Impact of the northern Pacific seastar *Asterias amurensis* on soft sediment assemblages, including commercial species, in southeast Tasmania

by

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Abstract

Introduced species are having major impacts in terrestrial, freshwater and marine ecosystems worldwide. In Australia, the introduced northern Pacific seastar (*Asterias amurensis*) was first recorded in southeast Tasmania in 1986, where it has become the dominant invertebrate predator in the Derwent River Estuary. Despite indirect indications based on seastar foraging behavior, stomach contents, and estimates of feeding electivity that suggest the potential for considerable impact on native benthic marine assemblages, the impact of the seastar has not previously been examined directly or quantitatively in either its native or introduced range. Because of the absence of baseline data prior to the arrival of the seastar and the presence of other anthropogenic stressors in the estuary, estimating the impact of the seastar is difficult. To overcome these difficulties and the limitations of any one method of impact assessment, I used multiple methods at different scales to provide independent tests of impact: (a) experiments in which seastar density is manipulated at several sites immediately beyond the current range of the seastar; (b) experiments in which seastar density is manipulated following recruitment of prey; (c) experiments in which the density of both seastars and another introduced benthic predator (*Carcinus maenas*) are manipulated to examine their interaction; (d) comparative analysis of prey taxa in the sediments and in seastar stomachs; and (e) spatially hierarchical surveys to examine the relationship between soft sediment assemblages and seastar abundance at several sites in southeast Tasmania. The combination of these methods provide, for the first time, a robust estimate of the impact of the seastar.

In the Derwent River Estuary where the seastar occurs at high densities, live adult bivalves are rare despite the presence in sediments of numerous recent remains (intact shells) of adults. Experiments conducted immediately beyond the current range clearly demonstrated a large impact of *Asterias amurensis* on adult bivalve populations and on the commercial cockles *Fulvia tenuicostata* and *Katelysia rhytiphora* in particular. Manipulative experiments also demonstrated that *Asterias amurensis* has a large impact on the survivorship of bivalve recruits in the estuary, effectively arresting significant recruitment events. Observations of diet and prey switching show that while the seastar has clear food preferences, it is a generalist predator able to switch to other prey when preferred prey become relatively rare. This finding and results of experiments conducted at several sites demonstrated that the exact nature of seastar effects is site and time specific given the inherent natural variability in soft sediment assemblages and the seastar's responses to them. In the event of spatial overlap with the introduced predatory European green crab (*Carcinus maenas*), experiments suggest that both predators may coexist because of resource partitioning on the basis of prey size and/or habitat requirements, and that the impact on bivalves may be greater in the presence of both species.

I use the results from experimental manipulations, feeding observations and large scale surveys to provide a broad synthesis of the immediate and predicted impacts on native assemblages and commercial species. There is strong evidence that predation by the seastar is responsible for the decline and subsequent rarity of bivalve species that live just below or on the sediment surface in the Derwent River Estuary. Recent modelling of dispersal of seastar larvae indicates that the large majority of larvae produced in the estuary are likely to be advected from it (Morris & Johnson in prep).

It seems clear that should seastar densities in other areas on the Tasmanian coast attain the levels that occur in the Derwent River Estuary, there are likely to be large direct effects on native assemblages, particularly on populations of large bivalves (including commercial species) that live just under or on the sediment surface. Given the seastar's ability to exploit a range of other food resources and the importance of bivalves as a functional component of native systems, I also predict broader direct and indirect effects on native assemblages. Overall, these important consequences of the establishment and potential spread of this introduced predator warrant management efforts to control its spread and impact.

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Chapter 1: General Introduction

1.1 Introduction

Biological invasions in marine and estuarine environments due to human mediated movement of species across and between continents are now recognised as a serious global environmental problem (e.g. Elton 1958; Carlton and Geller 1993; Cohen and Carlton 1998; Hewitt et al. 1999; Ruiz et al. 1999; Pimentel et al. 2000). In some marine and estuarine systems, the impact of marine invaders on the recipient community has been catastrophic, such as the well documented invasion of San Fransisco Bay by the Asian clam *Potamocorbula amurensis* (Nichols et al. 1990) and the introduction of the comb jelly *Mnemiopsis leidyi* in the Black Sea (Shushkina and Musayeva 1990). Although prevention of invasion is the most desirable management option, in many cases invasive species are already established before they are recognised. Eradication of most species already established is often not feasible, at least in the short term (but see Bax 1999; Culver and Kuris 2000; Willan et al. 2000), and particularly if they are widely established. Given that only a small percentage of exotics are likely to cause large ecological change (Carlton & Geller 1993; Williamson 1996), it is imperative that with limited resources for management and control efforts, management priorities are based at least in part on the best scientific assessment of immediate and anticipated impacts (Lodge et al. 1998).

Despite the geographic isolation of Australia, the coastal waters are the host of over 175 introduced marine species (Hewitt et al. 1999; Hewitt submitted ms). While scientists have been aware of introduced marine species in Australian waters since the late 1880s (e.g. MacGillivray 1869; Fulton and Grant 1902; Allen 1953; Pollard and

Hutchings 1990a, b), efforts aimed at minimising the impacts of exotic species have been, until recently, directed largely at terrestrial pests such as rabbits and foxes. The discovery of the conspicuous northern Pacific seastar (*Asterias amurensis*) in Tasmanian waters in the early 1990s, and more recently other high profile invaders (e.g. the Japanese kelp *Undaria pinnatifida* and the Mediterranean fanworm *Sabella spallanzanii*) have highlighted the problem posed by introduced pests entering Australia's marine environment. Widespread concern among the public, environmental managers and marine industries led to the establishment of a CSIRO National Centre in 1994 to carry out research on the impacts and management of exotic marine species in Australian waters (Hewitt et al. 1999).

The northern Pacific seastar was first recorded in southeast Tasmania in 1986 (Buttermore et al. 1994). Since its arrival the seastar has become the dominant invertebrate predator in the Derwent River Estuary where it is considered a major threat to benthic assemblages (Grannum et al. 1996). Of greater concern is the potential spread and impact on native assemblages and commercial species in areas outside the estuary, not just in Tasmania but nationally and internationally. Concentrations of larvae of seastars adjacent to wharf areas in the estuary are some of the highest reported for seastar larvae worldwide (Bruce et al. 1995). Furthermore, recent modelling of seastar larval dispersal indicates that the majority of larvae (> 99 %) produced in the estuary are likely to be advected from it (Morris & Johnson in prep). The recent discovery and subsequent population explosion of the seastar in Port Phillip Bay, Victoria, on mainland Australia is believed to be the result of larval translocation from Tasmania (Murphy and Evans 1998). Considered a threat internationally, New Zealand has enacted legislation preventing discharge of ballast water from boats coming from the Derwent River Estuary and Port Phillip Bay during the spawning season of the seastar (Biosecurity Act 1993, Annex 1 *cited by* Goggin 1998).

Few introduced echinoderms have been identified in global investigations of introduced species (e.g. Ruiz et al. 1999; Cohen & Carlton 1995; Hewitt et al. 1999; Hewitt submitted ms). However, the importance of asteroids in structuring benthic marine communities, their propensity for population outbreaks, and capacity to 'invade' and significantly impact fishery and mariculture grounds in their native ranges is well documented (see Sloan 1980; Menge 1982). In the northern hemisphere, *Asterias amurensis* causes considerable damage to commercial shellfish (e.g. oysters, cockles, scallops, other clams: Hatanaka and Kosaka 1959; Kim 1969; Nojima et al. 1986) and is known to be an opportunistic predator on a variety of other epifaunal and infaunal species including other molluscs, ascidians, bryozoans, sponges, crustaceans, polychaetes, fish and echinoderms (Hatanaka and Kosaka 1959; Fukuyama and Oliver 1985; Fukuyama 1994). In Tasmania, indirect indications via observations of seastar foraging behavior, stomach contents, and estimates of feeding electivity suggest the potential for considerable impact on native benthic marine communities. Nonetheless, the impact of the seastar on native assemblages and wild fisheries has not previously been examined directly or quantitatively in either its native or introduced range. With limited resources for management and control efforts as the number of high profile introductions continues to accumulate in Australia, it is imperative that management priorities are based on accurate scientific assessments of the immediate and anticipated impacts on native assemblages and commercial species. The aim of the work outlined in this thesis is to provide the first broad synthesis of the immediate and predicted impacts of *Asterias amurensis* on the soft sediment assemblages and commercial species in southeast Tasmania.

A major challenge for ecologists is how to conduct an assessment of the immediate and anticipated impacts of successful invaders that includes information such as the magnitude (and type) and pattern of impact in space and time (Lodge et al. 1998; Ruiz et al. 1999). A number of obstacles to this challenge exist. First, there is often little pre-impact data on native assemblages. Second, introduced species are often established before they are even discovered. Third, introduced species most often occur in areas that are subject to a broad spectrum of other anthropogenic stressors (Ruiz et al. 1999). It is difficult to separate the effects of the introduced species of interest from other anthropogenic stressors, particularly given their probable interaction (Ruiz et al. 1999). Finally, concern is often with impacts over large spatial and temporal scales, at which experimental work is difficult and normally not practical (see Lodge et al. 1998; Ruiz et al. 1999).

To help overcome these difficulties and the strengths and weaknesses of any single method of impact assessment (e.g. Diamond 1986; Schmitt and Osenberg 1996; Lodge et al. 1998; Ruiz et al. 1999), I used an integrated approach combining multiple methodologies. A combination of experiments and observations conducted at small scales was used because this provides a powerful assessment of the cause-effect relationship of interest, in this case the effect of seastar predation on the abundance of soft sediment organisms. However, it cannot be assumed that results measured at small scales in space and time necessarily 'scale up' (see Diamond

1986; Weins 1989; Thrush et al. 1997; Lodge et al. 1998). Therefore, large scale surveys were necessary to establish whether results detected at small scales were reflected in patterns described at larger scales. This combination of methods provides a more robust assessment of impacts because it includes independent tests of impacts conducted on different scales (e.g. Diamond 1986; Ruiz et al. 1999).

To contend with the lack of pre-impact data, experimental manipulations were conducted in similar habitats immediately beyond the current range of the seastar (with one exception, in chapter 3). In chapter 2, an experiment was conducted to assess the interaction and impact of the seastar and another introduced benthic predator (*Carcinus maenas*) because of the potential for interactions to modify impacts if their distributions should overlap. In chapter 3, a combination of feeding observations and an experiment was used to assess the impact of the seastar on the survivorship of bivalve recruits within the current range of the seastar. In chapter 4, the generality of the type and magnitude of the impact of the seastar is assessed in identical experiments conducted at several sites in southeast Tasmania. In chapter 5, large scale surveys to examine the relationship between soft sediment assemblages and seastar abundance at several spatial scales were undertaken to test whether large scale patterns reflected patterns anticipated from the small scale experiments and observations. Finally in the discussion chapter (chapter 6) I synthesise the results of the different methods, and for the first time provide an integrated picture of the role of the invasive seastar on benthic assemblages in southeast Tasmania. The reader should note that the thesis chapters are written as manuscripts for publication, and thus, some repetition in the introductions of the different chapters is unavoidable.

Chapter 2

Interaction and impacts of two introduced species on soft sediment assemblages in southeast Tasmania

(Submitted to Marine Ecology Progress Series)

2.1 Abstract

Introduced species are having major impacts in terrestrial, freshwater and marine ecosystems worldwide. Most investigations of invasion impacts have examined only one species at a time. While it is increasingly recognised that effects of multiple species often cannot be predicted from the effect of each species alone, due to complex interactions, few studies have examined the interactions among introduced species. I 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 assemblage in Tasmania. Spatial overlap in distribution of these invaders is just beginning, and appears imminent as their respective ranges expand, suggesting a strong overlap will exist in food resources as both species share a proclivity for bivalves. *A. amurensis* and *C. maenas* are good models to test the interaction between multiple predators because for a number of common prey taxa (bivalves and gastropods) they leave clear predator-specific traces of their predatory activity. 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*. In contrast, there was no detectable effect of predation on other potential prey. When both predators were present they consumed fewer *F.*

tenuicostata than when alone. 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; *A. amurensis* consuming the large and *C. maenas* the small bivalves. Thus, in the event of spatial overlap the effect on each predator is likely to be negative rather than facilitative when sharing a limited resource. Nonetheless, I predict the introduced predators may coexist because of resource partitioning according to size and/or different habitat requirements. In fact, 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. Because they are generalist predators, both *C. maenas* and *A. amurensis* have the potential to impact a large variety of taxa and have wider direct and indirect effects on soft sediment communities than the short term effects reported here.

2.2 Introduction

Biological invasions, or the establishment of non-native species outside their historic range, have become major forces of global change (Lodge 1993; Vitousek et al. 1996; Stachowicz et al. 1999). Although invasions have occurred for millions of years there has recently been a rapid increase in the rate of new invasions due to human aided movement across and between continents and oceans (Carlton and Geller 1993; Lodge 1993; Vitousek 1994; Cohen and Carlton 1998; Hewitt et al. 1999; Ruiz et al. 1999). 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).

A critical question when several introduced species occur together is their combined effects, an issue that has been addressed infrequently in invasion ecology (Simberloff and Von Holle 1999). The question of the combined effects of several sympatric introduced species is particularly important given the possibility that synergistic interactions may well lead to 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). In the few instances where interactions among introduced species have been studied, Simberloff and Von Holle (1999) report that facilitative interactions are at least as common as the negative interactions of resource competition and direct interference.

Marine communities have historically been important for experimental tests of ecological theory, due to our ability to manipulate multiple trophic levels over relatively small areas (e.g. Connell 1970; Dayton 1971; Paine 1974; Underwood 1978). Given the tens to hundreds of introduced species now established in bays and estuaries throughout the world (e.g. Cohen and Carlton 1995; Hewitt et al. 1999; Ruiz et al. 1999), marine environments also provide useful testing grounds for invasion ecology (e.g. Stachowicz et al. 1999; Grosholz et al. 2000).

Despite the degree of geographic isolation, the coastal waters of Australia have been the site of a number of significant introductions of exotic marine species (Pollard and Hutchings 1990a, 1990b; Jones 1991; Furlani 1996; Hewitt et al. 1999). Two of the more conspicuous introductions have been large, predatory species of sheltered low energy environments: the northern Pacific seastar, *Asterias amurensis*, and 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; Ruiz et al. 1999; Grosholz et al. 2000). Furthermore, both species are thought to have significant effects on native populations in Tasmania (Grannum et al. 1996; McKinnon 1997).

Asterias amurensis was introduced to southeast Tasmania in the early 1980s where it has become the dominant invertebrate predator in the Derwent River Estuary (Grannum et al. 1996). *Carcinus maenas* is thought to have been introduced to mainland Australia in the early 1900s (Fulton and Grant 1900; Hewitt et al. 1999), but it was not recorded in Tasmania until 1993 (Gardner et al. 1994) where its range has expanded rapidly. In their native ranges both species are important predators of a wide variety of epifaunal and infaunal species (e.g. Hatanaka and Kosaka 1959; Jensen and Jensen 1985; Fukuyama and Oliver 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).

Although the distributions of *Carcinus maenas* and *Asterias 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, I believe the direct biological interaction between the pest species is inevitable. Furthermore, I predict the interaction between *A. amurensis* and *C. maenas* will modify their effects. The seastar/crab/bivalve interaction is an excellent model to test for interaction modifications between predators because they leave clear traces of the relative proportions of prey loss associated with each predator, i.e. undamaged, empty shells identify bivalves eaten by seastars, whereas hinges with only a fraction of the shell remaining, identify bivalves eaten by crabs. To test these predictions I examine the separate and combined impacts of *A. amurensis* and *C. maenas* on a soft assemblage, with particular attention to 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 outside, but adjacent and between, their current ranges.

2.3 Methods

A manipulative experiment was undertaken in the sheltered upper reaches of King George Sound (42° 56' S 147° 51' E), southeast Tasmania at a depth of 2-3 m. Sediment in the area is composed predominantly of sand-mud. Because the area does not currently support populations of either *Asterias amurensis* or *Carcinus maenas*, to reduce the risk of establishing these species in the area the experiment was conducted in completely enclosed cages and only male specimens were used. The sex of seastars was determined via a minute incision made in the arm wall from which a small sample of gonads was removed with a hypodermic needle and examined for eggs or sperm under a high powered microscope. For crabs, the triangular shape of the abdomen and gonapore opening on the last pereiopod identified males.

Cages consisted of a rigid (1 m x 1 m base x 0.7 m high) steel frame with legs (0.5 m long) to securely anchor the cage in the sediment. The cage 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. Five treatments were used to investigate predation effects and test for potential cage effects, which included all possible combinations of presence (a single animal per cage) and absence of crabs and seastars in cages, and an unmanipulated 1 m^2 plot without either cages or added predators. The spatial scale of patchiness of infauna indicated in a pilot study suggested that a randomised complete block design was the most efficient option to test for treatment effects given the limited number of replicates possible due to logistical constraints in diving. In the pilot study, plots 3-5 m apart were similar to each other, but not to plots 30 - 60 m away. Thus, the five treatments were applied randomly to separate experimental units (≈ 5 m apart) in each of three blocks (≈ 30 m apart). By accounting for the variation between blocks I hoped to obtain a smaller experimental error and hence improve the power with which I could 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. Three replicate cores (150 mm diameter x 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 m x 1 m x 0.1 m depth) was inserted into the sediment to isolate the plot, and all contents then vacuumed into a 1 mm mesh bag.

Samples were sieved (1.0 mm mesh) prior to fixing in 10% buffered formalin with Rose Bengal stain, and then rinsed in freshwater before storing in 100 % ethanol. All infaunal and epifaunal organisms (> 1 mm) were sorted and identified to the lowest possible taxon in core samples. For suction samples, only the major macro-invertebrates were sorted and analysed, which included all bivalve species and the heart urchin *Echinocardium cordatum*.

Because both predators leave clear traces of their activities when consuming bivalves the number of commercial bivalves (*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 selectivity the length of uneaten bivalves and those eaten by seastars were measured in all treatments.

2.3.1. Statistical Analysis

The responses of dominant taxa to experimental treatments were determined using species abundance data obtained from suction samples of 1 m^2 plots, with the exception of polychaetes which were counted in cores. For polychaetes I used the arithmetic mean of the 3 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' (2 levels = cage present and cage absent, both without added predators) as a fixed factor, and 'block' as a random factor was used. The effects of *Asterias amurensis* and *Carcinus maenas* on native prey species were analysed using a two-way 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. Because I used a randomised complete block design there are two assumptions to consider: (i) no interaction between treatments and blocks and, (ii) constant variance from block to block. However, I adopted the more realistic non-additive model in which a treatment by block interaction is allowed and in which the test for treatments effects is statistically valid even if there is an interaction between treatment and block. While there is no test for 'block' or the treatment by block interaction in the non-additive model, the design is more powerful if there is no treatment by block interaction because in the presence of an interaction the residual variation will increase proportionately more than the treatment variation and result in a loss of power. Interpreting the test of treatment effects requires no, or a relatively small treatment by block interaction. To assess treatment by block interactions, plots of dependent variables *versus* block were examined. In cases where the interaction was clearly evident so that significant treatment effects could be misinterpreted, the analysis was not conducted. In regard to constant variance from block to block, variances are unlikely to be very different between blocks because the treatments were applied randomly to different experimental units within each block. Where prey depletion occurred and multiplicative effects were likely, as was the case for

Fulvia tenuicostata and *Katelysia rhytiphora*, I tested a multiplicative model by running the ANOVA on log abundances.

To test for size selection by seastars and crabs on the two commercial bivalves (*Fulvia tenuicostata* and *Katelysia rhytiphora*), I compared mean sizes between treatment groups using the Ryan-Gabriel-Elliot-Welsch procedure ('Ryan's test') for multiple range tests (Day and Quinn 1989). To assess size selection by crabs on *F. tenuicostata* in more detail the Kolmogorov-Smirnov test was used to compare the length frequency distributions of live bivalves remaining in the cage control (no predators added) with those in the treatment with crabs added (single crab per cage).

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*. The statistical package SAS® was used for univariate analyses. To depict the multivariate patterns among blocks and treatments, non-metric multi-dimensional scaling was done on Bray-Curtis distances calculated from 4th root transformed data, using the Primer® computer program (Clarke 1993).

2.4 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 *Fulvia tenuicostata*, *Theora* spp., *Kataleysia rhytiphora*, *Wallucina assimilis* and the echinoid *Echinocardium cordatum*.

2.4.1 Commercial Bivalves: *Fulvia tenuicostata* and *Katelysia rhytiphora*

There were no significant effects of cages on the abundance of *Fulvia tenuicostata* or *Katelysia rhytiphora* (Table 2.1).

	Predation effects						**Cage effects**	
	seastar		crab		seastar x crab		cage	
	F	*P*	F	*P*	F	*P*	F	*P*
Commercial Bivalves								
Fulvia tenuicostata								
Alive	37.05	**0.026**	0.69	0.495	0.18	0.711	0.36	0.611
Empty shell	13.44	0.067	1.10	0.404	1.58	0.336	1.08	0.408
Hinge	8.31	0.102	5.47	0.144	36.55	**0.026**	0.09	0.792
Katelysia rhytiphora								
Alive	10.18	0.086	0.44	0.573	1.69	0.323	0.43	0.580
Empty shell	37.99	**0.025**	1.33	0.369	0.49	0.558	0.14	0.742
Other bivalves and echinoderms								
Theora spp.	0.07	0.812	0.25	0.665	0.19	0.707	0.58	0.524
Wallucina assimilis	0.87	0.449	1.04	0.415	3.12	0.219	2.56	0.251
Echinocardium cordatum	1.69	0.324	0.35	0.612	0.13	0.756	1.09	0.406
Polychaetes								
Simplisetia amphidonta	5.88	0.136	4.99	0.155	0.64	0.507	11.94	0.075
Lysilla jennacubinae	0.52	0.547	0.05	0.843	0.44	0.574	0.57	0.529
Glycera spp.	6.49	0.126	0.05	0.845	0.69	0.493	12.00	0.074

Table 2.1 Results from analysis of predation and cage effects for the common taxa. Note *K rhytiphora* hinges were not present in samples. All of the tests in the table have 1,2 df. The tests for seastar and crab effects used the MS for seastar x block and crab x block as their respective error terms. The tests for the seastar x crab interaction and caging effects used the MS residual in their respective analysis as the error term.

2.4.1.1 Effect of predation by seastars

There was a major reduction in densities of *Fulvia tenuicostata* and *Katelysia rhytiphora* in all treatments containing *Asterias amurensis*; however, this difference was only significant for *Fulvia tenuicostata* (Table 2.1, Figure 2.1). The abundance of recently opened shells (indicative of seastar predation) of both species of bivalve was greater in treatments with seastars, however, this difference was only significant for *K. rhytiphora* (Table 2.1, Figure 2.1). Size selection by seastars was not apparent on both species of bivalves, given that nearly all bivalves were consumed. The mean size of both species eaten by *A. amurensis* was not significantly different from the mean size of live bivalves in the cage control treatment (Figure 2.2, Ryan's test P > 0.05).

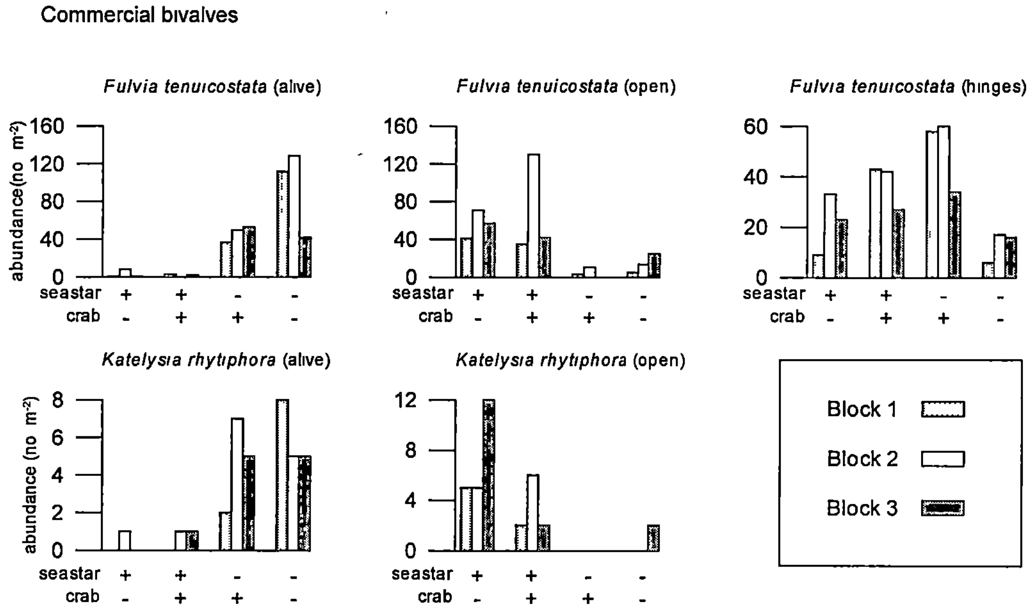


Figure 2.1 Densities of the commercial bivalves and their shell remains in each treatment plot in each block ($n = 3$ blocks). Abundances of are totals from 1m^2 suction samples. Seastars had a large and significant effect on the commercial bivalves, but not on other species. Crabs appeared to have an effect on *Fulvia tenuicostata* in 2 of the 3 blocks, but not on other species.

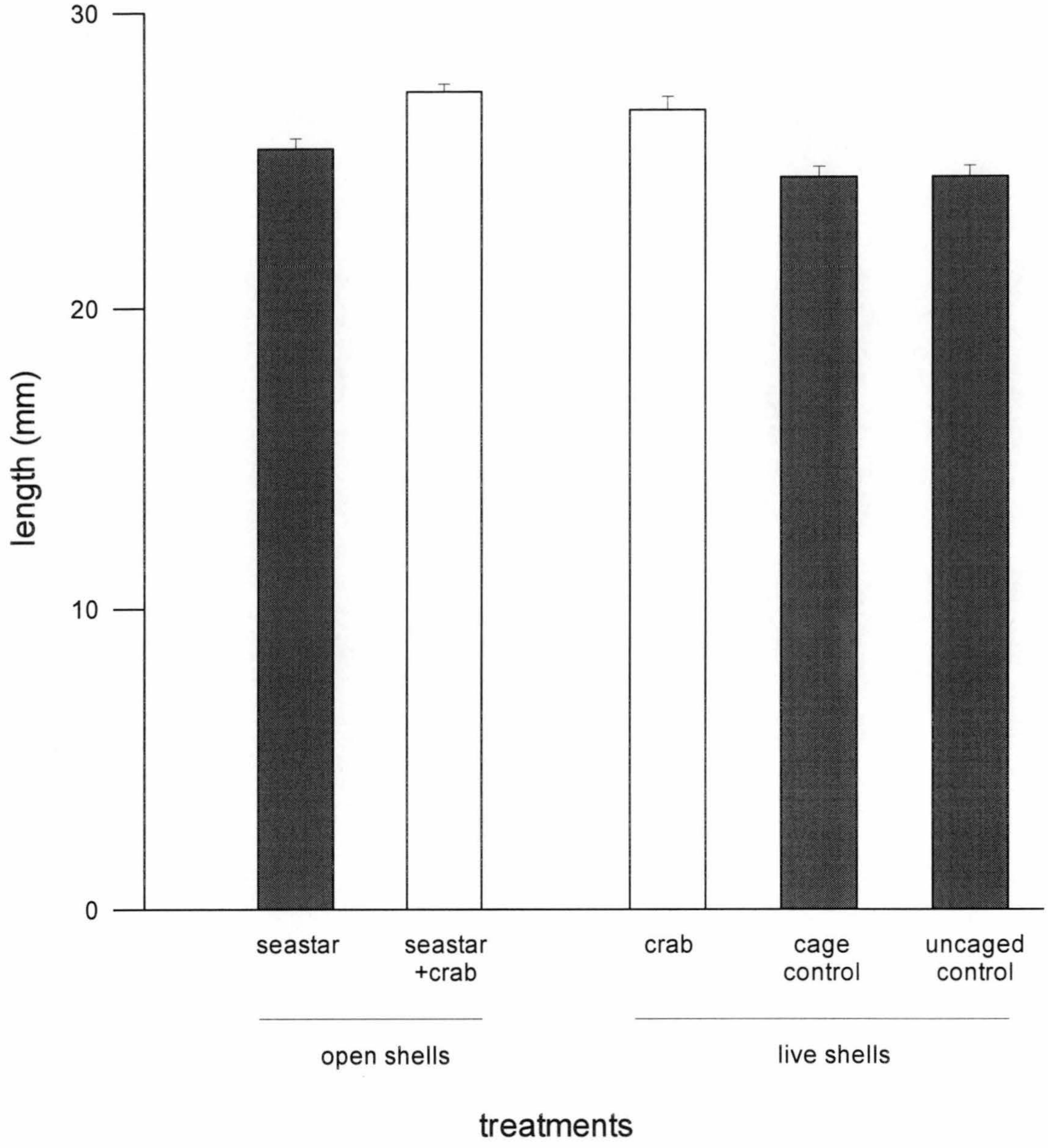


Figure 2.2 Mean size (+ SE) of open (treatments with seastar, and seastar + crab) and live (crab, cage control and uncaged control treatments) *Fulvia tenuicostata* remaining at the end of the experiment. The size of bivalves differed significantly across treatments ($F_{[4,\ 952]} = 16.09$ $P = 0.0001$). Unshaded and shaded bars represent significantly different treatments in the multiple comparison tests.

2.4.1.2 Effect of predation by crabs

In two of the three blocks, the abundance of *Fulvia tenuicostata* was reduced in all treatments containing crabs compared with the cage control, and the abundance of *F. tenuicostata* hinges (indicative of crab predation) was greater in all treatments containing crabs compared with the cage control (Figure 2.1). Comparison of the length frequency histograms of *F. tenuicostata* between the cage control (no predators added) and treatment with crabs (a single *Carcinus maenas* per cage) in these two blocks shows that *C. maenas* predation was greater on small (< 25 mm) bivalves (Figure 2.3). There were clearly fewer small bivalves remaining in the presence of crabs compared to the cage controls, however the difference in size frequency distributions was only significant for block 2 (Figure 2.3, Kolmogorov-Smirnov test: block1, P = 0.0901; block2, P = 0.0001). Because small (< 25 mm) bivalves were virtually absent in block 3 controls and treatments, the size frequency distributions of *F. tenuicostata* remaining in the treatments with and without crabs in block 3 were not significantly different (Figure 2.3, Kolmogorov-Smirnov test, P = 0.9619). The absence of a detectable effect of crabs in block 3 suggests that *C. maenas* is unable to consume bivalves > 25 mm in length. Size limitation in handling prey is consistent with the absence of any effects of crabs on *Katelysia rhytiphora*, given that the majority of *K. rhytiphora* in all experimental plots exceeded 25 mm in total length.

2.4.1.3 The interaction of crabs and seastars

The crab x seastar interaction was not significant for either bivalve species. This suggests that the combined effect of the predators can be predicted from the effect of each predator alone. Given that both species of bivalves were almost completely consumed in all treatments with seastars, the impact of crabs would need to be negligible for this to hold. Whilst this appears to be the case for crab predation on *Katelysia rhytiphora*, the results for *Fulvia tenuicostata* are indicative of a strong crab effect in 2 of the 3 blocks (Figures 2.1,2.3). Crabs did not show an effect in the third block because they appear unable to consume large bivalves (> 25 mm), and small bivalves were virtually absent from this block. This suggests that when small

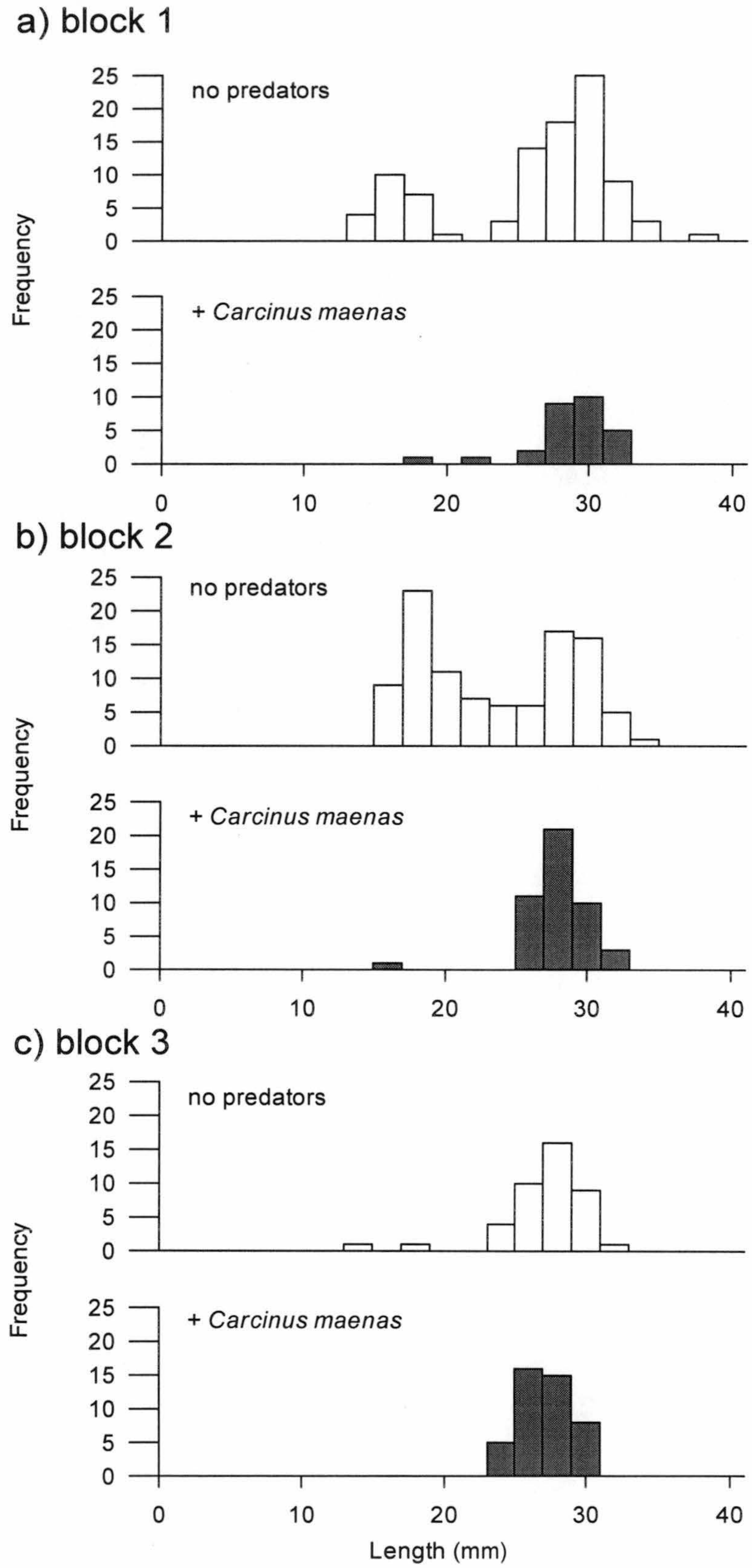


Figure 2.3 Length frequency histograms of the commercial bivalve *Fulvia tenuicostata* from the cage control (no predators added) and the treatment with added crabs (single *Carcinus maenas* per cage) in block 1 (a), 2 (b), and 3 (c). Predation by crabs has greatest impact on small (< 25 mm total length) bivalves. Differences in the size distribution of bivalves remaining in treatments with added crabs compared with the cage control was significant for block 2 (Kolmogorov-Smirnov test P = 0.0001), but not blocks 1 and 3 (Kolmogorov-Smirnov test: block 1, P = 0.0901; block 3, P = 0.9619).

(< 25mm) bivalves are present (e.g. *F. tenuicostata* in blocks 1 and 2) the combined effect of both predators cannot be predicted from each predator alone. In contrast, when small bivalves are absent (*F. tenuicostata* in block 3, and *K. rhytiphora* in all three blocks), the combined effect of both predators can be predicted from the effects of each predator alone. In the latter case, this is because the effect of *C. maenas* on large bivalves is negligible.

A clear picture of the interaction is evident from analysis of the shell remains. The effect of each predator on the abundance of *Fulvia tenuicostata* was reduced when both predators were present. The number of *F. tenuicostata* hinges (*Carcinus* predation) in the presence of both predators was reduced compared to when the crab was alone, but higher than when predators were absent (Figure 2.1). Similarly, with the exception of block 2, the number of open shells (*Asterias* predation) in the presence of both predators was reduced compared to when the seastar was alone, but higher than when predators were absent (Figure 2.1). The interaction between *C. maenas* and *A. amurensis* results in partitioning of predation on bivalves on the basis of size. In the presence of *A. amurensis, C. maenas* continued to consume small bivalves (Figure 2.2), but less than in the absence of *A. amurensis* (Figure 2.1). The mean size of *F. tenuicostata* not consumed by *C. maenas* in the presence *A. amurensis* (i.e. open shells eaten by *A. amurensis*) was not significantly different from the mean size of bivalves not eaten by *C. maenas* in the absence of *A. amurensis* (Ryan's test $P > 0.05$, Figure 2.2). While *A. amurensis* also consumed fewer *F. tenuicostata* in the presence of *C. maenas* (with the exception of block 2, Figure 2.1), the mean size of bivalves consumed (open shells) was significantly larger than when the crab was absent (Ryan's test $P < 0.05$, Figure 2.2).

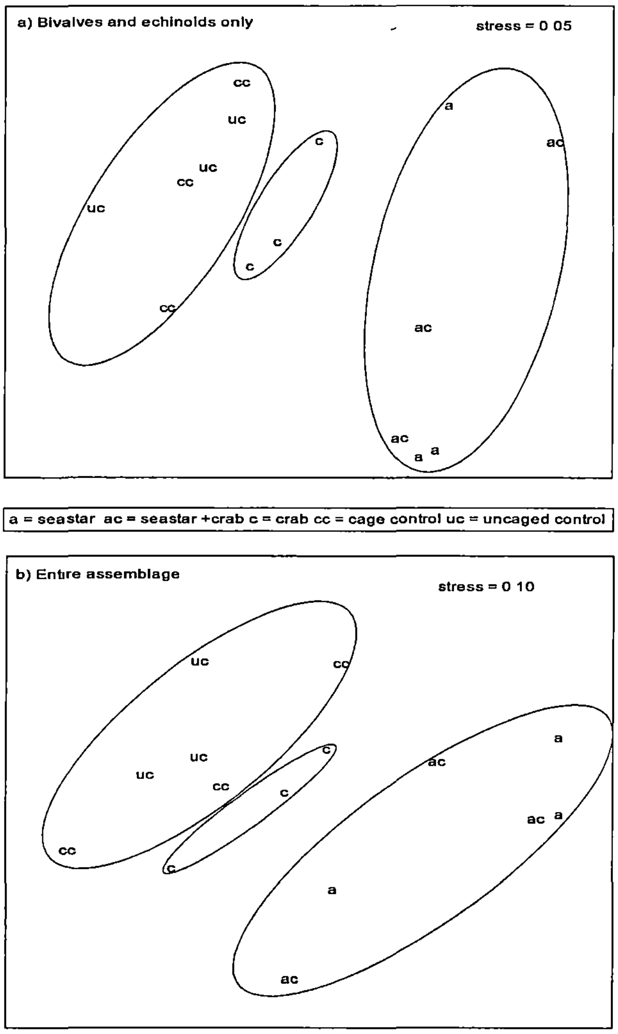


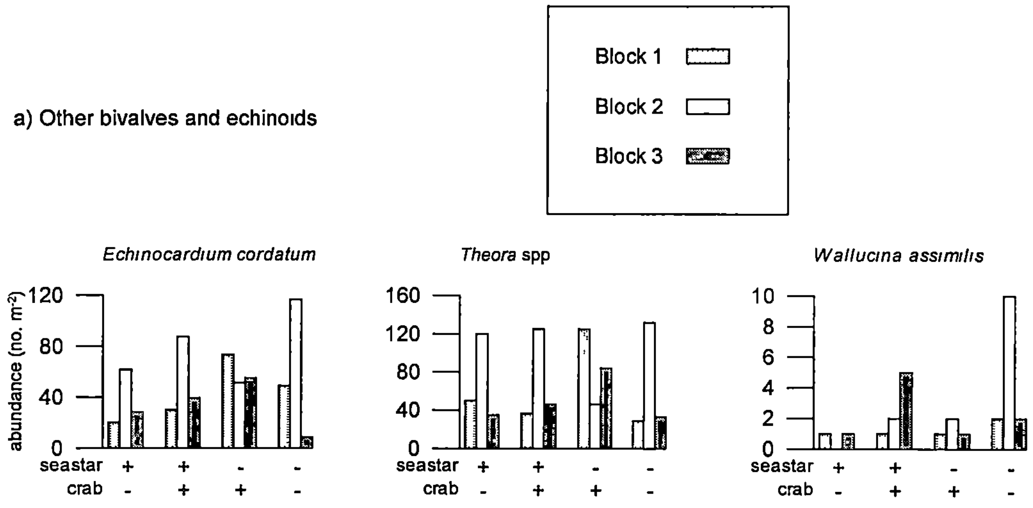
Figure 2.4 Ordination (nMDS) of treatment plots based on abundances of bivalves and echinoids (a), and on the entire assemblage (b). For both ordinations, plots with added seastars separate clearly from plots with only added crabs, and both are distinct to plots without added predators. The grouping is consistent with the general pattern described for the commercial bivalves in univariate analysis. Note the mean number per core in each treatment plot was used to estimate the number per m^2 for taxa found in cores for this comparison.

2.4.2 Other species

The general pattern described for commercial bivalves is evident graphically in the ordination (nMDS) of treatment plots based on abundances of bivalves and echinoids

(Figure 2.4a), and on the whole assemblage (Figure 2.4b). For both ordinations, plots with added seastars separate clearly from plots with only added crabs, and both are distinct to plots without added predators. It is important to note that bivalves and echinoids constituted approximately half the total abundance of organisms in the whole assemblage. Nonetheless, on the basis of individual species, there were no significant effects of added predators or cages detected for the echinoid *Echinocardium cordatum*; bivalves *Theora* spp. and *Wallucina assimilis* or for the polychaetes *Simplisetia amphidonta*, *Lysilla jennacubinae* and *Glycera* spp. (Table 2.1, Figure 2.5a,b).

a) Other bivalves and echinoids



b) Polychaetes

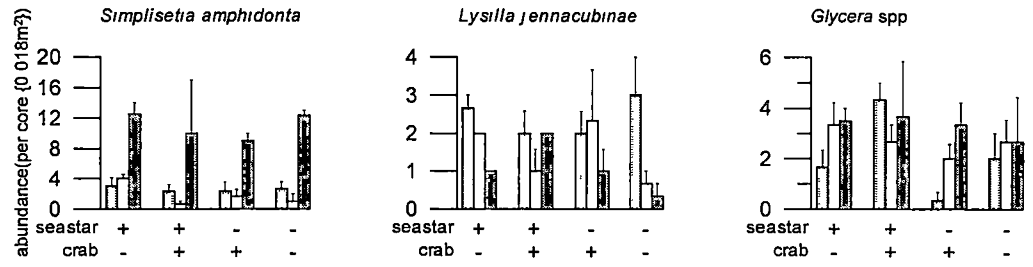


Figure 2.5 Densities of the other common species in each treatment plot in each block (n = 3 blocks). Abundances of bivalves and echinoids (a) are totals from 1m^2 suction samples, while polychaete densities (b) show mean (+ SE) numbers per core (n = 3 cores) in each plot. There were no significant effects of added predators detected for any of these species.

2.5 Discussion

The main effect of both predators was on the commercial bivalves, *Fulvia tenuicostata* and *Katelysia 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, this does not preclude that either or both predators may have direct and/or indirect effects on these and other species. For species in which variation between blocks was high (e.g. *Echinocardium cordatum*), or densities were very low (e.g. *Wallucina assimilis*), the power to test for treatment effects was low given only 3 replicates. More 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 the Derwent River Estuary where *Asterias amurensis* is abundant but large bivalves are rare, the echinoid *Echinocardium cordatum* (for which no effect was detected in this experiment) is a major prey item of *A. amurensis* (e.g. Morrice 1995; Grannum et al. 1996). While the commercial bivalves were clearly preferred over *E. cordatum* in this short term experiment, had the experiment run longer it seems likely that *A. amurensis* would switch to *E. cordatum* when the bivalves were exhausted. The echinoid can remain deeply buried (e.g. up to 15 cm), maintaining contact with the surface by a funnel-like opening over the aboral side of the animal (Buchanan 1966), compared with the bivalve, which is likely to be more available as it lives just below the sediment surface given its short siphon.

2.5.1 Impacts of *Asterias amurensis*

In this study, the reduction of the commercial bivalves *Fulvia tenuicostata* and *Katelysia rhytiphora* from densities upwards of 80 per m^2 and 5-7 per m^2 respectively, to virtually zero per m^2 in treatments with seastars at a density of 1 per m^2 demonstrates the impact of *Asterias amurensis* on bivalve populations. The abundance of recently opened shells increased for both bivalve species, indicating that seastar predation was largely responsible for the differences in densities between treatments. These findings are consistent with observed impacts of the seastar on bivalve populations in its native range (Hatanaka and Kosaka 1959; Kim 1969; Nojima et al. 1986). In the Derwent River Estuary, Grannum et al. (1996) calculated electivity indices based on field data and found that *A. amurensis* was highly selective of 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.

Despite the presence in the sediments of numerous remains (intact shells) of large adults of a number of bivalve species, living large adults are rare in the Derwent River Estuary. This is disturbing given the high prevalence of juveniles in the sediments and the diet of *Asterias amurensis* (Lockhart 1995; Morrice 1995; L Turner pers. comm.). 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 River Estuary. It is worth noting that the density of seastars in the cages (1 per m^2) is relatively high compared to that generally found in the Derwent River Estuary. However, similar or even substantially higher densities are common in large areas of the estuary (Grannum et al. 1996; Ling 2000), and are recorded commonly during population outbreaks in its native range (Nojima et al. 1986).

2.5.2 Impacts of *Carcinus maenas*

The lack of a significant effect of *Carcinus maenas* on *Fulvia tenuicostata* is largely due to spatial variability among blocks in densities of the bivalve. In two of the blocks the abundance of bivalves in the presence of the crab was 2-3 times lower than that in the control treatments. Given that the number of hinges was greatest in these plots, this indicates clearly that the reduced abundances are the direct result of predation by *C. maenas*. A comparison of the size frequency of *Fulvia tenuicostata* in the cage control and crab treatment in these blocks indicate that *C. maenas* prefers small bivalves. It is likely that *C. maenas* is unable to prey on larger bivalves given that 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* (Mackinnon 1997) and *Cerastoderma edule* (Mascaró and Seed 2000). Size constraints explain why no effect of crab predation was observed in block 3, since small *F. tenuicostata* were rare in all plots of this block. Similarly, size constraints in handling prey explain the absence of a detectable effect on *Katelysia rhytiphora*, given that the majority of *K. rhytiphora* in this experiment were large (> 25 mm) in all three blocks.

In similar short term experiments in intertidal soft sediment habitats, *Carcinus maenas* predation was shown to have similar effects on the abundance of the bivalves

Paphies erycinaea and *Katelysia rhytiphora*, in Tasmania (Mackinnon 1997), and *Nutricola* (as *Transenella*) *confusa* and *Nutricola* (as *Transenella*) *tantilla* in Bodega Harbor, California (Grosholz and Ruiz 1995). The results show that predation by *C. maenas* can also have a major impact on populations of small bivalves in subtidal soft sediment habitats where the crab becomes abundant. While the density of crabs in the cages was high compared to that generally found in nature, densities similar to and substantially higher than those in the cages have been recorded in Tasmania (Mackinnon 1997), and in its native range (e.g. Crothers 1968; Jensen and Jensen 1985)

2.5.3 Interactions of *Asterias amurensis* and *Carcinus maenas*

Spatial overlap of these invaders in southeast Tasmania is just beginning, and appears imminent as their respective ranges expand. Given their mutual preference for bivalves in sheltered low energy environments, they are likely to compete for the same prey. The question of the combined effects of several sympatric introduced species is particularly germane given the possibility of synergistic effects leading to accelerated impacts on native ecosystems (Simberloff and Von Holle 1999).

An important problem usually encountered in assessing interactions between multiple predators is identifying the relative proportion of prey loss associated with each predator (Sih et al. 1998; Weissberger 1999). This does not arise in the seastar/crab/bivalve interaction because seastars and crabs leave clear traces of their separate activities. Bivalves eaten by seastars manifest as undamaged shells with gaping valves, while hinges with vestiges of shells are a clear signature of feeding by the crab. The commercial bivalves, *Fulvia tenuicostata* and *Kataleysia rhytiphora,* are readily identifiable as intact live animals, as hinges or as gaping valves and provide ideal species to study the potential interactions between the two predators.

The effect of *Asterias amurensis* predation on *Katelysia rhytiphora* was apparently not affected by the presence of *Carcinus maenas*. This appeared to be due to an absence of small individuals and the inability of *C. maenas* to consume large ones. In contrast, the individual effects of each predator on the survival of *F. tenuicostata* were affected by the presence of the other. When both predators were present, they each consumed fewer *F. tenuicostata* than when alone. Thus, the interaction between *C. maenas* and *A. amurensis* appears to be direct competition for resources. *C. maenas* consumes only small bivalves. The seastar eats all sizes of *F. tenuicostata* in the absence of crabs, but fewer small animals when the crab is present.

While there are limitations in extrapolating to larger spatial scales on the bases of results of experiments conducted at small scales (e.g. Thrush et al. 1997; Lodge et al. 1998; Thrush 1999; Fernandes et al. 1999), there are nonetheless some predictions on the impact of *Carcinus maenas* and *Asterias amurensis* on a larger scale that are likely to be robust. The zone of overlap of these two species is likely to be largely restricted to the shallow subtidal given that *C. maenas* occurs predominately in the intertidal through to the shallow subtidal while *A. amurensis* occurs predominately in the shallow to deep subtidal. If the predators coexist in the shallow subtidal the results suggest that the effect on each predator is likely to be negative rather than facilitative when resources are limited. Whilst the densities in this experiment are high, they are well within the range observed for both species in their respective ranges in Tasmania, particularly where bivalves are abundant. On a larger spatial scale, 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. Grosholz and Ruiz (1995) suggested that the recent introduction of the predatory mollusc *Philine auriformis* into Bodega Harbor, and the potential for spatial and dietary overlap with *C. maenas*, may result in severe reductions of the abundances of infaunal invertebrates due to their combined impacts.

It is clear that the nature of interactions between introduced and native species is crucial to understanding the mechanisms that promote the successful establishment of introduced species (e.g. Wootton 1994; Petren and Case 1996). However, as invasions continue to homogenise the earth's biota, interactions between introduced pests are likely to be increasingly important in governing community dynamics. In Tasmania, I predict the interaction between *Asterias amurensis* and *Carcinus maenas* is imminent given the current rates of spread of *C. maenas* and strong preference of both predators for bivalve prey in sheltered low energy environments. When competing for a shared resource, the nature of the competitive interactions may be a major determinant of invasion success (Herbold and Moyle 1986; Byers 2000). I predict that partitioning of bivalves between the two predators according to size may allow for both introduced species to coexist in the shallow subtidal. On a larger spatial scale, coexistence would seem assured given partial spatial overlap in resource use. Bivalve populations in the intertidal and deep subtidal are not likely to be subject to seastar and crab predation respectively. This satisfies the general features that appear to be important in producing coexistence, namely: (1) structuring of the resource into distinct subunits, and (2) differential ability of the consumers to exploit these subunits (see Wilson et al. 1999).

2.5.4 Long-term effects

In coastal and estuarine systems bivalves are both important components of community structure and a major functional component as filter feeders, influencing the turnover of nutrients and coupling of the benthos and water column (Dame 1996). Thus, reductions in bivalve populations may significantly alter community structure and ecosystem function. Grosholz and Ruiz (1995) have speculated that *Carcinus maenas*, by reducing the abundance of *Nutricola* (as *Transennella*) spp. (bivalves) in western North America, may indirectly cause a reduction in filtration rates, influencing the turnover of nutrients and altering predator-prey populations.

It is not surprising, given the track records of both *Carcinus maenas* and *Asterias amurensis* that bivalve populations in particular may suffer serious impacts from predation. However, the plasticity of their respective diets is equally well documented. Predation by asteroids and portunids is thought to play a major role in organising many benthic marine communities as a result of their ability to exploit a wide range of food resources and habitats and the high rates at which they feed (e.g. Menge 1982; Cohen et al. 1995). The generalist nature of *C. maenas* and *A. amurensis* and their high rates of feeding have been well documented in Tasmania (Buttermore et al. 1994; Morrice 1995; Grannum et al. 1996; Lockhart 1995; Mackinnon 1997) and elsewhere (e.g. Hatanaka and Kosaka 1959; Fukuyama and

Oliver 1985; Jensen and Jensen 1985; Sanchez-Salazar et al. 1987; Raffaelli et al. 1989; Fukuyama 1994). Given the short time frame (2 months) of this experiment it is likely that indirect and other direct responses to the activity of these predators were not detected. Given the proclivity of *A. amurensis* and *C. maenas* for bivalves and their feeding plasticity it is likely that once the commercial bivalves were exhausted, they would have switched prey species and had wider community effects. For example in San Francisco Bay, California, a likely indirect effect of selective predation by *C. maenas* on native clams (*Nutricola tantilla* and *Nutricola confusa*) and native shore crabs (*Hemigrapsus oregonensis*) has resulted in significant increases in the abundances of two polychaetes and a tube-dwelling tanaid crustacean within a 2-year time frame (Grosholz et al. 2000).

2.5.5 Conclusions

The results of this short-term manipulative experiment suggest that predation by *Asterias amurensis* and *Carcinus maenas* may have a large impact on bivalve populations in shallow subtidal habitats in Tasmania where they become abundant. The reduction of bivalve populations has the potential to affect both community structure and ecosystem function. In the event of spatial overlap of predators, the results suggest that their interaction is likely to be mutually negative rather than facilitative, with both predators consuming fewer bivalves. However, the impact on bivalves may be greater in the presence of both species. Given their plasticity in feeding, both *C. maenas* and *A. amurensis* have the potential to also impact a large variety of taxa, and therefore to have wider direct and indirect effects than those reported here.

Chapter 3

Impacts of an introduced seastar (*Asterias amurensis*) on a soft sediment marine assemblage: reduced survivorship of recently settled recruits of a commercial bivalve

(Submitted to Marine Ecology Progress Series)

3.1 Abstract

The introduction and establishment of the predatory asteroid *Asterias amurensis* in southern Australia is considered a major threat to benthic marine communities and commercial bivalves. In this paper I quantify the impact of *A. amurensis* on a soft sediment assemblage in southeast Tasmania, with particular attention to effects of seastar predation on the survivorship of recruits of the commercial bivalve *Fulvia tenuicostata*. In a manipulative experiment, densities of *F. tenuicostata* recruits were reduced by ca. 15 fold (from 580 per m^2 to 35 per m^2) in the presence of seastars at background densities relative to control treatments without seastars. In a feeding survey, *A. amurensis* exhibited preference for *F. tenuicostata* following recruitment of the bivalve in January 1998, which comprised 80 % and 50 % of the seastar's stomach items in February 1998 and April 1998 respectively. The bivalves *Laternula rostrata* and *Paphies erycinaea* were the only other prey taxa affected by the seastar in the short-term experiment. However, *A. amurensis* preferred a variety of prey taxa when the abundance of *F. tenuicostata* was low, particularly other bivalves, gastropods and the echinoid *Echinocardium cordatum*; this indicates that the seastar may potentially affect other prey taxa. The results provide further support to the

hypothesis that predation by *A. amurensis* is responsible for the recent decline and subsequent rarity of large bivalves in its current distribution in Tasmania. The potential of seastar predation to have wider ecosystem level effects than the short term direct effects reported here is a major concern.

3.2 Introduction

In the late 20th century there has been a rapid acceleration of biological introductions due to human aided movement of species across and between continents (Carlton & Geller 1993; Lodge 1993; Mills et al. 1993; Vitousek 1994; Cohen & Carlton 1998; Ruiz et al. 2000). Introduced animals most likely to have a large impact on native communities are predators (Elton 1958; Lodge 1993; Lafferty & Kuris 1994) and, in marine benthic systems, asteroids are among the most important predators (see Menge 1982). In Australia, the introduced northern Pacific seastar (*Asterias amurensis*) has been highly conspicuous as a voracious generalist predator. It was first recorded in southeast Tasmania in 1986 (Buttermore et al. 1994; Byrne et al. 1997), but now occurs at high densities in Port Phillip Bay on mainland Australia. The introduction and establishment of this exotic asteroid is considered a major threat to benthic marine communities and commercial species (Grannum et al. 1996; Lockhart & Ritz 1998, chapter 2). Since its arrival in Tasmania, the seastar has become the dominant invertebrate predator in the Derwent River Estuary. Its population size in the estuary was estimated at 27.7 million in 1995/1996 (Grannum et al. 1996). Densities of the seastar recorded within the estuary (up to 46 per m^2; S Ling unpub. data) are far greater than any recorded during outbreaks of the species in the Ariake Sea, Japan (Nojima et al. 1986).

The key role of asteroid predation as a structuring force in benthic communities largely reflects their ability to exploit a wide range of food resources and habitats (Menge 1982). *Asterias* species are renowned for their capacity to form massive aggregations, and cause enormous damage to shellfish grounds (reviewed by Sloan 1980). *Asterias amurensis* is no exception. In its native range this species has caused considerable damage to commercial shellfishes (e.g. oysters, cockles, scallops, other clams; Hatanaka & Kosaka 1959; Kim 1969; Nojima et al. 1986), and is an opportunistic feeder on a variety of epifaunal and infaunal species including molluscs, ascidians, bryzoans, sponges, crustaceans, polychaetes, fish and echinoderms (Hatanaka & Kosaka 1959; Fukuyama & Oliver 1985; Fukuyama 1994). On this evidence alone, it has been anticipated that the successful establishment of *A. amurensis* in southeast Tasmania has the potential to profoundly affect native benthic marine communities and commercial species, particularly bivalves (Grannum et al. 1996; Lockhart 1995).

In contrast to the amount of work on exotic species in freshwater and terrestrial communities, the impacts of introduced species on native communities in marine and estuarine habitats have been quantified in only a handful of studies (e.g. Race 1982; Brenchley & Carlton 1983; Nichols et al. 1990; Lambert et al. 1992; Posey et al. 1993; Grosholz & Ruiz 1995; Grosholz et al. 2000, chapter 2). A major obstacle in assessing impact is often the absence of baseline data prior to the arrival of exotics, and this is the case regarding *Asterias amurensis* in the Derwent River Estuary (Grannum et al. 1996). Estimating the impact of *A. amurensis* on benthic communities in the estuary is further obfuscated by other large and long-term anthropogenic effects.

To help overcome these difficulties, experiments to assess the impact of the seastar were undertaken in areas that are similar in habitat type but do not currently support populations of the seastar (chapter 2,4). These experiments clearly demonstrated a major impact on the abundance of bivalves (including commercial species) that live just under or on the sediment surface. These results are consistent with the notion that predation by the seastar is responsible for the rarity of adult bivalves, particularly shallow infaunal and epifaunal bivalves, in the Derwent River Estuary. Furthermore, the high prevalence of juvenile molluscs, and particularly bivalves, in the diet of the seastar (Lockhart 1995; Morrice 1995) suggests that seastar predation on juveniles may be preventing the subsequent establishment and potential recovery of adult populations in the estuary. In early 1998, a massive recruitment pulse (≈300 per m^2) of the commercial bivalve *Fulvia tenuicostata* was recorded at Ralphs Bay at a site where seastars are abundant. In this paper I compare the abundance of prey taxa in the sediments and in seastar stomachs before, during and after the recruitment event, and conduct a manipulative experiment to test the hypothesis that seastar predation is limiting the survivorship of recently settled recruits of *F. tenuicostata* (and abundances of other species). Overall, the combined results of this study and those from related work (chapter 1,3,4,5) will provide for the first time a clear assessment of the impacts of *A. amurensis* on native assemblages, including commercial species, in southeast Tasmania.

3.3 Methods

The study was undertaken at Huxleys Beach (42° 58' S 147° 27' E) in Ralphs Bay, a large shallow embayment on the eastern side of the Derwent River Estuary, southeast

Tasmania, Australia, at a depth of 4-5 m. The sediment at this site is composed predominantly of fine to coarse sand.

3.3.1 Manipulative Experiment

Experimental design. The experiment to examine the effects of seastar predation on the survival of *Fulvia tenuicostata* recruits and the abundance of other prey taxa using cages was conducted over a 10-week period between January and April 1998. I consider that the vast majority of the *F. tenuicostata* present at the start of the experiment represent new recruits given both their small size (1-13 mm shell length, Figure 3.3a) and absence at the same site 3 months earlier. Cages consisted of a rigid (1 x 1 m base x 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 treatments used to examine the effect of seastar predation were: ($O_{initial}$) open unmanipulated plot, subject to background predation (sampled at 0 weeks); (O_{final}) open unmanipulated plot, subject to background predation (sampled at 10 weeks); (-S) caged exclusion, no seastars present, and (+S) caged inclusion, a single seastar added (thus at a density of 1 m^{-2}). Because of the scale of spatial patchiness of infauna indicated in a pilot study, a randomised complete block design was used in which each of the four treatments were represented once (each treatment ≈ 5 m apart) in each of three blocks (≈ 30 m apart) (see section 2.3 for the logic behind using this design).

Cage effects. While the potential for cage effects to confound true treatment effects is well documented, most of the tests to examine possible effects of cages have inherent limitations (e.g. Dayton and Oliver 1981). The design in this study contains several elements to account for potential effects of caging. Above all, cages were cleaned weekly and kept free of macroscopic fouling to minimise effects on water movement and light. In one approach to control for cage effects I compared plots with and without a cage in the presence of seastars (+S *vs.* O_{final}; but see later comments). In another approach to examine cage effects, I deployed a small cage inside a large cage with seastars excluded from both. In contrast to the outer cage, fouling built up rapidly on the inner cage where there was a decrease in abundance of most species and a reduction in growth of *Fulvia tenuicostata* in the inner compared to the outer cage. While these results may highlight the effect of fouling on abundance patterns and growth, the effect of the inner cage (a ‘ double cage’ effect) did not equate to the effect of single cages used elsewhere in the experiment (which were kept relatively free of fouling). For this reason the detailed results of this treatment are not presented. Nonetheless, it is worth noting that the growth of *F. tenuicostata* was similar in the outer cage compared to the unmanipulated plots suggesting that the effects of a single cage on water movement etc. are small. In any case, I rely primarily on the comparison of identical cages with and without seastars present to interpret seastar effects.

Sampling of invertebrates. Three replicate cores (150 mm diameter, 100 mm deep) were taken at random positions in each of the unmanipulated treatment (O) plots at the commencement of the experiment. After coring, the entire contents of treatment $O_{initial}$ plots were then 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 x 1 m x 0.1 m depth) was inserted into the sediment to isolate the plot, and all contents vacuumed into a 1 mm mesh bag. The experiment was monitored weekly to check the condition of the enclosed predators and remove fouling organisms from the cages.

Ten weeks after the commencement of the experiment, cages and predators were removed, and three cores were taken from the unmanipulated plots (O_{final}) and caged inclusion and exclusion treatments as described above. 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 all experimental plots were sampled to a depth of 0.1 m using the suction device as described above.

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 (2.0 mm mesh) and all bivalves, crabs and the echinoid *Echinocardium cordatum* sorted and identified to species. For core samples, all infaunal and epifaunal organisms (> 1 mm) were sorted and identified to the lowest possible taxon. In all core samples, the shell length of the commercial bivalve, *Fulvia tenuicostata* was measured to the nearest mm.

Statistical Analysis. The responses of numerically abundant taxa to experimental treatments were analysed using univariate statistics. Responses were determined using species abundance data from suction samples with the exception of polychaetes, gastropods and amphipods, which were counted in cores. For the analysis of cores, the arithmetic mean of the 3 replicate cores taken from each plot was used. A randomised complete block ANOVA, with 'treatment' (4 levels = $O_{initial}$, O_{final}, +S and -S) as a fixed factor, and 'block' as a random factor was used to test for the effect of seastars and cages (see below). 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). For a detailed description of how particular assumptions associated with a randomised block design were considered see section 2.3.1. The statistical package SAS® was used for analyses.

Three planned comparisons (one orthogonal and two non-orthogonal) were carried out following the initial analyses to test for seastar and caging effects. For planned comparisons, I adjusted the significance level using the conservative method of Todd & Keough (1994), i.e. α was reduced to α / (1 + the number of non-orthogonal contrasts). With two non-orthogonal and one orthogonal comparison, the significance level was adjusted to 0.016. Following Todd & 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:

$O_{initial}$ *vs.* O_{final} this assesses the change in invertebrate abundance over the experimental period in open unmanipulated plots. In particular, this will measure the natural change in abundance of *F. tenuicostata* recruits (and other taxa) in the presence of seastars at their background density over the course of the experiment. While this treatment is not critical to the

	assessment of seastar effects it provides useful biological information.
-S *vs.* +S	this assesses the effect of seastars on invertebrate abundances, contrasting treatments with and without seastars.
O_{final} *vs.* +S	this examines caging effects not associated with the removal of seastars, such as the exclusion of other predators and cage-induced changes to predator behaviour. In interpreting this comparison, it is recognised that the seastar density in the cage was higher (1 m^{-2}) than the mean background density (ca. 0.09 – 0.4 m^{-2} over the course of the study). Note, the distribution of seastars became highly aggregated during the experiment (see results) and densities at 1 m^{-2} were recorded in 5 x 2 m quadrats when belt transects dissected aggregations.

3.2.2 Comparison of macro-invertebrate abundance in the sediment and in seastar stomachs

Sediments. Invertebrate abundances were measured in one suction sample (as described above) and three infaunal cores (as described above, ≈ 1 m apart) at each of three random positions (≈ 30 m apart). These samples were taken in November 1997, January 1998 (at the start of the manipulative experiment), April 1998 (at the conclusion of the manipulative experiment), and November 1998. The samples obtained in January 1998 and April 1998 were those from the open plots in the manipulative experiment.

Stomach contents. Dietary information was assessed by examining the stomach contents of the first 50 seastars encountered on three randomly placed 50 x 2 m strip transects at the study site. Samples of seastars were taken in November 1997, February 1998 (4 weeks into the manipulative experiment), April 1998 (at the conclusion of the manipulative experiment), and November 1998. All seastars were placed immediately in sealed plastic bags upon collection to prevent the loss of regurgitated stomach contents. Because the seastar exhibits both extra and intraoral modes of feeding great care was taken in collecting them so that all prey items been fed on extraorally were collected in the plastic bags. Note that since evidence of intraoral feeding may be easier to detect because of longer residence times in the gut some biases may arise. Seastars were frozen within a few hours of collection, and thawed prior to examination.

Dietary analysis. Because of differential digestion rates, the ability to identify and count individuals in stomach samples varies between taxa. In contrast to bivalves and gastropods, polychaetes and crustaceans are more difficult to identify and count in stomach samples. In most cases it was clear that only a single individual was present, as evidenced by presence of a head capsule, limb, or complete body. However, when digestion was nearly complete (polychaetes) or when there were several small pieces of crustacean exoskeleton present, the exact number of individuals was uncertain. Accordingly I used two methods to calculate the proportion of each prey taxon in the diet of the seastar: (1) proportion of the total numerical abundance where presence of crab and polychaete parts were scored as a single animal, and (2) proportion of the total stomach contents based on a binary classification, i.e. all prey taxa were scored as either present (1) or absent (0). I compared patterns of prey composition and prey preferences (see below) calculated using both methods.

To identify prey species that were consumed disproportionately by *Asterias amurensis* relative to their occurrence in the environment, Vanderploeg and Scavia's (1979) relativised electivity index (*E*) was calculated. The index is defined as:

$$E_i = (W_i - \frac{1}{n}) / (W_i + \frac{1}{n})$$

Where $W_i = \frac{r_i / p_i}{\sum_i (r_i / p_i)}$, n = the number of kinds of food items, r_i = the proportion of the i^{th} food in the diet, and p_i = the proportion of the i^{th} food in the environment. The index for each taxon has a possible range from –1 to +1. A value of 0 denotes that the taxon is taken in proportion to its abundance; 1 signifies that the taxon is preferred and exclusive in the diet; and –1 indicates that the species is avoided. Taxa only found in stomach contents but not in the samples from the environment were given a value of +1 and not considered further in calculations of electivity. Given that the electivity coefficient confounds predator choice and ecological availability of prey (as it is based on numerical availability and not functional availability), preference does not necessarily imply active choice but may also indicate that a prey is ecologically unavailable to the predator. However, the primary question in this study is about the predator's impact on prey, rather than the behavioral mechanisms underlying it.

3.2.3 Seastar Density and Dispersion

Seastar density and dispersion were measured from the transects used to collect dietary information in November 1997, February 1998 (4 weeks into the manipulative experiment), April 1998 (at the conclusion of the manipulative experiment), and November 1998. Density and dispersion were estimated for each transect from counts of individuals present in 5 m x 2 m sections of the strip transect. Dispersion was described by Morisita's (1959) index of dispersion (I_δ). For comparison across surveys, the mean (± SE) of the density and dispersion calculated from each transect (n = 3) was used.

3.4 Results

3.4.1 Manipulative Experiment

Relative abundance of macro-invertebrates. The major groups found in the core samples were polychaetes, bivalves, amphipods and gastropods. The dominant taxa in each group in decreasing order of numerical abundance were the polychaete *Nephtys australiensis*, the bivalves *Theora* spp., *Fulvia tenuicostata* and *Mysella donaciformis*, and the gastropod *Nassarius nigellus*. Due to very low abundances and the taxonomic difficulties associated with species level identification, amphipods were not resolved below the level of order. The major species found in suction samples in decreasing order of numerical abundance were the bivalves *Fulvia tenuicostata*, *Theora* spp. and *Mysella donaciformis*; the native crab *Paragrapsis* *gaimardii*; the bivalve *Corbula gibba*; the echinoid *Echinocardium cordatum*; and the bivalves *Hiatella australis*, *Timoclea cardoides*, *Venerupis anomala*, *Soletellina biradiata*, *Laternula rostrata*, and *Paphies erycinaea*.

Changes in the abundance of macro-invertebrates. Abundances of *Fulvia tenuicostata* and *Mysella donaciformis* in unmanipulated plots decreased over the experimental period, however, the change was not significant at the adjusted level ($\alpha_{adjusted} = 0.016$) (Table 3.1: $O_{initial}$ vs. O_{final}, Figure 3.1). In contrast, densities of *Corbula gibba*, *Timoclea cardoides*, *Theora* spp., *Soletellina biradiata*, *Venerupis anomala*, *Echinocardium cordatum*, *Nephtys australiensis* and amphipods increased over the experimental period, however this change was only significant at the adjusted alpha level for *C. gibba* (Table 3.1, Figures 3.1, 3.2). *Laternula rostrata*, *Hiatella australis*, *Paragrapsis gaimardii* and *Nassarius nigellus* were absent or in very low densities in unmanipulated plots compared with the caged treatments (Table 3.1, Figure 3.1, 3.2).

Effects of seastars. There was a significant reduction in the abundance of *Fulvia tenuicostata* in the presence of seastars (Table 3.1: -S vs. +S, Figure 3.1). The mean size of *F. tenuicostata* increased from 3.79 (± SE 0.25) mm to 18.88 (± SE 0.59) mm in plots where seastars were excluded (Figure 3.3). This further demonstrates that recruitment into larger sizes was truncated by predation. At the end of the experiment, densities of *F. tenuicostata* in the cage inclusion and unmanipulated treatments were ≈ 17 m^{-2} and ≈ 35 m^{-2} respectively, while in the treatment protected from seastar predation densities were ≈ 580 m^{-2}. Abundances of *Paphies erycinaea*

	Main analysis		**Planned comparisons**		
	MS_{res}	Treat (*P*)	$O_{initial}$ vs. O_{final} (*P*)	-S vs. +S (*P*)	O_{final} vs. +S (*P*)
Degrees of Freedom	6	3	1	1	1
Bivalves					
Fulvia tenuicostata	0.878	**0.011**	0.025	**0.005**	0.236
Theora fragilis	$0.219*10^{-4}$	0.254	0.161	0.150	0.984
Mysella donaciformis	0.275	0.084	0.028	0.918	0.045
Corbula gibba	2.006	0.053	**0.014**	0.227	0.043
Timoclea cardoides	2.757	**0.046**	0.021	0.622	**0.015**
Soletellinna biradiata	11 005	0.826	0.505	0.836	0.962
Venerupus anomala	1.951	0 291	0.114	0.390	0.114
Hiatella australis	0.424	0.0001	*	0.020	*
Laturnula rostrata	0.465	**0.025**	*	0.020	*
Paphies erycinaea	2.621	0.124	0.284	0.045	0.284
Crabs					
Paragrapsis gaimardii	3.59	**0.038**	0.986	0.894	0.026
Echinoids					
Echinocardium cordatum	13.412	0.202	0.383	0.578	0.442
Gastropods					
Nassarius nigellus	23.942	0.513	0.552	0.486	0 838
Polychaetes					
Nephtys australiensis	19263	0.513	0.463	0.5791	0.673
Amphipods	1.030	0.275	0.099	0.669	0.242

Table 3.1 Analysis of effects of seastar predation and caging effects on the abundances of numerically abundant infauna. The table shows results for each taxon of the overall ANOVA comparing among treatments $O_{initial}$ (open unmanipulated plot, subject to background predation sampled at 0 weeks); O_{final} (open unmanipulated plot, subject to background predation sampled at 10 weeks); -S (caged exclusion, no seastars present), and +S (caged inclusion, a single seastar). Results of three planned comparisons are also given. All of the tests in the table used the MS residual as the error term. 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. * indicates that the species was absent in at least one of the groups being compared.

and *Laternula rostrata* were also greater when seastars were excluded, consistent with a seastar effect, however the differences were not significant at the adjusted level ($\alpha_{adjusted} = 0.016$) (Table 3.1: -S vs. +S, Figure 3.1). In contrast, the abundance of *Hiatella australis* was significantly higher in the presence of seastars (Table 3.1: -S vs. +S, Figure 3.1). For the remaining taxa, differences between treatments with and without seastars were not significant (Table 3.1, Figure 3.1, 3.2).

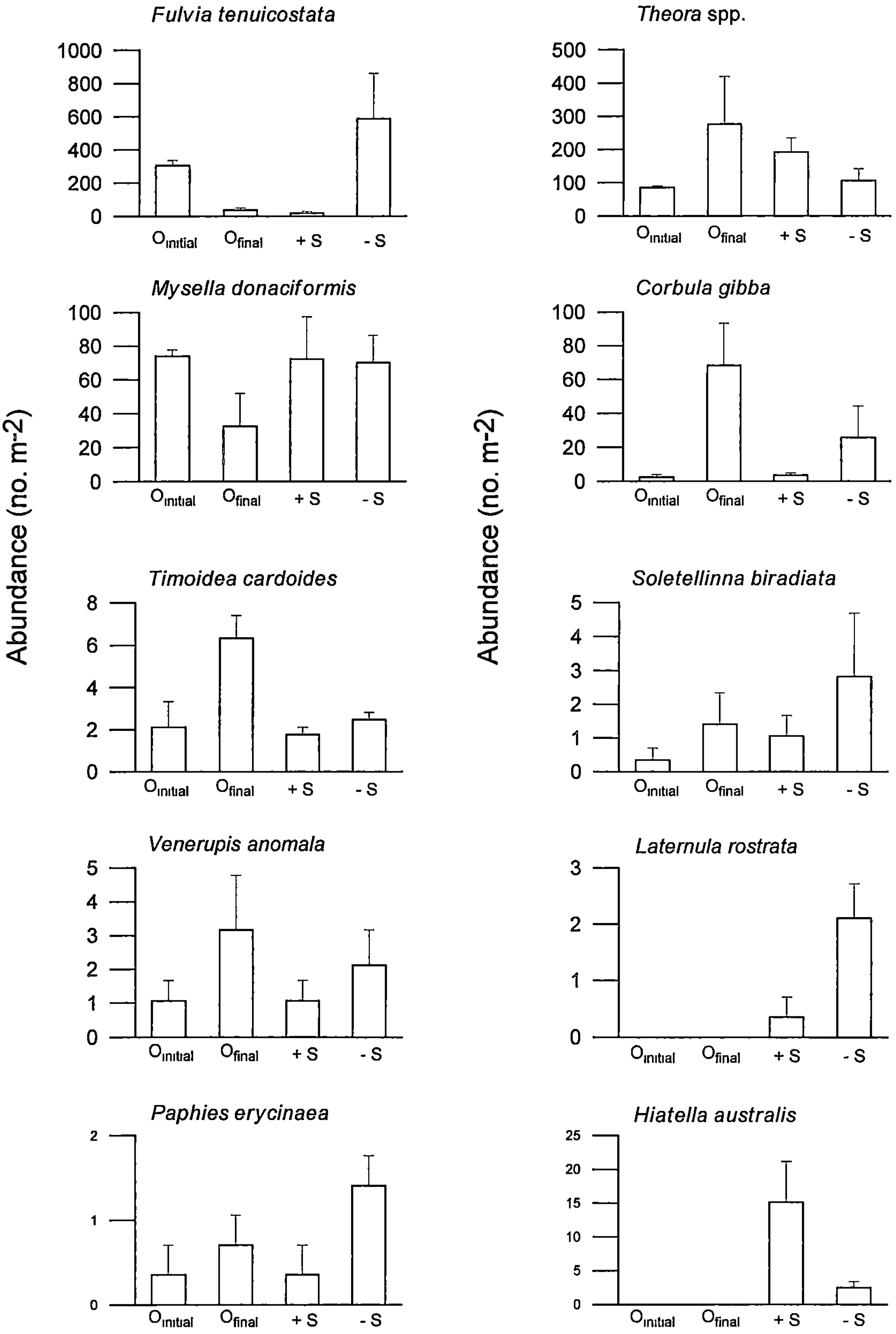


Figure 3.1 Densities of the most abundant bivalve species. Densities are means per 1 m^2 (+ SE) taken from suction samples to a depth of 100 mm ($n = 3$ plots). $O_{initial}$ = open unmanipulated plot, subject to normal predation (sampled at 0 weeks); O_{final} = open unmanipulated plot, subject to normal predation (sampled at 10 weeks); -S = caged exclusion, no seastars present; +S = caged inclusion, a single seastar added (thus 1 m^{-2}).

Figure 3.2 Densities of the most abundant polychaete, crustacean, gastropod and echinoid taxa in each treatment. Densities of the echinoid *Echinocardium cordatum* and the crustacean *Paragrapsis gaimardii* are means per 1 m^2 (+ SE) taken from suction samples to a depth of 100 mm (n = 3 plots). Densities of the polychaete *Nephtys australiensis*, gastropod *Nassarius nigellus* and amphipods are means per 1.m^2 (+ SE) scaled from counts in cores (n = 3 cores pooled, each 150 mm diameter, 100 mm depth) in each plot (n = 3 plots). Abbreviations are as in Fig. 3.1.

Caging Effects. In the presence of seastars, densities of the crab *Paragrapsis gaimardii*, bivalve *Mysella donaciformis* and gastropod *Nassarius nigellus* were greater in caged compared with uncaged treatments, however these differences were not significant at the adjusted level ($\alpha_{adjusted}$ = 0.016; Table 3.1: O_{final} vs. +S, Figure 3.1, 3.2). The bivalves *Laternula rostrata* and *Hiatella australis* occurred only in the presence of cages (Figure 3.1). In contrast, densities of *Timoclea cardoides*, *Venerupis anomala*, and *Corbula gibba* were reduced in caged compared with uncaged treatments, however this difference was only significant at the adjusted level ($\alpha_{adjusted}$ = 0.016) for *T. cardoides* (Table 3.1, Figure 3.1). For the remaining taxa, differences were not significant between the caged and uncaged treatments with seastars present (Table 3.1, Figures 3.1, 3.2).

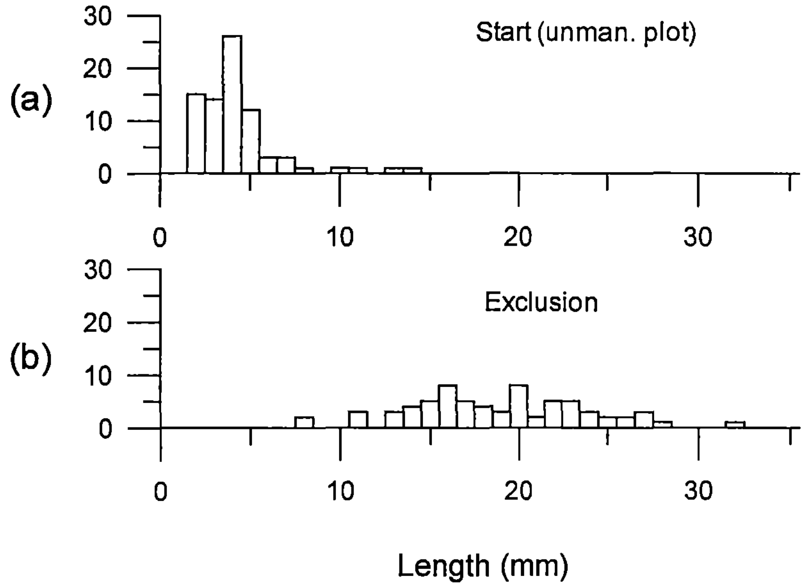


Figure 3.3 Length frequency histograms of the commercial bivalve *Fulvia tenuicostata* from (a) open unmanipulated plots at the start of the experiment, and (b) cages excluding seastars sampled at the end of the experiment.

3.4.2 Comparison of macro-invertebrate abundance in the sediment and in seastar stomachs

Sediments. The major groups found were polychaetes, bivalves, crustaceans and gastropods which represented 60%, 23%, 11% and 3% respectively of the total numerical abundance pooled across sampling times. However, the relative abundance and composition of each group varied considerably over the sampling period (Figures 3.4, 3.5), e.g. bivalves comprised 5 % and 9 % of the total abundance in November 1997 and November 1998 respectively, compared with 44% and 28% in January and April 1998 respectively. This pattern reflected recruitment of some species, particularly *Fulvia tenuicostata*, early in the year and subsequent mortality of nearly all the major bivalve species between November 1997 and November 1998 (Figure 3.5).

Stomach contents. Patterns of prey consumption calculated from numerical and binary data (binary data shown in parentheses below) were similar for all major groups and taxa (Figure 3.4, 3.5). The major groups found in seastar stomachs were bivalves, crustaceans, gastropods, polychaetes and the urchin *Echinocardium cordatum* representing 62 (52)%, 19(25) %, 8(9) %, 6(8) % and 4(6) % respectively of the total stomach contents of all seastars pooled across sampling times. With the exception of the bivalve *Mysella donaciformis*, which was never found in seastar stomachs, all of the major groups and taxa that were found in the sediments were present in the diet of *Asterias amurensis*. Temporal shifts in the occurrence of total bivalves, polychaetes and crustaceans in the diet of seastars tracked changes in relative abundance of these groups in the environment (Figure 3.4). Polychaetes and crustaceans were more common in the diet in the first and last surveys when their relative abundances were highest (Figure 3.4). In contrast, bivalves were clearly the most common prey items in the middle two surveys (February and April 1998) when their relative abundance was highest (Figure 3.4). *Fulvia tenuicostata* was clearly the major prey item in this period, representing 76 (69)% and 52 (39)% of the seastar's diet (Figure 3.5). Following the decline in abundance of *F. tenuicostata*, the absolute and relative abundances of the bivalves *Corbula gibba* and *Venerupis anomala*, and the gastropod *Nassarius nigellus*, increased in the sediments. These species were then consumed by the seastar until their densities in the environment were negligible (Figure 3.5). In November 1997 and 1998, polychaetes, crustaceans, *Echinocardium cordatum* and the bivalves *Theora* spp. and *Timoclea cardoides* were the major prey items of the seastar (Figures 3.4, 3.5).

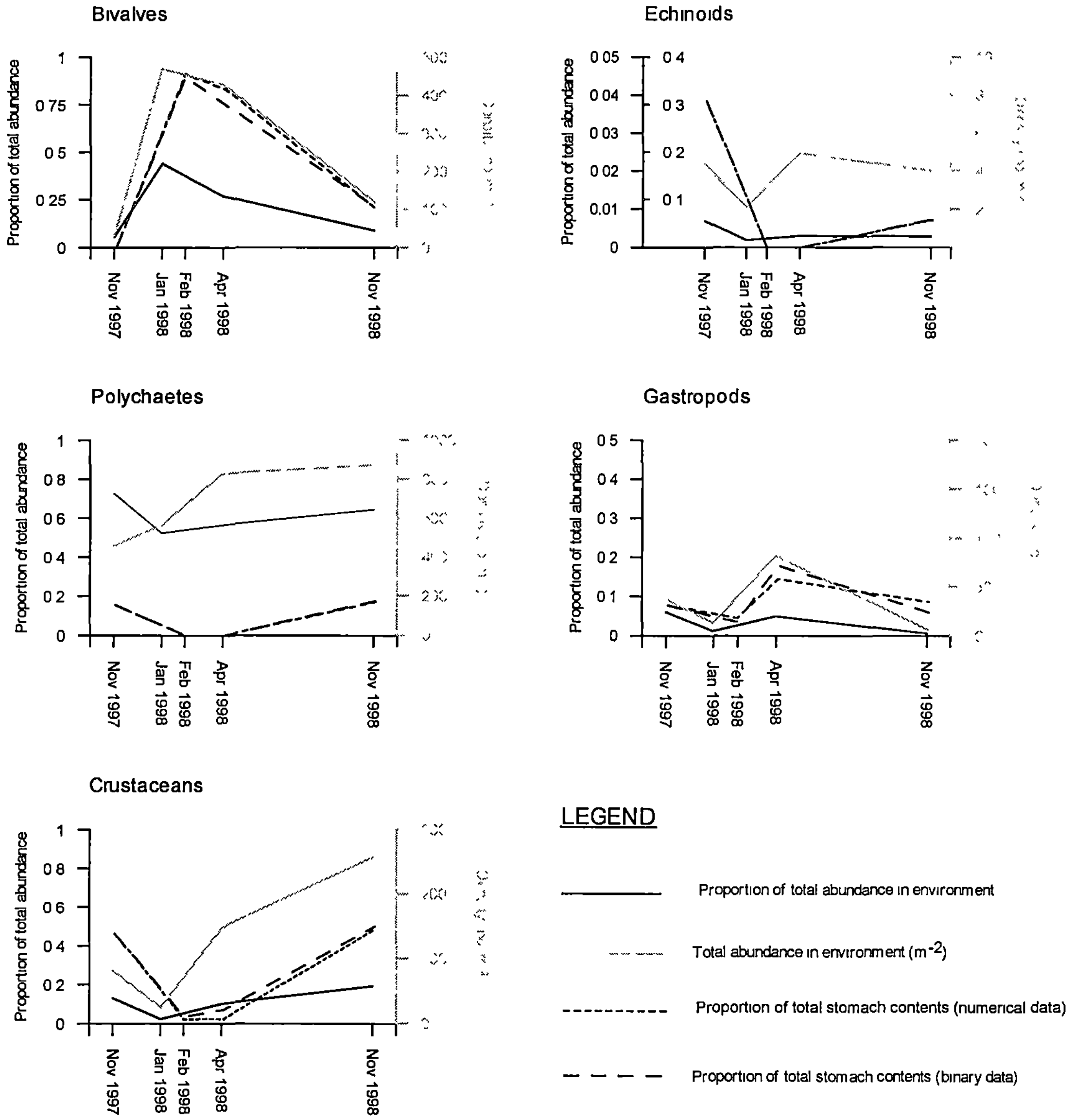


Figure 3.4 Proportion of the total abundance of the major groups of prey in seastar stomachs and in sediments, and the absolute abundance in the sediments. The Y-axis on the left depicts proportions in the diet and sediments [Note: when two scales are marked, the left-hand scale is the proportion of total abundance in the sediments]. The Y-axis on the right represents the absolute abundance in the sediments (m^{-2}). Densities are determined from 1 m^2 suction samples, with the exception of polychaetes, crustaceans and gastropods, which were extracted from core samples.

Dietary analysis. Prey preferences calculated from numerical and binary data were similar for the major taxa (Table 3.2). It is clear that the main prey items in summer (January – April 1998), i.e. the bivalves *Fulvia tenuicostata*, *Corbula gibba*, *Venerupis anomala* and the gastropod *Nassarius nigellus*, were consumed in much

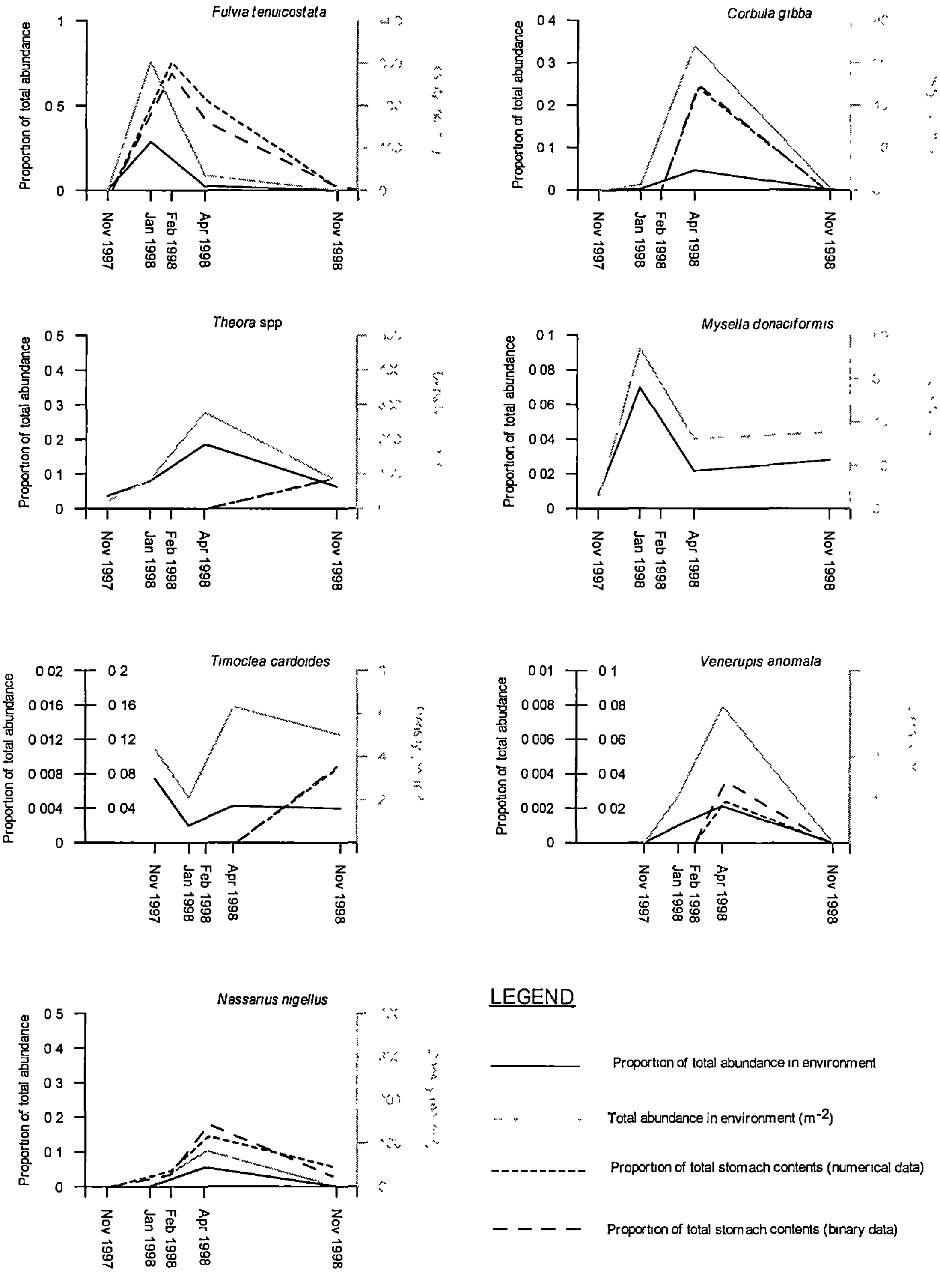


Figure 3.5 Proportion of the total abundance of the major bivalve species and the gastropod, *Nassarius nigellus* in seastar stomachs and in sediments, and the absolute abundance in the sediments The Y-axis on the left depicts the proportion in the diet and sediments [Note when two scales are marked, the left-hand scale is the proportion in the sediments]. The Y-axis on the right represents the mean absolute abundance (per m^2) in sediments. Densities are determined from 1 m^2 suction samples, with the exception of *Nassarius nigellus*, which was extracted from core samples.

Taxon	**November 1997**			**April 1998**			**November 1998**		
	Frequency (%)		Electivity index	Frequency (%)		Electivity Index	Frequency (%)		Electivity Index
	sub-stratum	stomach contents		sub-stratum	stomach contents		sub-stratum	stomach contents	
Bivalves									
Fulvia tenuicostata	0.1	0	-	2.8	51.8(39.3)	0.69(0.58)	0	2.9	+1
Theora spp.	3.4	0	-1	21.5	0	-1	5.9	8.6(8.8)	-0.43(-0.43)
Mysella donaciformis	0.7	0	-	2.5	0	-1	2.6	0	-1
Corbula gibba	0.1	-	-	5.3	24.1(25.0)	0.14(0.10)	0.1	0	-
Timoclea cardoides	0.7	0	-	0.5	0	-	0.4	8.6(8.8)	0.73(0.73)
Laternula rostrata	-	-	-	-	2.4(3.6)	+1	-	-	-
Venerupis anomala	-	-	-	0.2	2.4(3.6)	0.48(0.58)	-	-	-
Electroma georgina	-	-	-	Na	2.4(3.6)	-	-	-	-
Gastropods									
Nassarius nigellus	-	-	-	0.5	14.5(17.9)	0.80(0.82)	0	5.7	+1
Fusinus novaehollandiae	0	7.7	+1	-	-	-	-	-	-
Retusa pelyx	3.0	0	-1	0.5	0	-	-	-	-
Philine angasi	1.0	0	-1	-	-	-	2.3	0	-1
Gastro sp1	2.0	0	-1	-	-	-	-	-	-
Gastro sp2	1.0	0	-1	-	-	-	-	-	-
Gastro sp3	-	-	-	-	-	-	0	2.9	+1
Echinoids									
Echinocardium cordatum	0.7	30.8	0 87	0.5	0	-	0.3	5.7(5.9)	0.69(0.69)
Crustaceans	13.0	46 2	0.05	9.7	2.4(7.1)	-0.86(-0.67)	19.1	48.6(50 0)	-0.17(-0.17)
Polychaetes	73.2	15.4	-0.88	55.0	0	-1	64.7	17.1(17.6)	-0.86(-0.86)
Sipunculids	-	-	-	-	-	-	1.9	0	-1
Ascidians	1.0	0	-1	-	-	-	-	-	-
Flatworms	-	-	-	-	-	-	1 9	0	-1

Table 3.2 Frequency (%) and electivity coefficients for macro-invertebrates in the sediments and stomach contents of 46, 20 and 49 *Asterias amurensis* collected from Ralphs Bay during November 1997, April 1998 (week 8 of experiment) and November 1998 respectively. Frequency (%) of macro-invertebrates in the diet is calculated using the total stomach contents based on numerical and binary data. Results based on binary data are in parentheses. Taxa showing positive values of electivity are presented in bold face. - indicates taxa that were not recorded in both sediments and stomach contents.

greater proportion to their relative abundance in the environment (Table 3.2). However, in late spring (November) when the abundances of these species in sediments were very low, the echinoid *Echinocardium cordatum* and the bivalve *Timoclea cardoides* were preferred. Whilst polychaetes were major prey items in late spring, they were not preferred. In contrast, crustaceans were consumed in greater proportion to their abundance in the environment in November 1997 and consumed in (approximately) direct proportion to their occurrence in the environment in November 1998. Invertebrates that were relatively common in the sediment, but clearly not preferred were the bivalves *Mysella donaciformis* and *Theora* spp.; the gastropods *Retusa pelyx*, *Philine angasi*, plus two unidentified gastropod species; ascidians; flatworms and sipunculids. In contrast, the bivalve *Laternula rostrata*, gastropod *Fusinus novaehollandiae*, and an unidentified gastropod were found in the diet but not in the sediments.

3.4.3 Seastar density and dispersion

In November 1997 and 1998 seastars were dispersed randomly at scales of 10^1 m^2, but in February 1998 the dispersion of seastars was aggregated at this scale (Figure 3.6). In April 1998 the dispersion of seastars was random on two transects and aggregated on the other which is reflected in the high variation associated with the index of dispersion (Figure 3.6). The mean density of seastars was 0.39 (± 0.06 SE), 0.15 (± 0.04 SE), 0.09 (± 0.003 SE), and 0.40 (± 0.02 SE) m^{-2} in November 1997, February 1998, April 1998 and November 1998 respectively. When the mean density of seastars was at a peak in November 1997 and 1998, seastars were dispersed randomly.

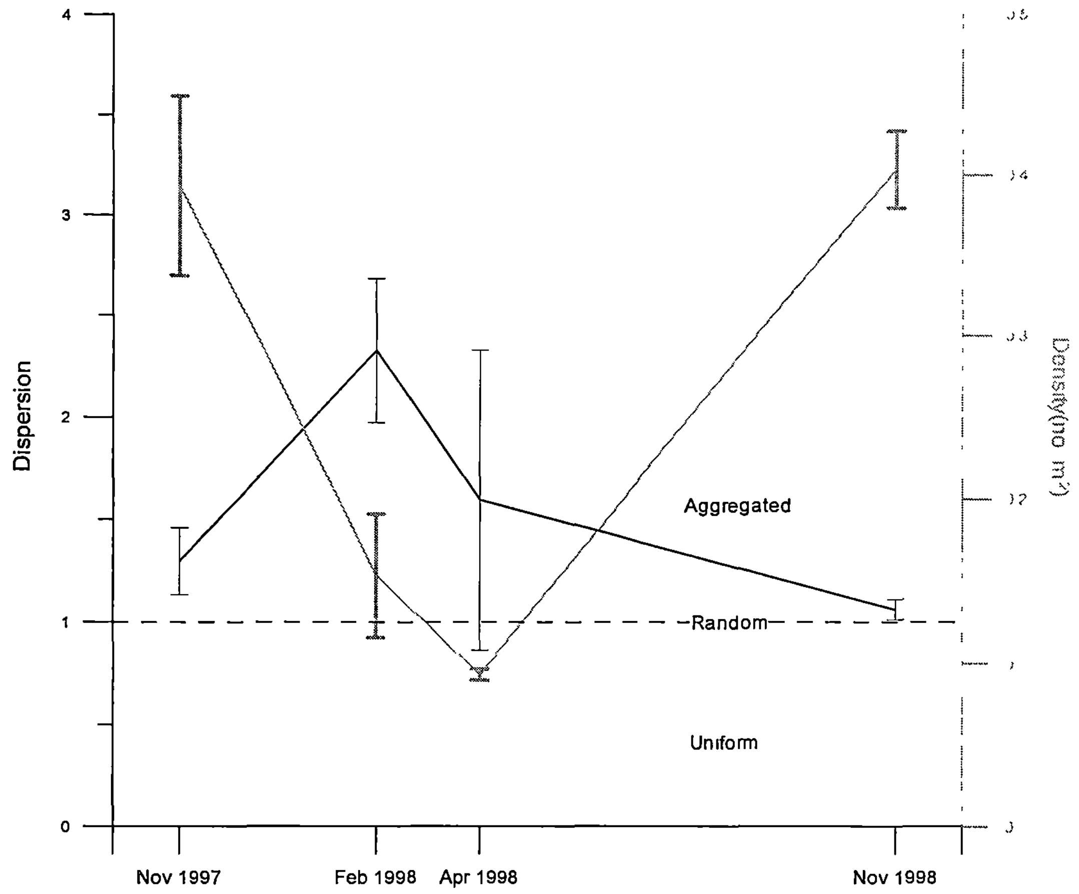


Figure 3.6 Density and dispersion of seastars. Density (light line) are means (± SE) determined from 50 x 2 m strip transects (n = 3). Dispersion (dark line) is given as the mean (± SE) Morisita's (1959) index of dispersion, I_δ, calculated from counts of seastars within ten 5 x 2 m quadrats that comprised the larger 50 m x 2 m strip transects (n = 3). I_δ has a value of 1 for random distributions, less than one for uniform distributions and greater than one for aggregated distributions.

3.5 Discussion

3.5.1 Direct effects of seastar predation on the survivorship of *Fulvia* recruits

There have been numerous observational studies to suggest that asteroids may play a major role in structuring bivalve populations in soft sediment habitats (e.g. Christensen 1970; Anger et al. 1977; Fukuyama & Oliver 1985; Nojima 1988). However, in contrast to hard bottom benthos (e.g. Dayton 1971; Paine 1974; Robles et al. 1995), far fewer studies have experimentally demonstrated the influence of asteroid predation on bivalve populations in soft sediments. Using a combination of experimental and observational approaches, the present study demonstrates the impact of *Asterias amurensis* on the survivorship of new recruits of the commercial bivalve *Fulvia tenuicostata*. After ten weeks, the mean density of *F. tenuicostata* was reduced from ca. 300 m^{-2} following recruitment at the beginning of the experiment, to ca. 35 m^{-2} in the presence of seastars at natural densities, and 17 m^{-2} in cage inclusions where seastar density was 1 m^{-2}. In marked contrast, in treatments from which *A. amurensis* was excluded, the mean density of *F. tenuicostata* was ca. 580 m^{-2} at the end of the experiment. The mean size of *F. tenuicostata* increased dramatically in seastar exclusions over the experimental period. Note the increase in density over the experimental period most likely reflects the growth of recruits into size classes that are retained on the 2 mm mesh sieve which was used to assess abundances. Densities of ca. 530 m^{-2} were recorded at the start of the experiment when recruits retained on a 1mm mesh sieve were counted. While it is possible that hydrodynamic effects caused by the cages (e.g. affecting food availability) and/or exclusion of other predators may have led to increased survival in the cage exclusion, the major reduction in bivalve density in the cage inclusion is most likely due to seastar predation. Moreover, the seastar clearly responded to the recruitment of *F. tenuicostata* in the unmanipulated area, as evidenced by a pronounced shift in diet. The bivalve was the most common prey species of *A. amurensis* following its recruitment, representing 50 - 80% of the seastar's dietary items in February and April 1998. These findings are consistent with observations in the native habitat of the seastar that show major damage to commercial shellfishes such as cockles, oysters, scallops and other clams (Hatanaka & Kosaka 1959; Kim 1969; Nojima et al. 1986).

The bivalves *Laternula rostrata* and *Paphies erycinaea* were the only other prey taxa for which the experimental results indicated an impact of the seastar. This is consistent with previous observations of feeding, which identified *P. erycinaea* as a common prey item of the seastar (Lockhart 1995; Grannum et al. 1996). Although it was absent from unmanipulated plots at the start and end of the experiment, *L. rostrata* was recorded in seastar stomachs and was present in both treatments from which seastars were excluded. Whilst the results are indicative of a seastar effect, the presence of *L. rostrata* at low levels in seastar inclusion treatments relative to open plots where it was absent, suggests that it is also subject to losses from other predators.

Bivalve populations in the Derwent River Estuary are characterised by very small size and rarity of live adults (Lockhart 1995; Ross pers. obs.). The presence in the surface sediments of numerous remains (intact shells) of large adults of several species suggests that this has not always been the case (Lockhart 1995; L Turner pers. comm.). The results of this study support the hypothesis that predation by *Asterias amurensis* may be largely responsible for the rarity of adult *Fulvia tenuicostata* in the Derwent River Estuary. A manipulative experiment conducted outside the current range of the seastar in Tasmania (chapter 2) demonstrated that *A. amurensis* at densities of 1 m^{-2} could quickly decimate adult populations of *F. tenuicostata.* In this study I have demonstrated that *A. amurensis* can have a dramatic impact on the survivorship of *F. tenuicostata* recruits in the short term. At the feeding rates observed in Ralphs Bay, the majority of a large settlement > 500 recruits m^{-2} could readily be consumed within 2-3 months of settlement.

3.5.2 Density and dispersion

Seastars became more strongly aggregated at the study site (at scales of 10^1 m^2) following recruitment of *Fulvia tenuicostata*. The quantitative data were also supported by observations of a large aggregation of seastars moving through the experimental area, leaving masses of empty *F. tenuicostata* shells in its wake. These aggregations may result from chemoattraction towards feeding conspecifics (Ormond & Campbell 1974; Scheibling 1980). This is supported by observations of Lockhart (1995) in which *Asterias amurensis* showed greater attraction to feeding conspecifics than to available prey. At the same time that seastars aggregated, their overall density dropped. This may reflect seasonal changes in the distribution of *A. amurensis*. In Tasmania and Japan, *A. amurensis* appear to migrate into shallower water during winter and move into deeper water during summer (Morrice 1995; Hayashi 1973).

3.5.3 Caging artefacts

Caging artefacts may have compromised the ability to detect seastar effects for some taxa. Whilst caging experiments have been important in elucidating the role of predators in structuring marine benthic communities (see Peterson 1979; Ólafsson et al. 1994; Thrush 1999), the potential for cage artefacts to confound true treatment effects is widely acknowledged (e.g. Virnstein 1978; Dayton & Oliver 1980; Hulberg & Oliver 1980; Hall et al. 1990; Ólafsson et al. 1994; Fernandes et al. 1999; Thrush 1999). At the end of the experiment, the abundance of the bivalves *Corbula gibba*, *Timoclea cardoides*, *Theora* spp. and *Venerupis anomala* were reduced in both caged treatments, compared with open plots. In contrast, the bivalves *Laternula rostrata* and *Hiatella australis* were only present in caged treatments. Artefacts of caging effects may have contributed to the change in abundance of these species in cages.

In contrast to *Fulvia tenuicostata*, which recruited prior to the experiment, all bivalves that were recorded in lower abundances in the caging treatments recruited during the experiment. Thus, settlement of new recruits may have been suppressed by changes in water flow and /or settlement behaviour around cages. Also, predation by the crab *Paragrapsis gaimardii* may have confounded the effect of manipulating seastars since densities of *P. gaimardii*, a known bivalve predator, were 60 – 110 times higher in all treatments with cages compared with open plots. *F. tenuicostata* recruited prior to the experiment and may either have reached a size refuge from crab predation (see chapter 2) or been too abundant for the crab to have much impact. In contrast, *Corbula gibba*, *Timoclea cardoides*, *Theora* spp. and *Venerupis anomala* were likely to be susceptible to crab predation as they recruited during the experiment, and were available to the aggregation of crabs in cages at a much smaller size. For the bivalves that had greater abundances in the caging treatments (*Laternula rostrata* and *Hiatella australis*), exclusion of other predators by the cages is a possible explanation. Given that *H. australis* is a nestling or boring species, recruitment of larvae may have been enhanced in cages. Furthermore, the accumulation of shell matter as a settlement substratum may explain their high abundance in the cages with seastars (and thus shell debris) compared with cages without seastars.

It is important to note that potential effects of cage artefacts are unlikely to compromise the tests for direct effects of the seastar. This is because the effects of caging are unlikely to account for lower abundances of some bivalves in cages containing seastars compared with cage exclusions. Moreover, *Fulvia tenuicostata*, *Laternula rostrata*, *Corbula gibba*, *Timoclea cardoides* and *Venerupis anomala* were identified as preferred prey items of *Asterias amurensis* in the feeding survey (Table 2). *Soletellina biradiata* and *Paphies erycinaea* have been recorded as common prey items of *A. amurensis* in other studies in the estuary (Lockhart 1995; Morrice 1995; Grannum et al. 1996). It is concluded that the lower densities of bivalves in cage inclusions compared with identical cages without seastars are indicative of a seastar effect.

3.5.4 Potential indirect effects of seastar predation

Another possible explanation for the low abundance of *Corbula gibba*, *Timoclea cardoides*, *Theora* spp. and *Venerupis anomala* in the caging treatment without seastars compared with open plots may be the indirect effects of reduced seastar predation. In the absence of seastar predation, *Fulvia tenuicostata* was clearly the dominant bivalve (mean density ~ 580 m^{-2}). The high density and large size of *F. tenuicostata* may have had negative effects on the recruitment success of the other bivalves. A number of studies on soft sediment communities have demonstrated that high densities of resident adult bivalves may exert a wide variety of effects on other macrofauna, including negative effects on the recruitment density of other bivalve species (see Thrush et al. 1996; Whitlach et al. 1997). In a review of field experiments in the marine environment Sih et al. (1985) noted that indirect effects following manipulation of predator densities are common, particularly in circumstances when predators prefer competitively dominant species, as may be the case with *Asterias amurensis* and *Fulvia tenuicostata*.

3.5.5 Prey Switching & Food Preferences

That significant impacts on only *Fulvia tenuicostata* were detected in the short term (10 weeks) caging experiment does not preclude that seastars may have effects on other taxa in the longer term. The importance of asteroids in structuring benthic marine communities stems largely from their ability to exploit a wide range of food resources (see Menge 1982). Given their generalist nature, the diet of asteroids often reflects changes in the relative availability of prey species. In this study seastars fed prominently on *F. tenuicostata* after its massive recruitment, but shifted to feed on other species when the bivalve became relatively rare. As the abundance of *F. tenuicostata* declined, other bivalves (*Corbula gibba* and *Venerupis anomala*), and the gastropod *Nassarius nigellus* were increasingly consumed by the seastar until their populations also declined to low levels by late spring (November 1998). This is consistent with previous studies in the estuary, in which *Asterias amurensis* was found to be highly selective of *V. anomala* (Lockhart & Ritz in press{b}), *Venerupis* spp. and *N. nigellus* (Grannum et al. 1996). *C. gibba*, an introduced bivalve, had not been previously reported from the Derwent River Estuary, although in Port Phillip Bay on mainland Australia, *C. gibba* is considered a major prey item of *A. amurensis* (G Parry pers. comm.). In both 1997 and 1998 these bivalve prey had peaked, declined and were rare by November, at which time the seastar largely fed on the echinoid *Echinocardium cordatum,* the bivalves *Theora* spp. and *Timoclea cardoides*, polychaetes and crustaceans.

The observed shift in diet correlates with the ecological availability of prey. Bivalves such as *Fulvia tenuicostata, Venerupis anomala*, *Corbula gibba* and *Timoclea cardoides* are relatively accessible because they have short siphons, live just below the sediment surface, and do not burrow deeply. In contrast, *Theora* spp. has long siphons and is likely to be less accessible to the seastar since it can live at depths several times its shell length (Willan 1998). Similarly, *Echinocardium cordatum* can remain deeply buried (up to 15 cm, Buchanan 1966), maintaining contact with the surface by a funnel-like opening over the aboral side of the animal (Buchanan 1966). This requires that the seastar actively dig to access the prey. The complete absence of the bivalve *Mysella donaciformis* in the seastar diet is enigmatic. Possible explanations include escape by leaping movements and/or their very small size, which may decrease the probability of their detection and/or capture (Fukuyama & Oliver 1985). Crustaceans are likely to be less available to seastars than bivalves due to their high mobility, while polychaetes may be less available because of behavioural avoidance (e.g. withdrawal into tubes). Interestingly, the majority of crustacean parts found in the stomach of *Asterias amurensis* in November 1997 were pieces of the crab *Paragrapsis gaimardii*. However, predation on this highly motile crab is likely to be incidental as a result of seastars preying on autotomised limbs or moults, both of which were abundant at the site during the survey. The clear pattern is that they eat the most accessible prey first, and shift to other less accessible prey only when availability of more accessible prey declines.

3.5.6 Potential Broader Impacts

Also of concern are secondary effects caused by the loss of species which represent a major functional component of the ecosystem. Bivalves in abundance filter large volumes of water, influencing water quality, the turnover of nutrients and coupling between the benthos and water column (Dame 1996). In Tasmania, thick shell layers close to the sediment surface over large areas of the Derwent River Estuary indicate that large bivalves were recently common and likely to have been important components of community structure and ecosystem function. These results support the hypothesis that predation by *Asterias amurensis* may be largely responsible for the rarity of bivalves such as *Fulvia tenuicostata*. The effect of such a major change in ecosystem function (e.g. on phytoplankton abundance) cannot be investigated by small scale manipulations such as reported here, but could be estimated by a combination of experimental studies and modelling.

3.5.7 Conclusions

Despite considerable speculation as to the potential effects of *Asterias amurensis* in Tasmania, the impact of the seastar has not previously been examined directly or quantitatively. The results of this and parallel studies provide for the first time a clear assessment of the impacts of *A. amurensis* in southeast Tasmania. Experiments conducted immediately beyond the current range (chapters 2,4) clearly demonstrated a large impact of *A. amurensis* on adult bivalve populations, particularly the commercial bivalves *Fulvia tenuicostata* and *Katelysia rhytiphora*. The present study showed that *A. amurensis* can have a large impact on the survivorship of bivalve recruits, effectively arresting significant recruitment events. These results provide strong evidence that predation by *A. amurensis* is responsible for the decline, and subsequent rarity of adult bivalves in the Derwent River Estuary. The observations of shifts in diet show that while the seastar has clear food preferences, it is a generalist predator able to consume other prey when preferred prey (bivalves) become rare. Thus, *A. amurensis* has the potential to impact a large variety of taxa and have wider effects on soft sediment communities than that demonstrated in short-term manipulative experiments. My overall conclusion is that at the high densities that can occur in southeast Tasmania, there are large direct and likely indirect effects on native communities, including several commercial species. These important consequences of the establishment of this introduced predator warrant efforts to limit its impact.

Chapter 4

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

(Submitted to Journal of Experimental Marine Biology and Ecology)

4.1 Abstract

The introduction and establishment of the predatory asteroid *Asterias amurensis* in southern Australia is considered a major threat to benthic marine communities and commercial species. I examine the impact of the seastar on soft sediment assemblages in experiments at three sites (ca. 10-35 km apart) beyond the current range of the seastar in southeast Tasmania. This allows me to assess the repeatability, and hence predictability, of the type and magnitude of the impact of *A. amurensis* on soft sediment assemblages. Given marked differences in assemblages among sites at both the species and functional group level, it is not surprising that responses to manipulations were dissimilar across sites. When potential prey taxa were separated into functional groups that are likely to reflect ecological availability (e.g. surface dwelling *versus* deep burrowing bivalves), seastar effects were largely restricted to the surface bivalves. While the effect of seastar predation on surface bivalves' was common to all sites, the magnitude of the impact varied among sites (scale = 10^4 m), and among blocks within sites (scale = 10^1 m). Variability in the impact of *A. amurensis* at both spatial scales 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 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.

4.2 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 & Geller 1993; Lafferty & Kuris 1994; Cohen & Carlton 1998; Ruiz et al. 2000). Most often, species are already widely established before they are first discovered and so eradication attempts are often not feasible. Management priorities for exotic species already established are based largely on the immediate, and in particular on the anticipated, impacts on native communities and/or commercial species. If either the nature and/or magnitude of impact vary in space and time, 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; Griffiths et al. 1992; Cloern 1996; Grosholz et al. 2000), quantitative data on the impacts of most introduced species in the marine environment is limited, and the amount of spatial and temporal variability of their direct and indirect effects remains uncertain.

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Relatively few studies of introduced marine species have investigated spatial and temporal variability in impacts (but see Allmon & Sebens 1988; Nichols et al. 1990;

Grosholz & 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. 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 & Hines 1986; Woodin 1978; Everett & 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 & Ritz 1998, chapter 2,3). In its native range the seastar causes considerable damage to commercial shellfishes (e.g. oysters, cockles, scallops, other clams; Hatanaka & 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 & Kosaka 1959; Fukuyama & Oliver 1985; Fukuyama 1994). Despite the strong rhetoric and publicity surrounding the establishment of *A. amurensis* in Tasmania (e.g. McLoughlin & Thresher 1994), the impact of the seastar on native assemblages had not been examined directly or quantitatively until recently (chapter 2,3). Feeding observations suggest that the impact of the seastar may vary in space and time due to variability in prey species composition and relative availability of prey taxa (chapter 3). In this study I assess the predictability of the impact of *A. amurensis* on soft sediment assemblages by examining the impact of the seastar in three sheltered bays separated by ca. 10-35 km in southeast Tasmania.

4.3 Methods

4.3.1 Sites and experimental protocol

Manipulative experiments were conducted on soft sediment habitats in three sheltered bays in southeast Tasmania at a depth of 3-5 metres (Figure 4.1). The experiments ran for ≈ 2 months, commencing in April 1997, May 1998 and July 1999 at Murdunna, Conningham and Saltwater River respectively. Because these areas do not currently support populations of *Asterias amurensis*, to reduce the risk of establishing the seastar the experiments were conducted in completely enclosed cages and only male seastars were used.

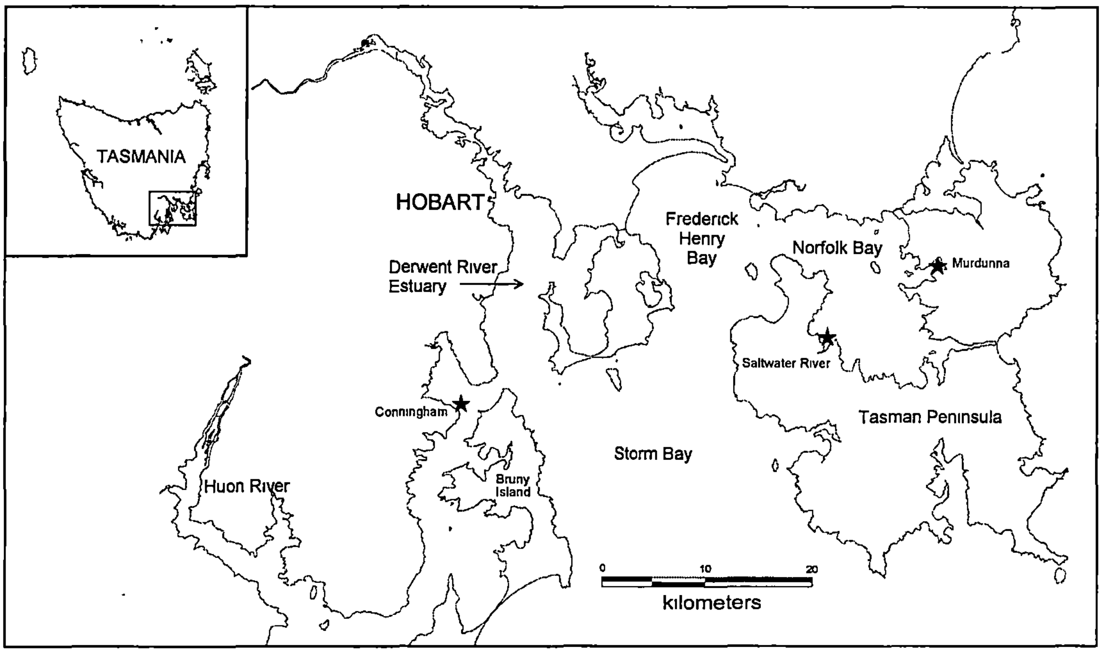

TASMANIA
HOBART
Derwent River Estuary
Frederick Henry Bay
Norfolk Bay
Murdunna
Saltwater River
Tasman Peninsula
Conningham
Storm Bay
Bruny Island
Huon River
0
10
20
kilometers

Figure 4.1 Map of southeast Tasmania showing study sites at Conningham, Saltwater River and Murdunna.

Cages consisted of a rigid (1 x 1 m base x 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 (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 or seastars.

Because of the spatial scale of patchiness of infauna 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) (see discussion of the logic behind using this design in section 2.3). 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 m x 1 m x 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, sipunculids), order (amphipods, isopods, leptostracons, cumaceans, tanaids), family (most polychaetes) or species (bivalves, echinoderms, gastropods and common polychaetes).

4.3.2 Statistical Analysis

Comparison of soft sediment assemblages. To depict differences in the structure of soft sediment assemblages among the three sites a non-metric ordination (MDS) was undertaken on Bray-Curtis distances calculated from 4th root transformed data using the PRIMER v4.0 software (Clarke 1993). The MDS was undertaken on data from the three unmanipulated plots at each site at the highest level of taxonomic resolution recorded. Data for all taxa are densities of individuals (per 1 m^2). For all bivalves, crabs and the echinoid *Echinocardium cordatum*, abundance was determined from suction samples. For the remaining taxa abundance was scaled from counts in the 3 cores in each plot.

A principal components analysis (PCA) and associated biplot was conducted on a covariance matrix after pooling taxa into broad functional groups, *viz.* surface bivalves (bivalves with short or non existent 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.

Responses to experimental treatments at each site. Effects of experimental treatments at each site were analysed for dominant taxa and functional groups (groupings as above) using univariate statistics. This permitted the appraisal of treatment effects on particular taxa within the broader context of effects at the level of functional groups within the macrobenthic assemblages.

Responses of bivalves, crabs and the echinoid *Echinocardium cordatum* were determined from suction samples. Responses of all remaining taxa were determined from core samples, in which case the arithmetic mean of the 3 replicate cores taken from each plot was used. To test for seastar and caging effects at each site a randomised complete block ANOVA was conducted, with 'treatment' (3 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). For a detailed description of how particular assumptions associated with a randomised block design were considered see section 2.3.1. The statistical package SAS® was used for analysis.

Two planned comparisons were carried out following the initial analysis for treatment effects. For planned comparisons I adjusted the significance level using the conservative method of Todd & Keough (1994), i.e. α was reduced to α / (1 + the number of non-orthogonal contrasts). With two non-orthogonal comparisons, the adjusted significance level was 0.016. Following Todd & 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.

4.4 Results

4.4.1 Comparison of assemblages between sites

Despite the fact that all of the sites were in sheltered, shallow bays the soft sediment assemblages were distinctly different at each site (Figure 4.2). 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 m^{-2} ± 362 SE), followed by Murdunna (1778 m^{-2} ± 351 SE) and Saltwater River (973 m^{-2} ± 222 SE). The separation of sites was also distinct at the functional group level (Figure 4.3a). The biplot analysis (Figure 4.3b) shows that Conningham and Murdunna have higher densities of sedentary polychaetes than Saltwater River (see also Figure 4.4). 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 polychaetes compared with the two other assemblages. At Murdunna, one of the plots (no. 3) supported 3 - times the density of polychaetes observed in other plots at this site. Given vastly different assemblages at each site, it was not sensible to include effects of 'sites' in the analysis of treatment effects. Thus, responses to experimental treatments were analysed separately for each site.

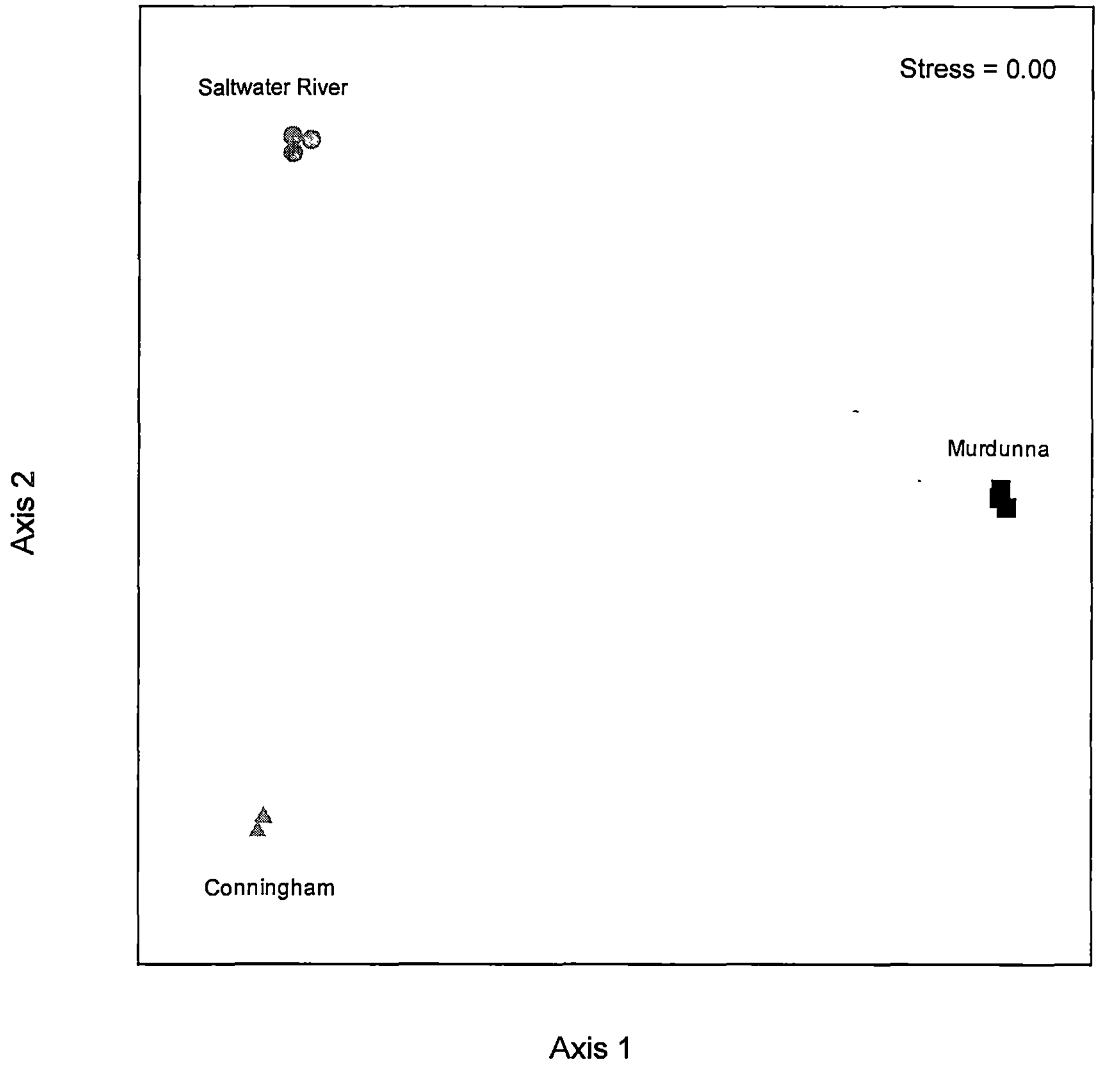
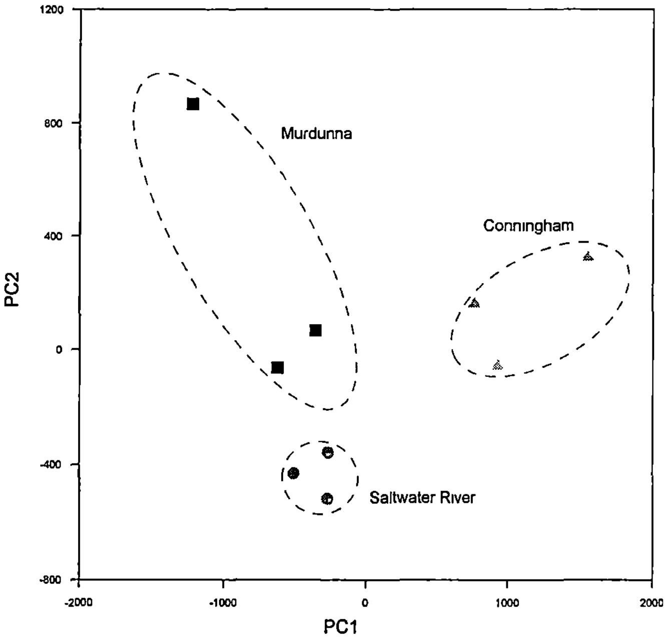


Figure 4.2. Ordination (MDS) of unmanipulated plots at each site based on Bray Curtis matrix of 4th root transformed data of densities of macro-benthic species. The macro-benthic assemblages are distinctly different at each site.

a. PCA



b. Biplot

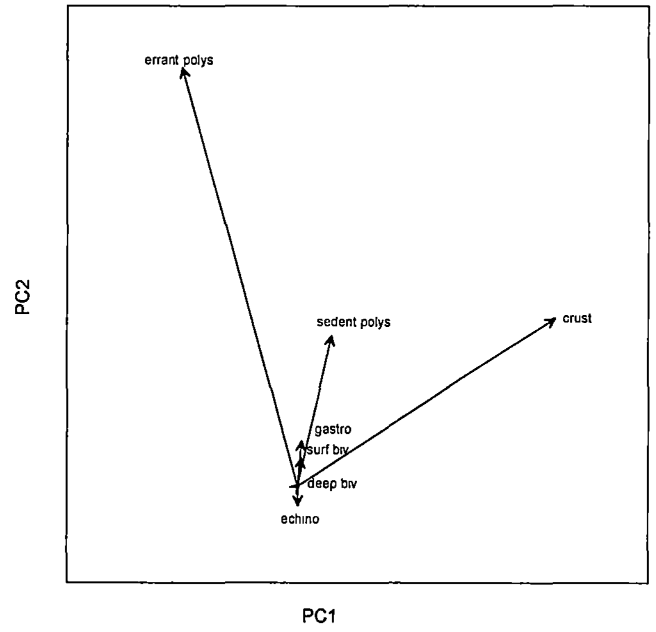


Figure 4.3 (a) The PCA plot of functional groups in unmanipulated plots (*n* = 3) across sites (M = Murdunna; S = Saltwater River; C = Conningham) shows distinct differences between sites. Principal components 1 and 2 accounted for 94 % of the total variance. (b) The associated biplot which identifies 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.

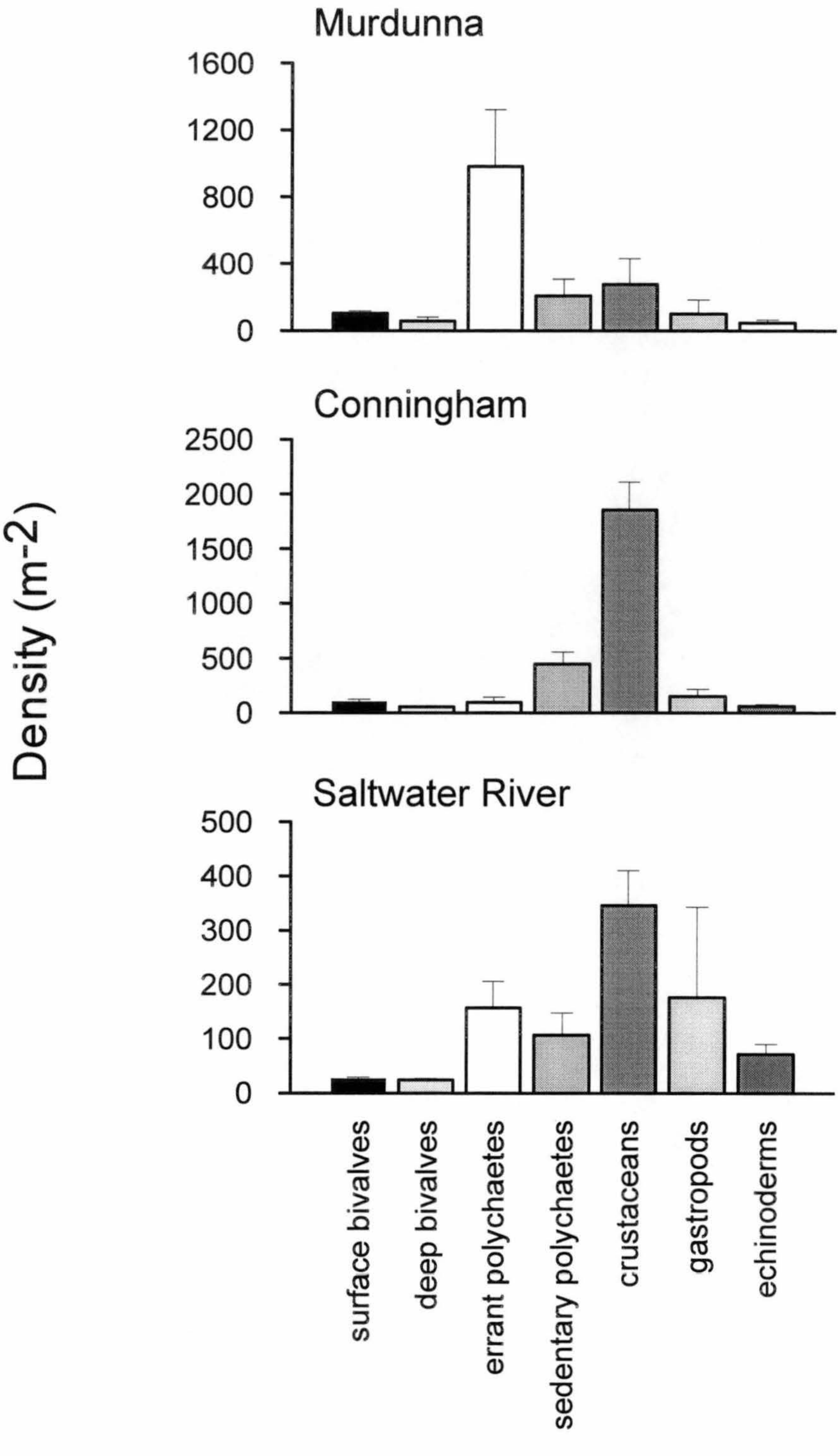


Figure 4.4 Densities of the major functional groups at each site. Data for all groups are means per 1 m^2 (+ SE). For bivalves and *Echinocardium cordatum* the data obtain from 1 m^2 suction samples (n = 3 plots per site). For the remaining taxa the means are scaled from counts in 3 cores (each 150 mm diameter, 100 mm depth) in each plot.

4.4.2 Responses to experimental treatments at each site

4.4.2.1 Murdunna

The most abundant taxa were the errant polychaetes *Simplisetia amphidonta* and *Glycera* spp.; the sedentary polychaete *Lysilla jennacubinae*; surface bivalves *Fulvia tenuicostata*, *Katelysia rhytiphora* and *Wallucina assimilis*; deep bivalves *Theora* spp. and *Laternula rostrata*; amphipods; gastropods (largely *Dialla variata*); and the echinoid *Echinocardium cordatum*.

Caging effects. There was a negative effect of caging on the abundance of the errant polychaete *Simplisetia amphidonta* and the functional group as a whole (largely attributable to *S. amphidonta*), however the difference was only significant for *S. amphidonta* at the adjusted alpha level (Table 4.1a, Figure 4.5). Although the abundance of sedentary polychaetes was also lower in the caging treatments than in the unmanipulated plots, this difference was not significant (Table 4.1a, Figure 4.5). The results for crustaceans (largely amphipods) and to a lesser extent gastropods are also indicative of a caging effect (Figure 4.5). 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, but rather a clear treatment by block interaction. Therefore, statistical analyses were not conducted on amphipods, gastropods and crustaceans as a group.

Seastar effects. There was a significant reduction in the abundance of the surface bivalves *Fulvia tenuicostata* (accounting for ≈ 85 % of the surface bivalves) and *Katelysia rhytiphora* in the presence of seastars (Table 4.1a, Figure 4.5). Abundances

a) Murdunna	Main analysis		Planned comparisons	
	MS$_{resid}$	Treat (*p*)	C vs P (*p*)	C vs. I (*p*)
Degrees of Freedom	4	2	1	1
Surface Bivalves	356.03	**0.0052**	0.7332	**0.0038**
Fulvia tenuicostata	0.0352	**0.0005**	0.7667	**0.0003**
Katelysia rhytiphora	1.9444	**0.0083**	0.4294	**0.0076**
Wallucina assimilis	4.2225	0.3331	0.6725	0.1729
Deep Bivalves	214.59	0.6612	0.4868	0.9120
Theora spp.	0.0305	0.4134	0.4499	0.5511
Laternula rostrata	2.8333	0.0803	0.1234	0.2920
Errant Polychaetes	36746	0.0966	0.0463	0.5322
Simplisetia amphidonta	5.8426	**0.0056**	**0.0103**	0.5862
Glycera spp.	0.2329	0.1237	0.1412	0.4571
Sedentary Polychaetes	0.6313	0.7154	0.4422	0.6586
Lysilla jennacubinae	0.8272	0.6595	0.4201	0.4960
Crustaceans	6.8748	0.2836	0.4874	*
Amphipods	6.5151	0.4023	0.7351	*
Echinoderms				
Echinocardium cordatum	0.0011	0.8769	0.8280	0.6304
Gastropods	3894.1	0.4145	0.2128	*

b) Saltwater River	Main analysis		Planned comparisons	
	MS$_{resid}$	Treat (*p*)	C vs. P (*p*)	C vs I (*p*)
Degrees of Freedom	4	2	1	1
Surface Bivalves	47.020	**0.0082**	0.0176	**0.0033**
Fulvia tenuicostata	0.0274	**0.0033**	0.0890	**0.0014**
Musculus impacta	1.7778	0.1045	0.0987	0.5734
Mysella donaciformis	3.4444	**0.0257**	**0.0117**	0.0299
Wallucina assimilis	0.1336	0.5399	0.2867	0.4863
Deep Bivalves	14.806	**0.0282**	**0.0143**	0.5383
Theora spp.	0.0113	**0.0256**	**0.0118**	0.3537
Errant Polychaetes	8638.2	0.7700	0.7570	0.4973
Nephtys australiensis	5099.9	0.8195	0.7625	0.5529
Sedentary Polychaetes	5099.9	0.3617	0.5529	0.1811
Capitellids	4309.2	0.3993	0.4577	0.2019
Crustaceans	21129	0.3679	0.6010	0.1872
Crabs	5.7778	**0.0137**	**0.0089**	1.0000
Amphipods	15457	0.1796	0.8616	0.1030
Echinoderms				
Echinocardium cordatum	1294.0	0.3056	0.2145	0.8837
Gastropods	1.6179	0.4855	0.9702	0.3114

c) Conningham	Main analysis		Planned comparisons	
	MS$_{resid}$	Treat (*p*)	C vs P (*p*)	C vs I (*p*)
Degrees of Freedom	4	2	1	1
Deep Bivalves	265.39	0.1946	0.0987	0.1708
Theora spp	0.0106	**0.0110**	0.0186	**0.0046**
Errant Polychaetes	6523.1	0.8839	0.7223	0.9286
Sedentary Polychaetes	72445	0.9738	0.8932	0.9357
Pectinaria sp	30520	0.9758	0.9012	0.8364
Capitellids	2376.4	0.8509	0.9605	0.6263
Crustaceans	201103	0.6241	0.4265	0.9871
Amphipods	112770	0.9530	0.9485	0.7805
Ostracods	19253	0.1156	0.0501	0.3086
Echinoderms	558.85	0.3158	0.7229	0.2625
Holothurians	50.516	0.4082	0.7362	0.2221
Echinocardium cordatum	10.903	0.4764	0.7153	0.4125
Gastropods	6997.5	0.3700	0.2670	0.2148
Nassarius nigellus	2767.4	0.6703	0.5048	0.8907

Table 4.1 Analysis of effects of seastar predation and caging effects on the abundances of functional groups and common taxa the study sites at (a) Murdunna, (b) Saltwater River and (c) Conningham. 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*), and of the two planned comparisons. * Indicates that the plot of the variable *versus* block was characteristic of a treatment by block interactions, and subsequently, the analysis was not conducted. 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. All of the tests in the table used the MS residual as the error term. 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. Note: there was unforseen incursion of seastars at Saltwater River during the course of the experiment (see text for details).

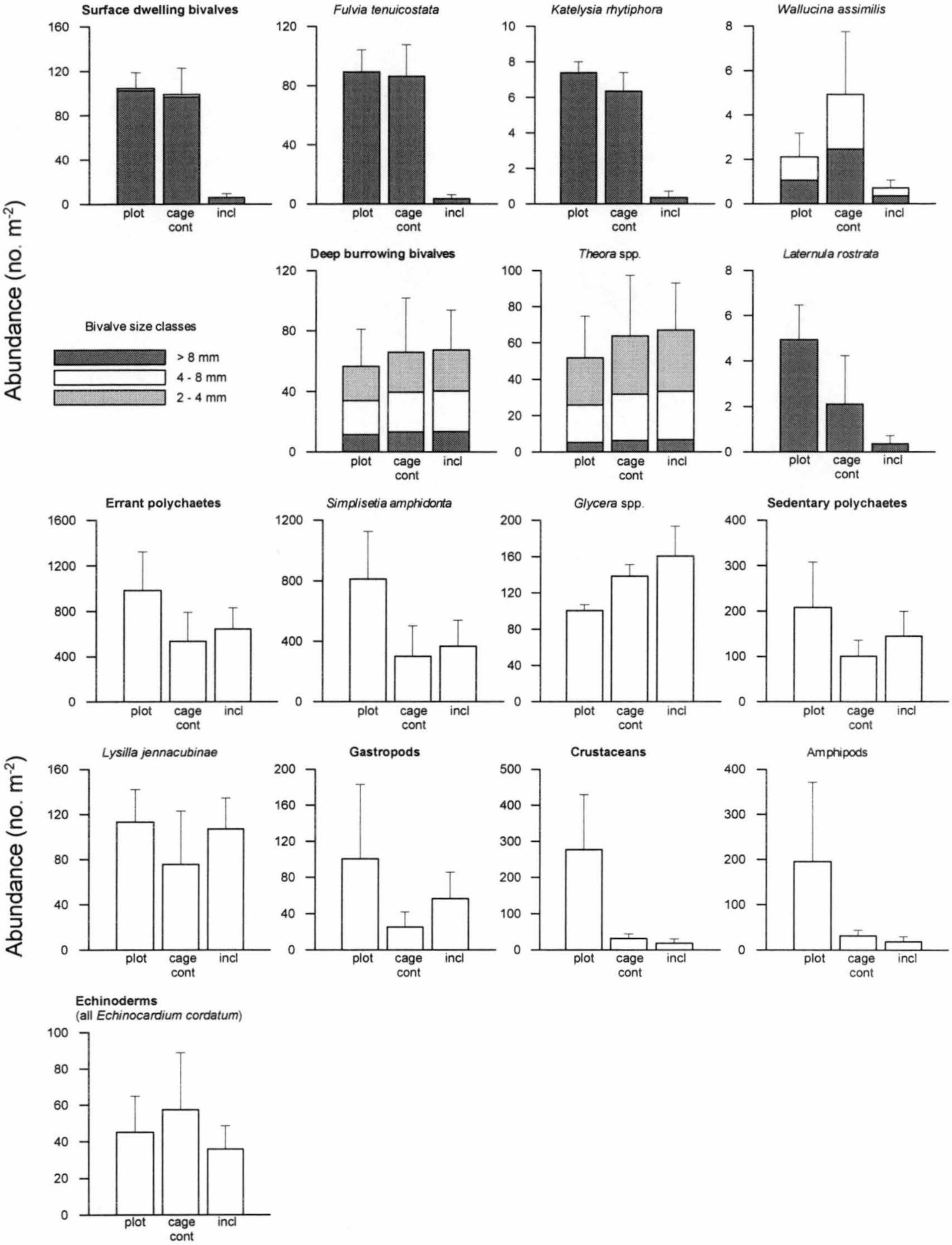


Figure 4.5 Densities of functional groups and common taxa in each treatment at Murdunna. Data for all groups and taxa are means per 1 m^2 (+ SE). For bivalves and *Echinocardium cordatum* the data obtain from 1 m^2 suction samples (n = 3 plots per site). For the remaining taxa the means are scaled from counts in 3 cores (each 150 mm diameter, 100 mm depth) in each plot. The proportion of bivalves retained on 2, 4 and 8 mm mesh are also depicted.

of *Wallucina assimilis* and *Laternula rostrata* were also lower in the presence of seastars compared with the two control treatments (Figure 4.5), although these differences were not significant (Table 4.1a).

4.4.2.2 Saltwater River

The most abundant taxa were amphipods; gastropods (largely *Dialla variata*); crabs (largely *Nectocarcinus integifrons*); sedentary capitellid polychaetes; the errant polychaete *Nephtys australiensis*; the echinoid *Echinocardium cordatum*; the surface bivalves *Fulvia tenuicostata*, *Mysella donaciformis*, *Musculus impacta* and *Wallucina assimilis*; and the deep bivalve *Theora* spp. It should be noted that two weeks into the experiment an aggregation of *A. amurensis* (not previously recorded at the site) moved into the experimental area. Whilst the majority (≈1500) were collected and removed from the site, almost all were feeding. Thus, I 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.

Caging effects. With the exception of *Musculus impacta*, the abundance of each of the major surface bivalves (and thereby for the functional group as a whole) and the echinoid *Echinocardium cordatum* was higher in the cage controls without seastars than in the unmanipulated plots (Figure 4.6). However, this difference was only significant for *Mysella donaciformis* at the adjusted alpha level (Table 4.1b). In contrast, the abundance of crabs (largely *Nectocarcinus integifrons*); *Theora* spp. and the deep bivalves' functional group (largely attributable to *Theora* spp.) were significantly lower in the caged plots without seastars compared with the unmanipulated plots (Figure 4.6, Table 4.1b).

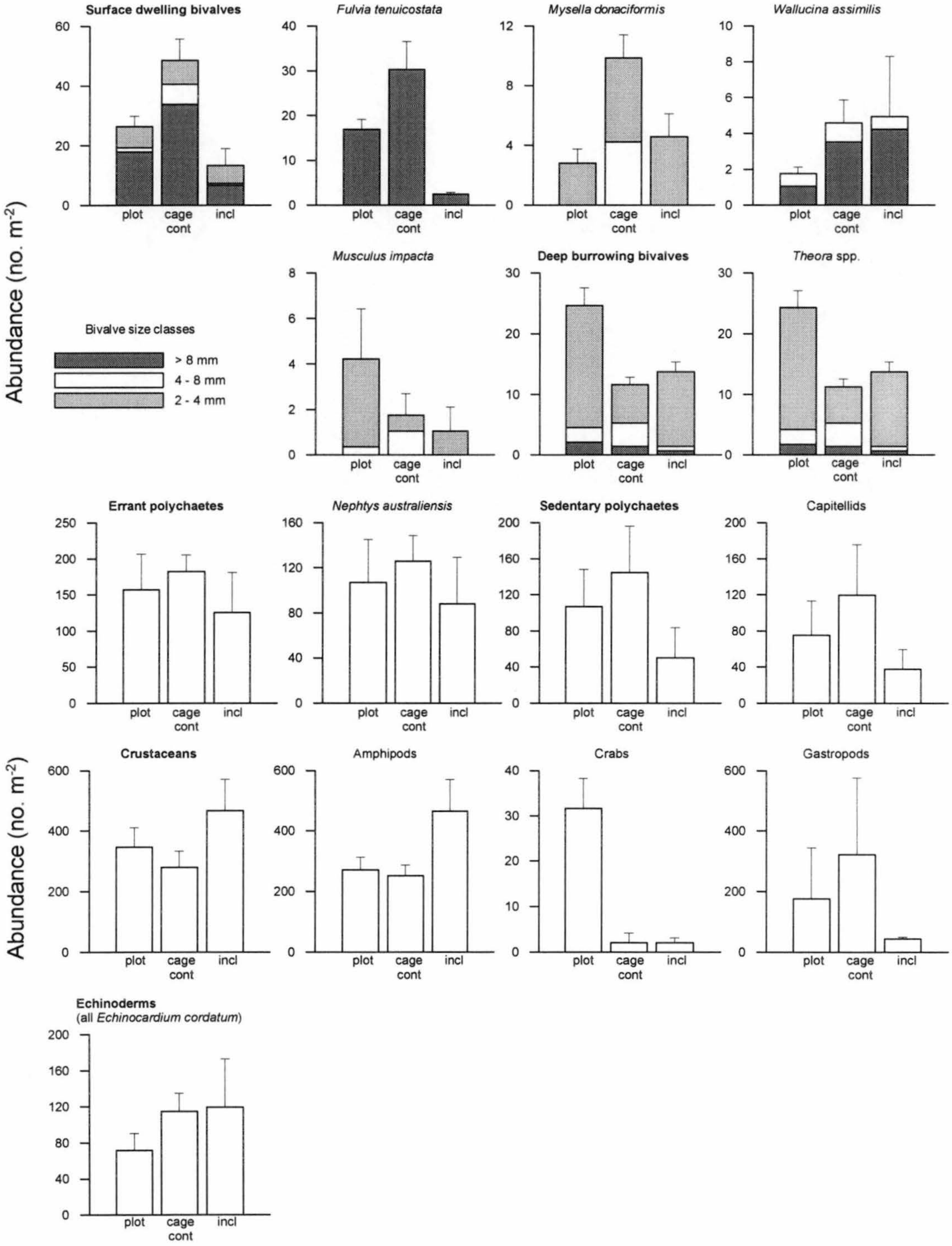


Figure 4.6 Densities of functional groups and common taxa in each treatment at Saltwater River. Data for all groups and taxa are means per 1 m^2 (+ SE). For bivalves and *Echinocardium cordatum* the data obtain from 1 m^2 suction samples (n = 3 plots per site). For the remaining taxa the means are scaled from counts in 3 cores (each 150 mm diameter, 100 mm depth) in each plot. The proportion of bivalves retained on 2, 4 and 8 mm mesh are also depicted.

Seastar effects. The abundance of *Fulvia tenuicostata* and *Mysella donaciformis* (and the functional group of surface bivalves) was reduced in the seastar inclusion compared with the caged control, indicative of a seastar effect (Figure 4.6). However, this difference was only significant at the adjusted alpha level for *F. tenuicostata* (which accounted for ≈ 56 % of the surface bivalves) and surface bivalves as a group (Table 4.1b). 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 4.1b, Figure 4.6). In contrast, the abundance of amphipods was higher in the presence of seastars, however this difference was not significant at the adjusted alpha level (Table 4.1b, Figure 4.6).

4.4.2.3 Conningham

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

Caging effects. The mean abundance of *Theora* spp., the deep bivalves' functional group to which they belong (largely attributable to *Theora* spp.) and ostracods was reduced in the caged compared with the unmanipulated plot (Figure 4.7). However, the differences were not significant at the adjusted alpha level (Table 4.1c).

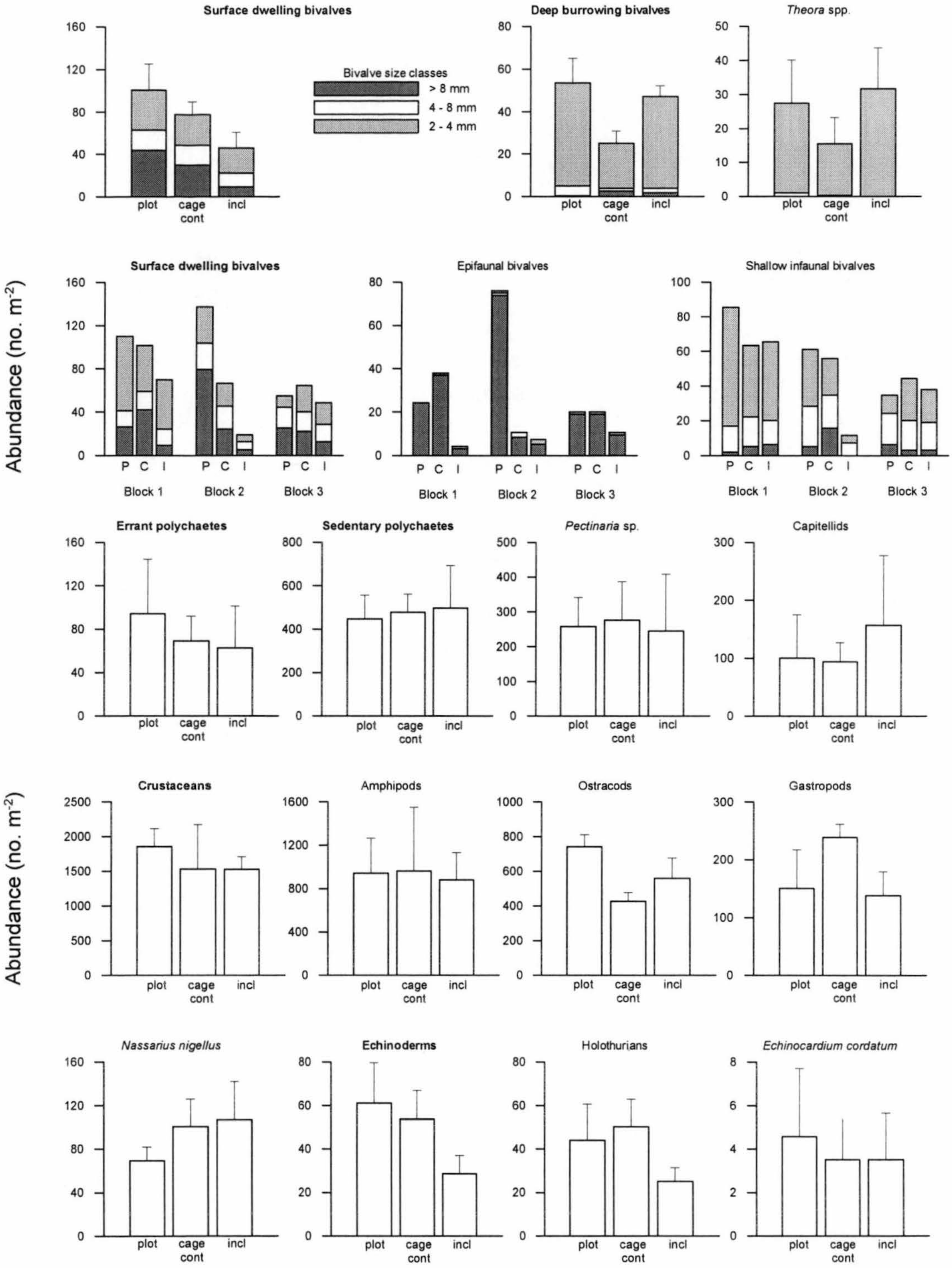


Figure 4.7 Densities of functional groups and common taxa in each treatment at Conningham. Data for all groups and taxa are means per 1 m^2 (+ SE). For bivalves and *Echinocardium cordatum* the data obtain from 1 m^2 suction samples (n = 3 plots per site). For the remaining taxa the means are scaled from counts in 3 cores (each 150 mm diameter, 100 mm depth) in each plot. The proportion of bivalves retained on 2, 4 and 8 mm mesh are also depicted. Note that for surface bivalves as a whole, and component groups of epifaunal and surface infaunal bivalves, the total number of individuals in each treatment in each block are displayed as evidence of an interaction of experimental treatments with block.

Seastar effects. 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 (Figure 4.7, Table 4.1c). While the mean abundance of surface bivalves was lower 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 (Figure 4.7), and thus, statistical tests were not conducted. Several interesting patterns were apparent when surface bivalves as a group were separated into epifaunal (*Electroma georgina* accounted for 99% of epifaunal bivalves) and infaunal groups, and examined at the level of blocks (Figure 4.7). In two of the three blocks (blocks 1 and 3), the abundance of epifaunal bivalves, but not surface 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 (Figure 4.7). Given that there were 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.

4.5 Discussion

4.5.1 Variability in assemblages

Marine soft sediment assemblages are characterised by spatial and temporal variability in the distribution and abundance of benthic organisms (e.g. Rhoads 1974;

Gray 1981; Underwood 1992; Morrisey et al. 1992a,b; Schmitt & Osenberg 1996; Thrush et al. 1999). It is not surprising therefore that the soft sediment assemblages in this study were distinctly different among sites, especially given that the experiments at different sites were conducted 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. The number of taxa recorded was much higher at Conningham (63) compared with Saltwater River (43) and Murdunna (38). While the average density of macro-invertebrates was also highest at Conningham (2766 m^{-2} ± 362 SE), followed by Murdunna (1778 m^{-2} ± 351 SE) and Saltwater River (973 m^{-2} ± 222 SE). At the functional group level the assemblage at Conningham was dominated by crustaceans (largely amphipods and ostracods), whereas at Murdunna errant polychaetes (largely *Simplisetia amphidonta*) were the most abundant group. Both of these sites were characterised by a greater abundance of sedentary polychaetes compared with Saltwater River. At Saltwater River, the site with the lowest overall abundance of macro-invertebrates, the more common groups were crustaceans (largely amphipods), gastropods (largely *Dialla variata*), errant and sedentary polychaetes (largely *Nephtys australiensis* and capitellids respectively) and echinoderms (all *Echinocardium cordatum*). Given marked differences in assemblages among sites, it is not surprising that responses to manipulations were qualitatively different across sites.

4.5.2 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. Dayton & Oliver 1980; Hulberg & Oliver 1980; Underwood 1986; Hall et al. 1990; Thrush 1999). Potential artefacts of particular concern in this study include effects on water movement and light, effects of inclusion and/or exclusion of other potential predators, and effects of caging on the feeding behaviour of the seastar. To minimise altering hydrodynamic conditions I chose a large mesh size (since I was 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 is the case at all sites in the present study.

By undertaking experimental manipulations immediately beyond the current range of the seastar in similar but unimpacted sites, the contrast of open plots with empty cages provides a straightforward test for cage artefacts. Significant caging effects were detected for the errant polychaete *Simplisetia amphidonta* (↓) at Murdunna, and *Theora* spp. (↓), the deep bivalves' functional group (largely attributable to *Theora* spp.)(↓) and *Mysella 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 likely to be able to move 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 *Asterias amurensis* (not previously recorded at the site) and influx of the crab *Nectocarcinus integifrons* during the experiment may have confounded the test for caging effects. Of the 1500 seastars that were removed during the experiment upwards of 80 % were feeding, consuming *Fulvia tenuicostata* exclusively (with the exception of one seastar). Given that *N. integifrons* also feeds on bivalves, predation by both species on surface bivalves could explain why the abundance of surface bivalves is lower in open plots compared with cage controls (in which both predators are excluded) at this site. However, the prevalence of empty bivalve shells (mainly *F. tenuicostata*) which are indicative of seastar predation and the much higher density of seastars compared with the crabs indicates that predation in the open plots was predominately due to the seastar. Importantly, neither the immigrating seastars (*Asterias amurensis*) nor crabs (*Nectocarcinus integifrons*) gained 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. In interpreting this contrast I assume that the cage has not greatly 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 higher than, those in the cages are frequently encountered in the Derwent River Estuary (Grannum et al. 1996; Ling 2000) for periods much greater than the 2 month experimental period. This occurs in several areas where there is an abundant supply of bivalves. I suggest it is not unreasonable to expect similar effects on native assemblages should the seastar attain the densities used in these experiments. This was supported from observations at Saltwater River where aggregations of seastars consumed virtually all the *Fulvia tenuicostata* in their path, as anticipated from the experiments.

4.5.3 Predation by seastars: consistent broad-scale effects

In both Tasmania (Morrice 1995; Grannum et al. 1996; Lockhart 1995, chapter 2,3) and overseas (Hatanaka & Kosaka 1959; Nojima et al. 1986), bivalves are most often the major food source of *Asterias 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 taxa 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 & 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 *Fulvia tenuicostata, Electroma georgina* and *Katelysia 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 *Echinocardium 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. Similarly, Virnstein (1977) demonstrated that 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.

4.5.4 Predation by seastars: site-specific effects

Although at a functional group level the effect of seastar predation on surface bivalves was common to all sites, the magnitude of the impact varied between sites. The differences in mean density between the seastar inclusion treatment and the cage control indicate 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 at each site is largely attributable to the decrease in abundance of larger (> 8 mm) bivalves. The decrease in percentage of surface bivalves at each site closely reflected the percentage of large (> 8 mm) surface bivalves at each site, i.e. 92 %, 67 % and 41 % respectively. However, it is unclear whether these patterns reflect selection on the basis of size or species composition (or both) given that the species most heavily impacted at each site were also the large (> 8 mm) species of surface bivalves. Given that previous work has demonstrated both size and species selection for *Asterias amurensis* (Lockhart and

Ritz in press{a, b}), changes in both the size and species composition may underpin variability in the magnitude of impact between sites.

While the effect of seastar predation on surface bivalves varied between sites, at Conningham it also varied among blocks at a scale of 10^1 m, which complicates the interpretation of effects. 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 when the surface bivalves are separated into epifaunal and infaunal groups which are likely to represent different availability. In contrast to the other two sites, epifaunal bivalves, predominately *Electroma georgina*, were common at Conningham. *E. georgina* was abundant in 2 of the 3 blocks at this site, and in these blocks the change in 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 abundance 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 *Timoclea cardoides*, *Venerupis anomala* and *Fulvia tenuicostata* were major prey items of the seastar except when *Electroma georgina* became available at high densities, at which time the epifaunal bivalve dominated the seastar's diet (Ross unpub. 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 sites as a whole, Conningham was characterised by a higher species diversity and evenness of surface bivalves than at the other sites, with *E. georgina*, *Corbula gibba, Wallucina 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 spatial differentiation in diet, and therefore impact, may arise.

4.5.5 Conclusions: Implications for impacts on native assemblages and commercial species in Tasmania

The potential impact of the northern Pacific seastar on native assemblages and commercial species is a major concern for natural resource managers in Tasmania. However, until this study there had been no direct quantitative assessment of seastar impacts on which to base accurate predictions of the immediate and future effects. 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 (L. Turner pers. comm.). Another manipulative experiment showed clearly that *Asterias amurensis* has a large impact on the survivorship of commercial cockle recruits (*Fulvia tenuicostata*) in the estuary, effectively arresting significant recruitment (chapter 3). 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 of the seastar in the Derwent River Estuary it is the potential spread and impact in coastal areas outside the estuary that is the immediate concern of management. Recent modelling of dispersal of seastar larvae indicates that the large majority of larvae produced in the Derwent River Estuary are likely to be advected from it (Morris & Johnson in prep). The results of the experiments reported here and evidence of strong food preferences (Grannum et al. 1996; Lockhart & Ritz in press {b}; chapter 3) indicate that the exact nature of seastar effects is site and time specific given the inherent natural variability in soft sediment assemblages and the seastar's responses to them. Nonetheless, the results indicate that the seastar will have major impacts in areas 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 leaving masses of *Fulvia tenuicostata* shells in its wake. 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 (chapter 3). 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.

Chapter 5

Patterns of association between soft sediment assemblages and the presence of the introduced predator, *Asterias amurensis*

5.1 Abstract

The northern Pacific seastar, *Asterias amurensis*, was first recorded in southeast Tasmania in 1986. It is now a conspicuous predator in soft sediment habitats in this region, and is considered a major threat to native assemblages and commercial species. I estimated variability in soft sediment assemblages at different spatial scales in southeast Tasmania, and correlated this variation with seastar abundances. I found that the structure of soft sediment assemblages is highly variable at a range of spatial scales from metres to tens of kilometres. Clear differences in the composition of assemblages and abundances of major taxa were detected between areas with and without seastars and between areas with low and high seastar densities. However, the nature of these patterns suggests that they are more likely due to differences in sediment characteristics than to impacts of the seastar. Thus, spatial differences in soft sediment assemblages might have been erroneously attributed to seastars without detailed information on important physical factors such as sediment characteristics. Because core samples were not expected to provide precise estimates of the abundance of larger and/or rare species a second survey using much larger samples (1 m^2) but across a more limited spatial extent was conducted. In this survey bivalves and heart urchins that were identified as important prey of the seastar in

observations of feeding and experimental studies at smaller scales were targeted. Large scale patterns of abundance and size structure were consistent with seastar effects anticipated from small scale experimental and feeding studies for some, but not all species. While the field survey ultimately provided evidence about the presence or absence of seastar impacts at large scales, the identification of key ecological variables in experimental and feeding studies proved crucial to both the design, and interpretation of patterns observed in the large scale surveys. Overall, this work highlights the utility of incorporating multiple lines of evidence rather than a single 'inferential' test in the absence of pre-impact data.

5.2 Introduction

The concentration of human activity in coastal zones worldwide has inevitably led to an increase in human mediated disturbances of marine and estuarine ecosystems (e.g. Allison et al. 1998). In recent years, the discovery of an increasing number of high profile invaders (e.g. the Asian clam *Potamocorbula amurensis* in San Fransisco Bay and the comb jelly *Mnemiopsis leidyi* in the Black Sea) has highlighted the threat posed by introduced species to the integrity of marine and estuarine ecosystems (Nichols et al. 1990; Shushkina & Musayeva 1990; Carlton & Geller 1993; Cohen & Carlton 1998; Ruiz et al. 1999, 2000). As public awareness and concern over impacts of exotics has heightened, so has the need to properly assess and quantify these impacts. A major challenge is to design assessment protocols that identify patterns of spatial and temporal variation in marine assemblages caused solely by the activity of introduced species. In the past 30 years, coastal marine ecologists have focused on manipulative experiments to test hypotheses about specific processes (see Underwood et al. 2000), but this approach is typically limited to small scales in space and time (e.g. Underwood 1996; Thrush et al. 1997). Given that concerns are often with assessing and managing putative environmental disturbances over large spatial and temporal scales, and that manipulative experiments cannot fully address questions at larger scales, large scale surveys are used widely as a basic tool in field assessments of environmental impacts (Osenberg & Schmitt 1996).

Discovery of the northern Pacific seastar (*Asterias amurensis*) in southeast Tasmania in the early 1990s highlighted the problem posed by introduced species entering Australia's marine environment. Despite the potential for enormous ecological change, understanding the influence of most introduced species on native assemblages is limited. Although the impact of the seastar on native assemblages has not previously been examined directly or quantitatively, indirect indications based on seastar foraging behaviour, stomach contents, and estimates of feeding electivity suggest the potential for major impacts on native soft sediment assemblages (Grannum et al. 1996; Lockhart 1995). In this paper I describe the results of large scale spatial surveys in southeast Tasmania in which soft sediment assemblages at locations with seastars ('impact' sites) were compared with assemblages at sites without seastars ('control' sites). Because of the cost involved in processing soft sediment samples, core samples were used in the initial survey because they are practical, cost effective, provide suitable precision for most taxa, and enable a broad spatial coverage (i.e. many cores can be processed). However, it was recognised that cores may not provide precise estimates of the abundance of large and/or rare species, or even necessarily detect these species. Thus, in a second survey much larger samples (1 m^2) were used but across a more limited spatial extent targeting some of the species (bivalves and heart urchins) that were identified as important prey species in small scale experiments and feeding observations.

Since its arrival in Tasmania the seastar has become the dominant invertebrate predator in soft sediment habitats in the Derwent River Estuary. At the time of conducting these surveys, the seastar appeared largely restricted to the estuary, with the infrequent sightings outside the estuary largely restricted to marine farms (Grannum et al. 1996). Therefore, the comparison of primary interest was between assemblages in the estuary where seastars were abundant and those in similar areas outside the estuary without seastars.

A critical limitation of this approach, and one that arises commonly when assessing the impact of introduced species, is the lack of baseline data prior to the species becoming established. Although differences between the ‘impact’ location and ‘control’ locations where the species is not established may be indicative of an impact, it is also possible that these differences reflect other mechanisms independent of seastars. To help offset this difficulty, it is important that environmental factors that may generate spatial variability are identified and accounted for when choosing control sites (Glasby 1997; Keough & Mapstone 1997; Glasby & Underwood 1998), and that they are at least recorded at all sampling sites. Even when control locations are carefully chosen, inferences about potential cause-effect relationships are only correlative. In this study, I consider lines of evidence from other studies in interpreting differences between the estuary (impact) and control locations. More specifically, the broad scale patterns observed in the survey are interpreted in light of results of the feeding observations and manipulation experiments designed to test the direct impacts of the seastar at smaller scales (chapters 2,3,4). I found that effects of seastar predation detected from feeding observations and manipulative experiments at smaller scales are consistent with patterns at larger scales for some species, but not others.

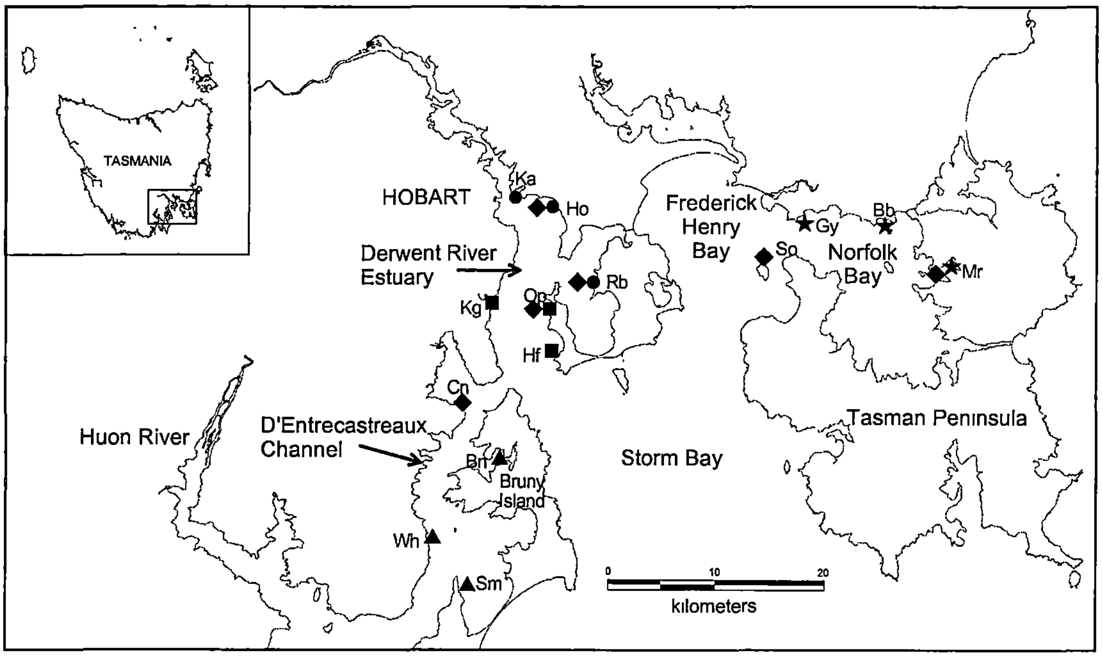
5.3 Methods

5.3.1 Spatial variation in soft sediment assemblages

Variability in soft sediment assemblages in southeast Tasmania was assessed at several spatial scales. Since impacts may vary with seastar density, sampling in the Derwent River Estuary was divided into regions of the upper and lower estuary which support high and low seastar densities respectively. It was not possible to have control sites in similar upper and lower estuarine regions in adjacent estuaries (they do not exist). To help alleviate this problem the two control regions (Norfolk Bay and the D'Entrecastreaux Channel) were chosen randomly from a limited number of 'regions' that did not support populations of the seastar but contained similar soft sediment habitats in similar sheltered shallow bays that covered the range of estuarine conditions found in the Derwent River Estuary regions (Figure 5.1).

In total twelve sites were surveyed in November 1996, three in each of the two regions inside the estuary where seastars occurred, and three in each of the two regions outside the Derwent River Estuary where seastars were absent or rare. At each site, three plots were randomly chosen approximately 30 metres apart. In each plot, two replicate benthic samples approximately 1 metre apart were collected with a

a. Map


TASMANIA
HOBART
Ka
Ho
Derwent River
Estuary
Kg
Op
Rb
Hf
Frederick
Henry
Bay
Gy
Bb
So
Norfolk
Bay
Mr
Cn
Huon River
D'Entrecastreaux
Channel
Br
Bruny
Island
Wh
Sm
Storm Bay
Tasman Peninsula
0
10
20
kilometers

b. Survey design

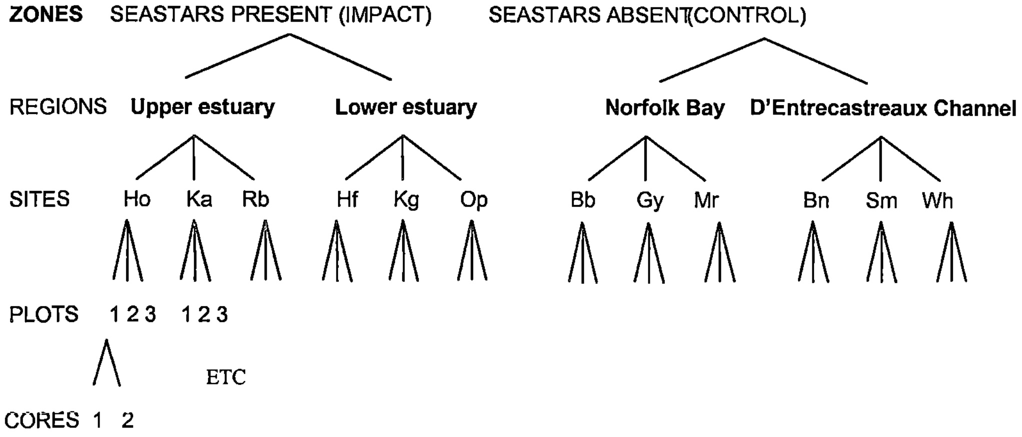

ZONES
SEASTARS PRESENT (IMPACT)
SEASTARS ABSENT (CONTROL)
REGIONS
Upper estuary
Lower estuary
Norfolk Bay
D'Entrecastreaux Channel
SITES
Ho
Ka
Rb
Hf
Kg
Op
Bb
Gy
Mr
Bn
Sm
Wh
PLOTS
1 2 3
1 2 3
ETC
CORES
1
2

Figure 5.1 (a) Map of southeast Tasmania showing the 12 sites sampled in the large scale survey in 1996 (= 3 sites in each of the four regions: two inside the estuary where seastars were present and were designated the [●] upper and [■] lower estuary, representing areas of high and low densities of seastars respectively; and two regions outside the estuary where seastars were absent at [★] Norfolk Bay and in the [▲] D'Entrecastreaux Channel). The sites of the 1998 survey [◆] of bivalves and heart urchins using 1 m^2 samples are also shown. (b) Summary of large scale spatial survey used in the 1996 large scale survey. Three plots (30 m apart) were nested within each of 3 sites (5-15 km apart), within each of 2 regions (5-50 km apart), both inside and outside the Derwent estuary. Two replicate cores (~ 1 m apart) were collected at each plot. Site codes stand for Howrah Beach (Ho), Kangaroo Bay (Ka), Ralphs Bay (Rb), Halfmoon Bay (Hf), Kingston Beach (Kg), Opossum Bay (Op), Breaknock Bay (Bb), Gypsy Bay (Gy), Murdunna (Mr), Barnes Bay (Bn), Simmonds Bay (Sm), Whaleboat Rock (Wh), Sloping Island (So) and Conningham (Cn).

corer (150 mm diam, 100 mm depth). Thus, the design incorporated 5 spatial scales of sampling (Figure 5.1b). Samples were sieved (1.0 mm mesh) prior to fixing in 10 % buffered formalin with Rose Bengal stain for a minimum of 24 hrs, and then rinsed in freshwater before storing in 100 % ethanol. All infaunal and epifaunal organisms (> 1 mm) were sorted and identified to the lowest practical taxon. This entailed identification to species (bivalves, echinoderms, gastropods and common polychaetes), family (remaining polychaetes), and class or higher taxa for other groups.

Since sediment characteristics are known to be a particularly important determinant of assemblages in soft sediment habitats (e.g. Rhoads 1974; Woodin 1978; Gray 1981), sediment characteristics were measured at all sites to minimise ambiguities of interpretation of differences between the estuary (impact) and control locations. A separate sediment core (45 mm diameter x 50 mm depth) was taken from each plot at each site. Sediment samples were oven dried at $30^{O}C$ for ≈14 days, weighed to the nearest 0.01g and then wet-sieved through a series of sieves: 8 mm, 4 mm, 2 mm, 1 mm, 0.500 mm, 0.250 mm, 0.125 mm, and 0.063 mm mesh . Each portion was oven dried for ≈10 days prior to weighing. The portion < 0.063 mm was estimated as the difference between the initial sample weight and the combined weight of all sieve fractions. Mean particle size (M_Z) and the sorting coefficient (σ_I) were calculated after the methods of Folk (1974).

In order to test for potential correlations between seastar density and composition of assemblages and abundance of major taxa, seastar density was estimated at each site from counts in three 50 x 2 m randomly positioned belt transects.

5.3.2 Spatio-temporal variation in soft sediment assemblages

Although temporal replication was not incorporated in the comparison of impact and control regions annual variability of benthic assemblages at three of the survey sites in the estuary was assessed. The sites (Opossum Bay, Ralphs Bay and Howrah Beach) were resurveyed in November 1997 and 1998 in the same manner as for the 1996 survey (including transects to estimate seastar density).

5.3.3 Macrofaunal abundance and seastar diet

To help identify benthic species that are most likely to prove reliable indicators of seastar impacts, the composition of taxa found in the stomachs of seastars was also measured at Opossum Bay, Ralphs Bay and Howrah Beach in November 1997 and 1998. The first 50 seastars encountered on each transect used in estimating seastar density were collected into separate sealed plastic bags to prevent the loss of any regurgitated stomach contents. Seastars were frozen soon after collection, and thawed prior to examination of stomach contents.

5.3.4 Spatial variation in abundances of bivalves and heart urchins

A total of six sites (3 sites inside and 3 sites outside the Derwent River Estuary) were surveyed in November 1998 (Figure 5.1). At each site, three 1m^2 plots approximately 30 metres apart were sampled. 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 m x 1 m x 0.1 m depth) was inserted into the sediment to isolate the plot, and all contents then vacuumed into a 1 mm mesh bag. Samples were sieved a second time through a nested series of sieves (2, 4 and 8 mm mesh).

Bivalves and heart urchins retained on each sieve size were identified to species and counted.

5.3.4 Statistical Analysis

5.3.4.1 Univariate analysis

A variety of univariate tests were undertaken on the most abundant taxa, the total number of individual animals, and the total number of taxa, using the SAS® software package. The spatial component of the 1996 survey was analysed using a 4-factor nested ANOVA, with 'zone' (i.e. inside and outside the Derwent River Estuary) as a fixed effect, and 'region', 'site' and 'plot' all random effects. The spatio-temporal component was analysed using a model II nested ANOVA, with main effects of site (random effect) and time (fixed effect), and a nested term of 'plot (site*time)' (random effect). Data were checked for normality and homoscedasticity, and transformed (usually by log $(y + 0.1)$ or $(y)^{0.5}$) as necessary depending on the relationship between standard deviations and means (Draper and Smith 1981).

5.3.4.2 Multivariate analysis

To depict and test for differences in the structure of whole assemblages, non-metric MDS and non-parametric 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 BIOENV procedure in PRIMER was used to identify the combination of 'environmental' variables best correlated with patterns in the biotic similarity matrix (Clarke & Ainsworth 1993).

5.4 Results

5.4.1 Spatial variation in soft sediment assemblages

A total of 78 taxa (comprising species, families, classes and higher taxa) were recorded across the 12 sites. The major groups were polychaetes, bivalves, amphipods, phoronids, tanaids, gastropods and ostracods. The numerically dominant polychaete families were Capitellidae, Spionidae, Magelonidae (all *Magelona* sp.), Nereidae (all *Simplisetia amphidonta*), Lumbrineridae, Nephtyidae (all *Nephtys australiensis*) and Terebellidae, and the most abundant bivalves were *Mysella donaciformis*, *Theora* spp. and *Timoclea cardoides*. Gastropods, amphipods, tanaids, ostracods and phoronids were analysed at these levels because of taxonomic difficulties and low numbers of individual species.

Significant differences in mean abundances were observed among plots, sites, regions and zones for the number of taxa, the number of individuals and the separate taxa analysed (Table 5.1, Figure 5.2). However, the level at which significant differences were detected varied depending on the taxonomic grouping. For example, there were significant differences among regions, sites and plots for lumbrinerid polychaetes, whereas abundances of the bivalve *Mysella donaciformis* differed significantly only at the scale of sites (Table 5.1f,m). Nonetheless, there was a clear overall trend of more significant differences at smaller spatial scales. For the total number of taxa and individuals significant differences were only observed among sites, and sites and plots respectively. For individual taxa, significant differences were far more common among plots (11 out of 18 taxa) and sites (16 out of 18 taxa) than among regions (2 out of 18 taxa) and zones (2 out of 18 taxa). However, patterns of significance were not necessarily paralleled by patterns in the

Source of Variation	df	a Total no. taxa				b Total no. individuals				c Errant polychaetes				d *Simplisetia amphidonta*			
		MS	F	p	% Var	MS	F	p	% Var	MS	F	P	% Var	MS	F	p	% Var
Zone	1	6.368	0.03	0.870	0%	0.02	0	0.957	0%	106	2.8	0.236	32%	49.77	6.18	0.131	37%
Region (Z)	2	185.2	1.98	0.200	19%	5.444	1.29	0.327	9%	37.8	3.98	0.063	28%	8.06	1.25	0.336	6%
Site (R(Z))	8	93.49	12.01	**<0.001**	56%	4.222	14.29	**<0.001**	71%	9.5	6.5	**<0.001**	23%	6.42	5.57	**<0.001**	30%
Plot (S(R(Z)))	24	7.786	1.15	0.352	2%	0.296	2.27	0.014	9%	1.46	2.79	**0.003**	10%	1.15	4.51	**<0.001**	18%
Residual	34*	6.794			24%	0.13			11%	0.52			8%	0.26			10%

Source of Variation	df	e *Nephtys australiensis*				f Lumbrinerids				g Sedentary polychaetes				h *Magelona* sp.			
		MS	F	p	% Var	MS	F	p	% Var	MS	F	P	% Var	MS	F	p	% Var
Zone	1	42.75	2.51	0.254	11%	39.64	1.91	0.301	25%	6.88	1.07	0.409	0%	17.31	104.31	**<0.001**	42%
Region (Z)	2	17.01	0.71	0.519	0%	20.72	4.48	0.05	35%	6.42	1.07	0.425	1%	82.55	98.66	**0.010**	0%
Site (R(Z))	8	23.85	8.42	**<0.001**	54%	4.63	12.94	**<0.001**	29%	6.73	6.71	**<0.001**	61%	0.84	0.05	0.953	51%
Plot (S(R(Z)))	24	2.83	1.37	0.198	4%	0.36	1.96	**0.035**	3%	1	3.8	**<0.001**	24%	0.75	4.52	**<0.001**	5%
Residual	34*	2.07			31%	0.182			8%	0.26			14%	0.17			2%

Source of Variation	df	i Capitellids				j Terebellids				k Spionids				l Bivalves			
		MS	F	p	% Var	MS	F	p	% Var	MS	F	P	% Var	MS	F	p	% Var
Zone	1	19.91	1.81	0.310	20%	19.77	3.09	0.221	22%	1.06	0.03	0.874	0%	97.39	1.49	0.347	9%
Region (Z)	2	10.98	6.82	**0.019**	45%	6.40	1.92	0.209	14%	32.52	2.57	0.137	24%	65.36	1.76	0.233	17%
Site (R(Z))	8	1.61	4.49	**0.002**	17%	3.34	4.28	**0.003**	28%	12.63	5.02	**0.001**	36%	37.13	21.15	**<0.001**	61%
Plot (S(R(Z)))	24	0.36	3.24	**0.001**	11%	0.78	2.74	**0.004**	18%	2.52	2.17	**0.019**	17%	1.76	1.32	0.226	2%
Residual	34*	0.11			8%	0.28			19%	1.16			23%	1.33			11%

Source of Variation	df	m *Mysella donaciformis*				n *Theora* spp.				o *Timoclea cardoides*				p Phoronids			
		MS	F	p	% Var	MS	F	p	% Var	MS	F	P	% Var	MS	F	p	% Var
Zone	1	165.9	3.1	0.22	27%	0.31	0.05	0.84	0%	3.23	0.59	0.522	0%	72.12	20.09	**0.046**	33%
Region (Z)	2	53.45	1.25	0.336	5%	5.79	2.88	0.114	20%	5.45	2.72	0.126	29%	3.59	0.34	0.723	0%
Site (R(Z))	8	42.6	45.74	**<0.001**	61%	2.01	2.13	0.073	17%	2.01	3.9	**0.005**	32%	10.64	2.29	**0.056**	17%
Plot (S(R(Z)))	24	0.93	0.93	0.564	0%	0.95	4.55	**<0.001**	33%	0.52	4.39	**<0.001**	26%	4.65	3.21	**<0.001**	28%
Residual	34*	1			6%	0.21			30%	0.12			12%	1.45			22%

Source of Variation	df	q Gastropods				r Amphipods				s Tanaids				t Ostracods			
		MS	F	p	% Var	MS	F	p	% Var	MS	F	P	% Var	MS	F	p	% Var
Zone	1	13.06	3.16	0.217	11%	50.45	11.78	0.075	34%	31.28	1.08	0.408	0%	39.56	4.77	0.161	22%
Region (Z)	2	4.13	0.61	0.569	0%	4.28	0.43	0.664	0%	29.02	1.85	0.219	17%	8.3	0.67	0.539	0%
Site (R(Z))	8	6.81	3.35	**0.01**	26%	9.95	6.63	**<0.001**	36%	15.68	10.6	**<0.001**	51%	12.4	9.38	**<0.001**	51%
Plot (S(R(Z)))	24	2.03	1.01	0.481	0%	1.5	1.51	0.132	8%	1.48	0.91	0.589	0%	1.32	1.45	0.158	6%
Residual	34*	2.01			63%	0.99			22%	1.63			32%	0.91			22%

* two cores were missing

Table 5.1 Summaries of ANOVAs for (a) the total number of taxa, (b) total number of individuals and (c-t) selected taxa identifying scales of significant spatial variation. Significant *P*-values (<0.05) are shown in bold face. The percentage contribution of the total variance for each level in the ANOVAs was also derived.

relative contribution of variance components. For example, the level of zone (Derwent River Estuary regions *versus* control regions) was a relatively important component of variance, contributing 37 % of the total variance for the nereid polychaete *Simplisetia amphidonta*, despite not being significant. The absence of a significant effect in these cases is likely to be due to large variances in abundance at smaller spatial scales (particularly among sites) and/or low degrees of freedom in error terms, and therefore low power in tests for the differences at larger spatial scales.

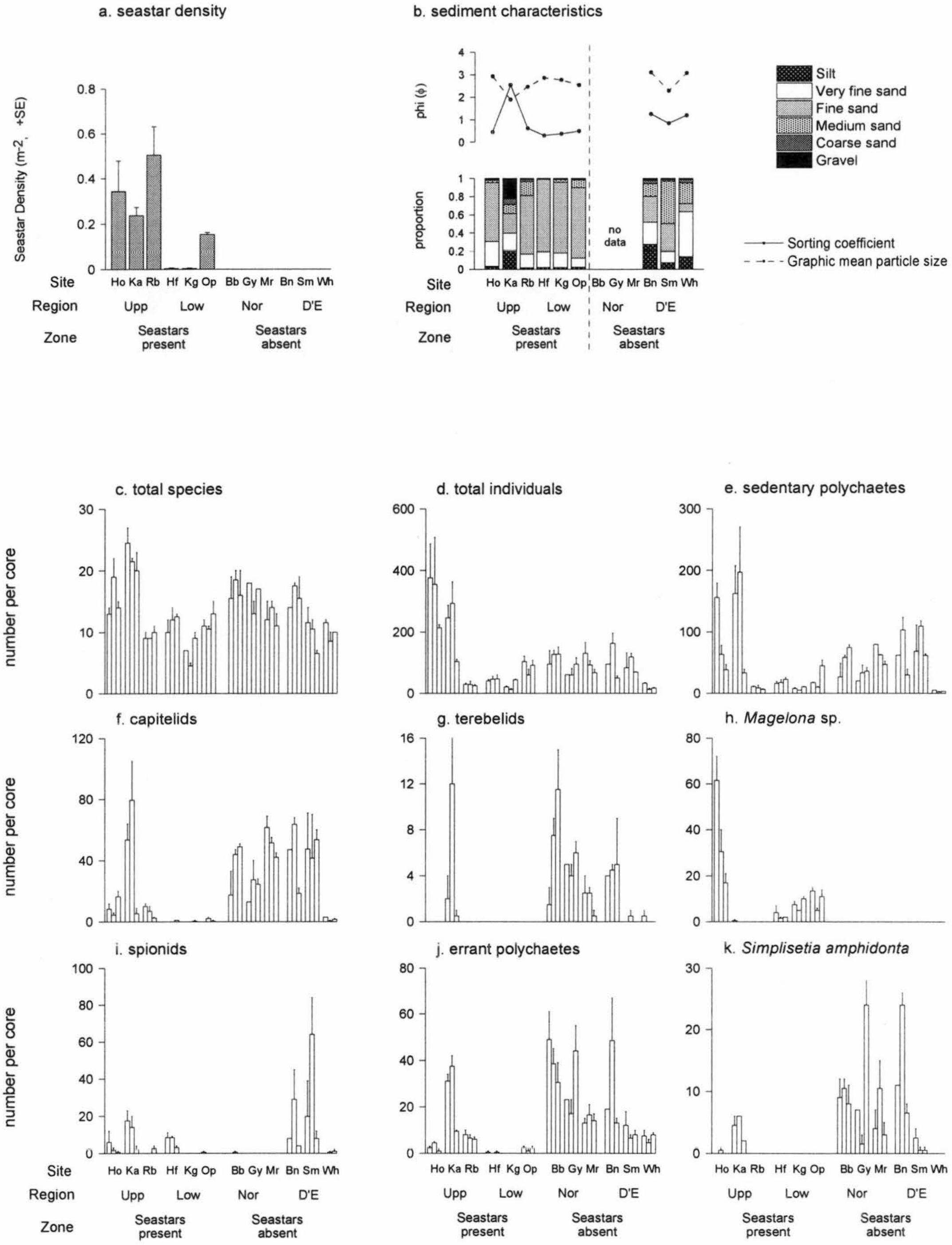


Figure 5.2 (contd on next page) (a) Seastar density at each site in November 1996. Densities are means (+ SE) determined from 50 x 2 m strip transects (n = 3). (b) Sediment characteristics at each site in November 1996: sorting coefficient, graphic mean particle size, and the percent content of each particle size fraction. Sediment characteristics are determined from sediment cores (n = 3). Note there was no sediment data available for the Norfolk Bay sites. (c-k) Mean (+ SE) numbers of taxa or individuals and per core (n = 2) in each plot (n = 3) in each site in November 1996. Site code descriptions are listed in the caption for figure 5.1.

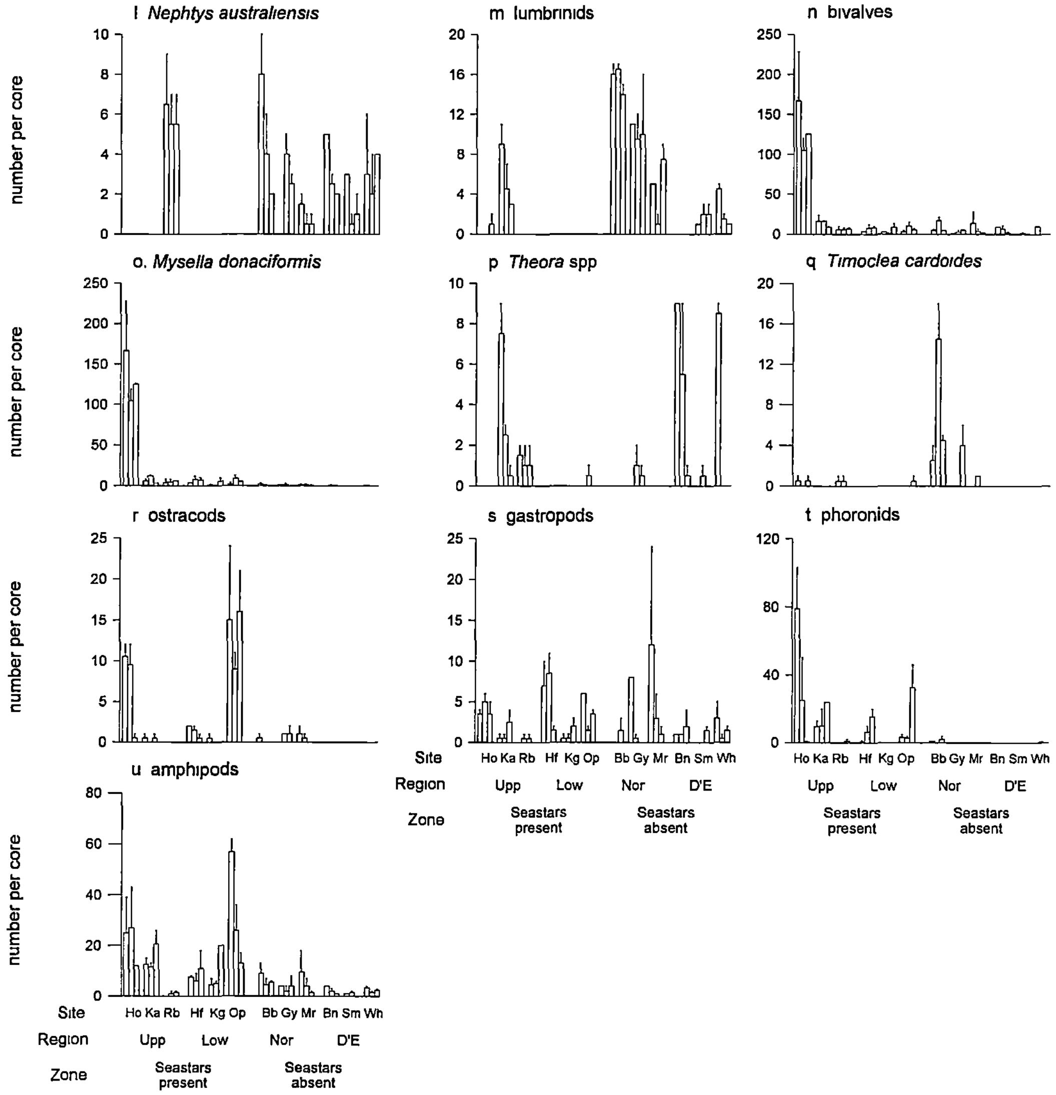
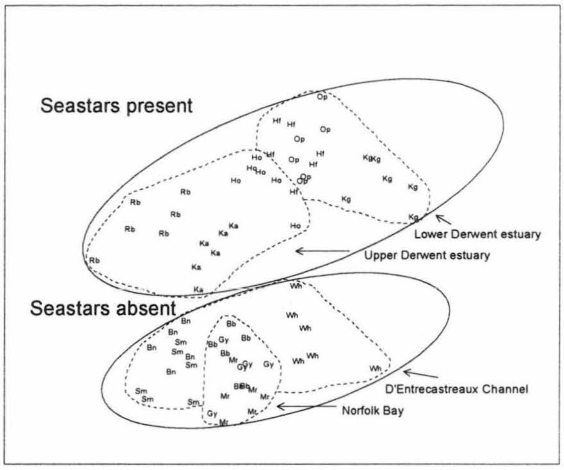


Figure 5.2 contd (l-u) Mean (+ SE) numbers of taxa or individuals and per core ($n = 2$) in each plot ($n = 3$) in each site in November 1996.

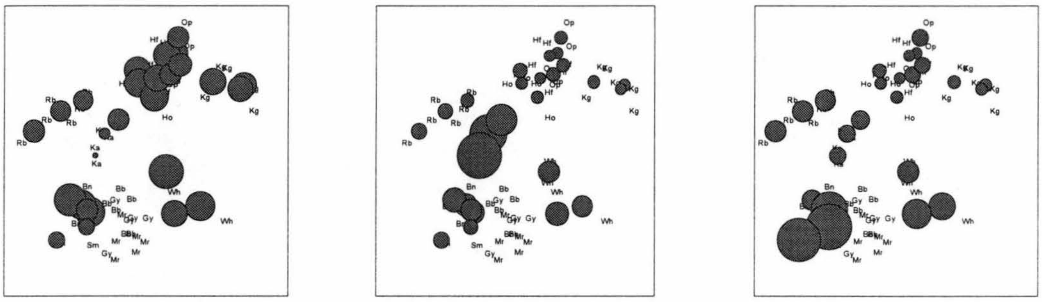
At the level of whole assemblages, the multivariate comparison indicated significant differences in macrofaunal assemblages among sites (npMANOVA, $F_{8,24} = 5.20$, $P = 0.003$) but not at other spatial scales (npMANOVA: Plot, $F_{24,34} = 1.75$, $P = 0.066$; Region, $F_{2,8} = 2.40$; $P = 0.090$; Zone, $F_{1,2} = 2.80$, $P = 0.335$). Although there was no significant effect at the level of zone, the Derwent River Estuary regions were clearly distinct from the two regions without seastars (Figure 5.3a). Moreover, within the estuary there was also a separation of the upper and lower regions (Figure 5.3a). In contrast, while sites in the D'Entrecastreaux Channel were more dispersed than those in Norfolk Bay on the MDS, these two regions were not clearly separated (Figure 5.3a). Although the stress value was high (0.20) for the ordination, comparison with a cluster analysis (group average sorting of a Bray Curtis matrix derived from 4th root transformed data) indicated a consistent pattern of grouping between the two approaches.

5.4.1.1 Relationships of soft sediment assemblages with seastars and sediment characteristics

Seastar density was variable both within and between the upper and lower reaches in the Derwent estuary, but overall abundance was clearly higher in the upper estuary than in the lower estuary (Figure 5.2a). No seastars were observed at sites outside the estuary. There were only two taxa, *Magelona* sp. and phoronids, where differences in abundance at the largest spatial scale (i.e. between the Derwent estuary where seastars were present and regions outside the estuary where seastars were absent) were significant (Table 5.1h,p). Both taxa were more abundant inside the estuary than outside (Figures 5.2h,t). At the scale of regions, both lumbrinerid and capitellid polychaetes were significantly less abundant in the lower Derwent estuary where seastars were at lower densities compared with the upper estuary (Table 5.1f,i; Figures 5.2e,f). However, lumbrinerid polychaetes also demonstrated significant variation among regions in the absence of seastars, with a lower abundance in the D'Entrecastreaux Channel than in Norfolk Bay (Table 5.1f, Figure 5.2m).



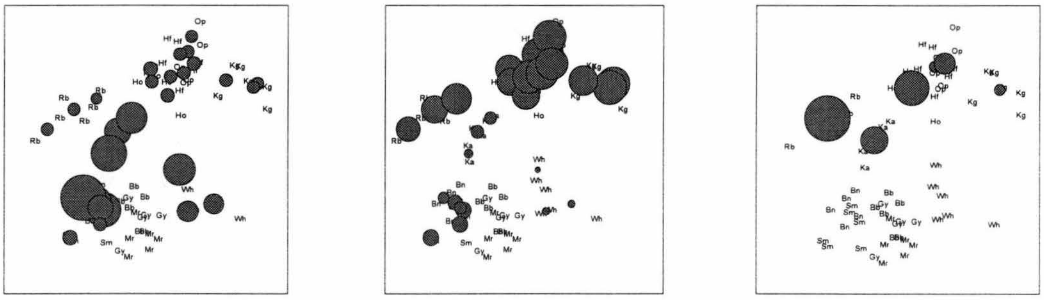
a. MDS



b. Graphic Mean

c. Sorting Coefficient

d. Silt



e. Medium Sands

f. Fine Sands

g. Seastar Density

Figure 5.3 (a) MDS ordination based on 4th root transformed taxon abundance data for all core samples in the large scale survey in 1996. The samples corresponding to assemblages in each region and regions in the presence and absence of seastars have been outlined for clarity. Bubble plot overlays of graphic mean particle size (b), sorting coefficient (c), percentage silt (d), percentage medium sand (e), percentage fine sands (g) and seastar density (h). Note there was no sediment data available for the Norfolk Bay sites. The bubble plots were overlayed on the centroids of each plot for sediment characteristics (b-g) and on the centroids of each site for seastar density (h). This reflects that I obtained a single sediment core from each plot and a single estimate of seastar density for each site. Site code descriptions are listed in the caption for figure 5.1.

At the level of the entire assemblage, the clear separation of the composition of macrofaunal assemblages in the Derwent estuary from the regions outside the estuary in both the ordination and cluster analysis is consistent with an effect of seastars (Figures 5.3a,g). However, sediment characteristics also showed clear trends when related to the multivariate composition of whole assemblages (note that sediment cores from sites in Norfolk Bay were lost). Bubble plot overlays of sediment characteristics on the MDS of faunal community structure indicates that trends in the composition of macrofaunal assemblages are correlated with gradients in the sorting coefficient, and percentages of silt (< 0.063 mm), fine sands (0.125 – 0.250 mm) and medium sands (0.250 – 0.500 mm) (Figures 5.3c-f). There is a clear grouping of assemblages with well-sorted sediments (top right of MDS, Figure 5.3c) that is distinct from assemblages with poorly to extremely poorly sorted sediments. A low percentage of silt and medium sands, but high proportion of fine sands relative to the other sites also correlates with this grouping (Figure 5.3d-f). Comparison of the structure of similarity matrices for the macrofaunal and sediment data, indicated that differences in macrofaunal structure was best correlated with the percentage of fine and medium sands (BIOENV procedure, $r_s = 0.516$). Because there was only a single estimate of seastar density at each site, the mean of sediment variables for each site was used to enable inclusion of seastar density as a potential 'environmental' correlate. The analysis indicated that the combination of percent silt, fine sand, medium sand and seastar density provided the maximum correlation with patterns of faunal similarity ($r_s = 0.463$). When each of these variables was analysed separately, only seastar density showed no correlation with the composition of assemblages.

The association between sediment characteristics and macrofaunal assemblages appears to be largely attributable to polychaetes (Figure 5.2). This is not surprising given their numerical dominance in benthic samples. The greatest abundances of both sedentary (in particular capitellids and terebellids) and errant polychaetes (in particular the nereid *Simplisetia amphidonta* and lumbrinerids) were in poorly sorted sediments with a low percentage of fine sands (< 30 %). The sedentary polychaete *Magelona* sp. was found only in the Derwent estuary where the percentage of medium sands was less than 10 % (Figures 5.2b,h). In contrast, *Nephtys australiensis* was found both inside and outside the estuary, but only where the percentage of medium sands was greater than 10 % (Figures 5.2b,l).

5.4.2 Spatio-temporal variation in soft sediment assemblages

Across years, seastar density was consistently greater at Ralphs Bay, followed by Howrah Beach and Opossum Bay (Figure 5.4). Seastar density declined at each site after the 1996 survey. This was most evident at Opossum Bay where only a single seastar was recorded in the later surveys. The MDS ordination showed that soft sediment macrofaunal assemblages were distinctly different among the three sites irrespective of year (Figure 5.5). Opossum Bay and Howrah Beach assemblages were more similar to each other than to the Ralphs Bay assemblage and this was particularly evident in 1997. The multivariate comparison indicated a significant site x time interaction (npMANOVA, $F_{4,18} = 2.58$, $P = 0.009$) suggesting that the magnitude of the differences among sites depended on the year of survey. The MDS ordination indicated that distinctions between assemblages at Howrah Beach and Opossum Bay were more pronounced in 1996 and 1998 than in 1997. At each site, assemblages in 1996 were similar to those in 1998, but 1997 showed clear separation from the other years (Figure 5.5). Results of the univariate analyses indicated a similar pattern to that described for whole assemblages. There was a significant time x site interaction for half of the taxa analysed (8 out of 17 taxa; Table 5.2). When the interaction term was not significant, differences among sites were significant for all taxa, while differences among years was significant only for capitellid polychaetes

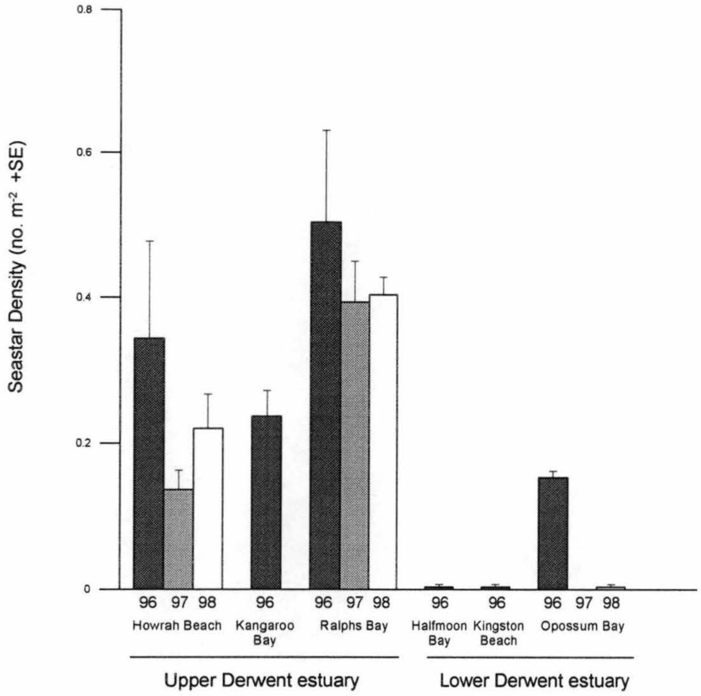


Figure 5.4 Seastar densities in November 1996, 1997 and 1998 at sites in the Derwent estuary. Note that only 3 sites were surveyed in 1997 and 1998 (Howrah Beach, Ralphs Bay and Opossum Bay). Densities are means (+ SE) determined from 50 x 2 m strip transects ($n = 3$).

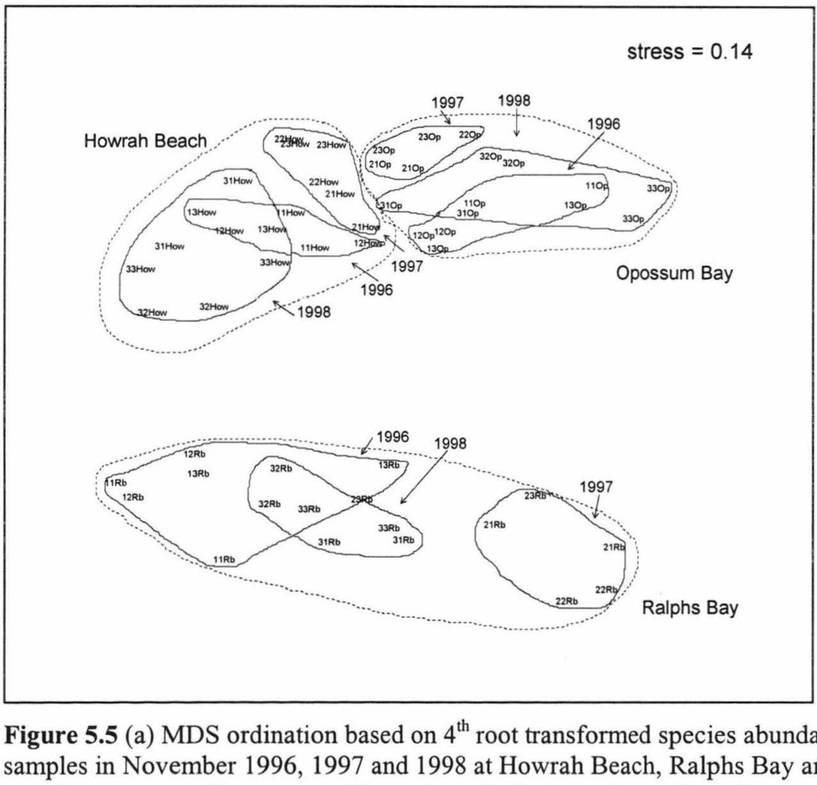


Figure 5.5 (a) MDS ordination based on 4th root transformed species abundance data for all core samples in November 1996, 1997 and 1998 at Howrah Beach, Ralphs Bay and Opossum Bay. The samples corresponding to assemblages in each site in each year have been outlined for clarity.

	a Sedentary polychaetes					b *Magelona* sp					c Capitellids					d Errant polychaetes				
Source of Variation	df	MS	F	p	% Var exp	df	MS	F	p	% Var exp	df	MS	F	p	% Var exp	df	MS	F	p	% Var exp
Site	2	24 86	12 87	**<0 001**	27%	2	71 61	27 93	**<0 001**	63%	2	10 90	10 32	**0.001**	17%	2	22 004	41 57	**<0 001**	66%
Time	2	13 21	1 8	0 277	9%	2	7 33	1 13	0 408	1%	2	17 57	7 49	**0.044**	33%	2	3 537	3 27	0 1441	7%
Site*Time	4	7 33	3 8	**0.021**	28%	4	6 48	2 53	0 077	12%	4	2 34	2 22	0 108	15%	4	1 0824	2 04	0 1309	5%
(Site*Time)	18	1 93	2 82	**0 008**	18%	18	2 56	6 87	**<0 001**	19%	18	1 06	1 74	0 097	10%	18	0 5294	2 34	**0 0236**	10%
Residual	26*	0 68			18%	26	0 37			5%	26	0 61			25%	26*	0 2263			11%

	e *Nephtys australiensis*					f Bivalves					g *Mysella donaciformis*					h *Theora* spp				
Source of Variation	df	Mean Sq	F	p	% Var exp	df	Mean Sq	F	p	% Var exp	df	Mean Sq	F	p	% Var exp	df	Mean Sq	F	p	% Var exp
Site	2	288 93	185 74	**<0.001**	84%	2	203 83	42 71	**<0.001**	61%	2	250 43	48 61	**<0.001**	65%	2	6 71	24 02	**<0 001**	57%
Time	2	8 03	0 99	0 447	0%	2	17 86	0 73	0 536	0%	2	30 24	1 32	0 364	2%	2	0 59	1 42	0 342	2%
Site*Time	4	8 10	5 21	**0 006**	6%	4	24 42	5 12	**0.006**	20%	4	22 96	4 46	**0 011**	15%	4	0 41	1 48	0 250	4%
(Site*Time)	18	1 56	0 79	0 691	0%	18	4,77	3,25	**0,003**	10%	18	5 15	3,27	**0.003**	9%	18	0 28	1.45	0 185	7%
Residual	26	1 96			9%	27	1 47			9%	27	1 57			8%	27	0 19			31%

	i *Timoclea cardoides*					j *Fulvia tenuicostata*					k Gastropods					l Phoronids				
Source of Variation	df	Mean Sq	F	p	% Var exp	df	Mean Sq	F	p	% Var exp	df	Mean Sq	F	p	% Var exp	df	Mean Sq	F	p	% Var exp
Site	2	1 49	6 53	**0 007**	0%	2	4 80	7 85	**0 004**	4%	2	20 22	6 62	**0 007**	17%	2	1 63	0 39	0 684	0%
Time	2	1 00	0 68	0 555	0%	2	5 69	1 43	0 339	8%	2	21 06	3 03	0 158	18%	2	18 40	0 8	0 509	0%
Site*Time	4	1 46	6 41	**0 002**	47%	4	3 96	6 48	**0 002**	47%	4	6 94	2 27	0 102	15%	4	22 91	5 47	**0 005**	50%
(Site*Time)	18	0 23	1 01	0 480	0%	18	0 61	1 57	0 140	9%	18	3 06	2 43	**0 018**	21%	18	4 19	1 98	0 055	18%
Residual	27	0 23			52%	27	0 39			32%	27	1 26			29%	26	2 12			33%

	m Ostracods					n Tanaids					o Amphipods					p Isopods				
Source of Variation	df	Mean Sq	F	p	% Var exp	df	Mean Sq	F	p	% Var exp	df	Mean Sq	F	p	% Var exp	df	Mean Sq	F	p	% Var exp
Site	2	80 51	44 84	**<0.001**	72%	2	41.25	14 55	**<0 001**	40%	2	67 37	47 56	**<0.001**	80%	2	17 45	8 7	**0.002**	34%
Time	2	2 61	0 75	0 529	0%	2	2 94	0 43	0 677	0%	2	1 02	1 05	0 429	0%	2	1 22	1 08	0 423	0%
Site*Time	4	3 48	1 94	0 148	5%	4	6 82	2 4	0 088	14%	4	0 97	0 69	0 611	0%	4	1 13	0 56	0 692	0%
(Site*Time)	18	1 80	2 02	**0.048**	8%	18	2 84	1 69	0 106	12%	18	1 42	3 79	**0.001**	11%	18	2 01	1 33	0 246	9%
Residual	27	0 89			15%	27	1 68			35%	27	0 37			8%	27	1 51			57%

	q Sipunculids				
Source of Variation	df	Mean Sq	F	p	% Var exp
Site	2	1 95	6 65	**0 007**	6%
Time	2	2 49	1 73	0 288	11%
Site*Time	4	1 44	4 91	**0 007**	37%
(Site*Time)	18	0 29	1 71	0 102	12%
Residual	27	0 17			34%

* polychaetes from one core were excluded

Table 5.2 Summaries of ANOVAs for selected taxa identifying significant site, time, and site x time effects. Significant *P*-values (<0.05) are shown in bold face. The percentage contribution of the total variance for each level in the ANOVAs was also derived.

At Howrah Beach bivalves were clearly the dominant group, with tanaids, amphipods and sedentary polychaetes also common in 1996 (Figure 5.6). Small mobile crustaceans, in particular amphipods and ostracods were the most common groups at Opossum Bay, with sedentary polychaetes and bivalves also reasonably abundant in each year (Figure 5.6). At Ralphs Bay where the total density of animals was lower than at the other two sites, errant and sedentary polychaetes and, to a lesser extent bivalves, were the most common groups (Figure 5.6). Regarding individual taxa, the polychaete *Nephtys australiensis* was found only at Ralphs Bay, the polychaete *Magelona* sp. only at Howrah Beach and Opossum Bay, while capitellid polychaetes were notably more common at Ralphs Bay and Howrah Beach than at Opossum Bay (Figure 5.7a). The high abundance of bivalves at Howrah

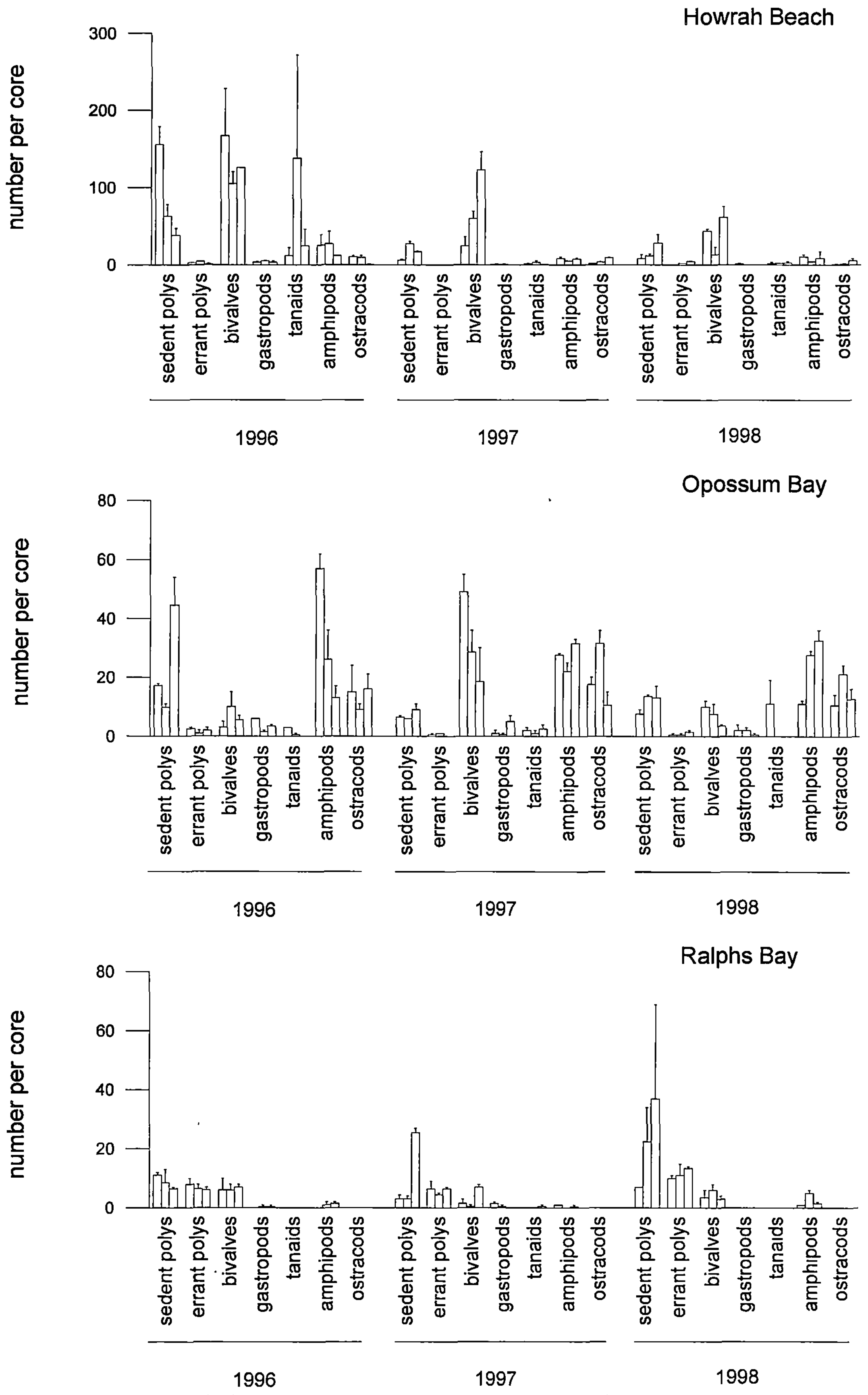


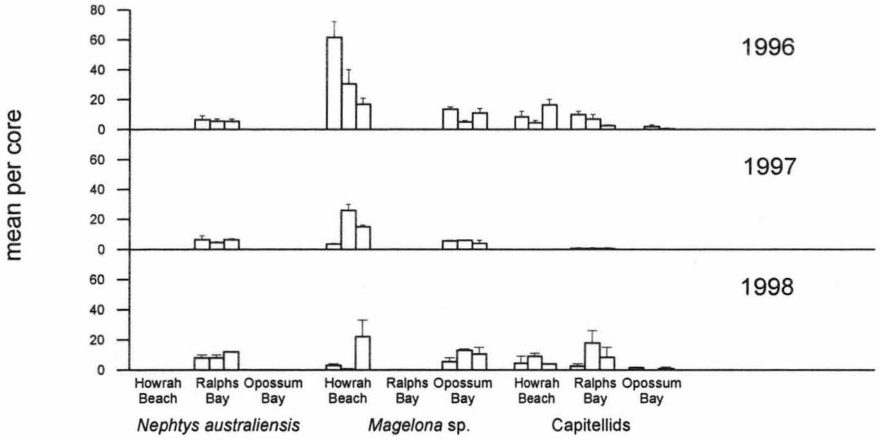
Figure 5.6 Mean (+ SE) abundances of major groups per core (n = 2) in each plot (n = 3) in 1996, 1997 and 1998 at (a) Howrah Beach, (b) Opossum Bay and (c) Ralphs Bay.

Beach was clearly attributable to the high density of *Mysella donaciformis* (Figures 5.6, 5.7b). Of the other bivalve species, *Theora* spp. was predominately found at Ralphs Bay, while *Timoclea cardoides* in 1998 and *Fulvia tenuicostata* in 1997 were common at Howrah and Opossum Bay respectively (Figure 5.7b). Of the remaining taxa sipunculids were common at Howrah Beach and Ralphs Bay but only in 1996; isopods were abundant at Howrah Beach and Opossum Bay in all years; while *Nassarius nigellus* was abundant at Opossum Bay in all years but at Howrah Beach only in 1996. Phoronids were recorded at all sites but were extremely patchy in space and time (Figure 5.7c).

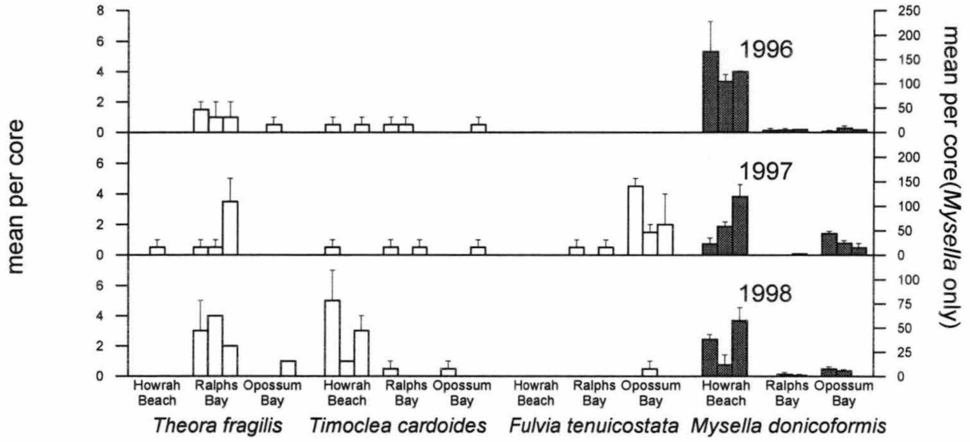
5.4.3. Macrofaunal abundance and seastar diet

Bivalves, polychaetes and crustaceans were clearly the numerically dominant groups in soft sediments at Howrah Beach, Ralphs Bay and Opossum Bay respectively (Figure 5.8a). However, this pattern wasn't always reflected in seastar stomach contents (Figure 5.8a). While bivalves were the most numerically common group in both the sediments and seastar diet at Howrah Beach, they were consumed in lower proportions relative to their occurrence in the environment. In contrast, gastropods and crustaceans were consumed in greater proportion to their occurrence in the environment. Similarly, while polychaetes at Ralphs Bay and crustaceans at Opossum Bay were the most common groups in the sediments, crustaceans and bivalves were the most common groups in seastar stomach contents at each site respectively.

a. Polchaetes



b. Bivalves



c. Other taxa

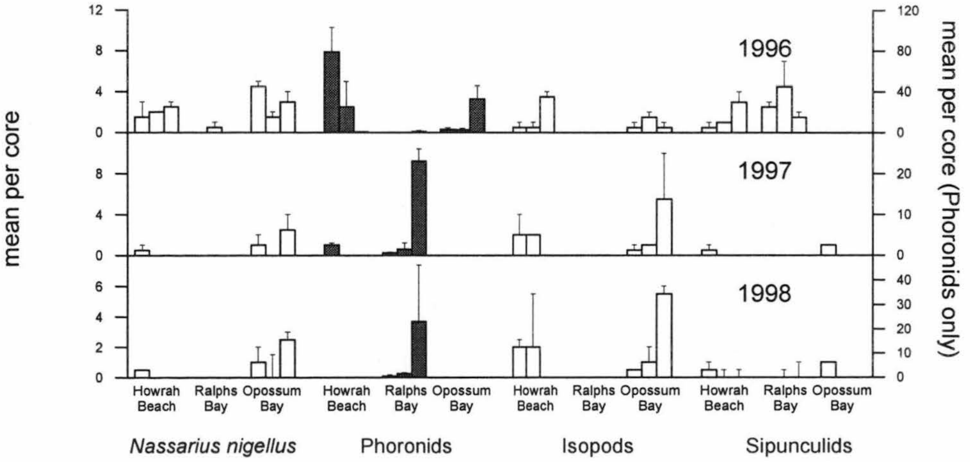


Figure 5.7 Mean (+ SE) abundances of major taxa per core ($n = 2$) in each plot ($n = 3$) at each site in 1996, 1997 and 1998 for (a) polychaetes, (b) bivalves and (c) other taxa.

It is also clear that when taxa are grouped, dietary preferences are not consistent across sites (Figure 5.8a). For example, crustaceans were more common in the diet of seastars at Howrah and Ralphs Bay than at Opossum Bay, despite that crustaceans were far more common in the environment at Opossum Bay. By considering individual taxa, clear dietary preferences emerge for certain taxa but not others (Figures 5.8b,c). Despite being extremely abundant in the sediments, *Mysella donaciformis* was invariably rare in seastar stomach contents. In contrast, most of the other bivalve species were more common in seastar stomachs than expected from their abundance in the environment. Thus, the relatively high abundance of *Mysella donaciformis* at Howrah Beach compared with Opossum Bay explains why bivalves as a group are ostensibly avoided at Howrah Beach, but disproportionately represented in the diet at Opossum Bay. Other taxa consumed in far greater proportion to their occurrence in the environment were the gastropod *Nassarius nigellus*, heart urchin *Echinocardium cordatum*, and an unidentified polychaete. This polychaete was unable to be identified because of its state of decomposition, although the remains indicated that it was clearly different from any of the intact polychaetes recorded from the sediments. Crustaceans that were disproportionately common in seastar stomach contents were tanaids and amphipods at Howrah Beach and pieces of the crab *Paragrapsis gaimardii* at Ralphs Bay. Despite being common in the environment at Opossum Bay, amphipods were extremely rare in seastar stomach contents.

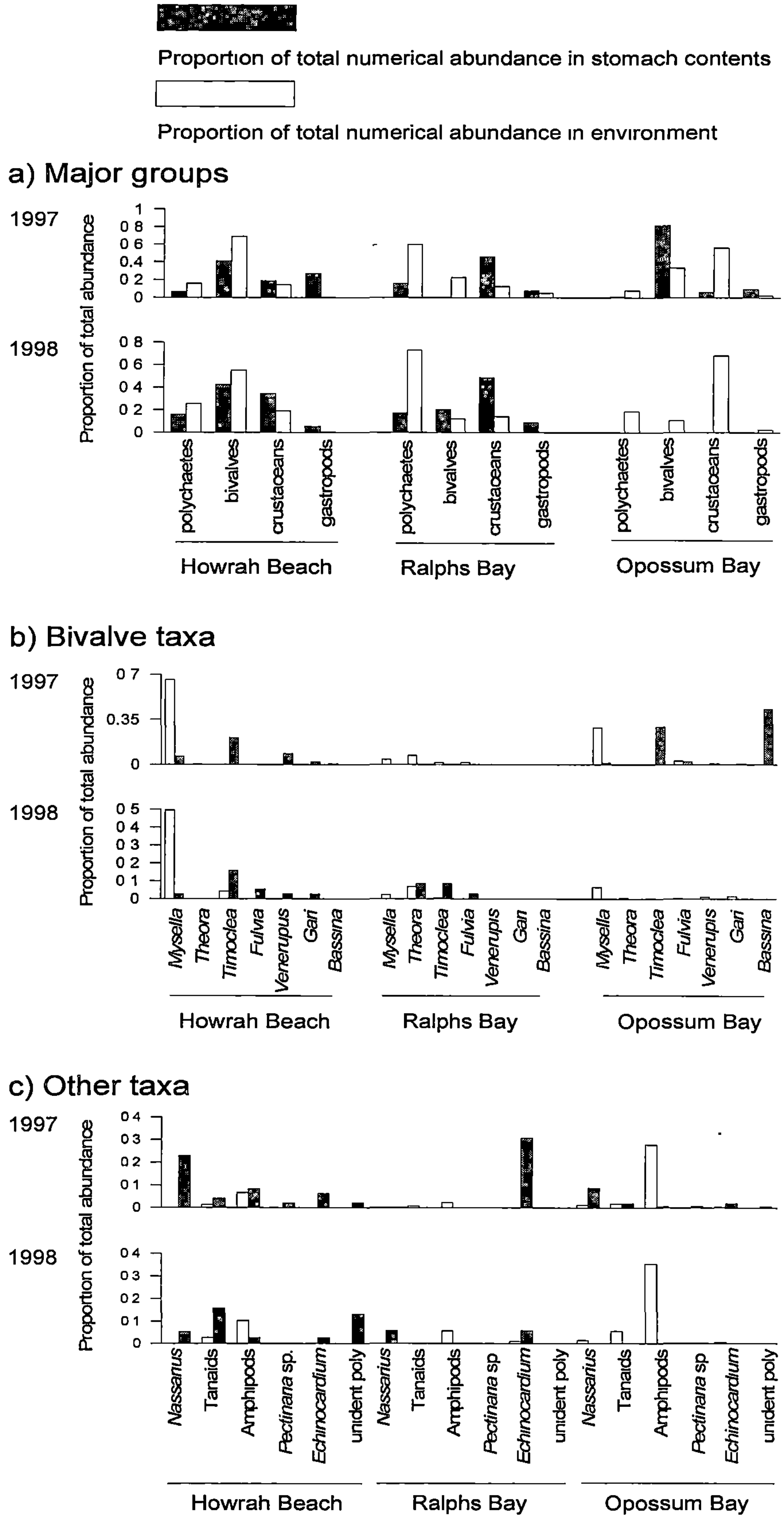


Figure 5.8 Proportion of total prey abundances in seastar stomachs and in sediments at Howrah Beach, Ralphs Bay and Opossum Bay in 1997 and 1998 for (a) major groups, (b) bivalve taxa and (c) other abundant taxa.

5.4.4 Spatial variation in abundances of bivalves and heart urchins

The survey based on 1m^2 suction samples provided more precise estimates of abundances (and even presence) of bivalves and heart urchins than did data from the smaller core samples, particularly for species that are either large and/or present at low densities (unpub data). However, the overall pattern of large variability among sites evident from cores was also clear from the suction samples of larger plots (Figure 5.9). Note that since seastars were virtually absent from Opossum Bay in 1997 and 1998 surveys (Figure 5.4), for the purposes of comparing patterns among sites with and without seastars in 1998, Opossum Bay was grouped with the other sites outside the estuary that did not support seastars.

Considering the total number of bivalves and heart urchins, there was no evidence of an overall effect of seastars on abundance (Figures 5.9a-c). However, bivalves were notably smaller at sites supporting large populations of seastars. (Figure 5.9c). At the level of species there were clear patterns in the abundance and size structure of some species, but not others, that correlated with the presence of seastars. The bivalves *Electroma georgina*, *Fulvia tenuicostata*, *Soletellina biradiata* and *Wallucina assimilis* were abundant only at sites where seastars were absent (Figures 5.9d–g). In contrast, the bivalves *Theora* spp., *Mysella donaciformis* and *Timoclea cardoides* were abundant at some sites supporting large populations of seastars (Figures 5. 9b,h-j). While there was no evidence that the seastar affected the abundance of *Timoclea cardoides* (Figure 5.9j), this bivalve was noticeably smaller in both the sediments and stomach contents of seastars at sites supporting large populations of seastars than at sites where seastars were absent (Figure 5.9k).

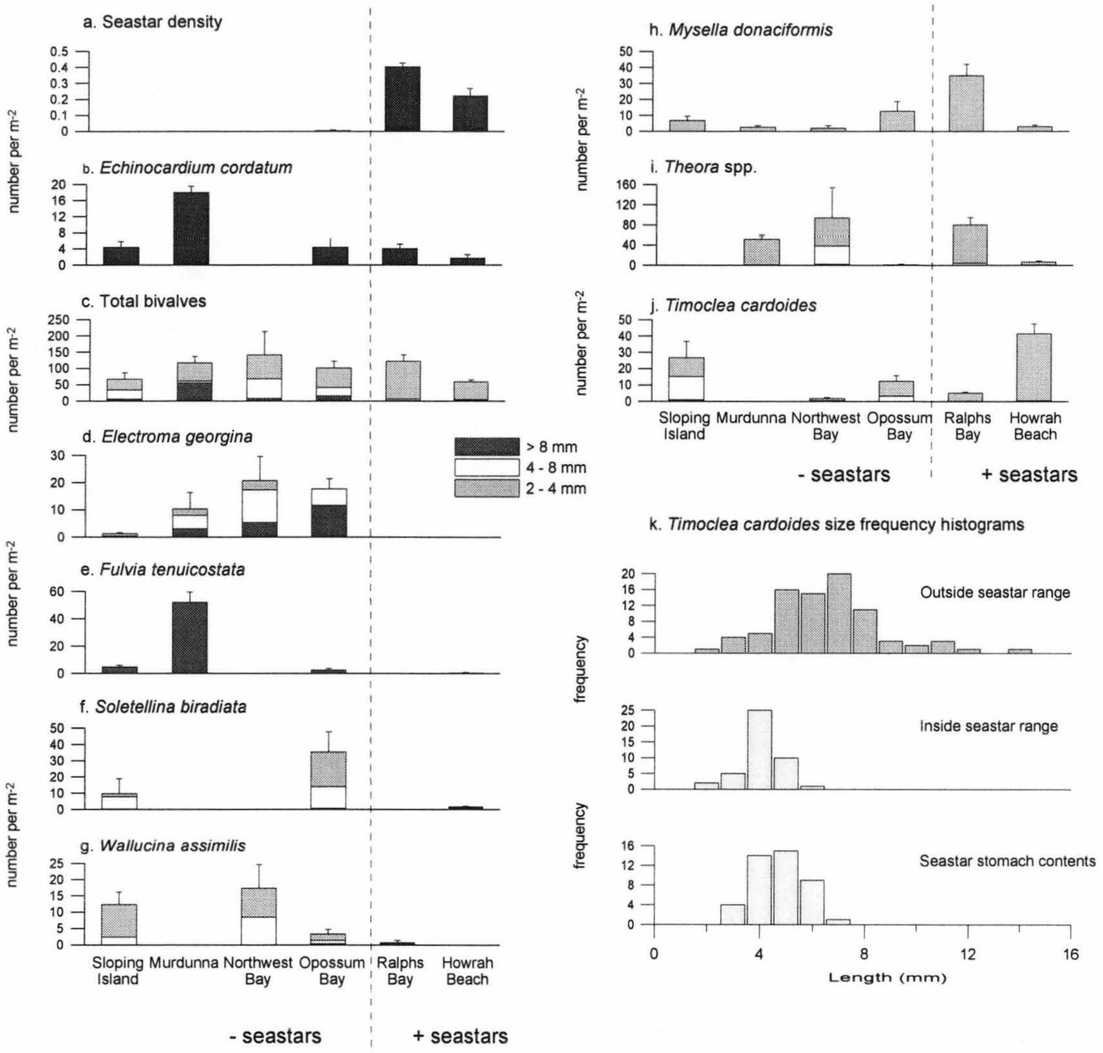


Figure 5.9 Mean densities (+ SE) of (a) seastars based on 50 x 2 m strip transects (n = 3), (b) *Echinocardium cordatum* (heart urchin), (c) total number of bivalves and (d-j) each of the major bivalve species based on 1 m^2 benthic samples (n =3) at each site in 1998. The proportion of bivalves retained on 2, 4 and 8 mm mesh are also depicted. (k) Length frequency histograms of the bivalve *Timoclea cardoides* from animals collected at sites outside the seastars range, inside the seastars range and from seastar stomach contents.

5.5 Discussion

5.5.1 Spatial variability in soft sediment assemblages

Variability in the distribution and abundance of benthic organisms is characteristic of marine soft sediment assemblages (e.g. Rhoads 1974; Gray 1981; Barry & Dayton 1991; Morrisey et al. 1992a,b). However, few published studies have examined patchiness in the distribution and abundance of benthic organisms in subtidal soft sediment habitats in Tasmania (but see Moverley & Jordan 1996; Edgar et al. 1999). The results of this study indicate large variability at a range of spatial scales, from metres to tens of kilometres in soft sediment assemblages in southeast Tasmania. For the total number of taxa, the total number of individuals, and the dominant taxa, significant spatial differences in mean abundance were observed at all scales. Most striking was the importance of variability among sites (over 1000s of metres), reflected in both the univariate analyses of dominant taxa and multivariate analysis of whole assemblages. The relative contribution of each scale to the total variance also confirmed the importance of variability at this scale. However, for some taxa, variance components indicated that differences among regions and zones were also important, although differences at these scales were not always significant in ANOVAs. The absence of a significant effect in these cases is likely to be due to large variances in abundance at smaller spatial scales (particularly among sites) and/or low degrees of freedom in error terms, and therefore low power in tests for the differences at larger spatial scales. Thus, in some instances, the large variability at smaller scales may have obscured the importance of variation at larger spatial scales. A similar pattern, and for the same reason, is noted by Morrisey et al. (1992a)

5.5.2 Spatio-temporal variability in soft sediment assemblages

At sites within the estuary, significant site x time interactions in both the multivariate and univariate analysis indicated that the temporal trajectories of whole assemblages and ca. 50 % of the dominant taxa varied between sites. Lack of concordance in temporal trajectories among sites has been demonstrated for many populations in other studies (see Osenberg et al. 1996). In the Derwent, variation in space (among sites) was considerably larger than variation in time (among years) at the sites that were surveyed annually. However, annual observations will not detect shorter-term fluctuations of populations among weeks or seasons (see Underwood 1991), and the importance of short-term fluctuations has been shown in other work at the Ralphs Bay site between the 1997 and 1998 surveys (chapter 3). Although most bivalves, including the commercial species *Fulvia tenuicostata*, were extremely rare at Ralphs Bay in the annual surveys reported here, a number of bivalve species recruited in the bay in large numbers in the period between the 1997 and 1998 surveys, but were virtually eliminated by seastar predation prior to the 1998 survey. These results highlight the importance of sampling at several temporal scales if questions of interest are not specifically concerned with a single particular scale (see Underwood 1996).

5.5.3 Relationships between macrofaunal assemblages and seastar abundance and sediment characteristics

There were only two taxa, *Magelona* sp. and phoronids, where differences in abundance at the largest spatial scale, i.e. between the Derwent estuary where seastars were present and regions outside the estuary where seastars were absent, were significant. Both taxa were more abundant inside the estuary than outside, which cannot be attributed to a direct effect of the predatory seastar. While it is possible that indirect effects of the seastar may provide the opportunity for enhanced recruitment and/or survival of polychaetes accounting for the greater abundance of polychaetes in the region with greater seastar abundance; such indirect effects are unlikely given what is known about the strong association of polychaetes and sediment characteristics (see below). Given that *Magelona* sp. was completely absent and phoronids were extremely rare outside the estuary, the differences are more likely to be attributable to spatial variability independent of seastars. Other evidence of variability in the abundance of *Magelona* sp. at this scale is evident from the statewide survey of Edgar et al (1999), where *Magelona* sp. was present at only 22 of 55 sites across 48 estuaries. In the present survey, the variability in the abundance of *Magelona* sp. appears to be associated with the degree of sorting and sand content of the sediments. In the estuary it was recorded in abundance only at sites with well sorted sediments that were comprised mainly of fine sands and with little medium sands. The absence of suitable sediment conditions provides a more likely explanation for the absence of *Magelona* sp. outside the estuary than the absence of seastars.

Within the estuary itself, all of the polychaetes with the exception of *Magelona* sp. were less abundant in the lower region where seastars were present at lower densities. Again this difference in abundance cannot be explained as a direct effect of the seastar, and is probably best explained in terms of sediment differences. For example, there was a clear trend that teribellids, capitellids and the nereid *Simplisetia amphidonta* were most abundant in poorly sorted sediments with a low percentage (< 30 %) of fine sands.

The importance of sediment characteristics, including grain size and the degree of sorting, as a correlate and/or determinant of patchiness is well established (e.g. Sanders 1958; Rhoads 1974; Gray 1974; Barry & Dayton 1991). Hughes (1972) showed that substratum characteristics accounted for 46 % of the variance in the frequency of occurrence of polychaetes and echinoderms in St. Margaret's Bay, Nova Scotia. Given the numerical dominance of polychaetes and their strong association with sediment characteristics, it is not surprising that in this study the composition of the assemblage as a whole correlated with sediment characteristics. The percentage of fine and medium sands provided the best correlation with the composition of assemblages at the scale of plots. Conducting the analysis after pooling data at the scale of sites (so that seastar density could be included), showed that the combination of percentage of silt, fine sand, medium sand and seastar density provided the best correlation with the composition of assemblages. Although seastar density helped explain the composition of assemblages it was the only variable that showed poor correlation with the composition of assemblages when examined on its own. Therefore, seastar abundance is likely to play a minor role relative to sediment characteristics in influencing the broad patterns across the entire assemblage that were observed here. Thus, although I endeavored to match the range of sediment types at sites inside and outside the estuary based on superficial observations, the results demonstrate that correlations with seastar abundance is confounded with sediment characteristics. Indeed, the inclusion of seastar density with the sediment variables as the optimum combination to explain infaunal composition may simply reflect a preference of the seastar for certain sediment types. Nojima et al. (1986) noted that the distribution of *Asterias amurensis* in the Ariake Sea suggested a preference of medium sands over muds, while Grannum et al. (1996) recorded a negative relationship between the density of seastars and the degree of sorting of sediments in the Derwent estuary. This further highlights the difficulties of interpreting comparisons among putative ‘impact’ and ‘control’ sites in the absence of data prior to the establishment of exotic species.

5.5.4 Comparison with results from manipulative experiments and feeding observations at small scales

Observations of diet and prey switching (chapter 3) demonstrate that while the seastar is a generalist predator able to switch between taxa it has clear food preferences. Most bivalve species, the gastropod *Nassarius nigellus* and the heart urchin *Echinocardium cordatum* are consumed in far greater proportion to their occurrence in the sediments. (chapter 3; Grannum et al. 1996; Lockhart & Ritz in press{b}). Results of manipulative experiments also demonstrated a large impact of the seastar on bivalves, particularly those that live just under or on the sediment surface (chapters 2,3,4).

It was not anticipated that core samples used to describe large scale patterns would provide precise estimates of the abundance (or even necessarily detect) of larger and/or rare species. The second survey using much larger samples (1 m^2) but across a more limited spatial extent, targeted some of the species (bivalves and heart urchins) identified as important prey in the small scale experiments and feeding observations. The large scale patterns of abundance and/or size structure of these species were consistent with the findings of the observational and experimental studies at smaller scales for most, but not all species. Although there was no evidence of an effect of seastars on the overall abundance of bivalves, bivalves were noticeably smaller at sites supporting large populations of seastars. This is consistent with experiments conducted immediately beyond the current range of the seastar, in which the decrease in abundance of bivalves in treatments with seastars present was largely attributable to a decline in the abundance of large bivalves (chapter 4). At the level of species, large scale patterns of abundance were consistent with the findings of the observational and experimental studies for most, but not all species. The abundance of species that were most heavily preyed on or preferred by seastars in experiments and/or feeding observations (i.e. *Fulvia tenuicostata*, *Electroma georgina*, *Soletellina biradiata* and *Wallucina assimilis*) were abundant only at sites where seastars were absent. In contrast, bivalves that were rare in stomach contents despite been common in the sediments (*Mysella donaciformis* and *Theora* spp.) were highly abundant at some sites irrespective of seastar abundance. Two species that I did expect to be correlated with the presence of seastars based on known feeding preferences were the heart urchin *Echinocardium cordatum* and the bivalve *Timoclea cardoides*, but these two were abundant at sites with and without seastars at high densities. A possible explanation of this pattern for *E. cordatum* is that it has a depth refuge from seastar predation in the presence of more accessible prey due to its ability to remain deeply buried (up to 15 cm: Buchanan 1966). For *T. cardoides*, even though patterns of abundance were not indicative of a seastar effect, differences in the size structure were suggestive of a seastar effect, as it was noticeably smaller at sites were seastars were present than at sites where they were absent. Seastar predation on small *T. cardoides* may be preventing recruitment into the larger size classes recorded at sites were seastars are absent. The potential impact of seastar predation on the establishment of adult populations of bivalve and gastropod prey is supported by previous feeding observations in the estuary that have noted the absence of adults in the sediments despite the presence of large numbers of juveniles in seastar stomachs (Morrice 1995; Grannum et al. 1996; Lockhart and Ritz in press{b}). Indeed, the results of a manipulative experiment conducted in the Derwent River Estuary demonstrated that the seastar had a large impact on the survivorship of recruits of the commercial bivalve *F. tenuicostata*, effectively arresting the recruitment event (chapter 3).

5.5.5 Conclusions

This study has highlighted the difficulty in selecting appropriate control locations in the absence of any data prior to putative impacts. The results demonstrate that choice of sites based on superficial similarity of sediment types was inadequate. Despite that mean particle diameter was similar across sites, the degree of sorting and relative contribution of particular sediment fractions was not. Similarly, in a study of marina impacts, Glasby & Underwood (1998) suggested that their seemingly appropriate control locations might have been totally inadequate because of differences in environmental variables that were not considered. The results of This study have confirmed the importance of carefully identifying and accounting for physical factors that may play an important role in determining the composition of assemblages when choosing control locations in a post impact study. If I had interpreted results of the large scale surveys on the basis of the abundance of seastars alone, I may have erroneously associated the distinct differences in assemblages inside and outside the Derwent River Estuary as related to the presence or absence of the seastar. However, in light of known responses of infauna to sediment characteristics and results of the manipulative experiments and feeding observations at small scales, I'm in a strong position to suggest that the observed patterns for some species reflect associations with particular sediment types, while large scale patterns in other species (several bivalves) are consistent with predatory impacts of the seastar.

Overall, this study highlights the need to employ multiple methodologies in assessing impacts in the absence of pre-impact data that enable more sophisticated analyses (e.g. Stewart-Oaten & Bence 2001). While the field survey ultimately provided evidence about the presence or absence of impacts at large scales, the identification of key ecological variables in experimental and feeding studies proved crucial to both the design, and interpretation of patterns observed in the large scale surveys. In the absence of pre-impact data, the assessment of impact ultimately rest with a 'weight of evidence' argument from several lines of enquiry rather than a single 'inferential' test.

Chapter 6 General Discussion

Assessing the immediate and predicting the future impact of an introduced predator, the northern Pacific seastar (*Asterias amurensis*), in Tasmania

(Submitted to Journal of Biological Invasions)

6.1 Abstract

Introduced species are having major impacts in terrestrial, freshwater and marine ecosystems worldwide. However, resources for management and control efforts of introduced species are likely to be limited, particularly as invasion rates increase. Given that only a small percentage of invaders are likely to cause large ecological change, it is imperative that management priorities are based on the severity of immediate and, in particular, anticipated impacts on native assemblages and commercial species. The work described in this paper provides a broad synthesis of a body of work on the immediate and predicted impacts of an introduced predator (*Asterias amurensis*) on soft sediment assemblages, including commercial species, in southeast Tasmania. Because of the absence of baseline data prior to the arrival of the seastar and the presence of other anthropogenic stressors in the estuary, estimating the impact of the seastar is difficult. To help overcome the weaknesses of any single method, this assessment of impact ultimately rests with a 'weight of evidence' argument from multiple lines of evidence. Results from several experimental manipulations and detailed observations of feeding at small scales, and spatially hierarchical surveys, provide strong evidence that predation by the seastar is

responsible for the decline and subsequent rarity of bivalve species that live just below or on the sediment surface in the Derwent River Estuary. Observations of diet and prey switching and results of experiments conducted at several sites demonstrated that the exact nature of seastar effects is site and time specific given variability in soft sediment assemblages and the seastar's responses to them. In the event of spatial overlap with the introduced predatory European green crab (*Carcinus maenas*), experiments suggest that both predators may coexist because of resource partitioning on the basis of prey size and/or habitat requirements, and that the impact on bivalves may be greater in the presence of both species. It seems clear that should seastar densities in other areas on the Tasmanian coast attain the levels that occur in the Derwent River Estuary, there are likely to be large direct effects on native assemblages, and particularly on populations of large bivalves (including commercial species) that live just under or on the sediment surface. Given the seastar's ability to exploit a range of other food resources and the importance of bivalves as a functional component of native systems, broader direct and indirect effects on native assemblages are also predicted. Overall, these important consequences of the establishment and potential spread of this introduced predator warrant management efforts to control its spread and impact.

6.2 Introduction

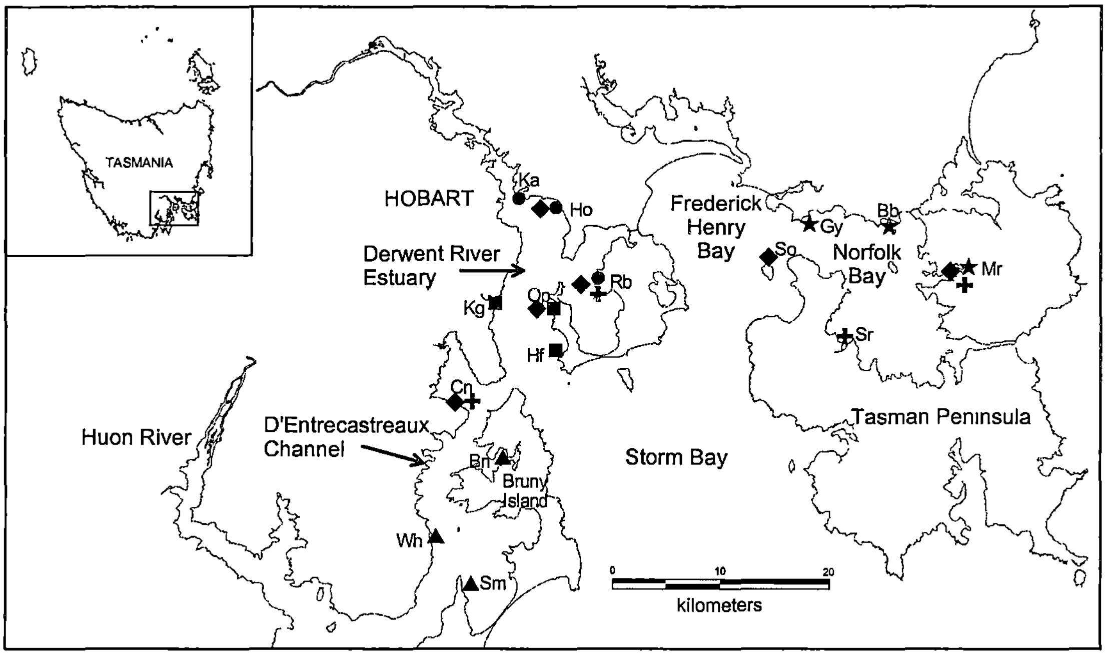
6.2.1 Background

Biological introductions due to human aided movement of species across and between continents and oceans are proving one of the greatest environmental and economic threats to native biodiversity and ecosystem function (Lodge 1993; Vitousek et al. 1996; Cohen & Carlton 1998; Pimental et al. 2000). In marine and estuarine systems, the number of introductions continue to accumulate (Cohen & Carlton 1998; Hewitt et al. 1999; Coles et al. 1999), yet our understanding of the nature and magnitude of ecological impacts is limited (Ruiz al. 1999; Grosholz et al. 2000). Of the handful of studies that have quantified impacts of marine invaders, in some cases the impact on the recipient community has been catastrophic, such as the invasion of San Francisco Bay by the Asian clam *Potamocorbula amurensis* (Nichols et al. 1990) and the introduction of the comb jelly *Mnemiopsis leidyi* in the Black Sea (Shushkina and Musayeva 1990). Although prevention of such invasions is the most desirable outcome for management, in many cases species are already established before they are recognised. Eradication of species already established is usually not feasible, at least in the short term and particularly if they are widely established (but see Bax 1999; Willan et al. 2000; Culver and Kuris 2000). Given that only a small percentage of exotics are likely to cause large ecological change (Carlton & Geller 1993; Williamson 1996), it is imperative that with limited resources for management and control efforts, management priorities are based on the severity of immediate and, in particular, anticipated impacts on native assemblages and commercial species (Lodge et al. 1998).

The coastal waters of Australia have been the site of a number of significant introductions of exotic marine species (Pollard & Hutchings 1990a, 1990b; Jones 1991; Furlani 1996; Hewitt et al. 1999; Hewitt submitted ms). One of the more conspicuous introductions has been the northern Pacific seastar (*Asterias amurensis*), first recorded at Hobart in the Derwent River Estuary in southeast Tasmania (Figure 1) in 1986 (Turner 1992; Buttermore et al. 1994). The seastar is a native of the coasts of Korea, Japan, China and Russia, but is also found across in Alaska and northern

Canada where it is possibly introduced (see McLoughlin and Bax 1993). It is thought to have been introduced to Tasmania as larvae in ballast water of ships from Japan, however, the discovery of adult seastars in the water intake ('sea chest') of a vessel confirms that other methods of transfer exist for this species (Talman et al. 1999).

Since its arrival in Tasmania, the seastar has become the dominant invertebrate predator in the Derwent River Estuary (Figure 6.1) where it is considered a major threat to benthic assemblages (Buttermore et al. 1994; Johnson 1994; McLoughlin and Thresher 1994; Grannum et al. 1996). Perhaps of greater concern is the potential spread to areas outside the estuary in Tasmania, and to other areas nationally and internationally. Concentrations of *Asterias* larvae adjacent to wharf areas in the estuary are some of the highest reported for seastar larvae worldwide (Bruce et al. 1995). Furthermore, recent modelling of seastar larval dispersal indicates that large majority of larvae produced in the estuary are likely to be advected from it (Morris & Johnson in prep). The recent discovery and subsequent population explosion of seastars in Port Phillip Bay Victoria (on mainland Australia) are believed to be the result of larval translocation from Tasmania (Murphy and Evans 1998). Considered a threat internationally, New Zealand has enacted legislation preventing discharge of ballast water taken up from the Derwent River Estuary and Port Phillip Bay during the spawning season of the seastar (Biosecurity Act 1993, Annex 1 *cited by* Goggin 1998).


TASMANIA
HOBART
Ka
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Derwent River Estuary
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Frederick Henry Bay
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Norfolk Bay
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Sr
Cn
Huon River
D'Entrecastreaux Channel
Bn
Bruny Island
Wh
Sm
Storm Bay
Tasman Peninsula
0
10
20
kilometers

Figure 6.1 (a) Map of southeast Tasmania showing experimental and survey sites used throughout this study. The 12 sites sampled in the large scale survey in 1996 (= 3 sites in each of four regions: two regions inside the estuary where seastars were present, designated as [●] upper and [■] lower estuary and representing areas of high and low densities of seastars respectively; and two regions outside the estuary where seastars were absent at [★] Norfolk Bay and in the [▲] D'Entrecastreaux Channel). Also shown are sites of the 1998 survey [◆] of bivalves and heart urchins using 1m^2 suction samples, and the sites where [✚] manipulative experiments were conducted. Site codes stand for Howrah Beach (Ho), Kangaroo Bay (Ka), Ralphs Bay (Rb), Halfmoon Bay (Hf), Kingston Beach (Kg), Opossum Bay (Op), Breaknock Bay (Bb), Gypsy Bay (Gy), Murdunna (Mr), Barnes Bay (Bn), Simmonds Bay (Sm), Whaleboat Rock (Wh), Sloping Island (So), Conningham (Cn) and Saltwater River (Sr).

While there are few examples of introduced echinoderms (e.g. Ruiz et al. 1999; Cohen & Carlton 1995; Hewitt et al. 1999; Hewitt submitted ms), the importance of asteroids in structuring benthic marine communities, their propensity for population outbreaks, and capacity to 'invade' and significantly impact fishery and mariculture grounds in their native ranges is well documented (see Sloan 1980; Menge 1982). In the northern hemisphere, *Asterias amurensis* causes considerable damage to commercial shellfishes (e.g. oysters, cockles, scallops, other clams; Hatanaka and Kosaka 1959; Kim 1969; Nojima et al. 1986) and is known to be an opportunistic predator on a variety of other epifaunal and infaunal species including other molluscs, ascidians, bryozoans, sponges, crustaceans, polychaetes, fish and echinoderms (Hatanaka and Kosaka 1959; Fukuyama and Oliver 1985; Fukuyama 1994). In Tasmania, indirect indications of impact from observations of seastar foraging behaviour, stomach contents, and estimates of feeding electivity suggest the potential for considerable impact on native species. Nonetheless, there is no direct quantitative evidence of impacts of the seastar on native assemblages or wild fisheries in either its native or introduced range. Given that resources for management and control efforts for introduced pests in Tasmania are likely to be limited, particularly as the number of high profile invaders continues to accumulate (e.g. the Japanese kelp *Undaria pinnatifida* and the European shore crab *Carcinus maenas*), it is essential that management priorities are based on a robust assessment of immediate and anticipated impacts on native assemblages and commercial species. The work described in this paper provides a broad synthesis of a body of work on the immediate and predicted impacts of *A. amurensis* on the soft sediment assemblages and commercial species in southeast Tasmania.

6.2.2 Estimating Impact

A major challenge for ecologists is how to assess impacts of successful invaders that includes information such as the magnitude (and type) and pattern of impact in space and time (Lodge et al. 1998; Ruiz et al. 1999). There are several obstacles to this challenge. First, there is often no pre-impact data on native assemblages. Second, introduced species are often well established before they are discovered. Third, introduced species most often arise in areas that are subject to a broad spectrum of other anthropogenic stressors (Ruiz et al. 1999). In this case it is difficult to separate the effects of the introduced species of interest from other anthropogenic stressors, particularly given the likelihood of interaction between the exotic species and other stressors (Ruiz et al. 1999). Finally, concerns are often with impacts over large spatial and temporal scales, at which experimental work is difficult and normally not practical (see Lodge et al. 1998; Ruiz et al. 1999).

To help overcome these difficulties and the strengths and weaknesses of any single method of impact assessment (see Diamond 1986; Schmitt and Osenberg 1996; Lodge et al. 1998), an integrated approach combining multiple methodologies was used. This provides a more robust assessment of impacts because it includes independent tests of impacts conducted on different scales (Diamond 1986; Ruiz et al. 1999). In this paper I integrate the results from: (a) experiments in which seastar density is manipulated at several sites immediately beyond the current range of the seastar; (b) experiments in which seastar density is manipulated following recruitment of prey; (c) experiments in which the density of both seastars and another introduced benthic predator (*Carcinus maenas*) are manipulated and their interaction assessed; (d) comparative analysis of prey taxa in the sediments and in seastar stomachs; and (e) spatially hierarchical surveys to examine the relationship between macrofaunal assemblages and seastar abundance at several sites in southeast Tasmania. This combination of approaches provides a readily interpretable estimate of the impact of *Asterias amurensis* on the soft sediment assemblages in southeast Tasmania.

6.3 Variability in impact

The capacity to predict the impact of introduced species will depend largely on the magnitude of spatial and temporal variability in impacts. I note, however, that relatively few studies of introduced marine species have investigated spatial and temporal variability of impacts (but see Allmon & Sebens 1988; Nichols et al. 1990; Grosholz & Ruiz 1996). 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 both the impacting species and its potential prey, the nature of functional responses to prey density, water temperature, current velocity, turbidity, non-linear functional responses and sediment characteristics (e.g. Lipcius and Hines 1986; Woodin 1978; Everett and Ruiz 1993; Skilleter 1994; Thrush 1999). For instance, an increase in the variability of impacts in space and time might be expected if prey populations are spatially and temporally variable and/or if the exotic is a generalist but with distinct food preferences.

The results of the initial large scale survey (chapter 5) highlights the magnitude of natural variability at a range of spatial scales (from metres to tens of kilometres) in the structure of soft sediment assemblages, sediment characteristics and seastar density (Figure 6.2). Results of temporal surveys conducted at a subset of the same sites were also indicative of significant intra- and interannual variability in benthic assemblages and seastar density (chapters 3,5). Based on this evidence alone it is anticipated that the impact of the seastar will vary in space and time.

To assess the variability, and hence predictability, of the impact of the seastar on soft sediment assemblages I used experiments to examine the impact of the seastar in three sheltered bays (separated by ca. 10-35 km) immediately beyond the current range of the seastar (chapter 4). Given that the experiments were conducted at different locations and at different times, it is not surprising to see marked differences in the soft sediment assemblages among sites at both the species and

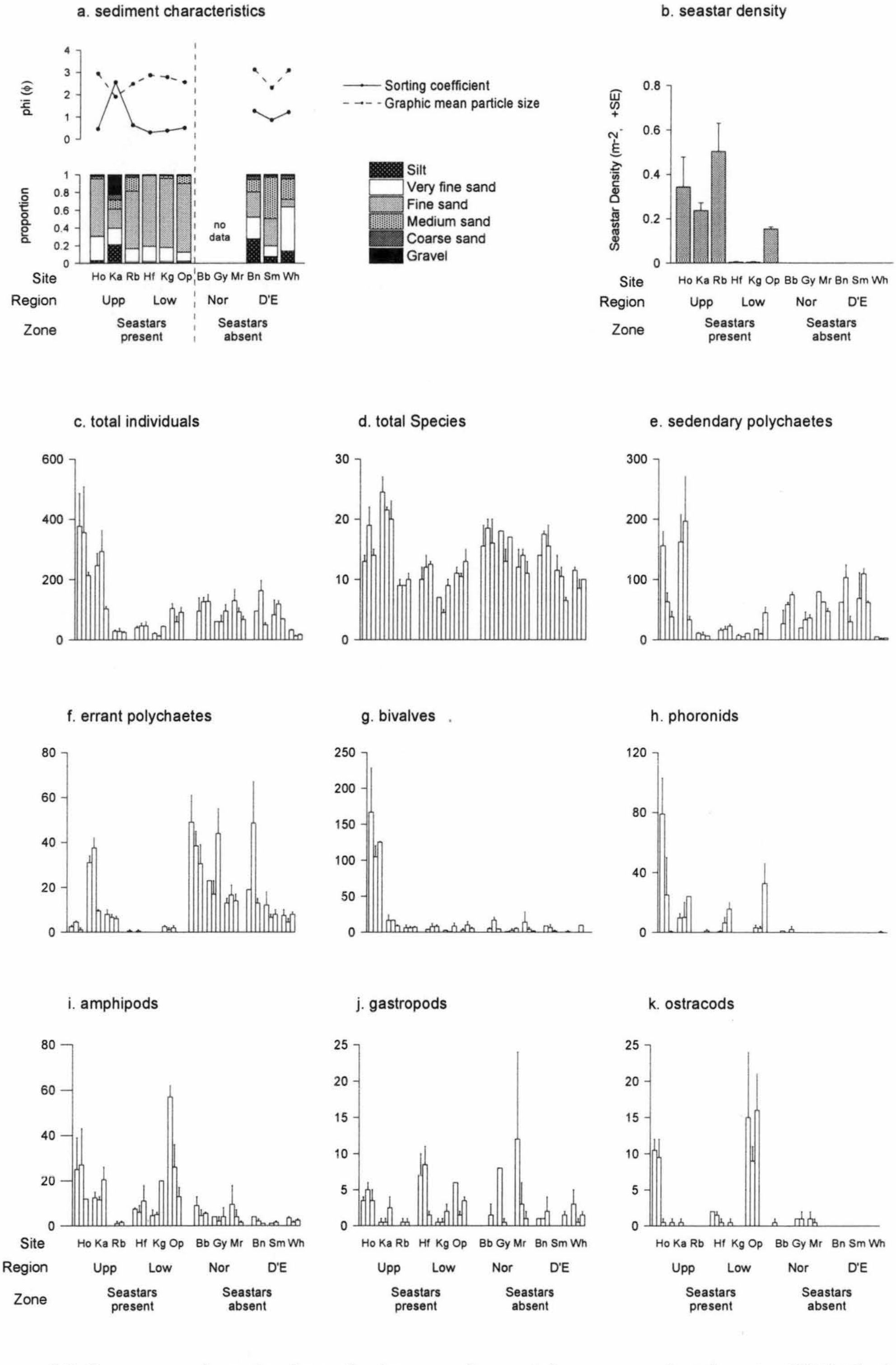

Figure 6.2 Summary of results from the large scale spatial survey undertaken in 1996 (design and abbreviations as in Figure 6.1). (a) Sediment characteristics at each site (determined from 3 sediment cores). Note there was no data available for the Norfolk Bay sites. (b) Seastar density at each site (densities are means (+ SE) determined from three 50 x 2 m strip transects). (c) Mean abundance of the total number of individuals, (d) total number of species and (e-k) the major groups. Data are the means (+ SE) of 2 replicate cores taken from each plot ($n = 3$) at each site. See figure 6.1 for site code descriptions. Figure adapted from chapter 5.

functional group level (Figure 6.3). Consequently, seastar impacts were not qualitatively identical across sites (chapter 4). Nonetheless, when potential prey taxa were separated into functional groups that also reflected their likely ecological availability to the seastar (e.g. surface *versus* deep burrowing bivalves), a consistent effect of the seastar on surface dwelling bivalves across all sites was clearly evident (Table 6.1).

	Murdunna	Saltwater River	Conningham
Surface Bivalves	S	S	*
Fulvia tenuicostata	S	S	-
Katelysia rhytiphora	S	-	-
Wallucina assimilis	NS	NS	-
Musculus impacta	-	NS	-
Mysella donaciformis	-	S	-
Deep Bivalves	NS	NS	NS
Theora spp.	NS	NS	S
Laternula rostrata	NS	-	-
Errant Polychaetes	NS	NS	NS
Simplisetia amphidonta	NS	-	-
Glycera spp	NS	-	-
Nephtys australiensis	-	NS	-
Sedentary Polychaetes	NS	NS	NS
Lysilla jennacubinae	NS	-	-
Capitellids	-	S	NS
Pectinaria sp.	-	-	NS
Crustaceans	NS	NS	NS
Amphipods	NS	S	NS
Ostracods	-	-	NS
Crabs	-	NS	-
Echinoderms	NS	NS	NS
Echinocardium cordatum	NS	NS	NS
Holothurians.	-	-	NS
Gastropods	NS	NS	NS

Table 6.1 Summary of results from experimental manipulations at Murdunna, Saltwater River and Conningham assessing the effects of seastar predation on the abundances of functional groups and common taxa. Results are from the planned comparison of interest to test for the effect of seastars i.e. cage control *versus* seastar inclusion. P-values < 0.016 are significant for the planned comparisons, indicated by S; NS = not significant (* no tests were undertaken due to a treatment by block interaction). Table adapted from chapter 4.

Bivalves are known to be a major food source of the seastar in both its introduced (Morrice 1995; Grannum et al. 1996; Lockhart & Ruiz in press{b}; chapter 2,3 & 4; G Parry pers. comm.) and native ranges (Hatanaka & Kosaka 1959; Nojima et al. 1986). Differential impacts on surface-living taxa and deeply burrowing taxa have been demonstrated for other predators in soft sediment habitats (e.g. Woodin 1974; Virnstein 1977).

While the effect of seastar predation on surface bivalves was common across all sites, the magnitude of the impact varied between sites. Seastar density at 1 per m^2 produced decreases of 92 m^{-2} (96 %), 35 m^{-2} (72 %) and 31m^{-2} (40 %) at Murdunna, Saltwater River and Conningham, respectively. This reflected the percentage of large surface bivalves (> 8mm) at each site (92 %, 67 % and 41 % respectively; Figure 6.4). Although there was a small decrease in abundance of the 2 smaller size classes (2-4 and 4-8 mm) in the presence of seastars, the change in abundance of larger bivalves was largely responsible for the overall decrease in bivalves in the presence of seastars. These results are consistent with the patterns evident in the large scale survey in which native assemblages at sites with and without seastars were compared; larger bivalves (> 8 mm) were extremely rare at sites where seastars were abundant relative to sites without seastars (Figure 6.5). However, it is unclear whether the observed patterns in the experiments and survey are a consequence of size or species selection (or both). In the experiments size and species selection can't be differentiated between because the species that were most heavily impacted at each sites were also the large (>8 mm) species of surface bivalves. However in the survey, bivalves species identified as important prey (in the small scale experiments and feeding observations) were rare in the presence of seastars irrespective of their size, which suggests that species-level selection operates. Given that laboratory and field observations has demonstrated both size and species selection for *Asterias amurensis* (Lockhart & Ritz in press{a, b}), changes in both the size and species composition may underpin variability in the magnitude of impact between sites.

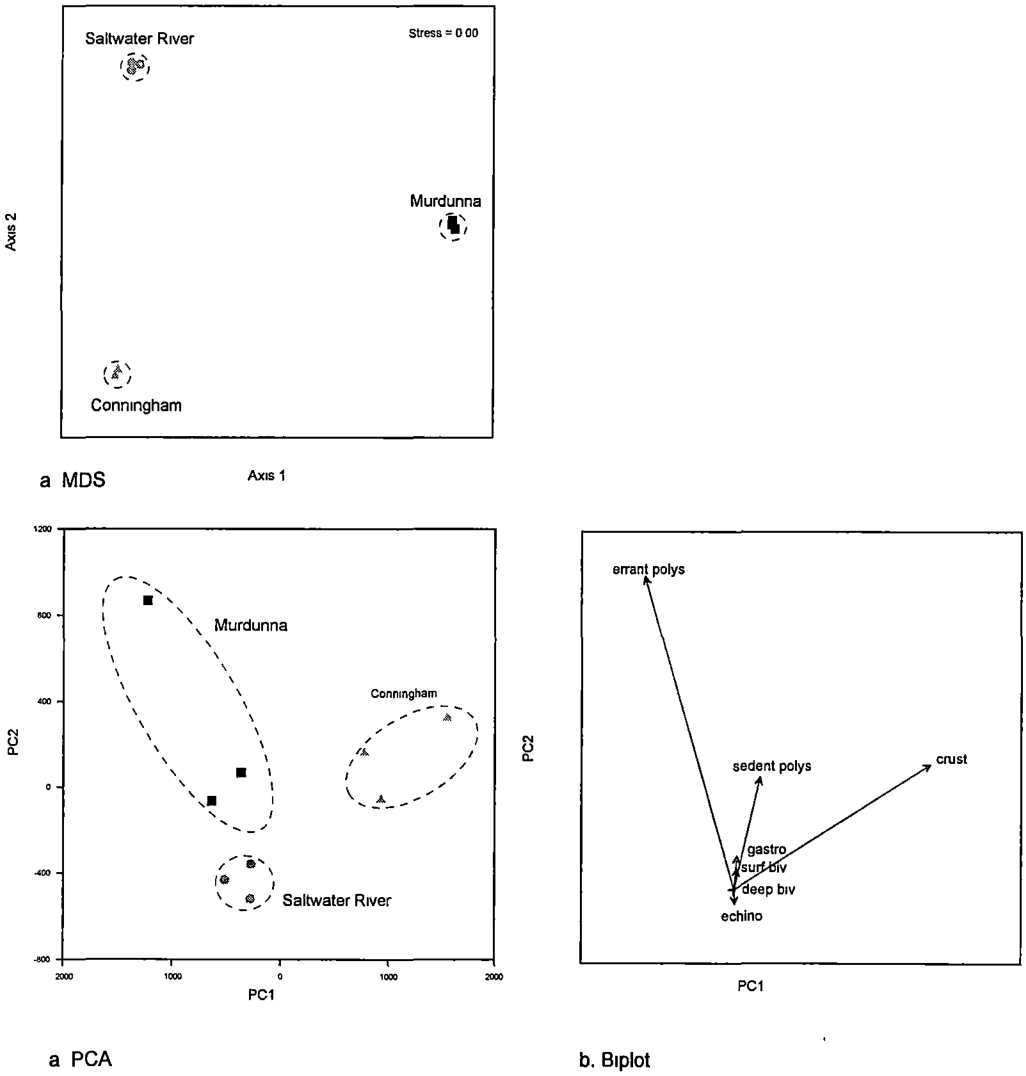

Figure 6.3 Composition of soft sediment assemblages at the three experimental sites where seastar effects were assessed. (a) MDS ordination of 3 replicate unmanipulated plots at each of three sites based the Bray Curtis matrix of 4th root data of densities of macro-benthic species and (b) PCA plot comparing functional groups across the same locations and plots reveal distinct differences in the composition of assemblages. Principal components 1 and 2 accounted for 94 % of the total variance. (c) The associated biplot identifies the groups most responsible for the patterns shown in the PCA plot. Figure adapted from chapter 4.

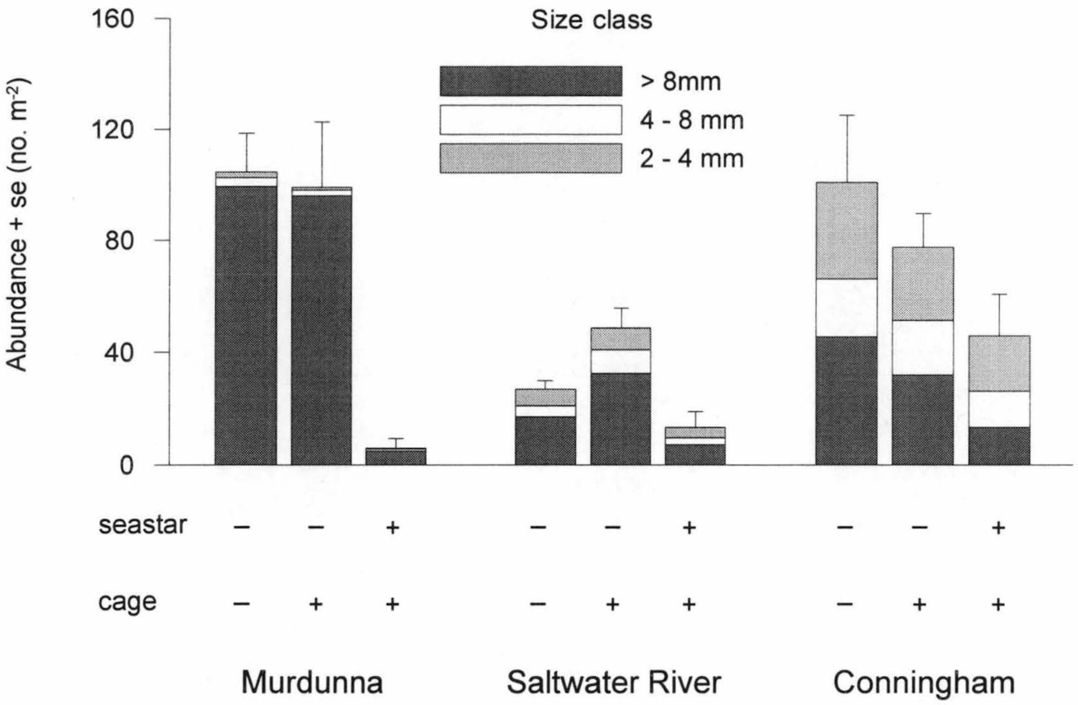

Figure 6.4 Results from experimental manipulations at Murdunna, Saltwater River and Conningham assessing the effect of seastar predation on native species, in this case surface dwelling bivalves. At each site there were 3 treatments: cage control (seastars absent); unmanipulated plot (seastars absent); and cage inclusion (single seastar added). Density is the mean per 1 m^2 (+ SE). The proportion of bivalves retained on 2, 4 and 8 mm mesh are also depicted. Figure adapted from chapter 4.

At Conningham the results indicated variability in impact at small spatial scales, i.e. among blocks separated by ca. 30 m. In contrast to other sites, epifaunal bivalves, predominately *Electroma georgina*, were common at Conningham. Reduced densities of *E. georgina* but not the other surface bivalves indicated predation by the seastar on *E. georgina* in 2 of the 3 blocks, but in one block where *E. georgina* was rare the opposite was true. I interpret this pattern to reflect both the ecological availability of prey and small scale patchiness of *E. georgina*. In patches where *E. georgina* is abundant, since it is epifaunal and directly accessible to the seastar, while other surface dwelling bivalves are infaunal, the seastar apparently preferentially consumes *E. georgina*. In patches when *E. georgina* is rare or absent, the seastar will readily consume other species of surface dwelling bivalves.

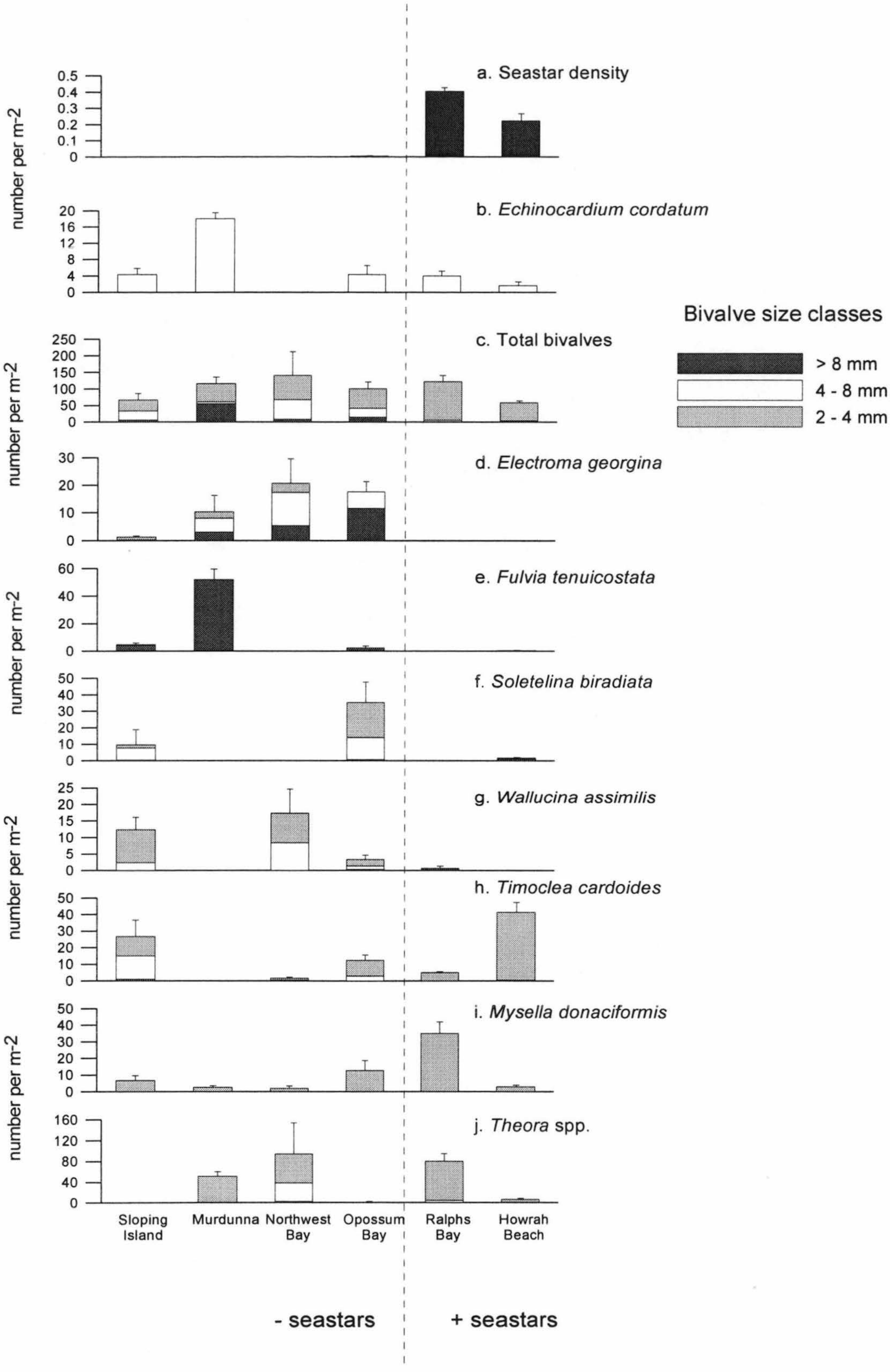

Figure 6.5 Results from the large scale survey in 1998 that used suction samples (1 m^2) to compare the abundance of bivalves and heart urchins between sites with and without seastars. Mean densities (+ SE) of (a) seastars based on 50 x 2 m strip transects (*n* = 3), (b) *Echinocardium cordatum* (heart urchin), (c) total number of bivalves and (d-j) each of the major bivalve species based on 1 m^2 benthic samples (*n* =3) at each site. The proportion of bivalves retained on 2, 4 and 8 mm mesh are also depicted.

In the nearby Derwent Estuary, observations of feeding highlight the likelihood that temporal changes in community composition also generate variability in impacts. At Opossum Bay the surface infaunal bivalves *Timoclea cardoides, Venerupis anomala* and *Fulvia 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 unpub data). Similarly, at Ralphs Bay the seastar fed predominately on bivalves after a massive recruitment event (largely attributable to *Fulvia tenuicostata*), but shifted to feed on other species (e.g. gastropods and the heart urchin *Echinocardium cordatum*) when bivalves became relatively rare (Figure 6.6).

The generalist nature of feeding in asteroids is well known (see Menge 1982), and is demonstrated clearly in that dietary composition often tracks changes in the relative availability of prey species. The results demonstrate that the exact nature of the effect of seastar predation on soft sediment assemblages is likely to be site- and time-specific depending on spatial and temporal variability of prey species at the time of arrival of the seastar at a site, and the length of time that seastar populations have been established at particular sites.

6.4 Impact on the survivorship of bivalve recruits

Despite the presence in the surface sediments of numerous remains (intact shells) of large adult bivalves (Lockhart 1995; J Ross pers. obs.), live bivalves >5 – 10 mm are now rare in the Derwent Estuary where seastars are abundant. The results of the

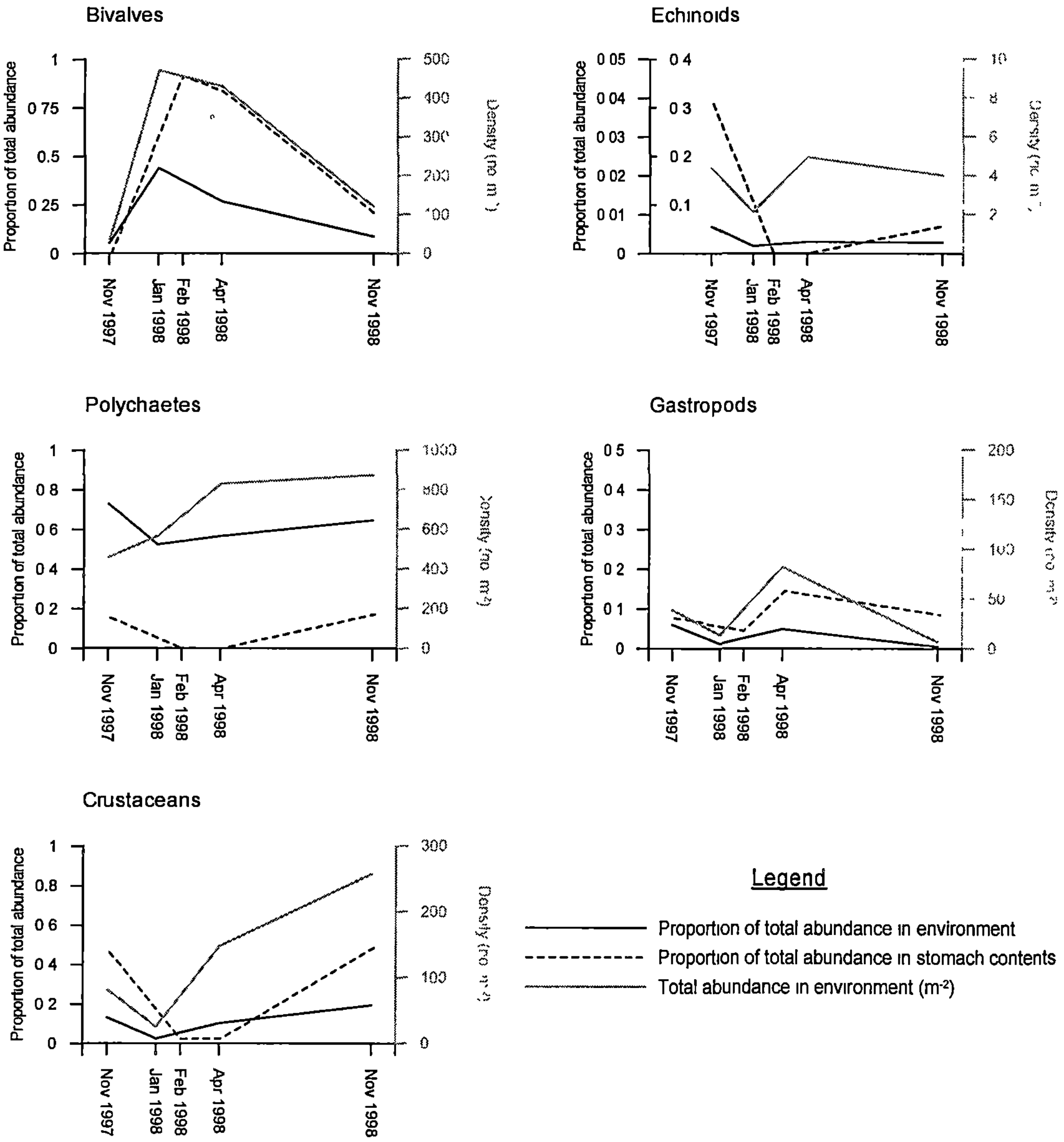

Figure 6.6 Results of surveys comparing the abundance of macrofaunal species found in the environment and seastar stomach contents. The proportion of the total abundance of the major groups of prey in seastar stomachs and in sediments, and the absolute abundance in the sediments. The Y-axis on the left depicts proportions in the diet and sediments [Note: when two scales are marked, the left-hand scale is the proportion of total abundance in the sediments]. The Y-axis on the right represents the absolute abundance in the sediments (no. m^{-2}). Densities are determined from 1 m^2 suction samples (1 m x 1 m x 0.1 m deep), with the exception of polychaetes, crustaceans and gastropods, which were extracted from core samples (0.15 diam x 0.1 m deep). Figure adapted from chapter 3.

experiments discussed above are consistent with the notion that predation by the seastar is responsible for the rarity of adult bivalves, particularly shallow infaunal and epifaunal bivalves, in the Derwent River Estuary. The high prevalence of juvenile molluscs, and particularly bivalves, in the diet of the seastar suggests that seastar predation on juveniles may be preventing the subsequent establishment and potential recovery of adult populations in the estuary. In early 1998, a massive recruitment pulse (≈ 530 per m^2) of the commercial bivalve *Fulvia tenuicostata* was recorded at Ralphs Bay, where seastars are abundant. This provided an ideal opportunity to test whether seastar predation might be limiting the survivorship of *F. tenuicostata* recruits (and potentially other species).

Using a combination of experimental and observational approaches, I detected a large impact of *Asterias amurensis* on the survivorship of *Fulvia tenuicostata* recruits (chapter 3). In a manipulative experiment, there was a ≈15-fold reduction in density of *F. tenuicostata* recruits (from 580 per m^2 to 35 per m^2) in the presence of seastars at background densities relative to control treatments without seastars (Figure 6.7a). In a feeding survey, the seastar clearly responded to the recruitment of *F. tenuicostata* in the unmanipulated area, as evidenced by a pronounced shift in diet. The bivalve was the most common prey species of the seastar following its recruitment, representing 50 - 80% of the seastar's dietary items in February and April 1998 (Figure 6.7b), before shifting to feed on other species when the bivalve became relatively rare.

Overall, these results have demonstrated that *Asterias amurensis* can have a dramatic and immediate effect on the survivorship of recruits of the commercial species *Fulvia tenuicostata*. The majority of a large settlement event (> 500 recruits m^{-2}) was readily consumed within 2-3 months of settlement. Furthermore, the feeding observations following the decline of *F. tenuicostata* indicated that seastar predation

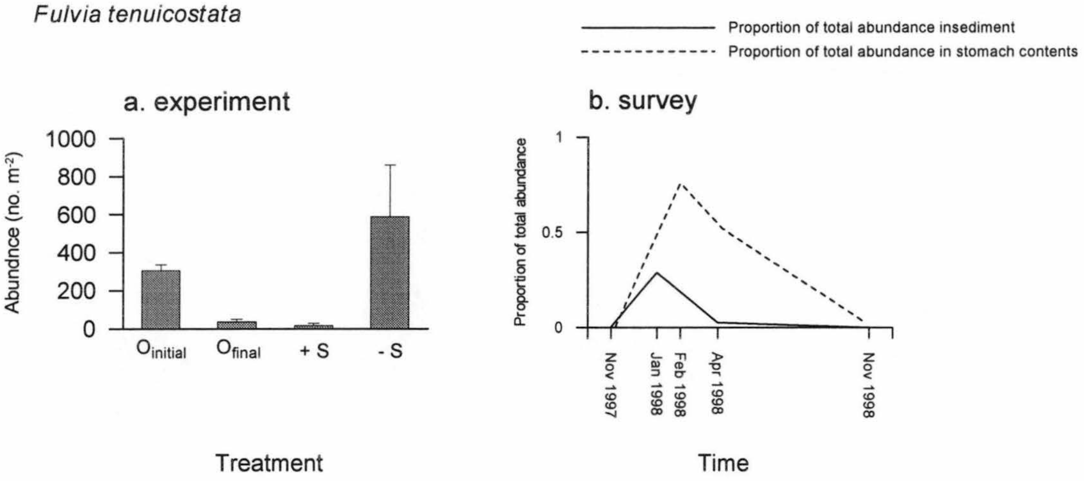

Figure 6.7 Results of the experimental manipulation and feeding observations following the recruitment of the commercial bivalve *Fulvia tenuicostata* at Ralphs Bay. (a) Density of *Fulvia tenuicostata* recruits in each of 4 treatments in a 10 week experiment. Treatments are unmanipulated plots sampled at the start of the experiment soon after the recruitment event; unmanipulated plots sampled at the end, subject to normal predation; caged inclusion sampled at the end with a single seastar added to 1 m^2 cages; caged exclusion sampled at the end, no seastars present. Density is the mean per 1 m^2 (+ SE, $n = 3$ plots). (b) Proportion of the total abundance of *F. tenuicostata* in seastar stomachs and in sediments, and the absolute abundance in the sediments. Figure adapted from chapter 3.

may be limiting the survivorship of recruits of the introduced bivalve *Corbula gibba*. Interestingly, *C. gibba* had not been previously reported from the Derwent River Estuary, but is present in high densities in the nearby D'Entrecastreaux Channel where seastars are comparatively rare. In Port Phillip Bay on mainland Australia, *C. gibba* is considered a major prey item of *A. amurensis* (G Parry pers. comm.). Thus, it is plausible that seastar predation on *C. gibba* recruits may be impeding the establishment of the bivalve in the Derwent River Estuary. The effect of seastar predation on bivalve recruits is also problematic in the mariculture industry, particularly in the collection of scallop spat, where losses of commercial spat over a settlement season may be as high as 50 %.

6.5 Interactions with other factors

Interactions between introduced species and other anthropogenic stressors may greatly influence the impact of introduced species (Ruiz et al. 1999). Estuaries and bays, which represent the most invaded habitats in coastal regions, are also often the most degraded coastal habitats. The Derwent River Estuary is no exception (Coughanowr 1997; Bennett 1999). A common generalization often touted is that disturbed habitats are more readily invaded than pristine ones, largely because of reduced competition or predation (see Elton 1958; Lodge 1993; Ruiz et al. 1999; Simberloff and Von Holle 1999). Given the degraded state of the Derwent River Estuary, a lack of native predators and/or competitors of the seastar may have played a major role in the successful establishment of the seastar in the estuary (Bennett 1999), although the idea has not been tested critically. Regardless, the seastar is clearly the most numerically dominant benthic invertebrate predator in the soft sediment assemblages of the Derwent River Estuary.

More recently, seastars have been increasingly recorded in more pristine areas outside the Derwent River Estuary in southeast Tasmania, and potential interaction with other predators and competitors appears inevitable. Ironically, potential spatial overlap and interaction with another introduced species, the European green crab, *Carcinus maenas*, is anticipated since both species are major predators of bivalves in sheltered low energy environments. It is often the case that effects of multiple species together cannot be predicted from estimates of the effect of each species alone due to complex interactions (Kareiva 1994). The question of the combined effects of several introduced species is particularly germane given the possibility that synergistic effects may lead to accelerated impacts on native ecosystems with the addition of each new species (Simberloff and Von Holle 1999). In a manipulative experiment where I examined the separate and combined impacts of *Asterias* and *Carcinus* (chapter 2), each predator had a major effect on the abundance of bivalves, reducing populations of the commercial bivalves *Fulvia tenuicostata* and *Katelysia rhytiphora*. However, when both predators were present simultaneously they consumed fewer *F. tenuicostata* than when alone (Figure 6.8). The interaction between *A. amurensis* and *C. maenas* appears to be one of resource competition, resulting in partitioning of bivalves according to size between predators; *A. amurensis* consuming the large and *C. maenas* the small bivalves. Thus, in the event of spatial overlap the effect on each predator is likely to be negative rather than facilitative in competing for a limiting resource. However, it is also predicted that the two introduced predators are likely to coexist because of resource partitioning according to size and/or different habitat preferences. *Asterias* is found predominately in the shallow to deep subtidal, whereas *Carcinus* is found predominately in the shallow subtidal and intertidal. Thus, it seems likely that the combined effect on bivalves will be greater than that due to each predator alone simply because their combined distribution covers a broader range of habitats.

6.6 Large scale patterns

Although manipulative experiments are powerful tools for identifying impacts, they are typically limited to small scales in space and time (e.g. Underwood 1996; Thrush et al. 1997; Lodge et al. 1998). Given that managers are often concerned with impacts over large spatial and temporal scales, large scale surveys are widely used as a basic tool in field assessments of environmental impacts (Osenberg & Schmitt 1996). In large scale spatial surveys I compared soft sediment assemblages at

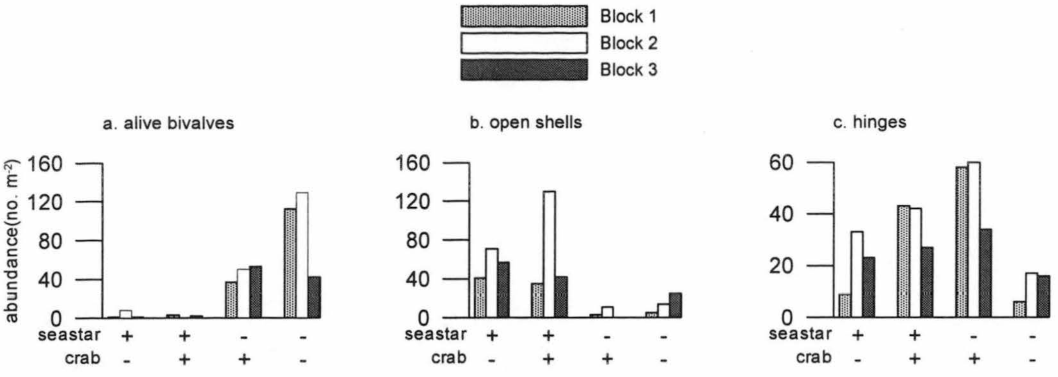

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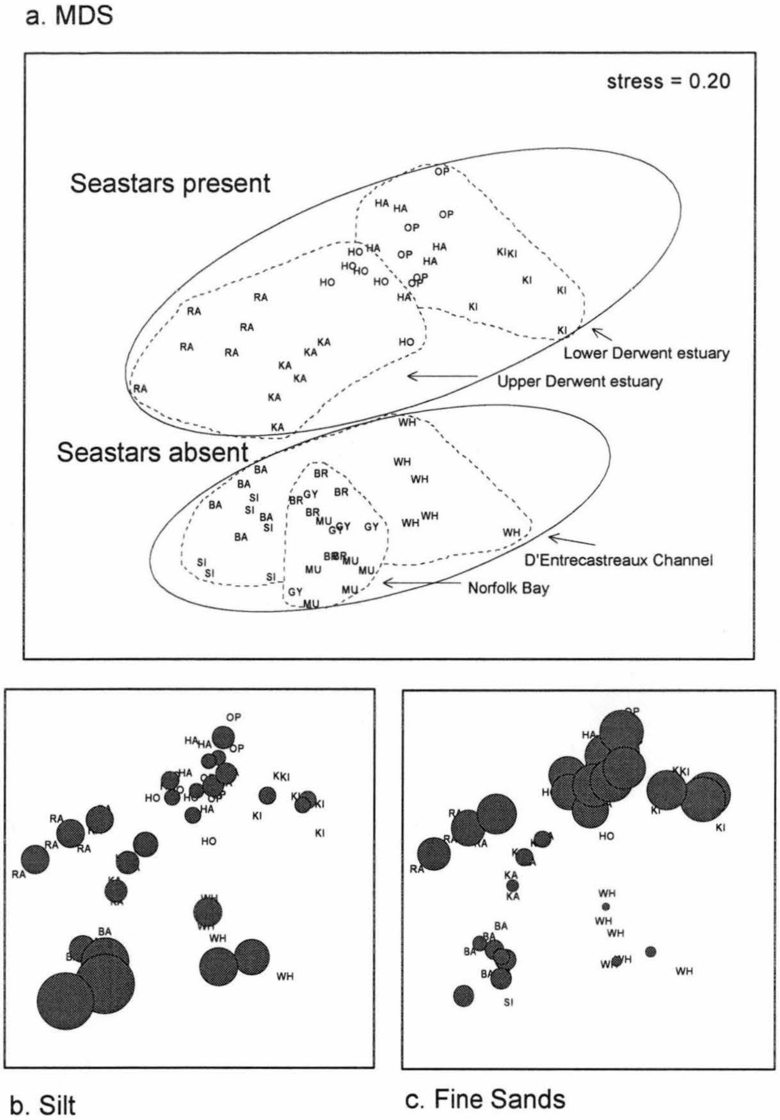
Figure 6.8 Results of experiment manipulations conducted at Murdunna that assessed the interaction and impact of *Asterias amurensis* and *Carcinus maenas* on soft sediment assemblages, in this case the commercial bivalve *Fulvia tenuicostata*. Densities of the number of (a) alive animals, (b) open shells (indicative of seastar predation) and (c) hinges (indicative of crab predation) in each treatment in each block (n = 3 blocks). Densities are totals from 1 m^2 suction samples of each plot. The four treatments include all possible combinations of presence (single animal per cage) and absence of crabs and seastars in cages. Figure adapted from chapter 2.

locations with seastars ('impact' sites) with assemblages at sites without seastars ('control' sites), and assemblages in areas with high seastar density with areas with low seastar density (chapter 5). The structure of soft sediment assemblages was highly variable at a range of spatial scales from metres to tens of kilometres (Figure 6.2). Clear differences in the composition of assemblages and abundances of major taxa were detected between areas with and without seastars and between areas with low and high seastar densities (Figure 6.9a). However, the observed differences are more likely due to differences in sediment characteristics than to impacts of the seastar (Figure 6.9b,c). While the combination of percentage of silt, fine sand, medium sand and seastar density provided the best correlation with the composition of assemblages, seastar density was the only variable that showed poor correlation with the composition of assemblages when examined on its own. Thus, seastar abundance is likely to play a minor role relative to sediment characteristics in influencing the broad patterns in the composition of assemblages that were observed.



a. MDS

b. Silt

c. Fine Sands

Figure 6.9 (a) MDS ordination based on fourth root transformed species abundance data for all core samples in the large scale survey in 1996 (design and abbreviations as in Figure 6.1). The samples corresponding to assemblages in each region and regions in the presence and absence of seastars have been outlined for clarity. Site codes are listed in figure 6.1. Bubble plot overlays of the percentage (b) fine sands and (c) silt at each site. Note there was no sediment data available for the Norfolk Bay sites. Figure adapted from chapter 5.

If I had interpreted these results on the basis of the abundance of seastars alone, I may have erroneously associated the distinct differences in assemblages inside and outside the Derwent River Estuary as related to the presence or absence of the seastar.

Because it wasn't anticipated that core samples would provide precise estimates of the abundance of larger and/or rare species (or even necessarily detect them) that may be important prey species, a second survey using much larger samples ($1m^2$) but across a more limited spatial extent was conducted. In light of the findings of feeding observations and experimental studies at smaller scales, species (bivalves and heart urchins) that were identified in feeding observations and experiments at small scales as preferred prey items were targeted. Large scale patterns of abundance and size structure were consistent with seastar effects anticipated from work at small scales for some, but not all species (Figure 6.5). For example, species that were most heavily preyed on or preferred by seastars in experiments and/or feeding observations (i.e. *Fulvia tenuicostata*, *Electroma georgina*, *Soletellina biradiata* and *Wallucina assimilis*) were abundant only at sites where seastars were absent (Figure 6.5d-g). Whereas bivalves that are rarely found in seastar stomachs (*Mysella donaciformis* and *Theora* spp.) were highly abundant at some sites irrespective of seastar abundance (Figure 6.5i,j). Two species that I did expect to be correlated with the presence of seastars based on known feeding preferences were the heart urchin *Echinocardium cordatum* and the bivalve *Timoclea cardoides*, but these two were abundant at sites with and without seastars at high densities (Figure 6.5b,h). For *E. cordatum* this may be because it has a depth refuge from seastar predation due to its ability to remain deeply buried (up to 15 cm: Buchanan 1966). While the pattern of abundance for *T. cardoides* was not indicative of a seastar effect, differences in the size structure were suggestive of a seastar effect, as it was noticeably smaller at sites were seastars were present than at sites where they were absent (see chapter 5 - Figure 5.9).

6.5 Multiple methods of impact assessment

There is no doubt that large scale monitoring programs can provide strong evidence about the presence or absence of impacts. However, when there are no pre-impact data, as is often the case with introduced species, inferences about potential cause-effect relationships are only correlative and may be based solely on spatial differences between ‘impact’ and ‘control’ locations. In this case it is impossible to determine whether impact sites have not always been different, because there is no evidence that any change has occurred (Keough & Mapstone 1995). While this highlights the importance of identifying and accounting for environmental factors that may generate spatial variability when choosing control sites (Glasby 1997; Keough & Mapstone 1997; Glasby & Underwood 1998), the results of the initial large scale survey demonstrated the difficulty in selecting appropriate control locations. On the other hand, while small scale experiments are extremely powerful at assessing cause-effect relationships it cannot be assumed that results measured at small scales in space and time necessarily ‘scale up’.

In assessing the impact of an introduced species with no pre-impact data, the results of this study highlighted the utility of employing a ‘weight of evidence’ approach from multiple lines of evidence. The combination of experimental and feeding results proved crucial in identifying key ecological variables most likely to be affected by seastars. This assisted in both the design, and interpretation of patterns observed in the large scale surveys which were ultimately consistent with impacts on some species but not others.

6.6 Indirect effects

In coastal and estuarine systems bivalves are important components of community structure and a major functional component as filter feeders, influencing the turnover of nutrients and coupling of the benthos and water column (Dame 1996). In Tasmania, thick shell layers close to the sediment surface over large areas of the Derwent River Estuary indicate that large bivalves were recently common and likely to have been important components of community structure and ecosystem function. The results of this study support the notion that the reported decline in large adult bivalves since the introduction of the seastar (L. Turner pers. comm.) is attributable to seastar predation. Thus, reductions in bivalve populations by *Asterias amurensis* in the Derwent River Estuary may have had secondary biotic and abiotic effects. Grosholz and Ruiz (1995) have speculated that *Carcinus maenas*, by reducing the abundance of *Nutricola* (as *Transennella*) spp. (bivalves) in western North America, may indirectly cause a reduction in filtration rates, influencing the turnover of nutrients and altering predator-prey populations.

6.6 Conclusions and implications for management

I conclude that there is now strong evidence that predation by the seastar is responsible for the decline and subsequent rarity of bivalve species that live just below or on the sediment surface in the Derwent River Estuary. Anticipated impacts on native assemblages, wild fisheries and mariculture operations in areas outside the Derwent River Estuary is of immediate management concern. Recent modelling of *Asterias* larval dispersal patterns indicates that the large majority of larvae produced in the estuary are likely to be advected from it (Morris & Johnson in prep). I predict that should the seastar attain high densities in areas outside the estuary that have occurred in the Derwent River Estuary, there are likely to large direct effects on native assemblages, particularly on large bivalves that live just under or on the sediment surface. Furthermore, as the spatial overlap with the introduced green crab *Carcinus maenas* appears imminent as their respective ranges expand, impacts on bivalve populations may be even greater. This is a particular concern to the small but growing number of commercial operations harvesting wild populations of the relatively large bivalves that live near the sediment surface such as *Fulvia tenuicostata*, *Katelysia* spp., *Venerupis* spp., *Bassina* spp., *Mactra* spp. and *Spisula* spp. Given the seastars' ability to exploit a range of other food resources and the importance of bivalves as a functional component of native systems, wider population, community and ecosystem level effects might also be expected. Overall, the important consequences of *Asterias* in the Derwent River Estuary and the anticipated effects in areas outside the estuary warrant management efforts to control the spread and impact of this introduced predator.

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