Mortality rates of juvenile starfish *Acanthaster planci* and *Nardoa* spp. measured on the Great Barrier Reef, Australia and in Okinawa, Japan

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ABSTRACT

Acanthaster planci (L.) and *Nardoa novaecaladoniae* (Perrier, 1875) are two coral reef asteroids having planktotrophic and lecithotrophic larval development, respectively. Comparative sizes at metamorphosis are 0.5 to 0.7 mm for *A. planci* and 1.2 to 1.6 mm for *N. novaecaladoniae*. Mortality rates of small juveniles (one month old) of each species were measured experimentally in the field on the Great Barrier Reef, Australia. Mortality rates of *N. novaecaladoniae* were low (1.5 %.d^{-1}) compared to 7.8 %.d^{-1} for *A. planci*. Survival of the two species was similar between habitats. However, mortality rates of *A. planci* were highly variable both within-sites and between-sites within-habitats (fore reef 15 m depth, reef flat 2 m and back reef lagoon 12 m). There was no apparent effect of density of *A. planci* on mortality rates. Mortality is thought to be principally due to predation by infauna which are abundant in the coral reef rubble. A study of survival rates of newly metamorphosed *Nardoa* sp. (1.0 to 1.2 mm) in Okinawa, Japan, found very low mortality rates of just 0.2 %.d^{-1}. The abundance of potential predators among the rubble infauna was very low on the Okinawan reef compared to the Great Barrier Reef. These studies provide evidence of the importance of predation as a determinant of survival rates of small starfish and that a reproductive strategy providing for a large size at settlement facilitates greater survivorship.

RÉSUMÉ

Taux de survie de l'astérie juvénile *Acanthaster planci* et *Nardoa* sp. mesurés dans la Grande Barrière de Corail australienne et à Okinawa, Japon.

Acanthaster planci (1) et *Nardoa novaecaladoniae* (Perrier, 1875) sont deux astéries de récifs coralliens dont le développement larvaire est respectivement planctotrophe et lécithotrophe. Les tailles comparées à la métamorphose sont de 0,5 à 0,7 mm pour *A. planci* et de 1,2 à 1,6 mm pour *N. novaecaladoniae*. Les taux de mortalité des petits juvéniles (âgés d'un mois) de chaque espèce ont été mesurés expérimentalement sur le terrain dans la Grande Barrière de Corail australienne. Les taux de mortalité de *N. novaecaladoniae* étaient faibles (1,5 %.d^{-1})

comparés à 7,8 %.d^{-1} pour A. planci. La survie des deux espèces était semblable entre habitats. Par contre, les taux de mortalité de A. planci étaient très variables, aussi bien intra-sites qu'entre-sites intra-habitats (prérécif 15 m de profondeur, platier de récif 2 m et lagon de récif extérieur 12 m). La densité de A. planci n'avait aucun effet apparent sur les taux de mortalité. On estime que la mortalité est principalement attribuable à la prédation par l'endofaune qui abonde dans l'éboulis du récif corallien. Une étude des taux de mortalité de Nardoa sp. juste après la métamorphose (1,0 à 1,2 mm) à Okinawa au Japon a trouvé des taux de mortalité très faibles atteignant tout juste 0,2 %.d^{-1}. L'abondance des prédateurs potentiels parmi l'endofaune de l'éboulis était très faible au récif d'Okinawa par rapport à la Grande Barrière de Corail. Ces études mettent en évidence l'importance de la prédation comme déterminant des taux de survie des astéries juvéniles et indiquent qu'une stratégie reproductrice caractérisée par une grande taille lors de la fixation favorise une plus grande survivance.

INTRODUCTION

One of the most poorly understood aspects of the ecology of echinoderms, or most marine invertebrates for that matter, is the consequences of variability in survival rates of very small (*i.e.* immediately post-settlement) juveniles on population dynamics (Keesing and Halford, 1992 *a*). The factors which affect survival during this period are also poorly understood but have been the subject of a number of recent studies which have highlighted the importance of predation and habitat differences on survivorship of small sea urchins, starfish and holothurians (Rowley, 1989, 1990; Scheibling and Hamm, 1991; Keesing and Halford, 1992 *b*; Wiedermeyer, 1994).

Keesing and Halford (1992 *b*) described ontogenetic changes in survival among small juvenile crown-of-thorns starfish *Acanthaster planci* (L.) (Acanthasteridae) and attributed very high mortality rates mostly to predation. That study did not examine whether mortality rates varied spatially or whether starfish density was likely to be an important factor affecting mortality rates. These aspects are examined in the present paper along with a comparison of mortality rates with another coral reef starfish with a contrasting mode of development and initial juvenile size; *Nardoa novaecaladoniae* (Perrier, 1875) (Ophidiasteridae), on the Great Barrier Reef.

Results of an experiment conducted in Okinawa, Japan to measure mortality rates of another *Nardoa* species are also presented and the survival contrasted with that observed for *N. novaecaladoniae* on the Great Barrier Reef.

MATERIALS AND METHODS

Great barrier reef experiments

Experimental work was carried out in January 1992 at Davies Reef (18° 50' S, 147° 39' E) in the central Great Barrier Reef (GBR). The study included an examination of the influence of starfish density and habitat on survival of *Acanthaster planci* as well as the interspecific comparison with *Nardoa novaecaladoniae*. Comparisons of the morta-

lity rates of starfish were made by deploying laboratory cultured juveniles of each species in small cages in the field. Methods for culture of *A. planci* were similar to that described by Birkeland and Lucas (1990) and for *N. novaecaladoniae* similar to that described below for *Nardoa* sp.

Survival of the species was compared in each of two habitats: front reef slope at 15 m depth and reef flat at 2 m. Adults of both species and juveniles of *A. planci* have been found in both habitat types (J.K.K. pers. obs.). The habitat of small *N. novaecaladoniae* is unknown but is likely to be in either or both these habitat types. The survival of *A. planci* was also measured in a third habitat, the back reef lagoon at 12 m depth.

Starfish of both species (one month old and *ca*. 1 to 1.6 mm in diameter) were deployed in small plastic boxes (26 × 18 × 8 cm) with 200 µm mesh sides and lids (*see* Keesing and Halford, 1992 *b*). The boxes were filled with dead coral rubble from the deployment site by divers and brought to the surface tender. Boxes were filled to the extent that the rubble was not compacted when the lids were fitted. No attempt was made to remove plants or animals from the rubble as it was placed in the boxes, except for some very large crinoids. Cultured starfish were then introduced to the boxes of rubble and then lid fitted. The boxes containing rubble and starfish were then taken back to the seabed by divers. The boxes were fixed to concrete blocks on the seabed with rubber straps made from tyre tubes. The straps did not come into contact with the rubble or the starfish. Boxes containing the natural substrate and cultured starfish are referred to hereafter as TREATMENT boxes. Three TREATMENT boxes each containing 50 *A. planci* were deployed at each of four sites in each of the three habitats (36 boxes, 1800 juvenile starfish total). Two TREATMENT boxes containing 30 *N. novaecaladoniae* were deployed at each of three sites in just the two habitats described above (12 boxes, 360 juvenile starfish total).

CONTROL boxes contained sun-bleached coral rubble which had been subsequently conditioned in the laboratory in flow-through seawater aquaria for several weeks. Thus the substrata provided habitat and food (diatoms) known to support growth of *A. planci* but was thought to be largely free of other fauna. CONTROL boxes for *A. planci* (n = 4)

were only deployed at one site on the back reef lagoon at 12 m depth and for *N. novaecaladoniae* (n = 3) at one site on the reef flat. Limited availability of starfish for the experiments dictated that controls be deployed only in one habitat. Physical variables which may vary between habitats are water quality, movement and depth. As factors which may affect mortality were considered to be less important when compared to predation, which was adequately controlled for with single site measurements of non-predation induced mortality (*i.e.* handling, caging and other unknown effects). The effect of starfish density on survival rate was examined by deploying TREATMENT boxes at the same back reef lagoon site as the CONTROL boxes.

Four replicates of each of four densities of *A. planci* (5, 20, 50 or 200 per box) were deployed. CONTROL and TREATMENT boxes were deployed on the seabed for nine days, during which time the outside mesh-covered surfaces were brushed daily to prevent build up of silt. Boxes were collected and the contents fixed in formalin and sieved through varying grade mesh sieves from 6 mm down to 100 μm. Small starfish were recovered and counted by sorting all fractions of the sieved material under a stereo microscope. Other nonsessile fauna retained on mesh sizes of 1 mm and larger were also recovered and counted.

Okinawa experiment

The *Nardoa* species used for this study (Fig. 1) is believed to be an undescribed species resembling *N. tumulosa* Fisher 1917. Type specimens have been lodged with the Western Australian Museum (*WAM catalogue number WAM 135.92*) and await description. Adult Nardoa were collected at Sesoko Is, Okinawa and maintained at the University of the Ryukyus in recirculating seawater aquaria. Three or four starfish of each sex were induced to spawn by an injection of 10^{-3} M 1-methyl adenine into the coelomic cavity. A small quantity of mixed sperm solution was added to the buoyant bright orange eggs which were released about six hours after injection. Fertilised eggs were maintained in a recirculating seawater aquaria. Eggs hatched after about 24 h at 28 °C, developed rapidly to a typical lecithotrophic type reduced brachiolaria after 2 to 3 days and settled after 5 to 6 days. Ten days after the spawning date, settled starfish were deployed on the reef at Sesoko Is. adjacent to the Sesoko Marine Science Centre (*see* Sakai and Yamazato, 1984, for detailed description of the site) in boxes with 500 μm mesh sides and lids (Fig. 2). The experiment differed from that on the great barrier reef in that the TREATMENT boxes were left open (no lid). This was done to permit the entry of nektonic predators and was a result of preliminary inspection of the reef rubble indicating that relative abundance of potential infaunal predators compared to the great barrier reef was low. Leaving the TREATMENT boxes open was enabled by including in the design of the experiment a method of determining escape rates from the open boxes. In all, three types of boxes were used to measure mortality and to correct for the incidence of escape from the TREATMENT boxes:

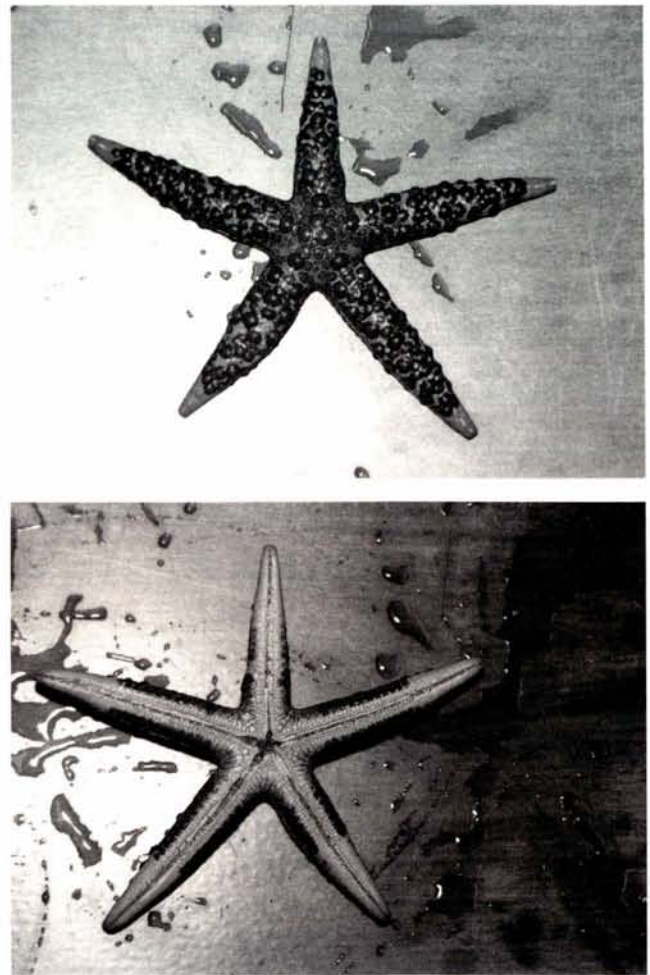CONTROL boxes measured 17 × 12 × 6 cm and had lids to prevent escape of starfish (n = 10).

Figure 1

Aboral and oral view of adult of Nardoa *sp. used in experiments in Okinawa. Radius (r) is approximately 6 cm.*

TREATMENT boxes were as above but without lids to allow free movement of starfish and predators (n = 14).

ESCAPE CONTROL boxes measured 30 × 20 × 9 cm with lids (n = 6). A TREATMENT box was placed inside this large box (*see* Fig. 2). This configuration allowed an assessment of the rates of escape from the TREATMENT. Using the escape rates as a correction factor it was possible to calculate the net mortality rate of the juvenile starfish in the TREATMENT boxes. Coral rubble was collected from around the deployment site as substrate for the juveniles. No attempt was made to remove plants or epifauna from the rubble in the TREATMENT and ESCAPE CONTROL boxes. For CONTROL boxes, rubble was taken ashore and visually inspected for any epifauna, which was removed before being returned to boxes. Thirty *Nardoa* sp. were placed in each of the boxes which were attached to bricks on the seabed at about 5 m depth. The water at the site was quite turbid over the study period. When possible the mesh on the boxes was brushed clean of silt every two days, however this was not done over the last few days of the experiment. After 11 days the boxes were recovered and the contents of each fixed in formalin and sorted under a stereo microscope. All *Nardoa* sp. and non-sessile fauna in the boxes were removed and counted as described above.
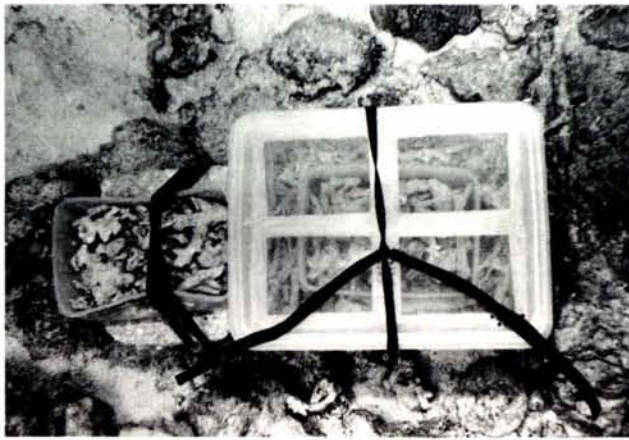
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Figure 2

TREATMENT (left) and ESCAPE CONTROL (right) boxes as deployed on seabed at Sesoko Is., Okinawa. By counting the number of surviving starfish which moved from the inner part of the ESCAPE CONTROL box into the outer part it was possible to partition reductions in abundance between the escape and mortality rates of starfish deployed in the TREATMENT box.

RESULTS

Great Barrier Reef

Interspecific comparison of survival

Mean survival of starfish in the CONTROL boxes was 74.5 % (SD = 10.6) for *A. planci* and 100 % for *Nardoa novaecaladoniae*. Survival of starfish from TREATMENT boxes pooled from all habitats and all sites was 22.5 % (SD = 16.9) for *A. planci* and 87.0 % (SD = 7.3) for *N. novaecaladoniae* (Fig. 3). When compared with the controls for each species these results constitute mortality 13 % or 1.5 %.d^{-1} for *N. novaecaladoniae* and 52 % or 7.8 %.d^{-1} for *A. planci*. Survival of *A. planci* in the front and reef flat habitats, where both species were deployed, differed little at 19.1 % (mortality = 8.6 %.d^{-1}).
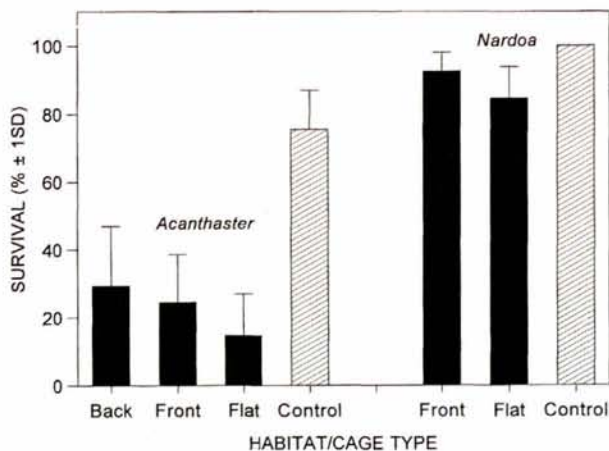

Figure 3

Comparison of survival (mean + 1SD) of juvenile Acanthaster planci *and* Nardoa novaecaladoniae *deployed in different habitats (sites within-habitats pooled) on Davies Reef during January 1992.*

Effect of habitat type on survival

No significant differences in survival between-habitats were detected for either species (two way ANOVA; p = 0.1296 for *N. novaecaladoniae*, p = 0.0524 for *A. planci, see* Fig. 3). There was no significant difference in survival of *A. planci* between-sites within habitats, (one-way ANOVA; front slope p = 0.1014, reef flat p = 0.2137, back reef lagoon p = 0.3844). Variability in mortality was very high at small spatial scales (within-sites) (Fig. 4). Between-site variability within habitats was also high with ratios of highest to lowest variances being 10 to 28 (Fig. 4). However, variability between habitats was low with variance ratios of 2 (Fig. 3). Mean survival of *A. planci* from TREATMENT boxes over nine days in each habitat were 24.0 % (front, SD = 17.2), 14.7 % (reef flat, SD = 13.4) and 29.3 % (back reef lagoon, SD = 17.6) (*see* Fig. 3). When compared with the CONTROLS, these levels of survivorship correspond to mortality 49.5 % or 7.3 %.d^{-1} (front), 59.8 % or 9.6 %.d^{-1} (reef flat) and 45.2 % or 6.5 %.d^{-1} (back reef lagoon).
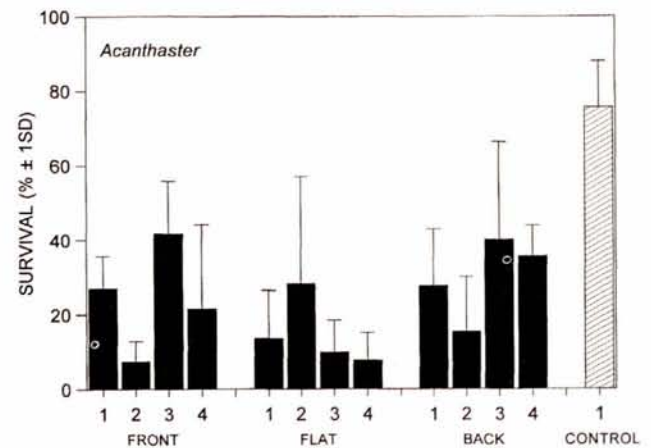

Figure 4

Survival (mean + 1SD) of juvenile Acanthaster planci *deployed at each site in different habitats on Davies Reef during January 1992.*

Effect of starfish density on survival

There was no significant difference in survival of *A. planci* between density treatments with survival varying between 35.5 % and 50.0 % (ANOVA; p = 0.8240) (Fig. 5). As expected, variability was much greater in the low density treatments due to the greater relative impact on mortality rate contributed by each individual death.

Possible effects of predation

Table 1 lists the numbers of the infauna in broad taxonomic groupings recovered with juvenile *A. planci* from the TREATMENT and CONTROL boxes. Few infauna were found in the CONTROL boxes compared to the large numbers of individuals in the TREATMENT boxes. Infauna consisted primarily of polychaete worms, crustaceans and gastropod molluscs. The inference from data on survival of *A. planci* are that some of these infauna would be respon-
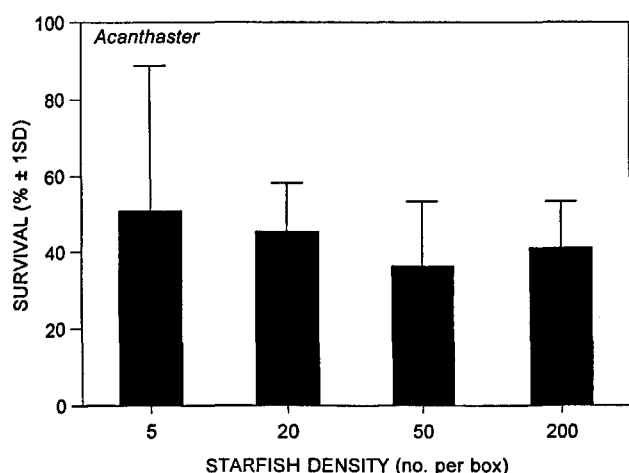
Figure 5

Survival (mean + 1SD) of juvenile Acanthaster planci *deployed at different densities on Davies Reef during January 1992.*
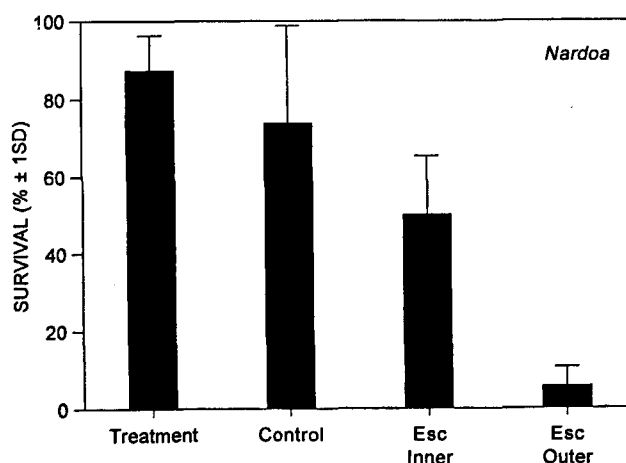

Figure 6

Survival (mean + 1SD) of juvenile Nardoa sp. deployed at Sesoko Is., Okinawa during June 1992. "Esc Inner" and "Esc Outer" refer to the inner and outer parts of the ESCAPE CONTROL boxes (see Fig. 2). High variability in survival rates in CONTROL and ESCAPE CONTROLS may be due to lack of water flow in some CONTROL boxes and all ESCAPE CONTROL boxes.

sible for the mortality rates attributed to predation. There were no strong differences in faunal type or abundance between habitats. Although a number of taxa varied in abundance inversely with surviving *A. planci* in the boxes, there were no significant correlations between the number of *A. planci* surviving in each TREATMENT box and the abundance of potential predators. Correlation coefficients for taxa tested were crabs (-0.26, $p > 0.1$), worms (-0.25, $p > 0.1$), stomatopods (-0.18, $p > 0.1$), gastropods (0.17, $p > 0.1$) and shrimps (0.31, $p > 0.05$).

Okinawa

Survival of *Nardoa* sp. is shown in Figure 6. Only 73.7 % and 55.7 % of starfish were recovered alive from the

CONTROL and ESCAPE CONTROL boxes respectively. The presence of some recently dead animals along with extensive clogging of the mesh suggested that mortality from lack of water exchange had occurred in these boxes late in the experiment when cleaning of mesh was not done. The higher rate of mortality in the ESCAPE CONTROL boxes can be explained by the greater amount of substrate and hence greater number of organisms that would have died and fouled the water.

In contrast, survival in the TREATMENT boxes was high (87.3 %) which is equivalent to a combined mortality and

Table 1

Contents of Acanthaster planci *TREATMENT and CONTROL boxes in three habitats after nine days at Davies Reef. CONTROL boxes were only deployed in the back reef lagoon habitat. *indicates asteroids other than experimental A. planci. Units are mean numbers + 1SD.*

Fauna recovered from rubble	Front slope n = 12	Reef Flat n = 12	Back reef lagoon n = 12	Controls n = 4
Worms				
mostly polychaetes	73.17 + 55.87	45.95 + 29.28	49.50 + 41.79	8.25 + 3.11
Crustaceans				
crabs	9.33 + 9.79	6.58 + 3.71	4.83 + 2.70	
shrimps	13.58 + 7.30	4.00 + 6.53	10.17 + 6.85	
others	29.83 + 10.58	26.08 + 12.47	24.25 + 16.21	4.00 + 2.55
Molluscs				
gastropods	46.25 + 28.24	80.17 + 57.60	53.50 + 28.96	1.75 + 1.79
opisthobranchs	2.25 + 3.09	0.08 + 0.28	0.58 + 0.76	
bivalves	6.00 + 6.23	5.25 + 5.05	3.08 + 3.25	
chitons	8.75 + 5.69	1.25 + 1.01	4.83 + 3.95	
Echinoderms				
echinoids	2.92 + 4.59	0.25 + 0.60	0.75 + 0.72	
ophiuroids	2.33 + 2.49	0.42 + 0.86	0.25 + 0.60	
holothuroids	0.08 + 0.28			
crinoids	0.08 + 0.28	0.08 + 0.28		
asteroids*	0.17 + 0.37	0.08 + 0.28		
Fish	1.08 + 0.95	0.25 + 0.43	0.92 + 0.95	

escape rate of 1.2 %.d^{-1}. The proportion of surviving star-fish that had moved into the outer part of the ESCAPE CONTROL boxes (10.2 %) can be used to estimate the escape rate from the TREATMENT boxes. However the possibility that movement rates may have been elevated by stagnant conditions inside the ESCAPE CONTROL boxes cannot be excluded.

Given the above, survival for the 10 day old *Nardoa* was estimated on that basis to be 97.5 % over the 11 day deployment. This constitutes a mortality rate of only 0.2.% · d^{-1}.

Relative abundance of potential predators

The abundance of non-sessile fauna other than the cultured starfish recovered from the TREATMENT and CONTROL boxes in Okinawa is shown in Table 2. A comparison of the non-sessile epifauna recovered from TREATMENT boxes at the end of the experiments in Okinawa and on the Great Barrier Reef is presented in Figure 7. Worms, mostly polychaetes were the most abundant taxa recovered in both Okinawa and the GBR. Gastropods were also abundant on the Great Barrier Reef. Few fish were found in any box but among all invertebrate taxa, abundances were much higher in great barrier reef samples than those from Okinawa. Although the volume of the boxes used on the great barrier reef was 2.7 times more than those used in Okinawa, the abundance of worms (up to 40 times greater) in the great barrier reef samples, gastropods (75 times), crabs (9 times) and shrimps (8 times) far exceeded this. The actual volume of substrata in each box was not measured.

DISCUSSION AND CONCLUSIONS

This study confirms the high mortality rates of 5 to 6 %.d^{-1} measured for *A. planci* of similar size and age by Keesing and Halford (1992 *b*) and provides detail on the spatial variability in mortality rates which was lacking from the previous study. Variability occurs over very small spatial

Table 2

Contents of TREATMENT and CONTROL boxes after 11 days at Sesoko Is, Okinawa. Units are mean numbers + 1SD.

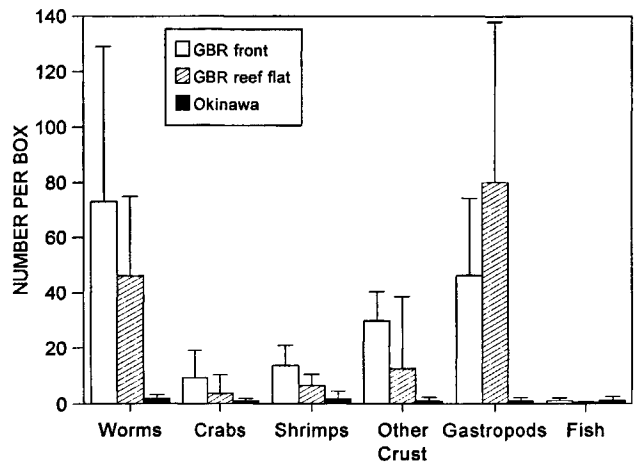| Fauna recovered from rubble	TREATMENT boxes n = 14	CONTROL boxes n = 10
Worms		
mostly polychaetes	1.78 + 1.31	1.70 + 0.95
Crustaceans		
crabs	1.07 + 0.83	0.20 + 0.42
shrimps	1.71 + 2.78	
galathaids	1.00 + 1.00	0.10 + 0.32
stomatopods	0.14 + 0.53	
pagurids	0.50 + 0.94	
Molluscs		
gastropods	1.07 + 1.21	1.40 + 1.07
Fish	1.21 + 1.31	

Figure 7

Comparison of common taxa of rubble infauna recovered from TREATMENT boxes (mean + 1SD) in experimental deployments of Nardoa novaecaladoniae *on the Great Barrier Reef and* Nardoa sp. *in Okinawa.*

scales across the range of habitats we examined. If this high mortality is mainly the result of predation, as suggested by Keesing and Halford (1992 *a*, *b*), then the observed variability is not surprising considering the potential variability in faunal composition among infauna assemblages when examined in small plots. Also given that movement rates of small echinoderms are very low (Rumrill, 1989; Keesing and Halford, 1992 *b*, Wiedermeyer, 1994) and that settlement rates of echinoderms vary spatially on coral reefs (Keesing *et al.*, 1993), localised variability in predator abundance will greatly affect survivorship. These factors will all contribute to high spatial variability in the abundance of juvenile echinoderms on coral reefs.

Variability in mortality rates for newly settled sea urchins has been recorded by Rowley (1990), who found mortality in kelp beds of 3.1 %.d^{-1} compared to 5.6 %.d^{-1} outside kelp beds. This difference is similar to our range of 6.5 %.d^{-1} (back reef lagoon) to 9.6 %.d^{-1} (reef flat). However, in our study within- and between-site replication in each habitat revealed that variability at the very small scale was at least equal to between habitat variability. Yokochi *et al.* (1988) recorded an order of magnitude variability in recruitment of small *A. planci* between the reef slope (0.82 .m^{-2}) and the reef flat (0.06 .m^{-2}) in southern Japan, although it is not known whether differential survivorship could explain this result as few details were provided.

This study found contrasting patterns for survivorship of *A. planci* and *N. novaecaladoniae* of similar age. We have found no other studies of survivorship between species of echinoderms conducted in the field under similar conditions. *Acanthaster planci* and *N. novaecaladoniae* have contrasting reproductive and larval development characteristics. *Acanthaster planci* produces many millions of small eggs (*ca.* 0.1 mm) giving rise to pelagic planktotrophic larvae which settle after two to three weeks and metamorphose into juveniles about 0.5 to 0.7 mm in diameter. In contrast *Nardoa novaecaladoniae* produces only a few hundred large eggs (*ca.* 0.75 mm) which give rise to pela-

gic lecithotrophic larvae which develop rapidly, settle after 5 to 6 days and are about 1.2 to 1.6 mm in diameter at metamorphosis. While we do not know if juvenile *N. novaecaladoniae* have chemical defences, it is likely that their relatively large size protects them from some predators and hence contributes to high survival rates. The results here confirm that lecithotrophic development, characterised by a tradeoff between low fecundity and large post-metamorphic size, provides the expected benefit of enhanced per capita survival. It is not possible to predict the comparative impacts of the differential mortality rates on eventual population size of two asteroids with contrasting development, since the growth rate of *N. novaecaladoniae* is presently unknown. However, if the estimated rates of mortality in this study are typical of the first month of life, a settlement of 1000 individuals of each species would result in 635 *N. novaecaladoniae* and just 87 *A. planci* surviving after 30 days.

While it is difficult to compare between experiments conducted in different places and times, the difference in mortality rates measured for the two *Nardoa* species, 1.5 %.d^{-1} versus 0.2 %.d^{-1} is significant. If all else were equal it would be expected that the mortality rate in Okinawa would have been higher given that the *Nardoa* sp. were a few weeks younger than those used on the Great Barrier Reef. Further, TREATMENT boxes used in Okinawa were open, allowing more mobile predators access to the starfish in addition to those predators actually introduced to boxes with rubble at the start of the experiment. Wiedermeyer (1994) used similar techniques to measure mortality of small holothurians and found higher predation when lids of cages were similarly removed. The results of our experiments (Keesing and Halford, 1992 *b*; Wiedermeyer, 1994; this study) on the Great Barrier Reef and in Okinawa lead to the conclusion that where predators among coral reef benthos are rare, survival should be much higher. This may in part explain the persistence of high densities of a number of echinoderms species on coral reefs in Okinawa relative to the Great Barrier Reef (Keesing, 1993).

Although we suggest that much of the high mortality experienced by *A. planci* in this study is due to predation, the actual numbers of infauna from the TREATMENT boxes were not correlated with survival of starfish in the boxes. This may be because epifauna were only classified into broad taxonomic groups irrespective of trophic category (which in most cases is not known), thus the epifauna would have included herbivorous and specialised feeders thus confounding the analysis. The other cause of mortality confounding this analysis may be death through contact with nematocysts of some sessile coelenterates. However,

regardless of whether mortality is due to motile or sessile predators, the combined effect on eventual adult population size will be significant. Wiedermeyer (1994) studied mortality rates of very small coral reef holothurians and found mortality rates of just 3.3 % month^{-1}, however 77 % of total mortality was attributable to predation. Scheibling and Hamm (1991) conducted caging experiments on very small urchins with a variety of potential predators and found significant rates of predation, particularly by crabs.

This study was not able to demonstrate any density-dependent influence on mortality of *A. planci*, however the techniques used may not have been entirely suitable because all densities tested could be considered "high" given the small size of the boxes and the variance structure observed in our results make experiments of this type difficult to interpret. Density-dependent mortality in newly settled non-sessile marine invertebrates such as abalone is known (McShane, 1991) and our results for starfish must be regarded as inconclusive at this stage. Despite these results further examination of mortality rates at very low densities of *A. planci* using much higher replication over longer periods may prove worthwhile given that the only replicates having 100 % survival were at the lowest density.

Acknowledgments

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