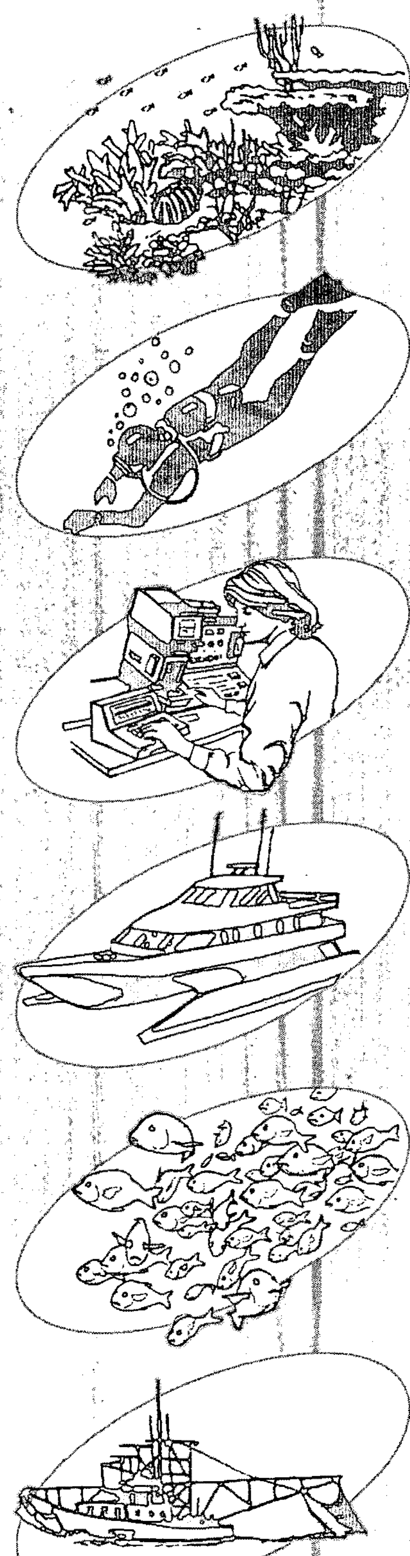
No. 10

CRC REEF RESEARCH

TECHNICAL REPORT



An investigation to describe the population dynamics of *Acanthaster Planci* (L.) around Lizard Island, Cairns section, Great Barrier Reef Marine Park

Richard Stump

MARENRE (Marine Environment Research)

CRC Reef Research Centre

Project Funded by the CRC Reef Research Centre

This project is part sponsored by the Environment Management Charge (EMC) paid by operators in the Great Barrier Reef Marine Park

CRC REEF RESEARCH TECHNICAL REPORT

AN INVESTIGATION TO DESCRIBE THE POPULATION DYNAMICS OF *ACANTHASTER PLANCI* (L.) AROUND LIZARD ISLAND, CAIRNS SECTION, GREAT BARRIER REEF MARINE PARK

Richard Stump

MARENRE
Marine Environment Research
2/5 Cleveland Terrace
Townsville Qld. 4810

A report funded by the CRC Reef Research Centre, the Crown-of-thorns starfish Research Committee and the Great Barrier Reef Marine Park Authority.

The CRC Reef Research Centre was established under the Australian Government's Cooperative Research Centres Program.

The Centre, established in 1993, undertakes an integrated program of applied research and development, training and education, aimed at increasing opportunities for ecologically sustainable development of the Great Barrier Reef and providing an improved scientific basis for Reef management and regulatory decision making.

CRC Reef Research Centre
c/- James Cook University
TOWNSVILLE QLD 4811
Phone: (077) 81 4976
Fax: (077) 81 4099
Email: crc.reef@jcu.edu.au

National Library of Australia Cataloguing-in-Publication entry

Stump, Richard.
An investigation to describe the population dynamics of *Acanthaster planci* (L.) around Lizard Island, Cairns Section, Great Barrier Reef Marine Park.

Bibliography.
Includes index.
ISBN 1 876054 09 3

1. Crown-of-thorns starfish - Queensland - Lizard Island. I. Cooperative Research Centre for Ecologically Sustainable Development of the Great Barrier Reef (Australia). II. Title. (Series: CRC Reef Research technical report; 10).

593.93

This publication should be cited as:
Stump, Richard. (1996)
An investigation to describe the population dynamics of Acanthaster planci (L.) around Lizard Island, Cairns Section, Great Barrier Reef Marine Park.
CRC Reef Research Centre
Technical Report No. 10
Townsville; CRC Reef Research Centre, 56 pp.

Published by the Cooperative Research Centre for Ecologically Sustainable Development of the Great Barrier Reef.

Further copies may be obtained from CRC Reef Research Centre, c/- James Cook University Post Office, Townsville, QLD 4811.

Printed by Image Print Townsville
Telephone (077) 755 933 Facsimile (077) 791 475
Email image@internetnorth.com.au

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

SUMMARY

Renewed reports of *Acanthaster planci* (L.) in the northern Cairns Section of the Great Barrier Reef Marine Park (GBRMP) have prompted opinion that a third episode of outbreaks, since about 1960, is developing in this region. Despite three decades of research effort there is little information about the early stages of outbreaks or their larval sources. This is primarily due to a lack of data on population dynamics and inconsistent use of survey methods that have failed to identify the early stages of outbreaks. To address this issue, this project aimed to investigate methods to describe *A. planci* population dynamics off Lizard Island through a series of three field exercises using mark/release/recapture (MRR) techniques and the application of a novel method of age determination. The specific aims of the study were to:

(a) determine changes in densities of *A. planci* by conducting adult (daytime) and juvenile (night) surveys and assess their impact on the benthic community.

(b) develop the methods of MRR and obtain data for population dynamics parameter estimation and analyses (i.e., age structure, population size, mortality, and recruitment).

(c) assess the method of identification of recaptures and establish a reliable protocol for identification.

(d) obtain morphometric data for growth analyses.

(e) analyse the capture/recapture data and investigate the use of the Jolly-Seber model (JOLLY) to determine population dynamics parameters.

The method to determine age in adult *A. planci* uses counts of pigment bands on cleaned aboral spine ossicles. Juveniles do not exhibit spine pigment bands but age can, in general, be determined from body size, due to the rapid growth phase leading to maturity. In the present study, individual ages were estimated assuming the validity of the method from evidence obtained in the first MRR study using *A. planci* on Davies Reef (Central Section). The recommended guidelines for field validation of annual bands involve recapturing marked individuals released for at least 12 months in all band classes from the population. This objective remains a priority for continuing research on *A. planci* populations.

Core research involved the development of a reliable procedure for individual identification based on coded madreporite patterns and an assessment of the potential for recapturing starfish marked with tetracycline. *A. planci* were collected from North Point and Granite locations and

transported to the Lizard Island Research Station (LIRS) for processing (identification and injecting with tetracycline to mark spine ossicles). They were maintained in aquaria prior to their release at the North Granite site. Of the 806 processed, 718 madreporite patterns were identified and 230 individuals shared 70 of these patterns (i.e., with one or more starfish). Therefore, 68% (488) of the starfish had unique madreporite patterns. Individuals with identical madreporite patterns can, in general, be distinguished using other characteristics (i.e., spine ossicle length, pigment band patterns on spine samples, arm-damage, colour patterns on the aboral body surface, body size and sex). A stepwise protocol was developed for identifying recaptures using these characteristics. Recapture rates derived from the estimated number alive following their release were 7.3% (8 recaptured) and 27.9% (80 recaptured) for the July and October field trips, respectively.

A broad, estimated age structure was determined from the spine ossicle samples, between 14 and 146 months (under the simplifying assumption that recruitment occurs in January each year). The oldest estimated age (14+ years) suggests a potential for this species to persist between recent outbreak episodes, with a similar interval to their estimated longevity (approximately 15 - 17 years). Assuming low adult mortality, the pattern in age structure reflects consecutive annual recruitment, increasing exponentially, over the past 6 to 8 years. This pattern is unlike those previously hypothesised from observations suggesting the sudden development of primary outbreaks.

Temporal changes in starfish densities showed a small but significant decline over the period of the three trips (nine months), particularly in the 1+ year class. The starfish relocated by the MRR experiments may have contributed to this pattern. Highest densities of both juveniles and adults were found at North Point (up to 867 ha^{-1}) and the North Granite release site (up to 1267 ha^{-1}) at 3 m depth where highest live hard coral abundances were found. Apart from the release site, high densities resulted from larval recruitment (1+ juveniles were found at all northern sites) and movement into those areas with higher resources (highest densities in areas of highest coral cover). Analyses of live hard coral and dead coral cover revealed no significant change in adjusted relative abundances with respect to site or depth over the study period, including the release site. The parameters relating to population dynamics were investigated using the general Jolly-Seber model for an open population. The large variation in recapture rates reflected the variation in mortality between the samples. This was considered to be the greatest influence on the error in the model calculations and the parameter estimates should be considered as first approximations only. Recommendations for marking starfish *in situ* were made to improve the accuracy of population dynamics parameter estimates in future studies.

The results have clear management implications for it is only through this type of study that accurate estimates can be made for recruitment, mortality and population size. These can be used to determine; the timing and effort required to implement effective control exercises (i.e., using the ratio of juvenile to adult sub-populations), the period of time taken to cause a reduction in the levels of hard coral cover (i.e., age structure), and the time taken for the population to attain its present size (i.e., age structure/MRR analyses). There is also potential for new applied research (i.e., before-and-after MRR studies for assessment of the efficacy of experimental control actions).

This study has demonstrated the potential significant contribution of MRR population dynamics studies in understanding how *A. planci* outbreaks occur. Therefore, with reasonable expectation of the third large-scale outbreak episode since the 1960's, a unique opportunity exists to describe the patterns of recruitment (temporal and latitudinal), population dynamics and growth. In addition, complementary data are required to assess the variation in the life-history characteristics of growth, mortality and reproduction. This could be achieved by immediate implementation of population dynamics and morphometry studies (including the MRR exercises) on representative reefs in the Cairns and Central Sections of the GBR.

1. INTRODUCTION

1.1 A history of *A. planci* in the Cairns Section

Early stages from two episodes *A. planci* outbreaks have been recorded in the Great Barrier Reef Marine Park (GBRMP) around Lizard Island, northern Cairns Section. The first occurred when significant spawning populations and recruitment were observed between 1957 and 1963 (Kenchington, 1977). He suggested that the parental stock of the original large populations was probably located north of 16°30', which included a large area behind the ribbon reefs including Lizard Island (14°38'). The second "wave" of starfish was recorded from the same area after 1981 with populations observed in the Lizard Island area as early as 1979. More recent analysis of the historical reports has concluded that if the hypothesised "seed" area north of Cairns really does exist, it may cover a relatively large number of reefs extending over 3 to 4° of latitude (see Reichelt, Bradbury and Moran, 1990).

In 1994, there were renewed reports of *A. planci* population growth in the Cairns Section of the GBR, particularly on reefs near Lizard Island. These sightings have prompted an opinion this may be part of a regional growth of populations that could lead to a third episode of outbreaks over the GBR (U. Engelhardt and B. Lassig, personal communication). Summarised Australian Institute of Marine Science (AIMS) surveys (unpublished data) showed there has been a consistent build-up in *A. planci* numbers around Lizard Island and a corresponding decrease in live coral cover since 1989 (Table A). The history of local sightings by researchers and research station staff around the island supports this pattern (L. Vail, personal communication).

Table A. Summarised AIMS survey data for coral cover (benthic transects) and *A. planci* counts (perimeter manta tow estimates) around Lizard Island (unpublished data, with permission).

Date	live coral %	dead coral %	*A. planci*	mean *A. planci*
5/10/88	12.53	5.0	1	0.011
7/12/89	15.73	3.29	0	0.011
2/11/90	11.63	3.84	1	0.012
1991	N/A	N/A	N/A	N/A
1992	N/A	N/A	N/A	N/A
10/10/93	23.72*	1.69*	17	0.23
16/10/94	19.83*	2.83*	48	0.53

* Technique changed from the line-intercept technique to video data collection and analyses (3 sites x 5 replicates).

The recurring phenomenon of *A. planci* outbreaks is potentially the most important issue for long-term reef management because of their immense impact and potential for long-term degradation of coral communities on the GBR. Despite this consideration, research directed towards addressing how *A. planci* populations develop into outbreaks has not been possible. This is because the techniques required to describe population dynamics were not available and the interpretation of historical data tended to be limited by inconsistent use of survey methods. To address this issue, the need for coordinated field research over several scales was recognised in the CRC Reef Research program on the regional environmental status of *A. planci* populations (1.6). Therefore, the results of this project may be used as an adjunct to the findings from the GBRMPA fine-scale regional surveys and the AIMS broadscale surveys.

1.2. A new approach to describing *A. planci* population dynamics

Surveys using manta-tow and limited, benthic-transect censusing methods have provided information that allows for general classification of reefs into outbreak or non-outbreak categories and simple estimates of parameters used to describe their population dynamics (i.e., density and size structure). However, with the real threat of another major episode there is now an urgent need for research to develop more detailed descriptions of the elements involved in population growth (i.e., age structure, population size, recruitment and mortality). To obtain this information, intensive, repeated field studies need to be undertaken in medium-term research programs. Only through such commitments to develop explicit population descriptions can we begin to understand how outbreaks occur, trace their source/s, and then set about determining their causes and predict the longer-term effects.

Detailed studies of populations include individual age since the age structure of a population is the key to understanding the population dynamics. Past attempts to study *A. planci* populations have revealed a number of problems in obtaining demographic data, in particular, it has not been possible to accurately determine age in *A. planci* (see Moran, 1986; Kettle, 1990; Johnson, 1992; Stump, 1994). Equally important, the introduction of studies on *A. planci* populations has been impeded by the requirement for the development of novel field techniques appropriate for this species (Moran, 1986; Stump, 1994).

Past attempts to describe *A. planci* populations interpreted age structure from modes in size frequency distributions. The relationship between size and age has continued to be used in *A. planci* studies until recently, despite increasing evidence of specific characteristics that are inconsistent with assumptions concerning their growth. Valid age determination in echinoderms has been achieved almost exclusively with echinoid species through skeletochronometric techniques. Periodic growth rings are generally found in larger skeletal elements such as the test plates, since the echinoderm skeleton consists of an open tridimensional network, the calcitic stereom. Unlike echinoids, the Asteroidea characteristically develop a skeleton of smaller ossicles that allows for a wide range of flexible movement, for locomotion, climbing, food handling and escape. An exception is *A. planci* which has large spines that join to pedicels, rooted in the aboral body wall, allowing battery-like protection as well as flexibility to bend so they do not restrict its cryptic habits.

Stump and Lucas (1990) showed that the aboral spine ossicles of adult *A. planci* have a linear growth pattern unlike the mode of development previously reported for echinoid spines. Numerous growth lines, perpendicular to the long axis were evident in spine sections and confirmed with tetracycline staining, apparently caused by frequent growth episodes. Spine growth in adults is by elongation with addition of new stereom at the base, preserving the entire growth history. Broad pigment bands develop parallel to the growth lines and are visible on the ossicle surface after the removal of soft tissues. It was hypothesised that spine growth continues throughout life and spine pigment band counts (SPBC) can be used to determine age in *A. planci*. Pigment banding commences after sexual maturity, in the third (2+) year at the time when body growth begins to slow and spine ossicle growth changes from enlargement in three dimensions to a mode primarily of elongation. Therefore, one SPBC (light and dark band pair) = 3+ years, two SPBC = 4+ years, etc,. A biosynthetic mechanism was proposed by Stump (1994) to explain the functional role of the pigment banding process, but was not investigated further.

The next step was to attempt to validate the SPBC method in the field. To address this task Stump (1994) introduced mark/recapture exercises on Davies Reef, Central GBR, between 1989 and 1991. He also collected morphometric data for seasonal and longer-term growth analyses. The recapture rate for marked individuals was 3.5 % (n = 661). Twelve of thirteen recaptured individuals whose release periods were at least twelve months supported the validation of age classes 3+, 4+ and 5+ years (i.e., one third of the estimated age classes). A further ten recaptures were obtained with release periods of less than twelve months, with incomplete band pair formation, also supporting the method. Further independent evidence was determined from morphometric results, including; annual incremental growth in the population SPBC classes, a significant increase in mean spine ossicle length but not body size, over the 38 month study period, consistent estimates of the growth constant ($K = 0.04\ mo.^{-1}$) between the recapture and population morphometric analyses; and the coincidence of the timing of the outbreak from AIMS survey results with the estimated age of the first outbreak cohort.

1.3. Aims of the present study

The study has sought to improve the techniques and procedures used in the previous population study by Stump (1994) and to trial new tagging technology as a potential adjunct to *A. planci* population dynamics studies. Investigations were based on a sampling strategy using the modified MRR methods in conjunction with standard benthic transect techniques. The principal aims of the study were:

(a) to estimate the densities of *A. planci* by conducting adult (daytime) and juvenile (night) surveys and assess their impact on the benthic community.

(b) to develop a mark/release/recapture (MRR) program to obtain data for population dynamics parameter estimation (i.e., age structure, population size, mortality, and recruitment).

(c) to assess the method of identification of recaptures, trial new tagging technology and establish a reliable protocol for identification, using; tetracycline for marking spine ossicles, the pattern of distribution of madreporites found in the aboral interarm areas, the extent of arm damage and pigment band patterns in aboral spine ossicles.

(d) to obtain morphometric data for growth analyses.

(e) to analyse the capture/recapture data and describe the population dynamics.

2. METHODS

2.1. Site selection around Lizard Island

Adult densities in the population around Lizard Island were estimated to be up to 160 ha^{-1} in the North Point area during 1994 (see Figure 1 for location) and dominated by a single cohort with body diameters of approximately 20 cm (U. Engelhardt and B. Lassig, in press) indicating an age class of 2+ years. By targeting smaller feeding scars in a preliminary manta-tow survey, circumnavigating the Island, permanent sites were set up in the areas with estimated high densities.

Using the estimated density as a guide, 50 x 3 m belt transects (150 m^2) were predicted to contain approximately 2.4 individuals each and therefore, considered to be a suitable trade-off between obtaining reliable estimates of errors and the time available. Two areas were selected for relatively high numbers of recent (white) feeding scars, from the manta-tow survey. These were North Point and the front reef of the island including South Island and Bird Islets. In consultation with the Lizard Island Research Station (LIRS) Directors, the area chosen to release marked starfish was Granite (see Figure 1). This area has a well-defined reef edge, with reasonable coral cover and would cause minimal interference to other studies conducted from LIRS. The two sites located off South Island were regarded as important due to the numbers of *A. planci* previously reported from the AIMS surveys on this side of the lagoon. However, the limited access due to exposure from the prevailing weather meant these sites could only be of secondary importance to the overall study.

2.2. Field research plan

The study was separated into two components, day and night. Daytime collections and belt transects involved estimates concerning the adult population, while night sampling enabled more accurate parameter estimates on the juvenile population. Depth-stratified collection of data was undertaken to determine any partitioning of habitat between the adult and juvenile populations.

The assessment of *A. planci* densities and gross live/dead coral cover estimates from three depths at each site served as a baseline to determine changes in population characteristics during interim periods. Some missing data occurred involving the NE site in the February study due to time restrictions and the SE and SW sites in the October study due to adverse weather. In the case of limited missing data and uneven periods between samples, it was considered appropriate to use linear regression techniques for data analyses.

2.3. Mark, release and recapture (MRR) exercise

The MRR techniques used were those recommended by Stump (1994), except for the removal of two adjacent arms to minimise invasive techniques that might affect the body growth analyses of recaptures (hence the use of tetracycline and the trial of the fluorescent elastomer micro-tags). All marked individuals were returned to one site (North Granite) to maximize the potential for obtaining recaptures and to determine the extent of migration in longshore directions and/or depth (i.e., migration distances could be estimated for recapture positions from this point of release).

Fluorescent elastomer micro-tags (Northwest Marine Technology Co.) were trialed as a permanent mark/tag. Field assessment of the red fluorescent micro-tag, formed from a two-part polymer, involved the injection of polymer intra-test from the oral surface into the "fleshy" junction between arms. A preliminary trial showed that this site on the starfish body facilitated the injection procedure and was the most likely position for tags to be retained within the body wall.

2.4. Belt transect exercise

Seven sites were marked by permanent sub-surface buoys. Two each of 50 x 3m isobathyic transects were set at 3 depths below MLW (9, 6 and 3m) per site (where possible). The transects were marked at each depth by a single point with replicates (2) laid in opposite directions maintaining isobathyic contours through use of a digital depth gauge. The northern site positions were recorded using a portable GPS (Magellan Nav 5000 DLX) during the third trip. The positions of two southern sites were not recorded due to adverse weather during the third trip which prevented safe anchorage off South Island.

Quantitative assessment of the fringing reef community was undertaken for each transect by estimating benthic cover in the major physiognomic categories using line-intercept techniques. Benthic transect video data were also collected for five northern sites during November 1995. The data is available as a 1995 baseline and to compare with the line-intercept data. Divers also counted and collected all starfish within 1.5 m each side of the tape placing them in catch bags or solid plastic baskets for return to the research station. Night exercises repeated the day sampling routine to obtain densities and samples of juveniles and young adult starfish (1+ and 2+ years) as well as additional adults. Remaining bottom time was used to collect all *A. planci* sighted within the area to increase the sample size and to increase the precision of estimates of parameters for the population dynamics analyses.

2.5. LIRS laboratory procedure

The collections were processed in the LIRS wet laboratories and the starfish held in large plastic bins (Nally) with flow-through seawater and airstones to maintain ambient temperature and supply oxygen. The following measurements were made for each individual: whole body diameter (BD), whole wet weight (WET), underwater weight (UW), sex (if possible), madreporite pattern, arm-injury pattern and descriptive secondary characteristics useful for individual recognition (i.e. colour patterns on the disk, arms and spines). Spine samples were taken by clipping 6-10 long, proximal arm spines close to the spine appendage base (i.e., through the pedicel) with one taken per arm, where possible, to reduce overall damage to the aboral spine battery. Spine samples were stored in plastic sample vials (30 ml) for protection during transfer to the CRC Reef Research Centre (JCUNQ) where they were processed and analysed.

The method of describing the madreporite pattern (after Glynn (1982)) was achieved by developing a string of numbers where each number in the sequence represents string counts of madreporites or their absence in consecutive interarm areas (see Stump, 1994). Counts always begin with the largest number of consecutive madreporites as the first number. Therefore, the 1st, 3rd, 5th, etc. (odd) numbers in the sequence involve madreporite counts (mads.) and the 2nd, 4th, 6th, etc. (even) numbers in the sequence involve absences in the interarm zones (i.e., 4 1 3 6 equals 4 mads. + 1 absence, + 3 mads. + 6 absences). To identify possible errors in the procedure the addition of the numbers in the string was used to check the number of interarm areas (or the total number of arms). The string always begins with madreporite counts, ends with an absence count and contains an even number of counts.

Tetracycline staining of spine ossicles was used to measure spine growth and as a tag to identify recaptures. Oxytetracycline was used in the form of commercially manufactured beads administered in prepared capsules (Doxycycline © Faulding Pharmaceuticals, an antibiotic in the tetracycline class), injected directly into the body cavity. Smaller starfish were given a solution of tetracycline by injection using crushed tablets (750 mg tetracycline hydrochloride; Aquasonic P/L, Australia). Approximately 100 - 150 $mg.kg^{-1}$ whole wet weight of tetracycline (as recommended by Stump (1994)) was used to stain the spine ossicles.

Potential recaptured starfish were screened through a preliminary series of criteria for identification before acceptance involving:

(a) identifying the tetracycline mark in prepared thin-sections of spines and measuring the additional skeletal growth from the mark to the spine ossicle base using fluorescence microscopy.

(b) matching madreporite patterns.

(c) matching pigment banding characteristics (band widths, pigment intensity and colour variations are similar within individuals).

(d) checking the difference in mean spine ossicle lengths (using the mark and recapture samples) with the growth measured from thin-section analyses of spines.

(e) comparing secondary characteristics; aboral colour patterns, signs of previously clipped spines in recaptures, arm-damage patterns, body size and sex.

In the July trip all processed individuals were double-marked using oxytetracycline and visible, fluorescent elastomer micro-tags (Northwest Marine Technology) (Buckley and Gomez-Buckley, 1992). The purpose of the elastomer tag (subject to its success) was to ID batches of recaptures in the field or, to use as a field guide to identify marked individuals without the need for the preparation of spine thin-sections. All potential recaptures had thin-sections of spine samples prepared and analysed for the tetracycline stain to confirm their identification as a recapture.

2.6. Laboratory procedure

Spine samples were placed in individual vials on collection and sealed for transport back to the CRC Reef Research laboratory (without fixative). The laboratory procedure involved processing spine ossicle samples prior to measurement and assessment of pigment band counts. Soft tissues were dissolved from the spines in 10% sodium hypochlorite over 1 to 2 days. The ossicles were then rinsed 3 times and allowed to stand in tap water for 1 to 2 days, then dried over several days in a fume cupboard. Care was taken with spine preparation and measurement as the tips of spines are easily broken. Spine ossicle lengths were measured with vernier calipers (to 0.1 mm) with ca. 5 spine ossicles per individual. Pigment band counts on spine samples from all individuals were conducted on three separate occasions to ensure consistency with counts.

Thin-sections of spine samples from all potential recaptures were prepared for ultraviolet light (UV) analysis to confirm the presence of the fluorescent tetracycline stain and their recapture status. Sections of spines and pedicels were prepared for UV microscopy by embedding ossicles in epoxy resin on glass slides. The ossicles were then abraded on fine emery paper to achieve a thin-section (approximately 200 μm).

2.7. Data handling and analyses

The methods for data collection and analysis in the present study can be summarised as:

MRR analyses accounted for the starfish population collected in the area around the release site at North Granite and North Point. Parameter estimates were obtained from the general open population model (including mortality and immigration), where recruitment was assumed to be negligible because the samples were all collected within one reproductive season (February to October). The capture/recapture data was analysed using the program JOLLY (the general Jolly-Seber open population model) which calculated standard errors and confidence intervals for each of the parameter estimates, where applicable (see Pollock et al. 1990). The equations used to estimate the population dynamics parameters are defined in Table B.

Table B. Jolly-Seber model parameters and equations used for their estimation.

Parameter	Equation
M_i	$m_i + \frac{R_i z_i}{r_i}$
N_i	$\frac{n_i M_i}{m_i}$
B_i	$N_{i+1} - \Phi_i(N_i - n_i + R_i)$
Φ_i	$\frac{M_{i+1}}{M_i - m_i + R_i}$
p_i	$\frac{m_i}{M_i}$ or $\frac{n_i}{N_i}$

Key:

M_i estimated number of marked starfish in the population at time i

N_i estimated population size at time i

B_i estimated number of recruits (birth + immigration)

Φ_i estimated probability that a starfish alive at time i survives to time i + 1

p_i estimated probability that a starfish alive at time i is captured in the ith sample

m_i the number of marked starfish captured in the ith sample

n_i total number of starfish captured in the ith sample

R_i the number of the n_i that are released after the ith sample

r_i the number of R_i starfish released at i that are not captured again

z_i the number of animals captured before i, not captured at i, and captured again later.

The assumptions involved in applying the model to *A. planci* were:

(a) that recruitment occurred over a period around mid-summer and therefore lies predominantly outside the sampling period (February to October), but immigration into the study area may have occurred at any time.

(b) every starfish present in the population at the time of the ith sample has the same probability of capture.

(c) every marked animal in the population after the ith sample has the same probability of survival (Φ_i) until the (ith + 1) sampling time.

(d) marked starfish are not overlooked or lost.

(e) all samples are instantaneous and each release is made immediately after the sample.

There are specific issues to address when applying statistical techniques to analyse *A. planci* populations, with an aim to optimize the accuracy in estimation of parameters. First, *A. planci* is a "contagious" starfish, i.e. it aggregates due to a number of factors including; density and coral cover (Moran, 1986), age (Zann et al., 1987; 1990; Stump, 1994) or the time of the year (Wilson and Marsh, 1974). Second, while juveniles are probably confined to small areas in their first 12 to 18 months, adults are relatively large and therefore, capable of moving over reef areas, depending on their condition and motivation (i.e., hunger, see Kettle, 1990; and Yokochi et al., 1992). Third, growth rates are relatively high such that very small juveniles have different habits and can occupy different habitats to young adults at approximately 2+ years. Apart from feeding scars, most juveniles are apparent on reefs only when they emerge from a cryptic habitat to feed at night (Kettle, Stump and Bell, unpublished). Therefore, the methods used to determine the juvenile and adult population densities were necessarily different so that the population was split into these two groups for the analyses and discussion.

Belt and line transect data were used for estimation of juvenile and adult population density and benthic cover. Minimal models were developed to assess changes in dead coral/coralline algae cover using backward elimination of variables in multiple regression analyses. Relative percentages of dead coral/coralline algal cover were arcsine transformed (Zar, 1984) prior to analysis. Multiple linear regression techniques were also used to analyze the starfish counts (discrete (Poisson) regression) in relation to independent parameters relating to time (3 sampling dates), location (7 sites), depth (3 levels) and replicate (2).

The SigmaPlot curve fitting program (Revision SPD-1.1; Jandel Scientific, 1992) was used to estimate the parameters of equations used to describe growth curves. The program fits curves iteratively using least squares to minimise the sums of the squares of the differences between the equation value and the sample data under the assumption that the standard deviations of each sample are equal. The significance of the curve parameters was tested using a t-test (where t = parameter coefficient/standard error of the parameter). The two growth functions were:

(a) von Bertalanffy growth function

$$y = L_{\infty} . (1-e^{(-K . t_o)})$$

(b) Logistic growth function

$$y = L_{\infty}.(1-(b.(e^{(-K . t_o)}))^{-1}$$

where:

L_{∞} = asymptotic body size

K = growth constant

b = growth parameter

t_o = age after initial resting phase (coralline algae feeding phase)

3. RESULTS

3.1. Timing and site selection

A. planci densities and benthic community descriptions were obtained from the 7 sites and 3 depths (3, 6 and 9m) around North Point, Granite Point and South Island in February, July and October (Appendix 1; GPS positions of sites: Figure 1; location map). Mark/recapture morphometrics studies in February, July and October when 128, 317 and 373 individuals were collected from the 5 northern sites, transported to the research station for processing, and maintained in aquaria prior to release. Body morphometry and aboral spine ossicle samples were obtained and individual identification was achieved using the pattern of madreporites in interarm area and other physical characteristics.

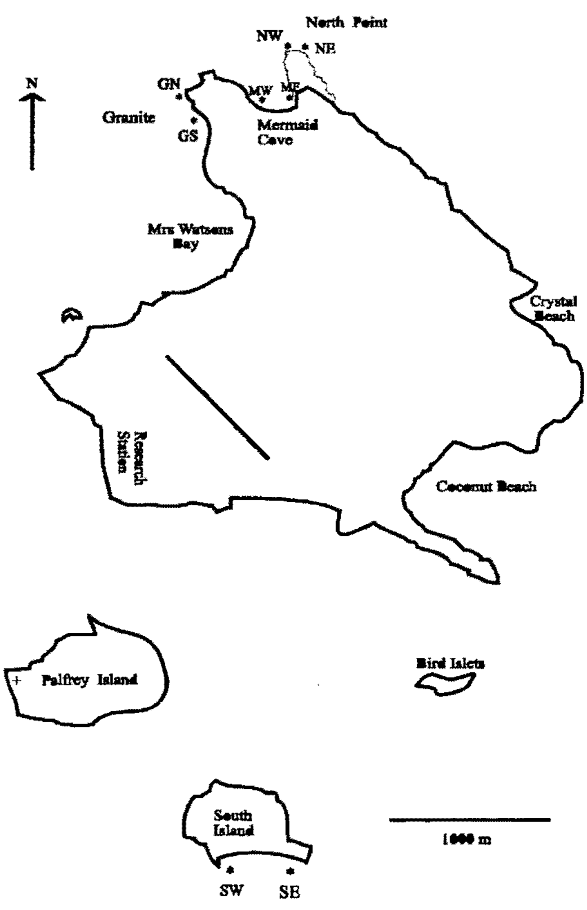


Figure 1. Map of Lizard Island showing permanent sites from North Point (2), Mermaid Cove (1), Granite (2) and South Island (2).

3.2. Benthic community analyses

Benthic community descriptions are presented as bar charts for each site and at each depth (mean) for each field trip (Appendix 2; see key). The multiple regression analyses are presented in Table 1.

Table 1. Final model from benthic line-intercept transect analyses using multiple regression techniques for arcsine transformed, relative percentages of dead coral/coralline algae cover.

Source	SS	DF	MS	F-ratio	P
Depth	9209.52	1	9209.52	238.4	< 0.01
Site	1360.55	6	226.76	5.87	< 0.01
Depth*Site	2033.94	6	338.99	8.77	< 0.01
Model	12604.01	13	969.54	25.095	< 0.01
Error	3283.95	85	38.635		
Total (corr.)	15888.0	98			

$r^2 = 0.79$; $n = 99$; SE = 6.216

The final model accounted for 79% of the variation found in the data and therefore was assumed to be an adequate description. There was significant variation in dead coral/coralline algae cover, consistently decreasing with depth (commensurate with live coral cover) at all sites. There was also significant variation among sites, confounded by an interaction with depth (Table 1). Highest levels of dead coral/coralline algae cover were at North Point (NE) and the Granite release site (GN). There were no significant changes in dead coral/coralline algae cover over the study period, including the release site.

3.3. Starfish identification

Of the 806 starfish processed, 718 individual madreporite patterns were identified and 230 of these shared 70 patterns with one or more starfish (68% (488) of starfish sampled had unique patterns). Individuals with identical madreporite patterns can generally be distinguished based on the pigment banding patterns in the spines.

The recommended protocol for identifying recaptured *A. planci* is:

(a) Identify the tetracycline stain; match madreporite patterns from database; compare; spine pigment band patterns, spine length, body size and other secondary characteristics.

If unable to match madreporite patterns, then proceed by:

(b) Calculating the predicted spine length at the time of release; subtracting the growth estimate determined by the thin-section analyses (tetracycline stain) from the mean spine length obtained in the recapture spine sample analyses.

(c) Using sorting methods on the database to select potential individuals with mean spine lengths within a small range of the predicted spine length at the time of release.

(d) Matching the pigment banding pattern of potential individuals with the recapture sample, then comparing secondary characteristics (i.e. body size, sex, arm-damage and colour patterns on the aboral surface).

(e) Comparing the madreporite patterns to confirm the identity (i.e. how close the string patterns match) and determine the reason for the discrepancy in interpretations.

3.4. Mark and recapture

Recapture rates were calculated using the number recaptured divided by the estimated number surviving following their release, these were 7.3% (8/109) and 27.9% (80/287) for the second and third field trips, respectively. Three individuals were identified as recaptures from their madreporite patterns and secondary characteristics, but did not exhibit the tetracycline stains in thin-section of spine samples. This may been due to the loss of the tetracycline capsules from the body cavity incision soon after processing. Only one individual with tetracycline stain in the spine thin-sections could not be traced to individual data from the time of its release. The increased rate obtained in October was probably due to several factors, including; new aquaria facilities at LIRS (capacity, water flow rate and equipment), stress mitigation through development of better handling and processing methods, and the lower ambient temperatures during winter and spring.

Trials of a new marking technique involving intra-body wall injection of fluorescent, elastomer micro-tags were deemed unsuccessful (retained in only 7.7% (6/78) of recaptures released in July). There was also evidence of imminent tag rejection and loss with the elastomer compound projecting out of the body wall in some of the recaptured starfish. This poor result was obtained despite efforts to modify particular techniques employed in the initial marking procedure (February) which had been identified as potential causes of tag rejection.

3.5. Population characteristics

(i) Size frequency patterns of body size and mean spine ossicle length

Plotted size frequency distributions of whole body diameter (cm) (BD), underwater body weight (g) (UW), whole wet weight (WET) (g) and mean spine ossicle length (mm) (S) used pooled data (3 samples) (Figures 2 - 5 respectively).

Multiple modes were apparent in all frequency distributions for BD, UW and WET representing juvenile (estimated 1+ years), young adult (2+ years) and adults (3+ years and older). Modal progression through time was apparent over the study period in the younger cohorts, but not in those adults approaching their asymptotic body size. However, the frequency distributions for spine ossicle length showed approximately five modes with apparent modal progression in both juvenile and adult cohorts.

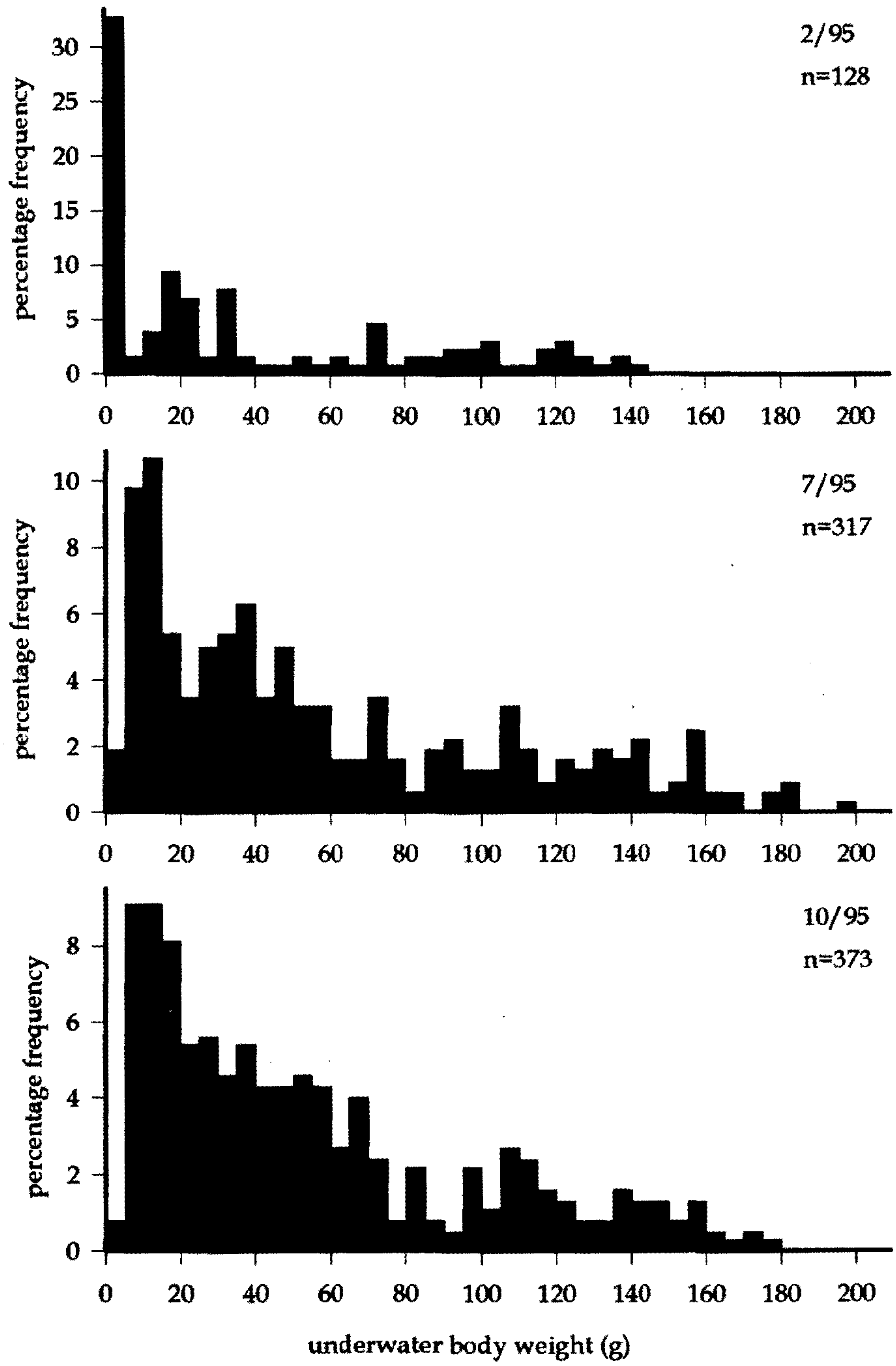


Figure 3. Size-frequency distribution of underwater body weight UW (g) of *A. planci* from Lizard Island, Cairns Section for February, July and October 1995.

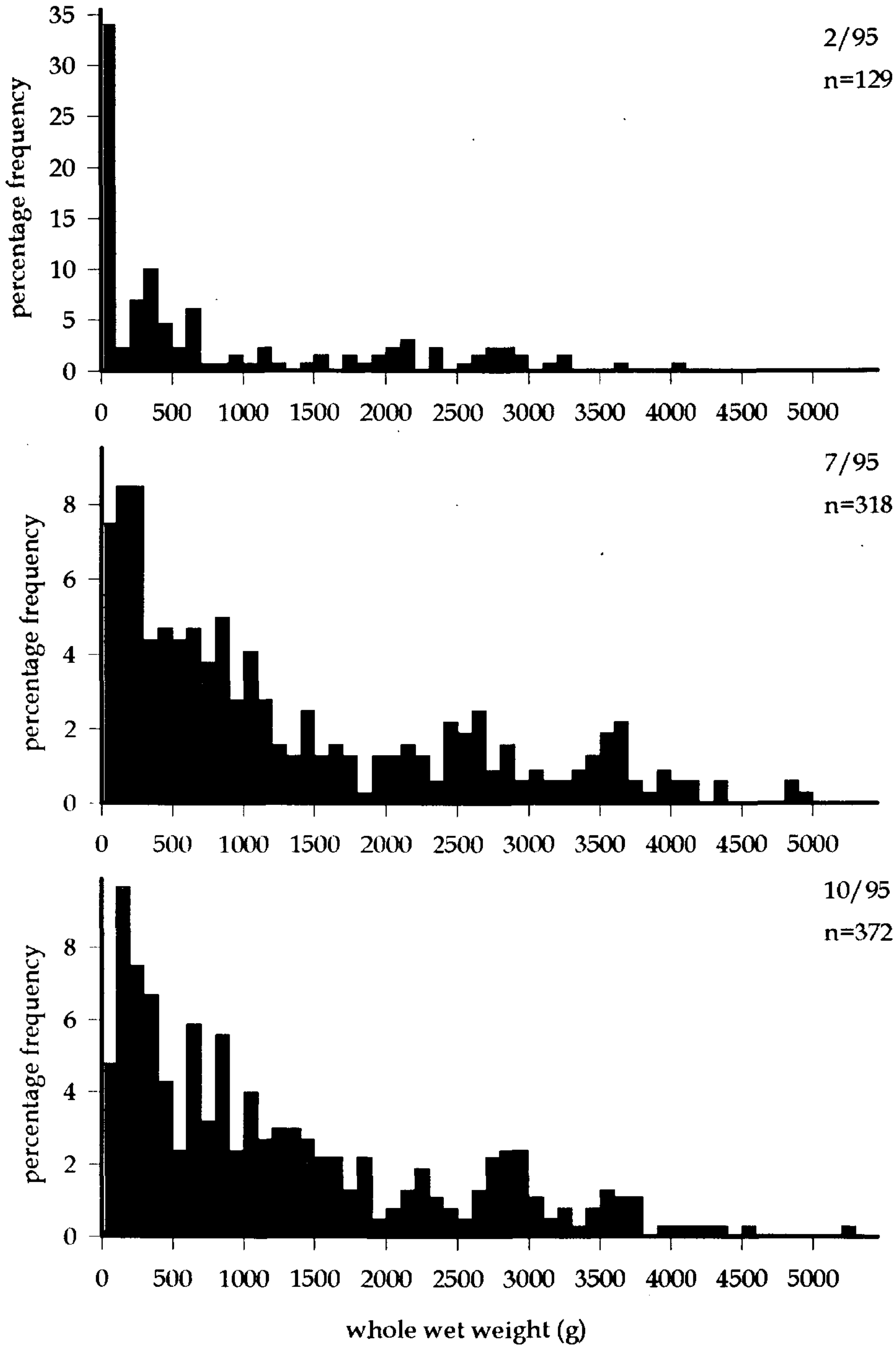


Figure 4. Size-frequency distribution of whole wet weight WET (g) of *A. planci* from Lizard Island, Cairns Section for February, July and October 1995.

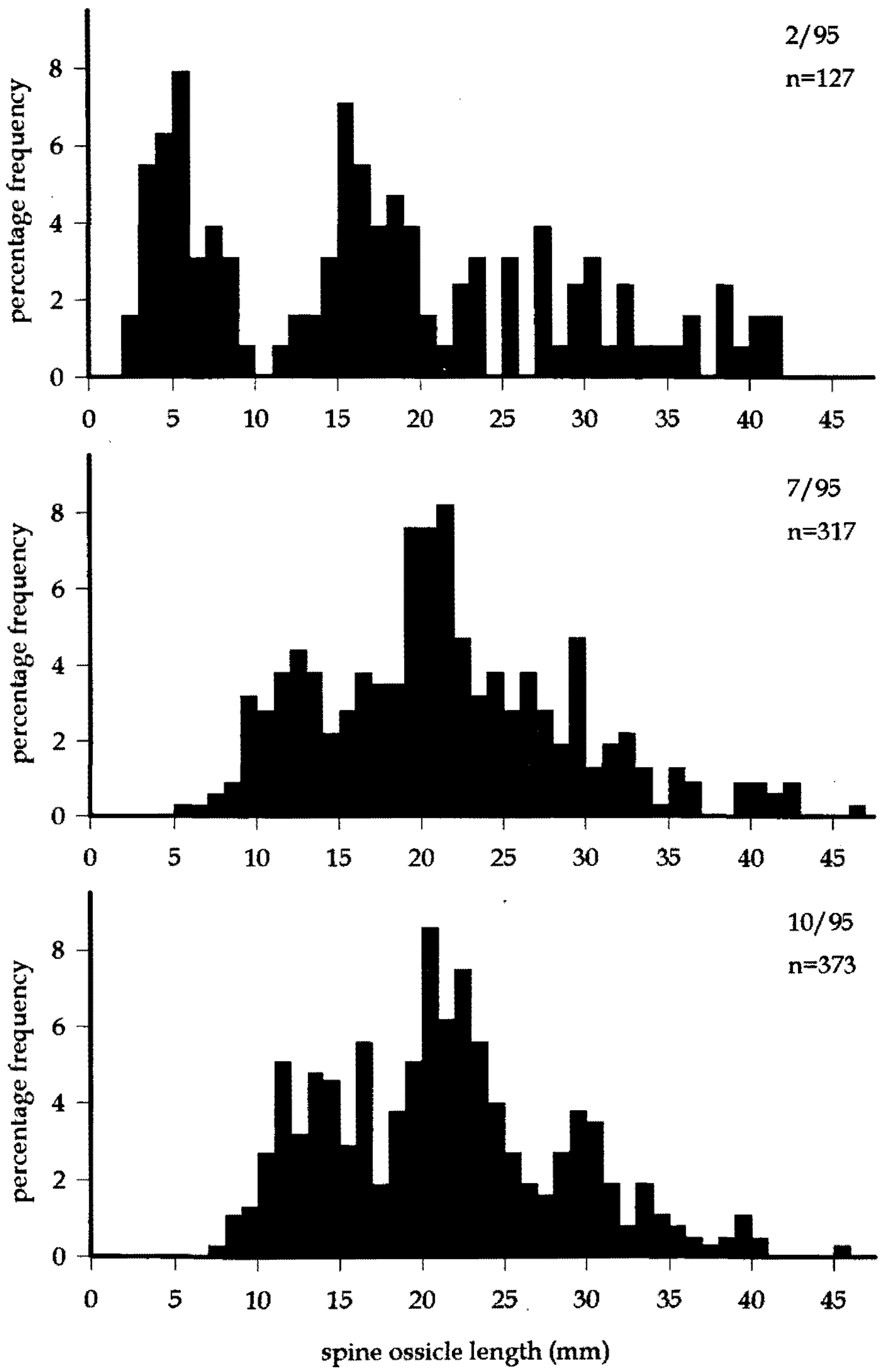


Figure 5. Size-frequency distribution of spine ossicle length (mm) of *A. planci* from Lizard Island, Cairns Section for February, July and October 1995.

(ii) Estimated age structure

The population comprised a broad estimated age structure between 14 and 146 months covering 12 estimated year classes (Figure 6a). However, the resolution of the banding patterns decreases with increasing band counts meaning that the upper age estimates may be less reliable. Variation in relative percentage composition of cohorts among sampling dates was evident in the younger estimated age classes. There was an apparent decline in the 1+ year cohort over the study period indicating that population growth was slowing. Repeated annual recruitment occurring over 8 estimated age classes including substantial representation of the 1+, 2+ and 3+ year classes (overall mean whole body diameters were; 13.6 cm, SE = 0.33 cm, n = 187; 25.3 cm, SE = 0.30 cm, n = 294; and 31.7 cm, SE = 0.44 cm, n = 139) respectively. Although there may have been some bias toward collecting relatively more adults (collected day and night) than juvenile starfish (collected predominantly at night), 58% of the sample was composed of individuals which had not yet undergone their first major spawning (at approximately 35 months). This pattern clearly described a population with a high ratio of young to old starfish indicating the adult population is currently increasing in size.

The overall size-frequency distribution of estimated age is used as an estimate of the population age structure (Figure 6b). The pattern showed that there have been elevated recruitment levels (above those expected between outbreak episodes) for approximately 6 to 8 years, a pattern not able to be identified in the body size-frequency distributions. The relative size-frequency distribution of ages showed exponential population growth up to the 2+ years cohort. There was also an indication that the population growth is slowing with a smaller sample of the 1+ year cohort than the 2+ cohort. The oldest estimated age (14+ years) was determined from spine samples with a mean spine length > 50 mm.

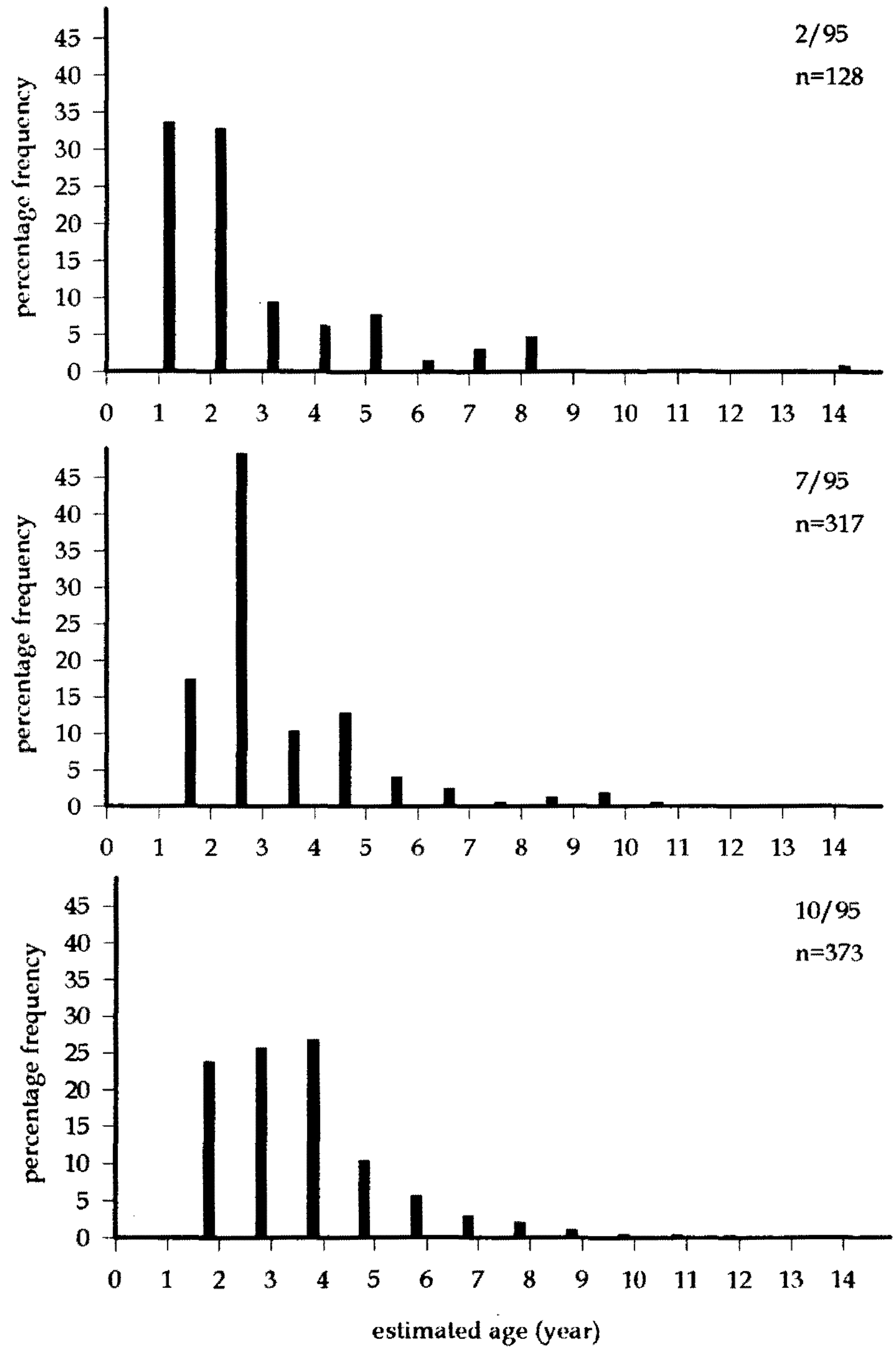


Figure 6a. Size-frequency distribution of estimated age (month) using pigment band counts from aboral spine ossicles in *A. planci* from Lizard Island, Cairns Section for February, July and October 1995.

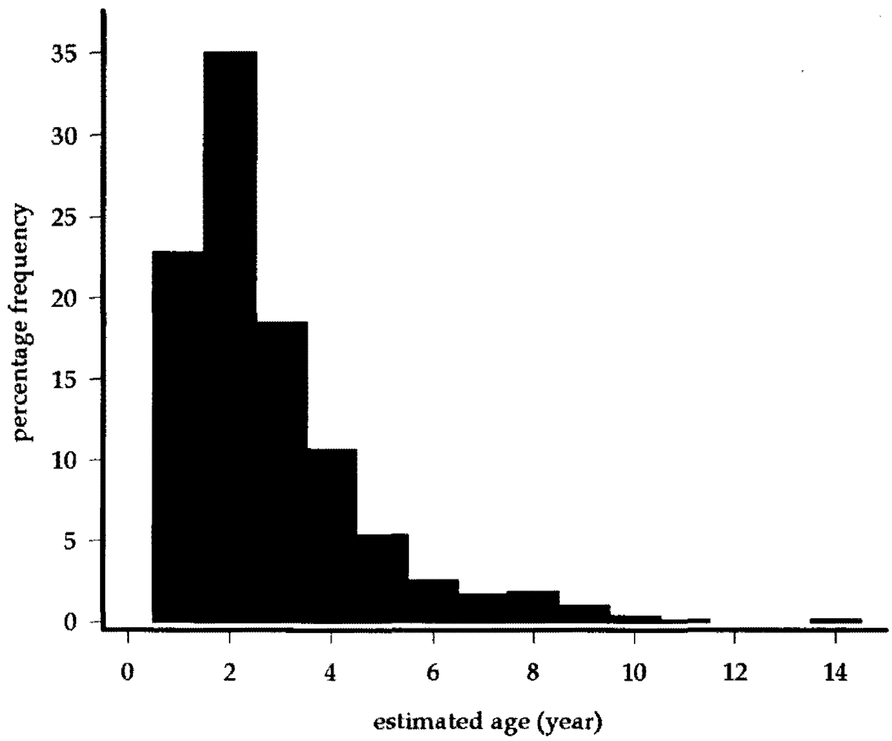


Figure 6b. Overall size-frequency distribution of estimated age (month) using pigment band counts from aboral spine ossicles in *A. planci* from Lizard Island, Cairns Section for combined data from February, July and October 1995.

(iii) Population density

Highest densities were found in the shallow zones of the fringing reefs around North Point (up to 867 ha^{-1}) and North Granite (1267 ha^{-1}). *A. planci* counts from belt transects were analysed using discrete (Poisson) regression, for all starfish counted in transects during the day (Table 2.1);

Table 2.1. Unweighted discrete (Poisson) regression of Lizard Island *A. planci* counts (juvenile and adults) in benthic belt transects over 7 sites, 3 depths (where possible) and 2 replicates from 3 samples, February, July and October.

Final model

Variable	Coefficient	SE	Coeff./SE	P
Constant	2.4728	0.1956	12.64	< 0.001
Sample 2 (July)	-2.0880	0.2110	-9.90	< 0.001
Sample 3 (Oct.)	-0.7236	0.1445	-5.01	< 0.001
GN site	0.8449	0.1319	6.40	< 0.001
Date * Depth	-0.0263	0.0036	-7.28	< 0.001
Deviance	181.76			
P	< 0.001			
Deg. Freedom	101			

Similarly, for juvenile/young adult starfish (estimated age 1+ and 2+ years) collected at night (Table 2.2.).

Table 2.2. Unweighted discrete (Poisson) regression off Lizard Island *A. planci* counts (juveniles only) in benthic belt transects over 7 sites, 3 depths (where possible) and 2 replicates from 3 samples, February, July and October.

Final model

Variable	Coefficient	SE	Coeff./SE	P
Constant	1.8155	0.3199	5.68	< 0.001
Sample 2 (July)	-1.0329	0.3134	-3.30	< 0.001
Sample 3 (Oct.)	0.7798	0.2399	3.25	< 0.001
NE site	0.4465	0.1770	2.52	< 0.011
Date * Depth	-0.0467	0.0061	-7.64	< 0.001
Deviance	197.82			
P	< 0.001			
Deg. Freedom	93			

Fitted values plotted against standardised residuals for both discrete regression analyses showed residual trends in data revealing that one or more additional variables were required to fit the data, P < 0.01 for both day (Figure 7a. all individuals) and night counts (Figure 7 b. juveniles/young adults). Despite the lack of fit, significant variation in the data was due to a small decrease in counts of starfish with time and depth (significant interaction term) except at the North Granite (release site) (day exercise) and at the NE site (night exercise) where counts of starfish generally increased during the year. This overall decline probably reflects the decrease in the relative numbers of 1+ year starfish in the collections over the three sampling periods.

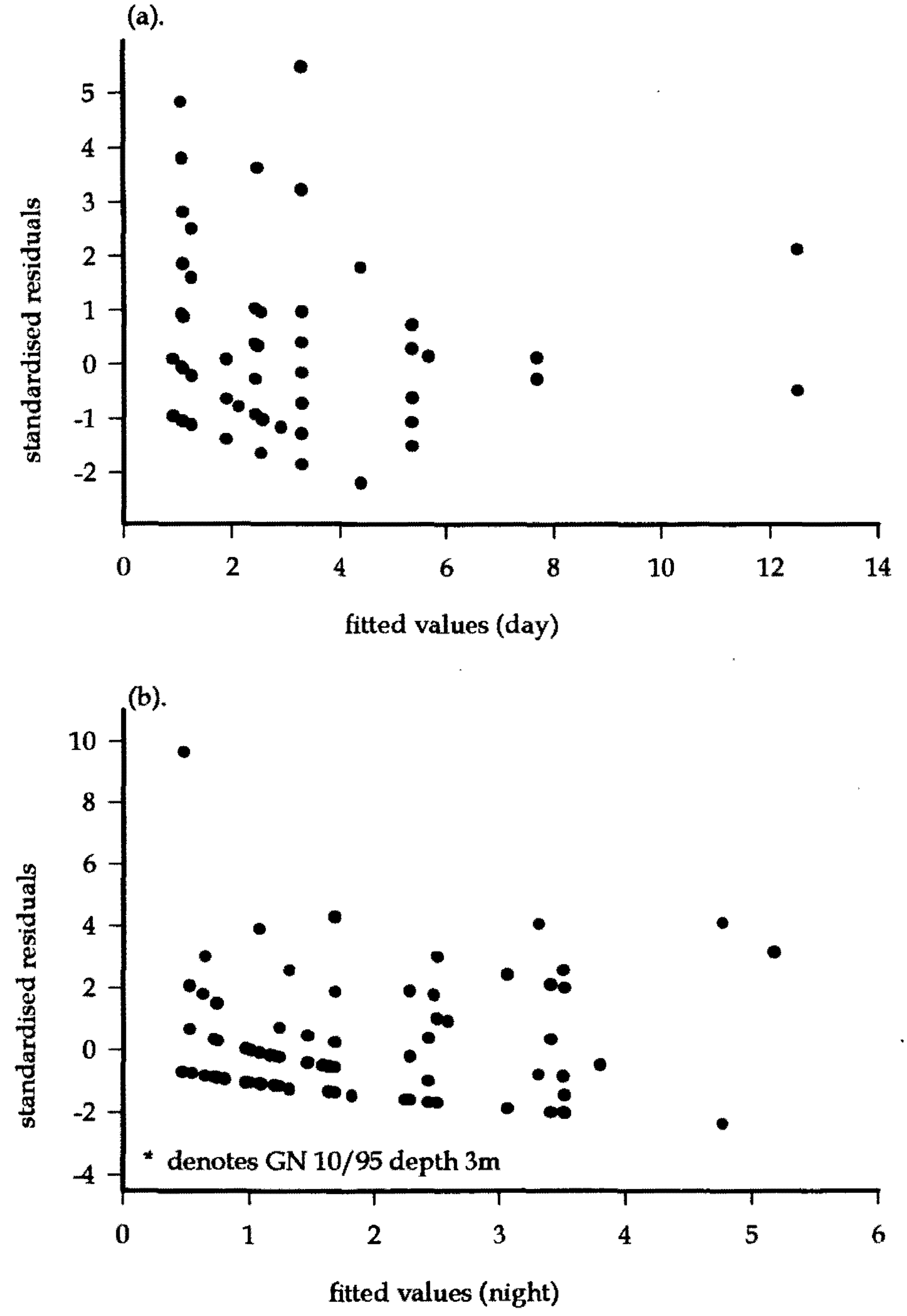


Figure 7. Plot of standardised residuals against fitted values for discrete (Poisson) regression models developed for (a) *A. planci* counts in belt transects by day and, (b) juvenile *A. planci* counts in belt transects by night.

(iv) Mark/recapture exercise

A total of 88 recaptures were obtained in the second and third sampling collections including 3 individuals recaptured twice (Table 3.1). There was a negative bias in the recapture rates due to higher rates of mortality among marked individuals. Evidence of this bias was found from casual observations sighting mortality following the release of batches of starfish on the North Granite site. The observations of *in situ* mortality accounted for at least 6 individuals (February), 3 (July) and 4 (October) within 10 metres radius of the release site, presumably from fish predation and processing/transportation trauma. No evidence of mortality among unmarked starfish was observed in the field during the 3 trips. Sub-lethal predation also increased following release of batches of marked starfish contributing to the negative growth found in many of the recaptures. Arm damage interpreted as sub-lethal predation occurred in 71% of juveniles/young adults (≤ 25 cm; n = 238) and 45% of adults (> 25 cm; n = 169).

Table 3.1. Summary of mark/release/recapture (MRR) data over 3 sampling trips, February, July and October.

	Feb.	July	October	Feb. and October	Total
Processed	128	310	373		811
Released	109	287	336		732
Recaptured		8	78 (3)*	2	88

* including 3 individuals recaptured twice.

(v) Parameter estimates for population dynamics

Parameters of the general Jolly-Seber model for mark and recapture data were estimated from the results of the MRR exercise over the three sampling occasions (February, July and October 1995). Estimates, SE's and 95% confidence limits were also derived from the data (Table 3.2).

Table 3.2. General Jolly-Seber model estimates of *A. planci* population dynamics in the area of North Granite, Lizard Island over three sampling exercises in February, July and October 1995.

Parameter	Estimate	SE	95% confidence limits
M_i	15.9	4.92	6.26 - 25.54
N_i	578	213.9	158.4 - 996.9
B_i	N/A		
Φ_i	0.680	0.053	0.577 - 0.784
pi	0.503	0.191	0.113 - 0.894

Key:

M_i estimated number of marked animals in the population at time i

N_i estimated population size at time i

B_i estimated number of recruits (birth + immigration)

Φ_i estimated probability an animal alive at time i survives to time i + 1

p_i estimated probability an animal alive at time i is captured in the ith sample

A $\chi 2$ goodness-of-fit test statistic = 0.443; 1 deg. of freedom; P = 0.506 (k-2 contingency test) was based on comparing observed and expected values for numbers of animals captured with each possible capture history. The non-significant result indicates that the model is an adequate fit of the data, but does not guarantee that the model assumptions have been met.

Given the short duration of the field trips, marked starfish were allowed to recover in aquaria for up to four days prior to their release on the North Granite site. Despite visual signs of recovery (i.e. body wall shape) there were casual observations of mortality *in situ* during the release exercises. This accounted for at least 6 (February), 3 (July) and 4 (October) individuals identified from arm-tip and body wall fragments, one to two days after release. This mortality was assumed to have been caused by fish predation and processing/transportation trauma.

3.6. Body growth analyses using cohort data

Growth curves were fitted for the three body size variables and mean spine ossicle length for all individuals; (Table 4.1). Applied growth functions were selected for goodness-of-fit.

Table 4.1. Growth function selection

ID	Parameter	Growth Function
BD	whole body diameter (cm)	von Bertalanffy (VBGF)
UW	whole underwater weight (g)	logistic
WET	whole wet weight (g)	logistic
S	mean spine ossicle length (mm)	von Bertalanffy (VBGF)

Fitted equations and curve fitting analyses for each of the applied growth functions are presented in Table 4.2.

Table 4.2. Growth function analyses

Variable	Fitted equation	ANOVA of curve-fit results
BD_t	$47.40(1-e^{-0.034(t-9.18)})$	r^2=0.84;SE=4.37;MSE=19.09;n=819
UW_t	$139.14(1-(-53.44(e^{-0.088(t-10.5)})))^{-1}$	r^2=0.77;SE=22.22;MSE=493.6;n=817
WET_t	$3369.3(1-(-91.71(e^{-0.097(t-10.5)})))^{-1}$	r^2=0.78;SE=545;MSE=3.0×10^5;n=819
S_t	$45.60(1-e^{-0.019(t-4.50)})$	r^2=0.90;SE=2.61;MSE=6.79;n=817

Growth curves fitted against body size data (UW and WET) using successive age classes (1+ to 8+ years) described a von Bertalanffy (Figure 8 (a)) or a logistic-type curve pattern (Figure 8 (b) and (c)). Continued body growth into the adult phase to approximately 80 months represents an indeterminate mode of growth. However, these analyses should be treated with caution for fitted growth curves among cohorts can be misleading because individuals within cohorts tend to show less variability in the mode of growth than between cohorts. In this population the adult body size range of 33 cm (18 to 51 cm) represented no more than two or three modes while the corresponding estimated age range was 10 consecutive year classes.

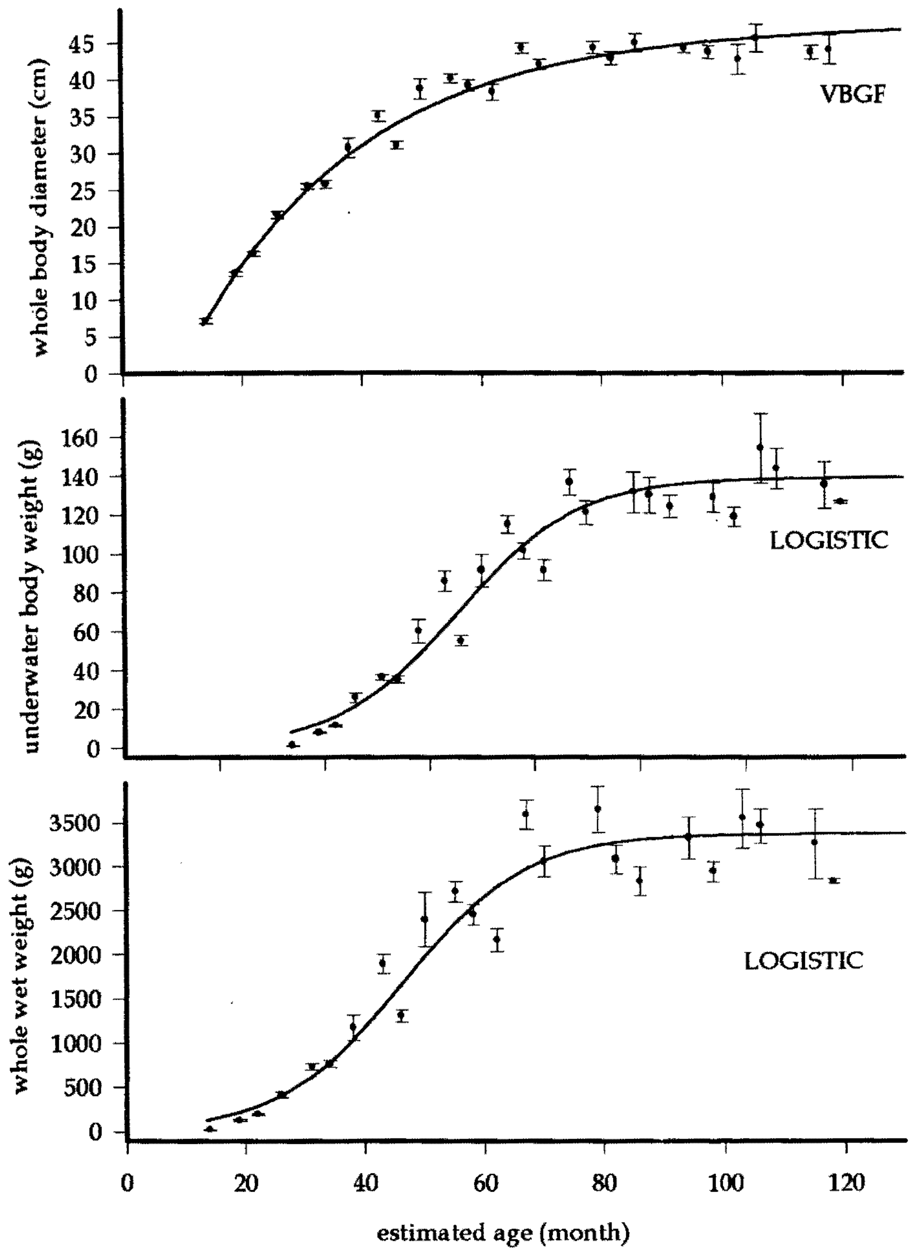


Figure 8. (a) Mean whole body diameter (cm) and SE (with fitted von Bertalanffy growth function (VBGF)), (b) mean underwater body weight (g) and SE (with fitted logistic growth function (LOGISTIC)) and (c) mean whole wet weight (g) and SE (with fitted logistic growth function (LOGISTIC)), at estimated age for *A. planci* from Lizard Island, Cairns Section for February, July and October 1995.

Assuming the method of age determination is valid, the interpretation of age from body-size frequency distributions of adult *A. planci* remains unjustified.

The mode of growth in spine ossicles (S) is described closely by the VBGF (r^2=0.90) (Figure 9) and supports the hypothesis that aboral spines continue to grow throughout life. The results from the spine thin-section analyses also support the claim where 85 of 88 identified recaptures retained the tetracycline stain. Continued spine growth throughout adult life allows for the consistent and periodic deposition of pigment bands.

3.7. Body growth analyses from recapture data

Data collected on recaptures included: subsequent spine growth from thin-sections showing the tetracycline marker (T), mean spine ossicle length (S), whole body diameter (BD), underwater body weight (UW) and whole wet weight (WET). Growth rates (units.month^{-1}) calculated from recapture data were plotted against estimated age class and analysed by linear regression techniques (Figure 10). The summary of the regression analyses for all recapture data is presented in Table 5.

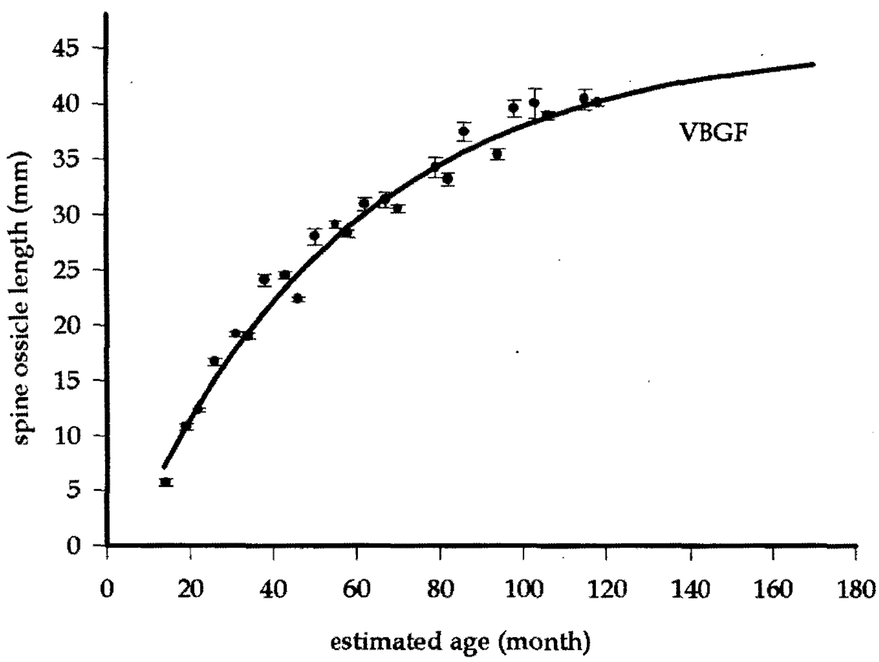


Figure 9. Mean spine ossicle length (mm) and SE at estimated age with fitted von Bertalanffy growth function (VBGF) (single line) for *A. planci* from Lizard Island, Cairns Section for February, July and October 1995.

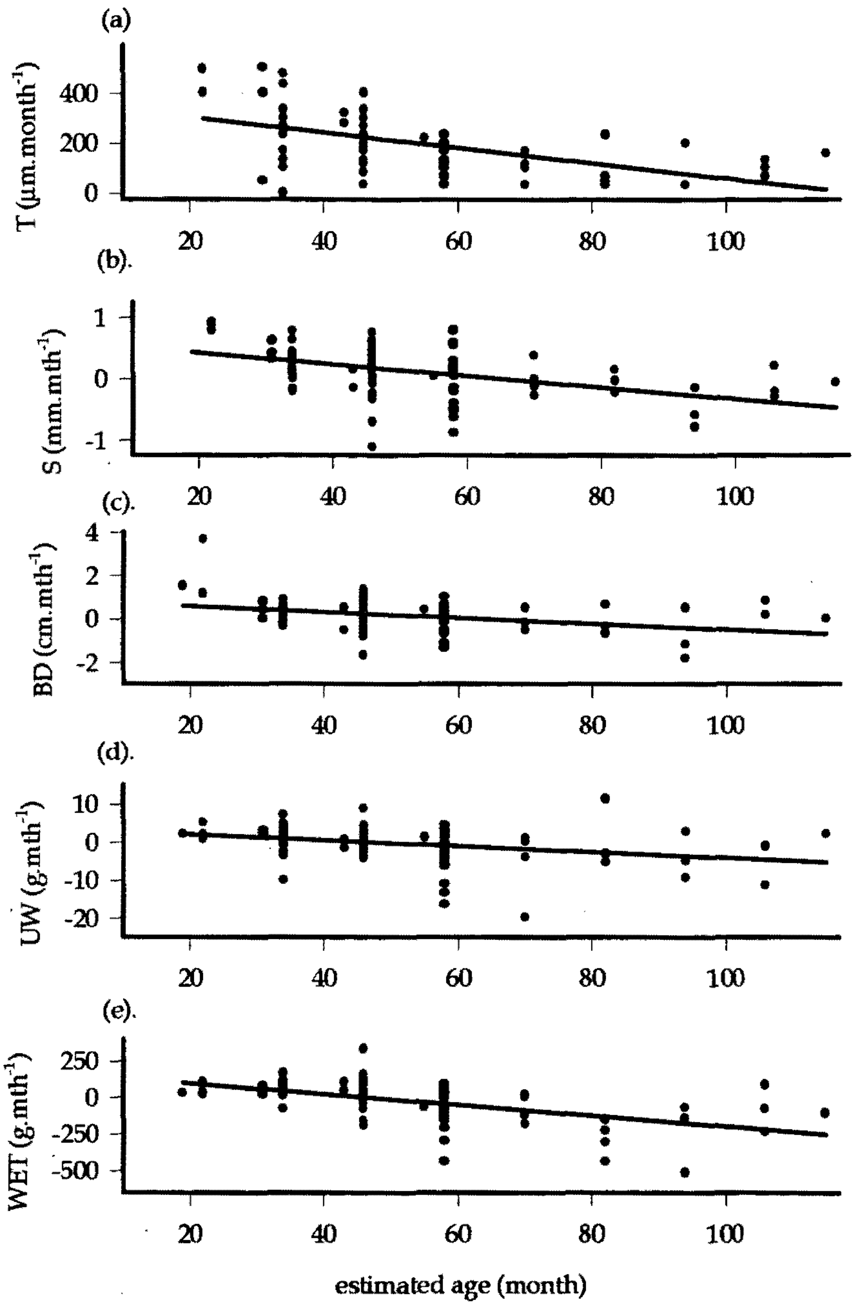


Figure 10. Recapture growth rate (month-1) versus estimated age for ; (a) basal spine ossicle growth after the tetracycline marker stain (thin-section analyses) (T), (b) mean spine ossicle length (S), (c) whole body diameter (BD), (d) underwater body weight (UW), (e) whole wet weight (WET).

Table 5. Linear regression analyses of morphometric data from recaptures.

Dependent	Equation	Regression analysis
T (μm.month^{-1})	3.651 - 0.031 x m	r^2=0.27; n=85; P< 0.01; MSE=0.999
S(mm.month^{-1})	0.609 - 0.009 x m	r^2=0.20; n=88; P< 0.01; MSE=0.143
D(cm.month^{-1})	0.833 - 0.013 x m	r^2=0.12; n=88; P< 0.01; MSE=0.532
UW(g.month^{-1})	3.514 - 0.077 x m	r^2=0.10; n=88; P< 0.01; MSE=21.74
WET(g.month^{-1})	171.50 - 3.717 x m	r^2=0.30; n=88; P< 0.01; MSE=13190.4

Key:

T spine growth (μm month-1) using fluorescent tetracycline marker in spine thin-sections.

S mean spine ossicle length (mm month-1).

BD whole body diameter (cm month-1).

UW underwater body weight (g month-1).

WET whole wet weight (g month-1).

m month

The general pattern of these analyses shows that growth rates are high in the juvenile/young adult stages and decreased with estimated age. Consistent negative growth rates in adult recaptures were determined from the three body-size measurements (BD, UW and WET). The apparent shrinkage increased with estimated age (and body size). Negative body growth results occurred from loss of coelomic fluid while processing out of the water, shrinkage from stress from handling and processing, and sub-lethal arm predation during the recovery period following their release.

4. DISCUSSION

4.1. Summary of results

(i) A new method of age determination was successfully applied to the Lizard Island population; approximately 500 marked remained in the vicinity of Granite Point starfish (using the Jolly-Seber estimate for population size as a guide) after the October field trip. There is now a unique opportunity to obtain validation data in a wide range of pigment band/estimated age classes. All marked starfish will have been released for at least 12 months after September 1996.

(ii) A reliable protocol for identifying individual *A. planci* was developed using; tetracycline staining, madreporite patterns, spine ossicle length, spine pigment band characteristics, aboral characteristics (previously clipped spines, colour pattern, arm damage), body size and sex.

(iii) 85 of 88 recaptures have shown that tetracycline is readily taken up in spine ossicles. It was assumed that the tetracycline capsules were lost from the body cavities of the 3 recaptures without staining soon after they were processed. The results are evidence of continued spine growth throughout life, satisfying an important assumption for their use in age determination.

(iv) Body growth analyses using cohorts with successive estimated ages, although potentially misleading (variance in growth mode between cohorts can be greater than within), showed an indeterminate mode of growth, increasing to estimated 6+ years. However, there can be large variations in growth when development is influenced by both extrinsic and intrinsic limitations. Assuming the validity of the method of age determination, body size frequency distributions showed up to 3 modes, while the distribution of estimated ages revealed 12 cohorts. With a variable mode of growth the interpretation of age structure from body size distributions of adult *A. planci* does not have a valid basis.

(v) Body growth analyses from recaptures showed that older (larger) starfish tended to lose weight (from sub-lethal predation, loss of coelomic body fluid from stress during transporting, processing and marking, and possibly senility). Modifications to improve the precision of estimates include; marking and processing in situ using SCUBA, photographing each starfish for madreporite patterns (deciphered in situ for confirmation) and colour patterns.

(vi) Assuming low mortality rates in adults, the population age structure showed exponentially increasing growth over approximately 8 years, dominated by the cohorts 1+, 2+ and 3+ years. A gradual build-up in population growth is quite different to views previously held about primary outbreaks and what has been observed in secondary outbreaks, where populations are dominated by one or two cohorts (see Stump, 1992; 1994).

(vii) Approximately half of the population had not yet matured to spawning condition by October 1995 (1+ and 2+ years). This showed the adult population was currently increasing in size, while the overall population growth was slowing with relatively smaller numbers of 1+ years compared with 2+ years.

(viii) Highest starfish density was from 3m depth at Granite release site (1267 ha^{-1}). This was less than 50% greater than the highest recorded, natural density at North Point (867 ha^{1}). Although artificially enhanced, there was no sign of aggregations in this area (or elsewhere) and no significant changes in coral cover were determined at the time of the third field trip in October.

(ix) Although coral mortality was obvious at all sites, no significant changes in coral cover were found over the 9 month study. The pattern of starfish age structure suggests that the decline in live corals will increase as individuals in the dominant cohorts achieve adult sizes.

(x) The estimates of the population dynamics parameters were considered to be first approximations only. This was because; only the minimum number of samples (3) for the analyses, a large difference in recapture rates (and interpreted mortality) between trips, and a potential for violation of the assumption of equal catchability from the effects of marking and releasing. Recommendations for new methods for the collection of MRR data have addressed this issue; see (v).

(xi) The hypothesis for primary outbreaks in the northern Cairns Section (Stump, 1992) described a gradual build-up in population size over many years, and starfish exhibit principal life-history characteristics of longevity and iteroparity. Lizard Island was one of the first populations in the area to achieve outbreak status from AIMS survey results (1995). To support this idea, the continuous age structure to estimated 11+ years was used as evidence that the Lizard Island population has been involved in the regional development of primary outbreaks.

4.2. Mark and recapture analyses

Capture probabilities of juvenile and adult starfish are likely to be different in daytime surveys of *A. planci* because the smaller juveniles are generally active only at night. The implementation of night surveys to estimate juvenile (1+) densities increases the probability of detection, approaching unity. In that life-history stage juveniles undergo exponential growth and therefore, are likely to be feeding or active on a nightly basis to maintain their growth rates. While smaller individuals are restricted by body size in movement around reefs, large adults have a significant potential for migration within reef areas. Migration of marked adult starfish included two individuals at Granite point (~ 100 m) and one individual from Mermaid Cove (~ 250 m) in just under three months. Under these circumstances overall migration was limited in this short period. Therefore, the proportion of marked animals in a random sample (m_i/n_i) should be close to the true proportion of marked animals (M_i/N_i), resulting in a relatively high precision in the population size estimator N_i.

The prediction of differences in the mortality rates between adults and juveniles can be justified on size differences, alone (where juvenile mortality is far greater than in adults). The nocturnal activity in juveniles indicates they are probably seeking refuge from a predator that uses vision to locate prey (i.e., fish). When survival probabilities are lower in young animals both the population size and survival estimators have been found to exhibit a positive bias (Pollock et al., 1990). Therefore, these parameter estimates are probably maximum values.

The decline in densities over the study period may have been due to the collection of starfish for the MRR exercises. However, if this influence was small it may be evidence of bias, either from variation in removal or mortality rates. Smaller *A. planci* are less mobile than large adults and their removal from the permanent transect areas may well have contributed to the decline in juvenile densities recorded from the transects. The introduction of a specific study for both juvenile and adult movement is therefore an important adjunct to further application of the open-population model analyses.

The results obtained from the population modelling exercise are considered to be a first approximation only. First, there were only 2 periods of collecting recaptures, a minimum requirement for this type of analysis, limiting the precision of estimation. Second, the variation in recapture and the related mortality rates between trips has reduced the reliability of the estimates. Third, the study has included some flexibility in the methods employed which has increased the variability in these results. This approach was taken to allow for exploitation of the new LIRS facilities and to implement new improvements in processing and handling methods to reduce stress on the starfish prior to release.

Further improvement in the methods is required for future population studies to reduce processing stress and improve the bias and precision of parameter estimates for the population dynamics models. It is recommended that the MRR procedure be tested *in situ* to minimise the effect of processing and handling on mortality. The method could be adapted for underwater processing by employing UW photography and using a sealed gun-injector for tetracycline marking. Photographs could be laminated for use underwater to characterise individual aboral colour patterns, arm-damage and possibly madreporite patterns (verified during processing). Marking a large sample within an area could be conducted by simply using the newly cut pedicel stubs, left after spine sampling, to identify previously marked individuals. The collection of some of the morphometric data (i.e., body weights) would not be possible with this approach but a representative sub-sample of starfish could be collected and sacrificed to obtain population sub-sample data.

4.3. Identification protocol

There was occasional difficulty in matching the madreporite patterns in a few recaptures. As with any naturally occurring mark, there are variations of patterns that lead to equivocal interpretation of the characteristics. The mapping procedure for the pattern can be time consuming (especially on large, dark starfish) and this exercise is the limiting factor in the process of marking large numbers of starfish. Sometimes the position of madreporites can be ambiguous (i.e., found outside the inter-arm area or may lie in an eccentric position) and can produce variation in the pattern description interpreted when recaptures are found.

By using sort techniques on the morphometric database (i.e., sorting by sampling trip and spine ossicle length) the number of potential candidates for identification can be reduced to a manageable size (i.e., approximately 20). The spine samples of the recapture are then matched with this group allowing for provisional identification of the released starfish. Finally, the madreporite patterns, aboral colour patterns and other secondary characteristics are compared to confirm the match with the recaptured individual. Therefore, the method for identification must include information on secondary characteristics to ensure correct identification of individuals when there is an error made in describing the madreporite pattern strings.

4.4. Arm damage

The incidence of arm damage in populations is likely to be a function of the density of predators and the age of the starfish (predator exposure). Despite the relatively high estimated densities in the Lizard Island population, the incidence of arm damage in adult size classes (49.5 %) is comparable to estimates obtained from persistent, low-density populations, as compiled by Lawrence (1991). He presented data for; Guam 1981, 1991 (43 %, 59 %), Papua-New Guinea (50 %), Western Australia (47 %, 64 %) and Hawaii (ca. 60 %) which were high compared with his tabled estimates from outbreak populations (i.e. GBR, 1967-8 (33 %) and 1987 (40 %); Suva Reef, 1984-5 (13 %); Ryukyu Islands, 1984-86 (~20-30 %, except Hamashima 40 %); and Sudan, 1969-70 (1.5 - 30 %)). According to Lawrence (1992) arm damage in asteroids may indicate total disturbance to the population when a large proportion of the population has lost only one or a few arms. The relatively high level of sub-lethal predation in juvenile/young adult cohorts (71 %), with damage to at least a half of one arm, suggests that predators (i.e., crabs and fish) may be exercising some control on the size of the population.

4.5. Benthic community descriptions

The use of line-intercept techniques to describe coral communities can be readily replaced by the more rapid technique using UW video. While the study aimed to describe changes in *A. planci* population dynamics in relation to variation in the coral communities, with limited field time there was some conflict concerning the allocation of effort to tasks. Video analyses are useful for describing communities to the level of physiognomic categories and therefore, would suit the aims of this project to quantify changes in live and dead coral. Costings for this technique should allow for hire of the requisite equipment and the subsequent analyses by an institution offering the service.

4.6. Body growth analyses

Growth rates and final sizes of marine invertebrates are often constrained by environmental conditions rather than by genetics i.e., they are plastic ontogenetic responses to local conditions (Sebens, 1987) resulting in a capacity to exhibit a wide range of habitat-dependent body sizes. Paine (1976) found that intraspecific competition (i.e. density dependence) had a clear effect on growth rate and ultimate size in the starfish *Pisaster ochraceus*, which exhibited indeterminate growth by reaching a much larger size in uncrowded populations with abundant prey, presumably from less competition. However, Lucas (1984) favoured the argument that variation in genotype or environment results in a broad range of ultimate sizes in *A. planci*, yet ultimate size is clearly determinate under experimental conditions.

The results from Stump's (1994) study also demonstrated a determinate growth pattern in *A. planci* under outbreak conditions. The analyses from the four principal cohorts on Davies Reef showed there was asymptotic growth because both pre- and post-outbreak groups (i.e., whether the cohorts settled before or during the outbreak) experienced a shortage of resources at the same time, but at different estimated ages. The mean body sizes of the pre-outbreak cohorts were significantly larger, reaching asymptotes at a later stage of the study, and suggesting they exhibited a more indeterminate-type mode. Therefore, the mode of growth is apparently not just determinate or indeterminate but more like a continuum between the two extremes of habitat dependence and asymptotic final size, as suggested by Sebens (1987). He noted that the mode depended on the degree of plasticity in growth, affected by extrinsic factors, that is exhibited in the adult stage. This characteristic of *A. planci* obviously precludes the attempt to interpret age structure from body size-frequency modes in populations.

A. planci is well suited to a plastic growth strategy, being relatively soft-bodied and capable of achieving very large body size compared with other tropical asteroid species that often develop thick, protective tests (see Lawrence, 1990). The Davies Reef study showed that older pre-outbreak starfish showed larger asymptotic body sizes while they coexisted with younger cohorts with smaller body sizes, being responsible for the outbreak. This pattern is similar to the description of population size structuring found in a study of Hawaiian *A. planci*, by Branham et al. (1971). In that study, larger starfish were located in lower densities nearby to the principal aggregation of smaller starfish, which presumably settled later and developed under conditions of greater competition for resources. Therefore, this type of population structure in size and age may be a relatively common characteristic of the species.

The variation in estimated reproductive effort found between pre- and post-outbreak cohorts from Davies Reef meant that lower mortality rates (longer lifespan) and a predicted slower growth rate during the juvenile phase (i.e., a smaller body size at maturity) occurred concomitantly (Stump, 1994). This is in accord with the predictions from the von Bertalanffy growth analyses. Therefore, body growth may appear to be determinate (i.e., expressed with higher reproductive effort and mortality rates) but under conditions of lower stress and disturbance the mode may be indeterminate. Therefore, the mode of growth may well be variable depending on the degree of plasticity in growth exhibited following maturity.

4.7. Pattern and prediction from *A. planci* population dynamics.

The observed large increases in *A. planci* around Lizard Island are due to exponential growth in consecutive recruitment events over the past 8 years, assuming relatively low mortality in the adult cohorts. Together with the persistence of older individuals (longevity), ongoing recruitment has caused a build-up in the spawning population. This is likely to promote an increase in the size of future recruitment in the region from spawning events by this population. There is now a regional increase in population growth within the Cairns Section (i.e., off the Daintree coast, where high numbers of juvenile/young adult *A. planci* were observed in February 1996 (personal observation)). These observations further support the conclusion that there is an ongoing escalation of recruitment in the northern GBR region.

The pattern of recruitment determined from the overall size frequency distribution of age structure explains the development of a primary outbreaking population by a slow incremental process leading to exponential growth in recruitment over a number of years. The pattern is in contrast with the previous reports of sudden appearances of primary outbreaking populations involving one or two massive events as found in secondary outbreaks from the Central Section (see Stump, 1992; 1994).

Since there is now evidence of a third outbreak episode, a unique opportunity exists to describe panmictic population growth over the GBR. The proposed study will determine parameters of individual reef population dynamics and compare variations in life-history characteristics from the low density and intermediate populations ahead of the 'wave' of outbreaks. The techniques required to obtain these types of data have previously been introduced for this species and further developed in this study. Through continued research on *A. planci* populations we can obtain data on the validation of the method of age determination and then address the issue of how outbreaks develop from low density populations. An exercise to obtain recaptures representing all estimated age classes that have been released for periods greater than 12 months is therefore important for further work on *A. planci* populations. The present study has shown that this objective is now both realistic and cost-effective.

To understand how outbreak episodes develop, data are needed on the quantitative assessment of estimated age structures associated with concomitant population dynamics and life-history studies. The collection of spine samples from representative reefs in the fine-scale regional surveys undertaken by GBRMPA has begun to address this question. Cross-regional age structures need to be determined in the very early stages of outbreak so those source populations with the oldest cohorts can be identified. This data should be collected concomitantly with population dynamics studies and descriptions of life-history characteristics. Recruitment observed on reefs 'downstream' can be compared with the larval output from the source allowing for estimation of survival in the post-settlement stages. With this approach the development of the outbreak episode can be mapped, variations in the biology and baseline information on the pattern of spread and size of outbreak populations can be made available for future reference and modelling exercises.

4.8. Conclusions and management implications

Recent progress in statistical ecology has seen the development of inference models for the design, analyses and interpretation of population dynamics studies (i.e., the Jolly-Seber model for open populations). These models are used to estimate the fundamental demographic parameters; recruitment, mortality and population size. After considering their precision, estimates can then be used to determine what is happening in the field, develop realistic population growth models and to test hypotheses, such as how outbreaks of *A. planci* occur.

This approach represents a potential for significant progress in *A. planci* research, for information derived from population models has direct implications for field assessments, reliable predictions and informed management decisions. However, this area of research has not been previously applied to *A. planci* populations because the appropriate methods to obtain the data required had not been developed.

In the present study, line and belt transect methods, mark, release and recapture (MRR) exercises and a new method of age determination were coordinated to obtain appropriate data to describe the population dynamics. Permanent, depth-stratified transects were established to allow estimation of the variation in densities and movement of marked starfish from repeated field exercises, conducted hand-in-hand with the MRR exercises. The data were applied to various statistical analyses (linear regression, multiple regression models) and capture-recapture inference using the general Jolly-Seber model for open populations.

The study has demonstrated the application and utility of populations dynamics techniques in *A. planci* research. This has been possible by the development of reliable marking and identification methods. Therefore, it introduces a new opportunity to develop an understanding of the development and spread of outbreak populations. The results are particularly important at this time because no other methods currently in use can provide such detailed information on *A. planci* population dynamics with known precision. The current window of opportunity to implement these research methods is available for a short time while the latest episode of outbreaks is still in its early stages. To follow the spread of outbreaks repeated studies need to be conducted on representative reefs over the Cairns and Central Sections. The recommendations include the commencement of population dynamics research on the contiguous reefs of Green Island to Arlington Reef. The data obtained will be used to document the timing of outbreaks and correlate life-history characteristics with environmental parameters. The reefs near Cairns are readily accessible with cost-effective support, given the availability of a research station and daily tour facilities.

The introduction of studies on the dynamics of *A. planci* populations will enable research to address specific issues related to their management, including; the time taken for populations to attain their present size (i.e., age structure/MRR analyses), the timing and effort required to implement effective control exercises (i.e., using the ratio of juvenile to adult sub-populations), and the time taken to reduce the levels of hard coral cover (i.e., transect techniques, age structure and mortality rates) and their subsequent recovery. In addition, before-and-after studies of population dynamics using these methods can be used for accurate assessment of the efficacy of small-scale control actions.

5. ACKNOWLEDGMENTS

I am grateful for the professional assistance from James Monkivitch, Kylie Pitt, Karen Diele and Andrew Heyward. Special thanks to my friend Kirsten McAllister for her patient help during the first field trip. Her cheerful support and encouragement throughout the project was my reward. The dedication of these assistants through long hours in field and the laboratory (day and night) ensured the successful completion of all tasks. Thanks also to Ray McAllister who kindly constructed several tools for collecting the starfish and for setting up the benthic transects. The Directors and staff of the LIRS were always on hand and offered invaluable solutions to the numerous logistical problems. Thanks also to Lisa Azzopardi (CRC Reef Research Centre) who gave help whenever it was needed. I acknowledge the continued assistance from Faulding Pharmaceuticals with their generous donation of tetracycline. This research was supported by the Australian Cooperative Research Centres Program through the Cooperative Research Centre for Ecologically Sustainable Development of the Great Barrier Reef and the Great Barrier Reef Marine Park Authority.

6. REFERENCES

Branham, J.M., Reed, S.A., Bailey, J.H. and J. Caperon (1971) Coral eating sea stars Acanthaster planci in Hawaii. Science 172:1155-1157.

Buckley, R.M. and M.C. Gomez-Buckley (1992) Internal micro-tag identification systems for teleosts, holothurians and decapods. Proc. 7th Int. Coral Reef Symp. Guam. Vol. 2. p.1029.

Glynn, P.W. (1982) Individual recognition and phenotype variability in Acanthaster planci (Echinodermata: Asteroidea). Coral Reefs 1:89-94.

Johnson, C.R. (1992) Reproduction, recruitment and hydrodynamics in the crown-of-thorns phenomenon on the Great Barrier Reef: an introduction and synthesis. In: Crown-of-thorns starfish on the Great Barrier Reef; Reproduction, recruitment and hydrodynamics. Ed. C.R. Johnson. Aust. J. Mar. and Freshwater Research. 43:1-8.

Kettle, B.T. (1990) Variations in biometric and physiological parameters of Acanthaster planci (L.) (Echinodermata: Asteroidea) during the course of a high density outbreak. PhD thesis. Zoology Dept. JCUNQ.

Kenchington, R. (1977) Growth and recruitment of Acanthaster planci (L.) on the Great Barrier Reef. Biol. Conserv. 5:11-20.

Lawrence J.M. (1990) The effect of stress and disturbance on echinoderms Zoo. Sci. 7:17-28.

Lawrence, J.M. (1991) Arm loss and regeneration in Asteroidea (Echinodermata). In: Echinoderm Research. Eds. L. Scalera-Liaci and C. Canicatti. Balkema, Rotterdam. p.39-52.

Moran, P. (1986) The Acanthaster phenomenon. Oceanogr. and Mar. Biol. Ann. rev. 24:79-480.

Paine, R.T. (1976) Size-limited predation: an observational and experimental approach with the Pisaster-Mytilus interaction. Ecology 57:858-873.

Pollock, K.H., J.D. Nichols, C. Brownie and J.E. Hines (1990) Statistical inference for capture-recapture experiments. J. Wildl. Manag. Supp. Vol. 54 No. 1. (Wildlife Monographs No. 107). 97pp.

Reichelt R.E., R.H. Bradbury and P.J. Moran (1990) Distribution of Acanthaster planci outbreaks on the Great Barrier Reef between 1966 and 1989. Coral Reefs 9:97-103.

Sebens, K.P. (1987) The ecology of indeterminate growth in animals Ann. Rev. Ecol. Syst. 18:371-407.

Stump, R.J.W (1992) Life-history characteristics of *Acanthaster planci* (L.) populations potential clues to causes of outbreaks. In: The possible causes and consequences of outbreaks of the crown-of-thorns starfish. Eds. U. Engelhardt and B. Lassig. GBRMPA workshop series No. 18. p.105-116.

Stump, R.J.W. (1994) Age determination and life-history characteristics of Acanthaster planci (L.) (Echinodermata: Asteroidea). PhD thesis. Zoology Dept. JCUNQ.

Stump, R.J.W. and J.S. Lucas (1990) Linear growth in spines from Acanthaster planci (L) involving periodic pigment bands. Coral Reefs 9:149-154.

Wilson, B.R. and L.M. Marsh (1974) Acanthaster studies on a Western Australian coral reef. In: Proc. 2nd Int. Symp. on Coral Reefs. Eds. A. Cameron et al. Vol. 1. Brisbane. p621-630.

Yokochi, H., S. Ueno, M. Ogura, A. Nagai and T. Habe (1992) Changes in diel feeding pattern in Acanthaster planci (L.): an experimental view of the effect of population density and food availability. In: Proc 7th Int. Coral Reef Symp. Guam. Vol. 2. p797-802.

Zann, L., J. Brodie, C. Berryman and M. Naqasima (1987) Recruitment, ecology, growth and behaviour of juvenile Acanthaster planci (L.) (Echinodermata: Asteroidea). Bull. Mar. Sci. 41:561.

Zann, L., J. Brodie and V. Vuki (1990) History and dynamics of the crown-of-thorns starfish Acanthaster planci (L.) in the Suva area, Fiji. Coral Reefs 9:135-144.

Zar, J.H. (1984) Biostatistical analysis. Prentice-Hall. New Jersey.

7. APPENDICES

Appendix 1.

GPS positions of sites for *A. planci* densities and quantitative benthic assessments around Lizard Island, Cairns Section GBR.

Site	GPS position
NE	14°38.435 S 145°27.017 E
NW	14°38.415 S 145°27.012 E
NW (3m)	14°38.455 S 145°27.018 E
MW	14°38.051 S 145°27.011 E
GN	14°38.052 S 145°27.000 E
GS	14°38.585 S 145°26.059 E
SE	N/A
SW	N/A

Key: NE (North Point, eastern); NW (North Point, western); NW (3m) (Mermaid Cove, eastern, 3m transects); (Mermaid Cove, western, 3m transects only); GN (Granite Point, northern); GS (Granite Point, southern); SW (South Island, western); SE (South Island, eastern). See also Figure 1 for locations.

Appendix 2.

Benthic physiognomic categories

Key:

%HC' = relative percentage of hard coral cover

%DC' = relative percentage of dead coral/coralline algae

DC = recently dead coral

FS = feeding scar (white)

HC = hard coral species

OT = other organisms

SC = soft coral species

SP = sponges

SR = sand and/or rubble

TA = turf algal cover

Sites

GN = North Granite

GS = South Granite

NE = East North Point

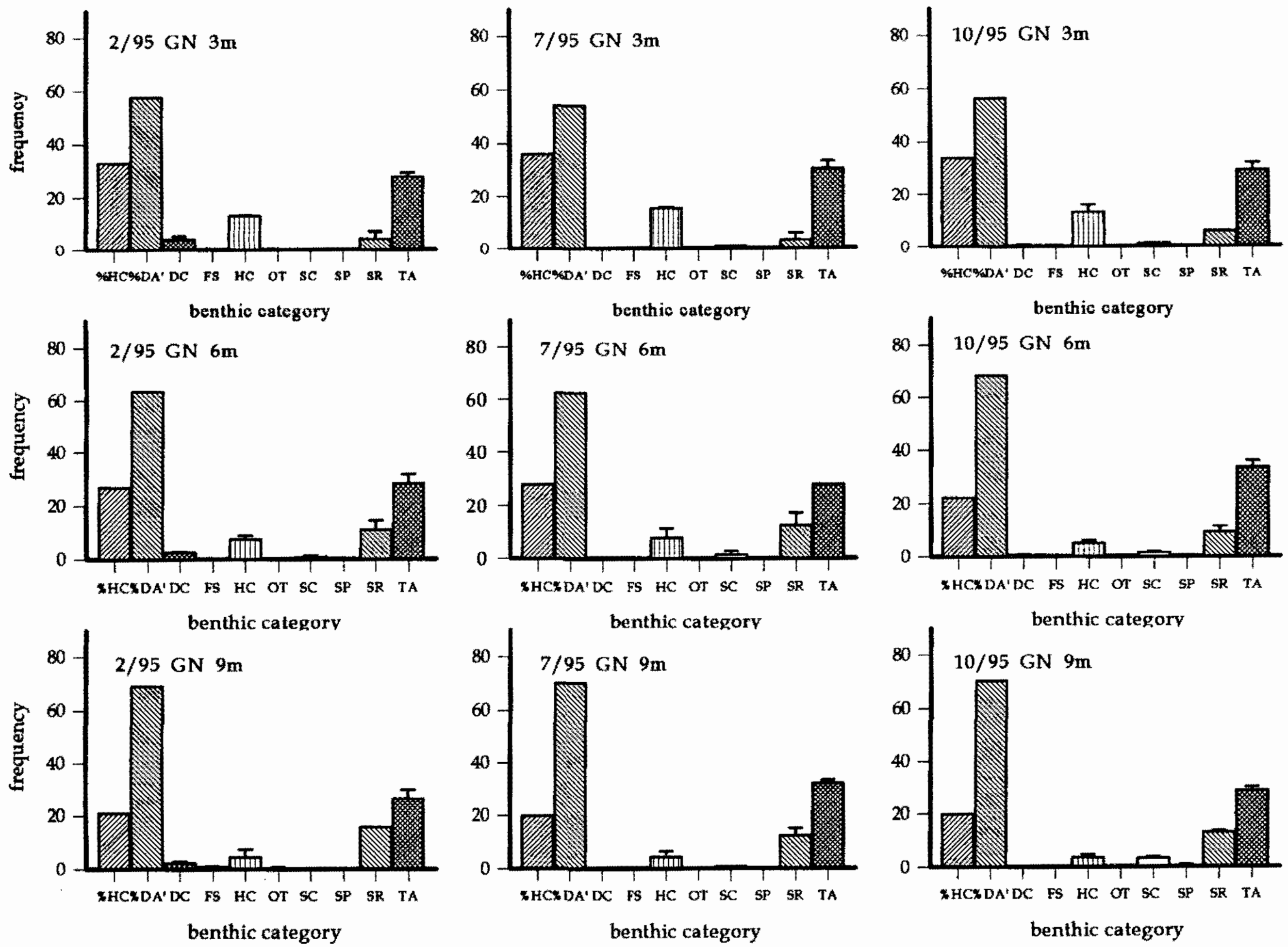
NW = West North Point

MW = West Mermaid Cove

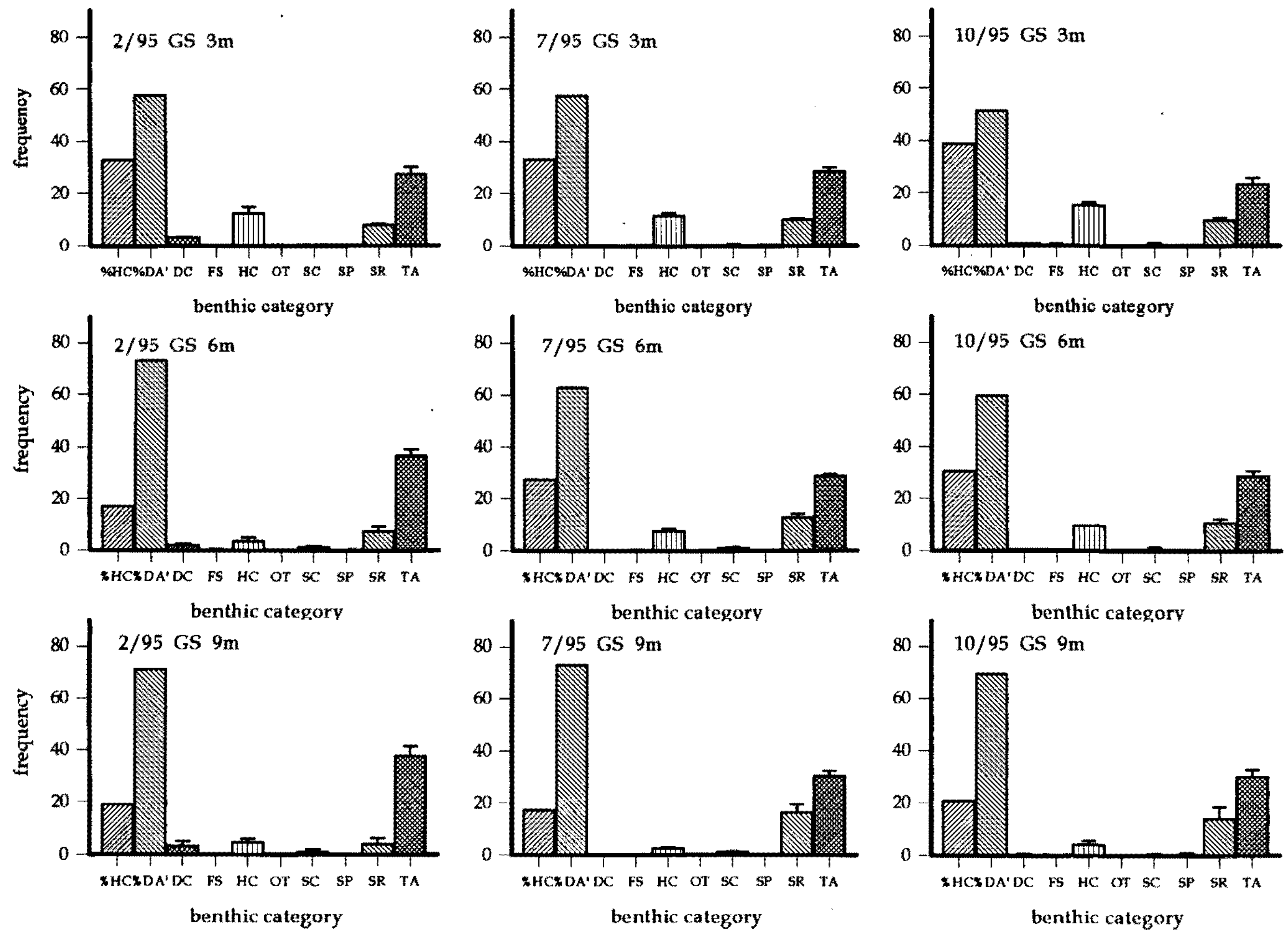
SE = East South Island

SW = West South Island

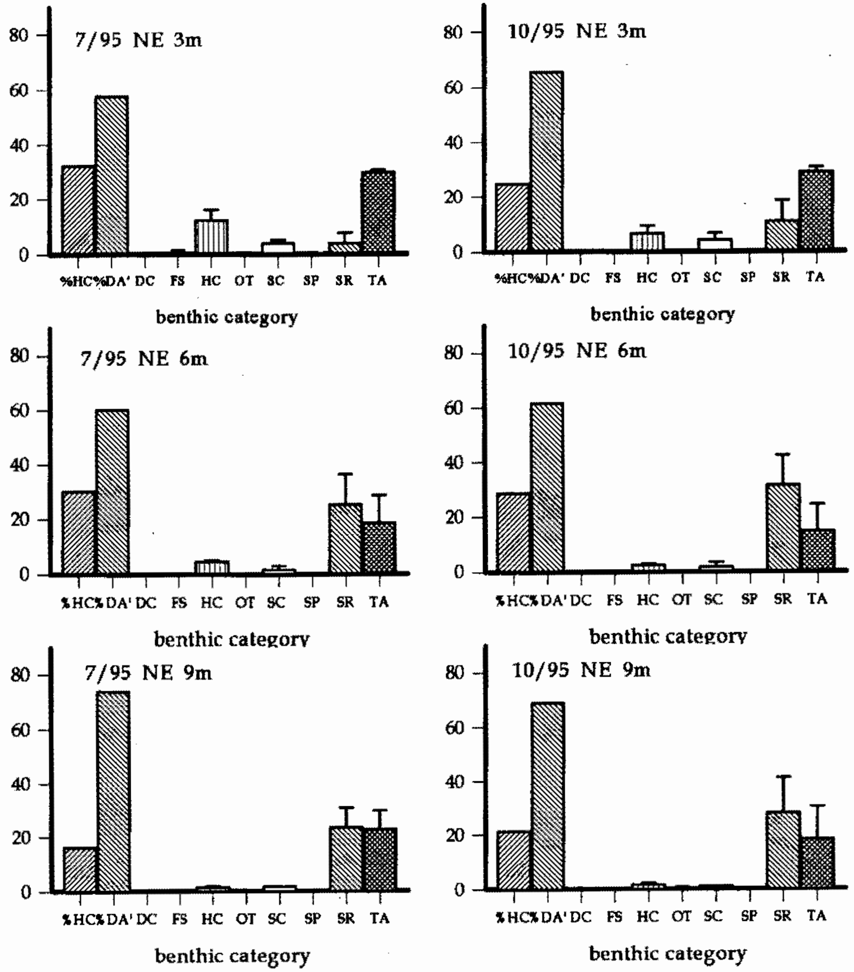
Appendix 2a. Histograms describing the benthic community at the North Granite site (2 x 3 depths; 3,6 and 9m) for February, July and October 1995, using physiognomic categories and relative percentages of live and dead coral/coralline algae.



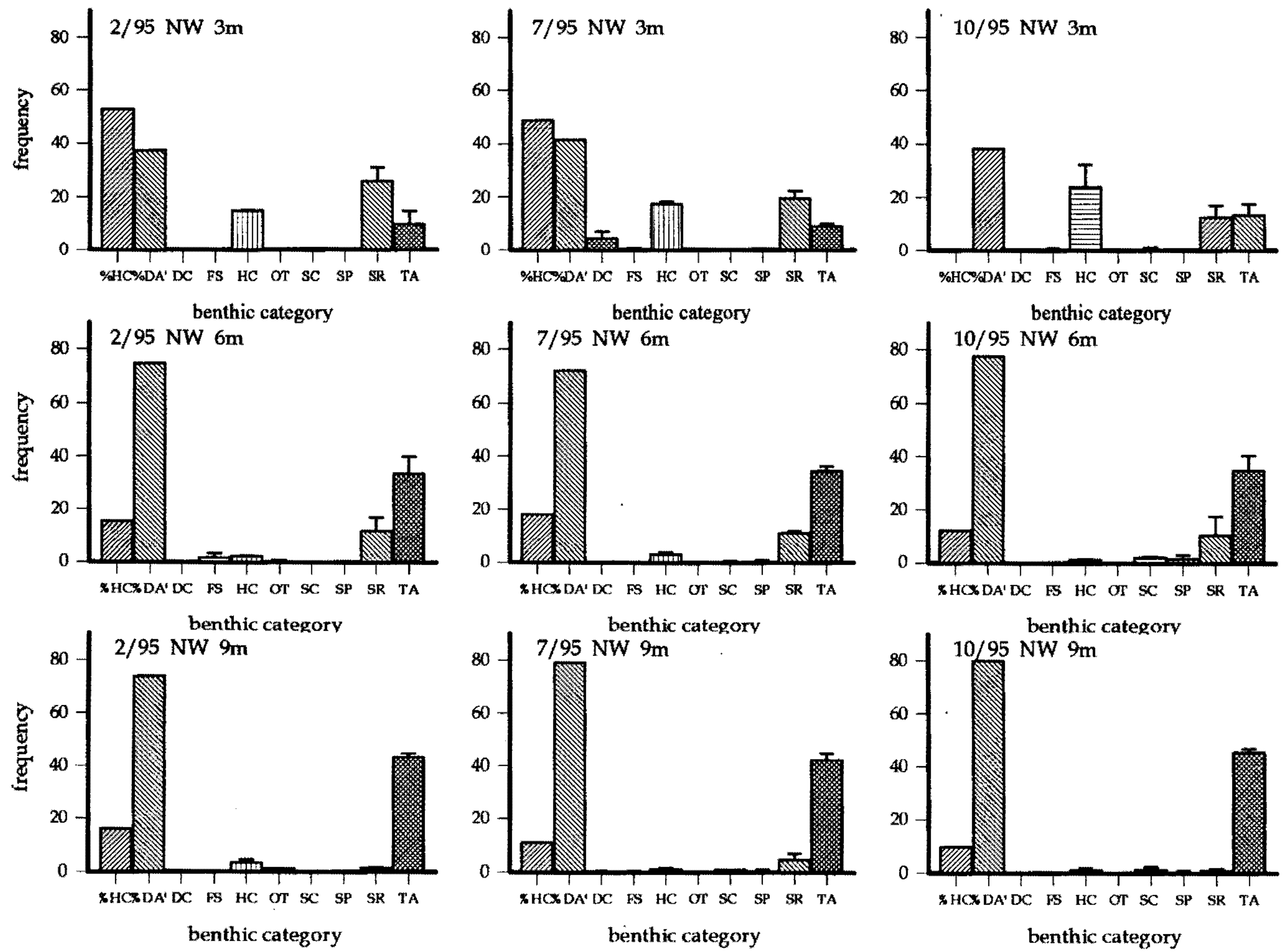
Appendix 2b. Histogram describing the benthic community at the South Granite site (2 x 3 depths; 3,6 and 9m) for February, July and October 1995, using physiognomic categories and relative percentages of live and dead coral/coralline algae.



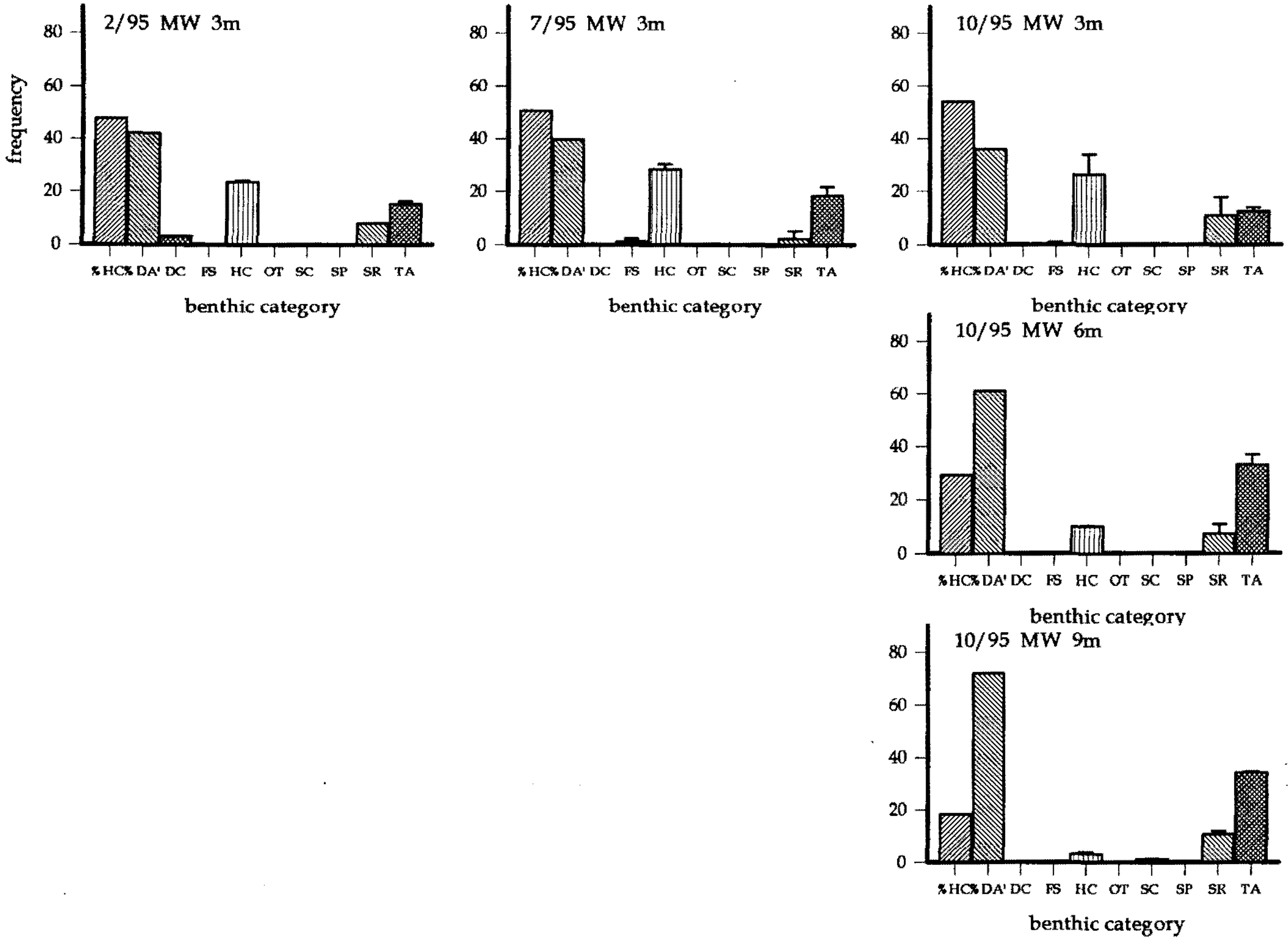
Appendix 2c. Histogram describing the benthic community at the East North Point site (2 x 3 depths; 3,6 and 9m) for February, July and October 1995, using physiognomic categories and relative percentages of live and dead coral/coralline algae.



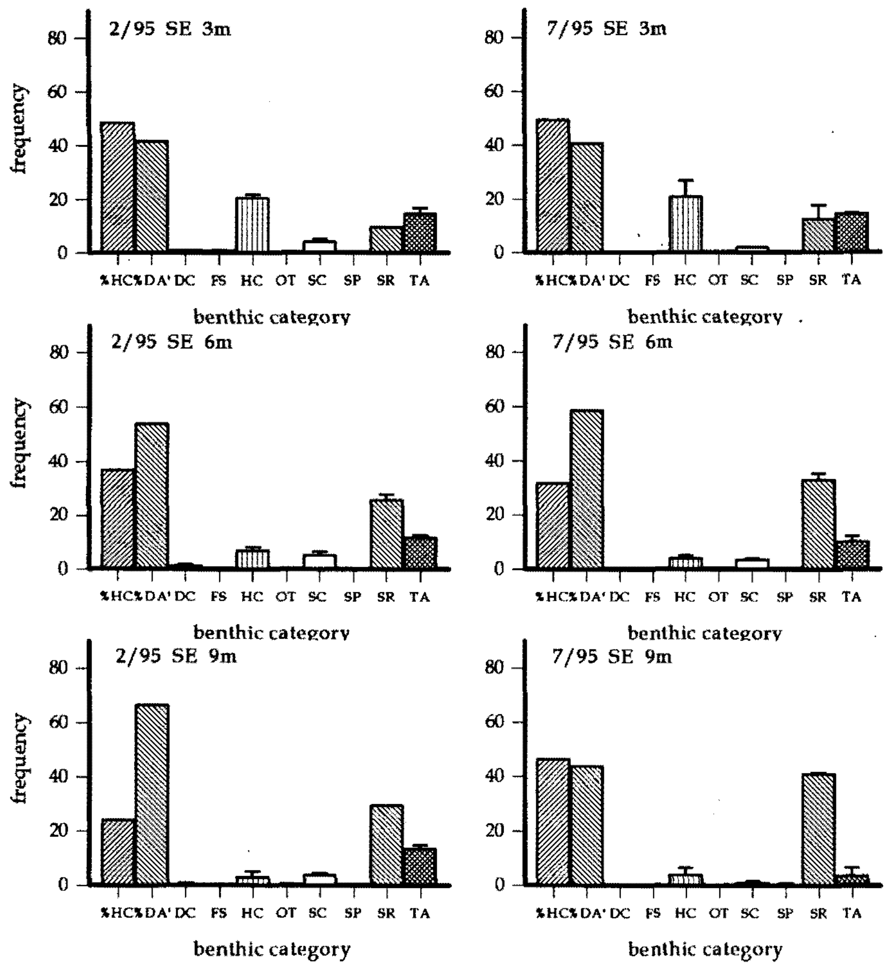
Appendix 2d. Histogram describing the benthic community at the West North Point site (2 x 3 depths; 3,6 and 9m) for February, July and October 1995, using physiognomic categories and relative percentages of live and dead coral/coralline algae.



Appendix 2e. Histogram describing the benthic community at the West Mermaid Cove site (2 x 3 depths; 3,6 and 9m) for February, July and October 1995, using physiognomic categories and relative percentages of live and dead coral/coralline algae.



Appendix 2f. Histogram describing the benthic community at the East South Island site (2 x 3 depths; 3,6 and 9m) for February, July and October 1995, using physiognomic categories and relative percentages of live and dead coral/coralline algae.



Appendix 2g. Histogram describing the benthic community at the West South Island site (2 x 3 depths; 3,6 and 9m) for February, July and October 1995, using physiognomic categories and relative percentages of live and dead coral/coralline algae.