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Predation on the exotic starfish *Asterias amurensis* by the native starfish *Coscinasterias muricata*.

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Executive Summary

Asterias amurensis is a starfish native to the northern Pacific that was introduced into Port Phillip Bay in 1995. While it is widely viewed as one of the most serious invasive marine pests in Australia, there are few methods available to control new or established populations.

This study was undertaken to determine if predation by the native starfish *Coscinasterias muricata* could be used to augment diver collections to eliminate any new *Asterias* infestations. This technique, recently termed “augmentative biocontrol”, uses native species to increase the mortality rate of an exotic, so that eradication becomes more likely.

This study involved laboratory and field-based components. Laboratory-based feeding trials measured the rate *Coscinasterias* consumed *Asterias* in the presence and absence of alternative mussel prey. During these trials, the effectiveness of *Asterias* escape behaviour was recorded using time-lapse cameras. Small *Asteria*s were usually pinned and quickly eaten, but larger *Asterias* wrestled with *Coscinasterias* for up to six hours before they were eaten or escaped. A few were partially eaten after they autolysed one or more arms.

Field studies involved analysis of extensive dredge surveys of the abundance of both *Asterias* and *Coscinasterias* in Port Phillip Bay collected between 1999 and 2003. In the bay, *Coscinasterias* is mostly found in water shallower than 15 m, while *Asterias* is mostly found in water deeper than 15 m. The relative density of *Asterias* to *Coscinasterias* increased with depth from 1.2 at 5-10 m, to 11.3 at 11-14 m, to 20 at 15 m, and beyond 16 m the ratio increased exponentially beyond 100. In the laboratory, *Coscinasterias* fed on *Asterias* at the rate of ~50/year, so if they fed at a similar rate in the field, they would be expected to exert significant control over *Asterias* populations at all depths less than 15 m.

This study suggests that *Coscinasterias* may be very helpful in eliminating newly-established populations of *Asterias*. But the efficacy of deploying large numbers of *Coscinasterias* on a new *Asterias* infestation would be difficult to evaluate. Consequently, it is recommended that a field trial is undertaken at a location where *Asterias* is already abundant (e.g. near a pier in Port Phillip Bay), and where the effectiveness of increasing the *Coscinasterias* population could be evaluated in the field

Contents

Index of figures

Index of tables

1. Introduction

Asterias amurensis is a starfish native to the northern Pacific that was introduced into Port Phillip Bay in 1995. It is widely viewed as the one of the most serious invasive marine pests in Australia (Hayes et al. 2005).

After its introduction the population of *Asterias* in Port Phillip Bay grew rapidly, and by 2000 its population peaked at 165 million (Parry et al. 2004), when its biomass equalled 56% of the total demersal fish biomass in central region of the bay (Parry and Hirst, 2015). In this region competition for food caused significant reductions in the biomass of three common fish species, whose diets overlapped with those of *Asterias* (Parry and Hirst, 2015)

Since its establishment in Port Phillip Bay further small populations have established at Andersons Inlet, San Remo and Tidal River. Whether these populations have been spread by people moving adults, or by larval dispersal is uncertain. However, *Asterias* larvae have been recorded offshore from Tidal River, and modelling suggests larvae from Port Phillip Bay could travel this far during their development (Hirst et al. 2013).

The populations at Andersons Inlet and San Remo appear to have been eradicated by diver removal, and no *Asterias* have been detected in Tidal River in the past 12 months (Brett Mitchell, Area Chief Ranger, pers. comm.). Eradication of newly established marine populations is difficult, as there is a paucity of suitable techniques.

This study was undertaken to determine if predation by the native starfish *Coscinasterias muricata* could be used to augment diver collections to eliminate the last few individuals of *Asterias* and make successful eradication more likely. This technique, recently termed augmentative biocontrol (Atlah et al. 2013), involves the use of native species to increase the mortality rate of an exotic so that eradication becomes more likely. This approach recognises that some damage to native communities is likely, but this damage will be temporary, and is well-justified if it leads to eradication of the exotic, as permanent ecological changes will be avoided.

Coscinasterias was considered the most suitable candidate for augmentative biocontrol as previous studies had shown that *Coscinasterias* readily eats *Asterias* in small laboratory tanks where no alternative prey were available (Botsios 2001). Botsios (2001) screened 11 species of potential *Asterias* predators, and found five species that consumed *Asterias* (Appendix 1). *Coscinasterias* consumed *Asterias* at a higher rate than other species trialled, except for hungry six-spined leatherjackets (Appendix 1). In addition, *Asterias* is usually attacked within minutes when placed adjacent to an undisturbed *Coscinasterias,* in field experiments (Parry pers. obs.).

This study had laboratory-based and field-based components. In the laboratory, *Coscinasterias* were held with *Asterias* in large corner-less tanks to determine their rate of consumption of small and large *Asterias.* Rates of consumption were measured when alternative mussel prey were and were not available, and the effectiveness of *Asterias* escape behaviour was recorded using time-lapse cameras.

This study also analysed rates of arm loss of *Asterias* throughout Port Phillip Bay, based on extensive field survey data from 1999-2003 (Parry et al. 2004). Correlations between rates of arm loss in *Asterias* and the densities of *Coscinasterias* and the spider crab *Leptomithrax gaimardi* in Port Phillip Bay were examined. Ramsay et al. (2000) found a correlation between the density of the starfish predator *Luidia ciliaris* and the proportion of arm loss in *Asterias rubens* and *Marthasterias glacialis*. While Ling and Johnson (2013) showed sublethal damage to *Asterias* due to spider crabs in Tasmania.

The relative densities of *Asterias* and *Coscinasterias* in different depth zones of Port Phillip Bay were also measured. These measurements enabled an assessment of the regions where *Coscinasterias* densities were high enough to appreciably reduce *Asterias* populations, if they consumed *Asterias* in the field at rates similar to those measured in the laboratory.

2. Methods

2.1 Laboratory studies

Feeding trials were conducted between 9 April 2015 and 7 June 2015 in flow-through tanks in the Victorian Marine Science Consortium (VMSC) aquarium. During trials, sea temperature was 15.1-17.5 ^{o}C and day length was controlled: daylight was from 6.00 am till 5.30 pm (E.S.T.) each day.

Behaviour of *Coscinasterias muricata* and *Asterias amurensis* was recorded in two identical 3 m x 1 m x 0.6 m deep tanks, with semi-circular ends (Figure 2.1). This design avoided corners, in which prey could be trapped. In field observations, Dayton et al. (1977) noted that most prey of the asteroid *Meyenaster,* appeared to be captured when they became trapped in crevices so they could not flee. Small rectangular tanks, as used by Botsios (2001), are likely to reduce the effectiveness of escape behaviours, especially when fleeing is the primary response.

A total of 20 trials were undertaken, each lasting four days. In each trial a *Coscinasterias* (24-35 cm diameter), a small (9-12 cm diameter) *Asterias*, a large *Asterias* (13-25 cm diameter) and five mussels (lengths 8.5-10.5 cm) were added to each tank. Two trials were conducted simultaneously, and in one tank mussels were added to the tank initially and removed after two days, while in the other, mussels were not added until the last two days of the trial. Any starfish eaten during the trials was replaced after two days, when mussels were added or removed.

Asterias used in the trials were collected from Williamstown and St Kilda, while *Coscinasterias* were collected from Portarlington and St Leonards. Both species were kept in separate large seawater holding tanks at the VMSC and fed mussels.

Handling of all starfish was minimised. Starfish were removed from holding tanks quickly, to avoid damaging their tube feet. They were transported between holding and experimental tanks on wet towels to prevent their tube feet from re-attaching firmly and being damaged subsequently.

The tanks were inspected daily and the number of dead mussels and starfish recorded. A Brinno time-lapse camera (Model TLC 200 Green), located above each tank, recorded the location of each starfish every minute for the four days, except at night.

The time-lapse videos were examined and the activity of all three predators recorded during daylight. For each starfish periods of inactivity and activity were recorded. Attacks between species were recorded and classified at chasing, wrestling and pinning. Pinning occurred when *Asterias* was held out of sight beneath *Coscinasterias*.

To compare the effectiveness of *Coscinasterias* in attacks on *Asterias* of different sizes, the ratio of their diameters was calculated, and attack durations and attack successes compared to this ratio.

2.2 Field studies

The distributions of *Asterias, Coscinasterias,* and *Leptomithrax* in Port Phillip Bay were surveyed using a calibrated scallop dredge in 1999, 2000, 2001 and 2003 (Parry et al. 2004). Between 63 and 176 (1 min) tows of the scallop dredge were undertaken annually throughout the bay. The efficiency of the dredge was estimated by comparing catch rates of *Asterias* with estimates of the density of *Asterias* obtained in the same area using a towed underwater video. Parry et al. (2004) should be consulted for details of the field surveys.

The distributions of *Asterias, Coscinasterias* and *Leptomithrax* in Port Phillip Bay were compared as both *Coscinasterias* and *Leptomithrax* are potential predators of *Asterias*.

The proportion of *Asterias* missing or regenerating an arm or arms was recorded at each site. Extensive field data on rates of arm loss of *Asterias* were analysed to detect patterns in the bay between 1999-2003. A GLM was used to examine factors potentially correlated with rates of arm loss. The factors examined were: year (1999, 2000, 2001, 2003), depth, the population densities of *Asterias*, *Coscinasterias* and *Leptomithrax gaimardii*, and the proportion of the *Asterias* population that was less than 11 cm in diameter. As *Leptomithrax* often occurs in dense aggregations the density of this species was log transformed prior to analysis.

Changes in the population density of *Asterias* and *Coscinasterias* with depth, and ratio of their densities with depth were calculated to better estimate the degree to which *Coscinasterias* may control the abundance of *Asterias* at different depths.

Figure 2.1 One of two experimental tanks used in the feeding trials, viewed through the lens of the time-lapse camera located above it. The tank is 3 m long × 1 m wide and approximately 0.6 m deep.

3. Results

3.1 Food preference of *Coscinasterias*

Coscinasterias ate a total of 14.6 *Asterias* (9.6 small*,* 5 large) and 14.5 mussels during the 20 four-day laboratory feeding trials (Table 1.1, Appendix 1), an average rate of consumption of ~0.2 *Asterias*/day. The numbers of *Asterias* eaten per trial was too low for statistical analysis, but several trends are suggested.

More *Asterias* and mussels were eaten during the first two days of the trials than during the second two days (8 cf 6.6 *Asterias*, 9 cf. 5.5 mussels, Table 3.1). More *Asterias* were eaten when mussels were not provided as an alternative prey (9 cf 5.6, Table 3.1). When mussels were available more mussels were eaten than *Asterias* (14.5 mussels cf. 5.6 *Asterias*, Table 3.2). More small *Asterias* were eaten than large *Asterias* (9.6 cf. 5, Table 3.1).

Table 3.1 . Total number of small and large *Asterias* and mussels eaten by *Coscinasterias* during 20 four-day trials. The numbers of *Asterias* eaten during the first two days, with and without mussels, and during the last two days, with and without mussels, are shown (0.2 *Asterias*= one arm eaten).

Prey	Days 1 & 2		Days 3 & 4		Total
	-Mussels	+ Mussels	-Mussels	+ Mussels	
Small *Asterias*	3.2	1.4	3	2	9.6
Large *Asterias*	2.4	1	0.4	1.2	5
Mussels	-	9	-	5.5	14.5

Table 3.2. Total number of small and large *Asterias* and mussels eaten by *Coscinasterias* during 10 four-day trials in which mussels were an alternative prey either on days 1 & 2 of the trial or days 3 & 4 of the trial (from Table 1.1).

Prey	Days 1 & 2	Days 3 & 4	Total
Small *Asterias*	1.4	2	3.4
Large *Asterias*	1	1.2	2.2
Mussels	9	5.5	14.5

3.2 Escape behaviour of *Asterias*

A total of 22 attacks were observed on time-lapse photos during daylight. Six of the 14.4 fatal attacks on *Asterias* occurred at night where attacks could not be observed. Attacks lasted between 1 minute and nearly six hours. Extended attacks consisted mostly of wrestling. The longest attack (5.8 h), between a 26 cm diameter *Coscinasterias* and a 16 cm diameter *Asterias*, resulted in the loss of two arms, and the escape of a 3-armed *Asterias*. The second longest attack, between a 31 cm diameter *Coscinasterias* and a 15 cm diameter *Asterias*, lasted 4.8 h and the *Asterias* escaped, apparently unharmed.

The success rate of *Coscinasterias* depended on the relative size of the predator and prey. *Asterias* less than 0.6× the diameter of *Coscinasterias* were usually pinned quickly and eaten completely. While *Asterias* larger than ~0.6× the diameter of the attacking *Coscinasterias* often escaped unharmed, or escaped after autolysing an arm, which *Coscinasterias* then ate (Figure 3.1).

Small *Asterias* seldom escaped from *Coscinasterias* once wrestling commenced. There were three occasions when small *Asterias* were found in tanks after autolysing one or two arms; one occurred at night; another was attacked and pinned for 67 min before nightfall, but next morning was only missing one arm; and in the other the *Asterias* autolysed an arm, escaped for <3 min and was then recaptured, pinned and eaten. Two large *Asterias* autolysed arms; one of these autolysed two arms after wrestling *Coscinasterias* for nearly six hours; while the other was repeatedly attacked over four days and progressively autolysed its arms until all that remained were two disarticulated arms.

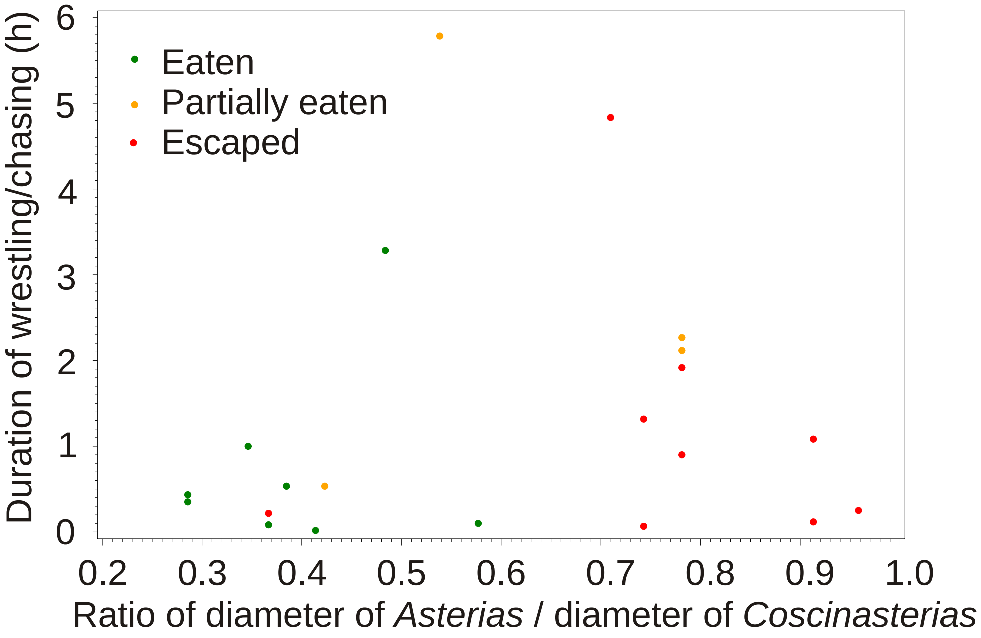

Figure 3.1. Duration and success of attacks of *Coscinasterias* on *Asterias* plotted against the ratio of their diameters. Attacks that resulted in *Asterias* being eaten, partially eaten or escaping are shown.

Both species frequently responded to the touch of the other species by changing direction, but on other occasions there was no obvious change in behaviour when they touched. Sometimes, after touching each other as they circled around the tank, they would avoid further contact, apparently as they could sense the proximity of the other starfish. On three occasions an *Asterias* attacked a much larger *Coscinasterias* (Appendix 1); the longest such attack lasted 18 min and resulted in a 28 cm diameter *Coscinasterias* fleeing an 18 cm diameter *Asterias*.

3.3 Densities of *Asterias, Coscinasterias* in Port Phillip Bay

3.3.1 Distribution of *Asterias, Coscinasterias* and *Leptomithrax*

The distribution of *Asterias amurensis, Coscinasterias muricata* and *Leptomithrax gaimardi* (giant spider crab) in Port Phillip Bay differed. *Asterias* was mostly found in depths greater than 15 m (Figure 3.2), *Coscinasterias* was mostly found at depths less than 15 m (Figure 3.3), while *Leptomithrax* was found mostly in the southern half of the bay (Figures 3.4).

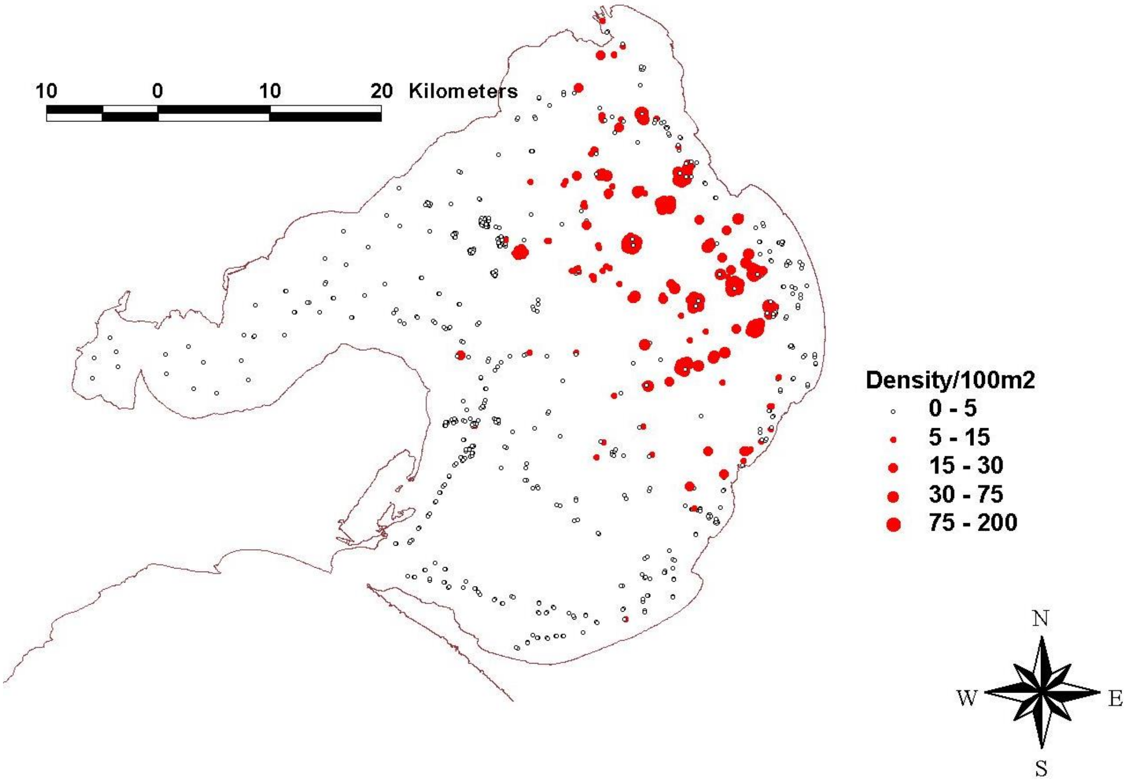

Figure 3.2 Distribution of *Asterias* in Port Phillip Bay, 1999-2003, from Parry (2004).

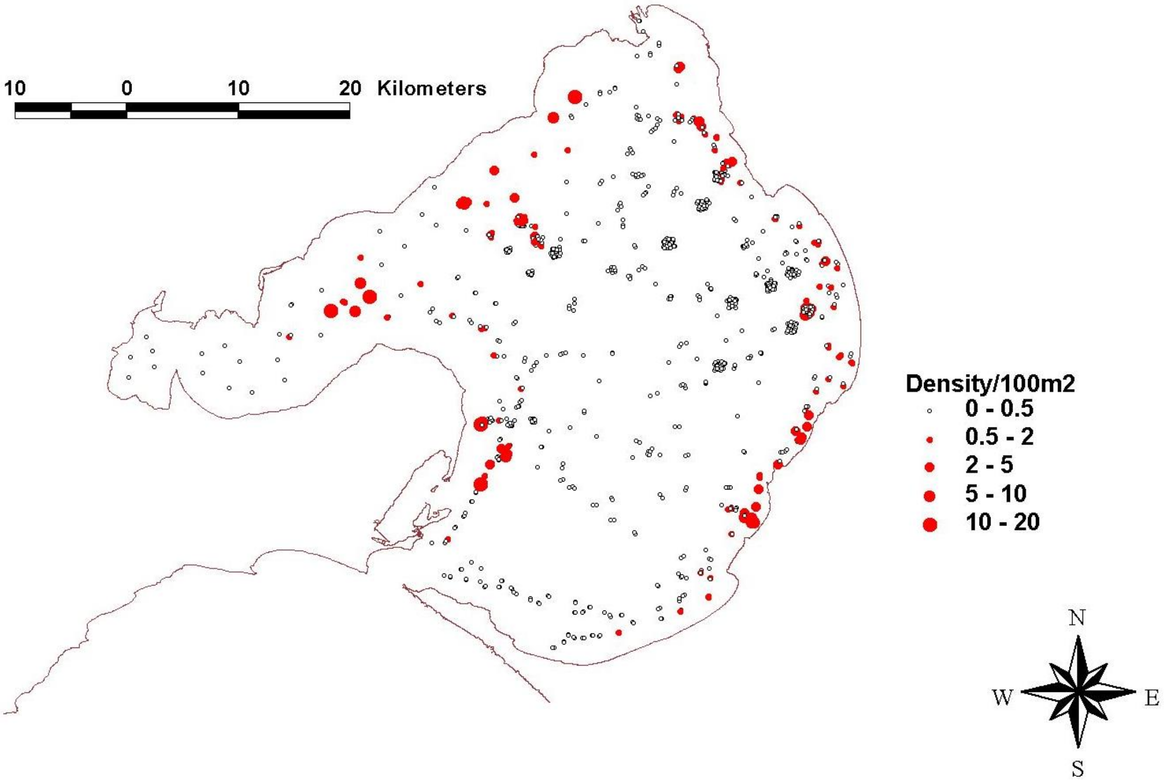

Figure 3.3 Distribution of *Coscinasterias* in Port Phillip Bay, 1999-2003, from Parry (2004).

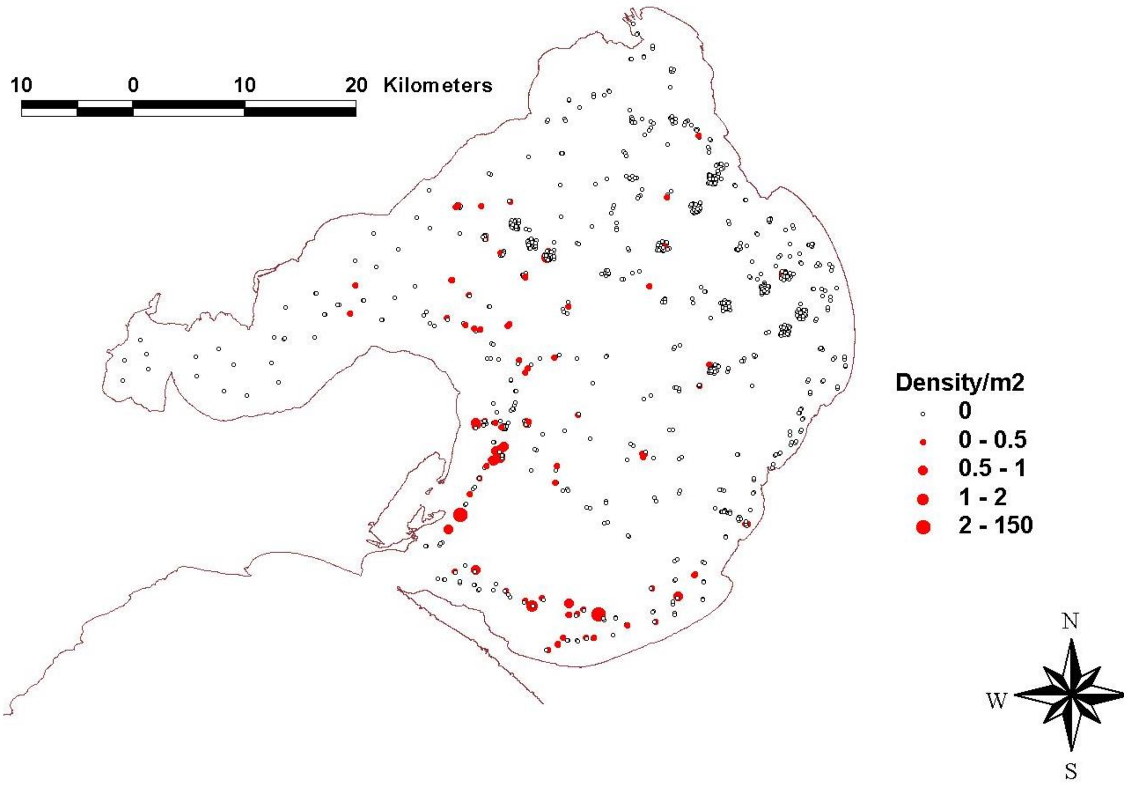

Figure 3.4 Distribution of *Leptomithrax* in Port Phillip Bay, 1999-2003, from Parry (2004).

3.3.2 Arm damage of *Asterias* in Port Phillip Bay

The proportion of the *Asterias* population missing or regenerating arms varied between regions and years from 3.2% to 13.8% (Table 3.3). The GLM indicated that rates of arm loss differed between years and were correlated with depth, the density of *Asterias* and the proportion of *Asterias* >11 cm in diameter, but there was no correlation with the density of *Coscinasterias* or *Leptomithrax* (Table 3.4). Rates of arm loss increased with depth (Figure 3.5a), were greater at lower densities of *Asterias* (Figure 3.5b), and increased with the proportion of *Asterias* larger than 11 cm (Figure 3.5c).

The density of *Coscinasterias* was highest in depths less than 15 m, while the density of *Asterias* was highest in depths greater than 15 m (Figure 3.6a). Consequently, the ratio of *Asterias* to *Coscinasterias* was low at depths less than 15 m, but it increased sharply above 15 m (Figure 3.6b). The mean ratio of densities of *Asterias/Coscinasterias* was 1.2 at depths of 5-10 m, 11.3 at depths of 11-14 m, but it increased to 20 at 15 m, and to more than 100 at greater depths (Figure 3.6b, Table 3.5). Annual rates of consumption of *Asterias* per *Coscinasterias*, if starfish feed at the same rates in the laboratory and the field, are shown in Table 3.6.

Table 3.3 Depth-related changes in Port Phillip Bay for different years for A. % *Asterias* arm loss, B. % *Asterias* with a diameter >11 cm, and C. Numbers of *Asterias* upon which estimates in A and B are based.

A.

Depth	1999	2000	2001	2003
< 12 m	3.2	11.5	16.5	7.9
12-15 m	5.8	7.8	13.3	10.1
15-20 m	7.3	8.2	11.1	9.6
>20 m	13.8	13.2	13.5	11.2

B.

Depth	1999	2000	2001	2003
< 12 m	29	12	36	59
12-15 m	58	17	34	57
15-20 m	82	38	53	62
>20 m	93	44	72	75

C.

Depth	1999	2000	2001	2003
< 12 m	31	591	297	216
12-15 m	1043	5265	1327	934
15-20 m	10338	17404	3720	1805
>20 m	927	1107	526	313

Table 3.4 GLM table showing significance levels for different factors influencing % arm loss in *Asterias*.

Source	DF	SS	Mean Square	F Value	Pr > F
Year	3	178421.8574	59473.9525	21.66	<.0001
Depth	1	14332.9332	14332.9332	5.22	0.0226
Density *Asterias*/100m^2	1	115862.0921	115862.0921	42.20	<.0001
Density *Coscinasterias*/100m^2	1	13.2325	13.2325	0.00	0.9447
Log(Density *Leptomithrax*/100m^2)	1	1031.0542	1031.0542	0.38	0.5402
% *Asterias* > 11 cm diameter	1	37322.5284	37322.5284	13.59	0.0002

Table 3.5 Ratios of densities of *Asterias* to *Coscinasterias* in different depth zones of Port Phillip Bay

Density *Asterias/Coscinasterias*				
5-10 m	11-14 m	15 m	16 m	17 m
1.2	11.3	20	95	173

Table 3.6 Estimated annual rate of consumption of *Asterias* per *Coscinasterias* based on rates of consumption observed in the laboratory.

	Consumption rate of *Asterias* per *Coscinasterias*	
	per 40 days	per annum
Alternative prey available	5.6	51.1
Only *Asterias* prey available	9.0	82.1

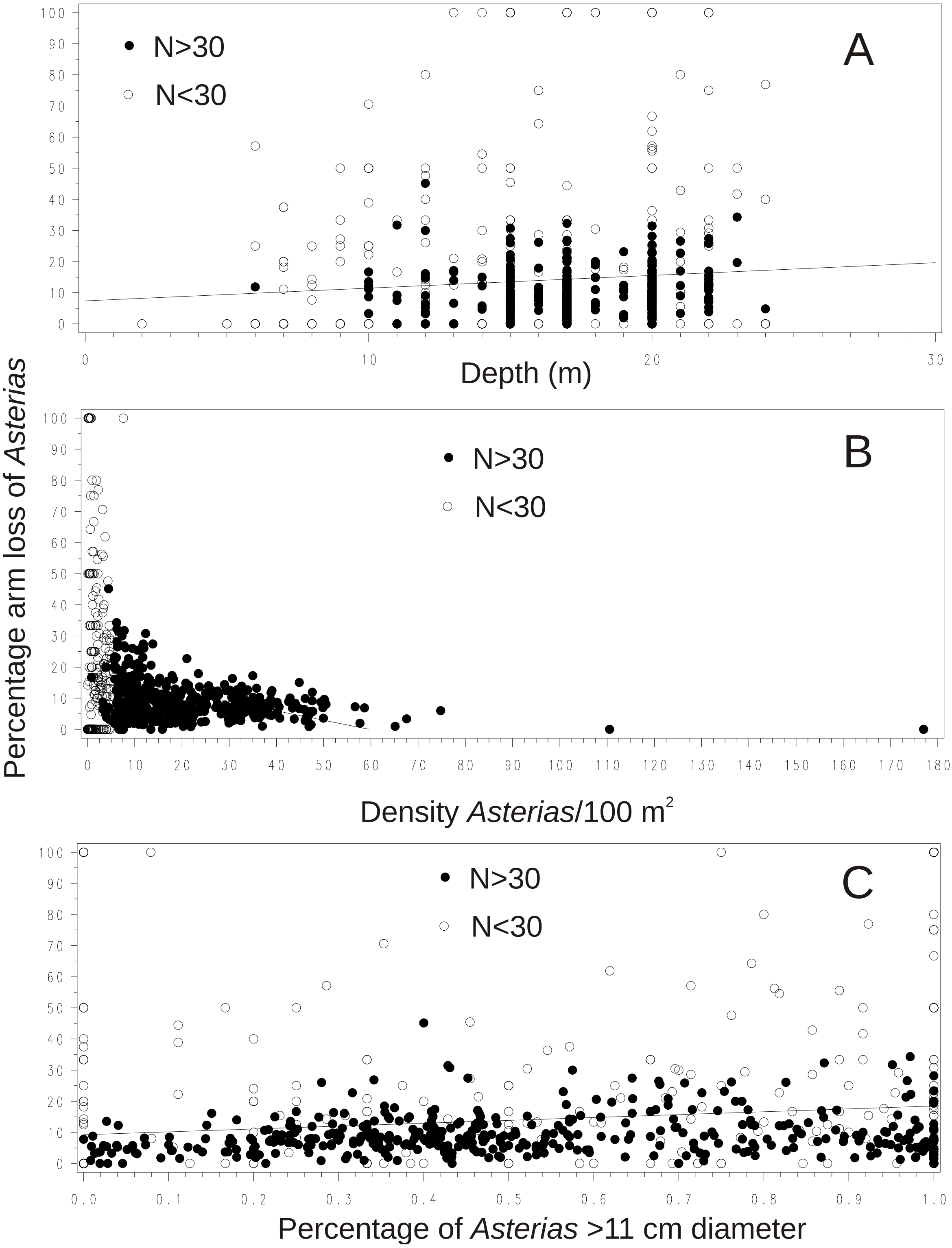

Figure 3.5. Correlations between % arm loss of *Asterias* and A. depth, B. the density of *Asterias,* and C. the % of *Asterias* >11 cm in diameter. N= the number of *Asterias* upon which the % Arm loss was based.

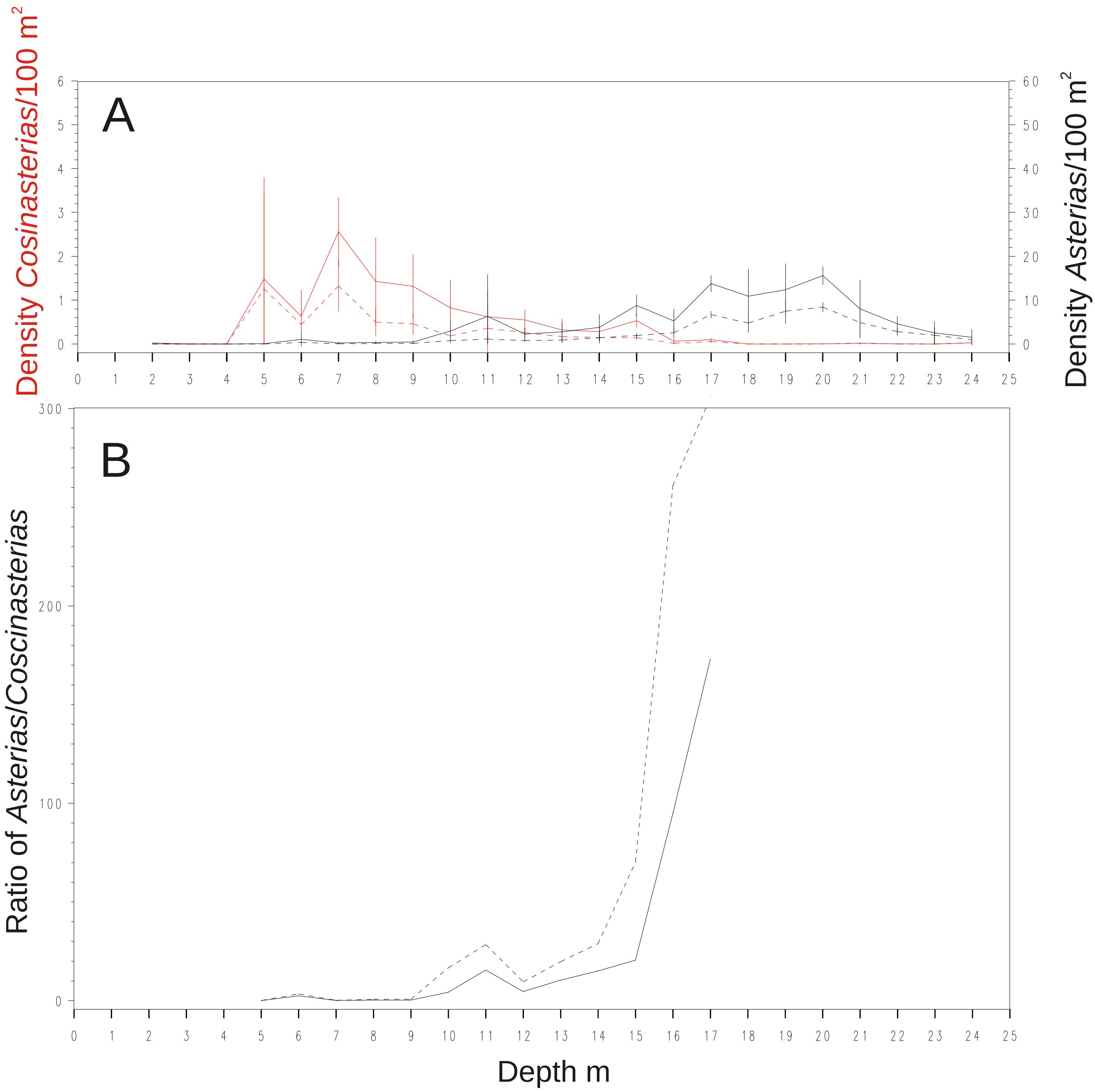

Figure 3.6 A. Change in densities of starfish/100m^2 with depth in Port Phillip Bay: *Coscinasterias* (red, solid line), *Coscinasterias*>24 cm diameter (red, broken line), *Asterias* (black, solid line), *Asterias*>11 cm diameter (black broken line). **B.** Change in ratio of *Asterias/Coscinasterias* with depth (Solid line) and *Asterias/Coscinasterias* >25cm diameter (broken line).

4. Discussion

The effectiveness of predatory control on a prey population depends on the rate of predation by individual predators and the size of the predator population. Whether a predator will eliminate a newly-established prey population, or effectively control a well-established population, will depend upon (1) the food preferences of the predator and the availability of alternative prey, (2) the effectiveness of prey escape behaviours, and (3) the size of the predator population relative to the prey population. Each of these factors is considered below.

4.1 Food preferences of *Coscinasterias*

In South Australia *in situ* observations of *Coscinasterias* showed they mostly fed on bivalves (Keough and Butler 1979), and on reefs in Port Phillip Bay they mostly fed on mussels (Day et al. 1995). Keough and Butler (1979) recorded one instance of cannibalism, but *Coscinasterias* were not observed to eat any other of the three smaller species of starfish present. Day et al. (1995) found that hungry *Coscinasterias* in the field immediately attacked other *Coscinasterias* from which an arm had been removed.

Coscinasterias appears to have a hierarchy of preferences where mussels and other bivalves, are eaten, then gastropods. Species with well-developed escape mechanisms such as abalone, and urchins are usually attacked only when *Coscinasterias* is starved and other prey are unavailable (Day et al. 1995). Observations of *Coscinasterias* by Day et al. (1995) in aquaria and in the field at night suggest that they digest prey at night, but do not forage for new prey. However, in this study six of the 14.4 *Asterias* eaten were attacked at night.

In the present study 14.4 *Asterias* were eaten during 80 days of feeding trials. In feeding trials when *Coscinasterias* had a choice between *Asterias* and mussels, more mussels were eaten than *Asterias* (13.5 mussels cf. 5.6 *Asterias*, Table 2). Fewer *Asterias* were also eaten when mussels were available as an alternative prey (5.6 cf 9 *Asterias* eaten, Table 1), and more small *Asterias* were eaten than large *Asterias* (9.6 cf. 5, Table 1).

These data suggest that *Coscinasterias*' food preferences are: mussels, small *Asterias* then large *Asterias*. However, the preference for mussels does not appear strong as in trials in which both mussels and *Asterias* were available as prey, there were always mussels available when *Asterias* were attacked.

Coscinasterias took approximately 19-20 h to open and digest a mussel (N=2 measurements), but not all attacks on mussels were successful. On four occasions unopened mussels were abandoned by *Coscinasterias* after attacking them for 15 min, 28 min, >1hr and 5.2 h. On one of these occasions *Coscinasterias* ceased attacking the mussel to attack an *Asterias*. Thus, while mussels cannot run away, they still have effective defence mechanisms against *Coscinasterias*. However, the large (85-105 mm) mussels used in these feeding trials (85-105 mm) would have been more difficult to open than smaller mussels. *Coscinasterias* are likely to have had greater success if smaller mussels had been available (Paine 1976).

4.1.1 Limitations of laboratory feeding trials

Behaviour of asteroids can be adversely affected by handling and captivity (Sloan 1980 p77). Handling, which was minimised in this study, can result in starfish refusing to eat or move (Sloan 1980 and references therein). In this study *Coscinasterias* did not eat during 4 of the 20 trials, and did not move during one of these (Appendix 1). The failure to eat and, especially lack of any movement in one trial, may have been the result of captivity-related stress.

The tanks in which observations were made had no corners in which escaping prey could be trapped. But both *Asterias* and *Coscinasterias* preferred the vertical edges of their tanks to their horizontal bottoms, and they often were located near the seawater-air interface. This meant that active starfish would often undertake circuits of the tank which would bring them into contact with other starfish, also moving near the air-water interface.

4.1.2 Learning and dietary preferences

Landenberger (1966) showed that starfish could be conditioned to associate light with food, but that if the light stimulus was maintained, but it was no longer was associated with food, the behaviour was unlearnt in 4-9 exposures (4-9 days). He also showed that the starfish *Pisaster* prefers mussels over chitons and gastropods, but *Pisaster* increased its preference for gastropods after being fed only gastropods for three months. However, after re-exposure of *Pisaster* to mussels its preference reverted back to mussels in one week (Landenberger 1968).

An asteroid's food preference may be influenced by "ingestive conditioning", where their recent feeding experience reinforces their preference for what has been eaten recently (Sloan 1980). In laboratory tests, the starfish *Luidia*, while initially showing no preference between shrimp or bivalve prey, developed a preference for each of these prey after being fed only one prey for 21 days (McClintock and Lawrence 1984). Similarly, Murdoch (1969) found that strong feeding preferences of snails feeding on mussels and barnacles could not be altered experimentally, but weak preferences could be altered by ingestive conditioning. Ingestive conditioning appears to have a role only where there are weak prey preferences, where energy yields per prey are similar, and it may then facilitate a decrease in recognition or handling times for prey (McClintock and Lawrence 1984). In the current study both starfish species were fed mussels prior to commencement of feeding trials. Thus, if "ingestive conditioning" influenced the diet of *Coscinasterias* in this study it is likely to have increased its preference for mussels.

4.2 Escape responses

4.2.1 Unpredictable nature of interactions between exotic species

The two species in this study evolved on opposite sides of the equator and have no shared recent evolutionary history. The two species did not interact in Port Phillip Bay until 1995, and individuals used in this study were collected from single species populations located 40 km apart. It is likely that most individuals of both starfish species used in these trials interacted for the first time during the trials themselves. Under these circumstances there is no certainty that interactions between these species have been optimised by natural selection.

Prey species, for example, may not recognise an exotic predator as a threat and will be eaten. For example, most scallops native to Port Phillip Bay do not show an escape response to *Asterias,* although all rapidly responded to the native *Coscinasterias* (Hutson et al. 2005). Similarly, the New Zealand grazing mollusc *Littorina unifasciata* escapes from their native predator *Lepsiella scobina albomarginata,* and the Australian predatory mollusc *Lepsiella flindersi,* but does attempt to escape from the Australian predatory mollusc *Lepsiella vinosa*, and is eaten (McKillop 1982). Presumably, in the above example, *L. flindersi*, but not *L. vinosa,* produces chemical signals similar enough to *L. scobina* to trigger an escape response.

Experiments undertaken at the Vancouver Public Aquarium (Sloan 1980) showed that three European species of starfish exhibited escape responses to three Pacific species, but only one of the Pacific species (*Solaster dawsoni,* a specialist predator of starfish) attacked the European species. The two remaining Pacific species showed either no response or tried to escape themselves.

4.2.2 Chemoreception in starfish

There is evidence of distance and contact chemoreception in 25 species of asteroids, but species that live in wave-washed rocky shores, may be unable to exploit odour gradients and rely instead upon fortuitous encounters for prey capture (Sloan 1980). Dayton et al. (1977) noted prey were able to detect the presence of *Meyenaster* at a distance of 0.5-1.3 m, but there was no indication that *Meyenaster* could perceive prey at a distance.

The starfish *Marthasterias glacialis* causes violent escape reactions in many molluscs and the substances responsible have been shown to be saponins, which are toxins found in many asteroids (Mackie 1975). Laurenson (1970 cited in Mackie 1975) showed that the escape behaviour of the New Zealand snail *Melagraphis aethiops* responds to saponins in the tube feet of the starfish *Coscinasterias calamaria (=muricata).* However, other studies have suggested that the chemical cues used by starfish to escape starfish predators may not be saponins, but instead two or three low molecular weight substances that act synergistically (Mayo 1974 cited in Sloan 1980).

Starfish are not always capable of distinguishing the unique biochemical factors of their predator from similar biochemical factors of other organisms. Biochemical similarities between species of starfish cause the starfish *Pycnopodia* to rapidly move away from *Crassoaster* and *Solaster stimpsoni* as well as from *S. dawsoni*, although only the latter preys upon it (Mauzey et al. 1968). In the current study, both *Asterias* and *Coscinasterias* often changed direction or speed when individuals touched, and on many occasions modified their direction of travel, when~30 cm apart, to avoid contact. These observations suggest that both *Asterias* and *Coscinasterias* have distance and contact chemoreception, and often try to avoid each other. In the current study *Coscinasterias* were always larger than *Asterias* in feeding trials, reflecting the usual size difference between these species. *Coscinasterias* usually attacked *Asterias,* but on three occasions *Asterias* attacked *Coscinasterias*. These attacks were always short and the longest lasted 18 min. In contrast, attacks of *Coscinasterias* were often sustained for hours. Occasional attacks of *Asterias* on larger *Coscinasterias*, suggest that chemical signalling between these species is imperfect.

Autolysing of arms is a commonly observed defence mechanism of starfish in response to attacks by predatory starfish (Sloan 1980). It has been observed when *Asterias rubens* is attacked by individuals of its own kind or by *Solaster papposus* (Hancock 1955), during attempted cannibalism of *Meyenaster* where large individuals attack smaller ones (Dayton et al. 1977), and when *Evasterias* and *Pycnopodia* are attacked by *Solaster dawsoni* (Mauzey et al. 1986).

In this study two large and two small *Asterias* escaped by autolysing arms. A further small *Asterias* autolysed an arm but was then recaptured within 3 min and eaten. Autolysing arms is unlikely to be an effective strategy for small *Asterias* as they are usually pinned quickly and eaten. It is probably also unnecessary for large *Asterias* as they can successfully wrestle *Coscinasterias*. Autolysis of arms appears to be employed by *Asterias* when attacked by *Coscinasterias* too small to pin it quickly, but large enough to wrestle it successfully.

4.3 Population density of *Coscinasterias* required to control *Asterias* populations.

That arm loss of *Asterias* and density of *Coscinasterias* or *Leptomithrax* were not correlated suggests that these potential predators are not the main cause of arm loss of *Asterias* in Port Phillip Bay. The highest rates of arm loss in *Asterias* also occurred at depths at which *Coscinasterias* was rare or absent, making it an unlikely cause of arm loss.

Arm autonomy is mostly used by forcipulate asteroids to escape other asteroid predators (Sloan 1980, p111). Cannibalism may be the main cause of arm loss in *Asterias*. This cause is consistent with the increased frequency of arm loss with depth, as the abundance of *Asterias* also increases with depth. Similarly, rates of arm loss increase as the density of *Asterias* decreases. Cannibalism is most likely when other food is scarce, and so is less likely where there are high densities of *Asterias,* which usually result from aggregations in regions with abundant food (often the bivalve *Electroma).* The increase in arm loss in *Asterias* populations with a higher percentage of larger individuals probably reflects that autolysis of arms is a less effective escape mechanism for small *Asterias*.

In Port Phillip Bay *Coscinasterias* and *Asterias* have disjunct populations. *Coscinasterias* is mostly found in water shallower than 15 m, while *Asterias* is mostly found in water deeper than 15 m. Is this distribution due to predation on *Asterias* by *Coscinasterias* or some other factor?

Depth-related differences in recruitment could cause the observed pattern, but settlement and feeding preferences of neither species is well-documented. Post-settlement juvenile asteroids are often herbivorous, but some, including *Asterias rubens,* feed carnivorously on barnacles and tubeworms immediately upon completing metamorphosis (Barker and Nichols 1983). *Coscinasterias* settles on “almost any hard substratum provided it was coated with a ‘primary’ film”, upon which the juveniles feed (Barker 1977). Day et al. (1995) found juvenile *Coscinasterias* “only on foliose algae, amongst mussels or under boulders”, suggesting that its recruitment may be restricted to shallower water where all these habitats are more available. Similarly, the only habitat in Port Phillip Bay where small *Asterias* (1-5 mm diameter) have been found is on *Ulva*, (D. Jindra and GD Parry pers obs), an alga found mostly in shallow regions of the bay. In the laboratory *Asterias* consumed algae until ~10 mm in diameter (Jindra pers obs). Thus, the limited evidence available, suggests that depth-related differences in recruitment are unlikely to explain the disjunct distributions of *Asterias* and *Coscinasterias*, as both may settle mostly in shallow regions where macroalgae is more available.

The lack of a relationship between rates of arm loss and the population density of *Coscinasterias* may result from a lack of predation, or because in areas of overlap in shallow water most interactions are between large *Coscinasterias* and small *Asterias*, which are eaten entirely.

If *Asterias* are eaten by *Coscinasterias* at the rate shown in the laboratory each would consume ~50 *Asterias* annually. Thus, they would be expected to have an appreciable impact on populations of *Asterias* until the ratio of *Asterias/Coscinasterias* exceeded ~50. This occurs at a depth of between 15 and 16 m, approximately the minimum depth at which high densities of *Asterias* are found. The exception to the above generalisation is that both species can be common around piers in shallow water (Parry, pers obs), where there may be enough alternative food for both to co-exist.

4.4 Potential of augmentative biocontrol

Augmentative biocontrol uses native grazers/predators of the invasive species to decrease their abundance. Used in conjunction with traditional control methods, it represents a promising tool for the integrated management of marine pests (Atalah *et al.* 2013). A recent attempt to eliminate a newly established *Undaria* population in Fiordland, New Zealand appears to have been successful (Environment Southland 2013). This well coordinated multi-agency response used divers and augmentative biocontrol, where 35,000 native sea urchins were introduced into the infected area to over-graze the *Undaria* (Figure 4.1).

Figure 4.1 Sea urchins about to be released to augment grazing pressure on a newly founded *Undaria* population in Fiordland, New Zealand.

The rate at which *Coscinasterias* feeds on *Asterias* in the laboratory suggests that predation helps control the depth distribution of *Asterias* in Port Phillip Bay. This further suggests that *Coscinasterias* may be very helpful in eliminating newly-established populations of *Asterias*.

In locations such as Tidal River small *Coscinasterias* are found occasionally (M Hoskins, Ranger Tidal River, pers. comm.), but they probably never grow naturally to a size capable of eating most *Asterias* as they are regularly eradicated during floods. *Asterias* appears more tolerant of low salinities and may be less impacted by floods. In locations such as Tidal River it is likely that any *Coscinasterias* added will only persist till the next flood. This may limit its effectiveness as a predator (or require new *Coscinasterias* to be added post-flood), but will also limit (undesirable) collateral impacts of a predator that doesn't usually exist at high densities in this location.

The effectiveness of augmentative biocontrol to eliminate a new *Asterias* population would be very difficult to evaluate in a location such as Tidal River. Consequently, before this technique was tried on a new infestation, it would be desirable to trial the technique in another location where *Asterias* is already abundant, and where the effectiveness of increasing the *Coscinasterias* population could be evaluated in the field.

There are a number of piers in Port Phillip Bay that would be suitable for such a trial. This would also enable a better estimate of the number of *Coscinasterias* that are needed to impact the *Asterias* populations. Estimates in this study suggest that after the *Coscinasterias* have been added that their ratio should be at least 1:1, and, if the aim is eradication, a ratio as high as 10:1 may be desirable. Higher densities may also result in more effective control as it is likely that hungry *Coscinasterias* will eat more *Asterias* than those that are well fed. Certainly hungry *Coscinasterias* rapidly attack damaged *Coscinasterias* (Day et al. 1995), and they could be expected to behave similarly with *Asterias*.

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Appendix

Appendix 1:

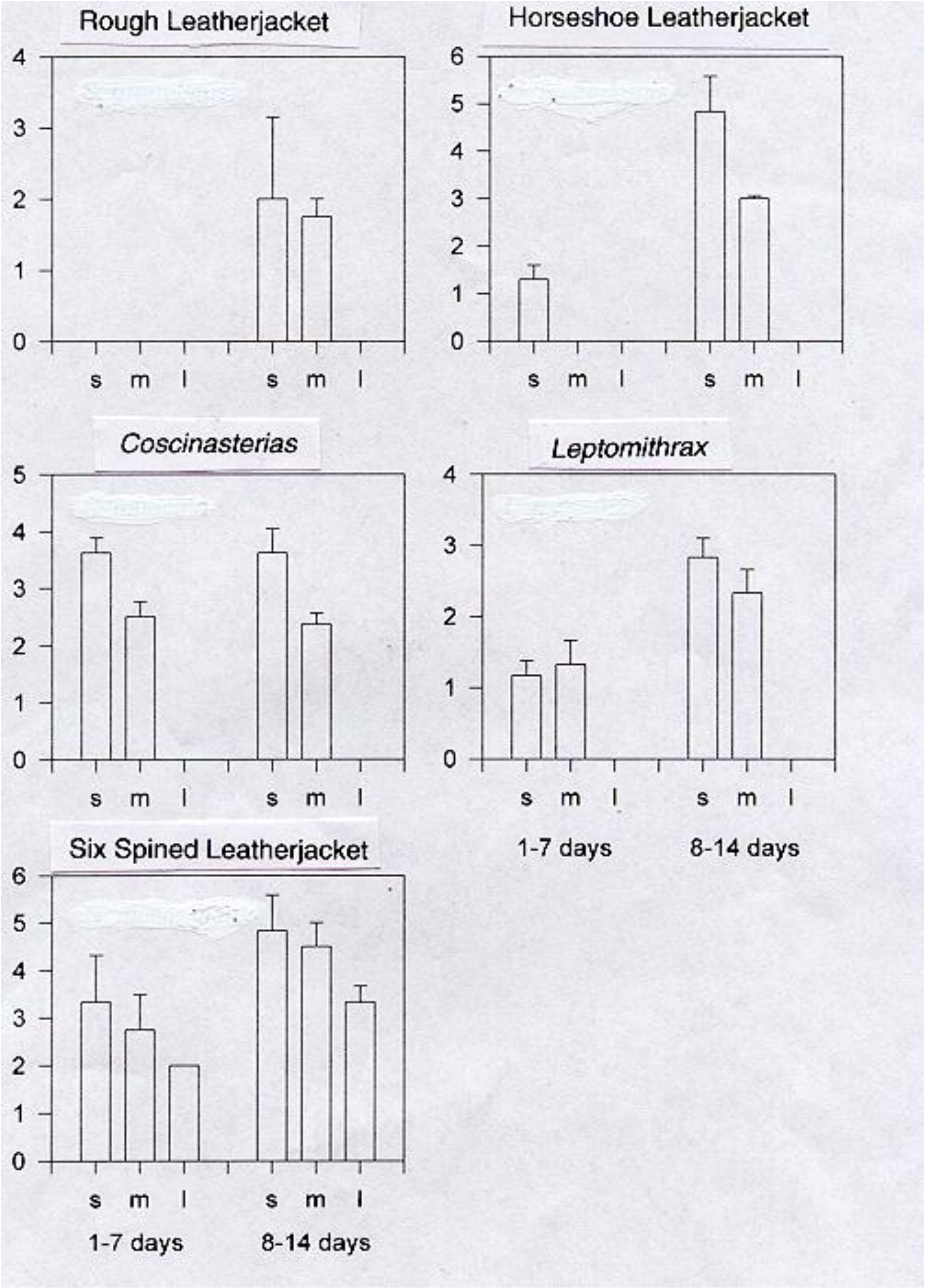

Figure (from Botsios 2001). Mean number (±se) of small (s, 3-10 cm diameter), medium (m, 10-16 cm) and large (l, >16 cm) *Asterias* eaten by five predators during days 1-7 and days 8-14 of two-week feeding trials. Trials were conducted in 20 aquaria (450 x 700 x 500mm), except that a large tank (600 x 1200 x 700mm) was used for large leatherjackets. Tanks contained either 5 small, 5 medium or 1 large *Asterias*.

Appendix 2:

Tank	1A	2A	1B	2B	1C	2C	1D	2D	1E	2E	1F	2F	1G	2G*	1H	2H	1I	2I	1J	2J	**Total**
Days 1 and 2																					
Diameter *Coscinasterias* (cm)	35	32	32	30	29	23	28	29	31	29	30	28	24	26	25	29	27	26	26	26	
Diameter *Asterias* (cm)	10,22	10,24	9,25	11,24	11,19	12,21	11,18	12,18	11,15	10,15	10,15	10,15	10,23	9,17	12,17	11,14	9,13	9,13	11,14	11,15	
small	1[A]	0	🟨 1	0	🟨 0.4	0	0	0	0	0	0	0	🟨 1	0	0	0	0	0	1[N]	0.2	**4.6**
large	🟨 1	0	0.4[B]	0[C]	0	0[D]	🟦 0[E]	0	1[F]	0	0	🟦 0	0[G]	0	0	0	0	🟨 1	0	0	**3.4**
mussels present/no. eaten	no	yes/2	no	yes/1.5	yes/1	no	yes/1.5	no	no	yes/1	yes/1	no	no	yes/0	yes/1	no	no	yes/0	yes/0	no	**8**
Days 3 and 4																					
Diameter (replacement) *Asterias* (cm)	10,26	-	9	-	10	-	-	-	22	-	-	-	10	-	-	-	-	16	10	10	
small	1	0	0	1[J]	0	0	0	1	0	0	🟨 1	0	0	0	🟩 0	0	0	0	1[P]	0	**5**
large	0[H]	0	0.2[I]	0	0	0[K]	0	0	0[L]	🟩 0	0	0	🟦 0	0	0	0	0	0.4[M]	0	1	**1.6**
mussels present/no. eaten	yes/1	no	yes/0	no	no	yes/0	no	yes/0	yes/1	no	no	yes/0	yes/1-2	no	no	yes/0	yes/2	no	no	yes/0	**5.5**

* *Coscinasterias* did not move during four day trial.

🟨 Eaten overnight, no observations of attack behaviour
🟦 *Coscinasterias* attacked **by** *Asterias,* but *Coscinasterias* escapes.
🟩 Unclear whether *Asterias* is chasing or being chased by *Coscinasterias*

A. *Asterias* escapes temporarily missing 1 arm, but recaptured within 3 min and eaten.
B. 2 arms of *Asterias* eaten: 1 arm eaten at night, then attacked 3 times. The first two attacks were unsuccessful, and these lasted 1hr:55min and 1hr:16min, while another arm was lost during the third attack which lasted 1hr:33min.
C. *Asterias* attacked the same mussels as *Coscinasterias* .
D. *Asterias* attacked for 1hr:5min, then escapes without damage.
E. *Coscinasterias* attacked **by** *Asterias* for 18min, then escapes.
F. *Asterias* attacked for 3hr17min, then eaten.
G. *Asterias* attacked for 15 min, then escapes.
H. *Asterias* attacked and chased for 1hr19min.
I. Partially eaten *Asterias* attacked six times, for 54min, 2hr:17min (another arm lost), 4min, 57min, 2:17 (another arm lost), >1hr (remaining 2 arms disarticulated but not consumed).
J. *Asterias* attacked for 13min then escapes, but is eaten on the next attack.
K. *Asterias* attacked for 7min then escapes.
L. *Asterias* for 4hr50min then escapes.
M. *Asterias* attacked for 5hr:47min, 3 arms escape, 2 arms eaten.
N. *Asterias* attacked for ~1hr before it was overwhelmed
P. *Asterias* attacked for ~32 min before it was overwhelmed.