Walbran + Henderson (1988a)

THE STATUS OF THE CROWN-OF-THORNS STARFISH (*ACANTHASTER PLANCI*) IN THE GREAT BARRIER REEF, AUSTRALIA, ASSESSED FROM THE SEDIMENT RECORD OF JOHN BREWER, GREEN ISLAND AND HERON ISLAND REEFS. A REPORT TO THE GREAT BARRIER REEF MARINE PARK AUTHORITY, TOWNSVILLE.

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Report to GBRMPA

Summary

Over the last 30 years the crown-of-thorns starfish (*Acanthaster planci*) has caused extensive damage to many reefs in the Great Barrier Reef Province. John Brewer Reef and Green Island Reef are among those worst affected by *A. planci* predation during this period. Surface sediment from these two reefs was exhaustively picked for *A. planci* skeletal elements and found to be greatly enhanced in element abundance when compared to that of Heron Island Reef which has historically maintained very low-density starfish populations. Carbon-14 accelerator mass spectrometry (AMS) dating indicates that skeletal elements from the surface sediment of John Brewer and Green Island Reefs are of contemporary age. Core sampling shows that subsurface sediment at John Brewer and Green Island Reefs contains *A. planci* element densities comparable to those found in the surface sediment at these localities. Physical and biological reworking of elements within the sediment precludes the recognition of individual outbreaks in core stratigraphy. AMS element dates and bulk sediment dates, obtained by conventional carbon-14 radiometry, show that subsurface elements are generally prehistoric and conform to an age structure preserved in the sediment pile. Assessed on a time-averaged basis, the density and distribution of subsurface elements suggest that *A. planci* outbreaks are not a recent phenomenon, but have been an integral part of the ecosystem for at least 7000 years on John Brewer Reef and 3000 years on Green Island Reef.

Introduction

The crown-of-thorns starfish (*Acanthaster planci* L.) has been responsible for the widespread destruction of scleractinian corals on many reefs in the Indo-Pacific region over the last 30 years. Coral devastation directly attributable to *A. planci* predation has occurred in areas as widespread as Micronesia (Chesher 1969; Marsh and Tsuda 1973), southern Japan (Nishihira and Yamazato 1974; Yamaguchi 1987), Polynesia (Devaney and Randall 1973) and Australia's Great Barrier Reef (GBR) (Endean and Stablum 1973; Pearson 1981; Done 1985).

Two distinct outbreaks have been recorded on the GBR since 1962. On both occasions, the outbreaks were first observed on Green Island Reef (Fig. 1) having apparently originated on reefs immediately to the north (Moran 1986). Following the initiation of each outbreak, reefs to the south have progressively been affected. To date, the majority of *A. planci* outbreaks have been reported between Princess Charlotte Bay (14°15'S) and Bowen(20°01'S) (Moran 1987; Fig 1). Isolated outbreaks have also been recorded in the Swain Reefs Complex, north-east of Gladstone (Pearson and Garrett 1978; Endean and Cameron 1985; Great Barrier Reef Marine Park Authority (GBRMPA) unpublished data base; Fig. 1).

Results from recent surveys (COT-CCEP Crown-of-thorns Study 1986-7) reveal considerable spatial variation in outbreak magnitude. Clearly however, the central third of the GBR has sustained most damage with 35% of reefs considered to be seriously affected and 30% affected to a lesser degree (Moran 1987).

Much of the current debate centres on the time-scale over which these outbreaks have occurred. Some commentators (Endean and Stablum 1975; Cameron and Endean 1981; Endean and Cameron 1985) regard the massive coral damage in the GBR as a recent phenomenon, directly attributable to the activities of man following European settlement of the north Queensland coast. Conversely, outbreaks may be long-standing and an integral part of the ecological framework under which the GBR has developed (Potts 1981).

Assessment of the sediment record offers a potential means of examining past patterns of *A. planci* activity on the GBR. A basic

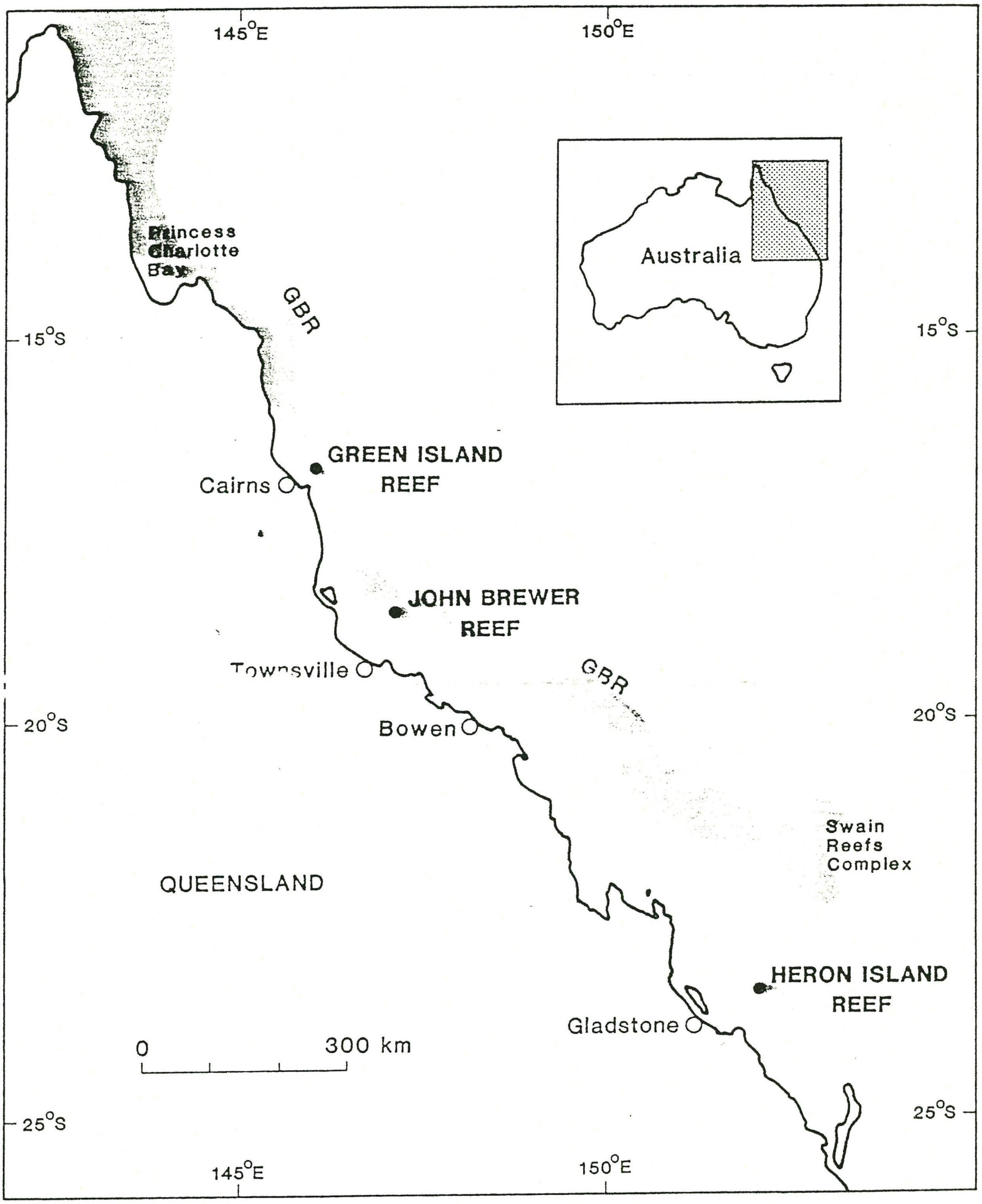

Fig. 1. Location of sampled reefs within the Great Barrier Reef (GBR). *A. planci* outbreaks have been recorded on reefs between Princess Charlotte Bay and Bowen and in the Swain Reefs Complex.

methodology for such a study was established by Frankel (1977, 1978). *A. planci* contains an intricate mesodermal skeleton of calcite elements which are released on death or predation and subsequent tissue decay and which must accumulate as inert grains in the reefal sediment record. Frankel (op. cit.) attempted to assess the late Holocene fossil record of *A. planci* in the GBR but his data base has been viewed as too small to sustain viable conclusions (Moran et al. 1986).

Our study was based on the following approach :

1. Extensive surface sediment sampling of selected reefs to evaluate the relationship between extremes in historic predation patterns and the density of *A. planci* skeletal elements in contemporary sediment;
2. Sampling of subsurface sediment cored from reefs known to have experienced saturation-level *A. planci* predation in the last 30 years;
3. Analysis of cored sediment for *A. planci* element contents and assessment, by carbon-14 dating techniques, of the age structure preserved within the cores;
4. Recognition of *A. planci* skeletal element density signatures in ancient sediment of known age on the basis of an established contemporary relationship.

Site Selection

Three reefs were targeted for surface sediment sampling (Fig. 1) based on their well-documented, and very different, recent histories of *A. planci* population levels. John Brewer Reef and Green Island Reef have both experienced two devastating outbreaks since 1962. Heron Island Reef has maintained a low-density population of *A. planci* during this period (GBRMPA unpublished data base) and was used as the control in this study.

An outbreak of *A. planci* occurred on Green Island Reef between 1962 and 1967 (Endean 1969). A second population increase was recorded on this reef in 1979. By 1980 the population was estimated to comprise 2 million starfish (Kenchington and Pearson 1981). Estimates of coral mortality were in excess of 90% (Endean and

Cameron 1985). *A. planci* was again rare by 1983 (Bradbury et al. 1985).

The first outbreak on John Brewer Reef occurred between 1969 and 1971 (Endean and Stablum 1973) and resulted in the almost total destruction of coral (Pearson 1981). The effects of the second outbreak, which commenced in May 1983, were at least as extensive as the first (Done 1985). By October 1984 starfish numbers on John Brewer Reef had declined markedly (Moran et al. 1985) and they are now scarce (Moran pers. comm.).

John Brewer and Green Island Reefs were also selected for subsurface sampling because of their susceptibility to *A. planci* predation over the last 30 years. If such predation is an enduring pattern, these reefs will contain *A. planci* skeletal elements within their ancient sediment bodies.

Element Identification

A detailed examination of the morphology and ultrastructure of *A. planci* skeletal elements (Walbran 1987) demonstrated that they are readily distinguished from the elements of other asteroids common on the GBR. Whilst *A. planci* elements are morphologically distinct, it is their colour, which ranges from a light mauve through to dark purple and, at times, an intense orange-red, that facilitates initial identification in a tray of mixed reefal sediment. A combination of colour, morphological features and a distinctive surface texture, reflecting detail of the stereom structure, permits the recognition of *A. planci* elements under a binocular microscope.

Methods

Surface sediment

Surface sediment samples (3-4 kg) were collected by a jawed grab sampler capable of retrieving approximately 3200 cm^3 of sediment to a maximum depth of about 4 cm at a time. In shallow areas ($\leq$10 m), where the coarse nature of the sediment rendered the grab sampler ineffective, samples were collected by SCUBA. John Brewer Reef was the first reef investigated with surface sampling down to 39 m water depth. In view of the enhanced skeletal element recovery for this reef at ≤20 m water depth, the surface sampling programs for Green Island and Heron Island Reefs were modified accordingly. Fifty eight surface samples were collected on John Brewer Reef 46 on Green Island Reef and 55 on Heron Island Reef (Fig. 2; Table 1).

Samples were washed in dilute sodium hypochlorite to remove organic coatings, soaked twice in tap water to remove salt, dried and split. One kilogram samples, dry sieved at 0·5-1·0, 1·0-2·0, 2·0-4·0, and ≥4·0 mm size intervals, were picked for *A. planci* skeletal elements under a binocular microscope.

<u>Subsurface sediment</u>

A pontoon-supported vibracorer was used for subsurface coring of sediment in shallow water. The leeward slope of John Brewer Reef was cored with a ship-deployed vibracorer. Sediment cores were collected in 76 mm I.D. aluminium piping measuring 5·8 and 4·5 m in length for the respective vibracorers. Finger core-catchers prevented sediment loss from the piping during core retrieval.

High frequency seismic profiles were utilised to assess leeward slope localities on John Brewer Reef for core recovery potential. All other sites were in sufficiently shallow water to allow for visual assessment of suitability. The absence of substantial sediment bodies rendered the windward slope unsuitable for coring.

Four cores were recovered from each site. Four replicate cores from site 11, three from site 12 and two cores from 5 other John Brewer Reef sites and the 6 sites on Green Island Reef were selected for picking (Fig. 3; Table 2) on the basis of environmental representation and core recovery length. Each core was split longitudinally. One half was subdivided into 250 g intervals (average length 8 to 10 cm), soaked 3 times in tap water, dried and sieved to the same size fractions as the surface samples. In addition to the above, the four cores from site JB11 were picked for elements in the 0·25-0·5 mm grain size range.

Variability in compaction between replicate cores and uncertainty as to how sediment behaves during the vibracoring process make accurate recalibration impossible. Recalculation of core recovery to penetration length (Table 2) assumes uniform

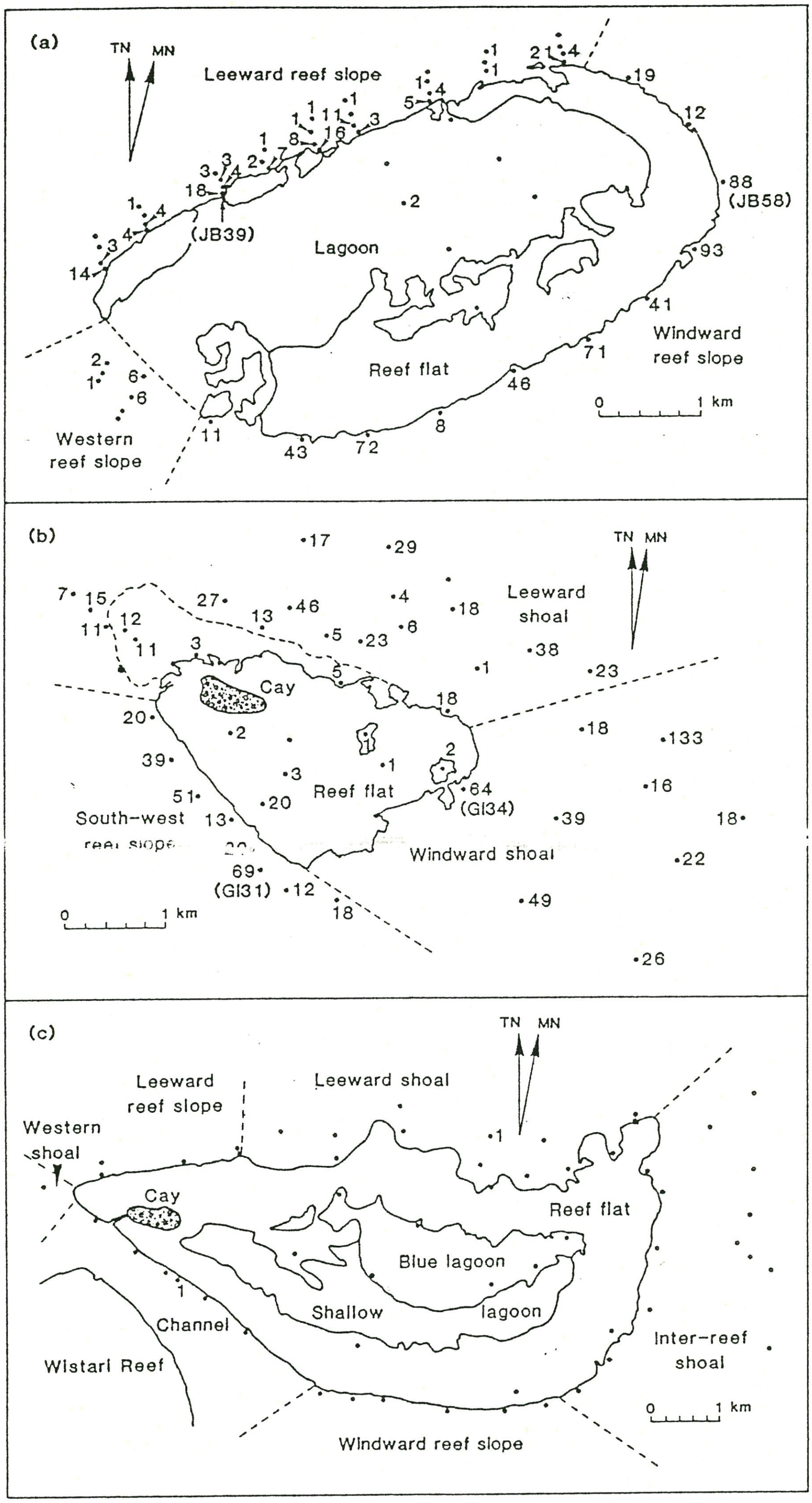

Fig. 2. Number of *A. planci* elements recovered from surface sediment sampling sites on (a) John Brewer Reef, (b) Green Island Reef, (c) Heron Island Reef. Unnumbered sites were barren. Bracketed numbers indicate surface sample sites for which bulk sediment and grouped element ages were obtained. Dating results are presented in Table 5.

Table 1. Details of surface sediment samples from John Brewer (JBR), Green Island (GIR) and Heron Island (HIR) Reefs picked for *A. planci* skeletal elements. Sample sites are given in Figure 2.

Key to Element Identification (see Walbran, 1987):
a = unidentified; b = abactinal spine; c = actinal spine;
d = primary abactinal ossicle; e = secondary abactinal ossicle;
f = actinal intermediate ossicle; g = ambulacral ossicle;
h = first ambulacral ossicle; i = adambulacral ossicle;
j = oral ossicle; k = interbrachial ossicle;
l = interbrachial plate; m = marginal ossicle;
n = pedicellarial cup.

<u>JBR Sample Totals</u>

Reef Environment	Water Depth (m)[1]	Sample Number (JBGS)[2]	Number of Elements Recovered	Element Types & Numbers Recovered
Windward reef slope	8	52	11	2a3b1c1d1f2g1h
	8	53	43	1a11b12c5d6e3f4g1i
	10	54	72	5a6b14c4d18e8f8g1h6i2j
	9	55	8	1a2b4c1i
	9	56	19	3a6c1d4e3f1g1i
	9	57	12	2a1b5c3e1i
	9	58	88	7a21b29c5d10e7f5g4i
	9	59	93	6a9b23c7d22e6f12g6i1j1n
	12	60	41	4a5b11c3d6e7f2g1i1j1l
	11	61	71	11a4b14c4d19e5f7g6i1l
	8	62	46	3a3b25c3d2e2f5g1h1i1m
Western reef slope	9	33	6	5a1e
	20	34	6	3a1b2g
	20	43	2	1b1c
	34	35	-	
	31	44	-	
	40	36	-	
	38	45	1	1e
Leeward reef slope	10	37	14	2a3b3c3d2e1g
	10	38	4	1a1d2g
	10	39	18	3a1b6c1d5e1f1g
	12	40	7	2b3e1g1i
	12	41	16	2a2b8c2e1g1i
	8	46	3	1c1e1j
	8	47	5	4c1f
	8	49	21	4a2b7c2d2e1g3i
	20	1	11	2a1b3c1d2g2i
	21	2	8	1a1b2d2e1f1i
	19	4	2	1b1c
	21	7	4	1a2b1e
	19	10	4	1a2e1g
	19	13	3	1c1e1g
	18	19	4	2c1e1i

Table 1 (continued)

JBR Sample Totals (continued)

Reef Environment	Water Depth (m)[1]	Sample Number (JBGS)[2]	Number of Elements Recovered	Element Types & Numbers Recovered
Leeward reef slope	19	50	4	2c1e1i
	19	51	1	1c
	34	3	1	1c
	34	5	1	1a
	33	8	3	1a1d1e
	33	11	-	
	33	14	-	
	33	18	-	
	32	20	1	1b
	33	22	-	
	33	25	-	
	39	9	3	1b1c1g
	39	12	1	1i
	39	15	-	
	39	16	1	1c
	39	17	1	1a
	39	21	-	
	39	23	1	1d
	39	24	-	
Lagoon	8	26	-	
	11	27	-	
	8	28	-	
	8	29	-	
	10	30	2	1e1j
	10	31	-	
	7	32	-	

1 - Water depths corrected to Low Water Datum
2 - No samples numbered 6, 42 or 48
n (all sites) = 58, $\Sigma = 663$, $x = 11{\cdot}2$
n (<20 m) = 39, $\Sigma = 649$, $x = 16{\cdot}6$

GIR Sample Totals

Reef Environment	Water Depth (m)[1]	Sample Number (GIGS)[2]	Number of Elements Recovered	Element Types & Numbers Recovered
South-west reef slope	8	26	20	3a3b8c2e3f1g
	8	27	39	2a7b13c2d6e3f5g1i
	8	28	51	4a13b16c5d5e2f3g1h2i
	8	29	13	2a7c1d2e1g
	8	30	29	3a5b3c1d6e6f3g1h1i
	8	31	69	2a16b25c1d15e2f6g2h
	8	32	12	1b2c1d5e2f1i
	8	33	18	1a6c5d4e1g1i

Table 1 (continued)

GIR Sample Totals (continued)

Reef Environment	Water Depth (m)[1]	Sample Number (GIGS)[2]	Number of Elements Recovered	Element Types & Numbers Recovered
Windward shoal	4	23	18	1a2b5c2e3f3g2i
	6	24	39	11a4b6c1d8e3f5g1i
	8	25	49	10a7b6c2d12e7f2g2i1l
	1	34	64	7a8b23c1d15e3f4g3i
	9	44	133	58a7b21c4d21e10f4g1h 4i1j1k1l
	20	45	18	6a2b4c2d2e1f1i
	8	46	16	1a1b11c2e1g
	17	47	22	1a1b9c1d4e3f2g1i
	20	48	26	4a2b12c1d3e1f2g1i
	11	2	27	5a3b7c1d6e1f3g1i
	6	3	13	8a1b1c1e1f1g
	7	4	5	1b3c1e
Leeward shoal	11	5	6	1a2b1d1e1g
	13	8	11	1a5c3e1g1i
	10	11	18	4a1b5c5e2f1g
	12	16	46	14a2b9c1d13e1f5g1i
	10	19	23	5a4b5c1d3e1f2g1i1h1j
	10	20	1	1c
	19	9	15	5a1b6c1g2i
	19	15	7	3c3e1g
	20	17	17	3a4b4c1d3e1g1k
	20	18	4	1a1d2e
	19	21	18	4a2b3c1d3e1f4g
	18	22	29	4a1b7c1d10e1f2g3i
	19	42	-	
	16	43	23	11a3c2d3e2g2i
	18	49	38	8a3b14c1d6e2f3g1i
Reef flat	3	35	2	1a1c1
	0	36	1	1a
	0	37	1	1c
	0	38	-	
	0	39	3	2c1g
	0	40	2	1b1g
	0	41	20	2a1b7c4e2f3g1i
	3	1	3	2e1f
	4	6	11	2a1b2c2e4f
	4	7	12	1b4c1d2e4f
	1	10	5	4a1f

1 - Water depths corrected to Low Water Datum
2 - No samples numbered 12, 13 or 14
n = 46, Σ = 997, x = 21·7

Table 1 (continued)

HIR Sample Totals

Reef Environment	Water Depth (m)[1]	Sample Number (HIGS)	Number of Elements Recovered	Element Types & Numbers Recovered
Channel	9	1	-	
	9	2	1	1c
	9	3	-	
	8	5	-	
	9	35	-	
	9	53	-	
Windward reef slope	9	4	-	
	7	25	-	
	10	31	-	
	5	32	-	
	6	33	-	
	9	34	-	
	9	54	-	
Inter-reef shoal	9	6	-	
	8	7	-	
	10	8	-	
	10	9	-	
	6	10	-	
	6	11	-	
	2	12	-	
	5	24	-	
	16	26	-	
	11	27	-	
	4	28	-	
	9	29	-	
	20	30	-	
Leeward shoal	3	14	-	
	6	15	-	
	9	16	-	
	9	17	-	
	6	20	-	
	8	21	-	
	7	50	-	
	18	13	-	
	18	18	1	1f
	21	19	-	
	15	22	-	
	16	51	-	
	19	52	-	
Western shoal	9	55	-	

Table 1 (continued)

HIR Sample Totals (continued)

Reef Environment	Water Depth (m)[1]	Sample Number	Number of Elements Recovered	Element Types & Numbers Recovered
Leeward reef slope	8	23	-	
	8	37	-	
	7	49	-	
	18	36	-	
	17	48	-	
Reef flat	0	40	-	
	0	41	-	
	1	45	-	
Lagoon	1	38	-	
	1	39	-	
	2	42	-	
	1	43	-	
	2	44	-	
	3	46	-	
	1	47	-	

1 - Water depths corrected to Low Water Datum
n = 55, Σ = 2.

Total Element Recovery

Reef	a	b	c	d	e	f	g	h	i	j	k	l	m	n	Total
JBR	73	84	187	45	117	45	60	3	39	6	-	2	1	1	663
GIR	201	107	270	40	187	71	76	6	31	4	2	2	-	-	997
HIR	-	-	1	-	-	1	-	-	-	-	-	-	-	-	2
Total	274	191	458	85	304	117	136	9	70	10	2	4	1	1	1662

Percentages

Reef	a	b	c	d	e	f	g	h	i	j	k	l	m	n	Total
JBR	11·0	12·7	28·2	6·8	17·6	6·8	9·0	0·5	5·9	0·9	-	0·3	0·2	0·2	100·1
GIR	20·2	10·7	27·1	4·0	18·8	7·1	7·6	0·6	3·1	0·4	0·2	0·2	-	-	100·1
HIR	-	-	50·0	-	-	50·0	-	-	-	-	-	-	-	-	100·0

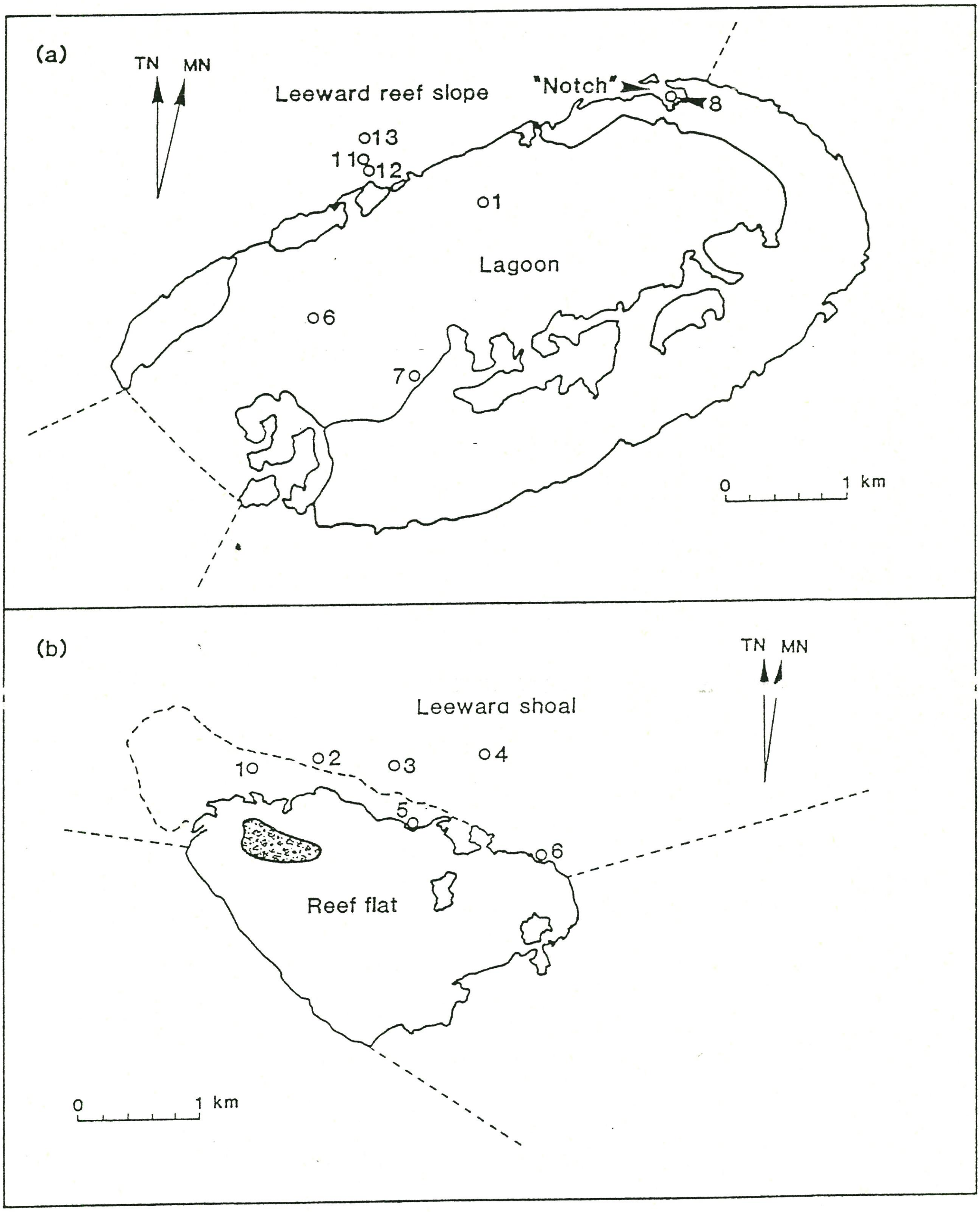

Fig. 3. Vibracore sites on (a) John Brewer Reef, (b) Green Island Reef.

Table 2. Details of John Brewer (JB) and Green Island (GI) Reef cores picked for A. planci skeletal elements in the ≥0·5 mm size range. Core localities are given in Fig. 3.

Core Number	Reef Environment/ Water Depth (m)[1]		Core Penetration Length (cm)	Core Recovery Length (cm)	Percent Compaction	Number of Elements Recovered	Element Types & Numbers Recovered
JB1a	Lagoon	8	271	225	17·0	23	5a2b6c1d3e4f2g
JB1c			282	233	17·4	26	2a2b8c2d5e5g1i1j
JB6a	Lagoon	9	423	326	23·0	74	17a15b22c1d9e7f2g1i
JB6c			464	375	19·2	78	16a17b20c3d11e1f7g2i1k
JB7c	Lagoon	7	473	400	15·5	61	15a12b17c2d5e2f6g2i
JB7d			408	368	17·9	53	16a11b13c1d5e2f4g
JB8a	'Notch'	16	501	392	21·8	132	35a13b51c7d13e2f8g3i
JB8b			484	375	22·5	129	21a14b51c8d14e6f12g3i
JB11c	Leeward	33	393	372	5·4	23	7a9c4e1f1g1j
JB11d	reef slope		311	311	0·0	6	1a2c1e1f1g
JB11e			374	357	4·6	17	7a1b4c1d2e1f1i
JB11f			361	361	0·0	26	6a2b8c2d5e1f2i
JB12a	Leeward	25	357	215	39·8	37	14a6b8c1d3e1f4g
JB12b	reef slope		318	138	56·7	27	10a2b8c4e2g1i
JB12c			385	154	60·0	29	10a5b10c1f3g
JB13a	Leeward	39	287	251	12·6	57	23a7b12c2d6e2f4g1i
JB13b	reef slope		306	180	41·2	7	5a1c1i
GI1b	Reef flat	3	517	415	19·8	251	96a22b58c12d32e14f11g6i
GI1c			522	416	20·4	217	87a17b50c11d32e6f12g2i
GI2b	Leeward		514	428	16·8	196	88a12b34c3d25e7f18g8i
GI2c	shoal	6	502	420	16·4	202	89a8b36c7d33e13f10g2h4i
GI3a	Leeward		454	418	8·0	71	17a8b12c6d12e9f7g
GI3b	shoal	7	506	396	21·8	93	32a7b18c4d10e7f9g1h4i1j
GI4a	Leeward		504	396	21·4	68	15a11b8c2d14e7f8g3i
GI4d	shoal	11	512	404	21·1	104	28a17b13c3d17e7f10g8i1j
GI5b	Reef flat	1	541	437	19·3	166	55a21b25c6d24e11f15g1h6i1j
GI5c			532	428	19·6	154	50a16b30c5d27e13f7g1h5i
GI6b	Leeward		539	333	38·3	177	37a28b55c8d23e12f9g5i
GI6c	shoal	10	497	350	29·6	175	42a27b54c9d21e9f11g2i

1 - Water depths corrected to Low Water Datum

Key to Element Identification (see Walbran, 1987):

a = unidentified; b = abactinal spine; c = actinal spine; d = primary abactinal ossicle; e = secondary abactinal ossicle; f = actinal intermediate ossicle; g = ambulacral ossicle; h = first ambulacral ossicle; i = adambulacral ossicle; j = oral ossicle; k = interbrachial ossicle.

sediment compaction throughout the core permitting a more direct comparison of element distribution between replicate cores than would be the case had no correction been taken into account.

Carbon-14 dating

Liquid scintillation counting (LSC) of bulk (50 g minimum weight) surface and core sediment samples was undertaken at the Radiocarbon Dating Laboratory, Australian National University (ANU), Canberra. Dating of individual and grouped *A. planci* elements (10-15 mg minimum weight) from within sampled intervals was carried out on the accelerator mass spectrometry (AMS) facilities at the Institute of Nuclear Sciences (INS), Department of Scientific and Industrial Research, Lower Hutt, New Zealand. Procedures followed at ANU are set out in Gupta and Polach (1985) and those at INS in Sparks et al. (1986), Lowe and Judd (1987) and Wallace et al. (1987).

Fifty four bulk sediment samples from the John Brewer and Green Island Reef core sets were dated by LSC (Figs 4, 5; Table 3). Sixteen AMS samples from the two core sets were submitted to INS (Figs 4, 5; Table 4). In addition, two bulk surface samples and the corresponding *A. planci* material from each of the two reefs were dated (Fig. 2; Table 5). AMS samples were washed in an ultrasonic bath for 30 minutes prior to submission. Minor amounts of secondary carbonate coating could not be removed (Tables 4 and 5). Scanning electron microscopy revealed these coatings to be thin surficial encrustations and volumetrically insignificant.

Dates presented in the text of this report are the real or reservoir-corrected ages in years B.P. determined by subtracting the Gillespie-Polach factor of 450 ± 35 years (Gillespie and Polach 1979) from the dates reported by the carbon-14 laboratories. Laboratory-reported conventional ages are given in the relevant tables.

Statistical analysis

Inter-reef variability in surface sediment element recovery on the three reefs and the comparability in element abundance per sample interval above and below 200 cm core depth for the John Brewer and

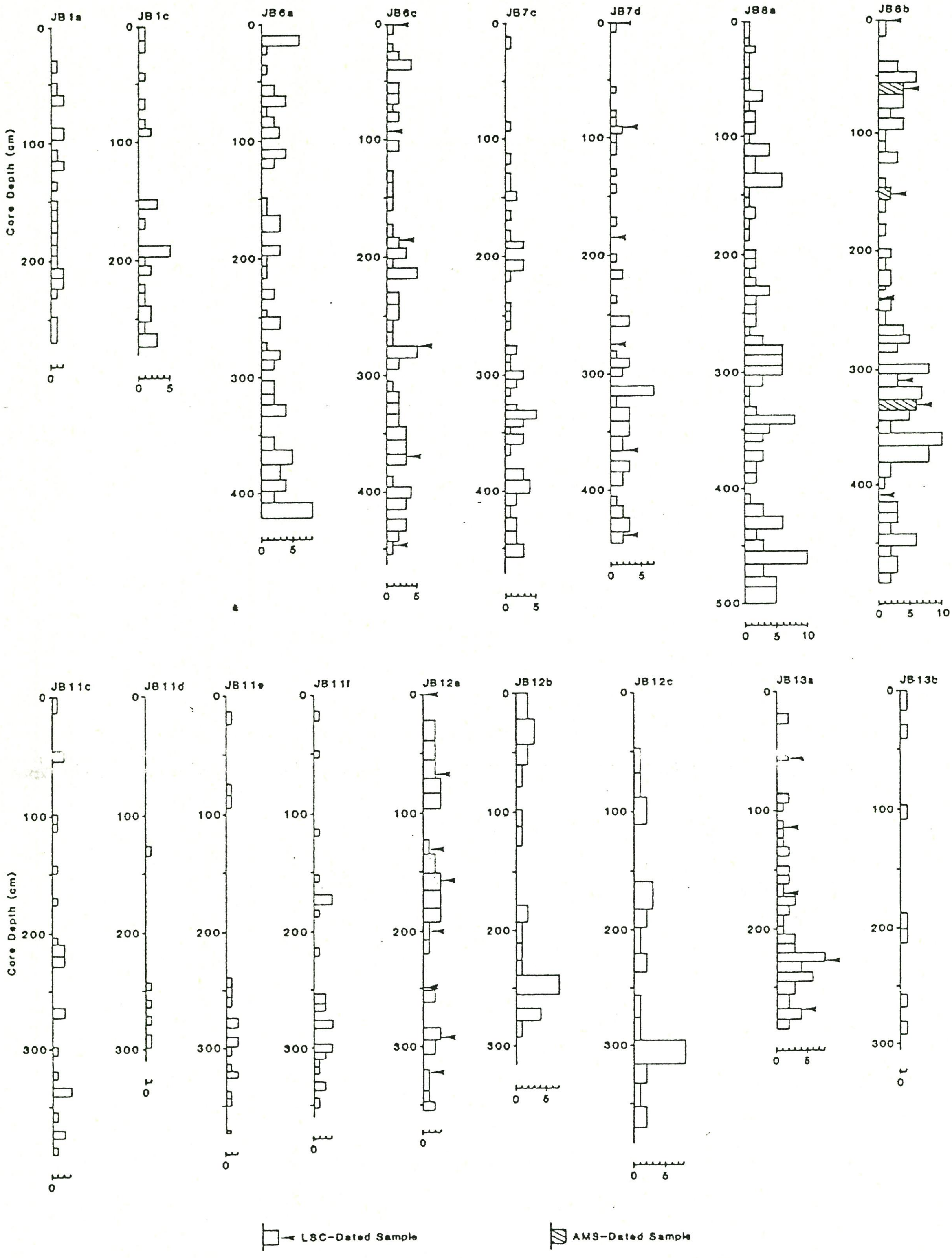

Fig. 4. Subsurface *A. planci* element recovery, John Brewer Reef, grain size ≥0·5 mm. Bar scales show element recovery in single units. Intervals sampled for Liquid Scintillation Counting and Accelerator Mass Spectrometry are indicated. Arrows represent median points of LSC-dated intervals.

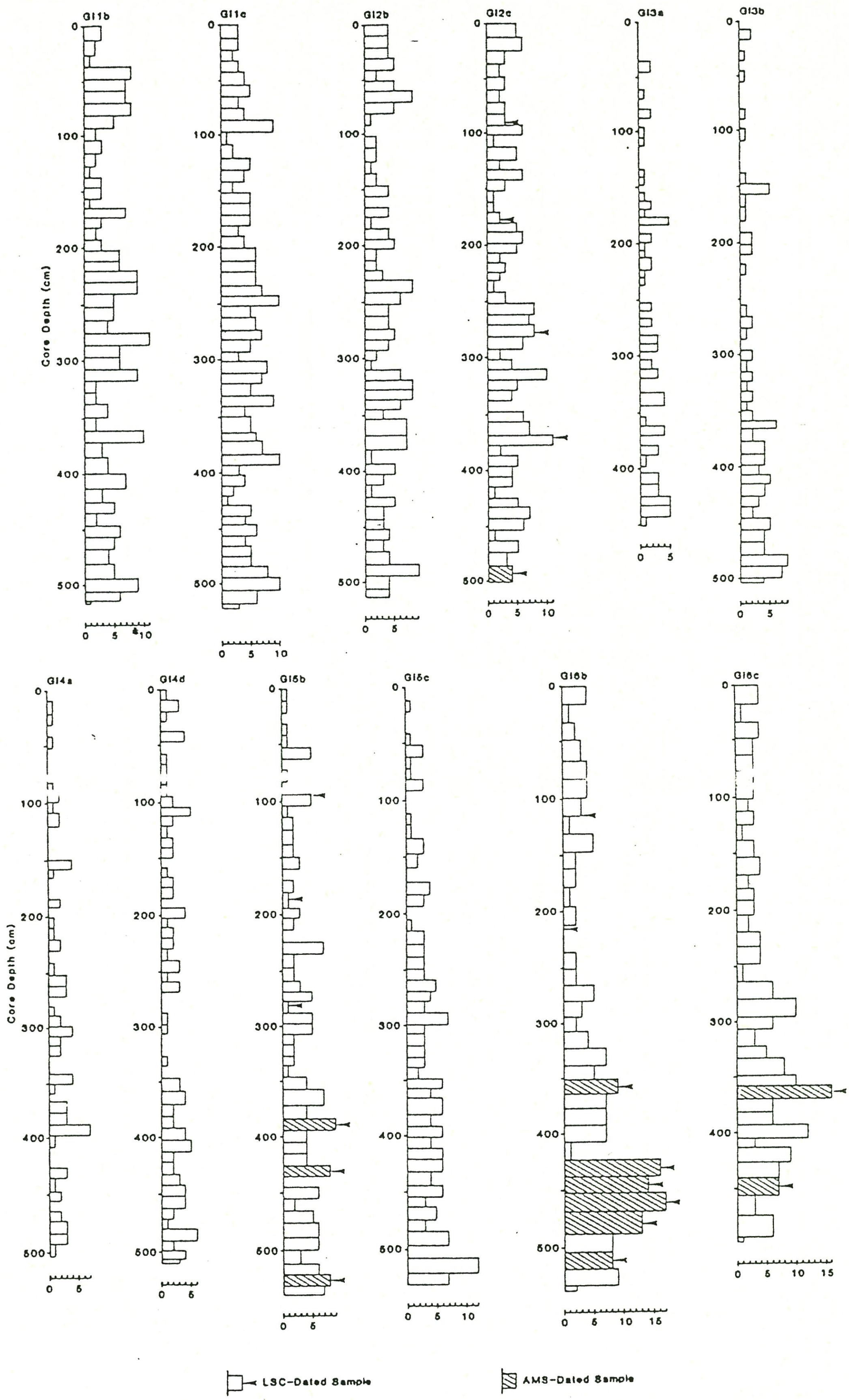

Fig. 5. Subsurface *A. planci* element recovery, Green Island Reef, grain size ≥0·5 mm. Bar scales show element recovery in single units. Intervals sampled for Liquid Scintillation Counting and Accelerator Mass Spectrometry are indicated. Arrows represent median points of LSC-dated intervals.

Table 3. Conventional and real ages of bulk sediment samples from John Brewer (JB) and Green Island (GI) Reef core sets dated by Liquid Scintillation Counting. Core localities are given in Fig. 3. S = fine- to coarse-grained sand; C = coral debris; G = very coarse-grained sand; M = mollusc; R = rubble.

Core Number/ Penetration Interval	Recovery Interval	ANU Reference Number	Material Dated	Conventional Age (± error)	Real Age (± error)
JB6c					
0·0-2·5	0·0-2·0	ANU-5863	S	2630 ± 80	2180 ± 90
90·5-94·5	73·0-76·5	ANU-5864	S	2640 ± 80	2190 ± 90
184·5-189·5	149·0-153·0	ANU-5865	S	2790 ± 80	2340 ± 90
273·5-276·0	221·0-223·0	ANU-5866	S	2620 ± 80	2620 ± 90
370·0-374·0	299·0-302·0	ANU-5867	S	3570 ± 80	3120 ± 90
445·5-448·5	360·0-362·5	ANU-5868	S/C	4980 ± 80	4530 ± 90
JB7d					
0·0-3·5	0·0-3·0	ANU-5870	S	2320 ± 80	1870 ± 90
91·5-94·5	75·0-77·5	ANU-5871	S	2390 ± 80	1940 ± 90
182·5-185·5	150·0-152·5	ANU-5872	S/G	2650 ± 80	2200 ± 90
274·0-277·0	225·0-227·5	ANU-5873	S/G	2930 ± 80	2480 ± 90
365·5-368·5	300·0-302·5	ANU-5874	S/G	3530 ± 80	3080 ± 90
441·0-444·0	362·0-364·5	ANU-5875	S	3840 ± 80	3390 ± 90
JB8b					
0·0-4·0	0·0-3·0	ANU-5853	S	760 ± 70	310 ± 80
54·0-66·0	42·0-51·0	ANU-5472	S	700 ± 60	250 ± [illegible]
146·0-156·0	113·0-121·0	ANU-5473	S	860 ± 60	410 ± 70
237·5-242·5	184·0-188·0	ANU-5654	S	1130 ± 60	680 ± 70
304·5-313·0	236·0-242·5	ANU-5655	S	1420 ± 70	970 ± 80
324·5-334·0	251·5-259·0	ANU-5474	S	1780 ± 60	1330 ± 70
405·0-413·0	314·0-320·0	ANU-5656	C	2760 ± 70	2310 ± 80
JB12a					
0·0-5·0	0·0-3·0	ANU-5854	S	1930 ± 80	1480 ± 90
66·5-71·5	40·0-43·0	ANU-5657	S	2040 ± 70	1590 ± 80
133·0-136·0	80·0-82·0	ANU-5658	S	2000 ± 70	1550 ± 80
166·0-171·0	100·0-103·0	ANU-5855	S	2770 ± 80	2320 ± 90
199·5------	120·0------	ANU-5659	M	2310 ± 70	1860 ± 80
246·0-252·5	148·0-152·0	ANU-5856	S	4950 ± 80	4500 ± 90
289·0-294·0	174·0-177·0	ANU-5857	S/R	5530 ± 90	5080 ± 100
320·5-328·0	193·0-197·5	ANU-5660	S	5770 ± 80	5320 ± 90
JB13a					
55·0-58·5	48·0-51·0	ANU-5670	S	2220 ± 70	1770 ± 80
113·5-116·7	99·0-102·0	ANU-5671	S	3840 ± 80	3390 ± 90
167·0-173·0	146·0-151·0	ANU-5672	S	4790 ± 80	4340 ± 90
226·5-232·5	198·0-203·0	ANU-5673	S	6330 ± 80	5880 ± 90
277·0-284·0	242·0-248·0	ANU-5674	S	8190 ± 90	7740 ± 100

Table 3 continued.

Core Number/ Penetration Interval	Recovery Interval	ANU Reference Number	Material Dated	Conventional Age (± error)	Real Age (± error)
GI2c					
89·5-92·0	75·0-77·0	ANU-5666	S	1860 ± 70	1410 ± 80
176·0-180·5	147·0-151·5	ANU-5667	S	2330 ± 70	1880 ± 80
275·0-277·5	230·0-232·0	ANU-5668	S	2510 ± 70	2060 ± 80
371·0-374·5	310·0-313·0	ANU-5669	S/G	2620 ± 70	2170 ± 80
484·5-496·0	405·0-414·5	ANU-5475	S	2800 ± 70	2350 ± 80
GI5b					
92·5-96·0	74·5-77·5	ANU-5661	S	1330 ± 70	880 ± 80
184·5-189·5	149·0-153·0	ANU-5662	S	2030 ± 70	1580 ± 80
279·0-282·5	225·0-228·0	ANU-5663	S	2570 ± 70	2120 ± 80
383·5-394·0	309·5-318·0	ANU-5645	S	2830 ± 70	2380 ± 80
425·0-434·5	343·0-350·5	ANU-5476	S	3000 ± 70	2550 ± 80
522·5-532·0	421·5-429·5	ANU-5477	S	3410 ± 70	2960 ± 80
GI6b					
113·5-116·5	70·0-72·0	ANU-5664	S	820 ± 70	370 ± 80
209·0-219·0	129·0-135·0	ANU-5665	C	490 ± 60	40 ± 70
210·5-219·0	130·0-135·0	ANU-5869	S	1030 ± 70	580 ± 80
351·5-364·0	217·0-224·5	ANU-5478	S/G	1380 ± 70	930 ± 80
423·0-439·0	261·0-271·0	ANU-5646	S/G	1820 ± 70	1370 ± 80
439·0-454·0	271·0-280·0	ANU-5647	S/G	1910 ± 70	1460 ± 80
454·0-469·0	280·0-289·5	ANU-5479	S/G	2030 ± 70	1580 ± 80
469·0-489·5	289·5-302·0	ANU-5648	S/G	1950 ± 70	1500 ± 80
505·0-520·5	312·0-321·0	ANU-5649	S/G	2000 ± 60	1550 ± 70
GI6c					
357·0-369·5	251·5-260·0	ANU-5480	S/G	1720 ± 70	1270 ± 80
440·5-456·0	310·0-321·0	ANU-5481	S/G	2210 ± 70	1760 ± 80

Table 4. Details of *A. planci* skeletal element batches recovered from John Brewer (JB) and Green Island (GI) Reef cores and dated by Accelerator Mass Spectrometry.

Core Number/ Penetration Interval	Recovery Interval	Number of Elements	Sample Weight (mg)[1]	% 2° Surface $CaCO_3$	Batch Number	Conventional Age (± error)	Real Age (± error)
JB8b							
54·0-66·0	42·0-51·0	2	12·77	<5	1	520 ± 514	70 ± 515
146·0-156·0	113·0-121·0	1	10·15	5	1	489 ± 371	40 ± 375
324·5-334·0	251·5-259·0	1	10·32	<3	1	2604 ± 346	2150 ± 350
GI2c							
496·0-502·5	405·0-420·0	1	10·78	<10	1	1932 ± 285	1480 ± 290
GI5b							
383·5-394·0	309·5-318·0	17	16·82	5	2	2709 ± 318	2260 ± 320
425·0-434·5	343·0-350·5	4	11·86	<10	1	2727 ± 727	2280 ± 730
522·5-532·0	421·5-429·5	8	11·04	<10	1	3545 ± 439	3100 ± 440
GI6b							
351·5-364·0	217·0-224·5	1	11·80	<5	1	1704 ± 376	1250 ± 380
423·0-439·0	261·0-271·0	28	14·55	<3	2	1255 ± 177	810 ± 180
439·0-454·0	271·0-280·0	24	17·02	5	2	1783 ± 210	1330 ± 215
454·0-469·0	280·0-289·5	3	10·22	<10	1	416 ± 455	Modern
454·0-469·0	280·0-289·5	21	10·02	<3	2	1886 ± 202	1440 ± 205
469·0-489·5	289·5-302·0	32	25·30	5	2	1876 ± 181	1430 ± 185
505·5-520·5	312·0-321·0	22	14·99	<3	2	2216 ± 299	1770 ± 300
GI6c							
357·0-369·5	251·5-260·0	6	10·57	<5	1	1050 ± 820	600 ± 820
440·5-456·0	310·0-321·0	1	14·65	<5	1	2889 ± 479	2440 ± 480

1 - Weight as submitted to INS

Table 5. Details of bulk sediment samples dated by Liquid Scintillation Counting (LSC) and grouped *A. planci* skeletal elements dated by Accelerator Mass Spectrometry (AMS) from corresponding surface sites on John Brewer (JB) and Green Island (GI) Reefs. Sample localities are given in Figs 2a and 2b.

LSC Details

Sample Number	ANU Reference Number	Conventional Age (± error)/ %Modern	Real Age (± error)
JB39	ANU-5650	700 ± 60	250 ± 70
JB58	ANU-5651	98·5 ± 0·7 %M	Modern
GI31	ANU-5652	290 ± 60	Modern
GI34	ANU-5653	99·2 ± 0·7 %M	Modern

AMS Details

Sample Number	Number of Elements	Sample Weight (mg)[a]	% 2° Surface $CaCO_3$	Batch Number	Conventional Age (± error)/ %Modern	Real Age
JB39	20	24·62	<3	2	111·1 ± 9·4 %M	>Modern
JB58	88	120·02	<5	2	111·3 ± 3·4 %M	>Modern
GI31	[illegible]	121·08	<5	2	104·8 ± 4·[illegible] %M	>Modern
GI34	64	28·98	<3	2	344 ± 342	Modern

a - Weight as submitted to INS

Green Island Reef core suites were assessed by the Mann-Whitney *U*-test for non-parametric data. The Kolmogorov-Smirnov 'two-sample' test was used to compare element recovery between replicate cores.

Results

Element Morphology and Preservation

Actinal spines, secondary abactinal ossicles and abactinal spines were the most abundant A. planci elements recovered from the surface and subsurface sediment on John Brewer and Green Island Reefs (Tables 1 and 2). Subsurface elements, in particular, were usually broken and/or abraded. An encrusting carbonate and detrital grains were commonly present as secondary surficial material. As a consequence of the poor preservational state, positive morphological identification of a large number of elements was not possible. This was especially so in the 0·25-0·5 mm size fraction in cores from site JB11 (Fig. 6), but generally more apparent in the Green Island Reef core suite as a whole than the John Brewer Reef suite (Table 2).

Element Recovery: Surface Sediment

A total of 663 elements were recovered from the 59 surface sample sites on John Brewer Reef (Fig. 2a; Table 1), an average of 11·2 elements per 1 kg sample. The windward slope 10 m and leeward slope 10 m environments were the most productive with maximums of 93 and 21 elements per sample respectively. With the apparent exception of the base of patch reefs, the lagoon is devoid of elements in the surface sediment. The vast majority of elements were recovered from water depths of 20 m or less. If results for depths of ≤20 m only are considered, the number of sample sites on John Brewer Reef is reduced to 39 and element recovery to 649, but average recovery per 1 kg sample increases to 16·6.

The 46 surface sample sites on Green Island Reef produced 997 *A. planci* elements (Fig. 2b; Table 1), an average of 21·7 per 1 kg sample. With the exception of the reef flat, no obvious pattern of element distribution is readily apparent on Green Island Reef. The morphology of Green Island Reef lacks the well-defined rim and

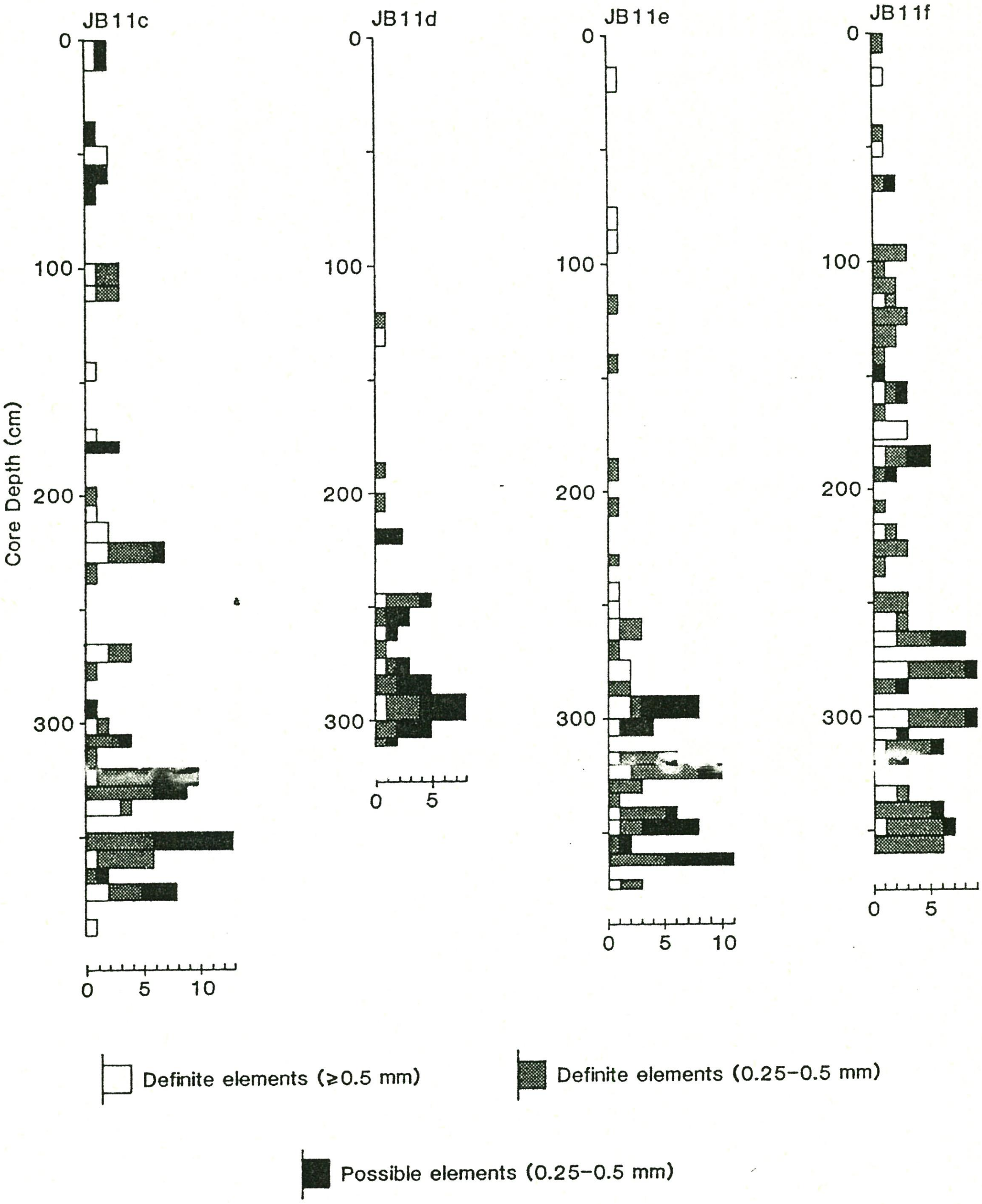

Fig. 6. *A. planci* element recovery from site 11 cores, John Brewer Reef, grain size ≥0·25 mm. Bar scales show element recovery in single units.

lagoon of John Brewer Reef. The somewhat erratic distribution of elements on Green Island Reef is thought to reflect this poor morphological differentiation.

Extensive sampling on Heron Island Reef produced only two elements from the 55 surface samples processed, each from markedly distinct environments (Fig. 2c; Table 1).

Mann-Whitney *U*-test analysis revealed surface sediment element recovery from John Brewer and Green Island Reefs to be significantly greater than that for Heron Island Reef ($P<0{\cdot}000$; Table 6). The difference in element recovery between John Brewer (≤20 m) and Green Island Reefs was also significant ($P=0{\cdot}024$; Table 6).

Table 6. Sample sizes, *Z* values and probability values derived by the Mann-Whitney *U*-test for comparison of *A. planci* element recovery from surface sediment samples on Heron Island, John Brewer and Green Island Reefs. HIR = Heron Island Reef, JBR = John Brewer Reef (all sites), JBR^{20} = John Brewer Reef (≤20 m water depth), GIR = Green Island Reef.

	n_1/n_2	*Z*	*P*
HIR/JBR	55/59	-6·40	<0·000
HIR/GIR	55/46	-8·22	<0·000
GIR/JBR^{20}	46/39	-2·25	0·024

Element Recovery: Subsurface Sediment

Core recovery on John Brewer Reef ranged from 271 to 501 cm (Table 2). Element distribution in the subsurface is discontinuous and subject to fluctuation (Fig. 4). Lagoon and "Notch" environments (Fig. 3a, sites 6, 7 and 8) provided the best record in terms of abundance, but recovery from the leeward slope environments at 25 and 39 m water depth (Fig. 3a, sites 12 and 13) was also substantial. Maximum element content for individual sample intervals was 10 from cores JB8a (454·5-466·0 cm) and JB8b (354·0-365·0 cm).

Core recovery on Green Island Reef varied between 454 and 541 cm (Table 2). As was the case with the surface sediment, element recovery in the subsurface of Green Island Reef was substantially greater than that for John Brewer Reef. Element distribution is continuous in most cores, although subject to fluctuation (Fig. 5). Site 6 contained the greatest abundance and highest concentration of elements with a maximum of 17 recovered from a single sampled interval (GI6b 454·0-469·0 cm).

Element recovery from cores JB11c-f points to a marked increase in the numbers of elements present in sediment finer than 0·5 mm grain size (Fig. 6). Coupled with this, however, is a higher degree of element breakage and abrasion and corresponding level of difficulty in morphological identification.

A visual inspection of both core sets suggests an increase in element abundance below 200 cm core depth (Figs 4, 5 and 6). This is borne out by statistical analysis of the ≥0·5 mm size fraction which shows that element abundance per sample interval is significantly greater ($P<0 \cdot 000$) below 200 cm core depth than above for John Brewer and Green Island Reefs (Table 7). Results of the Kolmogorov-Smirnov analysis indicate that, with the exception of site 13 on John Brewer Reef, sample suites from replicate cores reflect a common population and suggest that data for individual cores reasonably reflects the distributional pattern of elements within the sediment body as a whole (Table 8).

Table 7. Sample sizes, *Z* values and probability values derived by the Mann-Whitney *U*-test for comparison of *A. planci* element abundance (grain size ≥0·5 mm), per sample interval, above (<) and below (>) 200 cm core depth in the John Brewer Reef (JBR) and Green Island Reef (GIR) core sets.

	n_1/n_2	*Z*	*P*
JBR<200/ JBR>200	357/ 304	-7·32	<0·000
GIR<200 GIR>200	231/ 357	-7·97	<0·000

Carbon-14 Dating

Surface sediment ages for bulk samples ranged from Modern to 250 ± 70 years B.P. with corresponding grouped element giving Modern or >Modern dates (Table 5).

LSC dates reveal the preservation of an age structure in the subsurface sediment of John Brewer and Green Island Reefs (Fig. 7; Table 3). Broad correlation is displayed between the LSC and AMS dates for corresponding intervals although this is, in part, a function of large errors in the AMS results (Fig. 7). Two batches of skeletal elements were dated by AMS (Tables 4 and 5). The initial minimum sample weight of 10 mg proved to be insufficient and the resulting low yield of graphite for the first 10-sample batch (D. Lowe pers. comm.) gave rise to large dating errors. An increase in minimum weight for the second batch of 10 samples to 15 mg produced smaller errors and generally better correlation with bulk dates (Fig. 7).

Table 8. Sample sizes and values derived by the Kolmogorov-Smirnov test evaluating the comparability, in terms of *A. planci* element frequency, of replicate core sample suites for John Brewer (JB) and Green Island (GI) Reefs.

Core Pair	n_1/n_2	Maximum Frequency Differences	Critical Values
JB1a/JB1c	29/33	0·136	0·346
JB6a/JB6c	42/48	0·104	0·287
JB7c/JB7d	54/53	0·083	0·263
JB8a/JB8b	54/48	0·111	0·269
JB11c/JB11d	49/40	0·177	0·290
JB11c/JB11e	49/47	0·059	0·278
JB11c/JB11f	49/50	0·040	0·273
JB11d/JB11e	40/47	0·148	0·293
JB11d/JB11f	40/50	0·170	0·289
JB11e/JB11f	47/50	0·076	0·276
JB12a/JB12b	27/19	0·166	0·407
JB12a/JB12c	27/18	0·093	0·414
JB12b/JB12c	19/18	0·073	0·447
JB13a/JB13b	34/25	0·500	0·359
GI1b/GI1c	48/52	0·148	0·272
GI2b/GI2c	51/51	0·098	0·269
GI3a/GI3b	55/53	0·136	0·262
GI4a/GI4d	53/54	0·178	0·263
GI5b/GI5c	51/50	0·170	0·271
GI6b/GI6c	36/37	0·200	0·318

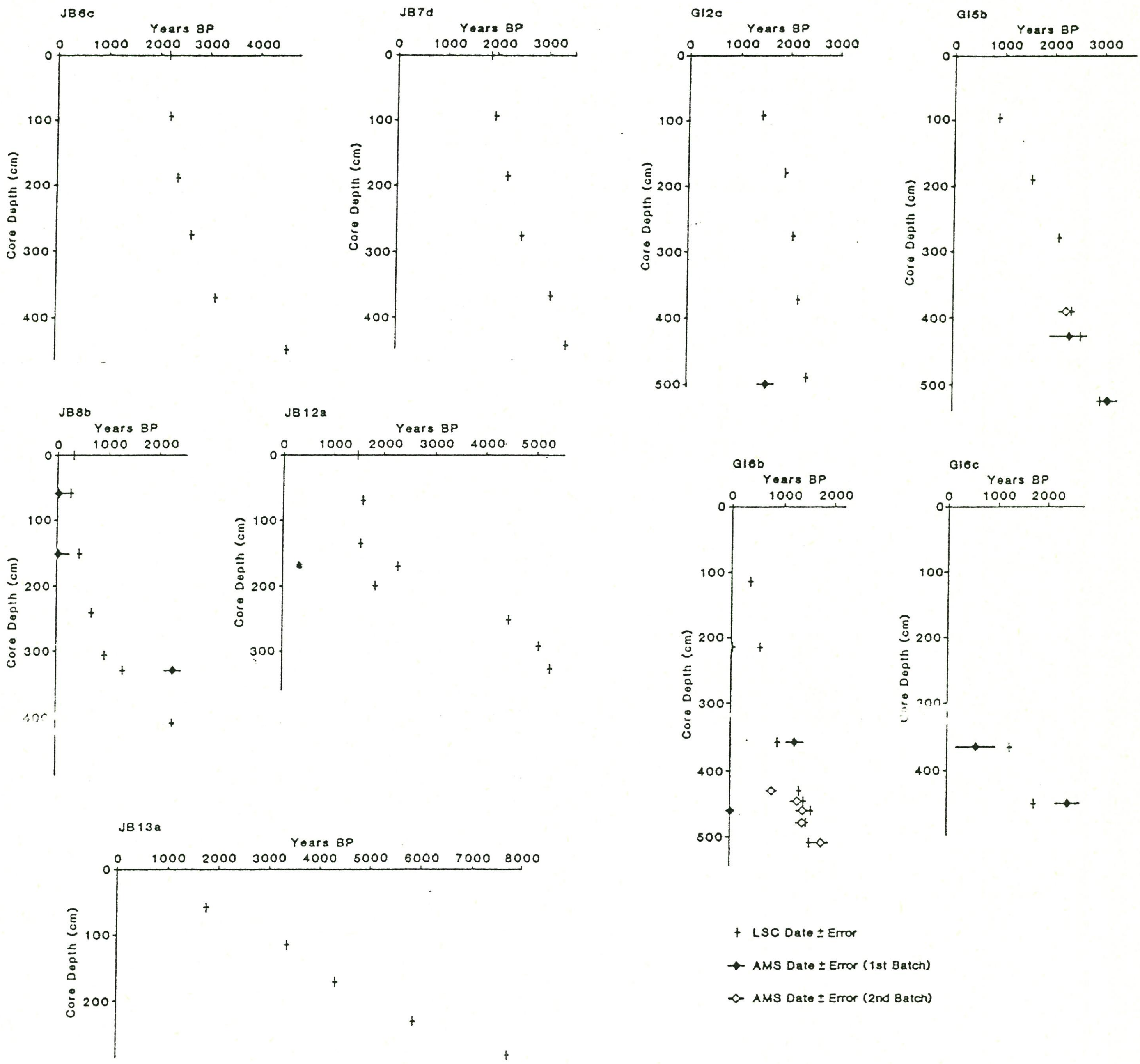

Fig. 7. Subsurface age profiles for John Brewer and Green Island Reefs established by Liquid Scintillation Counting and Accelerator Mass Spectrometry dating techniques.

Discussion

Surface Sediment

The abundance of *A. planci* elements in the surface sediment of John Brewer and Green Island Reefs contrasts markedly with that for Heron Island Reef. Although data were collected from only three reefs, they are the only reefs in the GBR for which the activity of *A. planci* has been adequately monitored over the last three decades. In addition, they represent population extremes for *A. planci* ranging from episodically very high (John Brewer and Green Island Reefs) to consistently very low (Heron Island Reef) starfish densities. Radiocarbon dating confirms that surface elements from John Brewer and Green Island Reefs are Modern or ≥Modern in age (Table 5). We infer a relationship between contemporary outbreaks and the broadscale contribution of *A. planci* skeletal elements to surface sediment.

This relationship is argued on the basis of extensive surface sediment sampling. Reports from the Red Sea (Ormond et al. 1973; Ormond and Campbell 1974) and Western Australia (Wilson and Marsh 1974) suggest that *A. planci* may aggregate from low density populations as a part of their normal feeding and/or breeding behaviour. Potentially misleading results may, therefore, be realised from limited sampling of reefs (see Moran et al. 1986), especially when compounded by poor data on contemporary *A. planci* activity.

For John Brewer Reef in particular, a relationship exists between zones of active coral growth and the density of *A. planci* elements in the surface sediment. Element recovery was best in areas adjacent to the reef rim, especially the windward rim, where coral cover is enhanced and decidedly poorer in samples from the lagoon and leeward slope sediment apron (Fig. 2a; Table 1). This observation is supported by the results of Moran et al. (1985) which showed the highest concentration of *A. planci* to be present on the windward slope. A similar pattern exists at Green Island Reef but is much less well-defined due to the poor morphological differentiation of this reef (Fig. 2b; Table 1). Accepting that *A. planci* population densities are related to coral cover during saturation outbreaks, the contribution of *A. planci* skeletal elements to the surface sediment appears to reflect the distribution of the animal in life.

Although mortality patterns for *A. planci* are poorly known, the inferred link between life assemblages and the sediment record has some biological support. Examination of individuals from high-density *A. planci* populations on Helix Reef, central GBR, has shown that tissue partitioning favouring gonad development at the expense of the body wall and caecae characterises post-juvenile growth (Kettle and Lucas 1987). For many *A. planci*, tissue-wasting terminates in death of the animal on the reef which hosted the outbreak and there is no evidence that any part of the population migrated from Helix Reef following the outbreak (Kettle pers. comm.). Studies of juvenile *A. planci* on Suva Reef, Fiji, lend further support to the view that outbreaks do not result from the migration of starfish between reefs (Zann et al. 1987).

<u>Subsurface Sediment</u>

Subsurface sediment on John Brewer Reef is somewhat depleted in *A. planci* elements relative to that of Green Island Reef. This may largely be a function of the availability of suitable vibracoring sites on John Brewer Reef which are, as a consequence of local bathymetry and substrate, restricted to lagoonal and leeward slope environments.

Core results indicate a more uniform geographic distribution of elements than that displayed in the surface sediment. This is especially apparent for John Brewer Reef where element recovery was particularly enhanced in the subsurface relative to surface sediment in lagoonal and leeward slope environments. We ascribe this to the reworking and dispersal of elements prior to their internment in the sediment body, as indicated by the generally poorer preservational state of subsurface elements. Grains in the upper few centimetres of sediment, including *A. planci* elements derived from contemporary outbreaks, are subjected to similar abrasion and dispersal prior to final burial.

In addition to problems arising from physical reworking, the detailed interpretation of element distribution within the cores is complicated by substantial biological reworking of the sediment pile. The dominant agents of bioturbation in tropical reef environments are Callianassid shrimps. These burrowers recycle vast quantities of sediment during feeding (Roberts et al. 1981; de Vaugelas and de Saint-Laurent 1984; de Vaugelas et al. 1986). Although *Callianassa* burrows in excess of 2 m depth have been reported from Eniwetok Atoll in the Marshall Islands (Suchanek et al. 1986), the active reworking of finer-grained sediment (≤1-2 mm) by *Callianassa* in reef lagoons of the GBR is restricted to the top 60 cm of the sediment pile (Tudhope and Scoffin 1984). Coarser material is stored in deeper chambers.

The storage of coarse and recycling of finer particles by *Callianassa* has important implications for this study. More than 82% of *A. planci* elements recovered from the subsurface are in the 0·5-1·0 mm size fraction and only 0·6% are ≥2 mm in size. The vast majority of contemporary elements are therefore retained within the zone of Callianassid activity. The abundance of skeletal elements in the 1·0-4·0 mm size range in a live A. planci specimen (Table 9) and the relative depletion of elements in this fraction in the subsurface sediment emphasises the importance of reworking as a determinant of grain-size distribution.

Table 9. Weight relationships between different size fractions of fresh *A. planci* skeletal elements. Live specimen was 25 cm in diameter with 14 arms.

Size Fraction (mm)	Dry Weight (g)	Weight Percent
≥4·0	4·07	4·36
2·0-4·0	35·46	38·02
1·0-2·0	45·63	48·92
0·5-1·0	4·99	5·35
0·25-0·5	2·40	2·57
<0·25	0·72	0·77
	93·27	99·99

The down-core distribution of elements is a legacy of physical and biological reworking. This, combined with overall sedimentation rates in the order of 1-3 m per thousand years, negates any prospect that short-term periodic events, such as individual *A. planci* outbreaks, will be preserved as a recognisable signature in the sedimentary record. It is noteworthy that element concentration in the uppermost interval of all cores is no greater than that of underlying intervals. Contemporary outbreaks are not recognisable in the sedimentary record as a unique layer discriminated by abnormally high quantities of *A. planci* elements.

The possibility that all the *A. planci* element contents of the cores represent biological reworking of contemporary material into the sediment pile can be eliminated on two grounds. Dating of individual and grouped elements obtained from the subsurface have, with one exception, realised old ages. In addition, *A. planci* elements are present within cores at depths of greater than 2 m, well beyond the range of contemporary *Callianassa* activity.

Reworking has doubtless impaired the age structure preserved in the core, especially those from shallower sites, but our dating results indicate that it has not been destroyed. A close relationship between core depth and bulk sediment age is apparent in all cores for which we have age data. Only two cases of age reversal (JB12a 199·5 cm and GI6b 209·0-219·0 cm) are represented in the bulk sediment age suites. Correlation between core depth and bulk sediment age is especially close for core JB13a ($r^2 = 0{\cdot}994$) which was taken in a water depth of 39 m. *Callianassa* activity is limited to about 20 m maximum water depth on nearby Davies Reef (Tudhope and Scoffin 1984) and the sediment record at site 13 may have escaped significant bioturbation.

Age data on individual and grouped elements from single core intervals broadly correspond to bulk sediment dates but show that some elements have different ages from that of the bulk sediment in which they occur. Age disparities range to at least 1000 years and possibly as much as 1600 years if the Modern age for GI6b (454·0-469·0 cm) is accepted. An age disparity also applies to the surface sediment at site JB39 (Fig. 2a) where the bulk sediment gave an age of 250 ± 70 years B.P. and the AMS age for *A. planci* elements returned a Modern age.

These data show that the stratigraphic integrity of individual grains within the sediment pile has been disturbed. Bioturbation, which clearly influences contemporary sedimentation, is the most likely cause of major disruption. The distribution of *A. planci* elements within the sediment body is most unlikely to reflect the temporal distribution of past populations.

The final question that has to be addressed is whether the core results demonstrate the presence of *A. planci* in outbreak proportions in prehistoric times. As we have discussed, the stratigraphy of sediment bodies in shallow-water reefal environments is not preserved in sufficient detail to permit the identification of short-term periodic events. The stratigraphic record of *A. planci* elements is time-averaged and shows only coarse trends. Knowledge of contemporary sedimentary processes indicates that *A. planci* elements derived from contemporary outbreaks on John Brewer and Green Island Reefs will become dispersed in the sedimentary record as it accumulates. The down-core distribution of *A. planci* elements documented here is consistent with a long period, at least 7000 years on John Brewer Reef and 3000 years on Green Island Reef, of repeated *A. planci* outbreak cycles, the skeletal record of which has become dispersed in the sedimentary record. Further, the enhanced element abundance apparent below 200 cm core depth implies a decrease in the prevalence of *A. planci* on these reefs over the last 1000-2000 years.

Present and past distributional patterns of *A. planci* elements in the sediment argues that repeated outbreak cycles should be adopted as the preferred view of *A. planci* activity. Any alternative hypothesis requires a long-term, stable, "intermediate level" *A. planci* population density on the two reefs in question which coincidentally has resulted in an element distribution in ancient sediment matching that now found at the surface and clearly related to contemporary outbreak cycles.

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