

## Taphonomy of crown-of-thorns starfish: implications for recognizing ancient population outbreaks

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**Abstract.** A field experiment was conducted to determine whether in situ mass mortality of *Acanthaster planci* subsequent to a simulated outbreak would leave a recognizable signature in surficial reef sediments. Constituent particle analyses comparing sediments that received starfish carcasses to those that did not revealed that, after a four year interval, the mass mortality was reflected by elevated abundances of starfish ossicles in 1–2 mm and 2–4 mm size classes, but not in > 4 mm and 0.5–1 mm size classes. Additional field study of starfish taphonomy revealed that the abundance of starfish ossicles in surficial sediments decreases through two orders of magnitude between two weeks and four years post-mortem, while tumbling experiments suggest that the size distribution of starfish ossicles is modified by physical processes: the < 0.5 mm size classes increases at the expense of the > 4 mm class. Taphonomic biasing increased the abundance of crown-of-thorns starfish (COTS) skeletal elements in the 0.5–1 mm size fraction, while the 1–2 mm size and 2–4 mm fractions produced the most reliable signature of starfish mass mortality based on element abundance. Our results demonstrate the importance of taphonomic processes in altering the original size frequency distribution of the COTS skeleton and their potential for biasing predictions of past population levels derived from constituent particle analyses of surficial reef sediments.

### Introduction

The ability of the reef sedimentary record to preserve evidence of population explosions of the crown-of-thorns starfish (*Acanthaster planci*) on the Great Barrier Reef has been the subject of intensive debate in recent years [e.g., Frankel 1977, 1978; Moran 1986; Moran et al. 1986; and two theme issues of Coral Reefs in vols 9 (1990) and 11

(1992)]. As pointed out by Wilkinson and Macintyre (1992), there is no dispute that *A. planci* has been part of the Great Barrier Reef ecosystem for many thousands of years. Rather, researchers disagree whether sedimentologic analysis of reef sediments provides conclusive evidence that the two damaging outbreaks in the last 35 years have historical precedent. All researchers agree that an assessment of the history of population explosions is crucial information for those determining contemporary management strategies (e.g., Kenchington 1978, 1987; and Kenchington and Kelleher 1992).

Establishing a relationship between outbreak events and the contribution of skeletal elements to surface sediment is a necessary though not sufficient prerequisite to any conclusions concerning past outbreaks based on analyses of subsurface sediments obtained from cores. Attempts to establish this relationship by Frankel (1977, 1978) and Walbran et al. (1989a, b) have been criticized for a variety of reasons. Among these is that two critical assumptions are invalid: (1) population outbreaks end with a mass mortality of adult starfish in situ; and (2) a post-outbreak mass mortality will contribute enough skeletal elements to significantly elevate total element numbers above background levels (see Moran 1986, 1992; Keesing et al. 1992; Pandolfi 1992). In response to this concern, Henderson and Walbran (1992) acknowledge the paucity of data concerning mortality patterns of *A. planci* (but see Moran, 1992) and suggest that, in the absence of these data, the incidence of skeletal elements in surface sediment may offer a perspective on mortality patterns. Subsequent data comparing the results of analyses of surficial sediments obtained from reefs with different outbreak histories, including Holbourne Island reef, where in situ mass mortality was certainly due to a mass poisoning program (Zann and Weaver, 1988), are presented by Henderson (1992). Henderson (1992) concludes that “evaluation of the incidence of *A. planci* skeletal elements in surface sediments has the potential to indicate outbreak history for individual reefs for which observational data on population levels is lacking” (p 107).

While the methodology utilized on Holbourne Island reef addresses the effect of in situ mass mortality on sediment composition, the approach utilized for the remaining 11 reefs examined by Henderson (1992) does nothing to mitigate concerns over the validity of both assumptions listed. What is required is a comparative analysis of sediments known to have received skeletal elements from starfish whose density is at outbreak proportions with sediments obtained from a similar habitat where the phenomenon has not occurred. The purpose of this study is to conduct this type of analysis. To achieve our objective, surficial sediments obtained from three permanent 4 m<sup>2</sup> quadrats were analyzed four years after dead starfish at outbreak density were emplaced and incorporated into the sediment. Comparison with results obtained from nearby control quadrats that did not receive additional starfish suggests that outbreak densities of dead starfish leave a recognizable signature in surficial sediments. However, this is not true for all size classes analyzed. We therefore present results on the size frequency distribution of COTS skeletal elements before and two weeks after a simulated outbreak and relate them to a tumbling experiment that investigates the effect of agitation on the size frequency distribution of the starfish skeleton.

## Methods

During December 1988, Moran (1992) established three permanent 4 m<sup>2</sup> quadrats in 9 m of water in the lagoon behind the eastern perimeter of Little Broadhurst Reef (Fig. 1). Nine freshly-killed starfish were placed randomly in each quadrat to simulate post-outbreak mass mortality and were observed to decay, disarticulate and become incorporated into the sediment over a period of seven days. In December, 1992, we established three 4 m<sup>2</sup> control quadrats in 9 m of water approximately 250 m south of the permanent quadrats. Five shallow (15 cm) sediment cores were obtained from each quadrat at both locations by SCUBA divers using a PVC pipe (diameter 15 cm) fitted with a removable watertight lid. The substrate at both locations consisted of a relatively coarse (see later) bioturbated calcareous sand.

Methods of sample preparation and analysis followed that of previous constituent particle analyses conducted by Walbran et al. (1989a, b) and Henderson (1992) to facilitate general comparisons of the results. Samples were oven-dried and sieved into >4 mm, 2–4 mm, 1–2 mm and 0.5–1 mm size classes. Each size class was weighed and COTS ossicles were identified using the criteria outlined by Walbran (1987). The numbers of COTS ossicles in each size class were converted to numbers of skeletal elements of COTS/kg (Table 1). An analysis of variance (ANOVA) was performed on square root-transformed data (closest approximation to normality). Cores within each quadrat were pooled in the analysis.

## Results

Previous workers have combined the four size classes listed when reporting values for skeletal elements of COTS/kg (e.g., Walbran 1989a, b; Henderson 1992). For all the size classes listed in Table 1 mean values based on 15 samples are 12.34 (SE = 2.73) skeletal elements of COTS/kg at the control site and 17.10 (SE = 2.80) skeletal elements of COTS/kg at the experimental site. The results

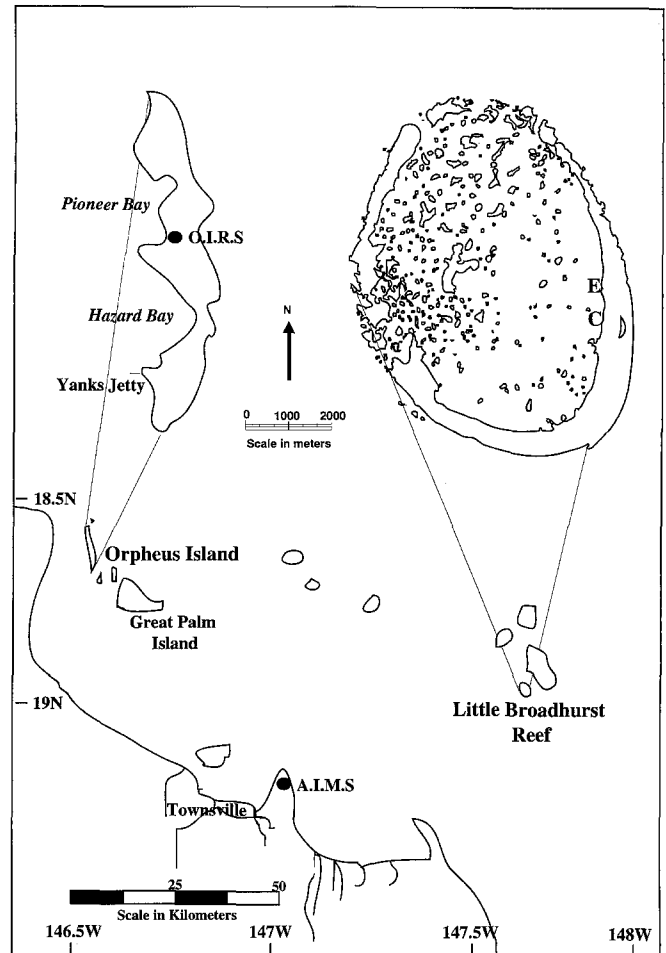


Fig. 1. Field localities. Fieldwork adjacent to Orpheus Island was supported by the Orpheus Island Research Station (O.I.R.S.). At Little Broadhurst Reef: E, experimental site; C, control site

of our ANOVA using the data from the four different size classes are presented in Table 2. There is a significantly greater likelihood ( $P = 0.0479$ ) of deposition of disarticulated *A. planci* into the sediments four years following the simulated outbreak than before the simulated outbreak. There are also significant differences in the number of skeletal elements of different size classes ( $P < 0.0001$ ). The nature of the size class versus treatment interaction ( $P = 0.0266$ ) is illustrated in Fig. 2: the two middle size classes (1–2 mm and 2–4 mm) show a significant difference between treatments whereas the >4 mm and 0.5–1 mm size classes do not. Chi square analysis of the sediment grain size distributions showed no differences between the experimental and control sites at Little Broadhurst Reef ( $P = 0.2428$ , Fig. 3).

## Discussion

During 1987, Little Broadhurst Reef experienced a COTS outbreak of extremely high proportions (Moran and De'ath 1992). Density of starfish was estimated to be 71,444 km<sup>-2</sup>; five times greater than on the other out-

**Table 1.** Data obtained from experimental and control sites established on Little Broadhurst Reef. Values are the number of skeletal elements of COTS/kg

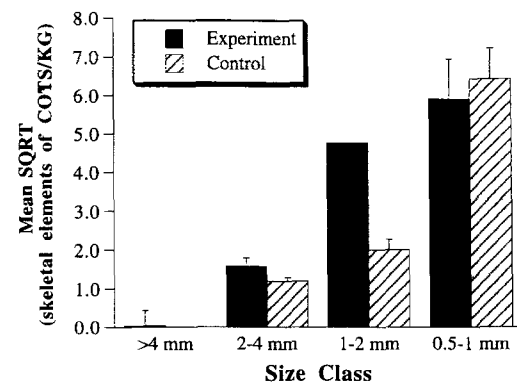
Experimental site:				
replicate	> 4 mm	2–4 mm	1–2 mm	0.5–1 mm
1	8.55	0.00	9.29	2.68
2	0.00	0.00	13.69	37.31
3	0.00	0.00	15.75	41.26
4	0.00	6.53	40.96	24.49
5	0.00	0.00	14.76	40.95
6	0.00	0.00	8.57	21.79
7	0.00	0.00	32.60	85.40
8	0.00	0.00	40.54	96.34
9	0.00	0.00	33.78	52.84
10	0.00	7.24	26.75	19.24
11	0.00	8.60	14.28	55.28
12	0.00	0.00	41.07	18.17
13	0.00	0.00	28.03	34.29
14	0.00	8.71	16.67	41.71
15	0.00	0.00	37.88	39.78
Average	0.57	2.07	24.95	40.77
Standard deviation	2.21	3.59	12.18	24.70
Control site:				
replicate	> 4 mm	2–4 mm	1–2 mm	0.5–1 mm
1	0.00	6.43	8.38	58.62
2	0.00	0.00	3.88	61.41
3	0.00	0.00	0.00	74.94
4	0.00	0.00	5.34	53.33
5	0.00	0.00	0.00	58.62
6	0.00	7.49	5.14	16.30
7	0.00	0.00	0.00	63.06
8	0.00	0.00	6.20	68.26
9	0.00	0.00	2.14	45.37
10	0.00	0.00	0.00	28.82
11	0.00	0.00	5.26	39.02
12	0.00	2.65	8.33	13.25
13	0.00	0.00	3.93	40.92
14	0.00	2.27	10.62	20.16
15	0.00	0.00	3.96	16.49
Average	0.00	1.26	4.21	43.90
Standard deviation	0.00	2.48	3.36	20.75

breaking reefs surveyed. The reef was estimated to have almost 430,000 individual starfish: fifty times the number observed on non-outbreaking reefs surveyed during the same study (Moran and De'ath 1992). Moreover, the highest densities were observed along feeding fronts on the southeast side of the reef, in the vicinity of our sample sites. Thus, data obtained from the control site represents (in terms of the abundance of COTS) sediment composition subsequent to the 1987 mortality event, while data obtained from the experimental site represent sediment composition resulting from the 1987 mortality plus the simulated outbreak approximately 1.5 years later.

Note that overall element abundance at the experimental and control sites (17.10 COTS/kg and 12.34 COTS/kg, respectively) is similar to that reported by Walbran et al. (1989b) and Henderson (1992) for reefs with previous histories of outbreaks (Table 3). The fact that a treatment effect was observed on Little Broadhurst Reef subsequent to the simulated population outbreak means

**Table 2.** ANOVA results for square root transformation of number of skeletal elements of COTS/kg (closest approximation to normality). These results indicate that there is a marginally higher proportion of COTS skeletal elements in surficial sediments after the simulated outbreak than before, but the frequency of skeletal elements retained varies enormously with size class

Source	df	Sums of squares	Mean square	F-value	P-value
Treatment (A)	1	3.4033	3.4033	4.59	0.0479
Size class (B)	3	123.4300	41.1420	55.48	0.0000
A*B	3	8.9013	2.9671	4.00	0.0266
Error	16	11.866	0.7416		



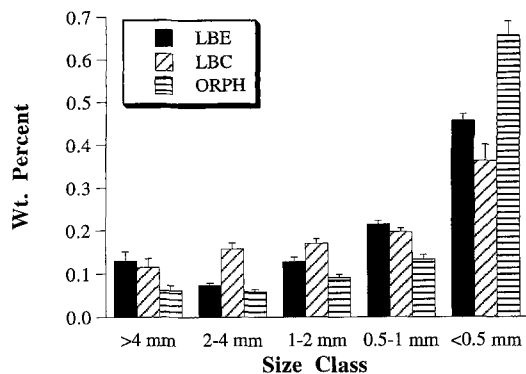
**Fig. 2.** Results of COTS skeletal elements abundances from each size class for both the experimental and control sites at Little Broadhurst Reef. Abundances are pooled from results of 15 cores (3 quadrats  $\times$  5 cores/quadrat) per treatment. Error bars are standard errors

that outbreak events may be recognizable over a four year interval. Using Frankel's (1977, 1978) data, Moran et al. (1986) demonstrated that the presence of starfish elements in surficial sediments was independent of the recent outbreak history of the reefs under study. Moreover, note the high variability apparent in Table 3: reefs with histories of high intensity outbreaks contain a range of 11.2–21.7 skeletal elements of COTS/kg, those with histories of low to moderate intensity outbreaks contain a range of 3.1–7.8 skeletal elements of COTS/kg, and reefs that have not experienced an outbreak contain a range of 0.0–7.50 skeletal elements of COTS/kg. These results suggest that the correlation between outbreak history and the abundance of starfish elements in surficial sediments may be masked by high variability or patchiness of the starfish elements. How do we reconcile these conflicting observations? Further analyses of the taphonomy of crown-of-thorns starfish provide some answers.

#### Significant loss of skeletal elements

An individual crown-of-thorns starfish is composed of over 25,000 individual elements (Keesing personal communication) and, during an outbreak, the number of individual starfish varies through several orders of magnitude (see Moran and De'ath 1992). Yet ossicles constitute a min-

### Grain Size Distributions



**Fig. 3.** Grain size distributions at sites established on Little Broadhurst Reef and adjacent to Orpheus Island. Chi square analyses of these distributions showed no difference between the experimental and control sites at Little Broadhurst Reef (LBE and LBC, respectively,  $P = 0.2428$ ). The distributions obtained from the sites at Little Broadhurst Reef were distinct from that obtained from Orpheus Island site (ORPH,  $P = 0.0035$ ). Error bars are standard errors

**Table 3.** Abundance of crown-of-thorns starfish ossicles retrieved from surficial sediments  $> 0.5$  mm in size and obtained from reefs with differing outbreak histories. Data from Henderson (1992); Walbran et al. (1989a, b) and this study

	Skeletal elements of COTS/kg	Standard deviation
High intensity:		
Green Island	21.7	23.50
Holbourne Island	13.1	6.10
Hope	16.0	9.37
John Brewer	11.2	21.50
Little Broadhurst <sup>a</sup>	12.34	21.13
Moderate to low intensity:		
Centipede	3.4	1.27
Davies	7.8	2.31
Gannet Cay	3.1	2.73
22-110	5.5	1.82
No outbreak		
Heron Island	0.04	0.00
Lady Musgrave	0.00	0.00
Myrmidon	7.50	3.85

<sup>a</sup> Average of 15 replicates from the control site

iscule and highly variable percentage of reef sediments. For example, the highest level of COTS ossicles reported for any reef is an average of 21.7/kg (standard deviation = 23.5) from 46 samples obtained from Green Island Reef, which experienced two major COTS outbreaks since 1962 (Table 3) (Walbran et al. 1989b). In order to investigate the discrepancy between the number of ossicles available for dissemination into reef sediments and the number observed subsequent to a mortality event, a second field experiment was performed adjacent to Orpheus Island (Fig. 1), where no previous outbreaks of starfish have been recorded (research station staff, personal communication).

Following the methodology described above, nine freshly killed starfish were placed randomly in each of

**Table 4.** Abundance of crown-of-thorns starfish ossicles in surficial sediments after two weeks post-mortem in Pioneer Bay, Orpheus Island, Great Barrier Reef. Values are the number of skeletal elements of COTS/kg. Note extreme variability within each size class

Replicate	> 4 mm	2-4 mm	1-2 mm	0.5-1 mm
1	0.00	37471.16	54.19	2316.22
2	146.34	759.41	389.00	295.62
3	0.00	688.86	51.62	176.94
4	37.85	1663.45	1649.83	408.47
5	0.00	156.20	73.52	90.48
6	0.00	3007.35	658.14	990.10
7	39.10	1858.27	497.80	526.60
8	0.00	764.58	1639.55	101.63
9	1567.00	878.45	2566.56	155.84
10	33.59	330.93	226.24	29.41
11	0.00	24.42	28.36.62	542.05
12	20.86	29.35	1010.53	326.48
13	15.75	1951.59	1543.87	24.65
14	15.38	908.94	7382.76	19.23
15	10.04	0.00	955.84	42.25
Average	125.73	3566.20	1435.74	403.06
Standard deviation	400.44	9473.88	1867.80	592.70

three 4 m<sup>2</sup> quadrats to simulate post-outbreak mass mortality. The substrate consisted of a bioturbated, relatively fine-grained calcareous sand with a grain size distribution distinct from that at Little Broadhurst Reef (Chi square analysis,  $P = 0.0035$ , Fig. 3). The starfish were allowed to decay for a two week interval. Although few of the starfish were still recognizable within the quadrats, individual spines and dental ossicles were readily apparent. The sediment was processed and analyzed as described. After two weeks post-mortem, the abundance of ossicles in the sediment is far greater than any data reported from the GBR (Table 4). Note also the extreme variability among replicates and that the majority of ossicles were counted in the 1-2 mm and 2-4 mm size classes. Henderson (1992, p 105) states that the best record of skeletal elements occurred in the 0.5-1 mm size class; our data from Little Broadhurst Reef, particularly from the control site, corroborate the statement (Table 1). These results suggest that, in addition to removing starfish ossicles from reef sediment in an area where mass mortality has occurred, taphonomic processes alter the original size distribution of skeletal components by degradation to smaller size classes and size-selective removal of COTS skeletal elements (either laterally or vertically) by physical and or biological processes. For example, some of the sediment burrowing callinastid shrimps in this region can rapidly modify the grain size distribution of surface sediments by physically removing larger grains to the sub-surface (Tudhope and Scoffin 1984). We conducted a series of tumbling experiments to further investigate physical degradation of COTS skeletal elements.

#### Change in size frequency distribution of skeletal elements

Tumbling experiments have a relatively long history of application to investigations of the behavior of bioclastic

particles (see for example the pioneering work of Chave 1964). Tumbling experiments have also been used to explore the effect of variations in skeletal durability and decay time on the preservation potential of marine invertebrates (see for example Allison 1986; Kidwell and Baumiller 1990; Greenstein 1991).

We conducted a series of tumbling experiments on a total of 17 crown-of-thorns starfish. Freshly killed starfish were preserved in 95% ethanol for transport to the lab and each was subsequently immersed in household bleach to remove all organic material. This treatment resulted in an initial "sample" of skeletal material much like that available in natural conditions after 7–9 days of decay (Moran 1992). Each skeleton was dried for several days under a laboratory hood, weighed and then placed in room temperature (22 °C) synthetic seawater (instant ocean) in a plastic tumbler attached to a variable speed motor. A 3 cm-wide "shelf" was glued along the length of the tumbler interior to ensure that the contents would tumble once with each rotation rather than slide around the outer wall. Five trials of 1, 10 and 100 h each were run at 25 rpm. This tumbling speed was selected as it provided moderate agitation to the contents of the tumbler. At the end of each trial, the contents of the tumbler were wet-sieved through a stack of nested sieves, and the stack was dried for several days under a laboratory hood. Once dry, the > 4 mm, 2–4 mm, 1–2 mm, 0.5–1 mm and < 0.5 mm size classes were weighed. Results are expressed as weight percent of each skeleton to normalize different sizes of starfish. Two additional starfish were subjected to the same bleaching process, and the size distributions of their skeletal elements were determined to compare to that obtained to the tumbled specimens.

Analysis of variance of the square root transformed tumbling data showed a significant effect for size class, tumbling time and their interaction (Table 5). Size class differences merely reflect the original distribution in the tumbled starfish. The significant tumbling time effect means that degradation of the starfish elements was caused by the tumbling. What is most interesting is the interaction between tumbling time and size class (Fig. 4). The > 4 mm size class showed a steady decrease with increased tumbling time. Over all tumbling intervals the largest percentage of starfish skeleton was present in the 2–4 mm size class. Both the 2–4 mm and the 0.5–1 mm size classes showed little change over 100 h of tumbling. The 1–2 mm size class increased between 1 and 10 h of tumbling, but bounced back to original levels between 10 and 100. Finally, the

**Table 5.** Analysis of variance of square root transformed tumbling experiment data

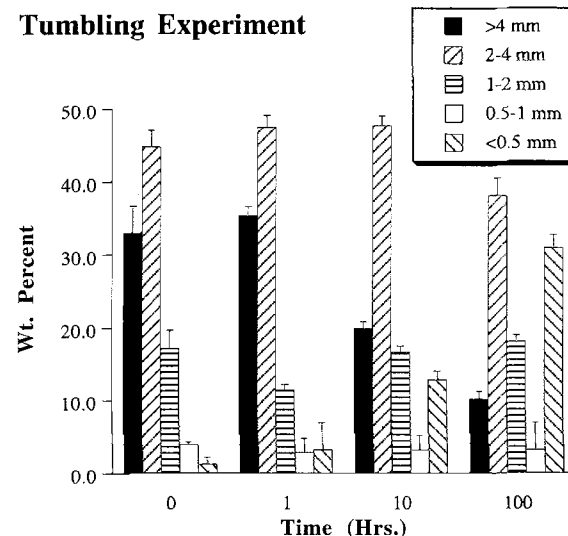
Source	df	Sums of squares	Mean square	F-value	P-value
Size class (A)	4	272.22	68.054	771.53	0.0000
Tumbling time (B)	3	1.5686	0.52288	5.93	0.013
A*B	12	88.793	7.3994	83.89	0.0000
Error	65				

< 0.5 mm size class increased steadily through each tumbling interval.

The results from this study can be summarized by the following statements:

1. Tumbling experiments show that there is a treadmill effect for the size breakdown in COTS ossicles. Over a 100 h tumbling interval, the < 0.5 mm size class increases at the expense of the > 4 mm size class while the other size classes remain at nearly constant levels.
2. Two weeks after a simulated outbreak event the order of abundance of COTS ossicles among size classes is 2–4 mm > 1–2 mm > 0.5–1 mm > 4 mm.
3. Four years after a simulated COTS outbreak, significantly elevated levels of COTS ossicles occur in the 2–4 and 1–2 mm size classes, while abundances of COTS ossicles in the > 4 mm and 0.5–1 mm size classes remained constant.

The great predominance of the 2–4 and 1–2 mm size classes segregated from sediments obtained two weeks after a simulated mass mortality (Orpheus Island) reflects the initial alteration of the original size frequency distribution of a starfish skeleton by the relatively rapid degradation (or removal) of the > 4 mm size class. We note that this result is corroborated by the results of the tumbling experiment (Fig. 4): after 100 h agitation, one would find that COTS ossicles in the 2–4 and 1–2 mm size classes predominate in a constituent particle analysis of sediments > 0.5 mm in size. Although ossicles from both experimental (1988 simulated outbreak) and control (1987 outbreak) sites at Little Broadhurst Reef were most prevalent in the 0.5–1 mm size class, the 2–4 and 1–2 mm size classes showed a significantly greater number of COTS ossicles in the 1988 simulated outbreak. A possible explanation for these results is that the 1987 outbreak is more represented



**Fig. 4.** Results of COTS tumbling experiment. Five starfish were tumbled for 1, 10 and 100 hours, two starfish (not tumbled) provide the original size frequency distribution. Error bars are standard errors

in the 0.5–1 mm size fraction while the 1988 simulated outbreak is more represented in the 2–4 and 1–2 mm size classes. We reject this hypothesis, however, because of the great difference in temporal scale between the results obtained at Orpheus Island (two weeks) and those obtained from Little Broadhurst Reef. Specifically, in order for the hypothesis to be correct, there would have to be some threshold time interval, presumably in the time between four and five years, for the transfer to the lower size class to occur.

Alternatively, we believe the 2–4 and 1–2 mm size classes have explanatory power for COTS skeletal element densities, whereas the 0.5–1 mm size class does not. The results suggest to us that the best indicators of COTS skeletal densities can be found in the 2–4 and 1–2 mm size classes. These are most abundant initially in the simulated, two-week, COTS outbreak; they showed significant differences in abundance before versus four years after the simulated outbreak at Little Broadhurst Reef; and processes of skeletal degradation (simulated by the tumbling experiments) predict no temporal changes in their relative abundances. Thus they should provide an accurate signature of their original relative abundances. Although the 0.5–1 mm size class also showed constant abundance during the tumbling experiments, it showed no significant difference before versus four years after the simulated outbreak at Little Broadhurst Reef.

Previous workers (e.g., Walbran et al. 1989a, b; Henderson 1992; Henderson and Walbran 1992) have pooled all size classes  $> 0.5$  mm when determining the number of COTS skeletal elements in a sediment sample. Moreover, Henderson (1992, p 105) comments on the predominance of elements in the 0.5–1 mm size class. While we acknowledge that this size class appears to contain the most skeletal elements, we argue that this is caused by a taphonomic bias in the breakdown of these organisms. We cannot identify whether the biasing is due primarily to physical factors (e.g., degradation, selective transport) or biological factors (e.g., selective removal by organisms).

There is a greater proportion of COTS skeletal elements in the 0.5–1.0 mm size class than one would reasonably expect from both the breakdown of skeletal elements two weeks after a simulation and their continued breakdown as evidenced from the tumbling experiments. Thus the 0.5–1.0 mm size class represents a biased sampling of COTS which, when pooled with other size fractions, would tend to overestimate the skeletal densities of COTS. We suggest that future work should take into account these biases, and past work be re-analyzed based on the results of these size frequency distributions, specifically by comparing COTS abundances within the 1–2 and 2–4 mm size classes.

We also note the limitations of the results of our study. We have identified the 2–4 and 1–2 mm size classes as the most important for investigating the relationship between original population size and the abundance of COTS skeletal elements in the surficial sedimentary record. A similar assessment needs to be made for the subsurface burial of COTS. Future experiments might include a simulated outbreak which is experimentally buried in the substrate and then sequentially sampled over

a several year interval. This would provide the very vital linkage needed between taphonomic biasing occurring in the surficial sedimentary record and that occurring in the subsurface sedimentary record. (In this way we can come to a greater appreciation of the nature and significance of the number of COTS skeletal elements per kilogram in the sedimentary record of the Great Barrier Reefs.)

The results of our field and laboratory investigations of the crown-of-thorns starfish suggest that taphonomic processes affect the size distribution of skeletal material subsequent to a mortality event. Hence an analysis of COTS elemental size frequency distributions is an essential component for recognizing past COTS outbreak events in surficial sediments. The results of the tumbling experiment suggest that the most abundant record of the dissemination of innumerable ossicles of *Acanthaster* following an outbreak may reside in the  $< 0.5$  mm size class.

## Conclusions

1. A simulated outbreak and subsequent mass mortality of *Acanthaster planci* on Little Broadhurst Reef was recognizable in the 2–4 and 1–2 mm size classes of surface sediments after a four year interval using sediment constituent particle analysis.
2. Field experiments conducted adjacent to Orpheus Island and at Little Broadhurst Reef revealed that abundance of starfish ossicles in surficial sediments decreases through two orders of magnitude between two weeks and four years post-mortem.
3. Tumbling experiments (100 h duration) revealed that starfish skeletal elements degrade into smaller size classes with increasing agitation. The weight percent of the  $< 0.5$  mm size class increased at the expense of the  $> 4$  mm size class, while the weight percent of intervening size classes remained nearly constant.
4. Taphonomic biasing increases the relative abundance of the 0.5–1.0 mm size class. The most reliable signature for elemental abundances appears to be from the 2–4 and 1–2 mm size classes. Future studies relating weight percent of COTS ossicles to COTS skeletal densities should use these size classes. Previous work has concentrated on the size classes where most elements are found (0.5–1 mm). Our results show, however, that these abundances are taphonomically enhanced and may prove to be misleading in estimating COTS elemental abundance.
5. Our results do not necessarily support the hypothesis that COTS outbreaks have occurred in the geologic past. We have demonstrated that the 1–2 mm and 2–4 mm but not the 0.5–1 mm size classes record elevated COTS skeletal element abundances in surficial sediments four years after a simulated outbreak. However we conclude that the size class frequency distribution of COTS skeletal elements from sediments is important and must be included in any analysis of COTS skeletal abundances. In previous studies, size classes have been pooled and thus the results may include a taphonomic bias. Re-analysis of these data bases with respect to size class frequency distribution,

are needed before the broader question of the antiquity of COTS outbreaks can be interpreted more accurately. We conclude that sediment constituent particle analysis of reef sediments has yet to demonstrate accurately the antiquity of COTS outbreaks.

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