

## PRELIMINARY OBSERVATIONS OF THE FEEDING PERIODICITY AND SELECTIVITY OF THE INTRODUCED SEASTAR, *ASTERIAS AMURENSIS* (LÜTKEN), IN TASMANIA, AUSTRALIA

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(with three tables and three text-figures)

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Field observations of the introduced north Pacific seastar, *Asterias amurensis*, in Tasmania showed that it feeds over the 24-h period with no obvious cycle of activity. Percentage of seastars feeding at any time ranged from 17.2% at 1600 h to 58.2% at 2000 h. Feeding periodicity did not correlate with the time of day or the height of the tide. A significantly higher proportion of juveniles than adult seastars were found to be feeding at any given time. A comparison of prey items found in the stomachs with the availability of prey items in sediments revealed that, in the field, *A. amurensis* selected some prey species and avoided others. A total of 15 species were consumed, with molluscan prey the most important (> 60%) in winter and spring and at the two depths studied (2 m and 5 m). It is concluded that *A. amurensis* is an opportunistic generalist predator but shows a certain degree of specialisation in local populations. All bivalves at the field site were found to be juveniles (most < 5 mm shell length). Whether this is a natural phenomenon or due to the presence of *A. amurensis* cannot be ascertained, as there are no data from these sites prior to the introduction of this seastar. Due to the dominance of juveniles, the resilience of the bivalve community is likely to be low.

**Key Words:** *Asterias amurensis*, asteroid, feeding periodicity, introduced species, prey selectivity, Tasmania.

### INTRODUCTION

*Asterias amurensis* was first collected in southeastern Tasmanian waters in 1986 but was not correctly identified until 1991 (Turner 1992, Buttermore *et al.* 1994, Byrne *et al.* 1997). The asteroid is thought to have been introduced as larvae transported in the ballast waters of ships (Turner 1992, Buttermore *et al.* 1994) from the North Pacific. *A. amurensis*, in its native habitat, is a notorious predator on commercial scallops and a great variety of other benthic invertebrates (Hatanaka & Kosaka 1959) and, thus, is considered a major threat to the native marine fauna of Tasmania. Unfortunately, little is known about the ecology of *A. amurensis*, despite this species being considered a pest even within its natural range.

Seastars are known to exhibit differing feeding intensities with the different seasons, due to (amongst other reasons) external temperature changes and/or internal physiological changes such as those associated with reproduction. At varying times feeding activity can slow or even cease altogether. The variations in asteroid feeding intensity over a 24-h period have been found to be controlled by light (Fenchel 1965, McClintock & Lawrence 1981), tidal variations (Paine 1969, Menge 1972), prey availability (Mori & Matutani 1952, Ribi & Jost 1978, McClintock & Lawrence 1985, Beddingfield & McClintock 1993) or a combination of these.

A predator's selectivity for prey can lead to the obliteration of preferred species populations (Murdoch 1969, McClintock & Lawrence 1985). Predators such as seastars, which exhibit intense prey species selectivity, can have considerable effects upon a number of ecological parameters such as

(1) the distribution of prey species and their competitors (Connell 1961, Landenberger 1968);

(2) community structure and species diversity (Paine 1969, 1976, Ormond *et al.* 1976, Lubchenco & Menge 1978, Menge 1982, Duggins 1983, O'Neill *et al.* 1983, Robles *et al.* 1990);

(3) the age structure (Fukuyama & Oliver 1985) and reproductive tactics of prey populations (Curio 1976 in Annett & Pierotti 1984).

Many important factors are involved in prey choice by predatory seastars (Menge 1971, Dayton *et al.* 1977, Sloan 1980a). These include availability, which is dependent on geographical and local community variability, caloric yield of prey and catchability, including pursuit and handling of prey, which, in turn, is dependent on prey and predator distribution, abundance and behaviour. Landenberger (1968) also lists past feeding experience as another variable affecting prey selectivity. To complicate the situation further, the attraction and/or repulsion of asteroids to various chemical cues can vary over the year (Castilla 1972a,b, Sloan 1980a).

Asteroids are known to exhibit intraspecific feeding diversity (Jangoux 1982), which has facilitated the success of these animals as keystone predators. Many prey species of *A. amurensis* are known from northern Pacific populations (Kim 1969a,b, Park & Kim 1985).

The work described here had two major objectives. It was designed firstly to investigate the diel feeding activity pattern of *A. amurensis* in the early winter, i.e. prior to spawning, and secondly, to determine whether *A. amurensis* in Tasmania exhibits prey selectivity or is a generalist on the most common species.

## MATERIALS AND METHODS

### Field Site and Collection

Field experiments were carried out at Nutgrove Beach, Sandy Bay, southeastern Tasmania (42°54'N, 147°20'E). Nutgrove Beach is considered to be typical of the Derwent River, where the Tasmanian population of *A. amurensis* is concentrated. The sediment is sandy-mud and the fauna is mainly infaunal. Very little zhard substratum exists, with the exception of rubbish which litters the riverbed. Macroalgae are also scarce at this site. Seastars were collected by hand and measured from the middle of the disc to the tip of the longest arm (Hancock, 1958); this is the radius ( $r$ ).

### Feeding Periodicity

To observe feeding activity in *A. amurensis*, SCUBA dives were conducted at Nutgrove Beach every two hours over a period of 24 h (from 1000 h, 31/5/95 to 0800 h, 1/6/95). Divers travelled parallel to the beach at a depth of 5 m. Seastars were overturned and recorded on underwater slates as digging, stomach extruded or neither, until approximately 100 seastars had been tallied. The presence of an extruded stomach is used in preference to the humped position, as *A. amurensis* remains flush with the substratum if the prey is very small. The seastars were further classified as juveniles ( $r < 55$  mm) or adults ( $> 55$  mm) (Byrne *et al.* 1997). Each successive dive was conducted up river from where the previous dive finished (approx. 50 m of beach per dive). This was done to prevent tallying seastars that had already been disturbed, which usually resulted in the expulsion of prey items. In addition, this procedure gave independence to each two-hourly sample.

The data (in percentage form) were transformed via angular transformation in order to comply with the assumptions of parametric statistics. Both single factor ANOVAs and two-factor ANOVAs without replication were carried out on the data.

### Selectivity in the Field

Three SCUBA dives were conducted off Nutgrove Beach, southeastern Tasmania. Two were conducted at 5 m, approximately three months apart (on 22/6/95 and 30/9/95), and the third was conducted at 2 m (on 19/9/95) for a depth comparison. Each dive was carried out between 0900 and 1200 h. All seastars within 1 m either side of a 50-m transect were examined. Each seastar was recorded on an underwater slate as feeding or not feeding. Any debris attached to the arms was carefully brushed off and the seastars were then placed into numbered plastic zip-lock bags to prevent loss of stomach contents. Along the same transect line, ten circular PVC cores (100 mm deep, 98 mm diameter) were pushed into the sediment and dug out in order to determine the faunal composition of the substrata on each of the three dives. In the laboratory each seastar was measured ( $r$ ) and its stomach folds examined for prey items. Pressure was applied to the aboral surface to expel engulfed food items. All prey items were measured and identified to the lowest possible taxon. Sediment from the core samplers was sieved (2 mm mesh) and any live animals were also measured and identified to the lowest possible taxon. Measurements taken were

anterior-posterior length (bivalves), columella length (gastropods), basal diameter (cirripedes), carapace width (brachyurans), columella length (anomurans) and greatest test length (irregular echinoids).

Dietary composition was compared to the sites' faunal composition by calculating Vanderploeg & Scavia's (1979) relativised electivity index ( $E^*$ ) as follows:

$$E^* = \frac{[W_i - (1/n)]}{[W_i + (1/n)]}$$

where  $W_i$  = selectivity coefficient calculated as

$$\frac{r_i / p_i}{\sum_i r_i / p_i}$$

$r_i$  = relative utilisation of food types in the diet

$p_i$  = relative availability of food types in the environment

$n$  = number of available food types

The electivity index ( $E^*$ ) given for each species has a range from  $-1$  to  $1$ . A value of  $0$  denotes that the species is taken in proportion to its abundance;  $1$  signifies that the species is preferred and selected at a greater proportion than is available; and  $-1$  indicates that the species is avoided strongly.

A number of electivity indices exist. All are versions of Ivlev's (1961) original, differing only slightly from one another. In a review of the sampling characteristics of the variety of electivity indices, Lechowicz (1982) concluded that no one index ideally satisfies all criteria and that food types shown as preferred by one index will frequently appear as avoided by another. The review led to the recommendation of the use of Vanderploeg and Scavia's index. The range of values ( $-1$  to  $+1$ ) with a zero value for random feeding is a convenient property. However, the maximum preference value can only be attained under the unrealistic conditions that  $r = 100$ ,  $p = 0$  and the number of food types is infinite. For a more detailed discussion on the advantages and disadvantages of Vanderploeg and Scavia's and the other indices available the reader is referred to Lechowicz (1982).

## RESULTS

### Feeding Periodicity

The percentage of seastars feeding over the 24-h period is illustrated in figure 1. The data were grouped around the high and low tide times and analysed by a single factor ANOVA which revealed no significant correlation between the percentage feeding and the tidal variations ( $F_{3,8} = 1.575$ ,  $p = 0.270$ ). The first high tide and the first low tide for the 24-h period occurred within a short time frame and did not differ in magnitude; therefore, a single factor ANOVA was calculated with these two periods considered as one. However, there was still no significant difference in feeding activity between the tidal levels ( $F_{2,9} = 1.928$ ,  $p = 0.201$ ).

The data were then grouped according to periods of the day (i.e. noon, dusk, midnight and dawn). Again, there was no significant variation between these ( $F_{3,8} = 0.340$ ,  $p = 0.797$ ). In addition, the data were grouped according to daylight hours and nighttime hours. The single factor

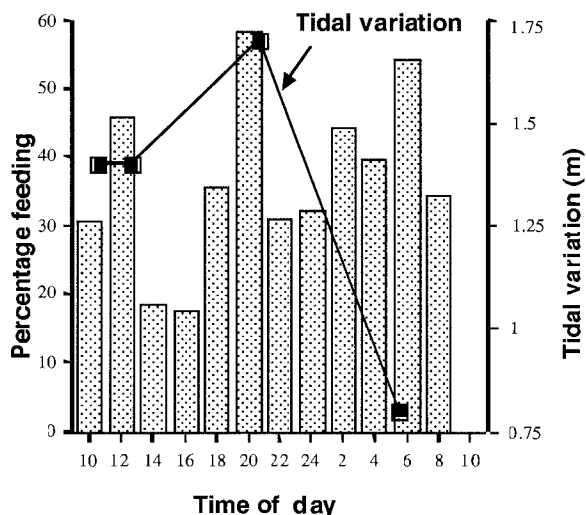


FIG. 1 — Percentage of *Asterias amurensis* feeding over 24 h. Graph shows tidal height variation over the same period.

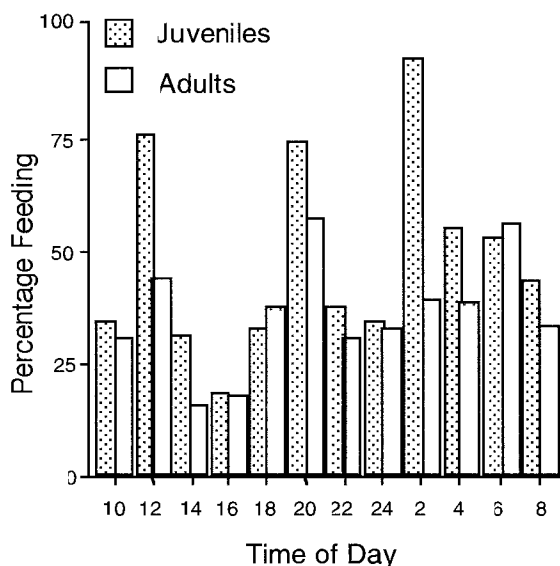


FIG. 2 — Percentage of juveniles and adults feeding over a 24 h period.

ANOVA again showed no significant difference between night and day ( $F_{1,10} = 0.960$ ;  $p = 0.350$ ).

A two factor ANOVA (without replication) revealed that the proportion of juveniles feeding was significantly higher ( $F_{1,11} = 6.510$ ;  $p = 0.027$ ) than the proportion of adults feeding (fig. 2).

### Selectivity in the Field

Combined June and Sept 1995 sample: 5 m  
 Dates of collections, seastar sizes and proportions feeding are given in table 1. Data from the two collections from 5 m were kept separate for a comparison of proportions of major prey types in stomachs but have been combined for the purpose of the electivity analysis. The percentage of seastars that were recorded as feeding was 44% (i.e. either had their

TABLE 1  
*A. amurensis* field data on size and percentage feeding

Date	Depth (m)	Av. radius (mm±SE)	Range of r (mm)	% feeding	% with items in stomach
22/6/95	5	69 ± 11.8	30-113	50.0	76.5
30/9/95	5	72 ± 10.5	40-103	36.4	69.1
19/9/95	2	81 ± 13.8	46-134	30.0	76.0

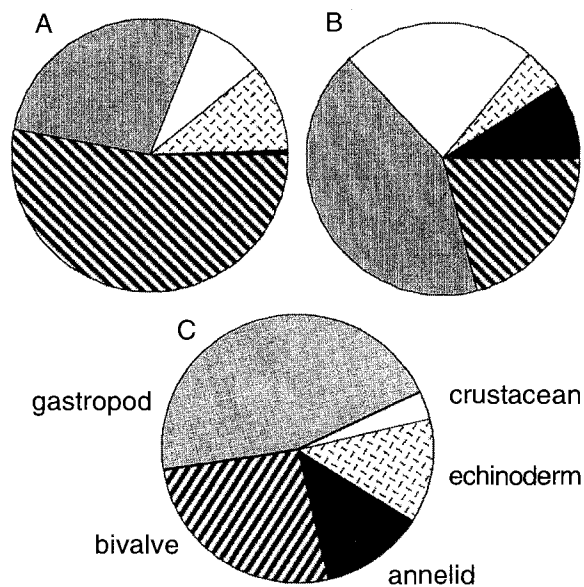


FIG. 3 — Proportions of prey types in the diet of *Asterias amurensis*. (A) June samples at 5 m depth; (B) September samples at 5 m depth; (C) September samples at 2 m depth.

stomach extruded or were in the process of digging). However, after examination of the stomach folds it was discovered that 73% contained at least one prey item. Hence both measures are included in the table for all occasions. The proportions of prey types in the diet are illustrated in figure 3. The results of the stomach content analysis, substrate faunal composition and the electivity indices are shown in table 2.

Bivalves were the most important prey type for this population of *A. amurensis* in June (fig. 3A), whereas gastropods were more important in the diet in September (fig. 3B). Non-molluscan prey types made up smaller proportions of the diet.

The most preferred prey was the bivalve *Notospisula trigonella* ( $E^* = 0.70$ ) followed closely by *Chioneryx striatissima*, Veneridae sp. and *Placamen placida*. The crustacean *Phlyxia* sp. was also taken selectively. *Nassarius nigellus* was one of the most abundant macrobenthic species in the substrate and was consumed in the greatest numbers. A small hermit crab (*Pagurixus handrecki*), which is common at this site and depth, occupies the shells of *N. nigellus*. In earlier laboratory experiments it was not consumed by *A. amurensis* (Lockhart & Ritz 1998). Thus, it was assumed

TABLE 2  
Numbers, proportions and size ranges of fauna found†

Species n = 20	Total number in 123 stars	Size range in 123 stars (mm)	Total number in 20 cores	Size range in 20 cores (mm)	r	p	E*‡
<b>Mollusca: Bivalvia</b>							
<i>Mysella donaciformes</i>	9	2.4–3.8	132	1.2–3.8	2.9	47.7	-0.92
<i>Placamen placida</i>	13	2.0–5.1	5	2.0–3.3	4.2	1.8	0.23
<i>Tawera gallinula</i>	5	2.1–5.9	5	1.4–2.6	1.6	1.8	-0.23
<i>Chioneryx striatissima</i>	94	1.2–5.0	11	2.0–5.6	30.6	4.0	0.68
<i>Katelysia</i> sp.	0		2	1.6–2.0	0	0.9	
<i>Venerupis anomala</i>	14	2.1–6.0	8	2.2–5.0	4.6	2.9	0.04
<i>Hiatella australis</i>	2	4.9–6.0	1	3.0	0.7	0.4	0.09
<i>Cyamiomacra mactroides</i>	0		1	2.0	0	0.4	
<i>Notospisula trigonella</i>	10	2.4–4.0	1	2.0	3.3	0.4	0.70
Veneridae sp.	3	2.5–3.5	1	1.6	1.0	0.4	0.27
<b>Gastropoda</b>							
<i>Nassarius nigellus</i> (gast.) §	98	1.8–10.0	62	1.8–10.2	31.9	22.4	-0.01
<i>Nassarius nigellus</i> (shell) §	10	2.2–7.4	0		3.3		
<i>Odostomia deplexa</i>	0		1	1.8	0	0.4	
<i>Sinuginella pygmaeioides</i>	0		1	5.1	0	0.4	
<i>Fusinus novaehollandiae</i>	0		6	6.6–110.0	0	2.2	
<i>Conuber conicus</i>	0		2	4.1–4.6	0	0.7	
<b>Crustacea</b>							
<i>Phlyxia</i> sp.	20	2.0–5.1	5	2.8–4.8	6.5	1.8	0.43
<i>Halicarcinus</i> sp.	5	3.2–5.2	3	6.0–10.0	1.6	1.1	0
<i>Pagurixus handrecki</i>	0		13	5.4–10.0	0	4.7	
<i>Elminius modestus</i>	18	1.0–5.4	0		5.9	0	
<b>Echinodermata</b>							
<i>Echinocardium Cordatum</i>	3	4.0–7.0#	7	9.0–38.0	1.0	2.5	-0.58
<b>Annelida</b>							
	3	#	10	#	1.0	3.6	-0.67
TOTAL	307		277		100	100	

† Found both in the stomach folds of *Asterias amurensis* (r) and in the substrate of Nutgrove Beach (p) at a depth of 5 m (combined June and September samples).

‡ Vanderploeg & Scavia's electivity index (E\*) shows those species which are preferred (positive E\*) and those which are avoided (negative E\*).

§ (gast.) & (shell) refer to those *N. nigellus* in the diet of *A. amurensis* in which remains of the gastropod were found or which were empty, respectively.

# denotes those prey items which were unmeasurable due to damage.

that the species consumed by *A. amurensis* was indeed the gastropod.

Species that were avoided (negative E\*) included (in decreasing order of avoidance) the bivalve *Mysella donaciformes*, the annelids, the echinoid *Echinocardium cordatum* and the bivalve *Tawera gallinula*. The annelids are most likely to have been underestimated in the diet as they are completely digested.

Some species were consumed but were not found in the core samples and, therefore, are considered to be taken selectively. These are *N. nigellus* empty shells and the barnacle *Elminius modestus*. The fact that no barnacles were found in the substrate is not surprising since, when they occur on soft substrates, they are usually associated with mussels (*Mytilus edulis*). The only mussels at the Nutgrove beach site were found attached to a chain that anchors a floating platform upstream of the immediate study area. A big storm had occurred just prior to the September dive, resulting in the detachment of the mussels (usually unattainable). The barnacles, therefore, were more

readily available to the seastars but would most likely be found in the direct vicinity of the floating platform.

Species were found in the core samples which were not found to be consumed and, therefore, are considered to be avoided. These include the hermit crab *Pagurixus handrecki* and the gastropods *Conuber conicus* and *Fusinus novaehollandiae*. However, the latter is known to be consumed occasionally by *A. amurensis* (pers. obs.).

#### September 1995 Sample: 2 m

Dates of collections, seastar sizes and proportions feeding are given in table 1. The percentage of seastars that were recorded as feeding was 36.0% (26.0% with stomach extruded and 10.0% digging). After examination it was found that 76.0% of seastars contained at least one prey item in the stomach folds. The proportions of prey types in the diet of *A. amurensis* at 2 m are illustrated in figure 3C. The results of the stomach content analysis, substrate faunal composition and the electivity indices are shown in table 3.

Gastropods make up the largest proportion of the diet followed by the bivalves (fig. 3C). Non-molluscan prey again make up smaller proportions of the diet. Numerically the most commonly consumed prey was again the gastropod *N. nigellus*, which was found to be taken selectively ( $E^* = 0.38$ ). Again no *P. handrecki* were taken and these, therefore, are considered to be avoided.

Species taken selectively included (in decreasing order of selectivity) the annelids, the echinoid *Echinocardium cordatum*, the gastropod *N. nigellus*, and the bivalves *Chioneryx striatissima* and *Placamen placida*. Species that were avoided are (in decreasing order of avoidance) the bivalves *Mysella donaciformes*, *V. anomala* and *T. gallinula*.

Other species considered to be preferred, as they were found in the stomach folds but not in the core samples, are the bivalve *Notocallista diemenensis*, the crab *Phlyxia* sp. and the barnacle *Elminius modestus*. Conversely, species considered to be avoided as they were found in the substrate

but not in the diet are the bivalves *Katelysia* sp., *C. mactroides*, *H. australis*, *Tellina deltoidalis*, unknown *Mysella* sp., *Lasaea australis*, unknown *Veneridae* sp., the gastropods *Odostomia deplexa*, *Conuber conicus*, *F. novaehollandiae*, and the crustacean *Pagurixus handrecki*.

## DISCUSSION

### Feeding Periodicity

The average percentage of feeding *A. amurensis* was found to be  $36.5 \pm 9.7\%$  with a range of between 17.2 and 58.2% of seastars feeding over all hours. This is surprising because asteroids are thought to remain inactive during most of the 24-h cycle (Valentinic 1983) and be relatively inactive in winter. The majority of non-feeding seastars were on the move with the tips of their arms curled in the characteristic

TABLE 3  
Numbers, proportions and size ranges of fauna found†

Species n = 23	Total number in 50 stars	Size range in 50 stars (mm)	Total number in 10 cores	Size range in 10 cores (mm)	r	p	E*‡
<b>Mollusca: Bivalvia</b>							
<i>Mysella donaciformes</i>	1	2.2	69	1.0–4.0	1.4	46.1	–0.93
<i>Mysella</i> sp.	0		2	2	0	1.3	
<i>Placamen placida</i>	3	3.2–4.0	6	1.8–3.0	4.3	4	0.11
<i>Tawera gallinula</i>	5	1.6–2.4	13	1.2–3.8	7.1	8.7	–0.03
<i>Chioneryx striatissima</i>	5	2.6–3.8	8	2.0–3.0	7.1	5.4	0.2
<i>Katelysia</i> sp.	0		2	2	0	1.3	
<i>Venerupis anomala</i>	3	3.0–6.0	11	1.4–5.6	4.3	7.4	–0.19
<i>Hiatella australis</i>	0		1	3.2	0	0.7	
<i>Cyamimactra mactroides</i>	0		1	1.4	0	0.7	
<i>Tellina deltoidalis</i>	0		1	11	0	0.7	
<i>Lasaea australis</i>	0		1	1.4	0	0.7	
<i>Notocallista diemenensis</i>	1	4.4	0		1.4	0	
<i>Veneridae</i> sp.	0		1	2	0	0.7	
<b>Gastropoda</b>							
<i>Nassarius nigellus</i> (gast.) §	20	2.2–10.0	22	1.6–4.4	28.6	14.8	0.38
<i>N. nigellus</i> (shell) §	10	1.4–9.4	0		14.3	0	
<i>Odostomia deplexa</i>	0		1	2.4	0	0.7	
<i>Conuber conicus</i>	0		1	4.4	0	0.7	
<i>Fusinus novaehollandiae</i>	0		1	61.9	0	0.7	
<b>Crustacea</b>							
<i>Pagurixus handrecki</i>	0		1	10	0	0.7	
<i>Phlyxia</i> sp.	2	–	0	2.9	0		
<i>Elminius modestus</i>	2	4.0–4.2	0	2.9	0		
<b>Echinodermata</b>							
<i>Echinocardium cordatum</i>	8	–	5	8.0–40.0	11.4	3.4	0.59
<b>Annelida</b>							
	10	#	2	#	14.3	1.3	0.85
TOTAL	70		149		100	100	

† Found both in the stomach folds of *A. amurensis* (r) and in the substrate of Nutgrove Beach (p) at a depth of 2 m (September).

‡ Vanderploeg & Scavia's electivity index ( $E^*$ ) shows those species which are preferred (positive  $E^*$ ) and those which are avoided (negative  $E^*$ ).

§ (gast.) and (shell) refer to those *N. nigellus* in the diet of *A. amurensis* in which remains of the gastropod were found or which were empty, respectively.

# denotes those prey items which were unmeasurable due to damage.

foraging pose (Sloan 1980b). In comparison, many asteroid species feed at a much lower rate than this over winter, increasing their activities over summer (Paul & Feder 1975, Mauzey 1966, Paine 1969, Menge 1972, Keesing & Lucas 1992). Mauzey (1966) found that less than 5% *Pisaster ochraceus* were feeding over winter, which increased to 60% over summer. Paine (1969) found a similar seasonal difference in this species. This seasonal variation was thought to be because *P. ochraceus* is a temperate species, which is heat tolerant and, therefore, feeds more intensively over summer, because of an increase in metabolism. However, over 22 months the average percentage of feeding *P. ochraceus* was 35.4% (Mauzey 1966), which is very similar to the results from the present study over 24 h. *A. amurensis* is also a temperate species and, therefore, possibly will also increase its feeding activity as summer approaches.

It was not so surprising that the feeding activities of *A. amurensis* in the Derwent River at this depth did not correlate with the tidal variations. The high and low tides do not differ a great deal in magnitude at this time of year. In addition, a lull in feeding activity over the winter among temperate climate asteroids appears more strongly among intertidal individuals (Paul & Feder 1975, Sloan 1980a), being more affected by low temperatures and bad weather due to low-tide exposure (Menge 1971, Sloan & Robinson 1983). Natural diel feeding activity patterns for this reason are likely to be suppressed in inlets, bays, harbours and protected waterways (Feder 1970) such as the Derwent River.

During the present investigation, the first low tide occurred around noon and was followed by a lull in feeding activity, while the second low tide occurred just before darkness, during which time the percentage of feeding activity did not vary greatly. No significant difference was found when the data were grouped according to the tidal variations. However, the possibility of the tides and light interacting, as Menge (1972) suggests, cannot be ruled out. Further work should test the interaction of light and tides on the feeding activities of *A. amurensis*.

The non-significant differences revealed when the data were grouped according to different times of the day suggest that light does not play a primary role in controlling the feeding activities of *A. amurensis*. In contrast, the feeding activities of many asteroid species are strongly influenced by light. Most of these prefer to feed at night, such as *P. brevispinus* (Smith 1960), *Luidia sarsi* (Fenchel 1965), *Asterias rubens* (Thain 1971 in Sloan 1980a), *Acanthaster planci* (Ormond *et al.* 1973) and *Astropecten latespinosus* (Nojima 1981). Other species are known to feed at dawn and/or dusk (Mori & Matutani 1952, McClintock & Lawrence 1981, Beddingfield & McClintock 1993). *L. clathrata* exhibits one peak at dusk, although there is never 100% activity or inactivity at any one time (McClintock & Lawrence 1981). *A. bispinosus* is active at dawn and dusk over the summer months, having different activity peaks from coexisting predators (Ferlin-Lubini & Ribi 1978 in Sloan 1980a). Beddingfield & McClintock (1993) also related the foraging peak of *A. articulatus* to avoidance of predators, such as fish, which decrease feeding activity at dawn and dusk. If predator activity is a controlling factor of *Asterias amurensis* activities then this may explain the lack of foraging peaks in this species. Having no predators in Tasmania (Turner 1992), *A. amurensis* need not reduce its activities according to those of its predators. *Astropecten polyacanthus* also feeds at dawn and dusk (the intensity of

activity being stronger at dawn), burying itself at noon and midnight (Mori & Matutani 1952). In this early study it was found that temperature played no role and that light and food were the controlling factors of this species' diel feeding pattern. Food was found to be a modifier of the intensity of activity, while light was shown to be the real controlling factor of the rhythm (Mori & Matutani 1952).

Prey availability cannot be ruled out as the factor controlling the feeding pattern of *Asterias amurensis* since prey appears to be scarce at this site. Thus, the level of hunger in these seastars may increase to the point where other controlling factors, such as tide levels and light, may be suppressed. Beddingfield & McClintock (1993) found that *Astropecten articulatus* spent significantly longer periods of time foraging when fed low quality food. A number of other researchers have reported similar findings e.g. Mori & Matutani (1952) studying the asteroid *A. polyacanthus*. Starved *L. sarsi* will consume a greater variety of prey species but at a reduced rate (Fenchel 1965). Such behaviour could explain the reason why species such as *F. novaehollandiae* are not preferred by *Asterias amurensis* but are consumed occasionally in the field (pers. obs.).

In the present investigation it was found that a significantly higher proportion of juveniles were feeding over 24 h than were adults. This could simply be an artefact of the very small number of juveniles found in the samples relative to the adults. Ferlin-Lubini & Ribi (1978 in Sloan 1980a), working on *Astropecten* spp., found that large individuals were active longer than smaller ones. Furthermore, the percentage of juvenile *Asterias vulgaris* found feeding was considerably less than that for the adults (Himmelman & Dutil 1991). Results from a laboratory experiment, comparing the feeding rates of a small size class and a large size class of *A. amurensis*, revealed that the former consumed a much greater percentage of its body weight than the latter, lending some support to the findings of the present diel investigation (Lockhart & Ritz 2001).

### Selectivity in the Field

The most disturbing finding of the selectivity investigation is the physical size of the prey species inhabiting Nutgrove Beach. The majority of the bivalves, which make up the largest proportion of the infauna, were just a few millimetres in length. The gastropod *Fusinus novaehollandiae* was found in its full size range, but this abundant species was shown to be avoided by *A. amurensis*. Almost the entire size range of the gastropod *Nassarius nigellus* was also found, though large individuals of this species were rare. Empty adult shells of all the other mollusc species were found, some with obvious carnivorous mollusc drill holes, but most appeared undamaged, as would be the case if an asteroid had attacked. Many dives were conducted at this site during 1995 and no live adult bivalve specimens were ever observed, even when digging deep into the sediment. One species, *Paphies (Mesodesma) erycinaea*, was an exception. Since it occurs at water depths shallower than 2 m, this species is likely to be in a refuge where *A. amurensis* cannot feed at low tides or in rough weather (Robles *et al.* 1990). *N. nigellus* has been observed displaying a range of defence techniques (Lockhart & Ritz 1998) and this is likely to be the reason why adults of this gastropod can be found.

The layer of aerobic sediment suitable for burrowing bivalves is very thin at the site sampled and possibly most

of the Derwent River. This means that even adult prey might not be able to find a depth refuge by digging beyond the reach of the tube feet of *A. amurensis*, which is a very common avoidance technique of bivalves to asteroid predators (Kim 1969a, Allen 1983, Fukuyama & Oliver 1985). *A. amurensis* is known to be able to dig no deeper than 50 mm (Arima *et al.* 1972, Fukuyama & Oliver 1985). Increasing size of prey may increase the probability of location and capture when behavioural and depth refuges are not effective (Fukuyama & Oliver 1985). Furthermore, *A. amurensis* at this site probably prefers intermediate or larger sizes of a bivalve species whenever they can be captured, as has been shown to be the case for *A. rubens* (Allen 1983) and demonstrated experimentally for *A. amurensis* (Lockhart & Ritz 2001). Adults of these species are, therefore, extremely vulnerable to predation by *A. amurensis*. The aerobic layer thickens as the intertidal zone is approached and is likely to be another important factor allowing the survival of *P. (Mesodesma) erycinaea*, since this species is known to be a common prey item of *A. amurensis* (pers. obs.).

Field observations revealed that *A. amurensis* selected some prey types and avoided others. However, it must be kept in mind that observations of feeding in the field might provide a biased reflection of dietary choices if the times spent feeding on various prey differ (Day *et al.* 1995). Also, what has been interpreted as avoidance of prey might actually be avoidance by prey, since some are known to have active avoidance mechanisms.

With the exception of *N. nigellus*, the gastropods were shown to be avoided. Grannum *et al.* (1996) showed that *Sinuginella pygmaeioides* was also strongly avoided in their samples from Howrah Beach, southeastern Tasmania, in November. Feder (1959, 1963) described a range of defence techniques by gastropods which provide these species with a means of escape from *P. ochraceus*. The only two gastropods which are in a great enough abundance for inferences to be made in the present study are *N. nigellus* and *F. novaehollandiae*. However, the data for these two gastropods are not consistent with the hypothesis that gastropod escape behaviour can account for low selectivity by asteroids. As has already been mentioned, the gastropod *N. nigellus*, has been observed to display a full range of defence techniques. However, it is consumed by *A. amurensis* selectively. In contrast, *F. novaehollandiae* is strongly avoided, as would be expected from the findings of Feder (1959, 1963). Nevertheless, this species, which has been observed to be an occasional prey item of *A. amurensis*, was never observed to display defence techniques. It may have other forms of defence such as toxins. The abalone *Haliotis rubra*, for example, is known to possess a toxin in its epithelium which acts as a chemical deterrent to the asteroid *Coscinasterias muricata*, which only feeds on this species when preferred prey such as scallops are scarce (Day *et al.*, 1995). Bivalves were generally being consumed selectively or avoided by *A. amurensis*. *Mysella donaciformes* was strongly avoided, despite its great abundance. This result was also reported by Grannum *et al.* (1996), and Morrice (1995) did not record *Mysella* in stomach contents of *A. amurensis*.

Unfortunately, the  $E^*$  index is not amenable to parametric analyses (Lechowicz 1982). In addition, as the number of food types increases,  $E^*$  becomes vulnerable to sampling errors for those species which are rare in the diet and rare to moderately common in the environment (Lechowicz

1982), as would be the case in this investigation. Hence, making a depth comparison is difficult. Nevertheless, some differences in the diet spectrum of *A. amurensis* in 2 m compared to 5 m can be seen. Annelids were strongly selected at 2 m but apparently avoided at 5 m. Grannum *et al.* (1996) also showed that annelids were strongly avoided by *A. amurensis* throughout most of the year in their samples from Howrah and Richardsons Beaches. However, these differences could have been due to the nearly complete digestion of annelids recovered from stomachs and damage sometimes suffered by those from cores.

Diet and preferences for prey can vary with depth. Himmelman & Dutil (1991), in a study of the asteroids of the Gulf of St Lawrence, Canada, stated that changes in diet with depth strongly reflect changes in the prey available, as most prey species are highly localised in their distribution. However, in the present study, the relative proportions of *Chioneryx striatissima*, *Echinocardium cordatum* and the annelids did not appear to change with depth, probably due to the relative uniformity of the substrate. Thus, the reason for the changes in diet between *A. amurensis* at 5 m and at 2 m is probably due more to the fact that the majority of prey at Nutgrove Beach were relatively rare. *A. amurensis* is a highly mobile asteroid (Grannum, pers. comm.) which often continues to forage while still digesting a formerly engulfed prey item and then expels a number of prey items at once (Lockhart & Ritz 1998). Also, *A. amurensis* was observed on a number of occasions to move around and up the walls of aquaria while clutching a prey item at the oral region or with just one or two distal tube feet, even after it had already been feeding on the prey item for a number of hours (Lockhart & Ritz 2001.). Thus, *A. amurensis* at one of the depths investigated in the present study may actually have travelled quite a distance before either settling down to feed, or whilst continuing to digest, when it was examined. This habit could, therefore, explain why little difference in the diets of *A. amurensis* at the two depths was seen, especially since the horizontal distance from 2 m to 5 m is only approximately 5 m as the riverbed slopes steeply between these depths.

Two major threats have become apparent from the findings of the present diel study. Firstly, native predators may be outcompeted if they feed according to some diel pattern other than over the entire 24 h, e.g. if the diel feeding activity pattern of native predators includes periods of 100% inactivity. For example, *Coscinasterias muricata*, a native of Tasmania, forages only during daylight hours, while the nocturnal hours are spent either near the shelter of rocks or continuing to digest prey items captured during the day (Day *et al.* 1995); it is, therefore, likely to be outcompeted by this most adaptable introduced pest. Secondly, predator behaviours are thought to assume greater importance if refugia do not exist (Robles *et al.* 1990). Therefore, due to the high proportions of the population feeding throughout a 24-h period, its locally high densities, and the apparent lack of prey refuges, including temporal, depth and size, as an introduced predator, *A. amurensis* is predicted to have major detrimental effects on the native marine fauna of Tasmania.

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