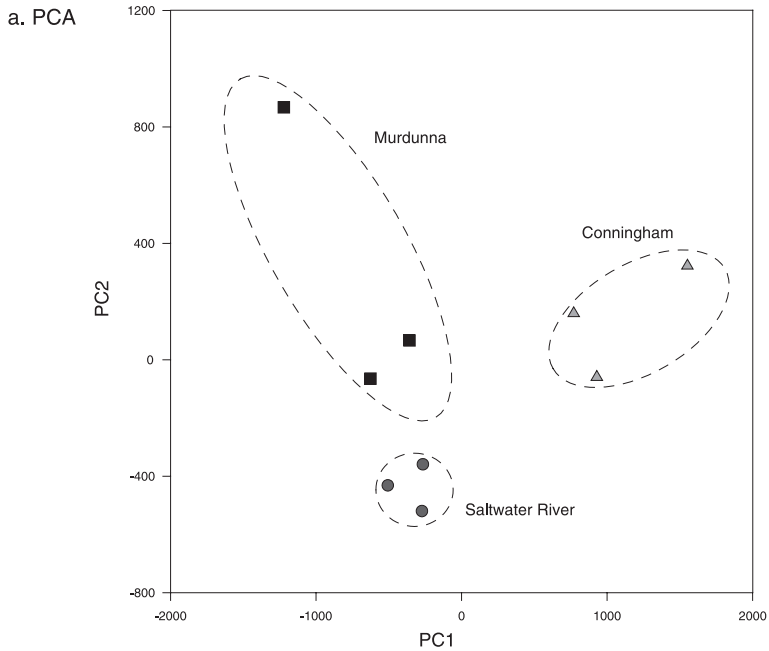
3.2. Responses to experimental treatments at each site

3.2.1. Murdunna

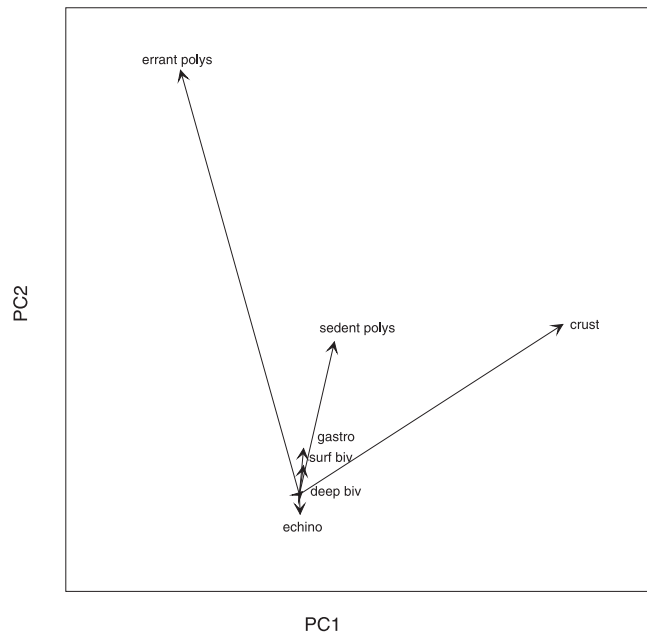
The most abundant taxa were the errant polychaetes *Simplisetia amphidonta* and *Glycera* spp.; the sedentary polychaete *Lysilla jennacubinae*; surface bivalves *Fulvia*

Fig. 3. (a) The PCA plot of functional groups in unmanipulated plots ($n=3$) across sites (M=Murdunna; S=Saltwater River; C=Conningham) shows distinct differences between sites. Principal components 1 and 2 accounted for 94% of the total variance. (b) The associated biplot that identifies the groups most responsible for the patterns shown in the PCA plot (see text for interpretation) which include (crust) crustaceans, (errant polys) errant polychaetes, (sedent polys) sedentary polychaetes, (surf biv) surface dwelling bivalves, (deep biv) deep burrowing bivalves, (gastro) gastropods and (echino) echinoderms.

tenuicostata, *Katelysia rhytiphora* and *Wallucina assimilis*; deep bivalves *Theora* spp. and *Laternula rostrata*; amphipods; gastropods (largely *Dialla variata*); and the echinoid *E. cordatum*.



b. Biplot



3.2.1.1. Seastar effects. The MDS ordination comparing differences among treatments showed that assemblages with and without seastars in the presence of cages among treatments were clearly separated; however, the analysis indicated that differences among treatments were not significant at the level of $\alpha=0.05$ (npMANOVA, $F_{2,8}=2.72$, $P=0.059$; Fig. 4a). However, at the univariate level, there was a significant reduction in the abundance of the surface bivalves *F. tenuicostata* (accounting for $\approx 85\%$ of the surface bivalves) and *K. rhytiphora* in the presence of seastars (Table 1a, Fig. 5).

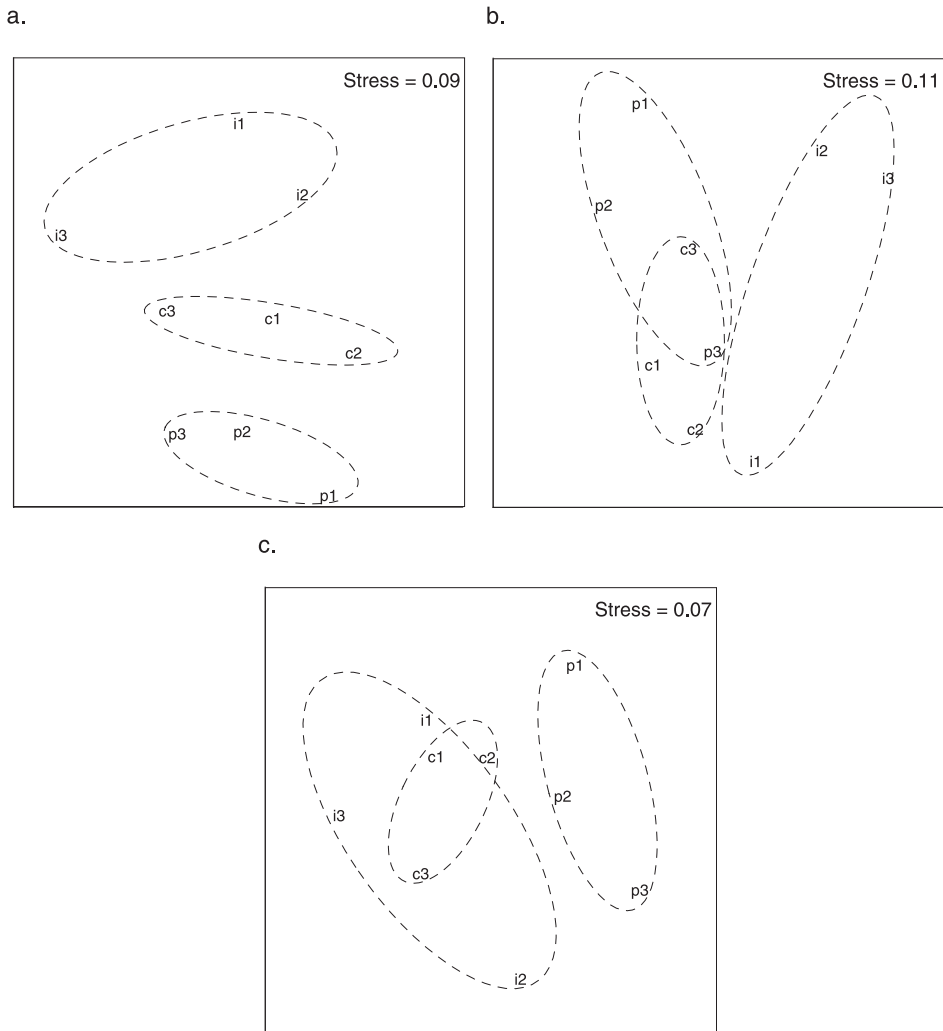


Fig. 4. Ordination (MDS) plots comparing assemblages among experimental treatments at (a) Murdunna, (b) Saltwater River and (c) Conningham. Plots for each site are based on a Bray-Curtis matrix of 4th root transformed data of the densities of macro-benthic species.

Abundances of *W. assimilis* and *L. rostrata* were also lower in the presence of seastars compared with the two control treatments (Fig. 5), although these differences were not significant (Table 1a).

3.2.1.2. Caging effects. The MDS ordination comparing differences among treatments showed that assemblages with and without cages in the absence of seastars were separated; however, these differences were not significant (npMANOVA, $F_{2,8}=2.72$, $P=0.059$; Fig. 4a). At the univariate level, there was a negative effect of caging on the total number of individuals, the abundance of the errant polychaete *S. amphidonta* and the functional group as a whole (largely attributable to *S. amphidonta*). However, the difference was not significant for errant polychaetes at the adjusted alpha level (Table 1a; Fig. 5). Although the abundance of sedentary polychaetes was also lower in the caging treatments than in the unmanipulated plots, this difference was not significant (Table 1a; Fig. 5). The results for crustaceans (primarily amphipods) and, to a lesser extent, gastropods are also indicative of a caging effect (Fig. 5). However, this is due to a high count of amphipods and gastropods in one of the three unmanipulated plots and does not reflect a consistent difference between the cage control and unmanipulated plot in each block.

3.2.2. Saltwater river

The most abundant taxa were amphipods; gastropods (largely *D. variata*); crabs (largely *Nectocarcinus integrifrons*); sedentary capitellid polychaetes; the errant polychaete *Nephtys australiensis*; the echinoid *E. cordatum*; the surface bivalves *F. tenuicostata*, *Mysella donaciformis*, *Musculus impacta* and *W. assimilis*; and the deep bivalve *Theora* spp. It should be noted that 2 weeks into the experiment, an aggregation of *A. amurensis* (not previously recorded at the site) moved into the experimental area. While the majority (≈ 1500) were collected and removed from the site, almost all were feeding. Thus, we interpret the comparison between the caged and uncaged control cautiously given that the incursion of seastars may have affected macro-invertebrates in the unmanipulated plots.

3.2.2.1. Seastar effects. The MDS ordination showed that assemblages with and without seastars in the presence of cages were separated but not tightly clumped (Fig. 4b). The lack of distinct separation in this pattern was reflected in the npMANOVA test, which did not identify significant treatment effects at the level of $\alpha=0.05$ ($F_{2,8}=2.10$, $P=0.218$; Fig. 4a). Species diversity and the abundance of *F. tenuicostata* and *M. donaciformis* (and the functional group of surface bivalves) were reduced in the seastar inclusion compared with the caged control, indicative of a seastar effect (Fig. 6). However, this difference was only significant at the adjusted alpha level for *F. tenuicostata* (which accounted for $\approx 56\%$ of the surface bivalves) and surface bivalves as a group (Table 1b). Sedentary polychaetes (largely capitellids) and gastropods were also less abundant in the seastar inclusion compared to the cage control; however, these differences were not significant (Table 1b; Fig. 6). In contrast, the abundance of amphipods was higher in the presence of seastars; however, this difference was also not significant at the adjusted alpha level (Table 1b; Fig. 6).

Table 1

Analysis of effects of seastar predation and caging effects on the total number of species and individuals, species diversity, and abundances of functional groups and common taxa in experiments at (a) Murdunna, (b) Saltwater River and (c) Conningham

	Main analysis			Planned comparisons	
	MS _{resid}	Block	Treat	C vs. P	C vs. I
<i>(a) Murdunna</i>					
Degrees of freedom	4	2	2	1	1
Total individuals	62,035	0.052	0.023	0.013	0.772
Total species	12.611	0.510	0.398	0.275	0.914
Species diversity (H')	0.006	0.036	0.522	0.292	0.716
Surface bivalves	356.03	0.096	0.005	0.733	0.004
<i>Fulvia tenuicostata</i>	0.0352	0.042	0.001	0.767	0.000
<i>Katelysia rhytiphora</i>	1.9444	0.805	0.008	0.429	0.008
<i>Wallucina assimilis</i>	4.2225	0.929	0.333	0.673	0.173
Deep bivalves	214.59	0.003	0.661	0.487	0.912
<i>Theora</i> spp.	0.0305	0.005	0.413	0.450	0.551
<i>Laternula rostrata</i>	2.8333	0.092	0.080	0.123	0.292
Errant polychaetes	36,746	0.013	0.097	0.046	0.532
<i>Simplisetia amphidonta</i>	5.8426	0.020	0.006	0.010	0.586
<i>Glycera</i> spp.	0.2329	0.139	0.124	0.141	0.457
Sedentary polychaetes	0.6313	0.482	0.715	0.442	0.659
<i>Lysilla jennacubinae</i>	0.8272	0.212	0.660	0.420	0.496
Crustaceans	6.8748	0.317	0.284	0.487	0.284
Amphipods	6.5151	0.439	0.402	0.735	0.335
Echinoderms					
<i>Echinocardium cordatum</i>	0.0011	0.129	0.877	0.828	0.630
Gastropods	3894.1	0.108	0.415	0.213	0.571
<i>(b) Saltwater River</i>					
Degrees of freedom	4	2	2	1	1
Total individuals	0.145	0.518	0.683	0.567	0.423
Total species	4.611	0.434	0.043	0.318	0.056
Species diversity (H')	0.001	0.840	0.024	0.648	0.020
Surface bivalves	47.020	0.123	0.008	0.018	0.003
<i>Fulvia tenuicostata</i>	0.0274	0.872	0.003	0.089	0.001
<i>Musculus impacta</i>	1.7778	0.038	0.105	0.099	0.573
<i>Mysella donaciformis</i>	3.4444	0.211	0.026	0.012	0.030
<i>Wallucina assimilis</i>	0.1336	0.844	0.540	0.287	0.486
Deep bivalves	14.806	0.635	0.028	0.014	0.538
<i>Theora</i> spp.	0.0113	0.612	0.026	0.012	0.354
Errant polychaetes	8638.2	0.943	0.770	0.757	0.497
<i>Nephtys australiensis</i>	5099.9	0.855	0.820	0.763	0.553
Sedentary polychaetes	5099.9	0.384	0.362	0.553	0.181
Capitellids	4309.2	0.327	0.399	0.458	0.201
Crustaceans	21,129	0.627	0.368	0.601	0.187
Crabs	5.7778	0.621	0.014	0.009	1.000
Amphipods	15,457	0.552	0.180	0.862	0.103
Echinoderms					
<i>Echinocardium cordatum</i>	1294.0	0.059	0.306	0.215	0.884
Gastropods	1.6179	0.344	0.486	0.970	0.311

Table 1 (continued)

	Main analysis			Planned comparisons	
	MS _{resid}	Block	Treat	C vs. P	C vs. I
<i>(c) Conningham</i>					
Degrees of freedom	4	2	2	1	1
Total individuals	0.45	0.072	0.630	0.415	0.961
Total species	42.33	0.866	0.817	0.602	0.602
Species diversity (<i>H'</i>)	0.046	0.609	0.769	0.665	0.500
Deep bivalves	265.39	0.864	0.195	0.099	0.171
<i>Theora</i> spp.	0.0106	0.000	0.011	0.019	0.005
Errant polychaetes	6523.1	0.948	0.884	0.722	0.929
Sedentary polychaetes	72,445	0.714	0.974	0.893	0.936
<i>Pectinaria</i> sp.	30,520	0.201	0.976	0.901	0.836
Capitellids	2376.4	0.463	0.851	0.961	0.626
Crustaceans	201,103	0.070	0.624	0.427	0.987
Amphipods	112,770	0.022	0.953	0.949	0.781
Ostracods	19,253	0.374	0.116	0.050	0.309
Echinoderms	558.85	0.416	0.316	0.723	0.263
Holothurians	50.516	0.408	0.408	0.736	0.222
<i>Echinocardium cordatum</i>	10.903	0.256	0.476	0.715	0.413
Gastropods	6997.5	0.499	0.370	0.267	0.215
<i>Nassarius nigellus</i>	2767.4	0.836	0.670	0.505	0.891

Results are of the overall ANOVA comparing among treatments I (cage inclusion, a single seastar added), C (cage control, seastars absent) and P (unmanipulated plot, seastars absent^a), and of the two planned comparisons. The comparison C vs. P tests for the effect of the cage, while C vs. I is the principal comparison of interest to test for the effect of the seastar. Significant *P* values are shown in bold face: *P* values <0.05 are significant for the main analysis, and *P* values <0.016 are significant for the planned comparisons.

^a There was unforeseen incursion of seastars at Saltwater River during the course of the experiment (see text for details).

3.2.2.2. Caging effects. The MDS ordination comparing differences among treatments showed that assemblages with and without cages in the absence of seastars were similar (Fig. 4b). The npMANOVA test confirmed this pattern showing no significant treatment effects ($F_{2,8} = 2.10$, $P = 0.218$; Fig. 4). Considering individual taxa, with the exception of *M. impacta*, the abundance of each of the major surface bivalves (and thereby for the functional group as a whole) and the echinoid *E. cordatum* was higher in the cage controls without seastars than in the unmanipulated plots (Fig. 6). However, this difference was only significant for *M. donaciformis* at the adjusted alpha level (Table 1b). In contrast, the abundance of crabs (largely *N. integrifrons*), *Theora* spp. and the deep bivalve functional group (largely attributable to *Theora* spp.) were significantly lower in the caged plots without seastars compared with the unmanipulated plots (Fig. 6; Table 1b).

3.2.3. Conningham

The most abundant taxa were amphipods; ostracods; the sedentary polychaetes *Pectinaria* sp. and capitellids; the surface bivalves *Electroma georgina* (epifaunal), *W. assimilis*, *Timoclea cardoides*, *Corbula gibba* and *F. tenuicostata*; deep bivalves *Theora* spp. and *Gari livida*; the gastropod *Nassarius nigellus*; the echinoid *E. cordatum* and holothurians.

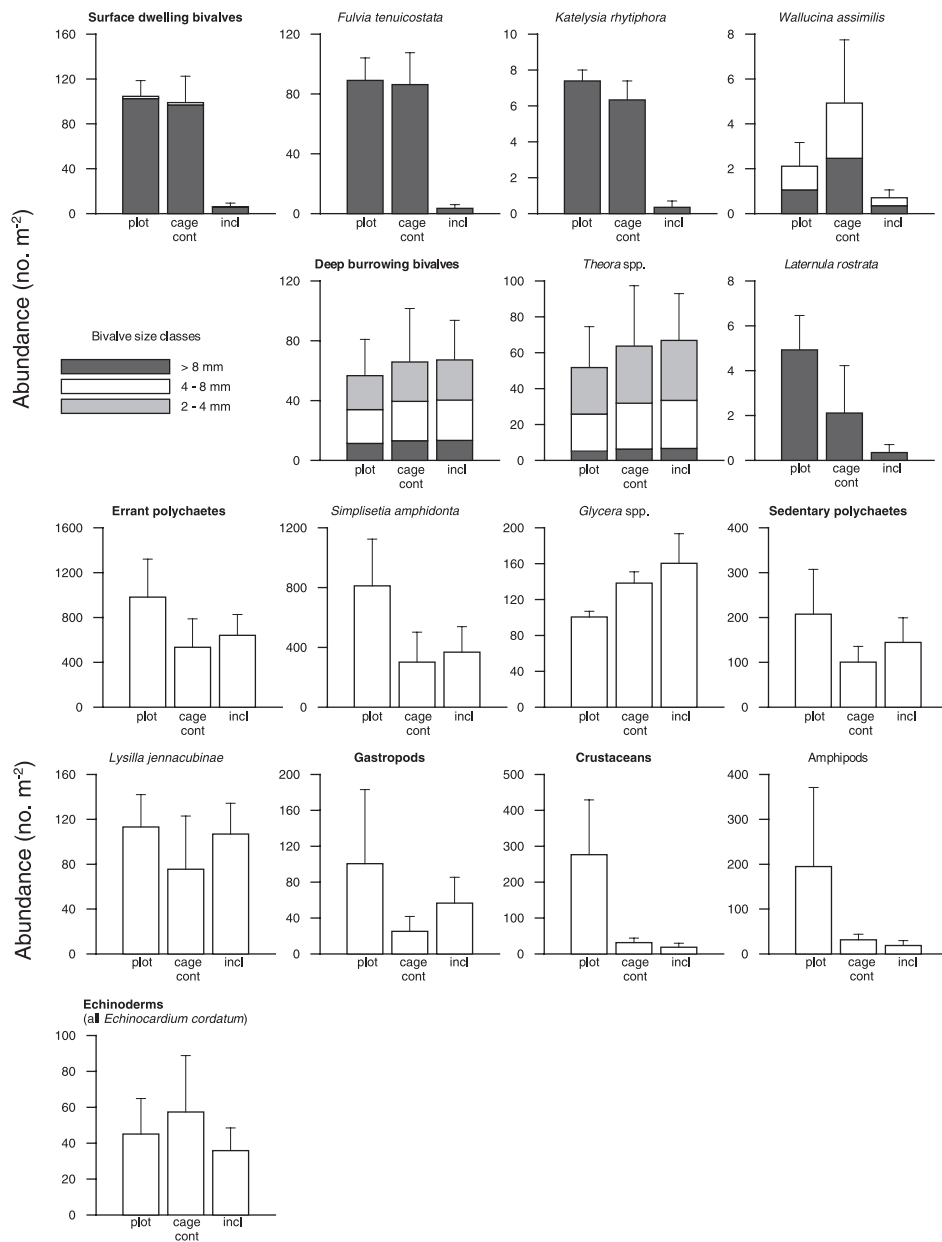


Fig. 5. Densities of functional groups and common taxa in each treatment at Mardunna. Data for all groups and taxa are means per 1 m^2 (+S.E.). For bivalves and *E. cordatum*, the data are obtained from 1-m^2 suction samples ($n=3$ plots per site). For the remaining taxa, the means are scaled from counts in three cores (each 150-mm diameter, 100-mm deep) in each plot. The proportion of bivalves retained on 2-, 4- and 8-mm mesh is also depicted.

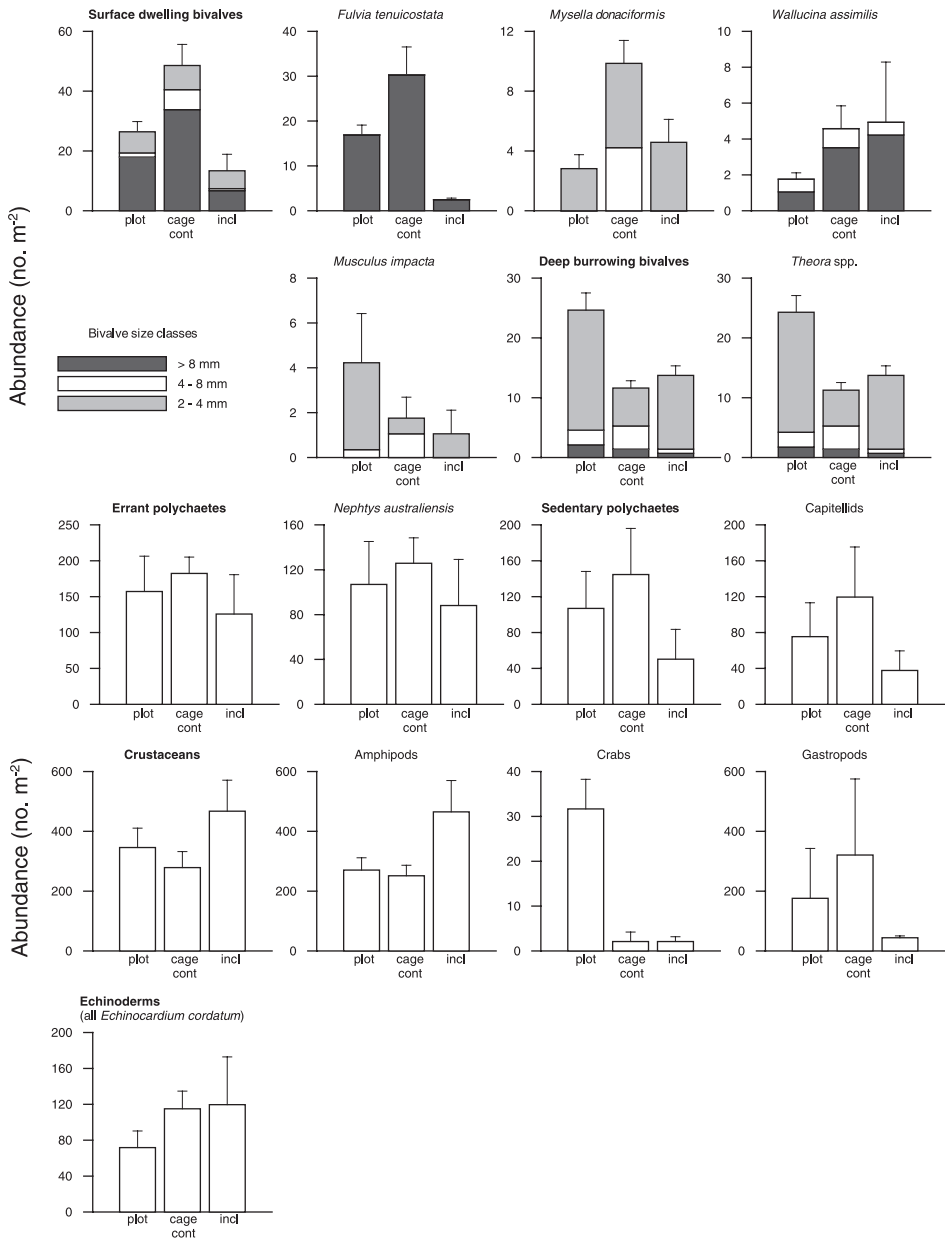
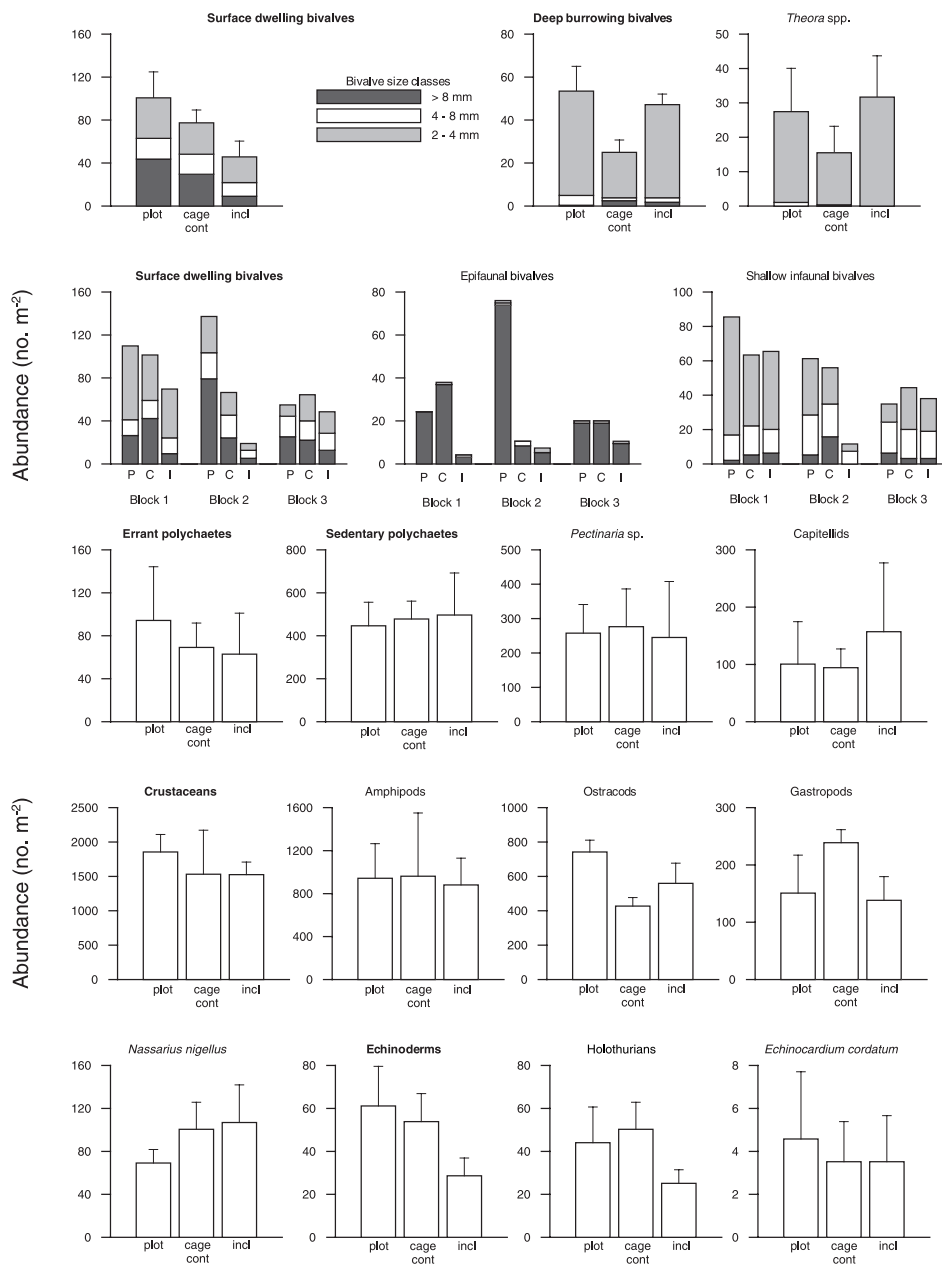


Fig. 6. Densities of functional groups and common taxa in each treatment at Saltwater River. Data for all groups and taxa are means per 1 m^2 (+S.E.). For bivalves and *E. cordatum*, the data are obtained from 1-m^2 suction samples ($n=3$ plots per site). For the remaining taxa, the means are scaled from counts in three cores (each 150-mm diameter, 100-mm deep) in each plot. The proportion of bivalves retained on 2-, 4- and 8-mm mesh is also depicted.

3.2.3.1. Seastar effects. Assemblages in treatments with and without seastars in the presence of cages were overlapping in MDS space (Fig. 4c). The npMANOVA test confirmed this pattern showing no significant treatment effects ($F_{2,8} = 1.96$, $P = 0.266$). The mean abundance of gastropods, holothurians and echinoderms as a whole (largely



attributable to holothurians) was reduced in the seastar inclusion compared with the cage control; however, these differences were not significant (Fig. 7; Table 1c). While the mean abundance of surface bivalves was also reduced in the seastar inclusion compared with the two control treatments, the magnitude of this difference varied markedly between blocks suggesting a treatment by block interaction (Fig. 7). Several interesting patterns were apparent when surface bivalves as a group were separated into epifaunal (*E. georgina* accounted for 99% of epifaunal bivalves) and infaunal groups, and examined at the level of blocks (Fig. 7). In two of the three blocks (blocks 1 and 3), the abundance of epifaunal bivalves, but not infaunal bivalves, was lower in the seastar inclusion cage compared with the caged and uncaged controls. In contrast, in block 2, the total abundance of infaunal bivalves (and each species separately) was lower in the seastar inclusion than in either of the control treatments (Fig. 7). Given that there was no characteristic shell remains of *E. georgina* recorded in either of the caged treatments in block 2, it appears that this epifaunal bivalve either emigrated from the cages or, more likely, was absent or rare in the plot when the cages were initially established. Either way, it is clear that the number of epifaunal bivalves present in caged treatments in block 2 was low compared with the other blocks.

3.2.3.2. Caging effects. Assemblages in treatments with and without cages in the absence of seastars were separated in MDS space; however, the npMANOVA test did not detect significant treatment effects ($F_{2,8} = 1.96$, $P = 0.266$; Fig. 4c). The mean abundance of *Theora* spp., the deep bivalves' functional group to which they belong (largely attributable to *Theora* spp.), and ostracods were reduced in the caged compared with the unmanipulated plot (Fig. 7). However, none of these differences were significant at the adjusted alpha level (Table 1c).

4. Discussion

4.1. Variability in assemblages

Marine soft-sediment assemblages are characterised by variability in the distribution and abundance of benthic organisms (e.g. Rhoads, 1974; Gray, 1981; Underwood, 1992; Morrissey et al., 1992a,b; Schmitt and Osenberg, 1996; Thrush, 1999). However, in Tasmania, variability in the distribution and abundance of benthic organisms in subtidal soft-sediment habitats has only been examined in a few published studies (Moverley and Jordan, 1996; Edgar et al., 1999). In this study the soft-sediment assemblages in each of three experiments were distinctly different. This is not surprising given that the experi-

Fig. 7. Densities of functional groups and common taxa in each treatment at Conningham. Data for all groups and taxa are means per 1 m² (+ S.E.). For bivalves and *E. cordatum*, the data are obtained from 1-m² suction samples ($n = 3$ plots per site). For the remaining taxa, the means are scaled from counts in three cores (each 150-mm diameter, 100-mm deep) in each plot. The proportion of bivalves retained on 2-, 4- and 8-mm mesh is also depicted. Note that for surface bivalves as a whole, and component groups of epifaunal and infaunal bivalves, the total number of individuals in each treatment in each block is displayed as evidence of an interaction of experimental treatments with block.

ments were conducted at different sites and at different times. There were major differences in species composition and abundance patterns of macro-invertebrates in each assemblage, and the distinction was also evident at the functional group level. There were also differences in the number of taxa and average density of macro-invertebrates in each assemblage. At the functional group level, the assemblage at Conningham was dominated by crustaceans (largely amphipods and ostracods), whereas at Murdunna, errant polychaetes (largely *S. amphidonta*) were the most abundant group. Both of these assemblages were characterised by a greater abundance of sedentary polychaetes compared with Saltwater River. At Saltwater River, the assemblage with the lowest overall abundance of macro-invertebrates, the more common groups were crustaceans (largely amphipods), gastropods (largely *D. variata*), errant and sedentary polychaetes (largely *N. australiensis* and capitellids, respectively) and echinoderms (all *E. cordatum*). Given the marked differences in the assemblages, it is not surprising that responses to manipulations were qualitatively different at the species level across the experiments.

4.2. Caging effects

Although caging experiments are generally considered to be a valuable tool in examining how predators influence the structure of marine communities (see Peterson, 1979; Ólafsson et al., 1994; Thrush, 1999), the potential for cage artefacts to confound true treatment effects is well recognised (e.g. Hulberg and Oliver, 1980; Underwood, 1986; Hall et al., 1990; Thrush, 1999). Potential artefacts of particular concern in our study include effects of altered water movement and light, and effects of inclusion and/or exclusion of other potential predators. To minimise altering hydrodynamic conditions, we chose a large mesh size (since we were examining the effect of a large predator), and kept the cages relatively free of fouling. Furthermore, hydrodynamic effects of cages are likely to be minimal in habitats where flow velocities are naturally low (see Ólafsson et al., 1994), as was the case in all experiments in the present study.

By undertaking experimental manipulations immediately beyond the current range of the seastar in similar but unimpacted areas, the contrast of open plots with empty cages provides a straightforward test for cage artefacts. Significant caging effects were detected for the errant polychaete *S. amphidonta* (↓) at Murdunna, and *Theora* spp. (↓), the deep bivalves' functional group (largely attributable to *Theora* spp.) (↓) and *M. donaciformis* (↑) at Saltwater River. There are a number of possible cage artefacts that may explain the changes in abundance in the presence of cages. Interestingly, all of these taxa that responded to cages are relatively mobile and small in size, and are thus able to move freely into or out of cages. Furthermore, they are unlikely to be significant consumers of the taxa for which seastar effects were detected. However, at Saltwater River, an unforeseen invasion of a large aggregation of *A. amurensis* (not previously recorded at the site) and influx of the crab *N. integrifrons* during the experiment may have confounded the test for caging effects. Of the 1500 seastars that were removed during the experiment, ca. 80% were feeding, consuming *F. tenuicostata* exclusively (with the exception of one seastar). Given that *N. integrifrons* also feeds on bivalves, predation by both species on surface bivalves could explain why the abundance of surface bivalves was lower in open plots compared with cage controls (in which both predators are excluded) in this experiment.

Importantly, the immigrating seastars (*A. amurensis*) and crabs (*N. integrifrons*) at Saltwater River did not gain access to the cages.

Notwithstanding any interpretation of caging effects, the contrast to examine seastar effects (comparing caged treatments with and without the seastar) is valid given that cage artefacts are held constant across both treatments. Nonetheless, in interpreting this contrast, we assume that the cage has not affected the behaviour of the seastar. While caging of a single animal may preclude any intraspecific inhibitory or facilitative behaviour that may influence feeding rate in nature, it needs to be emphasised that seastar densities similar to and substantially higher than those in the cages are frequently encountered in the Derwent Estuary (Grannum et al., 1996; Ling, 2000) and are maintained over periods much greater than our 2-month experimental period. Thus, we suggest that it is reasonable to expect similar effects on native species should the seastar attain the densities used in these experiments. This was supported from feeding observations at Saltwater River, where the majority of seastars that invaded during the experiment were feeding on *F. tenuicostata*, as anticipated from the experiments.

4.3. Predation by seastars: consistent effects among assemblages

In both Tasmania (Morrice, 1995; Grannum et al., 1996; Lockhart, 1995; Ross et al., 2002) and overseas (Hatanaka and Kosaka, 1959; Nojima et al., 1986), bivalves are typically the major food source of *A. amurensis*. Similarly, in this study, bivalves were the single group for which strongest effects of seastar predation were evident. The impact of the seastar on particular bivalve species reflects their ecological availability. Some prey find a depth refuge by digging beyond the reach of the tube feet of *A. amurensis*, which is a common response of bivalves to avoid asteroid predators (Kim, 1969; Allen, 1983; Fukuyama and Oliver, 1985). When bivalves are separated into functional groups reflecting their ecological availability (i.e. surface dwellers vs. deep burrowers), it is clear that effects of the seastar in short-term experiments are restricted to surface dwelling species. Bivalves such as *F. tenuicostata*, *E. georgina* and *K. rhytiphora* are likely to be more accessible because they live just below or on (*E. georgina*) the sediment surface so that their short siphons can project into the water column for ventilating and feeding. In contrast, *Theora* spp., the dominant deep burrowing bivalve at all three sites, has much longer siphons and is less accessible as it can live at depths several times its shell length (Willan, 1998). Similarly, the echinoid *E. cordatum* can remain deeply buried (e.g. up to 150 mm), maintaining contact with the surface by a funnel-like opening over the aboral side of the animal (Buchanan, 1966; Barnes, 1987). The seastar will readily consume *E. cordatum* if presented with it, but must actively dig to access this species. Crustaceans and polychaetes are likely to be less available to seastars than bivalves given their relatively high mobility or other avoidance mechanisms (e.g. tubicolous polychaetes and crustaceans can withdraw into tubes, some of which are relatively deep in the sediment).

Differential impact on surface-living taxa but not deeply burrowing taxa has been demonstrated for other predators in soft-sediment habitats. Woodin (1974) demonstrated that the abundance of surface-dwelling tube building polychaetes was reduced by *Cancer magister*, whereas deep burrowing infauna was unaffected. The portunid crab *Callinectes*

sapidus reduced the total infaunal density by affecting the species which were surface-living, e.g. spionid polychaetes and the bivalve *Mulinia lateralis*, whereas the deeper burrowing organisms were little influenced by this predator (Virnstein, 1977).

4.4. Predation by seastars: assemblage-specific effects

Although at a functional group level the effect of seastar predation on surface bivalves was common to all assemblages, the magnitude of the impact varied between assemblages. The differences in mean density of surface bivalves between the seastar inclusion treatment and the cage control indicates an absolute loss to seastars of 92 m^{-2} (96%), 35 m^{-2} (72%) and 31 m^{-2} (40%) at Murdunna, Saltwater River and Conningham, respectively. Once again, the impact of the seastar on particular bivalve species reflects the ecological availability of prey. When bivalves were separated into size classes (based on 2–4, 4–8 and >8 mm mesh sizes), the impact of the seastar on each assemblage was largely attributable to the decrease in abundance of larger (>8 mm) bivalves. The decrease in percentage of surface bivalves in each assemblage closely reflected the percentage of large (>8 mm) surface bivalves, viz. 92%, 67% and 41% at Murdunna, Saltwater River and Conningham, respectively. However, it is unclear whether these patterns reflect selection on the basis of size or species identity (or both) given that the species most heavily impacted in each assemblage were also the large (>8 mm) species of surface bivalves. Given that previous work has demonstrated both size- and species-specific selection for *A. amurensis* (Lockhart and Ritz, 2001a,b), changes in both the size and species composition may underpin variability in the magnitude of impact between assemblages.

While the effect of seastar predation varied between assemblages, at Conningham, it also varied among experimental blocks within the assemblage, complicating the interpretation. Our observations of seastar activity during the experiment and known feeding preferences of the seastar suggest that these results reflect a real biological interaction between predator and prey. In contrast to the assemblages in the other two experiments, epifaunal bivalves, predominately *E. georgina*, were common at Conningham. *E. georgina* was abundant in two of the three blocks in this experiment, and in these blocks the reduced density of *E. georgina*, but not of other surface bivalves, was consistent with a seastar effect. In the remaining block where *E. georgina* was rare, surface dwelling bivalves were significantly impacted by the seastar. This shift in diet at this scale correlates with both small-scale patchiness in abundances between blocks and ecological availability, since *E. georgina* is epifaunal and directly accessible to the seastar while the other surface bivalves are infaunal. In the nearby Derwent River Estuary, the infaunal bivalves *T. cardoides*, *Venerupis anomala* and *F. tenuicostata* were major prey items of the seastar, except when *E. georgina* became available at high densities, at which time the epifaunal bivalve dominated the seastar's diet (Ross, unpublished data). In this case, the switch in diet, and therefore in impact, is ostensibly the result of temporal changes in the abundance of *E. georgina*. It is also noteworthy that, across assemblages as a whole, Conningham was characterised by a higher species diversity and evenness of surface bivalves than in the other assemblages, with *E. georgina*, *C. gibba*, *W. assimilis*, *T. cardoides* and *F. tenuicostata* making up 29%, 24%, 22%, 15% and 6% of the total abundance, respectively.

This suggests that in an assemblage characterised by marked small-scale patchiness, but with high overall diversity and evenness of prey, small-scale differentiation in diet, and therefore impact, may arise.

4.5. Conclusions: implications for impacts on native assemblages and commercial species in Tasmania

The potential impact of the seastar on native assemblages and commercial species has been a major concern for natural resource managers in Tasmania since the early 1990s when it was found to be in high abundance in the Derwent River Estuary. However, prior to this study, no direct quantitative assessment of seastar impacts had been made on which to base predictions of the immediate and future effects on benthic assemblages. In the Derwent River Estuary, where the seastar occurs at high densities, live bivalves >5–10 mm shell length have become increasingly rare since the establishment of the seastar (Turner, personal communication). Another manipulative experiment showed clearly that *A. amurensis* has a large impact on recruitment of the commercial cockle *F. tenuicostata* in the estuary, effectively arresting significant recruitment (Ross et al., 2002). Combined with the results of this study, these findings are consistent with the notion that predation by the seastar is responsible for the decline and subsequent rarity of bivalves, including commercial species, that live just below or on the sediment surface in the Derwent River Estuary.

Notwithstanding the importance of impacts by the seastar in the Derwent River Estuary, it is the potential spread and subsequent impact in coastal areas outside the estuary that is of immediate concern for management. Recent modelling of dispersal of seastar larvae indicating that the large majority of larvae produced in the Derwent River Estuary are likely to be advected from it (Morris and Johnson, in preparation) is supported by empirical observations (Koch and Johnson, in preparation). The results of the experiments reported here and evidence of strong food preferences (Grannum et al., 1996; Lockhart and Ritz, 2001a; Ross et al., 2002) indicate that the exact nature of seastar effects is likely to be variable given the inherent natural variability in soft-sediment assemblages and the seastar's responses to them. Nonetheless, these results indicate that the seastar will have major impacts on assemblages that support populations of large surface bivalves (>8 mm) should the seastar invade at high densities. This is a particular concern for management of the small but growing number of commercial operations harvesting wild populations of several bivalve species, most of which grow large and live near the sediment surface. The potential implications of a seastar incursion were highlighted at Saltwater River where an aggregation of seastars moved through the experimental area causing high mortality of *F. tenuicostata*. These observations suggest that in the early stages of invasion, the seastar will track preferred prey, in this case a commercial cockle. In the Derwent River Estuary where surface bivalves have become rare, the seastar consumes a wide variety of other prey taxa (Ross et al., 2002). Thus, should the seastar invade and attain the high densities that occur in the Derwent River Estuary in other areas on the coast, it has the potential to have wider effects on soft-sediment assemblages than those demonstrated in these short-term manipulative experiments.

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