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Variations in biometric and physiological parameters of *Acanthaster planci* (L.) (Echinodermata; Asteroidea) during the course of a high density outbreak.

Thesis submitted by
Brett Thomas Kettle B.Sc. (Hons.)
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for the degree of Doctor of Philosophy
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In support of this thesis

The following publication has been derived from work connected with the production of this thesis, and a copy of the publication is included in the back of this thesis:

Kettle, B.T. and J.S. Lucas, 1987.
Biometric relationships between organ indices, fecundity, oxygen consumption and body size in *Acanthaster planci* (L.) (Echinodermata; Asteroidea)
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Abstract

The Crown–of–Thorns starfish, *Acanthaster planci* (L.), a large and voracious corallivore, has been the focus for a large number of scientific studies, few of which have examined aspects of starfish physiology or high density (outbreak) populations throughout the time course of a single outbreak event. This study sought to examine the variations in size, population density, morphology, respiration rates, fecundity and resource allocation, among starfish from a high density outbreak population throughout an outbreak event. The study sequentially examined three aspects: a) the effect of size *per se*; b) the effects of starvation on captive starfish; and c) changes occurring in an outbreak population in the field.

Starfish from the Great Barrier Reef have less skeletal material (one fifteenth to one thirtieth of whole wet weight over the size range 280g to 3000g) than starfish from Guam (generally one seventh of whole wet weight) and the proportion of skeletal material decreases markedly in larger starfish. Small starfish (less than ≈10g whole wet weight) allocate resources for growth of the body wall; but an increasing proportion of energy is accumulated in the caeca between weight ≈10g and ≈280g (the onset of sexual maturity), when it is diverted to gametogenesis. Starfish generally exhibited allometric growth – large starfish are thinner in the oral – aboral axis, perhaps being leaner as a consequence of low ration diets. Food limitation plays an important role in apparent levels of "sub lethal predation" – starving starfish apparently cannot maintain regeneration rates and therefore accumulate their injuries over longer periods. Fecundity increases relative to increasing whole wet weight such that small adults (220mm diameter) allocate ≈8% of their wet weight to reproduction and larger adults (≈400mm diameter) allocate ≈20%. Fecundity therefore increases rapidly with size (≈30 million eggs to ≈60 million eggs over the size range ≈2000g to ≈ 3000g whole wet weight) and the total potential fecundity of a population is strongly dependent on the size of individual starfish. Large starfish, the rare "giants" in excess of 500mm diameter, conform to the same size versus oxygen consumption relationship as do smaller starfish. There is no suggestion of any genotypic differences in metabolic rate in large animals. Rather, starfish size is likely to be commonly limited by low-ration diets towards the end of an outbreak or when food availability is low relative to the maintenance requirement of individuals within the population.

Acanthaster planci is, by comparison to other asteroids, relatively intolerant to food-limitation, surviving enforced starvation for only approximately six months. Responses to starvation are strongly influenced by starfish size. Small starfish can show continued growth and reproductive partitioning while large starfish quickly shrink and die. There is some suggestion that particulate organic films may be utilised by starving starfish to offset maintenance costs during starvation. Resources are readily resorbed from the caeca during starvation, and, as starvation becomes more severe, from the body wall and stomach. Gonadal growth is maintained and, after six months of starvation, starfish showed (on average) a fourfold increase in gonadal indices. Reproductive effort is thus extremely high even under conditions of extreme food shortage. Changes in the macroscopic appearance of starved starfish follow an interpretable pattern that can be rapidly used in the field to assess the gross health of starfish populations.

A two year field study on Helix Reef commenced in the initial stages of a high density outbreak and continued until starfish populations were too sparse to permit sampling. During this time, the estimated total population climbed to ≈37000 starfish and declined to ≈4000 starfish, while coral cover decreased from ≈40% total live cover to ≈1% live cover. The greatest fluctuations in both parameters occurred in a period of approximately 6 months. The outbreak population probably consisted not of one relatively long–lived cohort but of several successive cohorts. Cohorts of smaller starfish showed growth while cohorts of larger starfish were shrinking and being lost from the population. Size-specific reproductive potential was equivalent in the first year (abundant food) and the second year (very little food). *Acanthaster planci* is capable of very high reproductive effort during starvation. The wild population demonstrated similar compartmental priority systems to starved captive starfish. Reproduction can proceed without resorption from other compartments when food is abundant. As food supplies decrease, energy is partitioned from the caeca; but, if food limitation becomes acute, the body wall and the stomach will both yield resources to allow the continuation of high reproductive effort or to meet maintenance requirements. Marked changes in underwater weight frequency distributions suggest that decreases in population density result from mortality of large starfish.

Reproductive effort (energy allocated to reproduction as a fraction of energy acquired) is a key to the *A. planci* life strategy. That *A. planci* can achieve similar levels of reproductive output when food-limited as it does when food is plentiful is indicative of high reproductive effort. Previous work (Lawrence, 1990) has suggested that the active foraging, long-lived and highly fecund traits of *A. planci* in environments of high resource availability and long duration constitute a "competitive" life strategy. This study suggests that *A. planci* in high density outbreaks is short-lived and has very high reproductive effort in short duration environments of low resource availability – the same life strategy that produces a competitive species in conditions of excess food produces a ruderal species when food limitation becomes extreme.

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"Physiological adaptations of resource acquisition and use are not only the basis for the way organisms function physiologically but also the basis of their form (allocation of resources between different structures) and behaviour (allocation of resources between different activities)."

adapted from Sibly and Calow (1986).

1. General introduction

The Crown–of–Thorns starfish, *Acanthaster planci* (L.), is a large and voracious corallivore. It is frequently found in dense aggregations, and under these conditions can kill a large proportion of the corals in a given area of reef. As such, this starfish has become a focus for the attention of marine scientists. Major reviews of previous studies have been undertaken by Chesher (1969b), Walsh *et al.* (1970), Potts (1981), Moran (1986) and most recently by Birkeland and Lucas (1990).

A. planci exhibit a logistic growth pattern (Yamaguchi, 1975), with a slow absolute growth rate until switching from a coralline algal diet to a coral diet at approximately 7 months of age (approximately 10mm diameter) (Yamaguchi, 1974a). Subsequent workers have confirmed this and there has been good agreement between field (Zann *et al.*, 1987; Habe *et al.*, 1989) and laboratory studies (Yamaguchi, 1974a; Lucas, 1984). *A. planci* can reach sexual maturity at approximately two years of age (Yamaguchi 1974a; Lucas 1984; Zann *et al.*, 1987), although maturation is related to size as well as age. Small cohort members, which may have switched from the juvenile coralline algal diet to the adult coral diet late in their development, or otherwise suffered food shortages, may not mature until the subsequent year (Lucas 1984; Zann *et al.*, 1987). The ultimate size (L_∞) of adult starfish has variously been described as between approximately 170mm (Habe *et al.*, 1989) and 323mm diameter (Lucas, 1984), although individuals have been reported at 500mm diameter or greater (Chesher, 1969b; Laxton, 1974; Stanley, 1983; Lucas, 1984; Conand,1985; Moran *et al.*, 1985). Several authors attribute variations in growth and ultimate size to food limitation (Ormond and Campbell, 1971; Lucas, 1984; Zann *et al.*, 1987).

A. planci is a highly fecund starfish. Conand (1983, 1985) provided information on the relationship between fecundity and diameter for *A. planci* from New Caledonia, demonstrating an apparently exponential increase in gonad size with increasing starfish size. Pearson and Endean (1969) estimated that an average sized female (*ca.* 300 mm diameter) could contain 12–24 million eggs. Conand (1983) suggested that 400mm diameter starfish could produce up to 60 million eggs and Lucas (1984) noted the collection of more than 500ml of gonadal material from a single ripe female. Branham *et al.* (1971) suggested that engorgement of the body cavity with ripe gonads could be the cause of an increase in the mean diameter of *A. planci* prior to spawning, and that as a consequence of spawning mean starfish size decreased.

Despite indications that food limitation might regulate starfish size, and that reproductive effort constitutes a significant factor in the physiological processes of *A. planci*, there have been no attempts to examine the roles of reproduction and food limitation in the energetics of *A. planci*. Furthermore, with the exception of the unpublished work of Peckham (1984) and Keesing (1990), there has been no work done on the energetics of resource acquisition and use by *A. planci*, although other physiological studies include those on temperature tolerance and respiration (Yamaguchi, 1973b; 1974b). Several studies have made mention of related parameters, including tolerance to salinity (Piyakarnchana, 1981; Habe *et al.*, 1989) and starvation (Cheney, 1974; Lucas, 1984), their biometry (Nishihira and Yamazato, 1972; Conand, 1983), rates of growth (Yamaguchi, 1974a; Kenchington, 1977; Lucas, 1984; Zann *et al.*, 1987; Habe *et al.*, 1989) and regeneration (Owens, 1971) and reproductive biology (Pearson and Endean, 1969; Henderson, 1969; Branham *et al.*, 1971; Henderson and Lucas, 1971; Lucas, 1973; Yamazato and Kiyan, 1973; Yamaguchi, 1973a; Conand, 1983). The latest review of these works was by Birkeland and Lucas (1990).

One shortfall of most previous work has been the abbreviated temporal scale of the studies, and, in particular, the tendency to sample opportunistically from various populations rather than to return to the one population at repeated intervals. The gross dynamics of the predator (*A. planci*) and prey (coral) interaction, through a high density phase of the predator, have been generalised by Bradbury *et al.* (1985) as beginning with high coral cover and low starfish abundance (the coral phase), passing through a stage of high coral cover and high starfish abundance (the outbreak phase) to one of low coral cover and high starfish abundance (the starfish phase), before culminating in a "recovery" phase of low coral cover and low starfish numbers. The only study that has consciously sought to document population changes that occur throughout the time–course of a single outbreak is that of Moran *et al.* (1985), who found that the major changes in predator and prey populations can occur in as few as seven months. Studies that rely upon single or infrequent sampling of a particular population of starfish fail to account for the rapid and dramatic changes in this dynamic predator/prey interaction.

Renewed outbreaks of Crown–of–Thorns starfish appeared on the Great Barrier Reef in the late seventies, prompting a large multidisciplinary effort to determine more about the biology, ecology and management of *A. planci.* The studies described in this thesis were initiated in the midst of this renewed research effort, when it became apparent that few studies of the physiological processes of *A. planci* had been attempted. The objectives of this study were to:

1. examine resource acquisition and use by *A. planci* throughout the time–course of an outbreak, including periods of increase and decline in starfish numbers;
2. consider the general changes in physiological parameters (particularly energy partitioning) throughout the outbreak process and;
3. examine the life history strategies producing the observed patterns.

Given the degree of concern generated in Australia and within the international community by *A. planci*, the level of effort and expenditure on research and management relating to the Crown-of-Thorns issue, and the general applicability of Crown-of-Thorns related research to human interactions with echinoderms from around the world, a project meeting these objectives should contribute positively to human knowledge and to the resolution of social, political and economic issues.

The approach taken was to select a reef that was in the early stages of an outbreak and to measure a number of physiologically-related parameters at repeated intervals over the three year study period. There was no way of knowing *a priori* whether the selected reef would pass through an outbreak cycle in the study period. Helix Reef was chosen because it appeared to have both high coral cover and increasing numbers of *A. planci*, which were assumed to be precursors to a high density starfish outbreak. This thesis begins by examining the gross effects of body size using data from a single sample of the Helix Reef outbreak population (Chapter Two). It then considers the effects of enforced starvation, drawing on data from laboratory experiments (Chapter Three), before considering processes occurring within a discrete outbreak population on Helix Reef (Chapter Four), and examining the implications of those findings for life history strategies, the physiology of *A. planci* and starfish physiology in general.

2. The effect of size upon biometric relationships, compartmental indices and oxygen consumption of *Acanthaster planci*

2.1. Introduction

Acanthaster planci shows marked variation in size, diet and behaviour as it develops. Each of these compound the difficulties of interpreting trends in resource use for a wild population studied over a long period of time. The early juveniles feed on coralline algae and are very cryptic. They switch to coral predation as they reach about 10mm diameter (at ≈7 months of age). At about 200mm diameter (≈20 months) they show reproductive development and become less cryptic (Yamaguchi, 1974a; Lucas, 1984). In adult life they attain maximum sizes (L_∞) from ≈170mm (Habe *et al.*, 1989) to 323mm (Birkeland and Lucas, 1990). Evidence from laboratory studies (Lucas, 1984) suggests that they become "senile" between age 5 and 7 years, ceasing reproduction and undergoing shrinkage. Feeding preferences and rates during adult life vary with degree of aggregation, prey availability and seasonality (Keesing, 1990). These constitute a confusing suite of confounding parameters that we have good prior reason to believe will influence resource allocation patterns during the course of an outbreak event. This chapter focuses only on the effect of size *per se* on biometric relationships and resource allocation in *A. planci*.

Post-larval development encompasses an increase in linear dimensions of three orders of magnitude, from a post-metamorphic starfish 0.5mm diameter to an adult of up to 500mm diameter (and occasionally greater) and an increase in body mass of about seven orders of magnitude (Yamaguchi, 1974a). Previous workers have presented some data on size specific physiological and related biometric parameters of *A. planci*, although there has been no systematic study of these.

Relationships between size and weight (whole wet weight:W, underwater weight:U, and ash free dry weight:A – tabulated by Birkeland and Lucas, 1990) have been presented by Nishihira and Yamazato (1972), Yamaguchi (1974a), Peckham (1984) and Conand (1985). Whilst wet weight has never been demonstrated to vary allometrically with respect to diameter, values reported thus far are lower than the isometric coefficient of 3.

Fecundity / size relationships were investigated by Conand (1985). From a small sample (10 animals) it would appear that fecundity increases as $1.323 \cdot 10^{-4} \cdot D^{7.236}$ over the D range 250mm to 400mm. This is surprisingly high and, unless the form of the relationship varies beyond D=400mm, leads to unrealistic estimates of gonadal indices for large starfish (D>500mm).

The effects of size upon respiration rates have been investigated by Peckham (1984) and Habe *et al.* (1989). *A. planci* are oxyregulators over a wide range of ambient oxygen tensions[1], and the point at which they become oxyconformers varies according to size. Algal eating juveniles are oxyconformers below 0.5ml $O_2\ l^{-1}$ while the switching point for 100 to 150mm juveniles and 250 to 350mm adults is 1.5ml $O_2\ l^{-1}$ and 1.8ml $O_2\ l^{-1}$ respectively (Habe *et al.*, 1989). Yamaguchi (1974b) and Peckham (1984) provide data which suggest that metabolic rate increases approximately in proportion to $D^{0.87}$, indicating that *A. planci* have an oxygen transport system relatively effective when compared to other echinoderms. This study provides further data on the various biometric relationships of adult *A. planci* from the Great Barrier Reef (GBR). Unpublished data for juveniles (1+ years) (Peckham, 1984) are introduced to allow interpolation of the changing relationships between organ indices, respiration and fecundity for starfish in the size range 25mm to 500mm diameter.

This segment of the study seeks specifically to elucidate size-related phenomena in Crown-of-Thorns starfish, but may have wider implications for ecology in general. Study of allometric relationships is touted not only as "fundamental in understanding life history strategies and ecological systems" and a "vital and highly useful form of descriptive biology" (Western, 1979 and Calder, 1984, respectively), but as a subset of the general empirical theories that constitute the field of predictive ecology, a field seen as a replacement for "the old ecology", with which dissatisfaction is growing (Peters, 1983). Allometry is a powerful tool, the simplicity

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[1] Neither of these studies have determined the relative importance of behavioural modifications or rate-limited metabolic processes to "oxyregulation".

and generality of which may make a substantial contribution to biology (Reis, 1989).

In particular, this study meets two of the criteria set out as limitations in most studies of allometry (Peters, 1983): it examines a poikilotherm, an animal group less frequently studied than homeotherms; and it focuses intensively on the collection of field data, rather than laboratory data, as has often been the case.

Despite the potential value of this study to predictive ecology in general, this thesis focuses very heavily on the target organism, *A. planci*. Instead it is hoped that the data set will ultimately be used by others to it's greatest potential.

2.2. Methods

In order to minimise the influence of other environmental and intrinsic factors the starfish for this study were collected at a similar time of year, from populations that did not appear to be food limited and wherever possible, from the one population.

2.2.1. Study sites

In May 1985, reports indicated that numbers of *A. planci* were increasing on Helix Reef (Gazetteer Code 18–076, 18° 37.7'S, 147° 17.8'E), in the Central Section of the GBR adjacent to Townsville (Figure 2.1) (Dr P. Moran, *pers. comm.*).

Helix Reef is a mid–shelf patch reef and is small (≈700m diameter) by comparison to adjacent reefs (Figure 2.1). It rises steeply from the surrounding sea floor but, unlike many patch reefs, has neither prominent reef–front, lagoon nor back–reef bommie fields. Its accessibility to Townsville was ideal whilst it's small size suggested that the time required for a large number of starfish to become food–limited would be relatively short.

Starfish for respiration studies were collected from Pelorus Island (Gazetteer Code 18–048, 18° 33.4'S 146° 29.0E) (Figure 2.1) in the central section of the GBR, and from the lagoon at Lady Musgrave Reef (Gazetteer Code 23–082, 23° 54.1'S 152° 23.8'E) (Figure 2.2) in the southern section of the GBR.

2.2.2. Biometric relationships

Fifty specimens for biometric and organ index analyses were collected from a high density *A. planci* population on Helix Reef on 30 October 1985. Starfish from this population subsequently spawned in early December 1985, so that index data represent starfish one month prior to spawning and near peak reproductive condition. As such, the data reflect the energy channelled into reproduction, and do not represent the non–reproductive state of these starfish. The starfish collected ranged from 280g to 3000g whole wet weight (≈ 200mm to 410mm diameter).

Yamaguchi (1974a) found that relaxed specimens of *A. planci* could be as much as 20% larger in diameter than animals removed from the water. To minimise this source of variability, all diameter measurements were made with callipers on immersed starfish on a flat surface. Multiple measurements were taken to determine the greatest distance between optic cushions. This measurement, referred to as diameter (D or 2R), is in fact the "greatest chord" of the starfish.

Underwater weight (U) was determined using a submerged weighing tray suspended below a tared spring balance. Whole wet weight (W) was determined by allowing excess surface water to drain for 5 seconds, then placing the starfish in a deep tray. Emersion for periods of more than 5 seconds usually results in rupturing of the body wall and the loss of coelomic fluid. A deep weighing dish ensured that this fluid was retained for inclusion in the whole wet weight measurement. Rolling and pitching of the research vessel meant that it was difficult to resolve weights to less than 5g.

2.2.3. Compartmental Indices

Crown–of–Thorns starfish have approximately 15 rays (range 8 to 21; Moran, 1986; 7 to 23, this study), and thus complete dissections and body compartment analyses were impractical. Some workers have used single rays for gonad indices, noting that there were only small variations in organs between normal rays of *A. planci* (Pearson and Endean, 1969). The removal and analysis of a three–ray sector (including neither regenerating rays nor those immediately adjacent to them) was deemed prudent for this work .

Sectors were divided into four compartments for the analysis of resource allocation: (1) gonad, including gametes and supportive tissue; (2)stomach, including all associated organs except the pyloric caeca; (3) pyloric caeca; and (4) the remaining body wall, including tube feet and nervous tissue. Compartmental samples were wet weighed and dried at 60°C for three days, a regime determined by drying a number of samples to constant weight. Dried samples were homogenised as necessary in an electric coffee grinder and a representative subsample of each taken to determine calorific value by ballistic bomb calorimetry. Pen deflections on a strip recorder were used to plot thermistor-measured heat gains from weighed samples ignited in a pressurised oxygen environment under constant ambient conditions. Results were interpreted from a least squares regression developed using benzoic acid as an analytical standard. Standard corrections applied included ignition charge and wick combustion as well as endothermic corrections for inorganic salts. Relative indices of dry weight and calorific value were calculated for the various compartments of each 3–ray sector according to the method of Giese (1967):

$$\text{INDEX} = (\text{contribution of compartment}) / (\text{contribution of all body compartments}) \times 100$$

2.2.4. Oxygen consumption

Moderate sized starfish (280mm to 420mm diameter) were collected from Pelorus Island in June 1985 (ambient temperature: 22°C to 23°C). Large animals, ranging from 450mm to 680mm diameter, were collected from Lady Musgrave Reef in March 1986 (ambient temperature: 26°C to 28°C). Starfish from these locations had few gonads, being in an early stage of gonadal development and in a post–spawning state, respectively.

Oxygen uptake was determined with a polarographic oxygen sensor by measuring the rate of decline of partial pressure of oxygen in an enclosed chamber. A small centripetal pump ensured continual water circulation within the chamber. Previous workers (Peckham, 1984) had used blank runs prior and subsequent to each measurement so that the effect of bacterial oxygen consumption could be resolved. In this study it was found that twice rinsing starfish and filling the chamber with 0.2µm filtered seawater before each measurement resulted in an undetectable blank (bacterial) effect. These experiments were run at ambient sea temperature (ranging from 22°C to 28°C) and were standardised to 25°C by utilising the oxygen consumption/temperature relationship reported by Yamaguchi (1974b).

2.2.5. Fecundity

Fecundity measurements were made on a sample of 23 ripe females from a high density population on Helix Reef on 5 December 1985, immediately before their spawning[2]. All ovaries were dissected from each starfish and their total volume measured. Fecundity was determined from gonad weight (volume x seawater density) using the value of 90,190 oocytes.g^{-1} ovary determined by direct oocyte counts of weighed ovaries by Conand (1985). The values obtained represent potential fecundity rather than realised fecundity, as it is possible that spawning is incomplete.

2.2.6. Inter–ray variability

The *A. planci* population on Helix Reef had already reached outbreak levels when this project began, and the assumption that a three–ray sector was representative of the whole starfish could not be validated before the initial collection. Variability between rays was examined at a later date to assess the above assumption. Single normal rays were successively removed from healthy starfish and analysed for dry weight index in a similar manner to other samples. This exercise was repeated on other starfish removing two–ray sectors, and again removing three–ray sectors. In this manner the relative effectiveness of dissecting a one, two and three–ray sector could be judged from changes in the coefficient of variation of dry weight indices for particular sector sizes.

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[2] A subsequent collection on 12 December 1985 revealed that most starfish had shed most of their gametes, thus the 5 December sample could have been not more than seven days prior to the principal spawning event.

2.3. Results

2.3.1. Biometric relationships

Biometric relationships between diameter, whole wet weight and underwater weight are shown in Table 2.1. These include equations from Nishihira and Yamazato (1972), Yamaguchi (1974a), Peckham (1984) and Conand (1985), which have been modified to equivalent units where necessary.

In this study Student *t*–tests were used to test for deviations of slope coefficients from isometry. There was no significant difference between the power coëfficient for the relationship between diameter and wet weight (2.929) and the hypothetical value of 3. Over the range of animals examined in this study (200mm to 410mm diameter), *A. planci* demonstrate isometric growth.

The power coefficient of the relationship between underwater weight and diameter (2.264) was found to be significantly different from the hypothetical value of 3 ($t \approx 3.444$, N=50). There was also a significant difference between the hypothetical coefficient of 1 and that (0.764) found for the relationship between underwater weight and wet weight ($t \approx 4.049$, N=50). Since skeletal material is the only body component significantly denser than seawater, the degree of ossification of the body wall is decreasing relative to both diameter and wet weight in larger starfish.

2.3.2. Compartmental indices

Compartmental dry weight and calorific indices versus wet weight are displayed in Figure 2.3 [3]. Relationships between the dry weight indices (DWI) and calorific indices (CI) of the various body compartments and whole wet weight are shown in Table 2.2. Neither the DWI nor the CI of the stomach vary predictably over the whole wet weight range 280g to 3000g, having mean values of 5% and 8%,

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[3] Relationships in Figure 2.3a and 2.3b are calculated from least squares regression equations with one exception – predicted values are scaled in proportion to the cumulative total of stomach, caecal, gonadal and body wall indices ensuring that values sum to 100%. This adjustment is necessary because, while each regression minimises residual variation for its own data set, the method does not result in simultaneous minimisation of residuals for all four regressions.

respectively. Body wall dry weight and calorific indices (BDWI and BCI) decrease significantly with increasing wet weight, both gonad indices increase significantly. The caecal CI declines significantly with increasing wet weight, although the caecal DWI remains relatively constant. The general pattern emerging from these results is that with increasing size, mature starfish accumulate relatively greater amounts of energy in their gonads, at the expense of their body wall and caeca.

2.3.3. Fecundity

The relationships for fecundity (an absolute parameter) and gonad index (a relative parameter) versus whole wet weight are shown in Figure 2.4. The relationship between fecundity (F) and wet weight (W) is expressed by the equation:

$$F \approx 558 \cdot W^{1.439},$$

where the power coefficient (1.439) is significantly greater than the isometric coefficient of 1 ($t \approx 3.258$, N=23). Thus, the gonad wet weight index increases from about 10% for a starfish weighing 500g (≈230mm diameter) to about 24% for a starfish weighing 4000g (≈460mm diameter) and fecundity increases from about 4 million to 65 million eggs over this size range. Extrapolation of this relationship beyond W=4000g is to be done with caution. Gonadal indexes must stabilise for larger starfish – theoretical grounds suggest that there will be a point above which gonadal development cannot be supported by reduced somatic size.

2.3.4. Oxygen consumption

Figure 2.5 shows the relationship between oxygen consumption and wet weight using natural logarithm axes. A power coefficient of 0.67 would indicate that oxygen consumption is related to surface area (as surface area is proportional to $(\text{weight})^{0.67}$), while a coefficient of 1 would suggest that oxygen consumption is directly related to body mass. However, the observed coefficient (0.87) differs significantly from 0.67 and 1 ($t \approx 7.861$ and 5.052, respectively, N=75) – respiration rate is neither strictly limited by, nor free from surface area considerations. The result is that specific oxygen consumption decreases uniformly with increasing mass such that a small starfish (≈ 100mm diameter) consumes about 40µl

$O_2.(g.h)^{-1}$, while a 600mm diameter starfish consumes about 10μl $O_2.(g.h)^{-1}$. There is no suggestion in Figure 2.5 that the exceptionally large starfish from Lady Musgrave Reef exhibit an oxygen consumption/size relationship different from smaller conspecifics. Note that the data of Figure 2.5 were obtained for starfish at various times of the year with the exception that none were collected in early summer (i.e. near peak reproductive condition).

2.3.5. Inter–ray variability

The coefficient of variation between successively dissected sectors of an individual starfish decreases markedly as the number of adjacent rays in a sector increases. Table 2.3 and Figure 2.6 demonstrate, for the seven starfish sampled, the reduction in variability attained for each compartment. For single dissected rays the coefficient of variation was always greater than for sectors comprising three rays. The degree of improvement in the estimate of dry weight index varied between compartments. The greatest improvements occurred for the caeca and the body wall (variability reduced by a factor of 5 and 3 respectively). Estimates of stomach dry weight index showed a two-thirds reduction in variability when three rays were dissected. Improvement in the estimate of gonadal dry weight index was marginal and inconsistent.

The coefficient of variation (CV) can be utilised in an examination of the likelihood of a single measurement falling more than a given distance from the true mean.

Since

$$CV = \frac{S}{\bar{X}}$$

where S is standard deviation and $\bar{X}$ the mean, and

$$Z = \frac{X_i - \bar{X}}{S}$$

where X_i is a given measurement and Z is the number of standard deviations of X_i from $\bar{X}$ it follows that

$$Z = \frac{\frac{X_i - \bar{X}}{\bar{X}}}{CV} .$$

If the term X_f were used to denote the difference between X_i and $\bar{X}$ as a fraction of $\bar{X}$ then

$$Z = \frac{X_f}{CV} .$$

Tables 2.4 and 2.5 demonstrate the probability that a single measurement from the dissection of one, two and three adjacent rays will differ by ±10% and ±30%, respectively, from the measurement that would have been obtained by dissecting the entire starfish. If dissections had utilised only one ray then a 10% difference between real and measured values could be expected to occur 75%, 37%, 68% and 16% of the time for the stomach, caeca, gonad and body wall, respectively. The use of three adjacent rays reduced these values to 61%, <<1%, 61% and <<1%, respectively (Table 2.4). The poor precision of stomach and gonad estimates is further demonstrated in Table 2.5. The probability of ±30% error in any measurement is 32% and 31% for a single ray dissection of stomach and gonad, respectively, and 13% for three adjacent rays for both stomach and gonad.

2.4. Discussion

2.4.1. Biometric relationships

Power coefficients reported by Nishihira and Yamazato (1972) and Conand (1985) for the relationship between diameter and wet weight are substantially less than 3 (2.870 and 2.637 respectively, Table 2.1), although neither author examined this relationship statistically. The suggested allometric relationship is that body mass decreases relative to $(\text{diameter})^3$ for larger starfish, i.e., starfish become relatively thinner in the oral–aboral axis as they grow.

The results of this study (coefficient ≈ 2.929) are also less than 3, but not significantly so ($t \approx 0.45$, critical level≈ 2.01). Neither are they significantly less than the value reported by Conand ($t \approx 1.83$, critical level≈ 2.01). Analysis of more starfish and over a larger size range may clarify the status of the observed trend (4.3.4.2 and 4.4.5).

Yamaguchi (1974a) showed that underwater weight is primarily a measure of skeletal weight, as the ossicles of the skeleton are the only body components that are denser than seawater. He reported that the underwater weight of *A. planci* from Guam was generally about one seventh of their whole wet weight. Peckham (1984), however, found that the underwater weight for small GBR starfish was generally about one twentieth of their wet weight and values from this study are similar to Peckham's. *A. planci* from Guam are apparently much more heavily ossified, a morphological distinction that has not previously been recognised. This study shows that, in GBR starfish, over the size range 280g to 3000g, underwater weight varies from approximately one fifteenth to one thirtieth of whole wet weight, respectively (from Table 2.1). This reduction in the skeletal component of the body with increasing size coincides with a reduction in the body wall indices (2.4.2). It explains the fragility to handling of large individuals of *A. planci* (*pers. observ.*) and suggests a reason why small juveniles are sometimes found in more exposed sections of coral reefs than adults (Laxton, 1974).

Many other coral reef asteroids have a high degree of body wall development, and are very rigid (Blake, 1983). Many are also microphagous. Blake suggests that microphagy is a consequence of high body-wall development, while Lawrence (1990) suggests the opposite - high body-wall development results from microphagy (which in turn reflects a poor food supply). Blake suggests that *A. planci* avoids predation because of its pedicellariae and long spines, whereas Lawrence suggests that *A. planci* can afford a thinner body wall because food abundance is high and disturbance is offset by high growth rates. Whilst this study does support the notion that *A. planci*'s spines are of limited effectiveness (4.4.7) it provides no clear resolution to the impasse above. One point is quite clear though:

any generalisation that considers only one mode of living for *A. planci* is too simplistic. "Outbreak" populations, several orders of magnitude greater in density than "normal" populations, persist for brief periods of time (perhaps 6 to 12 months), and after commencing to feeding *ad libitum*, eventually die from food limitation.

The concept of "normal" populations as used in the literature to date is misleading. If averaged over time, "normal" populations would probably be low-density (these persist for longer). However, most individuals probably live and die within high density populations, and face very difference circumstances. Morphological, physiological or behavioral adaptations from either state (low density, high density) may well persist in the alternate state with no adaptive significance. It is even possible that traits offering increased survival at one density have a counterproductive effect on survival at the other.

2.4.2. Compartmental indices

Peckham (1984) demonstrated that the caecal, gonad and stomach indices of small juveniles (≈10g wet weight, 25mm diameter) were very low and that the body wall accounted for almost 95% of their dry weight. Interpolation between these 25mm juveniles and the small adults of this study (≈280g wet weight, 200mm diameter) (Figure 2.3a), shows that the body wall declined markedly as a proportion of the entire body over this size range. By contrast, the caecal and stomach indices increased during growth over this size range.

The marked increase in the caecal dry weight index for starfish between 10g (Peckham, 1984) and 280g wet weight (smallest starfish from this study) (Figure 2.3a) indicates strong partitioning of resources towards caecal development during juvenile development, a trend which is not continued in larger starfish (Table 2.2; no significant correlation). Thus, the dry weight of the caeca increases from less than 5% of the dry body weight to about 14% over the size range 25mm to 200mm diameter (onset of sexual maturity), and then remains relatively stable during further growth.

As expected, the dry weight index of the gonad remains very low (less than 5%) during growth to 200mm diameter, when it begins to increase rapidly. Voogt, Broertjes and Oudejans (1985) described the importance of the caeca in the accumulation of nutrients towards reproduction in asteroids and this has been experimentally demonstrated by Harrold and Pearse (1980). Increases in the caecal index of *A. planci* up until about 280g wet weight (near the onset of sexual maturity) are interpretable in terms of this role as an energy storage reservoir for reproduction. An increasing proportion of energy resources is accumulated in the caeca until the onset of sexual maturity, when it is diverted to gametogenesis (Figure 2.3b).

The organ index data presented here for adult starfish are from a population near peak reproductive condition. These data indicate the energy channelled into reproduction. It is likely that the pyloric caeca index would be much higher and the gonad index much lower for starfish in a non–reproductive state. An annual cycle of inverse changes in pyloric caeca and gonad indices has not yet been demonstrated for *A. planci*, but has been found in other asteroids (Voogt *et al.*, 1985). This subject is covered in detail in Chapter Four (4.4.9).

The rapid somatic growth (Yamaguchi, 1974a; Lucas, 1984) and high body wall indices of juvenile starfish (Peckham, 1984) suggest that these starfish prioritise their early allocation of resources in favour of the body wall. Thompson (1979) suggested that selective pressures from high mortality and competition result in the primary allocation of nutrients to support rapid somatic growth in juvenile echinoids. Selective pressures from high mortality may well be the ultimate cause for rapid initial somatic growth in *A. planci.* There are few observations of predation on juveniles, yet their extremely cryptic behaviour strongly suggests predator avoidance. Adults become less cryptic. They may be considered to have a "size refuge" where, by virtue of their large size, battery of now long spines and chemical defences, they achieve protection from predators, which either avoid them or cause only sublethal damage (Endean, 1977).

Birkeland (1989) suggested another benefit of reduced ossification in adult starfish – increased pliability for large multiarmed starfish permits them to prey upon arborescent and massive corals larger than those available to thick and heavily calcified asteroids. That *A. planci* channels increasingly greater proportions of energy to reproduction and ever decreasing proportions to maintenance of the body wall is an indication that bodily integrity is placed at risk for greater feeding and reproductive opportunity. Birkeland (1989) describes this as their "Faustian bargain" – *A. planci* appears to trade strength and structural integrity in their later years for rapid growth, the feeding advantages of a pliable body form and enhanced reproductive potential in their earlier years.

2.4.3. Fecundity

Nishihira and Yamazato (1972) observed an increase in the gonadal index for large *A. planci* from Sesoko Island, Japan, but did not describe the relationship mathematically. Conand (1985) reported a similar phenomenon for specimens from New Caledonia, with fecundity (F) increasing relative to weight (W) at an exceptional rate:

$$F \approx 0.009885 \cdot W^{2.322} \qquad (N=10)$$

In this study (N=23) the power coefficient for the relationship between F and W was somewhat less (1.439) (Figure 2.4), but still indicates a very marked increase in fecundity with increasing size. Results for the relationship between gonad wet weight index and whole wet weight reflect this phenomenon (Figure 2.4). Not only does fecundity increase with increasing size (as is expected), but the proportion of resources allocated to reproduction increases greatly. Small adults (≈220mm diameter) allocate ≈8% of their tissue production (wet weight) to reproduction. This increases to 13% at 300mm diameter and 20% for 400mm diameter starfish.

In energetic terms, the potential reproductive output of large *A. planci* can exceed 45% of the total energy content of the body (Figure 2.3b). The increasing allocation of energy to reproduction by large starfish must contribute to the decline in caecal and body wall indices (Figure 2.3b). It is notable, however, that the index of the stomach, essential to resource acquisition, does not decrease significantly with size.

The rapid increase in fecundity with size means that fecundity of an *A. planci* population depends not only on the population size but also on the size of individuals. A population of 25000 large adults (≈450mm diameter) may produce the same number of eggs as a population of 100 000 smaller (≈300mm diameter) adults. Conand (1985) noted that the greatest proportion of spawned eggs from a population with a polymodal size distribution would be from the largest cohort of starfish.

The accelerating relationship between the size of mature starfish and their potential fecundity (Figure 2.4) is particularly intriguing and may be hypothesised to result from several different reproductive strategies.

In a collapsing population (as is inevitable in a high density *A. planci* population), future progeny are worth more than current progeny (Pianka and Parker, 1975). If self-seeding of reefs is a significant source of recruitment (Cheney, 1974; Rowe and Vail, 1984; Williams *et al.*, 1984; Black and Gay, 1987; Black, 1988) and if size is related to age, then offspring produced at an early stage of an outbreak are less likely to survive than those produced in subsequent years. The latter may make the transition from feeding on coralline algae to feeding on coral (at ≈7 months of age, Yamaguchi, 1974a; Lucas, 1984) when there is sufficient regrowth of the faster growing corals to support them. It would be instructive to know whether, by leaving their largest reproductive effort until late, *A. planci* may be increasing the chances of their offspring finding sufficient regrowth of coral to survive. This reproductive strategy would appear well suited to a relatively sedentary animal (unable to navigate reliably to the next reef with high coral cover) that is capable of heavily exploiting its food source. It also assumes that corals regrow relatively rapidly and that reseeding (or at least settlement in an adjacent affected area) is a significant source of recruitment

Moore (1978) develops the view that *A. planci*'s bionomic features predispose it to large fluctuations in abundance. Late reproductive effort would be advantageous in these circumstances if it maximised the realised fecundity of *A. planci.* By growing, rather than reproducing, starfish may be maximising their potential fecundity for subsequent spawnings.

Alternatively, the assumption, implicit in the two above hypotheses, that larger starfish are older, may not be valid. This study acknowledges (2.4.6) that size and age are only loosely related. Size may not be related to age at all – starfish with large size and fecundity may have had a protracted period of surplus food while smaller starfish with fewer gametes may have been on a suboptimal diet.

The same accelerating relationship between fecundity and size could have resulted from a progressive transition (perhaps even over a few years) to full maturity, or it may have resulted from a progressive transition away from a strategy of initially supporting body growth to escape from size–dependent predation. Likewise, it may simply reflect the timing of the transition from a coralline algal diet to a coral diet, and the variable period of rapid growth prior to maturation.

An examination of the fecundity of the rare "giant" starfish may help to identify the cause of this relationship. If the relationship results from a "reckless" reproductive strategy, then these giants should have much higher gonad indices, i.e., the slope of the gonad index curve (Figure 2.4) should not rise asymptotically to zero. On the other hand, if the relationship results from a progressive transition (either away from favouring body growth or towards full maturity or both) then the gonadal index should stabilise (the slope of the gonad index curve in Figure 2.4 will approach zero) and fecundity will continue to increase as a simple proportion of body mass.

2.4.4. Oxygen consumption

The slope coefficient of 0.870 for ln (oxygen consumption) versus ln (wet weight) from this study (Figure 2.5) is similar to that reported for *A. planci* by Peckham (1984) (0.83), and to values found for other asteroids. Lawrence and Lane (1982) reviewed the literature on asteroid respiration and report slope coefficients ranging from 0.7 to 1.16 for various species, with most in the vicinity of 0.8.

The specific oxygen consumption values determined here appear to be somewhat less than data for juvenile *A. planci* from Guam (Yamaguchi, 1974b). In this study a 100mm diameter starfish consumed ≈40µl $O_2.(g.h)^{-1}$ at 25°C compared to ≈60µl $O_2.(g.h)^{-1}$ for a 120+mm starfish at the same temperature in Yamaguchi's study (derived from Figure 2 of Yamaguchi (1974b) and converted to wet weight). This suggests that there may be physiological differences in addition to different biometric relationships (i.e. underwater weight / whole wet weight) between

A. planci from these two regions. Reproductive condition should not have been a factor in the comparison between these juvenile starfish.

There is a profound increase in absolute oxygen consumption during the growth of *A. planci* resulting from the enormous change in mass, e.g., oxygen consumption increases from 0.14 ml.h^{-1} for a 45mm diameter starfish to 64 ml.h^{-1} for a 450mm conspecific, more than a 400–fold increase over this size range. This increase in metabolic rate is also reflected in changing feeding rates, which have been quantified by Yamaguchi (1974a). His study shows that a 300mm diameter starfish consumes more coral in a day than it did in its first year of life (which included about 7 months of feeding on coralline algae). This is one reason why populations of large *A. planci* seem to materialise on coral reefs without evidence of recruitment. Their initial feeding as juveniles has negligible effect in terms of gross coral damage and passes unnoticed. Their rate of coral consumption, however, increases dramatically with the rapid growth during their second year and their effect on the coral community becomes conspicuous over a short period.

2.4.5. Gigantism in Crown–of–Thorns starfish

Very large starfish, the rare "giants" in excess of 500mm diameter which have been reported mainly from the GBR, show nothing unique in their oxygen consumption versus wet weight relationship (highest values in Figure 2.5). Lucas (1984) discussed the origin of these exceptional individuals, including possible genotypic and phenotypic sources. There is no suggestion here of any genotypic difference in metabolic rate in these large animals – their respiration rate data are clearly part of the general metabolic rate versus wet weight relationship. Alternate explanations need be sought to account for the exceptional size of these "rare" *A. planci*, and to explain the existence of a small population (N $\approx$30) of these giants on Lady Musgrave Reef.

Starfish in high density populations, partitioning increasingly heavily towards reproduction and consuming their food resource rapidly are likely to be restricted in their maximum size by food limitations. Chesher (1969a) observed a 10% reduction in the size of 90mm diameter *A. planci* starved for 3 months. Crump (1971) found that specimens of *Patiriella regularis* lose 33% of their body weight after starving for

44 weeks. Feder (1970) found that individuals of *Pisaster ochraceus* could lose up to 35.2% of their body weight when starved for 18 months. The ultimate size of *A. planci* during population outbreaks may be commonly limited by low ration diets towards the end of the outbreak (Lucas, 1984). So–called "giants" need not be metabolically unique, but may simply have never been exposed to low ration diets. Thus, low population density or high coral availability (either in terms of percentage cover or extent of coral) favours larger adults (even "giants" in the extreme), while high starfish population density or low coral cover favours a small ultimate size. Lawrence and Lane (1982) draw a similar conclusion about "giant" *Pisaster ochraceus* and *Holothuria atra*, specifying that the asymptotic size may be population–specific according to environmental conditions.

2.4.6. Size and age

One limitation of this study stems from an inability to determine the age of individual starfish. Size in asteroids is only loosely related to age (Crump and Emson, 1978). The size distribution of *A. planci* in a given cohort shows marked variations, particularly after starfish begin the switch to a diet of coral. Successive cohorts of *A. planci* from Iriomote have distinct size ranges until ≈ 14 months old, at which point rapidly growing 1+ year starfish and slow growing 2+ year starfish overlap in size (Habe *et al.*, 1989). By the end of their second year, sizes can vary fourfold from ≈80mm to ≈ 250mm diameter. This represents a 27 fold difference in volume for siblings if W is proportional toD^3. Size / age discrepancies of a similar magnitude have been noted for cohorts from Suva Barrier Reef, Fiji (Zann *et al.*, 1987).

Lucas (1984) found that adult *A. planci* can shrink in diameter by as much as 31% (from maximum diameter down to 69% of maximum diameter, which corresponds to a reduction of ≈67% in volume, if W is proportional to D^3). Very clearly, the logical extrapolation of relationships involving size to similar relationships involving age should be done with caution. The assumption that larger starfish are older is only likely to be valid over a very large size range.

Knowledge of starfish age would help to determine the cause of the accelerating relationship between fecundity and size, and whether or not "giant" starfish are old or simply have never been subject to food limitation. Clearly a method of determining the age of individual *A. planci* is of paramount importance to understanding their ecology. Stump (1987) has demonstrated relatively high levels of the age-related intracellular pigment, lipofuscin, in caecal extracts of *A. planci*. Stump's results suggest that the accumulation of lipofuscin in the caeca of *A. planci* may provide an index against which starfish age can be estimated. Stump and Lucas (in press) have identified periodic growth lines in large skeletal ossicles from *A. planci*. While there is some debate over the use of such lines for ageing (Ebert, 1986), *in situ* mark-recapture studies by Stump and Lucas suggested that pigmented bands in the study population were laid down with annual periodicity. Further research on age-related intracellular pigments and skeletal banding should be pursued as a matter of priority.

2.4.7. Dissection techniques

Pearson and Endean (1969) suggested that there were only small variations in the gonadal index between normal rays of *A. planci*, using this as a justification for the estimation of fecundity from single rays. The coefficient of variation of the gonadal dry weight index for single normal rays dissected from healthy starfish was ≈ 24.5% in this study. The gonad biomass estimate obtained from a single ray has ≈31% chance of differing from the mean value for the entire starfish by 30%. If fecundity or gonad index measurements are to be made on a single ray then estimates may differ substantially from actual values.

There are clear gains in the accuracy of caecal or body wall measurements from dissecting three adjacent, intact rays - ability to detect real changes will be greatly enhanced by dissecting three rays rather than one. These improvements may not be worth the additional dissection time for the stomach or the gonads. Since the stomach lies compactly in the centre of the disc, small variations in the central point of incision introduce large variability into stomach measurements. Researchers wishing to examine biomass changes in the stomach should consider removing the entire stomach.

The gonads lie along either side of each arm and, where the rays join, along either side of the septum that extends into the disc cavity. It is relatively easy to ensure that all gonads from a ray are collected by cutting into the adjacent rays and trimming back the unwanted rays to the septum. Thus errors in gonadal measurements are unlikely to result from the dissection technique – variability between rays is likely to be real. However, researchers wishing to examine biomass or fecundity changes of the gonad at the population scale should consider taking a single ray only, but from a greater number of starfish, since the dissection of several adjacent rays makes little difference to the error in gonad biomass estimates and would only increase the time taken to complete the dissections[4]. In any event, researchers would be well advised to verify these findings on their own experimental populations prior to conducting a sampling program because variability between the rays of a particular starfish may be related to environmental factors (e.g. food availability, predator pressure).

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[4] Yamaguchi (*pers. comm.*) points out this is not applicable if the object of the study is to examine changes within individuals or between individuals within a population. In these cases, intra-individual variability may be minimised by randomisation (three single rays selected at random instead of three adjacent rays) or by greater sample size (more than three arms per individual). Yamaguchi notes that this would be particularly important if the object were to elucidate partial spawning of adjacent groups of rays. Babcock (*pers. comm.*) has chosen to dissect whole starfish, one ray at a time, for this reason.

Table 2.1 Correlations (r) between diameter (D:mm), whole wet weight (W:g) and underwater weight (U:g) for *Acanthaster planci* (L.) from Helix Reef, 30 October, 1985[5].

	Great Barrier Reef		Guam	New Caledonia	Sesoko Is., Ryukyus
	This study	Peckham, 1984	Yamaguchi, 1974a	Conand, 1984	Nishihira and Yamazato, 1978
W versus D	$W=6.29x10^{-5} .D^{2.929}$ r=0.394 N=50 D range = 200-410			$W=2.49x10^{-4}.D^{2.637}$ r=0.960 N=155 D range = 190-500	$W=8.58x10^{-5}.D^{2.870}$ r not given N=48 D range = 40-300
U versus D	$U=1.33x10^{-4}.D^{2.264}$ r=0.837 N=50 D range = 200-410		$U=8.20x10^{-5}.D^{2.320}$ r not given N=54 D range = 15-220		
U versus W	U=0.250.W r=0.884 N=50 D range = 200-410	U=0.046.W + 1.6 r=0.982 N=42 W range = 8-3,200	U=W/7 r not given, N=54 W range = ??		

Table 2.2 Correlations (r) for the dry weight index (DWI:%) and calorific index (CI:%) of four body compartments versus whole wet weight (W:g) for *Acanthaster planci* over the weight range 280 to 3000g whole wet weight, from Helix Reef, 30 October, 1985. Standard errors for the Y-intercept (SE(a)) and the slope coefficient (SE(b)) are included. N=50, $r_{0.05(2),48} \approx 0.279$.

Compartment	Dry weight index	Calorific index
Stomach	no significant correlation mean≈ 5	no significant correlation mean ≈8
Pyloric caeca	no significant correlation mean≈ 14	$CI \approx 111.4 \cdot W^{-0.176}$ $r \approx -0.402$ SE(a) ≈47.1 SE(b) ≈0.058
Gonad	$DWI \approx 3.59x10^{-4} \cdot W^{1.424}$ r ≈0.728 SE(a) $\approx 4.94x10^{-4}$ SE(b) ≈0.193	$CI \approx 3.00x10^{-4} \cdot W^{1.515}$ r ≈0.706 SE(a) $\approx 4.67x10^{-4}$ SE(b) ≈0.219
Body wall	$DWI \approx 147.2 \cdot W^{-0.114}$ $r \approx -0.535$ SE(a) ≈27.1 SE(b) ≈0.026	$CI \approx 113.2 \cdot W^{-0.157}$ $r \approx -0.414$ SE(a) ≈40.0 SE(b) ≈0.050

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[5] This table was compiled for publication in Kettle and Lucas (1987) (refer Appendix B). In that publication Yamaguchi's U versus D relationship was inadvertently entered as $W=8.2x10^{-5} . D^{2.320}$. This table is correct.

Table 2.3 Mean and Coefficient of Variation (%) of compartmental dry weight indices for *A. planci* dissected as sectors of one, two and three adjacent intact rays, from Helix Reef.

	Number of rays per sector						
	1			2		3	
	replicate			replicate		replicate	
	A	B	C	A	B	A	B
STOMACH	0.59 (27.9)	0.24 (19.0)	0.39 (43.9)	1.10 (23.8)	2.85(20.9)	1.40 (27.7)	1.31 (11.8)
CAECA	0.66 (5.6)	0.51 (14.5)	0.36 (14.2)	2.36 (3.9)	6.79 (3.9)	4.84 (2.6)	2.90 (2.8)
GONAD	0.04 (10.7)	0.02 (34.6)	0.01 (28.1)	0.80 (29.9)	0.40 (36.3)	0.07 (13.0)	0.06 (26.3)
BODY	9.49 (7.5)	6.93 (7.3)	8.26 (6.6)	16.18 (5.8)	31.02 (5.6)	25.44 (2.3)	19.14 (2.8)

Table 2.4 Probability that a single measurement from the dissection of one, two or three adjacent intact rays will differ by **10% or more** from the true value that would have been obtained by dissecting the entire starfish.

	Number of adjacent intact rays dissected		
	N=1	N=2	N=3
STOMACH	75%	65%	61%
CAECA	37%	1%	<<1%
GONAD	68%	76%	61%
BODY WALL	16%	8%	<<1%

Table 2.5 Probability that a single measurement from the dissection of one, two or three adjacent intact rays will differ by **30% or more** from the true value that would have been obtained by dissecting the entire starfish.

	Number of adjacent intact rays dissected		
	N=1	N=2	N=3
STOMACH	32%	18%	13%
CAECA	<<1%	<<1%	<<1%
GONAD	31%	36%	13%
BODY WALL	<<1%	<<1%	<<1%

Figure 2.1 Townsville region, central Great Barrier Reef, showing study sites at Helix Reef, Pelorus Island and Orpheus Island.

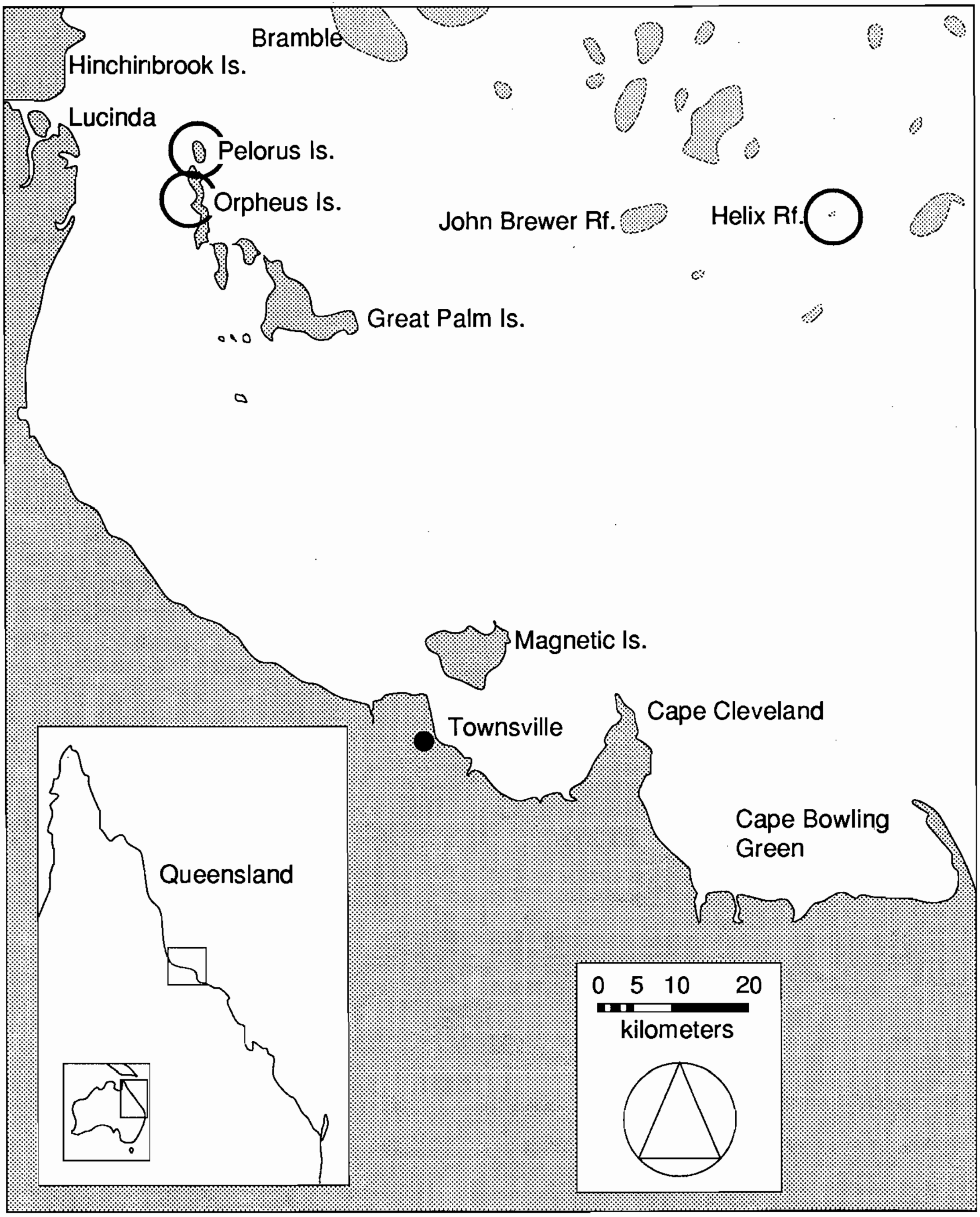


Figure 2.2 Collection site for large starfish from Lady Musgrave Reef, southern Great Barrier Reef.

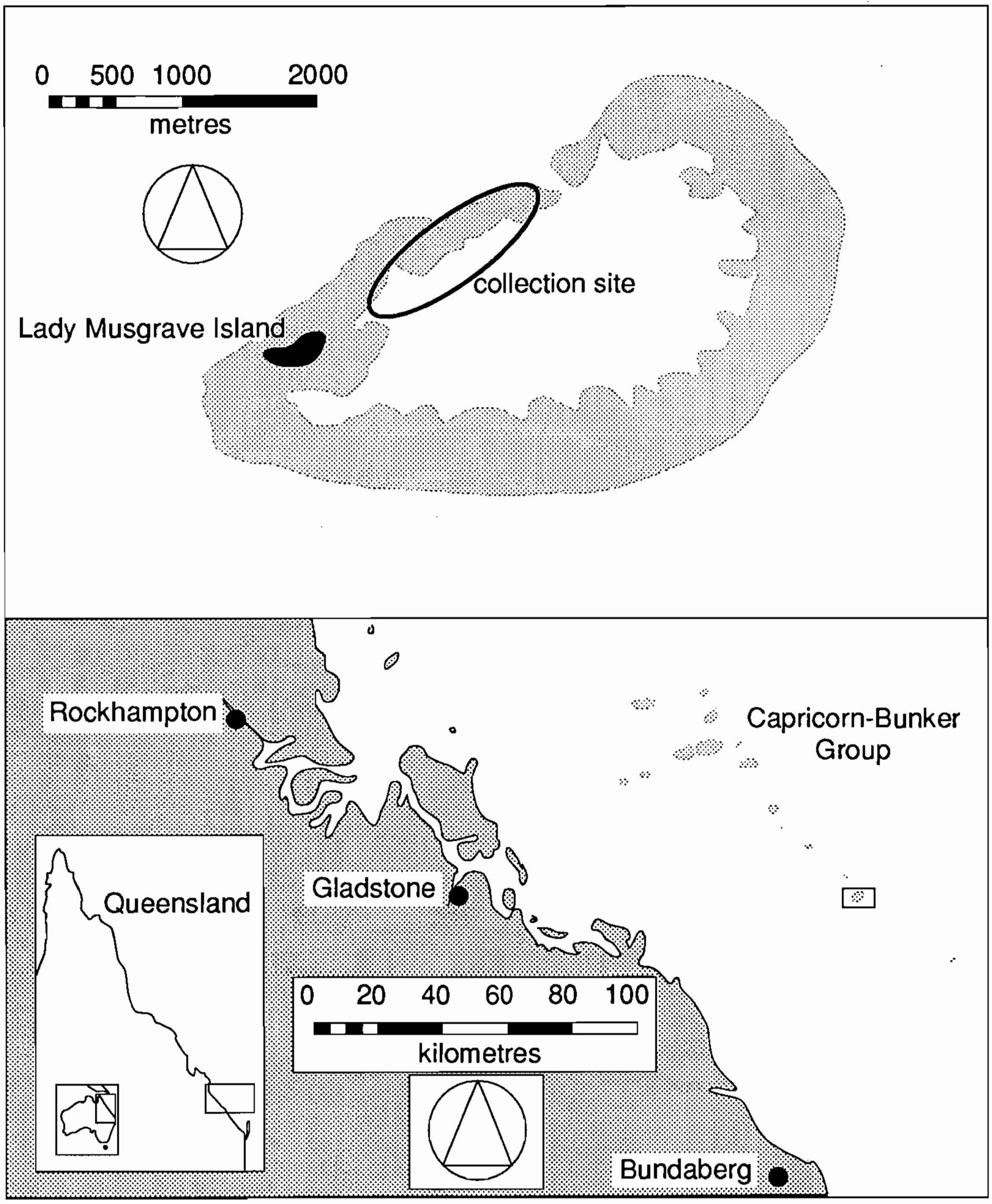


Figure 2.3 The relationship between; (a) the compartmental dry weight index (DWI:%) and whole wet weight (W:g), (b) the compartmental calorific value index (CI:%) and whole wet weight (W:g) for *A. planci* from the Great Barrier Reef (W range 10g to 3000g).

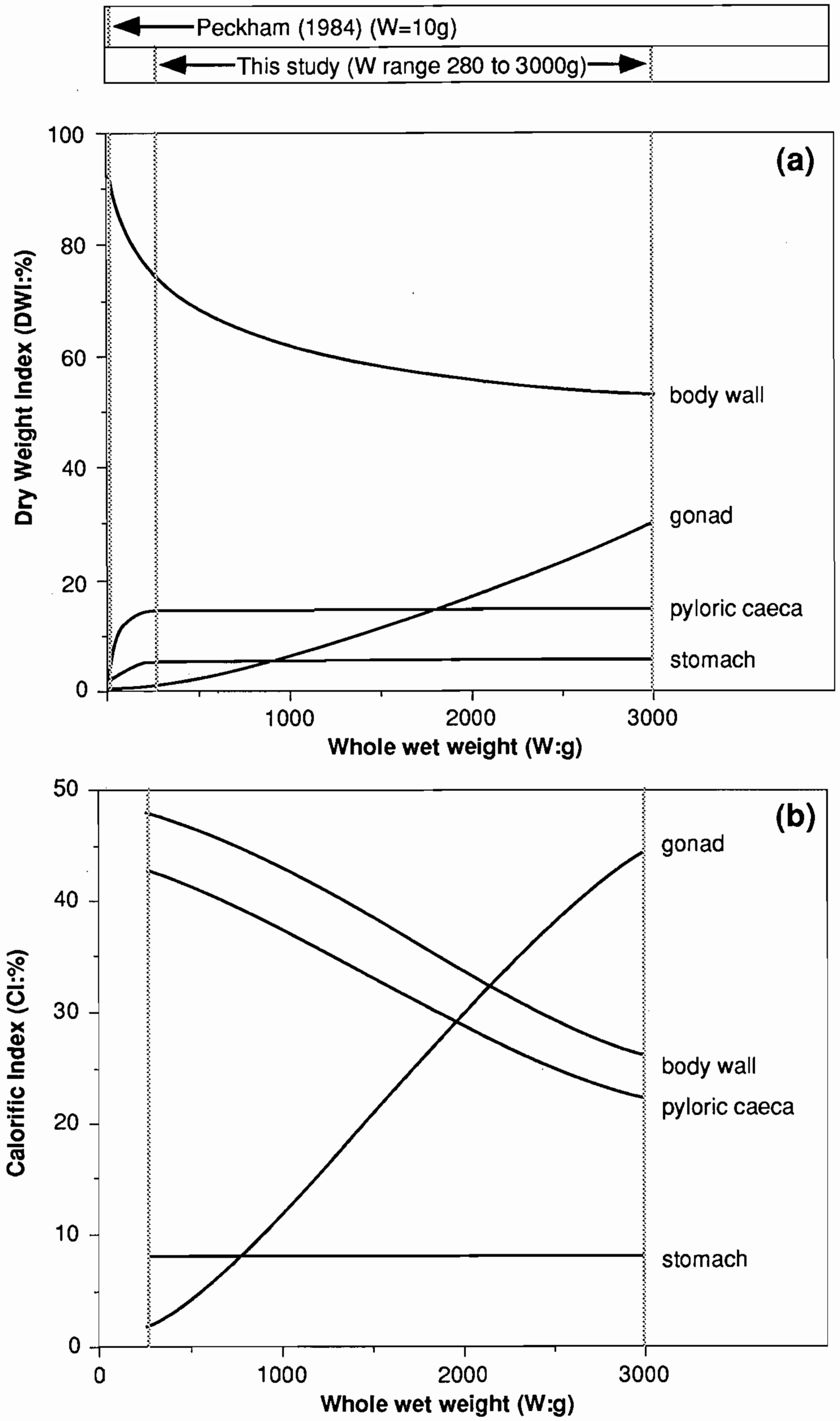


Figure 2.4 Gonad wet weight index and fecundity versus whole wet weight for female *A. planci* from Helix Reef (central Great Barrier Reef) approximately one week prior to spawning.

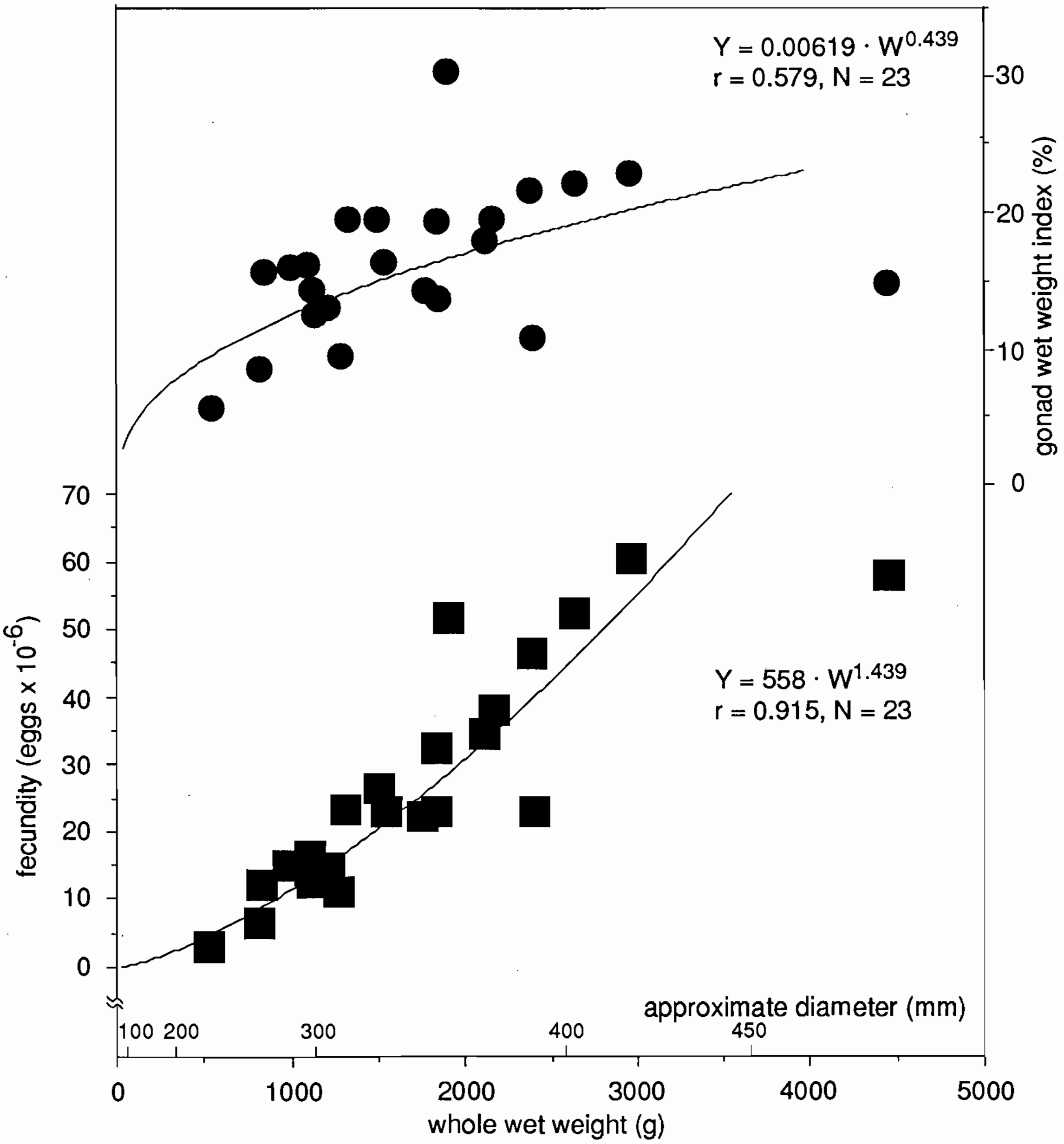


Figure 2.5 The relationship between ln(metabolic rate) (ml.O_2.hr^{-1} at 25°C) and ln(whole wet wt) (W:g) for starfish from the Great Barrier Reef. (▲) Peckham, 1984; (■) Lady Musgrave Reef; (●) Pelorus Island.

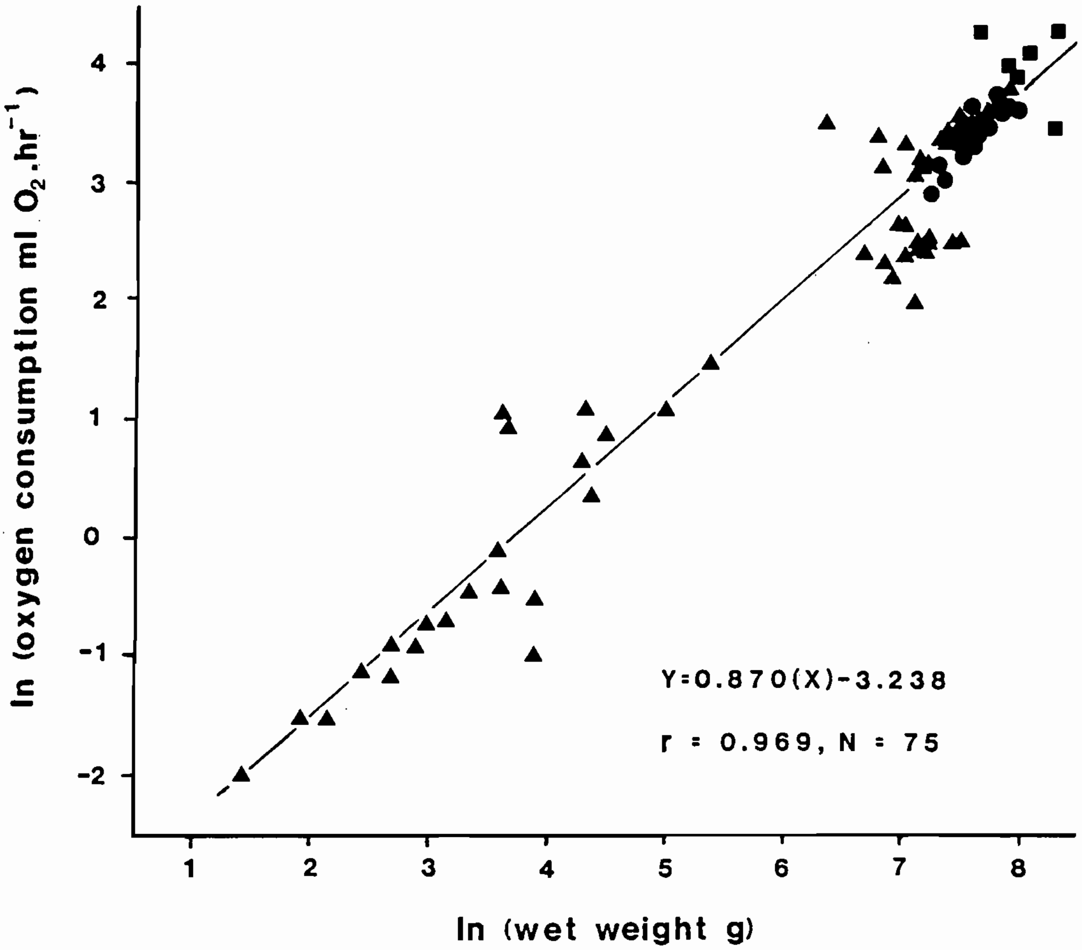
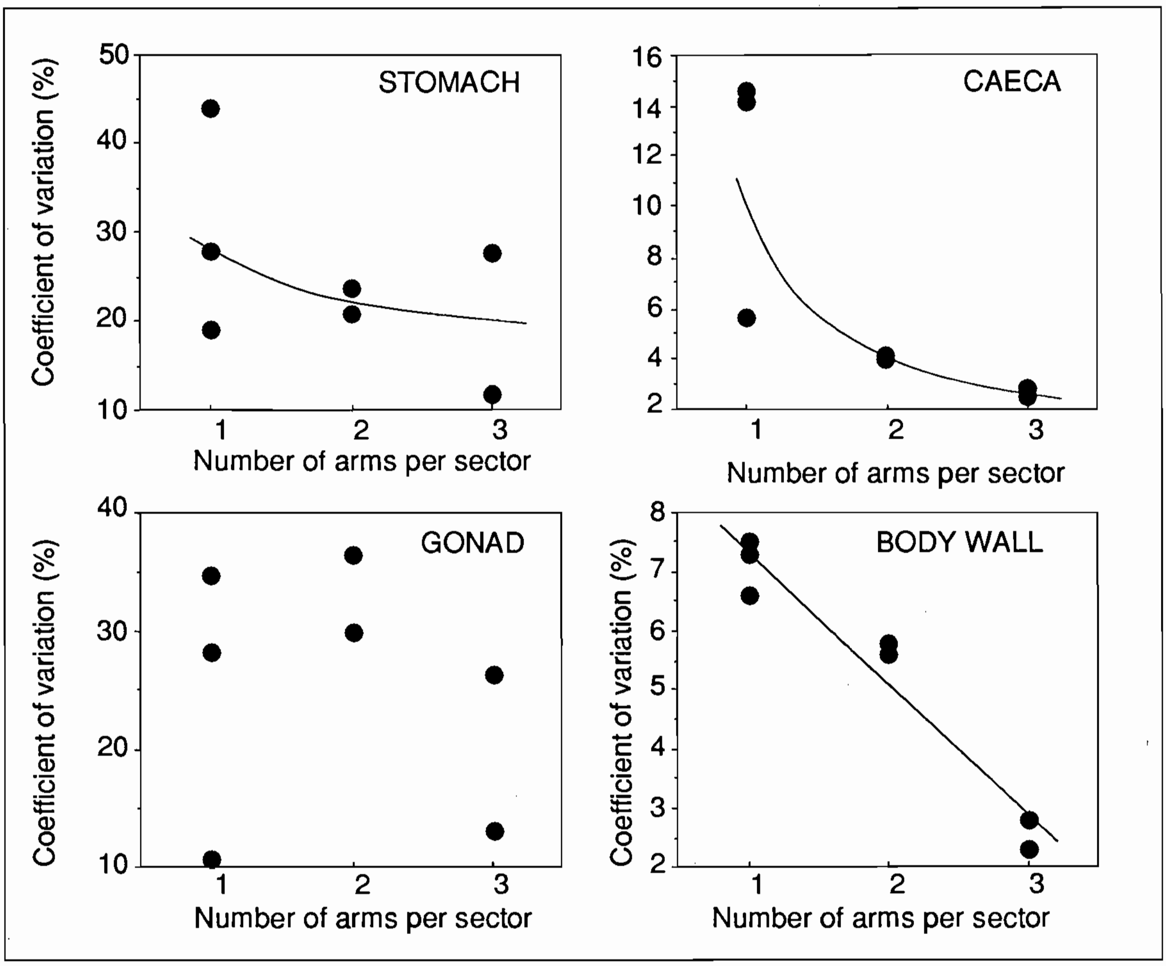


Figure 2.6 Effect of dissecting 1, 2 and 3–ray sectors on the Coefficient of Variation (%) of the dry weight index for the stomach, caeca, gonad and body wall of *A. planci* (n = 7).



3. The effects of starvation upon biometric relationships, compartmental indices and oxygen consumption of *Acanthaster planci*

3.1. Introduction

Life strategies of echinoderms can be described in terms of their response to environmental stress (factors that limit production) and disturbance (factors that cause partial or total destruction of biomass) (Lawrence, 1990). Low levels of food cause environmental stress as they limit production. Extreme food limitation causes disturbance – biomass is lost by shrinkage or mortality. Coral communities can be reduced to less than 1% cover (Colgan, 1987) and may take at least 10 to 15 years to recover (Pearson, 1981; Colgan, 1987; Done *et al.*, 1988) – *Acanthaster planci* causes the collapse of its niche's life support systems (Meredith, 1982). It follows that a study of the responses of *Acanthaster planci* to the stress of suboptimal food regimes, and the eventual disturbance resulting from near-total food exhaustion, will help to elucidate the life strategy of *A. planci.*

Asteroids grow, reproduce and deposit caecal reserves concurrently when food availability is high (Lawrence and Lane, 1982; Xu and Barker, 1990). As food availability declines, consumption debts can be overcome by translocating reserves between compartments or by reducing production to maintenance levels. Inverse relationships between the relative sizes of the gonads and other compartments may be interpreted as an allocation of energy to reproduction at the expense of those compartments. *Asterias rubens, Asterias vulgaris, Asterina gibbosa, Echinaster* sp., *Luidia clathrata, Odontaster validus, Oreaster herdmanni, Oreaster reticulatus, Patiriella regularis, Pisaster brevispinus, Pisaster ochraceus, Stichaster australis* (refer Table 5 of Lawrence and Lane, 1982) and *Sclerasterias mollis* (Xu and Barker, 1990) partition limited resources towards reproduction at the expense of other compartments, although the degree of partitioning can vary with absolute food availability. Notwithstanding its fundamental role in digestion, Voogt *et al.* (1985) concluded that the prime role of the caeca was the storage of energy for subsequent partitioning to reproductive development. Some species that are capable of continued reproduction under mild food limitation reverse their pattern of allocation as starvation becomes severe, ceasing reproduction and opting instead to maintain their form and functionality (e.g. *Pisaster giganteus*: Harrold and Pearse, 1980; *Asterias rubens*: Vevers, 1949). With prolonged starvation, compartments other than the caeca can contribute reserves (or forego maintenance) to support essential functions. Continued utilisation of nutrients from the body wall results in shrinkage. *Asterias rubens* has been observed to shrink in diameter by 37% (Vevers, 1949), *Patiriella regularis* by 33% of its body weight in 44 weeks (Crump, 1971), *Pisaster ochraceus* by 35.2% of its body weight in 18 months (Feder, 1970) and *Sclerasterias mollis* by 1.7% of its diameter in 4 months (Xu and Barker, 1990). Despite these sometimes marked variations in size, food limitation has not been demonstrated to cause mortality in echinoderm populations on low ration diets and, as a result, it is suggested that echinoderm populations are regulated through biomass changes rather than fluctuations in population numbers (Lawrence and Lane, 1982).

The effects of food limitation on *A. planci* have received little attention. Cheney (1974) reported that *A. planci* deprived of food for one month resorbed gonadal material, while Okaji (1989) found no resorption of gonads over a 90 day period, even though caeca underwent a marked reduction in size. Chesher (1969a) noted a 10% reduction in diameter of 90mm *A. planci* starved for a period of three months. Lucas (1984) noted shrinkage and cessation of reproduction after three years of age in laboratory–reared *A. planci* that were fed *ad libitum*, but did little eating, a situation that he described as "senility" in these older starfish. Peckham (1984) examined the effect of starvation on organ indices and oxygen consumption, but unfortunately his work was cut short by infection in his laboratory–kept animals.

The ultimate fate of Crown–of–Thorns starfish when they become food–limited is unknown and has been a subject of speculation. Some authors claim that *A. planci* can migrate from reef to reef in search of food (Endean, 1969; Talbot and Talbot, 1971; Dana *et al.*, 1972; Laxton, 1974; Glynn, 1976). Evidence for this hypothesis includes the trawling of at least one large *A. planci* from inter–reefal areas (Great Barrier Reef Marine Park Authority, unpublished), sightings of aggregations moving up from deep parts of reefs (Moran *et al.*, 1985), and time lapse photography of several starfish moving consistently down the reef slope and into deeper water towards the end of an infestation (cited in Moran, 1986).

On the first trip to the study reef, Helix Reef, many 2 minute manta tow segments around the reef perimeter recorded more than 100 starfish. The small size of Helix Reef, and its substantial outbreak population provided an *a priori* reason to believe that, among many possible influencing factors, starfish on Helix Reef would become food–limited within the 3 year study period. Thus it was prudent to study the effects of enforced starvation on captive *A. planci*, providing an insight into the effects of food–limitation in a laboratory environment where confounding factors could be controlled (or at least readily observed), thereby facilitating the interpretation of results of the subsequent *in situ* study of starfish on Helix Reef. This study examined the variations in biometric relationships, compartmental indices and respiration rates for a captive sample of starved *A. planci* from immediately after their capture until their eventual death.

3.2. Methods

Two large, plastic–lined, outdoor tanks (≈3 800 l each) were established in the flow-through, seawater system at James Cook University's Orpheus Island Research Station (Figure 2.1). The tanks were given similar flow rates (≈1 250 $l.h^{-1}$) and were both provided with additional circulation by means of submerged airlifts. In each tank, two sheets of compressed fibre cladding were erected in a crossed manner, perpendicularly bisecting each other to provide additional substratum upon which starfish could cling, thus facilitating higher stocking densities.

Tanks were stocked (14 June 1985) with adult starfish (D range 290mm to 460mm) from an outbreak population, with approximately 35 starfish in each tank. These starfish were collected from a high density population on a fringing reef on the north–western side of Pelorus Island (Figure 2.1). The population consisted of several hundred animals in an area approximately 50m by 50m. The distribution of starfish and recently killed coral suggested that starfish were moving in a southerly direction along the fringing reef. At the southern extremity of their distribution, starfish were formed into a narrow band, with individuals closely packed. Corals south of this band showed no evidence of Crown–of–Thorns predation; whilst north of the band only remnant pockets of live coral existed, and on these several starfish remained feeding. Starfish were collected from the "feeding front", and were assumed to be well fed due to the high coral cover (≈70%) existing at that time.

Starfish were individually identified at the time of their collection by noting their diameter, ray/madreporite pattern, number of anuses and the pattern of respiratory papillae and spines surrounding the anuses – a method originally utilised by Glynn (1982). Starfish were distributed haphazardly amongst the two tanks, no food was provided, and no attempt was made to remove algal growth that gradually accumulated on the walls of the aquaria throughout the study.

Peckham (1984) noted that some of his experimental *A. planci* had survived for approximately 7 months without food. This study was designed to allow four sets of 15 starfish to be sacrificed at approximately 8–weekly intervals (i.e. at the beginning of the study, and after every 8 weeks, for 6 months), with 10 additional starfish to allow for some mortality throughout the study period.

Starfish were sampled on 18 July 1985, 28 August 1985 and 20 November 1985 (after 5-, 10.5- and 22-weeks of starvation, respectively). Fifteen starfish were taken at random from the two tanks at each sampling. They were identified from the original capture records, measured for diameter, underwater weight, oxygen consumption and wet weight, and a 3–ray sector was removed for organ analysis. Dissection and measurement techniques used were the same as those specified in Chapter Two.

High water temperatures and algal growth within the aquaria were noted during the second sampling period after 10 weeks of starvation. There were pale circular patches resembling Crown–of–Thorns feeding scars on the short turf algal film. Canopies of 70% shade cloth were then erected over the tanks to minimise the incident light, algal growth and heating of the water. This procedure was maintained with the exception of the final sampling period, when a pump failure allowed water temperatures to rise. Animals became stressed and many died. At that time the six survivors were transfered to smaller holding tanks and were measured immediately.

3.3. Results

There was no attempt to control for starfish size, and thus both size and period of starvation could influence the results on any particular occasion. Whilst this design lends itself to analysis by multiple regression (where size and period of starvation are independent continuous variables), there was no prior reason to expect that the response of physiological parameters to long–term starvation would be continuous (i.e. a gradual transition between states). On the contrary, it was easy to envisage a situation where the value of a particular parameter would remain stable for some time before undergoing rapid change. Thus, the general approach was to proceed with an analysis of covariance, where regressions of effect versus size were compared between samples. If an effect was significant then *post hoc* tests were conducted to determine which pairs of consecutive samplings had differed significantly. Regression (and multiple regression) analyses were done only when it appeared that there was a significant and regular change in a dependent variable through time. The major advantage of such a procedure was its ability to determine the stage at which starvation effects became evident.

Two situations commonly hampered the above approach: in some cases there was no significant regression for a particular parameter versus size in one or more samples, and in all cases the size range of sacrificed starfish differed between samples.

In situations where size effects were observed in some samples but were absent in others, further analysis was possible only when size (whole wet weight) was partitioned into classes such that, within each class, there was no significant size effect; in which case analysis proceeded as a two factor (sample time and size) analysis of variance. In general, the procedure adopted was to use as few size classes as possible, thereby maintaining high cell (sample time by size) counts. Break points between size classes were selected to ensure similar numbers of observations per cell (never less than 3) and to ensure (as far as possible) that there were no significant weight effects within cells.

The extrapolation of regressions beyond the range of observed values is always suspect (Zar, 1984) and therefore regressions should only be compared over similar size ranges. A visual inspection of weight frequency histograms (Figure 3.1) reveals that the sample taken as SAMPLE D (the survivors at the end of the experiment) consisted of only small starfish. This compounded problems with subsequent analysis, even after recoding by weight into size classes, because the missing cells (large size classes from SAMPLE D) prevent an estimation of interaction effects over the entire time series. Interaction effects were estimated for SAMPLE A to C. SAMPLE D data were examined for effects of sample time only within the smallest size class.

Note that several conventions have been used throughout this text – capitalised words (e.g. SAMPLE and SIZE) denote names used in the statistical models, either as dependent variables (e.g. STDWI for stomach dry weight index), as independent variables (e.g. SAMPLE or SIZE) or as categories of a dependent variable (e.g. SMALL or LARGE as categories of SIZE), and in all cases α (alpha, the rejection criteria for the null hypothesis) was set at 0.05.

3.3.1. Biometric relationships

3.3.1.1. Change in diameter through time

Table 3.1 summarises the mean and range of starfish diameters animals sacrificed at each sampling occasion. The mean size of surviving starfish at each sampling event decreased regularly from $D \approx 397$mm (SAMPLE A) to $D \approx 342$mm (SAMPLE D). Differences among samples are significant (one way ANOVA; $F \approx 7.775$, df=(3,47), $P<.001$). *Post hoc* effects tests demonstrate that a significant decrease in diameter occurred between SAMPLE B and SAMPLE C ($F \approx 9.738$, df=(1,47), $P \approx 0.003$) (Figure 3.2), after 5 weeks of starvation.

It is possible to fit a highly significant regression to these data by using SAMPLE as a continuous variable, but such a regression is unlikely to be appropriate as it appears from Figure 3.2 that the rate of change of diameter varied markedly with respect to time.

Despite the consistent decrease of mean diameter (above), the mean change in diameter for remeasured starfish was positive. Furthermore, a plot of change in diameter (ΔD) versus initial diameter ($D_{initial}$) for the first and second starvation periods (Figure 3.3) shows that the change in diameter was inversely related to the size of starfish at the time the experiment began. Slopes on both occasions are equivalent ($F \approx 0.683$ df=(1,24) $P \approx 0.417$). Visual inspection of a plot of residuals versus estimates confirmed their non–heteroscedastic distribution. Small starfish increased in size while larger starfish shrank ($F \approx 18.708$, df=(1,25), $P < 0.001$). Size changes measured on SAMPLE C represented a greater reduction in $D_{initial}$ than those measured on SAMPLE B ($F \approx 5.302$, df=(1,25), $P \approx 0.030$).

The common $D_{initial}$ range for SAMPLE B and C was 350mm to 410mm. Based upon Figure 3.3, predicted ΔD for 350mm and 410mm starfish during SAMPLE B (5 weeks of starvation) is +25mm and –5mm, respectively; while ΔD for SAMPLE C (10.5 weeks of starvation) is +7mm and –40mm, respectively (Figure 3.4). These estimates are consistent with the observations (Figure 3.2) of a decrease in the mean size of survivors. However, reduction in the mean size of starved survivors (–41mm) was not due to shrinkage. The mean change in diameter for individual starfish that were positively reidentified after 5 weeks was +6.7mm. Even after 10.5 weeks remeasured individuals were, on average, 2.1mm larger. This pattern (growth of individuals whilst the sample mean was decreasing) would have resulted if successively smaller starfish were chosen from the holding tanks. The more likely explanation, given that starfish were selected at random from the tanks, is that large starfish were no longer present. This implies the selective mortality of larger starfish. This conclusion is supported by size–specific shrinkage rates. Smaller starfish ($D_{initial} \approx 350$mm) grew during 10 weeks of starvation (+7mm), while large starfish ($D_{initial} \approx 410$mm) shrank markedly (–40mm) (Figure 3.4).

3.3.1.2. Weight versus diameter

There were significant regressions for ln (whole wet weight: g) and ln (underwater weight: g) versus ln (diameter:mm) for SAMPLE A, B and C, but no significant relationship between these parameters for the smaller SAMPLE D (Tables 3.2 and 3.3).

Slopes of W versus D were homogeneous ($F \approx 2.137$, df=(2,39), $P \approx 0.132$; and $F \approx 0.318$, df=(2,39), $P \approx 0.730$ respectively) with similar elevations ($F \approx 1.849$, df=(2,41), $P \approx 0.170$, and $F \approx 0.376$, df=(2,41), $P \approx 0.689$ respectively). Relationships between W and D, and U and D were highly significant ($F \approx 64.138$, df=(1,43), $P < 0.001$, and $F \approx 49.235$, df=(1,43), $P < 0.001$ respectively) and could be described by the equations;

$W(g) \approx -3.165 \cdot D(mm)^{1.801}$ (SE(a)≈0.819, SE(b)≈0.225), and

$U(g) \approx -5.960 \cdot D(mm)^{1.789}$ (SE(a)≈0.903, SE(b)≈0.248).

Whole wet weight and underwater weight varied allometrically with respect to diameter ($t \approx 5.329$, N=45, $P < 0.005$, and $t \approx 4.883$, N=45, $P < 0.005$). Large starfish were "thinner" and had proportionally less skeletal material than small starfish, regardless of their state of starvation. Allometric variations in W versus D contrasts with earlier observations (see Chapter Two) that suggested isometric growth. Decreasing skeletal content has been noted for other *A. planci* (see Chapter Two), although in previous cases the power coefficient has been approximately 2.3. The value reported here (1.789) is significantly lower than 2.3 ($t \approx 2.060$, N=45, $P < 0.025$), perhaps as a consequence of size-specific mortality and shrinkage (3.3.1.1., 3.3.1.3).

3.3.1.3. Whole wet weight versus underwater weight

There were significant regressions between whole wet weight (W) and underwater weight (U) in each SAMPLE (Table 3.4). All slopes were homogenous ($F \approx 0.290$, df=(3,43), $P \approx 0.832$), and there were no significant SAMPLE effect ($F \approx 2.097$, df=(3,46), $P \approx 0.114$), however, a plot of ln(U) versus ln(W) suggests that interpretation is hampered by the dissimilar range of the independent variable (U) for each SAMPLE (Figure 3.5). Visual examination of Figure 3.5 suggests that elevation for SAMPLE D is greater than that for SAMPLE C (the only other data set where the ranges of the independent variable overlap). This relationship was examined further by reanalysis of SAMPLE C and SAMPLE D after limiting whole wet weight to less than 1640g. This included all six data points from SAMPLE D plus the lowest six data points from SAMPLE C (Figure 3.6). Slopes for this reduced data set are homogeneous ($F \approx 0.020$, df=(1,8), $P \approx 0.891$) and both weight (W) and SAMPLE effects are significant ($F \approx 15.260$, df=(1,9), $P \approx 0.004$, and $F \approx 5.537$, df=(1,9),

$P \approx 0.043$, respectively). Starfish had proportionally more skeletal material after 22 weeks of starvation. This suggests mobilisation of material from the soft tissues, resulting in a higher ratio of skeletal ossicles to soft tissues, an interpretation consistent with the observed shrinkage in size.

3.3.2. Compartmental indices

3.3.2.1. Stomach

There was a significant correlation ($r \approx 0.568$, $N=16$, $P \approx 0.022$) between stomach dry weight index (STDWI) and whole wet weight (W) ($a \approx 1.469$, $SE(a) \approx 2.122$, $b \approx 0.003$, $SE(b) \approx 0.001$) in the initial sample of unstarved starfish (SAMPLE A). This was neither observed in subsequent samples (Table 3.5) nor in the analysis of STDWI versus W in Chapter Two. Since the size effect was noted from only one SAMPLE, all starfish were recoded into two SIZE (weight) classes (SMALL and LARGE) with an upper exclusive class break point of $W \approx 1831$g. Weight effects were examined within each cell and were found to be insignificant, indicating that these SIZE classes were appropriate (cell means are presented in Table 3.6). The SAMPLE effect was also significant ($F \approx 5.08$; df=(2,23); $P \approx 0.015$) for SMALL starfish (SAMPLES A to D), for LARGE starfish (SAMPLE A to C), with a *post hoc* test for effects revealing a significant decrease between SAMPLE A and SAMPLE B. The SAMPLE effect was significant ($F \approx 4.061$, df=(3,22), $P \approx 0.019$) but *post hoc* tests revealed a decrease between SAMPLE C and SAMPLE D (Figure 3.7A). Thus, in general, the dry weight index of the stomach decreased throughout the period of starvation, but the period of greatest decrease was influenced by starfish size. The stomach dry weight index decreased markedly in the first month of starvation for large starfish (W range 1831 to 3000g), but not until after 2.5 months of starvation for small starfish (W range 900 to 1930g).

The water content of the stomach was independent of starfish size, but decreased markedly after 10 weeks of starvation (Table 3.7 and Figure 3.7B).

The calorific value ($kJ.g^{-1}$ AFDW) of the stomach was independent of size (Table 3.8), but mean values varied significantly ($F \approx 3.018$, df=(3,44), $P \approx 0.040$). *Post hoc* effects tests revealed that calorific value increased after 5 weeks of starvation

(F≈6.262, df=(1,44), P≈0.016) (Table 3.9 and Figure 3.7C). The overall trend of increasing calorific value contrasts with a general trend of decreasing stomach dry weight indices (above). The stomach was proportionally reduced in size but its calorific value increases, suggesting that shrinkage of the stomach was attributable to the preferential resorption of material with low energetic value.

Neither size nor period of starvation influenced the overall contribution of the stomach to the total calorific value of each starfish – the mean calorific index for the stomach was 10.7% (SE≈0.3). Evidently the synergistic effects of a decrease in stomach dry weight indices and the concurrent increase in calorific value (.g^{-1} AFDW) tend to balance out (Figure 3.7D).

3.3.2.2. Pyloric caeca

Regression coefficients of caecal dry weight index (PCDWI) versus WEIGHT for each SAMPLE (Table 3.10) reveal a significant WEIGHT effect (r≈.672, N=15, P≈0.006) for SAMPLE C (a≈5.721, SE(a)≈2.475, b≈0.004, SE(b)≈0.001) – large starfish had proportionally greater caecal dry weights. However, when caecal dry weight indices were analysed over three size classes (Table 3.11), the effect of SIZE *per se* became insignificant (F≈2.811, df=(2,41), P≈0.070). Mean caecal dry weight indices varied significantly during starvation (F≈29.217, df=(3,48), P<0.001) with *post hoc* tests demonstrating differences between all samples (F≈20.983, df=(1,48), P<0.001; F≈5.622, df=(1,48), P≈0.022; and F≈9.402, df=(1,48), P≈0.004) respectively (Figure 3.8A). Regardless of starfish size, caecal dry weight indices declined significantly as starvation progressed. This may have represented progressive consumption of energy stored in the pyloric caeca, or a gradual partitioning of energy from the caeca to the gonads as the spawning season (December to February) approached.

Caecal water content was independent of starfish size, but declined markedly after 10 weeks of starvation (Table 3.13 and Figure 3.8B).

Caecal calorific value was independent of starfish size (Table 3.14) for all samples, but mean values varied significantly (F≈7.099, df=(3,44), P≈0.001). *Post hoc* effects tests demonstrated that the only difference between consecutive samples was between SAMPLE C and SAMPLE D ($F \approx 14.521$, df=(1,44), $P \approx 0.001$) (Table 3.15 and Figure 3.8C) when values increased markedly. This contrasts with a consistent reduction in the dry weight index of the caeca over the same period and is an intriguing result, particularly given the high energy level attained by the caecal material ($\approx$ 31.5 kJ.g^{-1} AFDW) after 20 weeks of starvation.

Large survivors had higher caecal indices than smaller survivors after 10 weeks of starvation (Table 3.16). Throughout the study there was a highly significant SAMPLE effect ($F \approx 15.069$, df=(3,44), $P < 0.001$), with significant decreases between successive samples (Table 3.17 and Figure 3.8D).

Despite elevated weight specific calorific values, contribution of the caeca to the total energy content of the body declined steadily through the course of the starvation period, an effect that was independent of starfish size. This is in keeping with the suggested role of this organ in the storage of energy reserves and implies a progressive resorption of nutrients from the caeca during the period of starvation.

3.3.2.3. Gonad

After 5 weeks of starvation large starfish had higher gonad dry weight indices (GDWI) than smaller starfish ($F \approx 5.581$, df=(1,13), $P \approx 0.034$). The same relationship was insignificant on all other samples (Table 3.18) and WEIGHT effects were removed when the data were split into the same size classes as used for stomach dry weight indices. The mean gonadal dry weight index showed a significant increase during starvation ($F \approx 10.261$, df=(3,22), $P < 0.001$). *Post hoc* tests indicate that this occurred after 10 weeks of starvation ($F \approx 15.398$, df=(1,22), $P \approx 0.001$) (Table 3.19 and Figure 3.9A).

Gonadal water content was independent of starfish size but varied significantly between samples increasing after 5 weeks but decreasing after 10 weeks of starvation (Table 3.20 and Figure 3.9B).

Neither WEIGHT nor SAMPLE influenced gonadal calorific value ($F \approx 1.658$, df=(1,43), $P \approx 0.205$ and $F \approx 1.717$, df=(3,43), $P \approx 0.177$, respectively) (Table 3.21 and Figure 3.9C), which remained relatively stable at $\approx$19 kJ.g^{-1} AFDW.

Gonadal calorific indices were higher for larger starfish from SAMPLE B (F≈5.220, df=(1,12), P≈0.041) (Table 3.22). Weights were recoded into three classes to remove all within–cell WEIGHT effects leaving both SAMPLE and SIZE as significant factors (F≈4.395, df=(2,39), P≈0.019, and F≈5.578, df=(2,39), P≈0.007, respectively) (Table 3.23). Large starfish showed no change in gonadal calorific index, but medium sized starfish showed significant increases (F≈4.860, df=(2,11), P≈0.031) after 5 weeks (F≈6.507, df=(1,11), P≈0.027). Small starfish showed significant increases too (F≈15.640, df=(3,17), P<0.001), but not until 10 weeks into the starvation experiment (F≈31.899, df=(1,17), P<0.001) (Figure 3.9D).

Size dependent increases in gonadal dry weight indices were noted during the starvation period, while calorific value per gram was insensitive to either prolonged starvation or SIZE effects. These trends can be interpreted as indicating either active partitioning towards reproduction during the course of the experiment, or at least a maintenance of prior gonadal levels in the face of volumetric and energetic reductions in other compartments. The latter scenario is unlikely for two reasons: a) in the examination of biometric relationships it was concluded that shrinkage of individuals was less significant to the overall decline of starfish sizes than selective mortality of larger starfish, thus an increase in the GDWI is likely to represent a true increase rather than reductions in other compartments as a consequence of shrinkage, and b) gonad indices increase by a factor of between 5 and 10. If this had been due entirely to shrinkage then other compartments would have to have been reduced by a similar factor, a condition that was not observed. Thus, the observed increases represent growth of the gonads throughout the starvation period.

3.3.2.4. Body wall

Regression coefficients for the dry weight index of the body wall (BDWI) versus W indicate that the relationship approaches significance for SAMPLE A, is significant on SAMPLE C, but is insignificant on SAMPLE B and D (Table 3.24). SIZE and SAMPLE are significant (F≈4.493, df=(2,41), P≈0.017 and F≈14.874, df=(2,41), P<0.001, respectively) when data are recorded for three size classes (Table 3.25). LARGE starfish showed a significant increase in body wall dry weight index in the first five weeks of starvation (F≈6.698, df=(2,11) P≈0.013) as did small starfish

($F \approx 7.710$, df=(3,19), $P \approx 0.001$). MEDIUM sized starfish showed no change (Figure 3.10A).

Water content of the body wall was independent of size, but mean values varied significantly throughout the study ($F \approx 8.735$, df=(3,48), $P<0.001$) (Table 3.26 and Figure 3.10B). In the first 5 weeks the water content of the body wall decreased significantly, but increased thereafter.

Large, unstarved starfish had higher body wall calorific values than smaller unstarved starfish, ($F \approx 4.449$, df=(1,43), $P \approx 0.041$) a trend that was not evident for subsequent samples (Table 3.27). SIZE was not significant when analysed as two weight classes, but mean values varied significantly ($F \approx 8.472$, df=(3,44), $P<0.001$). *Post hoc* effects tests indicate a significant decrease in body wall calorific value after 10 weeks of starvation ($F \approx 5.553$, df=(1,44), $P \approx 0.023$) (Table 3.28 and Figure 3.10C). This is consistent with the hypothesis that energy reserves in the body wall are consumed, resulting in a higher proportion of skeletal material to tissue (dry weight indices) and a lower portion of energy per unit volume of the body wall (calorific value).

After 10 weeks of starvation, large starfish had lower body wall calorific indices than small starfish, a trend not evident at later stages of starvation (Table 3.29). In a two–factor analysis of variance utilising two size classes, significant variation in mean calorific index was noted ($F \approx 6.629$, df=(3,44), $P \approx 0.001$). The calorific index increased, independently of size, in the first 5 weeks of starvation ($F \approx 9.396$, df=(1,44), $P \approx 0.004$) (Table 3.30 and Figure 3.10D). This trend mirrors that of the dry weight index, both of which increase by slightly more than 10%. There was no significant change in the calorific value per gram in the first five weeks, thus it is likely that the changes in the calorific indices at that time simply mirror those changes in the dry weight indices.

3.3.3. Macroscopic changes to organ compartments

A great deal of time was spent observing and dissecting starfish throughout the starvation period. As a consequence of those observations it was possible to describe changes to the macroscopic appearance of starfish organs. Starfish in the first sample were dissected immediately after their collection from Pelorus Island and it was assumed that the characteristics displayed by the majority of starfish from that sample represented the state of healthy organs. Throughout this exercise notes were made only to describe starfish that differed from the norm. Table 3.31 summarises observations on the appearance of specific compartments of unstarved (presumed "healthy") starfish and those of starfish that appeared to have deteriorated dramatically in condition (presumed "unhealthy"), the latter being particularly common towards the end of the study.

3.3.3.1. Unstarved starfish

Sixteen starfish were dissected at the commencement of this work, and in four of these the pyloric caeca were discoloured. Whilst the caeca of other starfish were a uniform fawn (creamy brown) colour, the caeca of these four starfish had a mottled appearance, with small patches of dark brown tissues dispersed randomly among the paler caecal lobes. The degree of discolouration varied between starfish, with three showing only slight discolouration while the fourth showed very obvious changes. In the last starfish, the finely striated appearance of the caecal lobe tissue was absent, and most lobes were a uniform dark brown colour. The appearance of these caeca was intermediate between those described as healthy and unhealthy in Table 3.31.

3.3.3.2. Changes after 5 weeks

When 15 starfish were dissected after five weeks of starvation, four were noted to have discoloured caeca. Three showed only slight discolouration but caecal discolouration of the fourth was obvious. The latter starfish also had discoloured gonads, which were light brown in appearance rather than the usual pale creamy colour.

3.3.3.3. Changes after 10.5 weeks

Of the 14 starfish dissected after 10.5 weeks of starvation, one appeared to be normal but the remaining 13 had one or more compartments that had apparently deteriorated.

In three starfish only one organ was affected. In two of these the caeca were slightly discoloured and in the third the stomach was a little softer than usual. Eight starfish had two organ compartments which were affected – discolouration of the caeca was noted in all, but in five the skin was also weak, two had soft stomach tissues and one had discoloured gonads. In two of these the caeca were both discoloured and soft.

One starfish had three affected organs – caeca were discoloured, the skin was soft and the stomach weak.

In the worst affected starfish the caeca were discoloured, the skin was soft, the stomach weak and the gonads, in addition to being pale brown, appeared to be structurally degenerating, with a general softening of the tissue and a mucus–like surface film blurring the distinction between individual tufts on the gonadal lobes..

3.3.3.4. Changes after 22 weeks

Only six starfish remained alive in the final sample. None appeared to be healthy and all appeared to be stressed by high water temperatures in the holding-tanks caused by a pump malfunction the previous day. Organ conditions were readily interpretable as indicative of poor health in four severely affected starfish. Most aboral spines consisted of only the pedicel ossicle. Intact spines were typically bent, or, if pushed over intentionally, then failed to become erect. Pedicel ossicles could be grasped with forceps and easily torn from the surrounding skin, which was very soft. One starfish, with a ruptured body wall, lost several rays as it was removed from the holding tank.

The caeca of most of these starfish were not just mildly discoloured, but a dark brown colour with reddish tinges to some lobes. Caeca were short and thin relative to the rays of the starfish, and most caeca had degenerated structurally to the point where an attempt at their removal resulted in fragmentation.

Gonadal material in severely affected starfish consisted of very small lobes, each of which were dark brown in colour and appeared to be suffering structural breakdown – lobe and tuft structures were replaced by a dark brown gelatinous mass. However, it was noteworthy that the gonads of two surviving starfish appeared quite normal and healthy, even after 22 weeks of starvation.

The stomach of severely affected starfish was typically a brown or grey colour, tore easily when grasped with forceps and appeared to be producing an excess of mucus, again giving it an almost gelatinous appearance.

These observations suggest a hierarchy of partitioning whereby nutrients are withdrawn first from the caeca, then the body wall, the stomach, and finally the gonads. Figure 3.11 summarises the changes evident during starvation and suggests a general order in which organs became affected. The appearance of compartments did not change appreciably until approximately 10.5 weeks of starvation, when ≈85% of the sample had affected caeca. On this occasion the body wall ranked second, with 50% of the sample showing deterioration. Deterioration of stomach condition ranked third most common (36% affected). Very few starfish (14%) had gonads that were affected. By 22 weeks of starvation all starfish showed affected caeca and stomachs, 87% had affected body walls and 67% had affected gonads.

Despite a relatively consistent change in the macroscopic appearance of compartments, there was no significant correlation between caecal calorific value (kJ.g^{-1} AFDW) and appearance. Calorific values actually increased over the study period, even though the total energy of the caeca decreased. It may have been desirable to test for correlation against total energy of the caeca.

3.3.4. Oxygen consumption

Figure 3.12 depicts the relationship between the natural logarithms of oxygen consumption and whole wet weight throughout the starvation experiment. Both SAMPLE and ln(WEIGHT) had a significant effect on oxygen consumption ($F \approx 3.275$, $df=(3,46)$, $P \approx 0.029$ and $F \approx 44.043$, $df=(1,46)$, $P<0.001$, respectively). There was no detectable change in the first 10 weeks of starvation, but consumption declined after that ($F \approx 7.599$, $df=(1,46)$, $P \approx 0.008$) (Table 3.32). Figure 3.13 demonstrates a regression equation fitted to all data from the first 10 weeks, and a visual inspection indicates that the mean value for SAMPLE D starfish (approximately 1150g wet weight and 17.3ml O_2 h^{-1}) is approximately 5ml O_2 h^{-1} lower than previous values.

3.4. Discussion

3.4.1. Maximum period of starvation

Prior to this work there were four published observations of the effects of long term starvation upon *Acanthaster planci*: Chesher (1969a) noted a 10% reduction in the diameter of a 90mm starfish that had been starved for 3 months, Pearson and Endean (1969) noted that a starfish caged without food for four months remained alive and appeared to be healthy, Okaji (1989) noted maintenance of the gonad at the expense of the caeca over a 90 day period, and Cheney (1974) reported resorption of gonads after one month of starvation. This study suggests that *A. planci* can survive acute starvation for up to 5 months. Several unpublished observations (Moran, *pers. comm.*; Lucas, *pers. comm.*; Peckham, 1984; Trott *pers. comm.*; Stump *pers. comm.*) support these data. In contrast to many other asteroids and echinoderms, *A. planci* has limited ability to withstand starvation. *Patiriella regularis* survived 44 weeks of starvation (Crump, 1971), *Pisaster ochraceus* for 21 months (Feder, 1970), *Asterias rubens* for 12 to 18 months (Vevers, 1949) and *Astropecten irregularis* for 14 months (Feder and Christiansen, 1966). This may be due in part to the relatively high specific metabolic rate of *A. planci*, which varies according to size, but averages approximately 20 μl 0_2 g^{-1} (wet weight).h^{-1} (Peckham, 1984; Yamaguchi 1974b). Rates quoted for most temperate asteroids fall in the range 2.2 to 27 μl 0_2 $g^{-1}.h^{-1}$ (Lawrence and Lane 1982). The inability of *A. planci* to withstand starvation reflects a point made by Birkeland and Lucas (1990) – *A. planci* needs to maintain a high rate of food intake to offset costs associated with its rapid growth rate, high fecundity and multiarmed morphology.

Of great significance to the ecology of *Acanthaster* is the finding that starvation responses are size-specific, both in terms of mortality and shrinkage, and that alternative food sources may contribute significantly to maintenance requirements in times of low food availability. Thus, large starfish (greater than ≈380mm diameter) shrink and die within two to three months, whilst small starfish (less than ≈380mm diameter) may survive for more than 5 months with little change in size. In fact, small starfish continued to grow in size in the first five weeks of starvation, while larger starfish were shrinking, and even after 10.5 weeks of starvation remained larger than they had been at capture (Figure 3.4). The potential for similar trends in wild populations limits meaningful interpretation of size/frequency distributions.

The tendency for large starfish to be more susceptible to starvation may result simply from biomass considerations – large starfish require a great deal more energy for maintenance than do smaller starfish. When deprived of coral, they may utilise alternative food sources, thereby avoiding starvation or prolonging the starvation period. Evidence for this was found in the "feeding scars" evident on turf algae growing on the walls of the holding tanks. Feeding scars were not analysed to determine changes in turf algae composition or density, but algal feeding has been observed for *A. planci* in other studies. Adults have been observed feeding on coralline algae (Barham *et al.*, 1973) and on fleshy algae (Dana and Wolfson, 1970; Vine, 1972). Juveniles maintained on algae (Lucas, 1984) grew no more than 20mm – an indication that *A. planci* has difficulty gaining energy from this source.

While asteroids are in general carnivorous, many regularly feed on particulate organic detritus and some species feed on living or decaying plants (Jangoux, 1982). Araki (1964) examined feeding characteristics of *Patiria miniata*, an asteroid that appeared to commonly feed on algae and had previously been described as "largely vegetarian". Araki found that most algae were not degraded, but rather, *P. miniata* scavenged organic debris. Four *Patiria* maintained in running seawater without a macroscopic food supply for 18 months showed no external indications of ill-effects, (and may have even grown in size), although their caeca and gonads were emaciated. The only food sources available were dissolved and very fine organic particles (Araki, 1964). It is likely that *A. planci* "feeding scars" on the algal turf may have been related to uptake of organic detrital films rather than turf algae *per se*.

Echinoderms can uptake dissolved organic matter (DOM) across the external epidermis of the body wall (Bamford,1982). DOM has been shown to supply up to 79% of the energy requirements of larvae of the echinoid *Strongylocentrotus purpuratus* (Manahan *et al.*, 1983), and 50% of the maintenance requirement for juvenile *S. purpuratus* living near a sewage outfall (Clark, 1969). DOM uptake has been indicated for adult *Henricia sanguinolenta* and *Asterias rubens* (Pequingnat, 1972), *Dendraster excentricus* (58% of material for aerobic respiration; Stephens *et al.*, 1978) as well as *Lytechinus variegatus, Arbacia punculata, Mellita quinquiesperforata* and *Ophiophragmus filograneus* (37%, 11%, 25% and 19% of aerobic respiration, respectively; Ferguson 1980, 1982a, b). Lawrence (1987a) indicates that these values may even underestimate actual levels because they did not account for the potential uptake of fatty acids or sugars. Lawrence (1987b) suggests that external DOM uptake may free many structures from dependency on other food sources. Clearly, if *Acanthaster* has similar capabilities, the effects of severe starvation could be substantially mitigated by the uptake of DOM.

3.4.2. Macroscopic changes in appearance

Observations made throughout the period of enforced starvation suggest that there is a gradual but consistent change in the macroscopic appearance of starfish organ compartments that is related to the health of starving starfish. Whilst extreme changes in organ appearance (e.g. structural disintegration) were readily interpretable as indicators of poor health, many subtle changes (e.g. changes in the colour of organs) were not. However, the progressive nature of the changes that occurred, when interpreted in parallel with mortality and shrinkage, indicate a gradual transition from a state of good health to a state of poor health (Figure 3.11).

It is appropriate to note that these changes did not happen simultaneously, or even in the same sequence, in all starfish. Whilst general trends were evident, the organ compartments always exhibited a wide range of macroscopic characteristics at any one time. This is logical, since condition is likely to reflect the recent feeding history of individual starfish in the weeks or months prior to their capture. Some individuals (e.g. the stragglers feeding on remnant patches of coral behind the main group of starfish) are likely to have had fewer opportunities to feed and would therefore have had fewer stored energy reserves. Those that had been consistently feeding *ad libitum* (e.g. those at the advancing edge of the main feeding front) are likely to have had greater stored energy reserves. The former are likely to have displayed signs of ill–health quickly (if they hadn't already been doing so), whilst the latter may have greater stored energy reserves for utilisation, avoiding obvious changes in condition until these reserves began to be depleted.

Table 3.31, contrasting the colour, size, texture and integrity of each compartment of well fed ("healthy") and starved ("unhealthy") starfish , should be useful to future researchers wishing to make rapid field assessments of the condition of *A. planci.*

Changes in the macroscopic appearance of organ compartments were consistent with measured changes in biometry and organ indices reported above. When taken together, it would appear that the pyloric caeca, which has a known role as an energy reservoir in echinoderms (Voogt *et al.*, 1985), is the first compartment from which stored reserves are drawn. The trend from slight discolouration through to a very dark brown colour and ultimately to structural degeneration parallels the consistent decrease in the dry weight and calorific value indices of this organ. Energy reserves are drawn from the body wall throughout the starvation period and changes in the appearance of the body wall often followed changes in the appearance of the caeca. Changes in the appearance of the stomach manifest themselves at a similar time, although index data suggests that this does not happen until late in the starvation process. The gonad, which seemed to be the most resilient organ in its appearance, was the only organ which increased in both size and calorific value throughout the period of starvation.

3.4.3. The compartmental priority system

In various studies of echinoderms, the caeca, stomach, body wall and gonads have each been implicated as reservoirs of energy in times of food limitation (3.1). The priority system for mobilising nutrients from some organs in preference to the others can provide indications of that animal's survival strategy. Figure 3.14 (total energy of each compartment through time, derived from the mean values for dry weight index, calorific value and ash content[6]) demonstrates that changes in stomach and gonad parameters, while sometimes dramatic for each organ *per se*, had little effect on the gross dynamics of energy partitioning. Similarly, the marked changes in dry weight index and calorific value of the body wall are barely evident in terms of the redistribution of energy within the entire starfish. By contrast, the only organs that showed marked variations in total energy content were the pyloric caeca.

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[6] Calculated mean values per dissected sector were multiplied by an overall average for (W / [combined wet weight for each compartment]) to provide an estimate of the total energy for an intact starfish.

Gonadal growth is maintained, albeit at reduced levels, while resorption is occurring from all other compartments. Few starfish showed adverse changes to the gonad and, in these, changes usually occurred only when all other organs had been affected. This experiment represents an extreme case of prioritised gonadal development, for (with the possible exception of particulate films and dissolved nutrients) starvation was both absolute and prolonged. The dramatic changes in organ parameters and macroscopic appearances make it unlikely that starfish could have survived much longer. Thus, these starfish had starved near to death, yet during the starvation period there was (on average) a four–fold increase in the dry weight index of the gonads, with a maintenance of gonadal calorific values. In these circumstances, reproductive effort (the proportion of energy intake allocated to reproduction) was extremely high.

3.4.4. Shrinkage versus size-specific mortality

This work demonstrated that gross changes in the size structure of the sampled population resulted from selective mortality of large starfish even though shrinkage of starfish did result after prolonged starvation. *A. planci* has long been known to shrink in response to starvation, but there has been no prior indication that starvation–related mortality is size specific, and can produce changes in size frequency distributions that appear to be caused by shrinkage.

These findings suggest that alternative interpretations of previous work may be valid. Faced with little evidence of a progression in the modes of size/frequency histograms, several authors have postulated low adult growth rates (Branham *et al.*, 1971; Kenchington, 1977). These situations could equally have been produced by simultaneous growth in lower size classes and progressively higher mortality rates in larger size classes. Anyone attempting to ascertain starfish age distributions from size frequency curves, a technique that has been popular for *A. planci* in the absence of alternate methods (Ormond and Campbell, 1971; Nishihira and Yamazato, 1972; Endean and Stablum, 1973; Ormond and Campbell, 1974; Laxton, 1974), should exercise extreme caution.

Other workers have made anecdotal reference to starfish sizes that are consistent with size specific mortality. Moran *et al.* (1985) noted that the mean diameter of starfish on John Brewer Reef when first measured was 350mm, but 6 months later consisted of two distinct size modes, one at 100mm and one at 300mm. Coral cover in the intervening period decreased from approximately 30–45% to less than 10%. The apparent decrease in mean size of the larger mode may have been a consequence of mortality of large starfish due to food–limitation, or shrinkage, or a combination of both.

3.4.5. Reproductive success during starvation

Lawrence (1973), in studying starving *Luidia clathrata,* noted large differences between compartmental quantity (gravimetrically determined) and quality (biochemically determined). Lipid reserves of the gonads, which appeared to maintain their original size, had decreased significantly. The quantity / quality distinction will be very important for gonadal material, since marked decreases in fertilisation success and larval survival could be expected to result from poor egg quality. In this experiment, there was no decrease in the calorific value of gonadal material concurrent with increases in the gonadal dry weight index and it appears that gonad lipid levels were maintained. Biochemical and histological studies on eggs would need to have been done to determine the precise nature of embryonic reserves, and direct measurements of fertilisation rates made to determine fertilisation success. Unfortunately the failure in the water pumping system that halted this experiment occurred before conspecifics in the field would have spawned. It would have been instructive to have known whether these starfish could have spawned, in what quantities, and whether these gametes were viable at the time of spawning.

Even if successful spawning did not occur, the production of gonads at the expense of other organs during a period of prolonged starvation represents extreme "reproductive effort". *A. planci*, with its high density outbreaks, ability to rapidly deplete its food source, potential to undergo population collapses, and extreme reproductive effort, conforms to the "reckless" reproductive strategy described by Parker and Pianka (1975). High reproductive effort, an evolutionary consequence of rapid population expansion and decline (Parker and Pianka, 1975), supports the assertion that *A. planci* has a natural propensity to outbreak (although this has no bearing on questions relating to severity, frequency or duration of present-day outbreaks).

3.4.6. Respiration rates

Starvation typically has the effect of reducing respiration rates of echinoderms (Farmanfarmaian, 1966). This occurs rapidly in some species (within the first 24 hours of starvation for *Eucidaris tribuloides*; McPherson, 1968), and slowly in others (over three weeks for *Arbacia punctulata*; Boolootian and Cantor, 1965).

The respiration rate of *Acanthaster planci* decreases as a result of starvation. Peckham (1984) noted a decrease after six weeks starvation at 20°C and after four days at 25°C. Yamaguchi (1974b) recorded a reduction but did not specify the timing of onset. In this study a marked decrease was observed after 11 weeks (Figure 3.13), however there is some doubt as to whether this is a direct effect of starvation. The fourth sample was collected one day after a pumping failure that allowed water temperatures to climb and dissolved oxygen levels to drop. Stress resulting from high temperature conditions may have reduced metabolic rates, as has been observed for juvenile *A. planci* from Guam (Yamaguchi, 1974b) and adult *A. planci* from two locations on the Great Barrier Reef (Peckham, 1984).

Giese (1967), who found no variation in the respiration rate of *Strongylocentrotus purpuratus*, may have missed a rapid depression in rates, since his measurement period extended only between days 3 to 40 of the starvation period. Likewise, two respiration studies of *Acanthaster* failed to adequately examine respiration changes in the first 24 hours (Peckham, 1984 and this study) – Yamaguchi (1974b) did not describe this aspect. All three studies were consistent only in that declines were noted. None were able to elucidate the importance of short term and long term changes. In fact, it may be generalised that echinoderm respiration studies have failed to explore the potential for both rapid and long–term responses to starvation, since the monitoring regime of most experiments has precluded both intensive measurements in the first few days and regular measurements until the eventual death of the starfish, a period that could extend to at least 12 to 18 months in many echinoderms.

Table 3.1 Mean, (standard error) and range of diameters (D:mm) for starved A. *planci.*

Period of starvation (weeks)	SAMPLE	Mean	(SE)	range
0	A	397	(10)	320–470
5	B	394	(7)	360–450
10.5	C	357	(7)	320–410
22	D	342	(7)	320–360

Table 3.2 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between ln (**whole wet weight**:g) and ln(**diameter**:mm) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.821	16	<0.001
5	B	0.889	14	<0.001
10.5	C	0.741	15	0.002
22	D	0.074	6	0.889

Table 3.3 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between ln (**underwater weight**:g) and ln(**diameter**:mm) for starved A. *planci.*

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.687	16	0. 003
5	B	0.767	14	0. 001
10.5	C	0.708	15	0. 003
22	D	0.490	6	0. 324

Table 3.4 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between ln (**whole wet weight**:g) and ln (**underwater weight**:mm) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.761	16	0. 001
5	B	0.858	14	<0. 001
10.5	C	0.911	15	<0. 001
22	D	0.894	6	0.016

Table 3.5 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between the stomach dry weight index (%) and weight (W:g) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.568	6	0.022
5	B	0.143	15	0.611
10.5	C	0.054	15	0.849
22	D	0.644	6	0.168

Table 3.6 Mean and (standard error) of the stomach dry weight index (%) for starved *A. planci.* Data have been recoded for starfish size. NA , No data available.

		SIZE Class	
Period of starvation (weeks)	SAMPLE	SMALL	LARGE
0	A	5.9 (0.9)	7.4 (0.5)
5	B	6.0 (0.6)	5.9 (0.4)
10.5	C	5.4 (0.3)	5.8 (0.3)
22	D	3.6 (0.2)	NA

Table 3.7 Mean and (standard error) of the water content (%) of the stomach of starved, *A. planci.*

Period of starvation (weeks)	SAMPLE	mean	(SE)
0	A	80.4	(0.2)
5	B	82.0	(1.3)
10.5	C	81.6	(0.1)
22	D	79.3	(0.3)

Table 3.8 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between the stomach calorific value (kJ.g^{-1} AFDW) and weight (W:g) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.204	16	0.449
5	B	0.001	14	0.998
10.5	C	0.302	14	0.293
22	D	0.048	4	0.952

Table 3.9 Mean and (standard error) of stomach calorific values (kJ.g^{-1} AFDW) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	mean	(SE)
0	A	20.5	(0.2)
5	B	20.1	(0.2)
10.5	C	21.0	(0.3)
22	D	21.4	(0.6)

Table 3.10 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between the pyloric caeca dry weight index (%) and weight (W:g) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.313	16	0.238
5	B	0.272	15	0. 326
10.5	C	0.672	15	0. 006
22	D	0.355	6	0.491

Table 3.11 Mean and (standard error) of pyloric caeca dry weight index (%) for starved *A. planci.* Data have been recoded for starfish size. NA , No data available. Overall means and standard errors for each sample are included.

Period of starvation		SIZE class			
(weeks)	SAMPLE	SMALL	MEDIUM	LARGE	TRIP means
0	A	22.4 (1.8)	20.4(1.6)	25.4 (1.8)	22.6 (1.1)
5	B	16.1 (2.1)	16.8 (1.2)	17.2 (1.6)	16.7 (1.0)
10.5	C	11.8 (0.9)	13.7 (0.7)	16.1 (2.0)	13.6 (0.8)
22	D	8.3 (0.6)	NA	NA	8.3 (0.6)

Table 3.12 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between the pyloric caeca water content (%) and weight (W:g) for starved *A. planci.*

Period of starvation (weeks)	r	N	P
0	0.412	16	0.113
5	0.273	14	0.325
10.5	0.392	14	0.149
22	0.854	4	0.031

Table 3.13 Mean and (standard error) of the pyloric caeca water content (%) for starved *A. planci*.

Period of starvation (weeks)	SAMPLE	mean	(SE)
0	A	73.7	(1.3)
5	B	74.2	(1.2)
10.5	C	74.8	(1.4)
22	D	69.8	(1.0)

Table 3.14 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between the pyloric caeca calorific value (kJ.g^{-1} AFDW) and weight (W:g) for starved *A. planci*.

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.061	16	0.822
5	B	0.287	14	0.321
10.5	C	0.233	14	0.422
22	D	0.689	4	0.311

Table 3.15 Mean and (standard error) of the pyloric caeca calorific value (kJ.g^{-1} AFDW) for starved *A. planci*.

Period of starvation (weeks)	SAMPLE	mean	(SE)
0	A	26.7	(0.5)
5	B	27.2	(0.5)
10.5	C	27.3	(0.6)
22	D	31.5	(0.5)

Table 3.16 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between the calorific index (%) of the pyloric caeca and weight (W:g) for starved *A. planci*.

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.008	16	0.975
5	B	0.236	14	0.417
10.5	C	0.575	14	0.031
22	D	0.857	4	0.143

Table 3.17 Mean and (standard error) of the pyloric caeca calorific index (%) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	mean	(SE)
0	A	46.6	(1.2)
5	B	39.3	(1.8)
10.5	C	35.0	(1.7)
22	D	29.7	(2.0)

Table 3.18 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between the gonad dry weight index (%) and weight (W:g) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.219	16	0.414
5	B	0.548	15	0.034
10.5	C	0.277	15	0.318
22	D	0.539	6	0.269

Table 3.19 Mean and (standard error) of the gonad dry weight index (%) for starved *A. planci.* Data have been recoded for starfish size. NA , No data available. Overall means and standard errors for each sample are included.

Period of starvation		SIZE Category		
(weeks)	SAMPLE	SMALL	LARGE	TRIP means
0	A	0.6 (0.1)	1.9 (0.4)	1.4 (0.3)
5	B	1.2 (0.3)	1.7 (0.6)	1.4 (0.3)
10.5	C	1.9 (1.0)	3.1 (0.9)	2.5 (0.7)
22	D	6.2 (1.1)	NA	6.2 (1.1)

Table 3.20 Mean and (standard error) of the water content (%) of the gonad for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	mean	(SE)
0	A	81.7	(0.7)
5	B	81.4	(0.7)
10.5	C	84.1	(1.0)
22	D	78.7	(1.1)

Table 3.21 Mean and (standard error) of the calorific value (kJ.g^{-1} AFDW) of the gonad for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	mean	(SE)
0	A	17.7	(0.7)
5	B	19.7	(0.5)
10.5	C	19.2	(0.8)
22	D	19.2	(1.1)
all samples combined		18.9	(0.4)

Table 3.22 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between the calorific index (%) of the gonads and weight (W:g) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.177	16	0.512
5	B	0.551	14	0.041
10.5	C	0.297	14	0.302
22	D	0.471	4	0.529

Table 3.23 Mean and (standard error) of the gonad calorific index (%) for starved *A. planci.* Data have been recoded for starfish size. NA , No data available.

Period of starvation		SIZE class		
(weeks)	SAMPLE	SMALL	MEDIUM	LARGE
0	A	0.9 (0.2)	2.9 (1.0)	2.2 (1.0)
5	B	1.6 (0.5)	3.2 (0.7)	3.5 (2.1)
10.5	C	1.8 (0.9)	9.3 (2.8)	5.3 (2.6)
22	D	10.3 (2.2)	NA	NA

Table 3.24 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between the body wall dry weight index (%) and weight (W:g) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.459	16	0.074
5	B	0.413	15	0.126
10.5	C	0.601	15	0.018
22	D	0.231	6	0.659

Table 3.25 Mean and (standard error) of the body wall dry weight index (%) for starved *A. planci.* Data have been recoded for starfish size. NA , No data available.

Period of starvation (weeks)	SAMPLE	SIZE Class		
		SMALL	MEDIUM	LARGE
0	A	71.5 (2.3)	71.1 (1.8)	64.5 (2.7)
5	B	77.0 (0.3)	75.7 (1.5)	75.0(2.4)
10.5	C	81.7 (1.0)	76.2 (1.8)	75.6(2.1)
22	D	81.9 (1.0)	NA	NA

Table 3.26 Mean and (standard error) of the water content (%) of the body wall for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	mean	(SE)
0	A	76.0	(0.3)
5	B	74.0	(0.5)
10.5	C	75.8	(0.4)
22	D	77.4	(0.5)

Table 3.27 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between the calorific value (kJ.g^{-1} AFDW) of the body wall and weight (W:g) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.523	16	0. 037
5	B	0.162	14	0. 579
10.5	C	0.221	14	0. 449
22	D	0.372	4	0. 628

Table 3.28 Mean and standard error of the body wall calorific value (kJ.g^{-1} AFDW) for each size class, on each trip, including overall sample means. Na , No data available.

Period of starvation (weeks)	SAMPLE	SIZE class		
		SMALL	LARGE	overall mean
0	A	7.1 (0.3)	7.5 (0.2)	7.4 (0.2)
5	B	6.9 (0.2)	7.0 (0.3)	7.0 (0.1)
10.5	C	6.5 (0.2)	6.8 (0.3)	6.7 (0.2)
22	D	5.9 (0.1)	NA	5.9 (0.1)

Table 3.29 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between the calorific index (%) of the body wall and weight (W:g) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	r	N	P
0	A	0.324	16	0. 221
5	B	0.398	14	0. 159
10.5	C	0.598	14	0. 024
22	D	0.171	4	0. 829

Table 3.30 Mean and (standard error) of the body wall calorific index (%) for starved *A. planci.*

Period of starvation (weeks)	SAMPLE	mean	(SE)
0	A	40.3	(1.3)
5	B	47.4	(1.9)
10.5	C	49.0	(2.0)
22	D	51.6	(1.0)

Table 3.31 Characteristic appearance of specific compartments of well fed and starved *Acanthaster planci*.

Organ compartment	General state of starfish well fed (healthy)	 starved (unhealthy)
Stomach	Pale creamy colour. Can be excised intact and rarely tears when grasped with forceps. Membrane structure is distinct and tissues are relatively free of mucus.	Brown or greyish in colour. Tears easily when grasped with forceps. Membrane structure is indistinct and there is often an excessive production of mucus.
Pyloric caeca	Occupies most (up to 80%) of the length, and fills ≈50% of the cross-sectional area of the ray. Fawn colour with fine, pale striations on the surface of the caecal lobes. Can be removed intact if grasped with forceps at the proximal end.	Mottled brown colour ranging to very dark with red patches in extreme cases. Reduced in size to half (or less) of the length of the ray, and in width to <10% of the cross-sectional area of the ray. Disintegrates when forceps are used to remove it from the ray.
Gonad	Pale yellow colour with distinct tufts clustered in separate lobes. Distinction between males (creamy white colour) and females (pale yellow with larger lobes) becomes noticeable as spawning season approaches. Tufts and lobes can be readily removed from the body wall with forceps.	Tuft and lobe structure becomes indistinct. Males and females cannot be distinguished. Shrunken gonads become brown and gelatinous in appearance. Tufts disintegrate and adhere to the inner body wall when their removal is attempted.
Body wall	Spines intact and robust, quickly becoming erect after being depressed. Pedicel ossicles are difficult to pull from the body surface when they are grasped with forceps. Body wall will rupture after starfish is removed from the water, but this generally takes more than 5 seconds. The aboral body surface is relatively thick and firm and cuts cleanly with a sharp scalpel.	Spine ossicles frequently missing. Spines usually droop and fail to become erect when intentionally depressed. Pedicel ossicles are easily torn from the body wall. Body wall ruptures easily and quickly when the starfish is removed from the water. Aboral surface is thin and soft, and cannot be cut (even with a fresh scalpel) without tearing the tissue laterally for several centimetres.

Table 3.32 Regression coefficients (r), number of observations (N) and probability (P) of "nil effects" for the regression between ln(OXYGEN CONSUMPTION) and ln(WEIGHT) for starved *A. planci*.

Period of starvation (weeks)	r	N	P
0	0.822	16	<0.001
5	0.523	14	0.045
10.5	0.730	14	0.003
22	0.615	4	0.194

Figure 3.1 Whole wet weight frequency distributions for *A. planci* sacrificed after 0 weeks (SAMPLE A), 5 weeks (SAMPLE B), 10.5 weeks (SAMPLE C) and 22 weeks (SAMPLE D) of starvation.

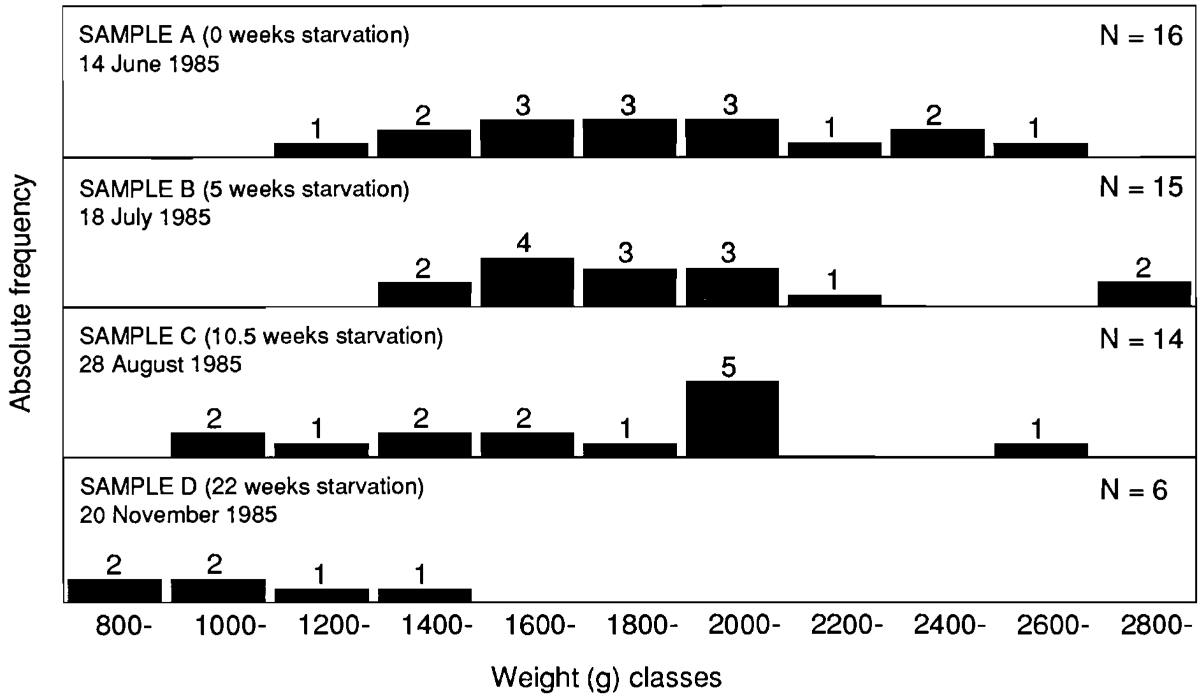


Figure 3.2 Changes in the mean diameter (D: mm) of *A. planci* sacrificed after 0 weeks (SAMPLE A), 5 weeks (SAMPLE B), 10.5 weeks (SAMPLE C) and 22 weeks (SAMPLE D) of starvation. Significant changes between successive samples are shown with a bold line.

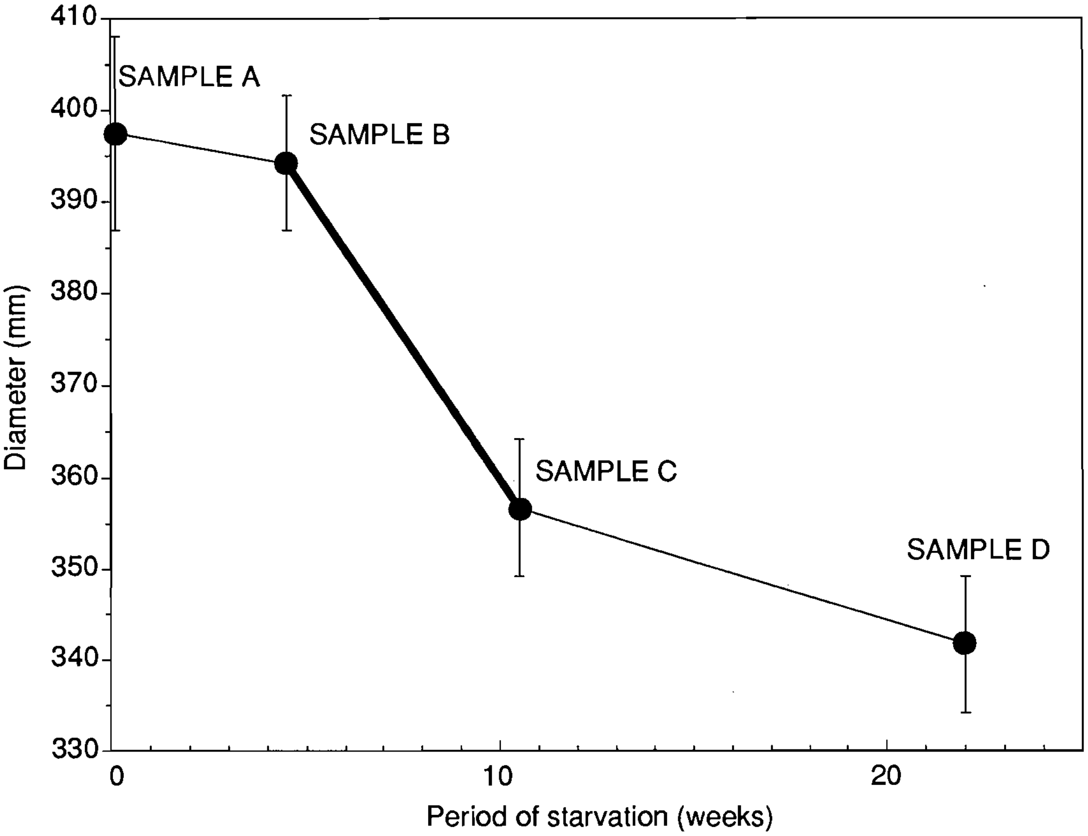


Figure 3.3 Change from initial diameter (ΔD) versus initial diameter ($D_{initial}$) for *A. planci* sacrificed after 5 weeks (SAMPLE B) and 10.5 weeks (SAMPLE C) (data are presented only for starfish that were positively re-identified).

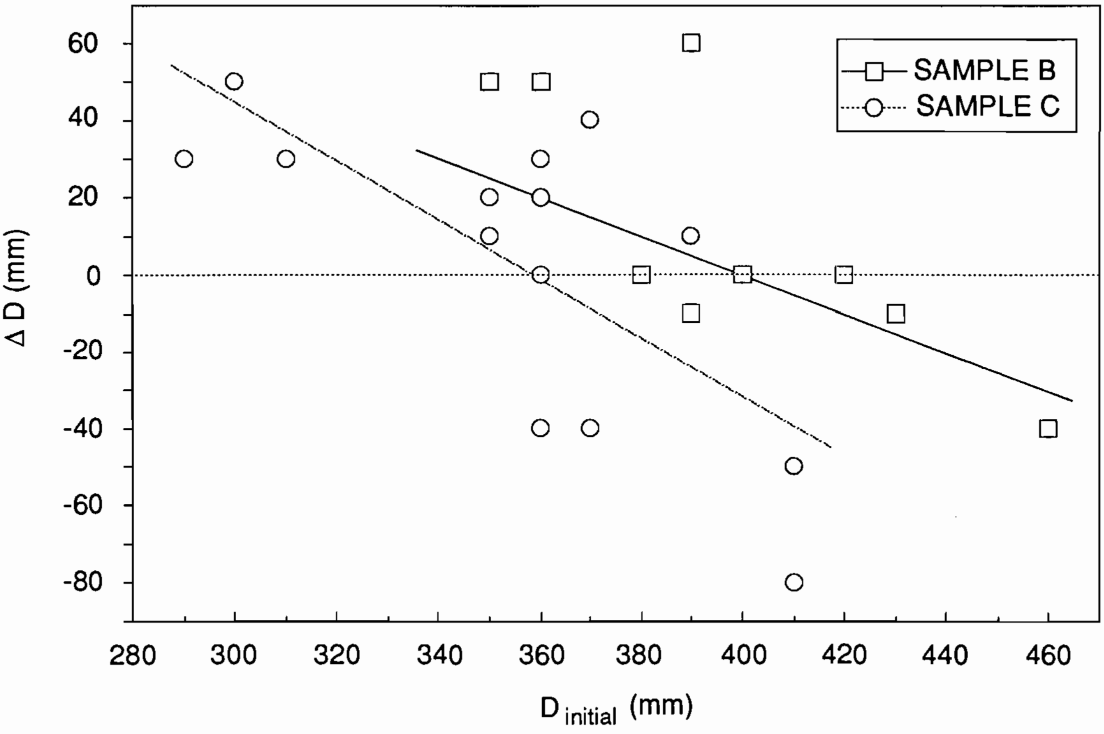


Figure 3.4 Estimated change in diameter (ΔD) versus period of starvation for *A. planci* of 350 and 410mm initial diameter ($D_{initial}$) after 5 and 10.5 weeks of starvation. Error bars indicate standard errors.

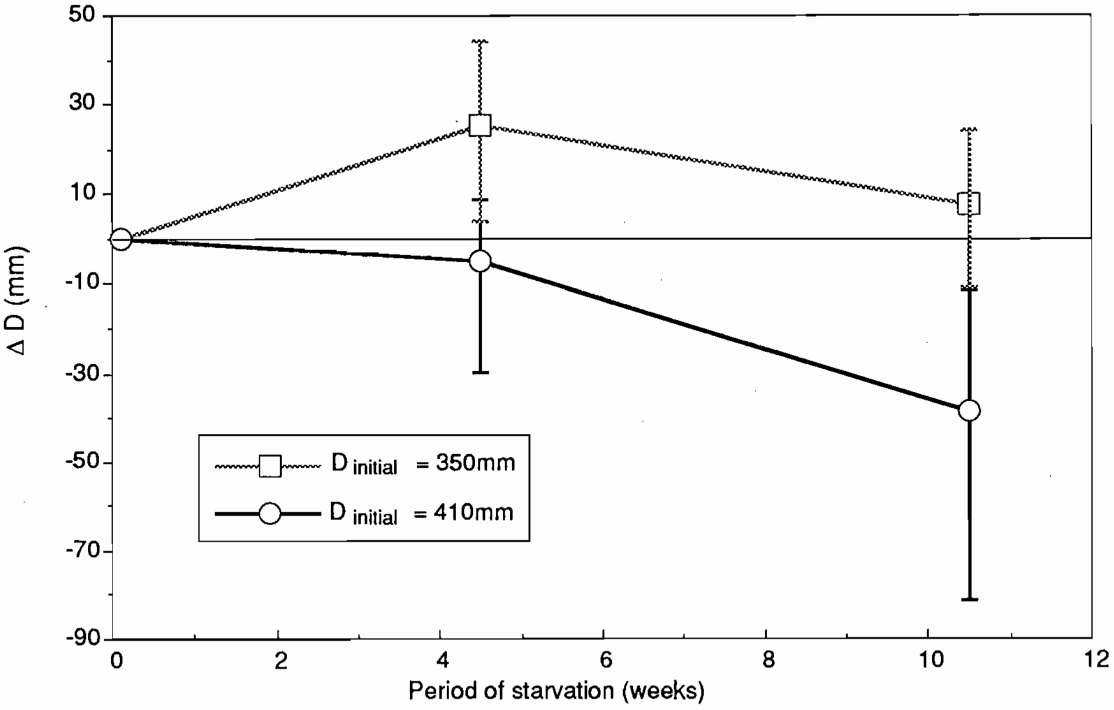


Figure 3.5 The relationship between ln (underwater weight) (U:g) and ln (whole wet weight) (W:g) for *A. planci* after 0 weeks (SAMPLE A), 5 weeks (SAMPLE B), 10.5 weeks (SAMPLE C) and 22 weeks (SAMPLE D) of starvation.

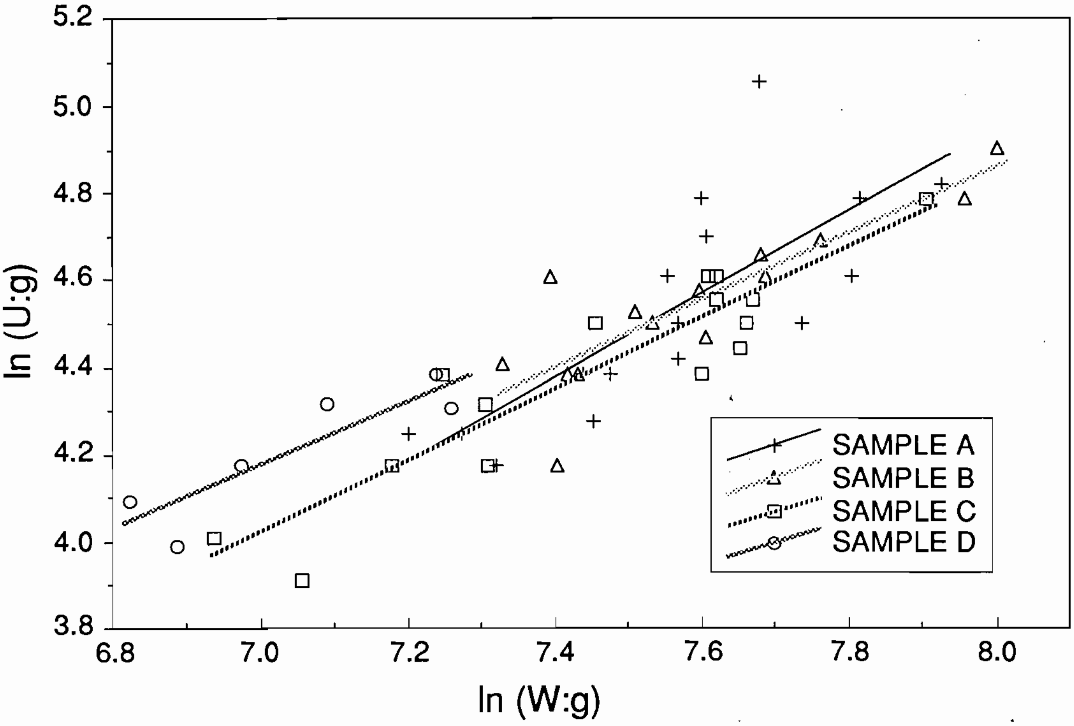
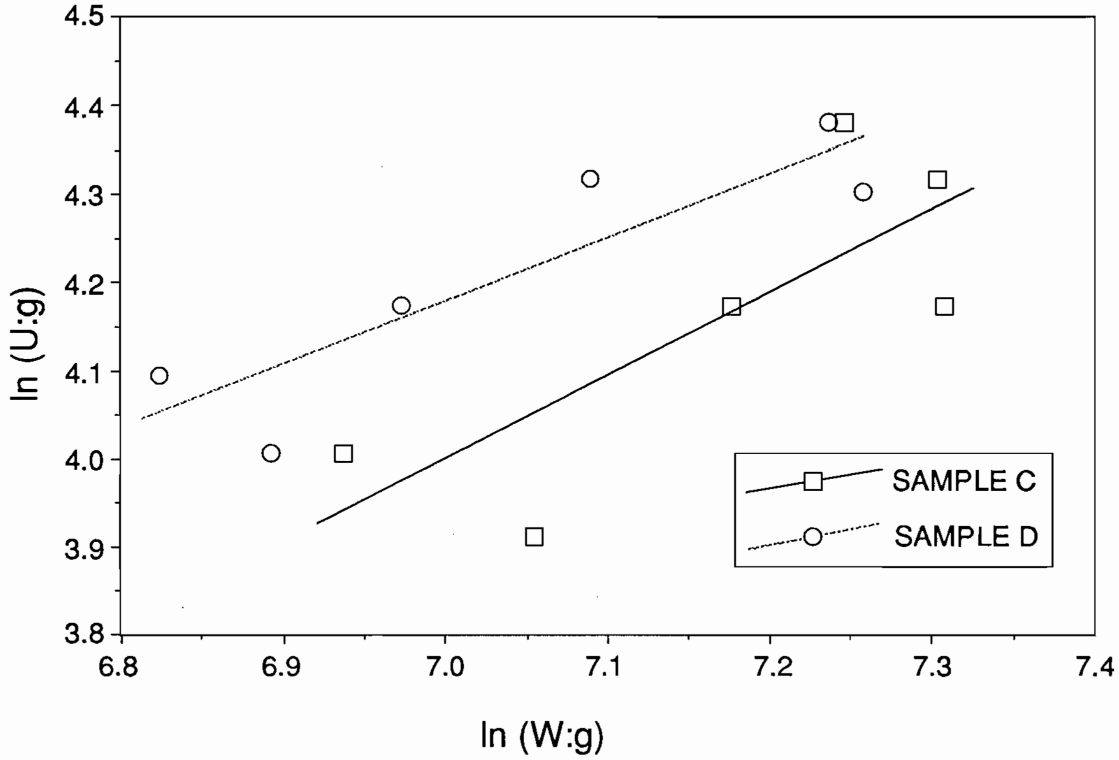


Figure 3.6 A comparison of the relationship between ln (underwater weight) (U:g) and ln (whole wet weight) (W:g) for small *A. planci* (W range: 920 to1640g) after 10.5 weeks (SAMPLE C) and 22 weeks (SAMPLE D) of starvation.



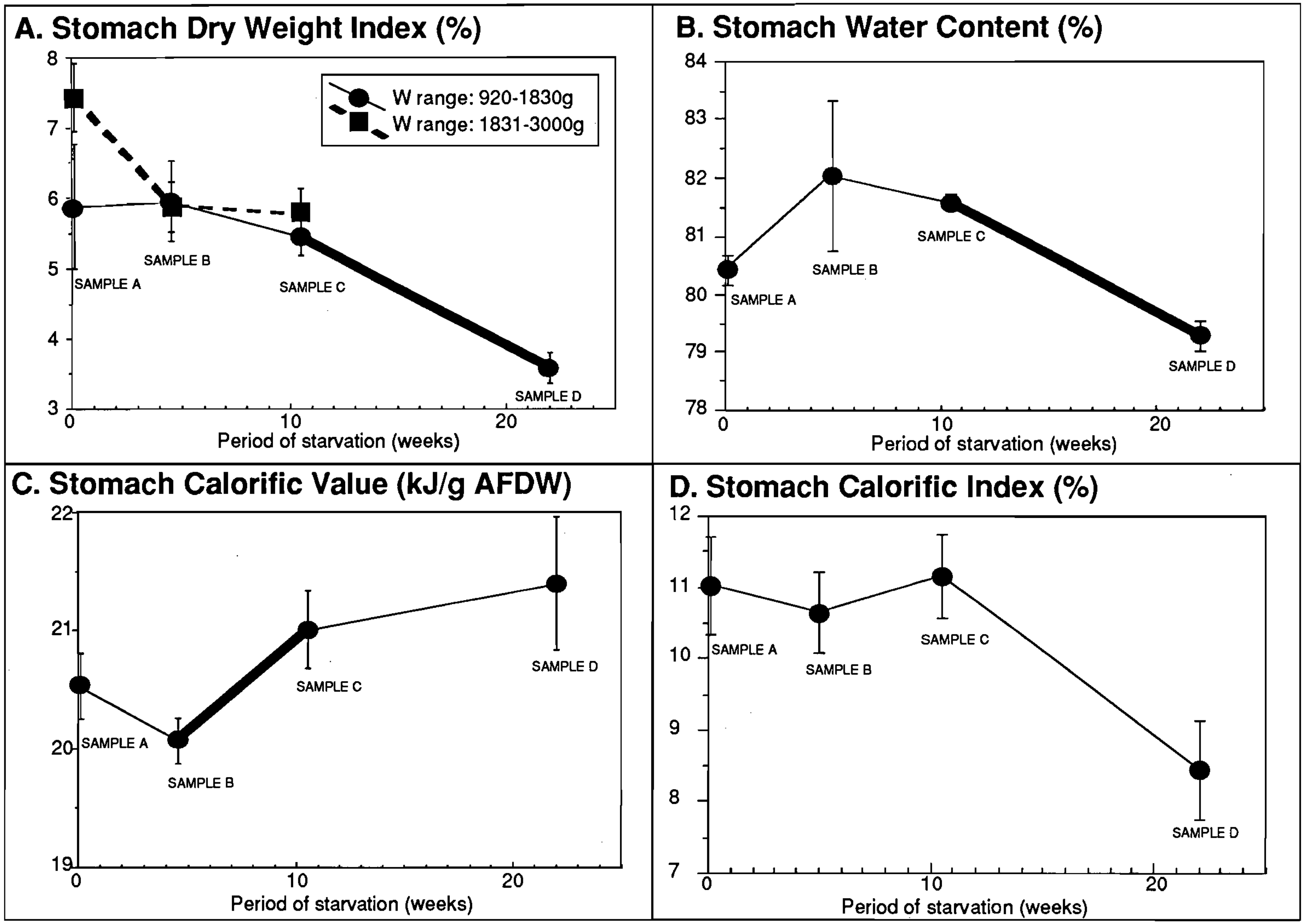


Figure 3.7 Effect of starvation upon the **stomach** of starved *A. planci*: (A) Dry Weight Index (%); (B) Water Content (%); (C) Calorific Value (kJ.g^{-1} AFDW) and; (D) Calorific Index (%). Standard errors are indicated and significant effects between successive samples are shown in bold.

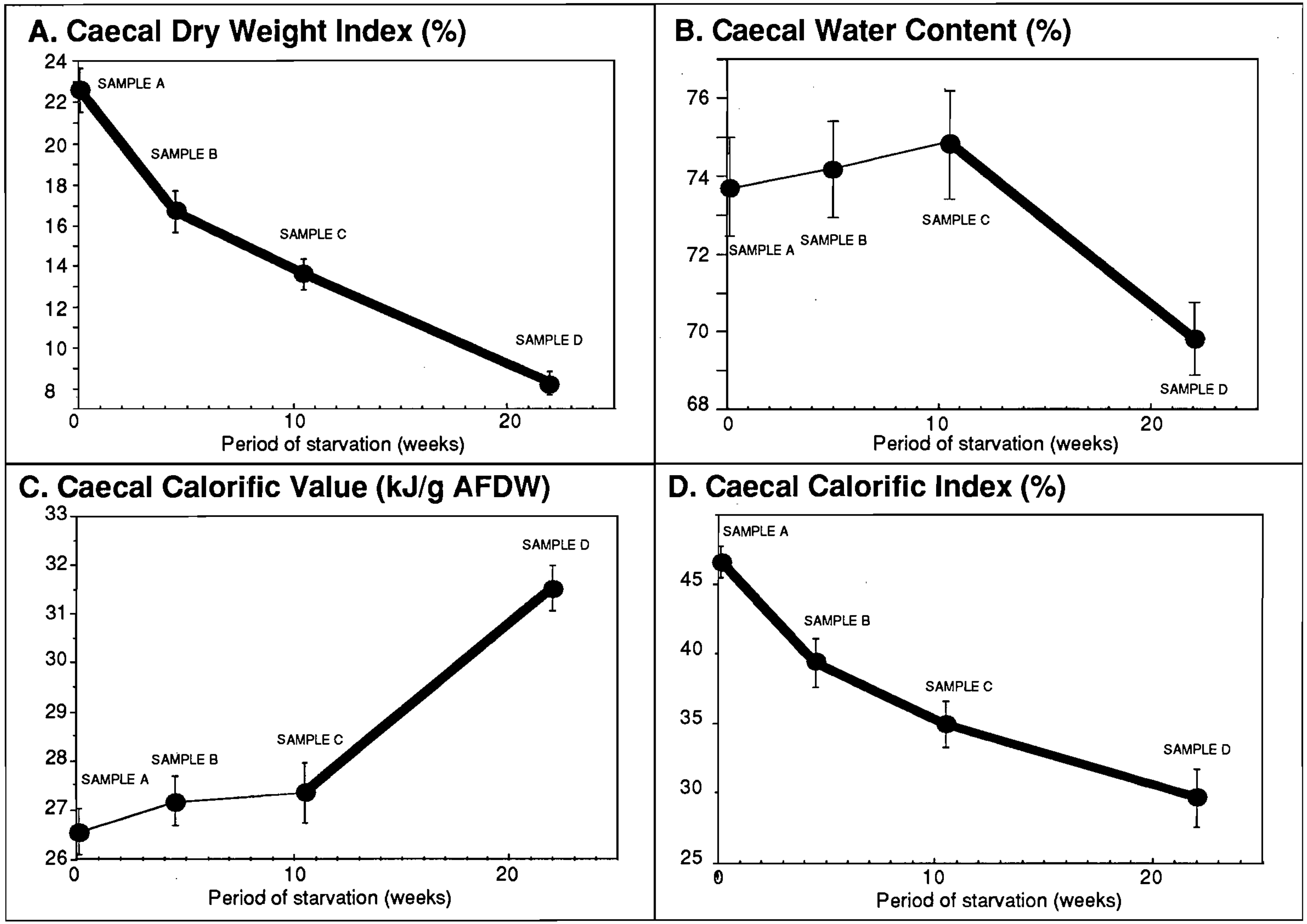


Figure 3.8 Effect of starvation upon the **pyloric caeca** of starved *A. planci*: (A) Dry Weight Index (%); (B) Water Content (%); (C) Calorific Value (kJ.g^{-1} AFDW) and; (D) Calorific Index (%). Standard errors are indicated and significant effects between successive samples are shown in bold.

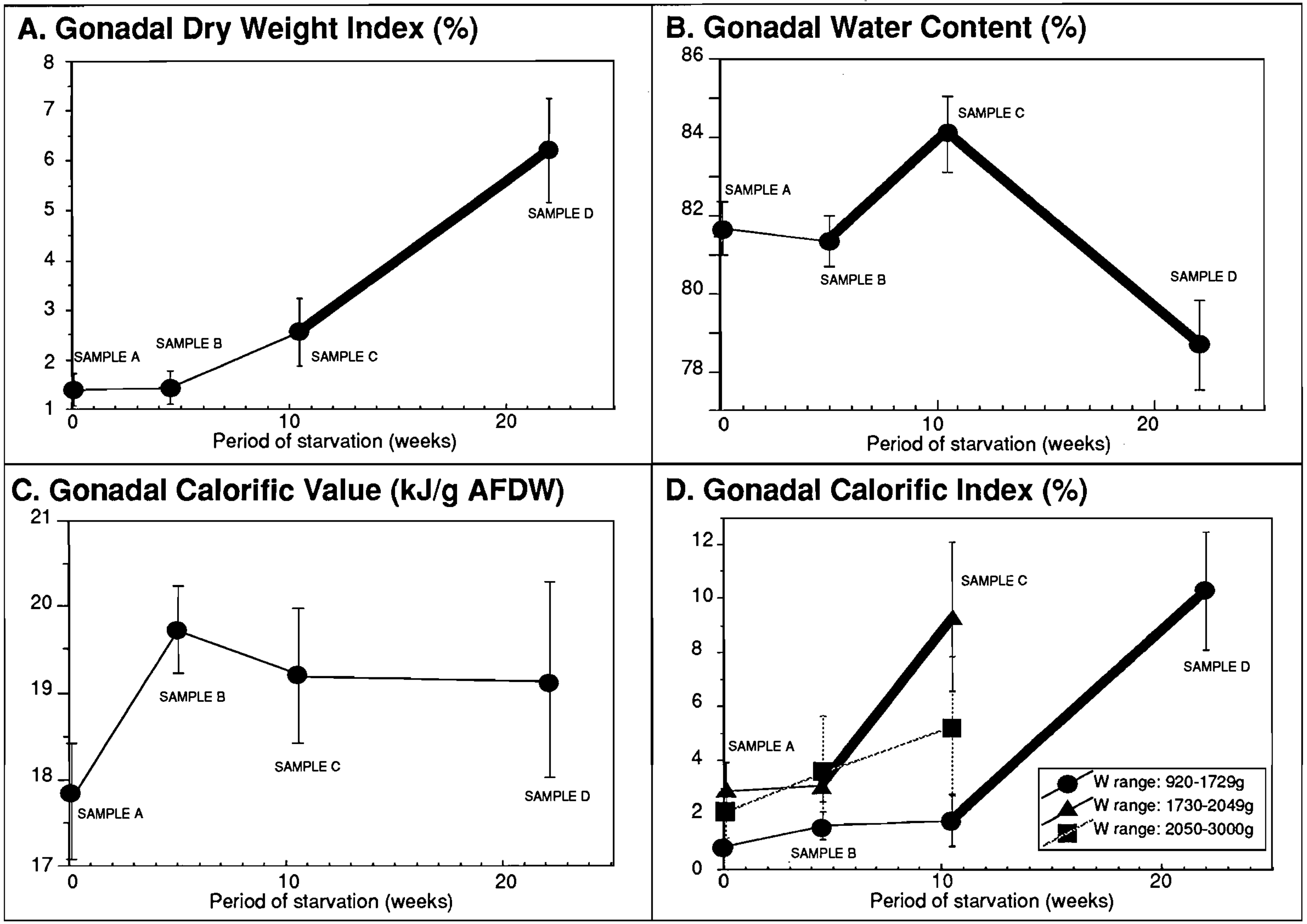


Figure 3.9 Effect of starvation upon the **gonads** of *A. planci*: (A) Dry Weight Index (%); (B) Water Content (%); (C) Calorific Value (kJ.g^{-1} AFDW) and; (D) Calorific Index (%). Standard errors are indicated and significant effects between successive samples are shown in bold.

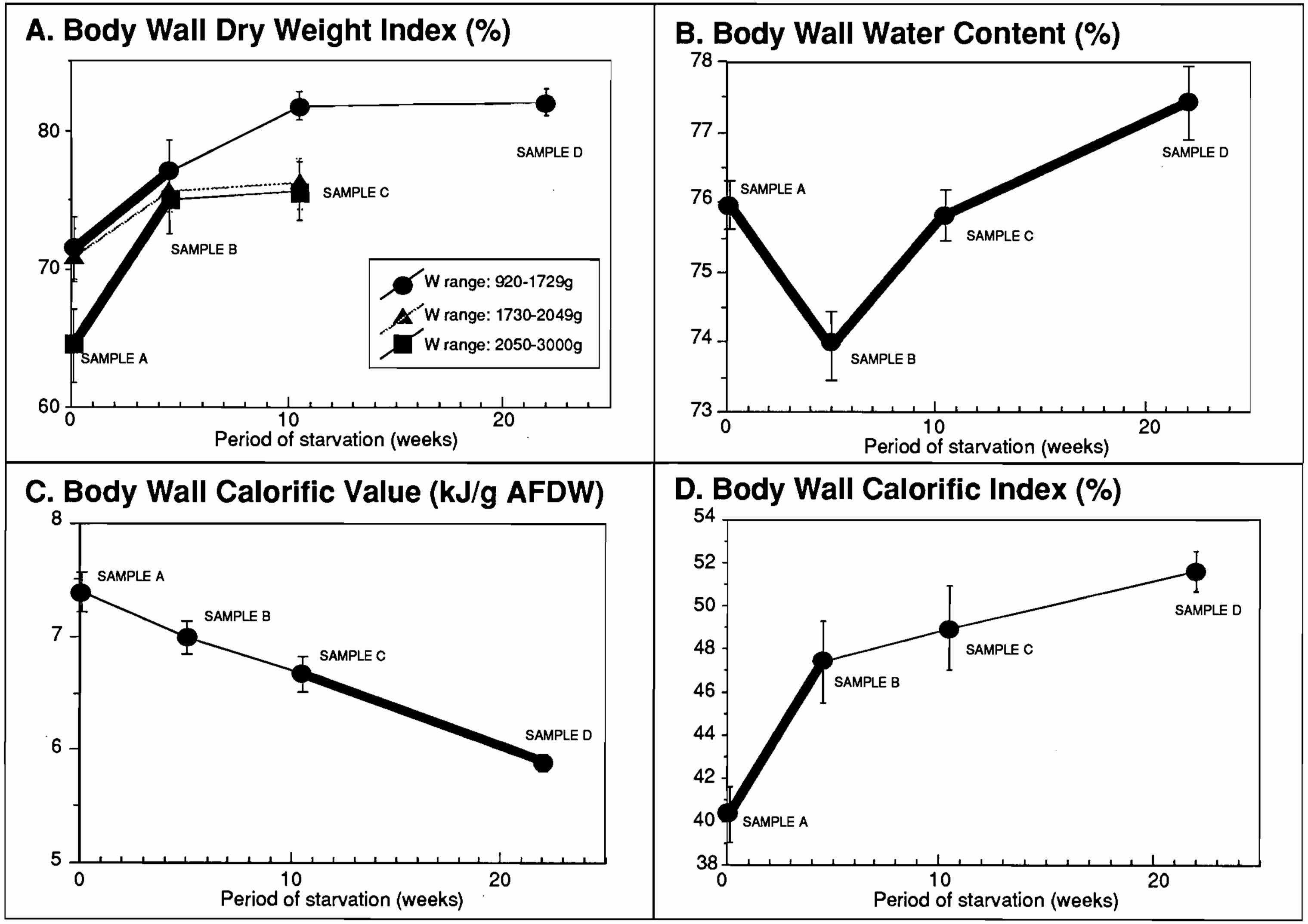


Figure 3.10 Effect of starvation upon the **body wall** of *A. planci*: (A) Dry Weight Index (%); (B) Water Content (%); (C) Calorific Value (kJ.g^{-1} AFDW) and; (D) Calorific Index (%). Standard errors are indicated and significant effects between successive samples are shown in bold.

Figure 3.11 Percentage of starved *A. planci* showing deterioration in the macroscopic appearance of the stomach, caeca, gonad and body wall throughout a 22 week period of starvation.

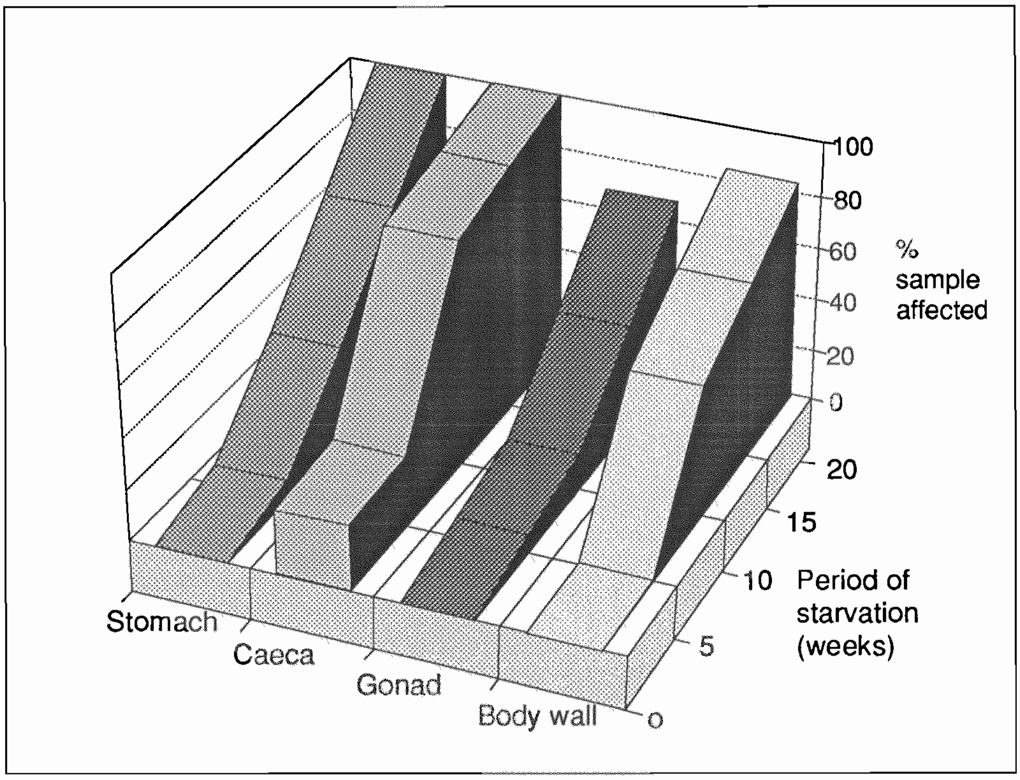


Figure 3.12 Effect of ln (weight:g) upon ln (oxygen consumption:ml O_2hr^{-1}) of *A. planci* after 0 weeks (SAMPLE A), 5 weeks (SAMPLE B), 10.5 weeks (SAMPLE C) and 22 weeks (SAMPLE D) of starvation.

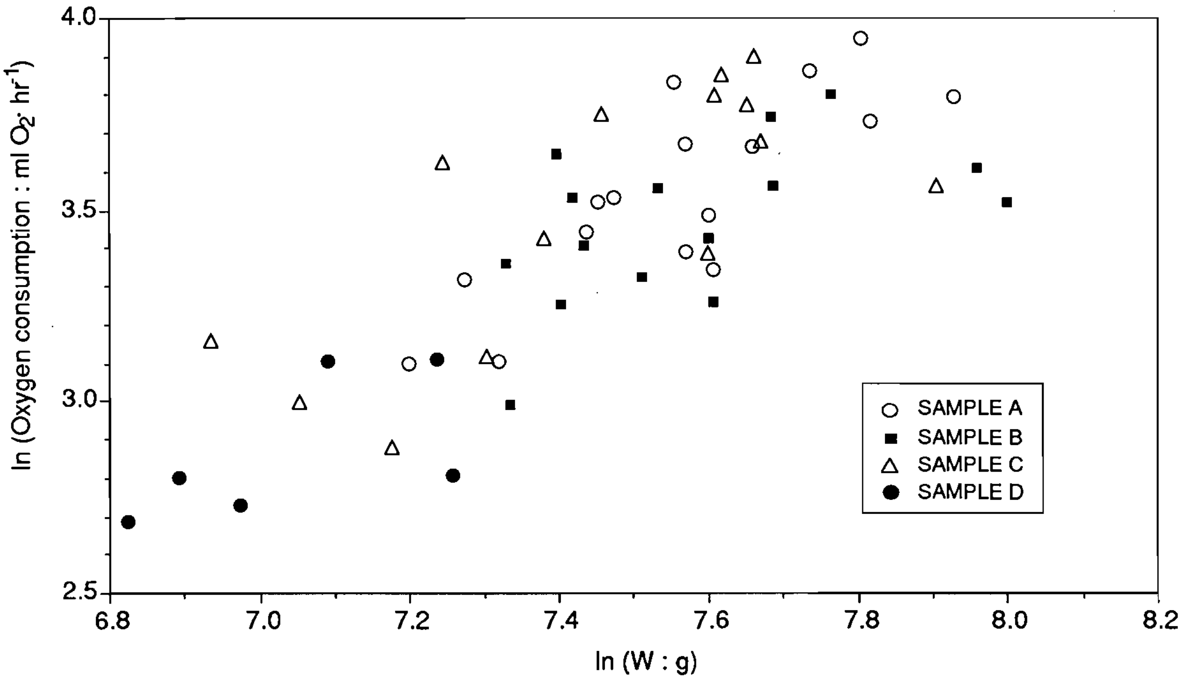


Figure 3.13 Effect of prolonged starvation on the relationship between ln (whole wet weight:g) and ln (oxygen consumption:ml O_2hr^{-1}) for *A. planci*. Open circles represent starfish starved for not more than 10.5 weeks, closed circles represent starfish starved for 22 weeks. Note that SAMPLE D data cannot be described by a significant regression (Table 3.3).

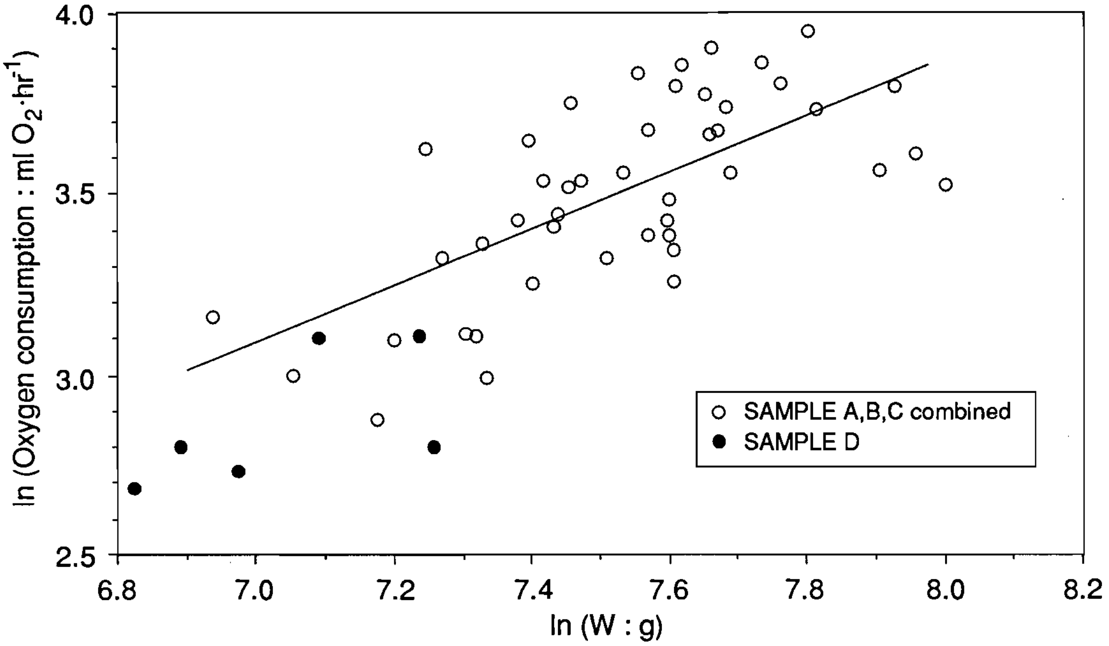
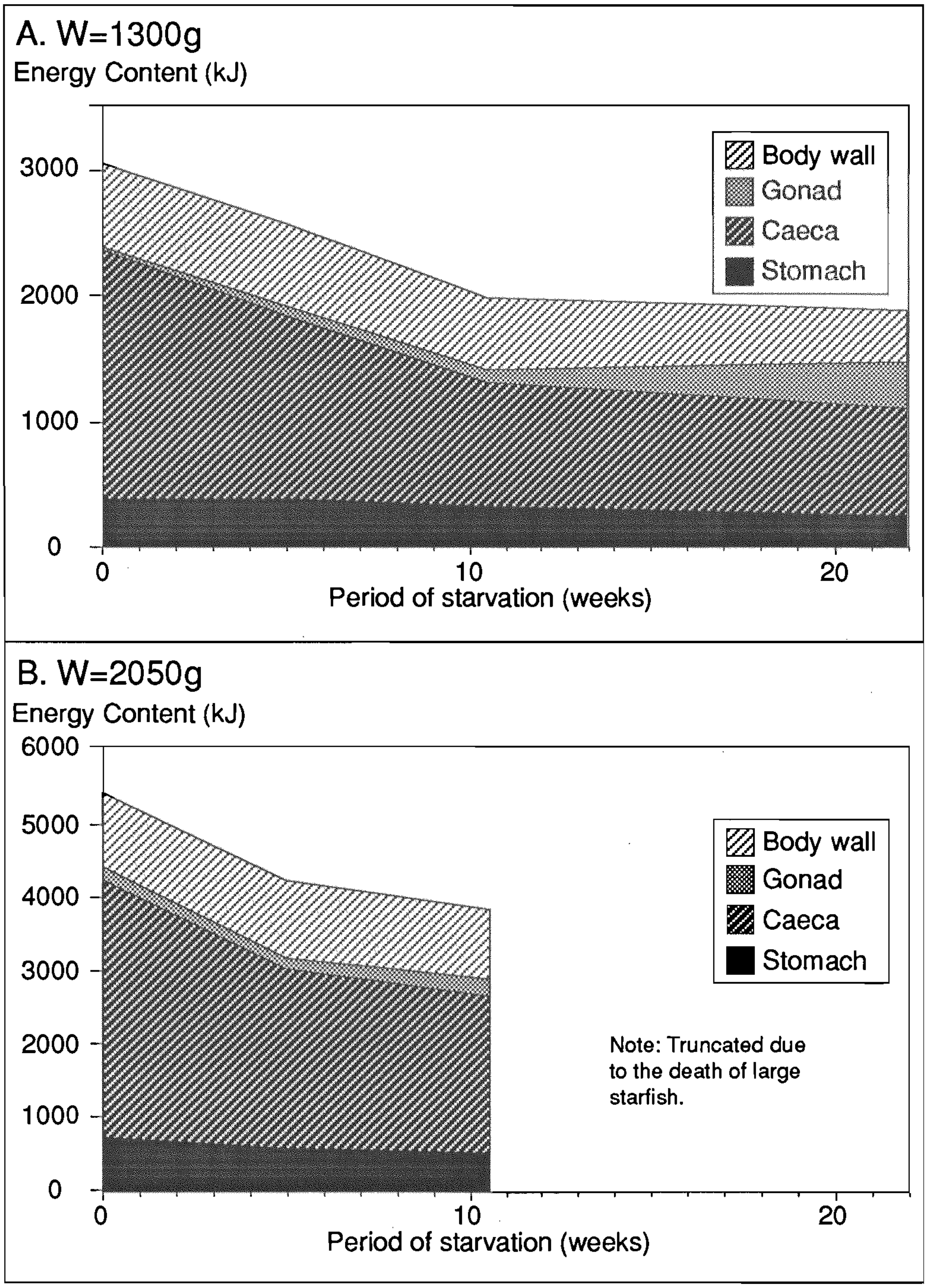


Figure 3.14 Effect of starvation upon the energy content (kJ) of whole SMALL (W≈1300g) and LARGE (W≈2050g) starved *A. planci*. Estimates are derived from mean values for organ dry weight indices and calorific value found elsewhere in this Chapter.



4. Variations in biometric relationships and compartmental indices of an outbreak population

4.1. Introduction

The object of the work described in this chapter is to examine the variation in some of the biometric and physiological parameters of *A. planci* throughout the course of an outbreak cycle on Helix Reef. Previous chapters have examined the effects of size *per se*, and of starvation *per se*, on starfish physiology, and conclusions drawn from those chapters will form the basis for interpreting the observations of a wild population under natural conditions.

4.2. Methods

Helix Reef (Figure 2.1) was selected as the study site in June 1985 when high coral cover and a large number of Crown–of–Thorns starfish were observed. These factors, combined with the relatively small size of Helix Reef, suggested that an outbreak event was beginning and would proceed to completion in a relatively short time.

4.2.1. Sampling regime

The Helix Reef population was sampled in June 1985 and at approximately three–monthly intervals over the subsequent two year period. Sampling ceased in May 1987 when it became difficult to locate sufficient starfish to collect a sample of 50 animals.

On each sampling occasion (unless prevented by weather or time limitations) the perimeter of the reef was surveyed using a manta tow technique based upon that of Done *et al.* (1982). An observer towed behind a vessel at approximately two knots counted the number of starfish seen in consecutive two minute intervals. After surveying the entire reef perimeter in this manner, the observer estimated the damage to coral cover. On most occasions two observers were towed simultaneously with counts and estimates averaged for recording purposes.

Collections on each occasion consisted of the first 50 starfish encountered from the region of the reef supporting the highest density of starfish. Recent recruits (less than 120mm diameter) were excluded[7]. Collections were made by hand to minimise damage to starfish, which were transfered immediately to seawater–filled containers while awaiting measurement on board the research vessel.

4.2.2. Field and laboratory measurements

Starfish were measured for diameter, underwater weight and whole wet weight using the techniques described in Chapter Two.

The incidence of damaged rays was established by recording the number of missing rays, rays of 1/4 length, 1/2 length, 3/4 length, and intact rays (Figure 4.1). "Arm spine length" (ASL) was recorded as the mean length of several of the longest spines (spine ossicle and pedicel ossicle on which it articulates) above the surrounding aboral (dermal) surface.

Starfish were dissected and subsequently analysed as previously described (2.2). Experience gained after dissecting 50 starfish (June 1985 sample) and throughout the starvation experiment (Chapter Three) suggested that starfish condition might be reflected in the macroscopic appearance of the various compartments. Notes were made during subsequent dissections of the qualitative appearance of each compartment (stomach, caeca, gonad, body wall and spines) so that relationships between macroscopic appearance and physiological condition could be examined. Each compartment was categorised as being of poor, fair or good condition. This categorisation follows the tabulated descriptions from Chapter 3 (Table 3.31).

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[7] Starfish with D less than 120mm were found occasionally, but were consistently excluded from the sample.

4.2.3. Long term data storage

Field and laboratory data sheets, including strip recordings from ballistic bomb calorimetry, have been retained and are presently archived at James Cook University. Data have been entered into dBASE databases, the structure and content of which are described in Appendix A. Copies of these databases are held by the Department of Zoology at JCUNQ, by the author and by the author's supervisor, Associate Professor John Lucas.

4.2.4. Statistical analysis

Statistical analysis of this data set proceeded in a format typical of analysis of covariance with two variations: a) the standardising techniques of Packard and Boardman (1987) were used in cases where size confounded interpretation, and b) seasonal and longer term variations in this two year data set were analysed by nonlinear regression. Figure 4.2 and its explanation (below) have been included to minimise the subsequent requirement for repetition in describing the results. All analyses were undertaken with the microcomputer-based statistical analysis package "SYSTAT"®

4.2.4.1. Terminology employed in analysis

Discussion of statistical analysis is facilitated throughout this chapter by the use of upper case nouns (SIZE, TRIP and TIME) to describe the parameters used in statistical models. Comparisons between different field collections are initially examined on a nominal scale by considering collections as a series of ordered, discrete, but otherwise unrelated "TRIPs". "SIZE" effects are examined for each TRIP by regressing dependent parameters against independent SIZE measures, usually the whole wet weight of starfish. TRIP is therefore the covariate when comparing the slope of these regressions between the various TRIPs.

The true temporal relationships between TRIPs were examined only after significant differences between successive TRIPs were elucidated. "TIME" is the continuous variable embodying not only the ordered sequence of discrete TRIPs, but the true temporal relationships between those TRIPs (TIME was set equivalent to "months since 1/1/1985" to facilitate plotting). This chapter examines changes in a population over a two year period and thus it is valid to attempt to interpret temporal variations. It is not valid to examine temporal effects *per se* beyond differences between successive TRIPs if a sequence of measurements does not extend more than twelve months (e.g. the starvation study of Chapter Two) since there is no possibility of distinguishing between seasonal and non–seasonal trends.

4.2.4.2. Data verification and treatment of outliers

Data verification began with the plotting of all parameters versus size, from which obvious outliers were visually identified. Outlier values were checked against raw data sheets and those that appeared correct were removed from the analysis only if they represented extreme deviations from overall trends (the assumption being that data sheet values had originally been incorrectly transcribed). Data were then submitted to an analysis of outliers by studentised residuals (available in the SYSTAT® package). These outliers, which were not evident by visual inspection, were verified against raw data but not excluded.

4.2.4.3. Homoscedasticity

Parameters were plotted against size (whole wet weight) after the removal of positively identified outliers, to ascertain visually that variance was uniform over the range of the independent variable. In several cases (specifically gonadal dry weight, gonadal dry weight index and gonadal calorific index) there was an obvious tendency for residuals to increase with increasing size. Size effects were examined for successive 600g weight classes. Standard deviations were approximately proportional to mean values, indicating that a logarithmic transformation ($X'=\ln(X+1)$) was desirable (Zar, 1984).

Analyses of heteroscedastic data sets were subsequently performed on transformed data and the results were reverted to natural units for interpretation in the following manner;

$$\bar{X} \approx \exp(\bar{X}') - 1$$

and

$$SE \approx \exp(\bar{X}' + SE') - \exp(\bar{X}')$$

where the superscript $'$ indicates transformed values.

Reverted means and standard errors determined in this manner are biased estimates of the true mean and standard error. The above method provides a more conservative estimate than the alternative of subtracting the transformed error from the mean.

Variations in the slope of "parameter versus SIZE" relationships of various TRIPs can not be tested on transformed data since the SIZE range of starfish on each occasion varies greatly – towards the end of the study, the largest starfish were approximately one third the weight encountered in the first few collections. When these distributions are log-transformed, slope values increase markedly due to the curvilinear nature of the logged relationship.

4.2.4.4. Analysis of covariance

In cases where results were homoscedastic and did not require log transformation, homogeneity of slopes was examined by testing the significance of the interaction term (SIZE by TRIP) with the Multivariate Generalised Linear Hypothesis (MGLH) module in SYSTAT®. Heterogenous slopes were examined further with multiple slope comparisons (refer 4.2.4.6). Homogenous slopes permitted an analysis of covariance with TRIP (a nominal scale variable equivalent to sample number) as the treatment and SIZE (whole wet weight) as the covariate. There are four possible outcomes to this test: a) neither factor is significant, in which case the gross mean of the dependent variable must be reported; b) SIZE is significant but TRIP is not, in which case the regression of independent variable versus SIZE is reported; c) TRIP is significant but SIZE is not, in which case variations in standardised mean values between TRIPs can be further examined (see below); or d) both TRIP and SIZE are significant, in which case the parameter versus SIZE relationship for each TRIP is reported before standardising to a mean SIZE (see below) and comparing means between TRIPs.

4.2.4.5. Standardising to remove confounding size effect

Packard and Boardman (1987) recommend adjusting values of the variable of interest to a standard size if the size range is inconsistent across several data sets. In this study, an analysis of covariance could not proceed beyond simultaneously examining the significance of the variable of interest and the covariate (unless there was no significant relationship between dependent and independent variable), because the size range of starfish varied markedly between successive TRIPs.

The Packard and Boardman technique is only valid when the size ranges for the various occasions overlap, since it is unwise to extrapolate any regression beyond the range of the independent variable. Furthermore, caution must be exercised as the distributions of the independent variable become more disparate. "Standardised" values are more sensitive to errors in slope estimates when distributions have only a small overlap. In this study, the size range of the various samples always overlapped (4.3.4), but the degree of overlap was only slight, particularly on latter trips.

Significant SIZE effects were obvious on only a few of the eight sampling occasions. Standardising was only necessary for those particular occasions when a significant SIZE effect was evident. The standardised data set was subsequently examined with a one way analysis of variance where mean values were tested for differences between samples.

4.2.4.6. Multiple comparisons of slopes

Tukey tests were used to determine similarities between slope coefficients when several samples had significant but dissimilar slopes. A mean slope was determined for each group of similar data sets using the equation

$$\hat{b} = \frac{\sum_{i=1}^{k} (\Sigma xy)_i}{\sum_{i=1}^{k} (\Sigma x^2)_i} .$$

4.2.4.7. Seasonal and long–term effects

All analyses to this point have considered time effects only in terms of differences between specific samples. At this point of the analysis, it is desirable to consider TIME as a continuous variable and to examine for seasonal and longer term trends.

The sampling period on Helix Reef extended from June 1985 until May 1987, a period encompassing almost two years. In hypothesising a statistical model to fit these data, it is reasonable to expect both annual variations (perhaps related to seasonality in breeding or to water temperature) and longer term variations (perhaps related to ageing of the population or to starvation effects becoming apparent as coral cover decreased). The latter effect would normally be tested with the linear model $Y = A + (B \times X)$ but the former effect requires a periodic model. The regular periodic cosine function $Y = A + (B \times \cos(\emptyset))$ (where $\emptyset$ represents TIME) was chosen as a general periodic model.

Linear and periodic effects must be examined simultaneously for the analysis to be valid. Figure 4.3 demonstrates the terminology employed to test these effects simultaneously. This model assumes the simplest form of change, a steady drift in the mean value over time. There is no theoretical basis for such an assumption and it is conceivable that some processes would accelerate as coral cover declines. Likewise, the proposed model assumes a regular periodic function when some seasonal fluctuations (e.g. spawning) are unlikely to result in gradual increases and decreases to the mean value. Nonetheless, the sampling regime (8 samples in 2 years) does not justify the use of more complex models.

In the model expression;

$$Y = A + (B \times \cos(X - C)) + (D \times X),$$

the term "A" is the deseasonalised mean value of the dependent variable at the commencement of the study, "B" is the amplitude of the seasonal effect (its displacement either side of the mean), "C" is the offset of the function's seasonal maxima from TIME = 0 (1/1/85) and "D" is the slope coefficient of the longer term effects (the tendency for the mean value to drift over TIME). For convenience, X (TIME) is left as "months since 1/1/1985" and the term (X – C) is multiplied by 0.524 to arrive at an annual seasonality expressed in radians. "C" is therefore the number of the month in which the function is locally maximised (0.5 being equivalent to the middle of January). The range of seasonal variability is twice the displacement from the mean (2 x B) and "D" is the monthly movement in the deseasonalised mean value. Note that a negative B value implies that C is an annual minimum.

The SYSTAT® package NONLIN was used to test the nonlinear model. Analyses were performed using a least squares loss function and a Quasi–Newton minimisation technique. Tolerance levels for convergence were set at 0.1 and starting values for each parameter were found by first analysing mean values only. In all cases the maximum number of iterations was set to 20 and the nonlinear model was deemed inappropriate if no solution could be found within the first 20 iterations. The significance of each of the resulting coefficients was determined by testing their difference from zero with a *t*–test (*t* = coefficient / standard error of the coefficient).

4.3. Results

4.3.1. Population density

Table 4.1 lists the dates of each collection of starfish, along with the total number of starfish observed around the perimeter of the reef and the estimate of the damage to coral cover. Live coral cover is derived from the damage estimate, assuming an initial coral cover of 40% across the entire reef[8]. Starfish were already apparent in high numbers on parts of Helix Reef when this study commenced (June 1985) and population density peaked in October 1985. Numbers declined rapidly after their peak. Coral cover declined markedly in the 11 month period between June 1985 and May 1986.

Figure 4.4 shows the temporal scale of fluctuations in total perimeter starfish count as well as fluctuations in estimated live coral cover throughout the course of this study. The eleven month period from June 1985 to May 1986 included both an increase and rapid decrease in starfish numbers and a significant decline in the amount of live coral cover.

Figure 4.5 depicts the approximate extent of utilisable habitat on Helix Reef, assuming that *A. planci* will be found on all areas from the reef crest to ≈30m depth. This amounts to ≈29ha of utilisable habitat on Helix Reef. The length of the tow path for a typical manta tow was ≈2km. If observers restricted their observations to a band ≈10m wide then they would be counting starfish in ≈2ha (7%) of the utilisable habitat.

Helix Reef differs from many Great Barrier Reefs by having no lagoon and no identifiable back–reef bommie fields (Figure 4.5). As a consequence of its small size, it rarely has poor visibility. The sightability estimates of Fernandes (1989), for manta tow observers restricting their observations to a band 9 to 10m wide in the windward zone with good visibility, suggest that approximately 29% to 36% of starfish in that band are observed[9]. If one assumes a random distribution of starfish throughout the utilisable habitat, then the total population of starfish on Helix Reef at any time is likely to be ≈40 to ≈50 times the total perimeter count.

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[8] This value was obtained by consensus by manta tow observers and divers from the first sampling trip, who made allowance for reef areas (relatively small at that time) where recent *Acanthaster*-related coral mortality was evident.

[9] Alternatively, Fernandes reports that observers see between 1.4% and 10% of the population on an entire reef. This provides a more cautious estimate (with total population between ≈10 to ≈71 times the total perimeter count) but is unlikely to be applicable to this study – the reef slope on Helix Reef was commonly greater than 30m wide, visibility was never poor, Helix Reef has no back-reef bommie fields, the perimeter count integrated ≈2km of tow–path, the same reef was censussed each time and in most cases the count was averaged from the counts of two observers.

Based on the above population multipliers, it would appear that the adult population peaked somewhere between ≈33000 and ≈41000 starfish in late October 1985, but declined within a period of five weeks to between ≈12000 and ≈15000 starfish. In the same period live coral cover fell from ≈36% to ≈20%. On December 12 one week after the latter trip, an additional excursion was made to Helix Reef to collect starfish for fecundity studies. Gonad sizes were noted to be markedly smaller in many animals than during the previous week, suggesting that most of the population had spawned most of their gametes in the intervening week. Thus it appears that the greatest decline in starfish numbers (a reduction of ≈23 500 starfish) occurred **prior** to starfish spawning.

By May 1986, when the perimeter count (147) suggested a total population of ≈6000 to ≈7000 starfish, coral cover had decreased to ≈4%. The rate of decline of coral cover and starfish numbers had begun to stabilise at this point.

Sampling ceased when it became difficult to collect a sample of 50 starfish in the available time. The perimeter count at that time indicated a total population of ≈4000 to ≈5000 starfish.

4.3.2. Distribution

Figure 4.6 (A to F) portrays the distribution of starfish around Helix Reef as determined by each manta tow survey. Initial user-reports and observations by AIMS staff (Moran *pers. comm.* and unpublished data) had suggested that starfish were becoming evident on localised sections of the back–reef (leeward zone, NW sector, Figure 4.5)(Figure 4.6A). On the first trip study, large numbers of starfish were found on the back–reef (mean 43 per two minute manta tow) with highest numbers on the ENE sector (Figure 4.6B). The front of the reef (exposed windward zone, SE sector, Figure 4.5) was unable to be surveyed on this occasion due to rough conditions.

By late October 1985 most starfish (mean 74 per two minute tow) were found on the NNE sector (Figure 4.6C), with a lesser aggregation (mean 43 per two minute tow) diagonally opposite on the down–current SSW sector. In early December (immediately after the apparent decrease in starfish numbers and immediately prior to spawning), the tendency to aggregate in one area became even more obvious, with 60% of the population observed within the NNW sector, an arc approximately one eighth of the entire reef perimeter (Figure 4.6D). Starfish numbers were substantially reduced in May 1986 and starfish were dispersed relatively uniformly around the reef perimeter (Figure 4.6E). Many starfish were seen on the top of the reef rather than the reef slope, as had previously been the case. Little live coral remained on the reef slopes.

The only remaining aggregation of starfish in August 1986 was found in the SSW sector (Figure 4.6F). This was confined to a small area on the reef-top near to the south–west reef crest. Additional manta tows across the reef top revealed that this small pocket contained the only significant area of coral remaining on the reef. Manta surveys were discontinued on subsequent trips, and coral cover and starfish density had decreased by May 1987 to such an extent that sampling was abandoned.

It is clear from these results that the distribution of starfish around the reef varied markedly during the study. There was also a tendency, not evident in the data, for the vertical distribution of starfish to change through time. Starfish did not appear on the reef top in significant numbers until twelve months into the study (May 1986).

4.3.3. Size structure

Figure 4.7 examines changes in the mean diameter, whole wet weight and underwater weight of starfish from Helix Reef through time. Each parameter showed a general tendency to lower values at the end of the study, and in most cases, a tendency towards higher values in November / December each year. However, trends between successive samples were not consistent. These effects were tested with the nonlinear model. Deseasonalised long term declines were significant for each parameter: diameter decreased from ≈360mm in June 1985 to ≈280mm in May 1987 ($D \approx -0.344 \pm 0.040$, $N=350$, $P<0.001$); wet weight from ≈1500g to ≈650g ($D \approx -39.428 \pm 5.685$, $N=380$, $P<0.001$); and underwater weight from ≈75g to ≈45g ($D \approx 0.975 \pm 0.190$, $N=350$, $P<.001$). Similarly, seasonal fluctuations for all parameters were significant: average annual fluctuations in diameter were 20mm ($B \approx -0.966 \pm 0.347$, $N=350$, $P<0.005$); ≈450g for wet weight

($B^t \approx -1.714 \pm 0.746$, $N=380$, $P<0.05$); and $\approx$ 25g for underwater weight ($B \approx -13.170 \pm 2.470$, $N=350$, $P<0.001$). Maximum annual values occurred in mid-December for diameter and whole wet weight ($C \approx -6.725 \pm 1.047$, $N=350$, $P<0.001$ and $C \approx -6.534 \pm 0.521$, $N=380$, $P<0.001$ respectively) and in mid-September for underwater weight ($C \approx 2.307 \pm 0.247$, $N=350$, $P<0.001$).

Figure 4.8 shows the relative frequency distributions for starfish diameter (D), whole wet weight (W) and underwater weight (U) measurements on each sampling period throughout this study. Starfish ranged in size from 140mm to 480mm diameter (smaller starfish were observed infrequently but excluded from the sample) and up to 3100g whole wet weight. There is some suggestion of bimodality in D, W and U distributions in the first sample, but this is not pronounced and does not recur in subsequent samples. Changes in these frequency distributions allow an interpretation of whether starfish might be recruiting, growing, shrinking or dying (assuming samples are randomly drawn from the population): growth should result in consistent increases in D, W and U; shrinkage would decrease W and perhaps D, leaving U unaffected; and mortality of large starfish would cause consistent decreases in D, W and U distributions towards smaller values.

On the basis of these assumptions, interpretation of Figures 4.7 and 4.8 suggests that: a) mortality of large starfish was greatest in the periods December 1985 to February 1986 (14% of sample with $U>100$g no longer present) and August 1986 to January 1987 (20% of sample with $U>90$g no longer present); b) recruitment occurred in the periods December 1985 to February 1986 and December 1986 to May 1987 (% of sample with $U<20$g increased from 2% to 36%); and c) growth of smaller starfish occurred concomitant with mortality of large starfish in the period August 1986 to December 1986 (no change in D, W increased markedly, mean U decreased, U truncated for 10% of the sample with $U>130$g).

4.3.4. Changes in starfish morphology

4.3.4.1. Ray number

Acanthaster planci sampled for this study averaged 15 or 16 rays, although the range of ray number varied from 10 to 20. This falls within the range commonly reported for *A. planci* (Moran, 1986).

During the course of the study, ray number (as distinct from the number of intact rays) varied significantly (F≈2.130, N=392, P≈0.040), increasing between August and December 1986 (Figure 4.9). *A. planci* add rays in the first six months after metamorphosing, and ray number becomes fixed by the time juvenile starfish reach ≈ 10mm in diameter (Yamaguchi 1973a, Lucas 1973). Yamaguchi (*pers. comm.*) indicates that the number of rays regenerated is variable when rays are lost to the disc. The increase in ray number in this study (D range = 140 to 480mm) is therefore unlikely to have resulted from the addition of new rays, but may have resulted from a period of unusually high ray replacement. It is more likely that the increase in ray number represents the appearance within samples of a different subpopulation.

4.3.4.2. Wet weight versus diameter

The theoretical cubic relationship between whole wet weight and diameter provides a reasonable basis for logging both whole wet weight (W), underwater weight (U) and diameter (D) prior to statistical analysis. Logged W and D values were examined for homogeneity of slopes. The relationship varied significantly (F≈2.542, N=390, P≈0.014). Tukey multiple comparisons were made between regression coefficients for each TRIP. These indicated that the slope coefficient for October 1985 was significantly higher than values for all other samples. Mean slopes were b≈2.929 for October 1985 and b≈2.446 for all other samples.

The highest slope coefficient occurred approximately 6 weeks prior to spawning in the first year of the study (October 1985, b≈2.929), by coincidence, the sample upon which SIZE effects were examined in Chapter Two. In October 1985 and August 1986, slopes were not significantly different from isometry (t ≈0.444, N=50, P>0.5 and $t \approx 1.907$, N=49, P<0.10 respectively), but was significantly less than 3 on all other occasions, indicating that Crown–of–Thorns starfish in this study most frequently exhibit allometric growth. Large starfish are usually thinner in the oral – aboral axis.

4.3.4.3. Underwater weight versus diameter

Slopes for the relationship between ln(U) and ln(D) varied significantly over time (F≈6.332, N=390, P<0.001). Tukey tests indicated no change between June 1985 and December 1986 (mean slope b≈2.146), nor between January 1987 and May 1987 (mean slope b≈3.282) but that the latter group had significantly higher slopes than the former. Skeletal content declined with increasing body size during the early stage of this study. Large starfish became more heavily ossified during the latter stages.

4.3.4.4. Spine length versus diameter

SIZE (W) had no effect upon the "arm spine length" versus diameter (ASL/D) ratio (analysis of covariance F≈0.953, N=342, P≈0.122), but mean values varied throughout this study (Figure 4.10). ASL/D increased immediately after spawning (December 1985 to February 1986) in the first year of this study. This coincides with the first period of significant decline in mean wet weight (Figure 4.7). The observed increase is unrelated to changes in mean population size *per se,* since the ASL/D ratio is independent of starfish size. Apparently individual starfish shrank after the 1985 spawning event.

4.3.5. Occurrence of injured starfish

Approximately 27% of the population exhibited ray damage in June 1985 (Figure 4.11). This portion increased throughout the study period, with the exception of one period immediately prior to spawning each year. About 90% of the population showed ray injuries by May 1987. These results are similar, though more pronounced, than those of Nakamura (1986), whose data reveal an increase in injury within a Sesoko Island population, from ≈20% in 1984 to ≈30% in 1986.

The severity of ray injury averaged 3% of the total free ray length for affected starfish in June 1985 (Figure 4.12). Severity averaged 9% by May 1987 – starfish with 15 rays were typically missing the equivalent of 1.35 whole rays. The severity of ray injury varied markedly throughout the study period, but showed no significant long term trend (F≈1.098, N=230, P≈0.273).

4.3.6. Compartmental Indices

4.3.6.1. Stomach

Mean water content of the stomach increased, principally as a result of a marked elevation between June and October 1985 (Table 4.2 and Figure 4.13A). The nonlinear model indicated that seasonal variations were small but significant (≈2%) with annual maxima in December and that the longer term tendency to increase was also significant (≈78% to ≈81%). These changes correspond to an overall tendency for the macroscopic appearance of the stomach to change from being firm with distinct membranous structure to being weak, losing its distinct membranous structure and producing excessive mucus (4.3.9). The long term increase in water content may therefore reflect the loss or weakening of structural materials and/or the increase in mucus production evident as overall condition declined.

The overall mean slope for stomach dry weight versus whole wet weight is ≈0.00738. Seasonal trends were insignificant but the mean value for a 1100g starfish declined from ≈9.5g to ≈7.9g throughout the two year study period. Most of this decrease is attributable to a decline that occurred between February and August 1986 (Table 4.3 and Figure 4.13B). This represents a relative decrease of ≈17% in stomach size, and if stomach surface area decreased, as well as wall thickness, then the net effect is one of reduced capacity for food intake, since the amount of coral able to be enveloped for extra–oral digestion is proportional to stomach area.

In December 1986, large starfish had significantly higher stomach calorific values than small starfish (Table 4.4) (≈4.7 $kJ.g^{-1}$ AFDW over the weight range W≈500g to W≈2500g), otherwise SIZE had no effect on stomach calorific value (Table 4.4). Mean stomach calorific values varied markedly over TIME (Figure 4.13C). These changes were most evident immediately before and after spawning in the first year of sampling. There were no seasonal fluctuations in the calorific value of the stomach (Table 4.4), but values declined consistently from June 1985 (≈25 $kJ.g^{-1}$ AFDW) to May 1987 (≈19 $kJ.g^{-1}$ AFDW).

The relationship between ash content of the stomach and SIZE varied significantly between TRIPs (Table 4.5). Whilst small starfish (W ≈500g) maintained ≈13% ash content, that of large starfish (W ≈2500g) changed from ≈12% (October 1985) to ≈18% (January 1987). Seasonal fluctuations in mean ash content were absent, but mean values increased significantly from ≈12% to ≈13.5% (Table 4.5 and Figure 4.13D). This can be interpreted as arising from shrinkage of the stomach (4.3.7) by the resorption of tissues. Inorganic material, being less readily mobilised, would remain in higher proportions as stomach size decreases[10].

4.3.6.2. Caeca

SIZE effects on caecal water content were variable throughout the study period (Table 4.6). When SIZE effects were significant, (June, October and December 1985, August 1986 and May 1987) large starfish (W≈2500g) had significantly lower caecal water contents than small starfish (W≈500g) (71% versus 75%). Mean caecal water content increases significantly (≈76% to ≈82%) over the study period (Table 4.6 and Figure 4.13E), with no significant seasonal component. Significant increases were found in October 1985, August 1986 and January 1987. The only significant decrease occurred immediately prior to spawning in the second year (December 1986). As with variations in stomach water content, increases in caecal water content correspond to the overall deterioration in structural integrity of the caeca.

The slope of the relationship between caecal dry weight and SIZE varied markedly between TRIPs (Table 4.7). Large starfish (W≈2500g) had higher caecal dry

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[10] AFDW, which may be more meaningful than ash content, is unlikely to vary substantially from dry weight unless variations in ash content are substantial. Variation in ash content from 12% to 15% (a relative change of 25%) will be more readily detectable (in a statistical sense) than the corresponding change from 88% to 85% for organic content (a relative change of 3.5%). It may aid interpretation to remember that % ash content is the compliment of % organic content on a dry weight basis.

weights on the first TRIP of this study (June 1985, ≈68g for a three ray sector) than on any subsequent occasion (≈40g for a three ray sector). This coincided with high food availability in the period leading up to June 1985. After this time coral cover declined markedly and, by February 1986, large starfish had begun to disappear from the population(U frequency distribution, Figure 4.8). Mean caecal dry weight varied markedly but could not be described by the seasonal model (Table 4.7 and Figure 4.13F). A long term decrease in caecal dry weight resulted in a relative reduction of 34% (from ≈28g to ≈18.5g for a three ray sector, for W≈1100g) over the study period.

On four of the eight TRIPs (June and October 1985, August 1986 and May 1987) large starfish had significantly higher caecal calorific values that smaller starfish (a difference of ≈3.2 $kJ.g^{-1}$ AFDW over the W range 500g to 2500g) (Table 4.8). Mean values declined significantly throughout the study, falling from ≈29 $kJ.g^{-1}$ AFDW to ≈21 $kJ.g^{-1}$ AFDW (a relative decrease of ≈28%). Significant decreases occurred between October 1985 and August 1986. In all other periods the same trend was consistent (Figure 4.13G). Seasonal trends are not significant.

Slopes for regressions between caecal ash content and SIZE varied significantly over the course of this study (Table 4.9). Standardised mean values varied significantly (≈7.5% to ≈10%, Figure 4.13H) with seasonal trends indicating October values 5% lower than values throughout autumn and winter. The relative increase in caecal ash content (≈33%) corresponds well to the decrease in caecal dry weight (≈34%) noted above and is likely to be directly related to that size reduction[11].

Energy levels for *A. planci* caecal tissues are within the range of those reported for other asteroids (13 to 26 $kJ.g^{-1}$ dry weight), as are those for caecal ash content (5% to 30% dry weight) (McClintock *et al.*, 1990). *A. planci* energy levels fall within the upper portion of this range (19 to 25$kJ.g^{-1}$ dry weight), while ash contents (≈10%) are relatively low.

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[11] Organic content (the compliment of ash content) would have decreased from 92.5% to 90% throughout the study.

4.3.6.3. Gonad

Gonadal water content was unrelated to starfish SIZE (Table 4.10), but marked changes occurred between successive TRIPs (Figure 4.13 I). Seasonal fluctuations were not significant, but mean values increased from 74% to 78%. This parallels similar changes in stomach and caecal water contents.

Variability in the relationship between gonadal dry weight and whole wet weight (W) increased markedly as W increased. Gonadal dry weight values were logged as a means of reducing heteroscedasticity, with the result that variations in slope between TRIPS could not be tested. Individual regression equations were used to standardise gonadal dry weights for starfish of W≈1100g (Table 4.11). Mean values varied significantly between TRIPs (Figure 4.13J). Seasonality was confirmed but no long term trends were evident. In 1985, mean gonadal weight for a three ray sector increased from ≈15g to ≈27g in a six week period immediately prior to spawning. The 1986 pre-spawning collection may have occurred up to six weeks prior to spawning and therefore the difference between maximal values in 1985 and 1986 may have been due to differences in the period between sample collection and spawning.

The calorific value of gonadal material is independent of starfish SIZE but varies greatly between TRIPs (Table 4.12 and Figure 4.13K)). Seasonal trends were absent but a significant decline from ≈25 $kJ.g^{-1}$ AFDW to ≈18 $kJ.g^{-1}$ AFDW occurred over the two year study period. This represents a relative decrease in energy levels of ≈28%.

Gonadal ash content is independent of starfish SIZE (Table 4.13 and Figure 4.13L). Seasonal cyclicity is very pronounced (annual variations of ±≈4% from a mean value of ≈14.5%) and maximum values occur in early February, after the release of gametes. There is no long term variation in mean gonadal ash content.

4.3.6.4. Body wall

TRIP and SIZE influenced the water content of the body wall significantly (Table 4.14). The mean slope of these regressions indicates that large starfish (W≈2500g) usually had body wall water contents ≈3% higher than small starfish (W≈500g) (72% versus 69%). Mean values differed significantly between TRIPs (Figure 4.13M), but neither the nonlinear model nor a simple linear model could determine significant trends.

The slope of the relationship between dry weight of the body wall and SIZE varied significantly throughout the course of this study (Table 4.15). Low slope coefficients occurred immediately prior to spawning (Oct '85, Dec '85 and Dec '86); high values after spawning and throughout the intervening winter periods. Body wall dry weight for large starfish (W≈2500g) was typically 60g less immediately prior to spawning than during intervening periods. Marked variations in mean values occur throughout the study period, but do not conform to the hypothesised seasonal cyclicity (Figure 4.13N). An overall trend towards increasing body wall dry weight is evident. Starfish of W≈1100g would have increased the dry weight of a three ray sector of their body wall from ≈118g to ≈123g during the study period. In the light of shrinkage processes that have been identified elsewhere (4.3.3), this increase in body wall material can be interpreted as increased skeletal ossification levels resulting from the progressive shrinkage of larger starfish to a size of W≈1100g.

In August 1986 large starfish (W≈2500g) had body wall calorific values ≈4.5 $kJ.g^{-1}$ AFDW higher than smaller starfish (Table 4.16), a trend not observed on other TRIPs. Mean values differed significantly between TRIPs (Figure 4.13O). Seasonal effects are significant; annual elevations in body wall calorific value of about 2.4 $kJ.g^{-1}$ AFDW peak in January, coinciding approximately with highest gonadal indices. Annual cyclicity is superimposed on an overall trend of decreasing calorific value (≈24 $kJ.g^{-1}$ AFDW to ≈17 $kJ.g^{-1}$ AFDW) which leads to a relative decrease in energy content of ≈30%. However in the period June 1985 to February 1986, when all other compartments had undergone substantial decreases in calorific value, the value for the body wall rose from ≈20.5 $kJ.g^{-1}$ AFDW to ≈22.5 $kJ.g^{-1}$ AFDW.

Large starfish (W≈2500g) had body wall ash contents 6% lower than small starfish (Table 4.17). This trend is consistent with the reduction in skeletal content of the body wall determined in Chapter Two and in the previous study of Peckham (1984). Mean ash contents differed significantly between TRIPs (Figure 4.13P). Annual variations in body wall ash contents were significant with peak annual levels occurring in the post–spawning period February to March, when ash contents were ≈4% higher than the deseasonalised average. Long term effects were not significant. Elevated body wall ash contents in post spawning periods may reflect shrinkage of large adults with a resultant increase in relative ossification levels.

McClintock *et al.* (1990) reports calorific values and ash contents for the body wall of asteroids from the Gulf of Mexico in the range 8 to 12kJ.g^{-1} dry weight and 51% to 88%, respectively. Values found from this study (6 to 8kJ.g-1 dry weight ; and 64% to 70%, respectively) are similar. The slightly lower calorific values are more in keeping with those reported for asteroids from other regions (McClintock *et al.*, 1990).

4.3.7. Biomass partitioning

Figure 4.14 (A to D) and Tables 4.18 to 4.21 summarise dry weight indices for the stomach, caeca, gonad and body wall respectively (calculated as given in Chapter 2). Stomach and caecal dry weight indices (Figure 4.14 A and B) declined significantly throughout the study period (Table 4.18 and 4.19 respectively); body wall indices increased (Figure 4.14 D and Table 4.21).

The most striking seasonal variations in biomass partitioning is the clear inverse relationship between gonadal and body wall dry weight indices. A strong seasonality also exists in the declining stomach dry weight index (Figure 4.14 A and Table 4.18). Stomach size, relative to other compartments, is maximised in summer and reaches an annual minimum in winter. The periodicity of these changes is out of synchrony with fluctuations in gonadal and body wall dry weight indices, suggesting a different causality.

4.3.8. Energy partitioning

Figure 4.15 (A to D) depicts fluctuations in the relative proportions of energy within stomach, caecal, gonadal and body wall structures. Tables 4.22 to 4.25 summarise statistical analyses of these variations. In general, these relationships resemble those given previously for dry weight indices (4.3.7). This is not surprising, since there is little difference between the general pattern of decline in calorific value per gram AFDW for each of these compartments (Figure 4.13 C, G, K, and O, respectively). Only two points stand out: a) caecal dry weight did not vary significantly in the period June to October 1985, when caecal calorific index slumped substantially, and b) the dry weight of the body wall increased significantly in the period February to August 1986, but the body wall calorific index remained stable. The former may have been due to the concurrent increase in gonadal size and energy reserves, and suggests an energy reservoir role for the caeca. The latter may have been due to the dramatic decline in calorific value of the body wall (kJ.g^{-1} AFDW) that occurred in that period (Figure 4.13O), and suggests that the body wall may have been an energy source during winter.

4.3.9. Macroscopic changes in appearance

Figure 4.16 shows the varying proportions of starfish whose compartments were ranked on macroscopic appearances as being of "poor", "fair" or "healthy" condition. Large fluctuations, apparently cyclical and annual, dominate the graph. Most starfish appear healthy immediately prior to spawning in both years of this study. The macroscopic condition of all compartments declines in winter.

The general form of this figure matches resource partitioning trends noted earlier. There is a pronounced annual cyclicity and a tendency for a deterioration in the macroscopic appearance of compartments over time. It is of interest that the annual improvement in macroscopic appearance in the gonad is parallelled closely for all other compartments. As the summer of 1986 approached, caecal and then body wall resources were diverted to facilitate reproductive partitioning. In particular, the period between August 1986 and December 1986 resulted in a substantial decrease in dry weight, dry weight index and calorific index of the body wall (Figure 4.13 N, 4.14 D, 4.15 D, respectively), at a time when the macroscopic appearance of the body wall increased noticeably.

4.4. Discussion

4.4.1. Population density

There is no universally accepted definition of an "outbreak population" based on population density. Birkeland and Lucas (1990) review population densities and support the outbreak threshold of 100ha^{-1} utilised by Dana *et al.* (1972). One year prior to this study, starfish density on Helix Reef was estimated to be ≈12000 km^{-2}. At the commencement of this study, population density was estimated to be ≈87000 km^{-2}. Thus, the outbreak on Helix Reef was well under way before sampling began.

Starfish density peaked four months into the study at ≈141000 km^{-2} (i.e. 33000 to 41000 in ≈ 29ha of utilisable habitat). Even though the outbreak had commenced some time in the preceding year, this study was initiated before starfish density peaked or began to decline and was terminated when insufficient numbers could be found to collect a sample of 50 starfish. In this regard the original objective of examining changes in an outbreak population was successfully met.

If adult starfish had travelled from adjacent reefs then immigration rates of ≈4000 starfish per month must have been maintained between June and October 1985 to explain the observed increase in population density. Birkeland and Lucas (1990) review short and long term movement rates of *A. planci;* at a maximum rate of 580m/week it would have taken ≈ 4.5 months to travel from the nearest reef (Grub Reef: 11km distant); at an average rate of ≈ 22m/week the journey would take ≈13.1 months. Even if starfish could navigate over this distance, or were fortunate enough to "stumble upon" Helix Reef, it is unlikely that they could have survived for 4.5 months (or more) in inter-reefal areas with little, if any, corals. Chapter Two suggests that 6 months is about the maximum extent of starvation before death. If, despite these difficulties, they were migrant recruits, it is reasonable to expect that compartmental calorific values and caecal dry weight would have resembled those of the Helix Reef population towards the end of the outbreak. On the contrary, calorific values and caecal dry weights in October 1985 were very high (Figure 4.13C,G,K,O and 4.13B,F, respectively). An alternative explanation is that starfish had settled on Helix Reef as juveniles and were only then becoming apparent as they switched from their cryptic juvenile behavioral phase. Figure 14 of Birkeland and Lucas (1990) shows this relationship for a hypothetical outbreak.

The starfish population on Helix Reef peaked at ≈37000 starfish in October 1985 and by December 1985 had fallen to ≈13500 starfish. In the five week period immediately **prior** to spawning ≈23500 starfish (almost $^2/_3$ of the population) had disappeared (4.3.1). Several alternative explanations exist: a) the starfish migrated off the reef; b) they moved out of the manta tow survey area; or c) they died. In December 1985, the remaining starfish were aggregated in the NNE sector (Figure 4.6D). Under these circumstances the manta tow census may have missed a major aggregation of the population. Two factors support this: a) the manta tow survey samples a belt 5 to 10m wide on the reef slope whereas the reef slope in the NNE sector of Helix Reef consists of an extended rugged bommie field; and b) aggregation *per se* increases the likelihood of an underestimated census by causing two minute counts to exceed saturation levels for observers.

Starfish may have migrated off the reef prior to spawning, but this is less likely since *A. planci* are known to aggregate and to perch on high corals for spawning (Owens, 1971), both of which would imply that movement away from the reef would be counter–productive in terms of spawning success. Whilst coral cover had decreased markedly in the period prior to spawning, observers estimated that live coral remained at ≈20% total cover (Figure 4.4). It is difficult to perceive a mechanism or evolutionary advantage allowing starfish to disperse off the reef in anticipation of starvation conditions some months hence, when coral cover remained at ≈20% and spawning would have occurred in ≈5 weeks.

Mortality is also unlikely to have caused the decrease in population density immediately prior to spawning. Live coral cover of ≈20% in December 1985 (Figure 4.4), relative stability of stomach and caecal dry weight and calorific value (Figure 4.13B,C,F,G), large increases in gonadal dry weight (Figure 4.13J), and increased energy levels in the body wall (Figure 4.13(O)), combined with the apparent health of the remaining population (Figure 4.16) suggest that starvation was unlikely to have been the cause of such mortality. Disease–related mass mortality has been observed in captive *A. planci* (Lucas, 1984) and in wild populations in Fiji (Zann *et al.*, 1987; Campbell *et al.*, 1987; Copeman *et al.*, 1988) and may have occurred on

Helix Reef. Of the ≈23500 starfish that disappeared, about 8000 ($^1/_3$ of the estimated population) would have been obvious to a manta tow observer. If starfish were aggregated within half of the utilisable area (say 15ha) and, assuming that dead starfish remain as sightable as live starfish for 5 days[12], then a steady mortality rate over the 5 week period would have resulted in ≈88 dead-but-sightable starfish per hectare throughout that period. A diver viewing a strip 5m wide at a swim rate of ≈0.25 kts would cover ≈0.15ha in a 40 minute dive, and would therefore expect to see ≈13 dead starfish. However, neither manta tow observers nor divers collecting and measuring starfish reported seeing moribund or decaying starfish.

Steady-state mortality over long periods of time may be an unreasonable assumption (Yamaguchi, *pers. comm.*). Disease-related mortality is more likely to occur as a focussed episode, in which case the probability of encountering moribund or decaying starfish would have been greatly reduced. Even so, a disease outbreak in the five week intervening period should have left evidence of partially affected starfish in the build-up or decline phases of the outbreak.

Considering the likelihood of erroneous manta tow counts, the failure to find moribund or decaying starfish, and the failure of a concurrent microbiological survey to determine the presence of pathogens (Trott, *pers. comm.*) it is concluded that the decline in starfish density prior to spawning most likely resulted from aggregation of starfish in shallow areas that were not surveyed by the manta tow.

4.4.2. Poly-cohort outbreaks

Whilst size (diameter) is a poor indicator of age in echinoderms (2.4.6), underwater weight (U) is expected to behave more conservatively. Increases in U provide no insight to age relationships, but decreases in U within a sample may be a strong indication that large starfish (high U) emigrated or died, and/or that small starfish (low U) starfish immigrated or were recruited as young. Shrinkage or cessation of growth would not cause a substantial short term decrease in skeletal ossification. On this basis, U frequency distributions (Figure 4.8) may be interpreted as indicating four cohorts in the Helix population (Figure 4.17). This scenario can be reasonably

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[12] Moran (1986a) indicates 4 to 6 days on the GBR.

expected to result from successive recruitments from up-current seed reefs (Dight *et al.*, 1988), and is a scenario envisaged by Birkeland and Lucas (1990) in their definition of secondary outbreaks. Whilst this interpretation is favoured, the same patterns may have resulted from other causes: a) small "cohorts" were present in the sampled population but sample size (N= 50) was insufficient to reliably recapture them; b) small "cohorts" may have been retarded in their growth by a delay in locating sufficient coral; or c) small "cohorts" were present on different sections of the reef and "appeared" when the sample location coincided with that area. Given the significant variation in mean ray count that occurred in December 1986, and the fact that ray count in *A. planci* is fixed after approximately six months of age, there is clearly some degree of variation attributable to incomplete randomisation of samples within the outbreak population.

4.4.3. Population distribution

Moran *et al.* (1985) surveyed starfish distribution around nearby John Brewer Reef (Figure 2.1) several times during the course of an outbreak event. They noted that starfish appeared on the exposed (SW) front and progressed gradually around the reef in an anticlockwise direction before reaching the back–reef area and dispersing approximately one year later. Similarly, starfish distribution around Helix Reef varied markedly through time.

Aggregation patterns on Helix Reef could be attributed to three different causes throughout this study. The first of these is recruitment–related. In the broadest sense, the entire outbreak on Helix Reef is a consequence of at least one year and probably several years of high recruitment on this reef. Even within Helix Reef, differential recruitment success may have influenced the spatial pattern of starfish distribution. At smaller spatial scales (tens of metres to kilometres), recruitment-related distributional patterns can only persist until starfish grow into adults and switch to non–cryptic behaviour. Adults are relatively mobile and once starfish reach adulthood, small scale distributional patterns are less likely to be recruitment–related.

The second cause of starfish aggregation on Helix Reef relates to starfish feeding. Ormond *et al.*, (1973) first demonstrated that *A. planci* can use olfactory cues from corals and in particular from conspecifics feeding on nearby corals, to home in on their prey. *A. planci* has also demonstrated learning behaviour by showing modified responses to non–preferred coral species (Collins, 1975; Ormond *et al.*, 1976) and to coral extracts versus corals (Huxley, 1976). Behaviour–modified search patterns acting synergistically with olfactory cues from live or preyed upon corals may have resulted in the distributional changes that were observed on Helix Reef throughout this study. These included distributional patterns at the scale of metres (many starfish on one coral) and at the scale of tens to hundreds of metres, as observed during manta tows (Figure 4.6 A to F).

Spawning behaviour is the third potential cause of starfish aggregation patterns on Helix Reef. Spawning pheromones are known to occur in *A. planci* (Beach *et al.*, 1975; Lucas, 1984). Owens (1971) noted the movement of hundreds of *A. planci* from deeper water to shallow areas prior to spawning and the dispersal of this aggregation soon after spawning. Spawning has been observed in groups of starfish over scales of up to 10m (Pearson and Endean, 1969; Owens, 1971; Gladstone, 1987; Yokochi, 1985 cited in Birkeland and Lucas, 1990). In this study starfish became progressively more aggregated as spawning approached – 60% of the population occurred on less than 15% of the total reef perimeter in the week prior to spawning in 1985. The sector in which starfish aggregated (NNE) is up–current of the reef (Figure 4.5) during the generally southerly currents that prevail in the summer spawning season (December to February) (Kenchington, 1977). It is therefore feasible that down–current starfish on the remainder of Helix Reef were able to detect pheromonal cues and to congregate in the upcurrent sector. As indicated previously (4.4.1), spawning-related behaviour may also have contributed to the apparent decline in population density immediately prior to spawning in 1985. Thus pheromonal cues may have resulted in a redistribution of starfish to the up-current sector and innate behavioral patterns, perhaps independent of any olfactory cues, may have resulted in large numbers of starfish seeking shallower waters near the reef crest.

4.4.4. Size structure

Changes in population size structure cannot be interpreted in isolation from an examination of total population size, wet weight and underwater weight versus diameter relationships, size frequency histograms, and compartmental dry weight, calorific value and ash content measurements. The size structure of the Helix Reef outbreak population at any one time reflected a combination of growth, shrinkage, recruitment, mortality and reproductive processes. The two year study period encompassed several major periods when the relative importance of these processes altered dramatically.

If one accepts the premise that the reduction in apparent population immediately prior to spawning in 1985 was due to aggregation of the population reducing the effectiveness of the manta tow assessment, then the three samples prior to spawning in 1985 suggest growth and recruitment of a healthy population. The apparent decrease in mean diameter and underwater weight in October 1985 (Figure 4.7) was simply the result of an increased portion of 1+ year recruits. Large starfish remained abundant with their decreasing relative abundance offset by increases in the total population size. Calorific values of most compartments had begun to decrease (Figure 4.13) but compartments appeared healthy (Figure 4.16) and starfish gained weight as they swelled with reproductive material (Figure 4.7).

The two summer months (December and January) after spawning were characterised by post–reproductive morbidity of large starfish in particular. Overall population size decreased and the D, W and U size frequency distributions were markedly truncated (Figure 4.8). Whole wet weights decreased in part due to loss of gametes and in part due to shrinkage, but truncation of underwater weight distributions suggest that large starfish died. Caecal and stomach calorific values of survivors decreased (Figure 4.13C,G). Survivors of W ≈1100g showed increased body wall dry weight (Figure 4.13B), maintained the calorific value of their body wall (Figure 4.13O), and showed significant increases in body wall ash content (Figure 4.13P). Shrinkage and mortality of large starfish may have occurred simultaneously, in a manner similar to starvation effects noted in Chapter Three. Live coral cover was ≈ 50% of initial values (Figure 4.4), suggesting that even these levels constituted food limitation for the population.

Autumn/winter of 1986 (February to August) was a period when mean diameter and whole wet weight declined markedly, but when mean underwater weight increased (Figure 4.7). Population size continued to decline but increasing mean underwater weight suggests that some larger starfish remained in the population as small shrunken animals. This period saw the most dramatic decrease in body wall calorific value (Figure 4.13O), suggesting that most energy resources that could be sequestered from the body wall were taken during the winter period. At the end of this period the macroscopic appearance of starfish and their organs was the poorest seen during the study (Figure 4.16).

Despite low coral cover and a continuing decrease in overall population density, the spring and early summer period of 1986 (August to December) resulted in growth of the recent cohort and an increase in the mean whole wet weight of surviving starfish. Calorific values of the stomach, caeca, gonad and body wall remained stable (Figure 4.13C,G,K,O) as did dry weights of the caeca and stomach (Figure 4.13B,F). Gonadal dry weights increased dramatically (Figure 4.13J), and body wall dry weights declined (Figure 413N). Starfish health increased significantly (Figure 4.16). Gonadal dry weight and calorific indices for starfish of W ≈1100g reached ≈12% and ≈14% respectively (Figure 4.14 and 4.15). There is no reason to believe that maximal pre-spawning indices were different from those observed in 1985 (when coral cover was relatively high) – gonadal dry weight and calorific indices increased from ≈4% and ≈5% respectively (Figure 4.14 and 4.15) in the 5 weeks immediately preceding spawning in 1985, and the 1986 spawning took place up to 6 weeks after December 1986 sampling (4.3.6.3).

The post–spawning period from December 1986 to January 1987 resulted in simultaneous decreases in the mean diameter, wet weight and underwater weight of starfish (Figure 4.7), and population density (Figure 4.8), suggesting selective mortality of larger starfish. Ash contents of all compartments showed significant increases (suggesting resorption of organic material), while calorific values continued to decline (Figure 4.13). In the period between December 1986 and January 1987 samples (6 weeks), the proportion of starfish in the population with $U < 20g$ increased from 2% to 22% (Figure 4.8). This suggests recruitment of small starfish to the population rather than shrinkage, since underwater weight is expected to be conservative (4.3.3). Shrinkage, post–reproductive morbidity and recruitment may each have been significant in this period.

4.4.5. Morphology

Ray number in *A. planci* varies from 7 to 23 (2.2.3) and typically varies from approximately 12 to 18 at any one site (Moran, 1986; Nakamura, 1986). Significant differences in mean arm number between geographic areas have been identified for Panama and Guam (Glynn, 1982), south-east Polynesia and New Caledonia versus the Ryukyus, and Indonesia versus the Ryukyus (Nakamura, 1986). These differences have been independent of starfish size (Glynn 1982; Nakamura, 1986) and within the Ryukyus, independent of sex, sampling time or collection sites (Nakamura, 1986). The significant increase in mean ray number noted in this study (Figure 4.9 and 4.3.4.1) occurred in consecutive samples from the same reef within several hundred metres of each other, and approximately three months apart, supporting the hypothesis that the Helix Reef population was a heterogenous grouping of subpopulations.

The existing data set provides no way of determining whether these subpopulations resulted from external influences on planktonic larvae or juveniles, or from a different genetic stock. Nakamura (1986) suggested that differences in ray count between widely separated geographic areas, and similarities within regions may be related to the degree of genetic similarity. However, Nishida and Lucas (1988) concluded that GBR populations were, in general, homogenous in their genetic composition.

Several authors have presented data for *A. planci* that indicate power coefficients for the relationship between diameter and whole wet weight less than the isometric coefficient of 3 (Nishihira and Yamazato, 1972; Conand, 1985). Neither of these authors examined the statistical significance of this relationship and none suggested that *A. planci* exhibit allometric growth. A previous publication resulting from this work (Kettle and Lucas, 1987), and based upon the October 1985 sample, indicates that growth of W and D occurs isometrically. However, analysis of the present samples over a two year time period suggests that allometric growth of W and D is the norm – large starfish are usually thinner in the oral/aboral axis than smaller conspecifics. This may simply reflect the difference between "fatter" (unrestricted food supply) and "leaner" (suboptimal food availability) starfish, given the decline in coral cover and starfish density that occurred after this point.

A similar trend was evident with respect to underwater weight. The power coefficient for the relationship between diameter and underwater weight (≈2.15) was significantly less than 3 throughout most of the study. This is likely to arise from the synergistic combination of allometric growth in whole wet weight (above) and a decreasing proportion of skeletal material in large starfish (2.4.1). Slope coefficients rose dramatically in the last two samples of the study (January 1987 and May 1987) when large starfish were proportionately heavier than small starfish . Large starfish were not becoming "fatter" (W versus D did not change: 4.3.4.2). Shrinkage of individuals probably resulted in elevated skeletal contents. This suggests that the occurrence of shrinkage in the population was most prominent after spawning in the second year of the study.

4.4.6. Spine length ratios as an indicator of physiological status

Changes in the "arm spine length" (ASL) to diameter (D) ratio (ASL/D) of *A. planci* may be effected by: a) allometric growth of spines with respect to diameter; b) spines continuing to grow while starfish growth rate decreases or ceases or c) spine length remaining constant while starfish diameter decreases. Alternative (a) can be rejected since analysis of covariance demonstrated that SIZE had no significant effect upon ASL/D ratio (4.3.4). Alternative (b) may occur, although preferential growth of spines when bodily growth rates are reduced appears to contradict the suggestion (Chapter Two) that mature A. *planci* reach a size refuge from predation. Alternative (c) would result during starvation if resorption of soft tissues occurs. Starfish diameter would decrease because the skeleton is comprised of dispersed ossicles throughout the body wall tissue. Calcified ossicles would be resorbed only slowly (if at all) by contrast to the resorption rate for soft tissues. Spines, which have but one tissue–separated joint, would remain of fixed length, effectively increasing the ratio of ASL/D.

The stabilisation of the ASL/D ratio after February 1986 (Figure 4.14) has many potential explanations: a) starfish and their spines grew (or shrank) allometrically after this point in time; b) starfish were able to subsist on the decreasing quantity of coral without further shrinkage; c) recruits entering the population after February 1986 were more healthy and had an averaging effect on the increasing ASL/D ratio of older starfish within the population; or d) starfish collected in subsequent samples were from a different population. Movement of starfish between remnant corals patches would have delayed the starvation process and given the appearance that starfish were subsisting on low ration diets. Alternatively, a fixed upper limit of ASL/D may reflect the upper limit of shrinkage for starfish, above which populations switch from biomass-limitation to density-limitation and mortality becomes significant. It would be difficult to ascribe the pattern of variation in ASL to any one cause, and is probably unwise to attempt to do so.

4.4.7. Starfish injury

Several workers have reported the presence of starfish missing some or all of the free segment of one or more rays (Pearson and Endean, 1969; Owens, 1971; Branham, 1973; Glynn, 1982, 1984; Zann *et al.*, 1987). This is most commonly regarded as an outcome of a sublethal predation event. Some workers have suggested that the incidence of injured starfish may be inversely related to ambient predation levels (Birkeland and Lucas, 1990), while others (Endean *pers. comm.*) have suggested that the level of sublethal predation in a population was a direct indication of the abundance of large fish predators. Endean cited low levels of sublethal predation and high levels of commercial and recreational fishing at Holbourne Island (central GBR) as supporting evidence. Implicit in Endean's statement is the assumption that the proportion of incomplete predation attempts is independent of the total number of predation attempts. Endean's assertions appear to directly contradict those of Birkeland and Lucas, but in fact refer to different effects. Birkeland and Lucas refer to "predator pressure" rather than "predator density" – a large number of predators making fewer predation attempts may in fact be equivalent to a small number of predators making many attempts. Endean did not distinguish between predator density and predator pressure.

Two factors govern the incidence of injury within any population: the rate of injury and the rate of regeneration. Birkeland and Lucas acknowledge this as a complication that may confound interpretation of partial predation. Whilst the apparent rate of injury may be inversely proportional to predation pressure, it will also be inversely related to the regenerative capacity of the starfish. It is not known whether predators of adult *A. planci* showed a numerical or functional response on Helix Reef. However, throughout the study, food availability declined dramatically, as did the calorific value of each compartment and the overall energy levels of starfish (4.4.8, 4.4.9). Starfish populations declined and large starfish shrank as they resorbed mobiliseable reserves (4.4.4). Under these circumstances it is unlikely that starfish were able to rapidly regenerate damaged tissue. Injuries would have remained apparent in starfish for increasing periods of time and the proportion of injured starfish would have gradually increased as a consequence. That the incidence of injury increased from ≈27% to ≈93% on Helix Reef in a period of less than two years (Figure 4.11), as opposed to a variation from 17% to 60% attributed to predation pressure (Birkeland and Lucas, 1990), is an indication that nutritional status may be more important in determining the incidence of ray damage than predator pressure *per se*. Certainly any future analysis of "sublethal predation" as judged by the incidence of ray injury should simultaneously test the effects of both predation pressure and regeneration rate.

4.4.8. Resource partitioning through time

Simultaneous (and sometimes disparate) variations in biomass (dry weight) and mass-specific energy levels (calorific value g^{-1} AFDW) confounded interpretation of the dynamic variations in energetics of whole animals. Presentation of variations in total energy, the product of these two parameters, simplifies the interpretation of variations in energy partitioning throughout the study (Figure 4.18). It is immediately clear that the body wall **always** contained more energy than any other compartment, and that pronounced annual cyclicity was evident only in the gonads.

When coral cover was high (prior to October 1985) the accumulation of large amounts of energy in the gonad (a six fold increase) had no adverse effect on any other compartment. However, in the month prior to spawning (November 1985), as coral cover began to decline noticeably, energy was withdrawn from the caeca to enable further reproductive partitioning. In the latter part of that summer, when starfish were presumably recuperating from their spawning effort, and as food availability decreased markedly, energy was consumed from the body wall. In the winter period, when body wall and gonadal energy levels were stable, energy was consumed from the caeca and to a lesser extent the stomach.

During the accumulation of spawning material in the second year, gonadal energy levels were elevated at the expense of body wall energy levels. The tendency to consume energy from the body wall became even more apparent immediately after spawning in 1986 and continued into the winter of 1987. Thus, while there was a pronounced inverse cyclicity between body wall and gonadal partitioning, overshadowing a similar relationship between caeca and gonads, there was a clear priority that the caeca were sacrificed first, and the body wall only under extreme circumstances. The generalised hierarchy of partitioning is as follows: reproduction can proceed with no adverse effects on the energy levels of any other compartments in conditions of high food availability; the caeca yield energy for reproduction as food becomes limiting and, along with the stomach, for maintenance during winter; under extreme food limitation the body wall yields energy to allow reproductive partitioning or to allow maintenance in post–spawning or winter periods.

4.4.9. Compartments functioning as energy reserves

In some asteroids annual growth of gonads results in inverse changes in the size of the pyloric caeca (Lawrence, 1973; Ferguson, 1974, 1975; Jangoux and Van Impe, 1977; Crump and Emson, 1978). In others, inverse changes can be noted in the body wall (Hatanaka and Kosaka, 1958 cited in Lawrence and Lane, 1982). Giese (1976) considered that the size of the echinoderm body wall gave it the potential to be a major nutrient store. In this study several indications support Giese's hypothesis: a) there was a distinct inverse cyclicity in the dry weight of the gonad and the body wall (Figure 4.14 and 4.15); b) the initially high energy level of the body wall was substantially utilised during this study (4.4.8); and c) the implied shrinkage of large adults indicates resorption of those resources from the body wall (4.4.5).

Acanthaster in this study showed no clear annual cyclicity between dry weight or calorific value of the gonads and caeca (Figure 4.14 and 4.15), but this may have been an artefact of particular site and timing conditions. The spawning period in 1985 coincided with the period of greatest period of impact on food availability (Figure 4.4). Starvation had undoubtably set in by the winter of 1986 . These dramatic changes in food availability may have obscured cyclical fluctuations in the caeca by retarding recovery of the caeca in post–spawning periods. Caecal energy levels declined markedly, and those of the gonad increased markedly (Figure 4.18), in the sample period preceding spawning in 1985, suggesting that caecal reserves were utilised for gamete production. Figure 4.18 suggests that caecal reserves continued to decline over the winter of 1986, and the absence of an inverse relationship prior to spawning in 1986 probably reflects the low levels of reserves present in the caeca at that time. Under other circumstances, particularly lower starfish density or a greater extent of corals, an inverse cyclical relationship between caeca and gonads may have been obvious, and that between body wall and gonads may have been absent.

The relative contributions of each compartment are evident in Figure 4.18 – the body wall of a three-ray sector yielded ≈150kJ over the two year period, the caeca yielded ≈125kJ and the stomach yielded ≈30kJ. The principal reservoir of energy available to starving *A. planci* is therefore the body wall. The caeca plays a secondary but still substantial role, and the stomach provides a minimal contribution. The prime difference between the role of the body wall and the caeca is not the magnitude of energy resorbed, but the pattern of resorption. Caecal reserves were utilised first – the body wall was utilised only after consumption of approximately half of the total caecal energy levels (Figure 4.18).

4.4.10. Macroscopic indicators of health

Throughout the Helix Reef study (this Chapter) and the previous Orpheus Island starvation experiment (Chapter 3), trends in the macroscopic appearance of starfish compartments facilitated the interpretation of changes in starfish health as determined by biomass and energy partitioning, and by changes in population density and size structure. In the Helix Reef study there was no gradual and consistent deterioration in the macroscopic appearance of individual compartments. Longer term trends were evident, but were confounded by a strong annual pattern (Figure 4.16). The macroscopic condition of all compartments improved noticeably during the two summer spawning periods (Figure 4.16), even though compartmental calorific values and dry weights showed no noticeable improvements (Figure 4.13). Nonetheless, gross changes in condition were mirrored by the macroscopic appearance of compartments. Of particular value were the spines *per se*. Even before beginning dissections, the relative proportion of spine length to diameter, the erectness of the spines and the presence of missing spine ossicles provided useful clues as to the likely condition of internal starfish compartments. These would serve as useful field indicators of starfish condition.

4.4.11. Variations in reproductive success

Neither the dry weight, the dry weight index nor the calorific index of the gonad varied appreciably between the first major spawning of the population (December 1985) and the second (December 1986) (Figure 4.13J, 4.14C, 4.15C respectively) although the calorific value per gram AFDW decreased from ≈24 $kJ.g^{-1}$ to ≈21.5 $kJ.g^{-1}$ (Figure 4.13K). Schmidt-Nielsen (1988) presented data on the energetic value of carbohydrate and protein (≈17.5 to 18 $kJ.g^{-1}$ AFDW) and lipid (≈39 $kJ.g^{-1}$ AFDW). On a simple basis of the proportions of each required to reach the observed calorific values these suggest lipid contents of ≈15.4% and 9.0% respectively for the first and second observed spawning. Energy levels (and presumably lipid contents) may have increased between 1 December 1986 and the actual spawning period in that year (4.3.6.3), but the suggestion from these data is that spawned gametes from the second spawning event may have had 40% less lipid storage material relative to gametes spawned in December 1985. Yolk, the principal energy storage site in the echinoderm egg, is composed of oil droplets and yolk platelets (Cognetti, 1982). The former are comprised largely of lipids (88.1% in *Strongylocentrotus intermedius*) and the latter may have a significant protein composition (56% lipids + 44% protein in *S. intermedius*) with lipid composition in each case comprising in order of decreasing abundance, triglycerides, phospholipids and cholesterol (Chelomin and Svetcher, 1978 cited in Cognetti, 1982). If energy levels in the gonads did not subsequently increase then the survivorship of larvae may have shown a significant decrease in the second year.

Gonad weight achieved similar levels in both years. Considering the change in population size (≈13000 starfish versus <4500 starfish) and the change in mean starfish size (≈1600g versus ≈1200g), it is clear that the maximum potential fecundity of the Helix Reef population in the second year would have decreased to ≈23% of that in the first year (≈14.8×10^{10} eggs versus 3.4×10^{10} eggs). Of course, spawning success may have decreased due to the smaller population size and larval survival may have been effected by lower energetic content. The overall effect is that of diminishing the contribution from subsequent spawnings – the greatest reproductive success from an outbreak population will be achieved prior to food limitation even if survivors linger over several years.

Table 4.1 Dates, data prefix (refer Appendix A), number of starfish censussed around the reef perimeter, estimated damage to coral cover (%) and estimated living coral cover (%) for collections from Helix Reef throughout this study. Live coral cover is estimated from coral damage assuming 40% mean live coral prior to the outbreak.

Trip date	Date reference	Data prefix	Perimeter count	Damage to coral	Estimated live coral
24/5/1984	May 1984	*	80	5%	38%
25-30/4/1985		A "			
24-28/6/1985	June 1985	B +	473	10%	36%
26-31/10/1985	October 1985	C	830	25%	30%
1-5/12/1985	December 1985	D	295	50%	20%
26-30/2/1986	February 1986	E^			
20-23/5/1986	May 1986	F #	147	90%	4%
25-29/8/1986	August 1986	G	100	95%	2%
30/11-6/12/1986	December 1986	H^			
25-28/1/1987	January 1987	I^			
12/5/1987	May 1987	J^			

* Data courtesy P. Moran, Australian Institute of Marine Science (AIMS).

" Preliminary survey only - no sample from Helix Reef

\+ Extrapolated from a survey of ≈3/4 of the reef perimeter during rough weather.

\# No physiology data available

^ Manta survey not undertaken

Table 4.2 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **water content (%) of the stomach** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance **STH2O**

Slopes are homogenous?

F≈	1.152	N=	384	P≈	0.330

TRIP is not significant?

F≈	31.821	N=	384	P≈	0.000

SIZE is not significant?

F≈	9.913	N=	384	P≈	0.002

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85							
12'85	81.380	0.368	-0.00045	0.00022	0.287	48	0.048
02'86							
08'86							
12'86	81.387	0.649	-0.00133	0.00052	0.379	42	0.013
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope
12'85 12'86	-0.00070

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	76.453	0.611	140.215	0.000
10'85	80.984	0.158		
12'85	81.004	0.142		
02'86	81.233	0.165		
08'86	80.771	0.240		
12'86	79.873	0.222	5.037	0.025
01'87	80.981	0.126	7.512	0.006
05'87	81.530	0.156		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	78.322	0.402	198.831	<0.001
seasonality	0.882	0.139	6.345	<0.001
offset	-0.404	0.433	0.933	>0.200
slope	0.111	0.021	5.286	<0.001

Linear regression model

	coefficient	±SE	t	P
elevation				
slope				

Table 4.3 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **dry weight (g) of the stomach** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance STDRY

Slopes are homogenous?

F≈ 0.636 N= 385 P≈ 0.726

TRIP is not significant?

F≈ 4.203 N= 385 P≈ 0.000

SIZE is not significant?

F≈ 532.441 N= 385 P≈ 0.000

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85	0.451	1.307	0.00776	0.00084	0.799	50	0.000
10'85	0.734	1.453	0.00788	0.00094	0.770	50	0.000
12'85	1.497	1.482	0.00736	0.00086	0.782	49	0.000
02'86	1.341	1.429	0.00718	0.00110	0.686	50	0.000
08'86	0.691	0.581	0.00499	0.00076	0.694	48	0.000
12'86	-1.376	1.164	0.00762	0.00092	0.800	41	0.000
01'87	0.845	0.648	0.00636	0.00079	0.765	48	0.000
05'87	0.231	0.482	0.00573	0.00080	0.723	49	0.000

Slopes grouped by Tukey tests

TRIP	Mean slope
06'85 10'85 12'85 02'86 08'86 12'86 01'87 05'87	0.00738

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	9.172	0.564	9.800	0.002
10'85	9.612	0.661		
12'85	9.654	0.629		
02'86	9.287	0.517		
08'86	7.208	0.246		
12'86	7.109	0.383		
01'87	8.267	0.262		
05'87	7.520	0.209		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	9.747	0.415	23.487	<0.001
seasonality	-0.584	0.334	1.749	>0.050
offset	-4.812	0.892	5.395	<0.001
slope	-0.076	0.022	3.455	<0.001

Linear regression model

	coefficient	±SE	t	P
elevation	9.637	0.377	25.537	0.000
slope	-0.066	0.020	-3.330	0.001

Table 4.4 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **calorific value (kJ/g-1 AFDW) of the stomach** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance STCAL

Slopes are homogenous?

F≈	1.244	N=	385	P≈	0.278

TRIP is not significant?

F≈	28.692	N=	385	P≈	0.000

SIZE is not significant?

F≈	1.784	N=	385	P≈	0.182

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85							
12'85							
02'86							
08'86							
12'86	17.634	1.286	0.00237	0.00103	0.336	44	0.026
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	25.162	0.302		
10'85	24.585	0.240	13.470	0.000
12'85	22.700	0.329	5.355	0.021
02'86	21.500	0.360		
08'86	20.607	0.326		
12'86	20.216	0.426		
01'87	19.649	0.505	3.854	0.050
05'87	18.630	0.414		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	26.150	0.391	66.880	<0.001
seasonality	-0.560	0.373	1.501	>0.100
offset	2.259	0.500	4.518	<0.001
slope	-0.267	0.021	12.714	<0.001

Linear regression model

	coefficient	±SE	t	P
elevation	26.405	0.328	80.539	0.000
slope	-0.282	0.018	-15.865	0.000

Table 4.5 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **ash content (%) of the stomach** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance STASH

Slopes are homogenous?

F≈ 2.437 N= 368 P≈ 0.019

TRIP is not significant?

SIZE is not significant?

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85	13.478	0.533	-0.00081	0.00034	0.326	49	0.022
12'85							
02'86							
08'86							
12'86							
01'87	12.239	1.027	0.00280	0.00125	0.316	47	0.030
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope
10'85	-0.00081
01'87	0.00280

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	13.710	0.480	6.434	0.012
10'85	12.326	0.346		
12'85	12.604	0.265		
02'86	13.609	0.425		
08'86	14.619	0.360	5.435	0.020
12'86	13.253	0.409	9.825	0.002
01'87	15.040	0.508	6.894	0.009
05'87	13.524	0.318		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	12.807	0.419	30.566	<0.001
seasonality	-0.409	0.276	1.482	>0.100
offset	-1.675	2.076	0.807	>0.200
slope	0.051	0.023	2.217	<0.050

Linear regression model

	coefficient	±SE	t	P
elevation	12.637	0.355	35.629	0.000
slope	0.056	0.020	2.881	0.004

Table 4.6 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **water content (%) of the caeca** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance PCH2O

Slopes are homogenous?

F≈ 1.101 N= 385 P≈ 0.362

TRIP is not significant?

F≈ 26.450 N= 385 P≈ 0.000

SIZE is not significant?

F≈ 24.606 N= 385 P≈ 0.000

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85	72.307	1.853	-0.00238	0.00119	0.281	49	0.050
10'85	77.616	0.829	-0.00168	0.00054	0.414	49	0.003
12'85	76.023	0.949	-0.00111	0.00057	0.276	48	0.057
02'86							
08'86	81.654	1.077	-0.00402	0.00139	0.389	49	0.006
12'86							
01'87							
05'87	80.209	0.918	-0.00332	0.00149	0.306	50	0.031

Slopes grouped by Tukey tests

TRIP	Mean slope
06'85 10'85 12'85 08'86 05'87	-0.00195

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	69.569	0.791	15.043	0.000
10'85	74.366	1.537		
12'85	73.790	1.446		
02'86	75.230	0.409	5.200	0.023
08'86	78.050	0.427	9.937	0.002
12'86	73.998	0.519	6.988	0.009
01'87	77.430	0.467		
05'87	77.321	0.388		

Nonlinear regression model

	coefficient ±SE	t	P
elevation seasonality offset slope	Failed to fit after 20 iterations		

Linear regression model

	coefficient	±SE	t	P
elevation	70.533	0.790	89.276	0.000
slope	0.265	0.043	6.158	0.000

Table 4.7 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **dry weight (g) of the caeca** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance PCDRY

Slopes are homogenous?

F≈ 4.251 N= 386 P≈ 0.000

TRIP is not significant?

SIZE is not significant?

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85	-2.314	4.455	0.02782	0.00295	0.809	49	0.000
10'85	6.774	3.443	0.01911	0.00223	0.777	50	0.000
12'85	3.914	2.591	0.01563	0.00150	0.836	49	0.000
02'86	3.987	3.411	0.01683	0.00262	0.679	50	0.000
08'86	-3.180	2.512	0.01975	0.00324	0.664	49	0.000
12'86	-5.027	2.672	0.01879	0.00213	0.813	42	0.000
01'87	1.539	1.619	0.01570	0.00197	0.761	48	0.000
05'87	-0.802	0.911	0.01438	0.00151	0.812	49	0.000

Slopes grouped by Tukey tests

TRIP	Mean slope
06'85	0.02782
10'85 12'85 02'86 08'86 12'86 01'87 05'87	0.01729

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	28.572	1.887		
10'85	28.462	1.547	22.800	0.000
12'85	20.503	1.113		
02'86	22.623	1.234	8.493	0.004
08'86	17.766	0.980		
12'86	15.942	0.877	4.214	0.041
01'87	19.538	0.648		
05'87	16.798	0.393		

Nonlinear regression model

	coefficient ±SE	t	P
elevation	Failed to fit after 20 iterations		
seasonality			
offset			
slope			

Linear regression model

	coefficient ±SE		t	P
elevation	28.246	0.987	28.605	0.000
slope	-0.401	0.052	-7.775	0.000

Table 4.8 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **calorific value (kJ/g^{-1} AFDW) of the caeca** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance PCCAL

Slopes are homogenous?

F≈	N=	P≈
1.349	384	0.226

TRIP is not significant?

F≈	N=	P≈
62.832	384	0.000

SIZE is not significant?

F≈	N=	P≈
20.890	384	0.000

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85	27.927	0.711	0.00117	0.00046	0.351	48	0.014
10'85	27.082	0.620	0.00143	0.00041	0.450	49	0.001
12'85							
02'86							
08'86	19.744	0.928	0.00344	0.00120	0.386	49	0.006
12'86							
01'87							
05'87	18.006	0.964	0.00329	0.00157	0.291	50	0.041

Slopes grouped by Tukey tests

TRIP	Mean slope
06'85 10'85 08'86 05'87	0.00161

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	29.046	0.315		
10'85	28.579	0.277	18.833	0.000
12'85	26.134	0.328	15.896	0.000
02'86	23.876	0.361	7.210	0.008
08'86	22.363	0.555		
12'86	21.889	0.468		
01'87	21.481	0.433		
05'87	20.684	0.408		

Nonlinear regression model

	coefficient ±SE	t	P
elevation seasonality offset slope	Failed to fit after 20 iterations		

Linear regression model

	coefficient	±SE	t	P
elevation	30.821	0.370	83.235	0.000
slope	-0.388	0.020	-19.332	0.000

Table 4.9 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **ash content (%) of the caeca** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance PCASH

Slopes are homogenous?

F≈ 3.722 N= 376 P≈ 0.001

TRIP is not significant?

SIZE is not significant?

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85	8.592	0.565	-0.00109	0.00037	0.396	50	0.004
12'85	9.182	0.525	-0.00077	0.00032	0.343	46	0.020
02'86	11.685	0.985	-0.00190	0.00075	0.345	49	0.015
08'86	15.342	1.059	-0.00423	0.00133	0.432	46	0.003
12'86							
01'87	8.165	0.923	0.00279	0.00113	0.346	47	0.017
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope
10'85 12'85 02'86	-0.00114
08'86	-0.00423
01'87	0.00279

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	8.238	0.370		
10'85	7.403	0.256		
12'85	8.090	0.303	8.676	0.003
02'86	9.503	0.360	5.915	0.015
08'86	10.689	0.384	15.621	0.000
12'86	8.686	0.289	21.481	0.000
01'87	11.011	0.426	4.865	0.028
05'87	9.930	0.327		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	7.483	0.509	14.701	<0.001
seasonality	-0.500	0.230	2.174	<0.050
offset	-2.203	0.569	3.872	<0.001
slope	0.107	0.025	4.280	<0.001

Linear regression model

	coefficient	±SE	t	P
elevation				
slope				

Table 4.10 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **water content (%) of the gonad** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance GH2O

Slopes are homogenous?

F≈ 1.897 N= 350 P≈ 0.069

TRIP is not significant?

F≈ 21.921 N= 350 P≈ 0.000

SIZE is not significant?

F≈ 0.201 N= 350 P≈ 0.654

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85							
12'85	81.184	0.905	-0.00116	0.00054	0.301	48	0.037
02'86	81.128	0.997	0.00256	0.00074	0.463	46	0.001
08'86							
12'86							
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope
12'85	-0.00116
02'86	0.00256

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	69.569	0.791	13.584	0.000
10'85	74.366	1.537	6.945	0.009
12'85	77.796	1.655	24.801	0.000
02'86	84.415	0.354	22.929	0.000
08'86	78.050	0.427	8.973	0.003
12'86	73.998	0.519	6.311	0.012
01'87	77.430	0.467		
05'87	77.321	0.388		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	Failed to fit after 20 iterations			
seasonality				
offset				
slope				

Linear regression model

	coefficient	±SE	t	P
elevation	74.147	0.936	79.194	0.000
slope	0.145	0.051	2.857	0.005

Table 4.11 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **dry weight (g) of the gonad** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance LGDRY logged

Slopes are homogenous?

F≈ 5.360 N= 383 P≈ 0.000

TRIP is not significant?

SIZE is not significant?

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85	-0.134	0.195	0.00072	0.00013	0.635	50	0.000
10'85	1.253	0.204	0.00123	0.00013	0.802	50	0.000
12'85	2.135	0.179	0.00095	0.00010	0.801	48	0.000
02'86	-0.060	0.116	0.00059	0.00009	0.696	49	0.000
08'86	-0.353	0.173	0.00130	0.00022	0.648	49	0.000
12'86	1.289	0.310	0.00143	0.00025	0.661	45	0.000
01'87	-0.331	0.159	0.00158	0.00019	0.783	45	0.000
05'87	-0.072	0.043	0.00041	0.00007	0.649	47	0.000

Slopes grouped by Tukey tests

TRIP	Mean slope
06'85 12'85 02'86 05'87	0.00078
10'85 08'86 12'86 01'87	0.00131

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	0.644	0.084	366.770	0.000
10'85	2.602	0.093	41.099	0.000
12'85	3.264	0.078	671.665	0.000
02'86	0.574	0.044	25.333	0.000
08'86	1.094	0.067	287.225	0.000
12'86	2.882	0.102	207.975	0.000
01'87	1.328	0.064	46.026	0.000
05'87	0.609	0.030		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	1.427	0.063	22.651	<0.001
seasonality	1.355	0.057	23.772	<0.001
offset	-1.992	0.067	29.731	<0.001
slope	-0.003	0.003	1.000	>0.200

Linear regression model

	coefficient	±SE	t	P
elevation				
slope				

Table 4.12 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **calorific value (kJ/g^{-1} AFDW) of the gonad** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance **GCAL**

Slopes are homogenous?

F≈ 0.761 N= 287 P≈ 0.621

TRIP is not significant?

F≈ 20.716 N= 287 P≈ 0.000

SIZE is not significant?

F≈ 1.070 N= 287 P≈ 0.302

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85							
12'85							
02'86							
08'86							
12'86							
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	25.414	0.313	8.180	0.005
10'85	23.817	0.238		
12'85	23.882	0.301	11.790	0.001
02'86	22.164	0.334		
08'86	21.727	0.439	17.351	0.000
12'86	21.447	0.381		
01'87	19.205	0.571		
05'87	18.352	0.922		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	Failed to fit after 20 iterations			
seasonality				
offset				
slope				

Linear regression model

	coefficient	±SE	t	P
elevation	26.690	0.364	73.407	0.000
slope	-0.274	0.021	-12.963	0.000

Table 4.13 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **ash content (%) of the gonad** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance GASH

Slopes are homogenous?

F≈ 0.354 N= 206 P≈ 0.928

TRIP is not significant?

F≈ 13.470 N= 206 P≈ 0.000

SIZE is not significant?

F≈ 0.048 N= 206 P≈ 0.827

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85							
12'85							
02'86							
08'86							
12'86							
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	12.647	0.545		
10'85	11.326	0.446		
12'85	14.976	0.489	32.001	0.000
02'86	18.370	0.441	16.386	0.000
08'86	11.413	0.409	41.535	0.000
12'86	13.869	0.651	6.674	0.010
01'87	15.835	0.559	4.685	0.032
05'87	nil	nil		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	14.591	0.687	21.239	<0.001
seasonality	4.258	0.492	8.654	<0.001
offset	2.208	0.189	11.683	<0.001
slope	-0.015	0.043	0.349	>0.500

Linear regression model

	coefficient	±SE	t	P
elevation				
slope				

Table 4.14 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **water content (%) of the body wall** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance BH2O

Slopes are homogenous?

F≈ 1.193 N= 385 P≈ 0.306

TRIP is not significant?

F≈ 21.481 N= 385 P≈ 0.000

SIZE is not significant?

F≈ 19.558 N= 385 P≈ 0.000

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85	70.513	0.716	0.00099	0.00046	0.293	50	0.039
12'85	72.795	0.590	0.00093	0.00035	0.361	48	0.012
02'86	71.119	0.742	0.00141	0.00057	0.336	50	0.017
08'86	67.948	0.929	0.00344	0.00120	0.386	49	0.006
12'86	71.205	0.666	0.00177	0.00053	0.326	43	0.033
01'87	69.626	0.695	0.00209	0.00085	0.345	47	0.018
05'87	67.073	0.764	0.00343	0.00124	0.371	50	0.008

Slopes grouped by Tukey tests

TRIP	Mean slope
10'85 12'85 02'86 08'86 12'86 01'87 05'87	0.00138

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	68.481	0.735	4.733	0.030
10'85	71.477	0.327		
12'85	72.104	1.518		
02'86	72.659	0.268		
08'86	69.530	1.435	5.272	0.022
12'86	72.465	0.223	4.288	0.039
01'87	70.175	1.513		
05'87	69.722	0.329		

Nonlinear regression model

	coefficient ±SE	t	P
elevation seasonality offset slope	Failed to fit after 20 iterations		

Linear regression model

	coefficient ±SE	t	P
elevation slope	Not significant		

Table 4.15 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **dry weight (g) of the body wall** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance BDRY

Slopes are homogenous?

F≈ 6.425 N= 390 P≈ 0.000

TRIP is not significant?

SIZE is not significant?

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85	15.562	6.855	0.10092	0.00442	0.957	50	0.000
10'85	22.240	7.718	0.08007	0.00500	0.918	50	0.000
12'85	34.197	8.780	0.07549	0.00507	0.909	49	0.000
02'86	10.981	9.378	0.10755	0.00722	0.907	50	0.000
08'86	32.965	7.545	0.10701	0.00974	0.848	49	0.000
12'86	28.062	12.183	0.08406	0.00971	0.797	45	0.000
01'87	16.773	3.733	0.10939	0.00451	0.964	47	0.000
05'87	6.896	2.747	0.12060	0.00446	0.969	50	0.000

Slopes grouped by Tukey tests

TRIP	Mean slope
06'85 02'86 08'86 01'87 05'87	0.10544
10'85 12'85 12'86	0.07872

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	126.298	2.982	12.086	0.001
10'85	111.475	3.507		
12'85	117.224	3.736	9.711	0.002
02'86	130.578	3.395	22.981	0.000
08'86	151.122	2.925	44.462	0.000
12'86	121.771	4.002	11.431	0.001
01'87	136.804	1.488		
05'87	132.391	1.281		

Nonlinear regression model

	coefficient ±SE		t	P
elevation seasonality offset slope	Failed to fit after 20 iterations			

Linear regression model

	coefficient ±SE		t	P
elevation	117.760	2.635	44.683	0.000
slope	0.625	0.137	4.546	0.000

Table 4.16 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **calorific value (kJ/g^{-1} AFDW) of the body wall** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance BCAL

Slopes are homogenous?

F≈ 1.029 N= 383 P≈ 0.410

TRIP is not significant?

F≈ 37.821 N= 383 P≈ 0.000

SIZE is not significant?

F≈ 4.450 N= 383 P≈ 0.036

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85							
12'85							
02'86							
08'86	16.137	0.669	0.00229	0.00086	0.360	49	0.011
12'86							
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	20.552	0.247	6.836	0.009
10'85	21.780	0.207		
12'85	21.941	0.300	83.103	0.000
02'86	22.548	0.459		
08'86	18.286	0.411		
12'86	18.429	0.238		
01'87	17.712	0.403	6.830	0.009
05'87	16.478	0.301		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	24.024	0.296	81.162	<0.001
seasonality	1.188	0.174	6.828	<0.001
offset	12.617	0.519	24.310	<0.001
slope	-0.268	0.017	15.765	<0.001

Linear regression model

	coefficient	±SE	t	P
elevation				
slope				

Table 4.17 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **ash content (%) of the body wall** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance BASH

Slopes are homogenous?

F≈ 1.904 N= 386 P≈ 0.068

TRIP is not significant?

F≈ 30.314 N= 386 P≈ 0.000

SIZE is not significant?

F≈ 72.313 N= 386 P≈ 0.000

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85	67.800	1.623	-0.00277	0.00105	0.357	50	0.011
10'85	68.829	1.166	-0.00303	0.00076	0.501	50	0.000
12'85	70.014	1.145	-0.00181	0.00069	0.357	49	0.012
02'86	75.237	1.334	-0.00248	0.00102	0.334	49	0.019
08'86	71.839	1.056	-0.00617	0.00136	0.551	49	0.000
12'86	72.294	1.455	-0.00278	0.00118	0.344	43	0.024
01'87	74.037	1.081	-0.00405	0.00132	0.416	47	0.004
05'87	77.455	0.999	-0.00783	0.00161	0.578	49	0.000

Slopes grouped by Tukey tests

TRIP	Mean slope
06'85 10'85 12'85 02'86 08'86 12'86 01'87 05'87	-0.00300

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	64.851	0.699		
10'85	65.515	0.529		
12'85	67.399	1.249		
02'86	72.602	0.484	15.282	0.000
08'86	66.310	0.432	22.128	0.000
12'86	66.286	2.145		
01'87	69.980	0.438	7.157	0.008
05'87	71.466	0.453		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	66.905	0.886	75.714	<0.001
seasonality	4.027	0.656	6.139	<0.001
offset	-9.576	0.202	47.406	<0.001
slope	0.075	0.046	1.630	>0.100

Linear regression model

	coefficient	±SE	t	P
elevation				
slope				

Table 4.18 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **dry weight index (%) of the stomach** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance **STDWI**

Slopes are homogenous?

F≈	0.323	N=	384	P≈	0.944

TRIP is not significant?

F≈	13.146	N=	384	P≈	0.000

SIZE is not significant?

F≈	0.687	N=	384	P≈	0.408

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85							
12'85							
02'86							
08'86							
12'86							
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	5.412	0.205		
10'85	5.502	0.201		
12'85	5.333	0.194		
02'86	5.568	0.230	59.966	0.000
08'86	3.449	0.191	7.417	0.007
12'86	4.229	0.141		
01'87	4.574	0.180	6.737	0.010
05'87	3.853	0.201		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	6.364	0.130	48.954	<0.001
seasonality	0.708	0.091	7.780	<0.001
offset	1.597	0.117	13.650	<0.001
slope	-0.099	0.007	14.143	<0.001

Linear regression model

	coefficient	±SE	t	P
elevation				
slope				

Table 4.19 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **dry weight index (%) of the caeca** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance PCDWI

Slopes are homogenous?

F≈ 3.362 N= 385 P≈ 0.002

TRIP is not significant?

SIZE is not significant?

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85							
12'85							
02'86							
08'86	2.773	1.522	0.00713	0.00196	0.468	49	0.001
12'86							
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	16.560	0.750		
10'85	16.412	0.619	32.177	0.000
12'85	11.980	0.383	4.408	0.036
02'86	13.612	0.574	16.315	0.000
08'86	10.487	0.581		
12'86	9.231	0.518		
01'87	10.689	0.487	11.563	0.001
05'87	8.004	0.423		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	18.449	0.561	32.886	<0.001
seasonality	-0.291	0.151	1.927	>0.050
offset	-3.021	1.539	1.963	>0.050
slope	-0.372	0.031	12.000	<0.001

Linear regression model

	coefficient	±SE	t	P
elevation	18.300	0.501	36.513	0.000
slope	-0.365	0.027	-13.345	0.000

Table 4.20 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **dry weight index (%) of the gonad** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance **GDWI logged**

Slopes are homogenous?

F≈ 10.536 N= 391 P≈ 0.000

TRIP is not significant?

SIZE is not significant?

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85	0.259	0.159	0.00023	0.00010	0.348	43	0.022
10'85	1.518	0.173	0.00060	0.00011	0.618	49	0.000
12'85	2.206	0.129	0.00041	0.00008	0.603	47	0.000
02'86	0.204	0.085	0.00018	0.00006	0.387	46	0.008
08'86	-0.067	0.173	0.00077	0.00021	0.490	43	0.001
12'86	1.700	0.256	0.00067	0.00020	0.460	42	0.002
01'87	0.040	0.156	0.00093	0.00019	0.610	44	0.000
05'87	0.011	0.117	0.00040	0.00017	0.427	28	0.023

Slopes grouped by Tukey tests

TRIP	Mean slope
06'85 02'86	0.00021
10'85 12'85 08'86 12'86 01'87 05'87	0.00059

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	0.521	0.063	367.153	0.000
10'85	2.180	0.079	22.358	0.000
12'85	2.581	0.051	648.988	0.000
02'86	0.391	0.029	13.193	0.000
08'86	0.710	0.061	366.775	0.000
12'86	2.432	0.086	277.288	0.000
01'87	0.943	0.063	17.246	0.000
05'87	0.527	0.040		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	1.163	0.076	15.303	<0.001
seasonality	1.200	0.050	24.000	<0.001
offset	-2.000	0.078	-25.641	<0.001
slope	-0.008	0.004	-2.000	<0.050

Linear regression model

	coefficient	±SE	t	P
elevation				
slope				

Table 4.21 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **dry weight index (%) of the body wall** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance **BDWI**

Slopes are homogenous?

F≈ 2.980 N= 385 P≈ 0.005

TRIP is not significant?

SIZE is not significant?

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85	80.976	2.026	-0.00275	0.00131	0.291	50	0.041
10'85	73.363	1.985	-0.00495	0.00129	0.488	49	0.000
12'85	71.472	2.459	-0.00352	0.00148	0.327	49	0.022
02'86							
08'86	94.859	1.990	-0.00972	0.00257	0.483	49	0.000
12'86	86.179	3.630	-0.01083	0.00288	0.511	42	0.001
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope
06'85 10'85 12'85 08'86 12'86	-0.00481

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	78.607	0.894	44.976	0.000
10'85	66.631	1.572		
12'85	67.169	1.392	53.206	0.000
02'86	80.194	0.753	10.880	0.001
08'86	86.114	0.801	70.973	0.000
12'86	70.492	2.623	45.225	0.000
01'87	83.087	0.677	6.546	0.011
05'87	87.751	0.547		

Nonlinear regression model

	coefficient ±SE	t	P
elevation seasonality offset slope	Failed to fit after 20 iterations		

Linear regression model

	coefficient	±SE	t	P
elevation	67.927	1.375	49.415	0.000
slope	0.574	0.075	7.645	0.000

Table 4.22 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **calorific index (%) of the stomach** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance STCVI

Slopes are homogenous?

F≈ 0.429 N= 278 P≈ 0.884

TRIP is not significant?

F≈ 6.034 N= 278 P≈ 0.000

SIZE is not significant?

F≈ 0.340 N= 278 P≈ 0.560

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85							
12'85							
02'86							
08'86							
12'86							
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	6.145	0.315	10.065	0.002
10'85	5.789	0.232		
12'85	5.419	0.226		
02'86	5.329	0.249		
08'86	4.155	0.268		
12'86	4.483	0.171		
01'87	5.029	0.255		
05'87	4.471	0.472		

Nonlinear regression model

	coefficient ±SE	t	P
elevation	Failed to fit after 20 iterations		
seasonality			
offset			
slope			

Linear regression model

	coefficient	±SE	t	P
elevation	6.380	0.231	27.618	0.000
slope	-0.076	0.013	5.680	0.000

Table 4.23 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **calorific index (%) of the caeca** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance **PCCVI**

Slopes are homogenous?

F≈	0.814	N=	277	P≈	0.577

TRIP is not significant?

F≈	34.451	N=	277	P≈	0.000

SIZE is not significant?

F≈	0.994	N=	277	P≈	0.320

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85							
12'85							
02'86							
08'86							
12'86							
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	24.790	1.048	13.767	0.000
10'85	20.655	0.848	51.725	0.000
12'85	13.660	0.458		
02'86	15.413	0.813	8.024	0.005
08'86	12.159	1.003		
12'86	10.585	0.702	3.968	0.047
01'87	12.738	0.605		
05'87	11.893	0.906		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	24.263	0.960	25.274	<0.001
seasonality	-1.890	0.540	3.500	<0.001
offset	-0.802	1.412	0.568	>0.05
slope	-0.513	0.052	9.865	<0.001

Linear regression model

	coefficient	±SE	t	P
elevation				
slope				

Table 4.24 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **calorific index (%) of the gonad** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance **GCVI logged**

Slopes are homogenous?

F≈ 1.564 N= 275 P≈ 0.146

TRIP is not significant?

F≈ 172.663 N= 275 P≈ 0.000

SIZE is not significant?

F≈ 40.758 N= 275 P≈ 0.000

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85	1.826	0.172	0.00044	0.00012	0.494	49	0.001
12'85	2.242	0.133	0.00041	0.00008	0.597	48	0.000
02'86							
08'86							
12'86	1.776	0.261	0.00067	0.00021	0.460	48	0.002
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope
10'85 12'85 12'86	0.00047

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	0.777	0.083	207.633	0.000
10'85	2.295	0.072	16.604	0.000
12'85	2.671	0.050	524.053	0.000
02'86	0.455	0.029	8.443	0.004
08'86	0.773	0.089	268.734	0.000
12'86	2.524	0.090	214.210	0.000
01'87	1.041	0.088	18.077	0.000
05'87	0.433	0.081		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	1.364	0.080	16.825	<0.001
seasonality	1.337	0.052	25.712	<0.001
offset	-2.033	0.079	-25.734	<0.001
slope	-0.015	0.004	-3.750	<0.001

Linear regression model

	coefficient	±SE	t	P
elevation				
slope				

Table 4.25 Summary statistics for tests of homogeneity of slopes, analysis of covariance, significant regressions on particular occasions, and variation in standardised mean values for **calorific index (%) of the body wall** of *Acanthaster planci* of W≈1100g from Helix Reef.

Analysis of covariance **BCVI**

Slopes are homogenous?

F≈ 3.092 N= 278 P≈ 0.004

TRIP is not significant?

SIZE is not significant?

TRIP regressions (when significant)

TRIP	A	SE(A)	B	SE(B)	r	N	P
06'85							
10'85	67.050	2.702	-0.00380	0.00186	0.301	44	0.047
12'85	69.627	2.432	-0.00416	0.00148	0.382	48	0.007
02'86							
08'86							
12'86	84.665	4.201	-0.01200	0.00333	0.499	41	0.001
01'87							
05'87							

Slopes grouped by Tukey tests

TRIP	Mean slope
10'85 12'85 12'86	-0.00541

Temporal variations (standardised SIZE)

TRIP means, SE & PΔ (when significant)

TRIP	Mean	SE	F	PΔ
06'85	67.652	1.257	13.869	0.000
10'85	57.820	2.478	4.611	0.033
12'85	62.691	1.747	43.087	0.000
02'86	78.547	1.003		
08'86	82.234	1.254	25.690	0.000
12'86	68.499	2.211	18.492	0.000
01'87	79.546	0.892		
05'87	82.229	1.114		

Nonlinear regression model

	coefficient	±SE	t	P
elevation	62.060	1.721	36.060	<0.001
seasonality	-9.464	1.126	8.405	<0.001
offset	-2.189	0.170	12.876	<0.001
slope	0.732	0.097	7.546	<0.001

Linear regression model

	coefficient	±SE	t	P
elevation				
slope				

Figure 4.1 Categorisation of ray damage for injured *Acanthaster planci*.

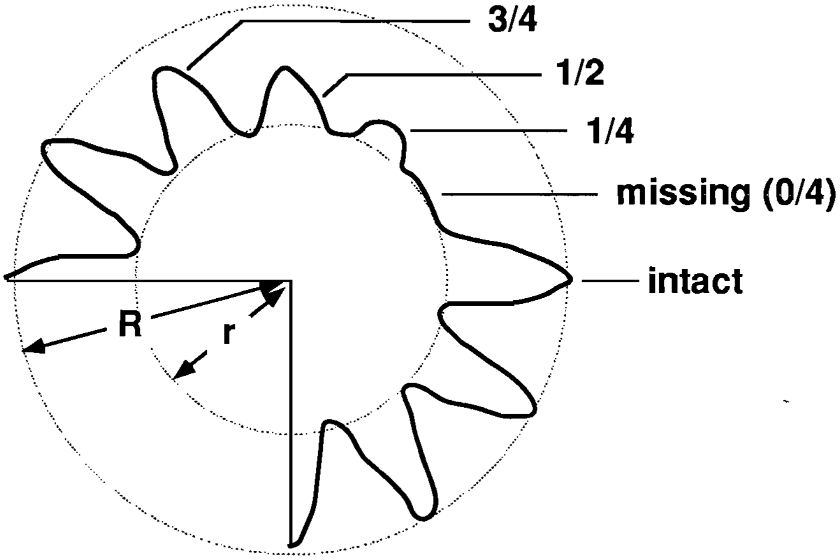


Figure 4.2 Generalised statistical procedure used to examine the variations of a particular parameter versus starfish size for successive collections of *Acanthaster planci* from Helix Reef.

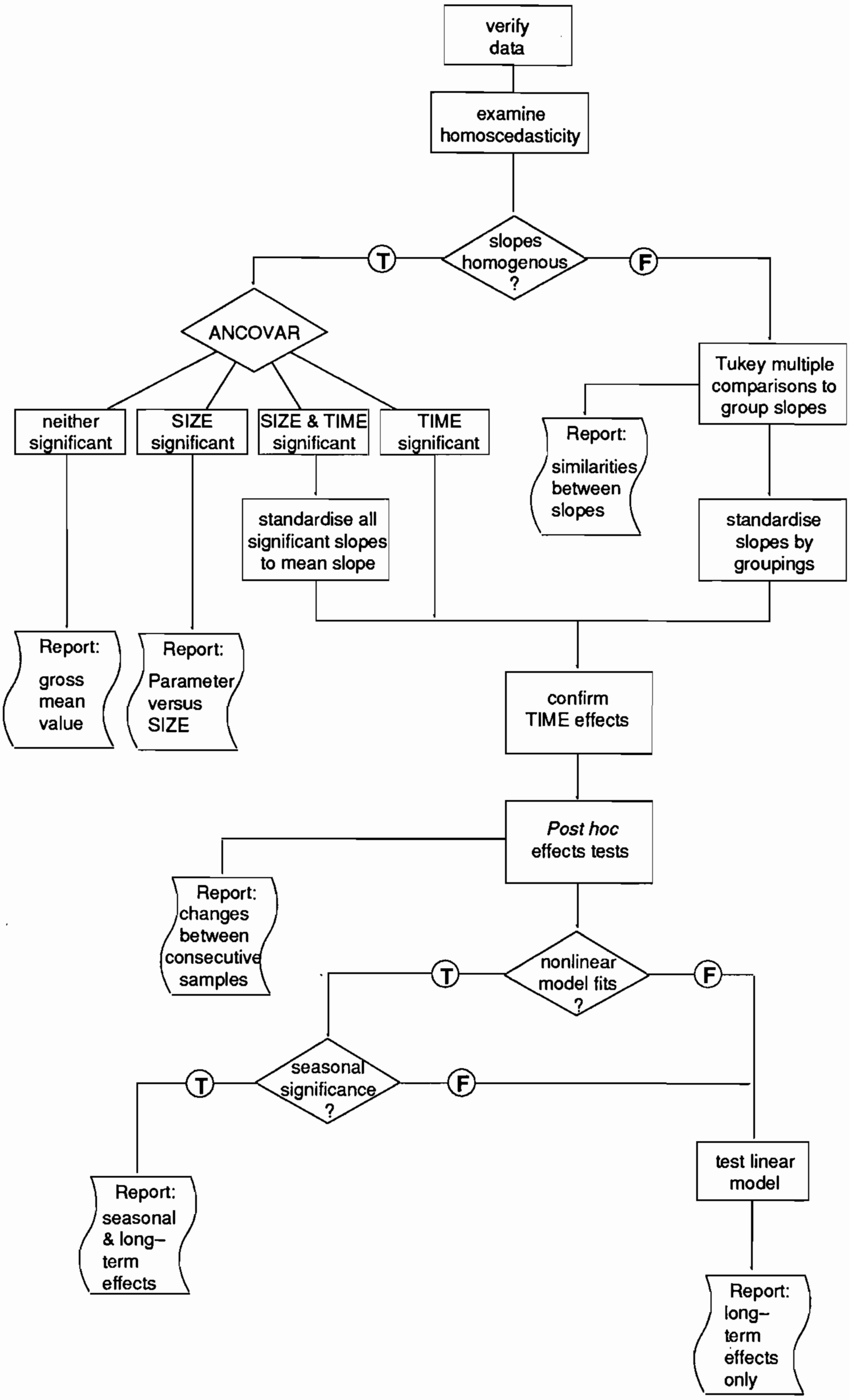
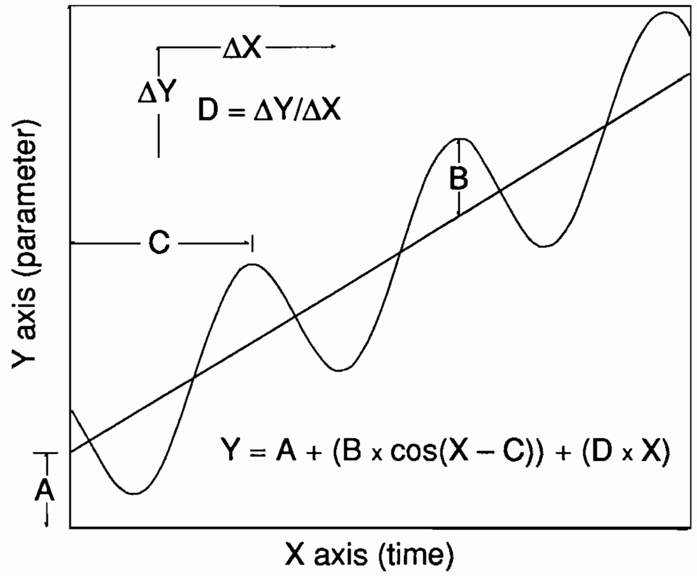


Figure 4.3 Generalised nonlinear model used to test for coincident seasonal and longer term effects on a particular parameter.



A = $\bar{Y}$ at time = 0
B = seasonal fluctuation of Y about $\bar{Y}$
C = offset (months) of annual maxima time = 0
D = long–term drift in $\bar{Y}$

Figure 4.4 Temporal variation in total perimeter *Acanthaster planci* count and estimated live coral cover on Helix Reef.

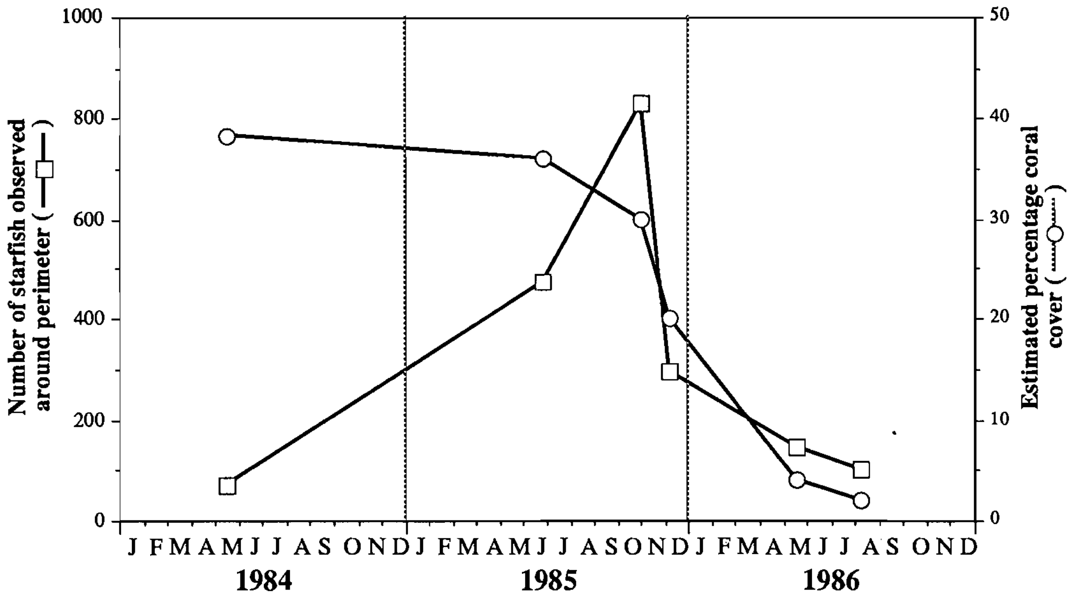


Figure 4.5 Prevailing winds and currents, broad scale reef zonation, approximate extent of utilisable habitat and position and length of a typical manta tow survey on Helix Reef.

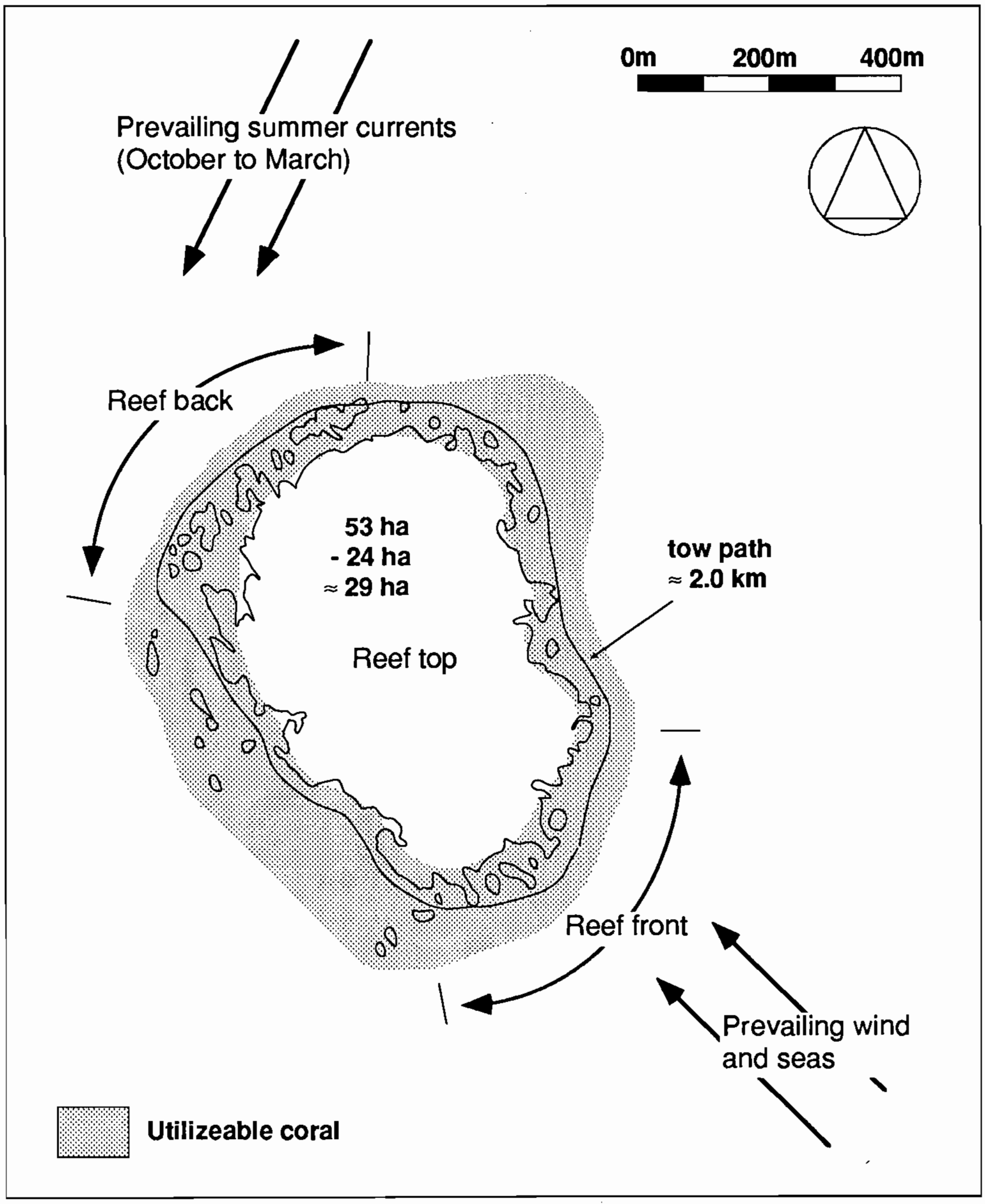
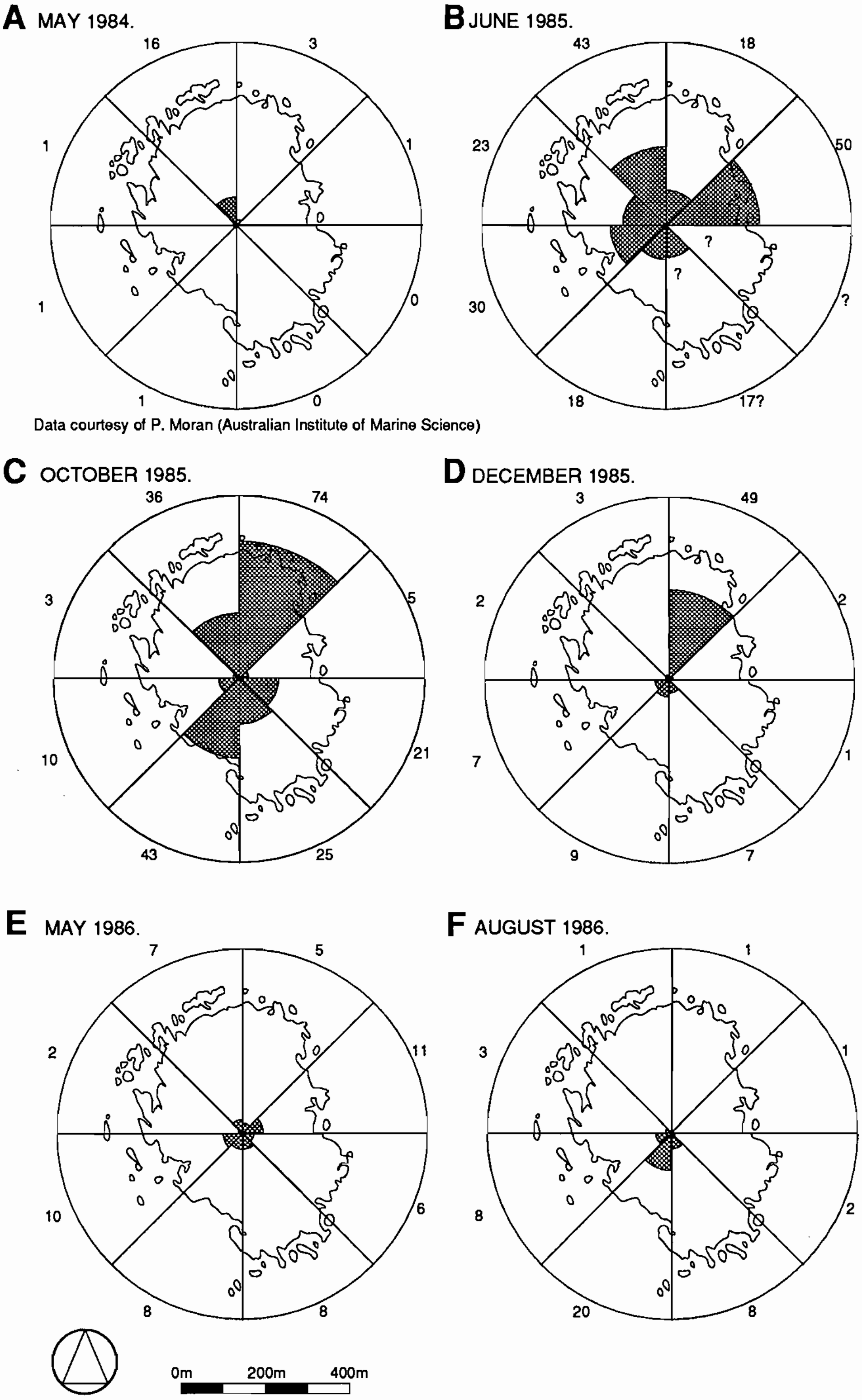


Figure 4.6 (A to F) Distribution and relative density of *Acanthaster planci* around Helix Reef. Numbers in each sector represent the mean starfish count for successive two minute segments of manta tows.



Data courtesy of P. Moran (Australian Institute of Marine Science)

Figure 4.7 Variations in mean diameter (D:mm), whole wet weight (W:g) and underwater weight (U:g) for *Acanthaster planci* from Helix Reef. Standard errors are shown (vertical bars), as are significant differences between successive trips (bold lines joining points).

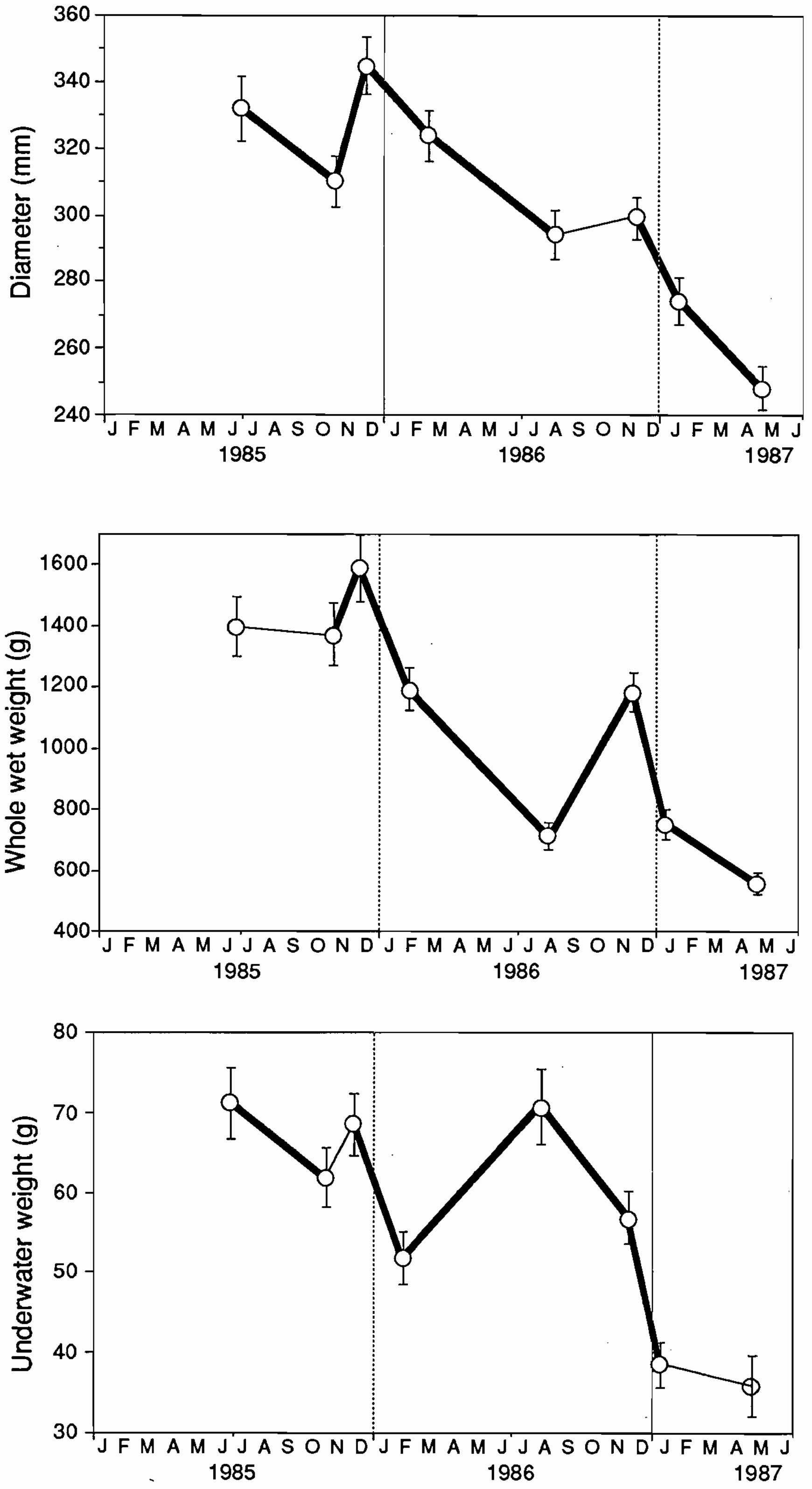


Figure 4.8 Frequency distributions of diameter (D:mm), whole wet weight (W:g), and underwater weight (U:g) for collections of *Acanthaster planci* from Helix Reef. Note: Sample size consisted of 50 starfish on all occasions.

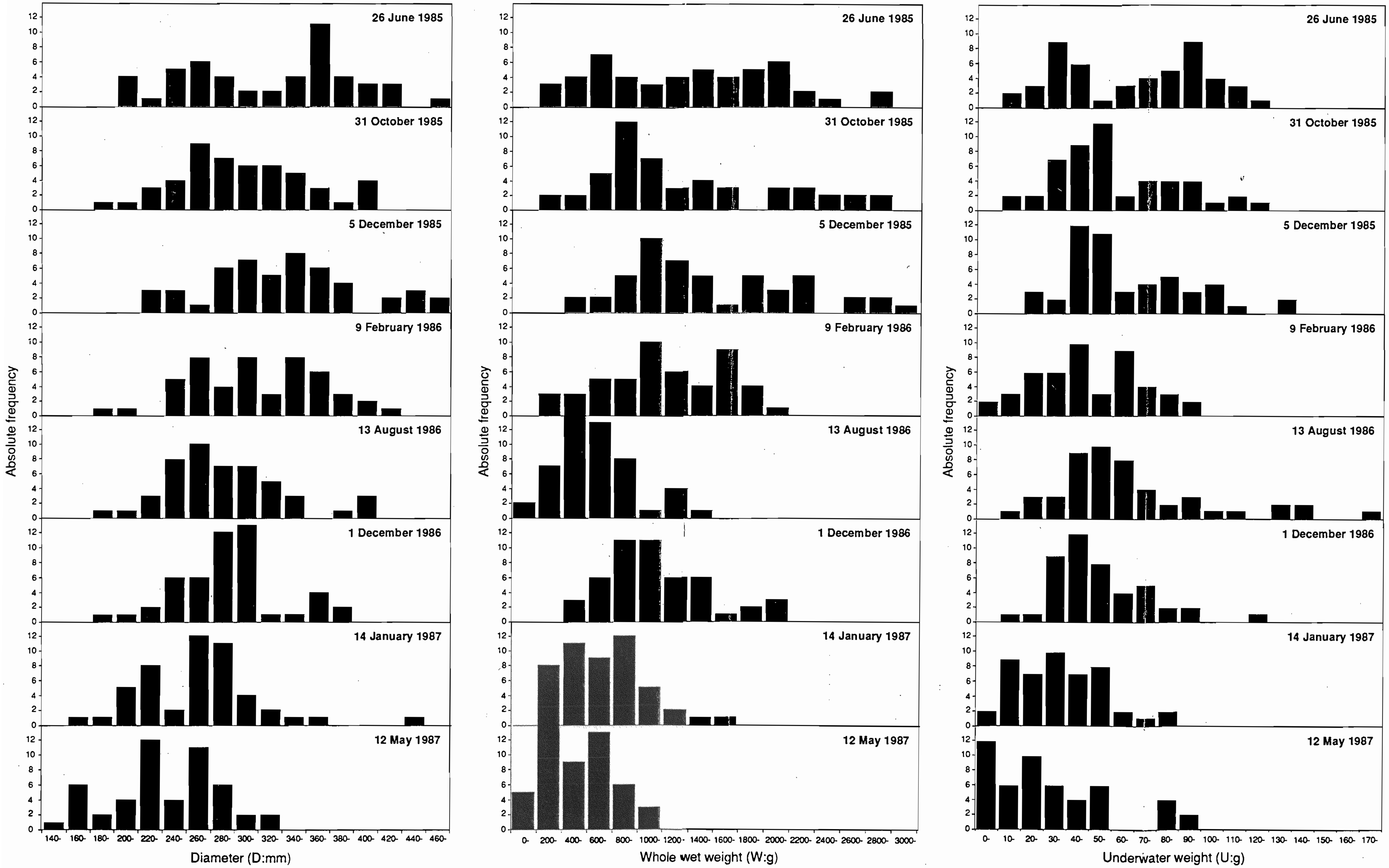


Figure 4.9 Mean ray count for *Acanthaster planci* collected from Helix Reef. Standard errors are shown (vertical bars), as are significant differences between successive trips (bold lines joining points).

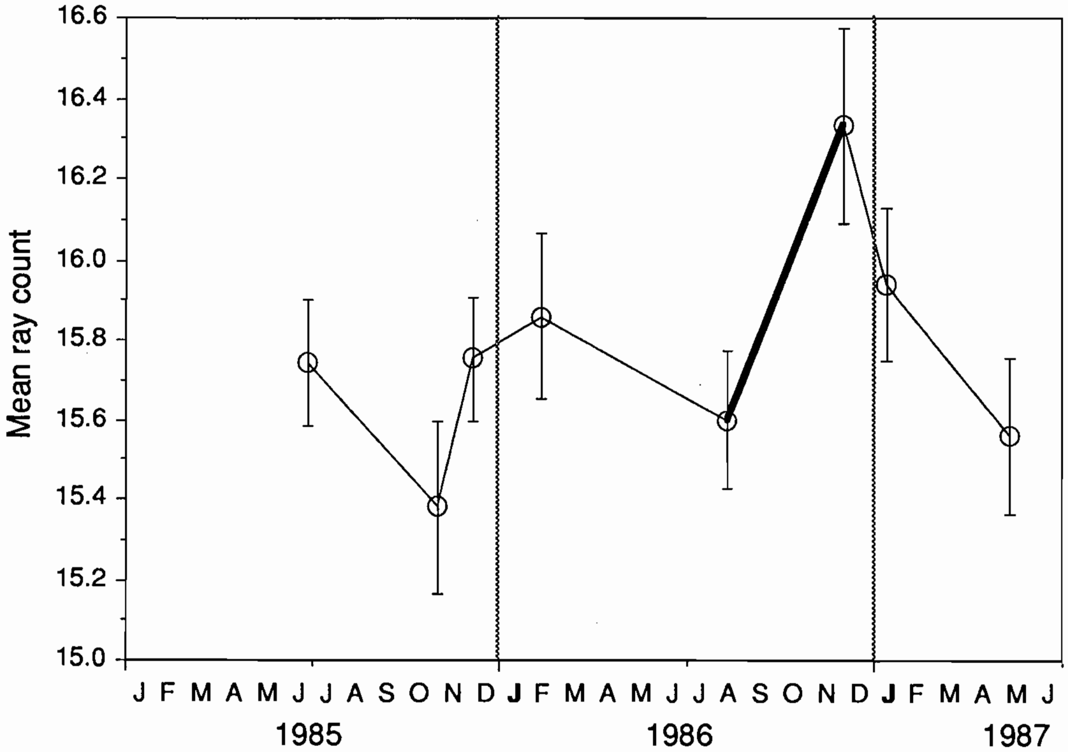


Figure 4.10 Mean arm spine length (ASL) to diameter (D) ratio (ASL/D) for *Acanthaster planci* from Helix Reef. Standard errors are shown (vertical bars), as are significant differences between successive trips (bold lines joining points).

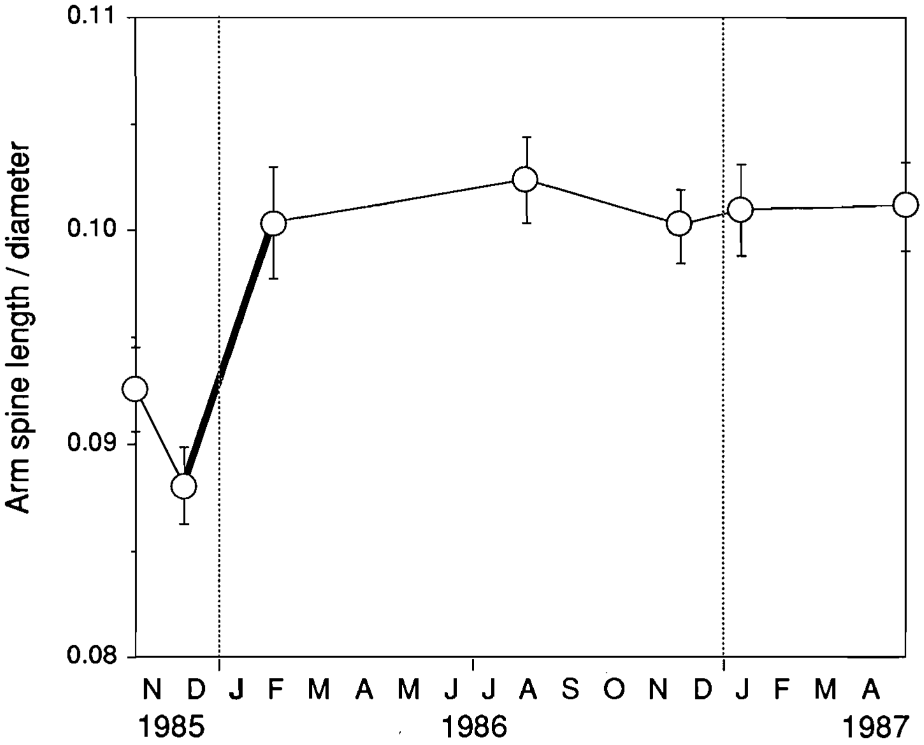


Figure 4.11 Percentage of individual *Acanthaster planci* with one or more injured rays versus time for successive samples from Helix Reef.

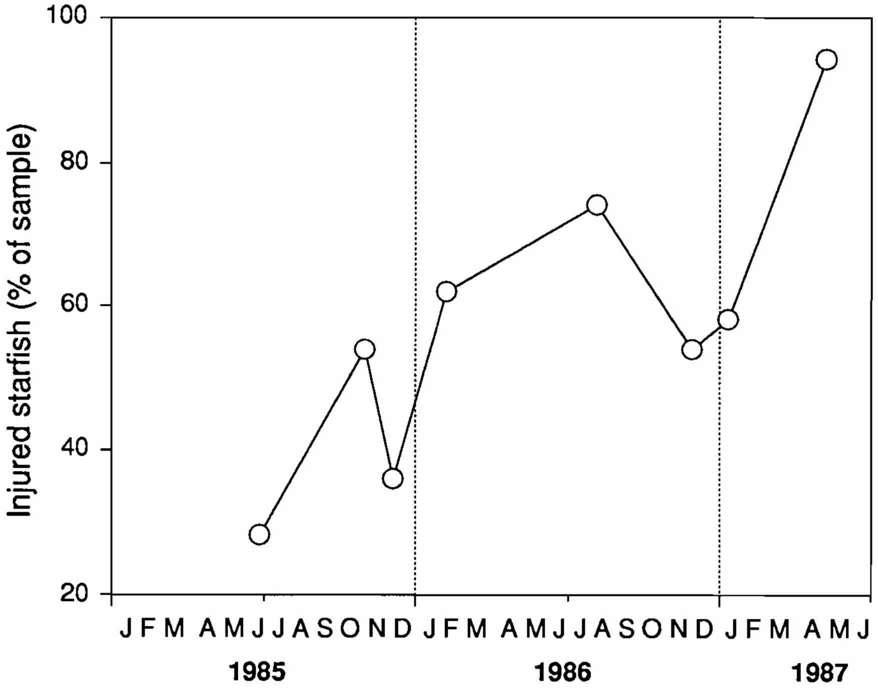


Figure 4.12 Severity of injury (missing % of total free ray length) for injured *Acanthaster planci* versus time for successive samples from Helix Reef.

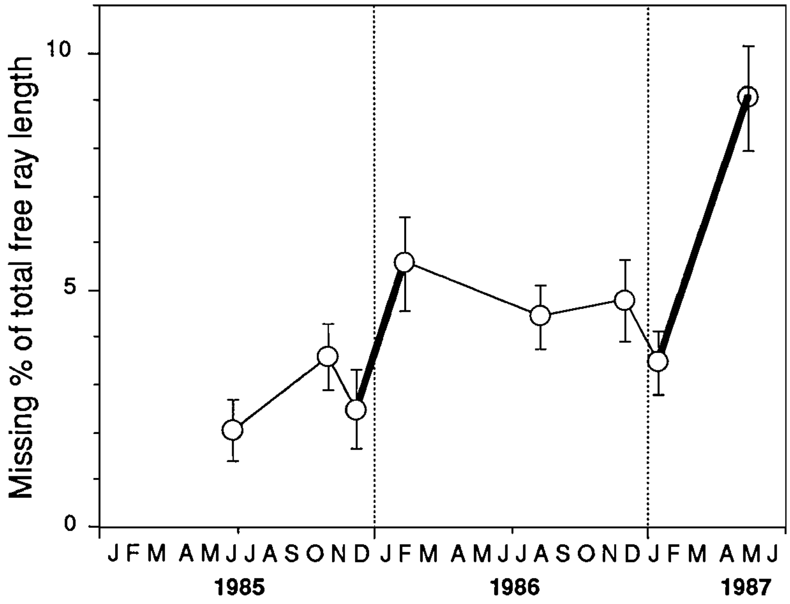


Figure 4.13 (A to P) Relationships between standardised mean water content (%), dry weight (g), calorific value (kJ.g^{-1} AFDW) and ash content (%) versus time for the stomach, caeca, gonad and body wall compartments of a three ray sector of *Acanthaster planci* W ≈1100g from Helix Reef. Mean values (circles), standard errors (vertical bars) and significant differences between successive trips (bold lines joining points) are indicated.

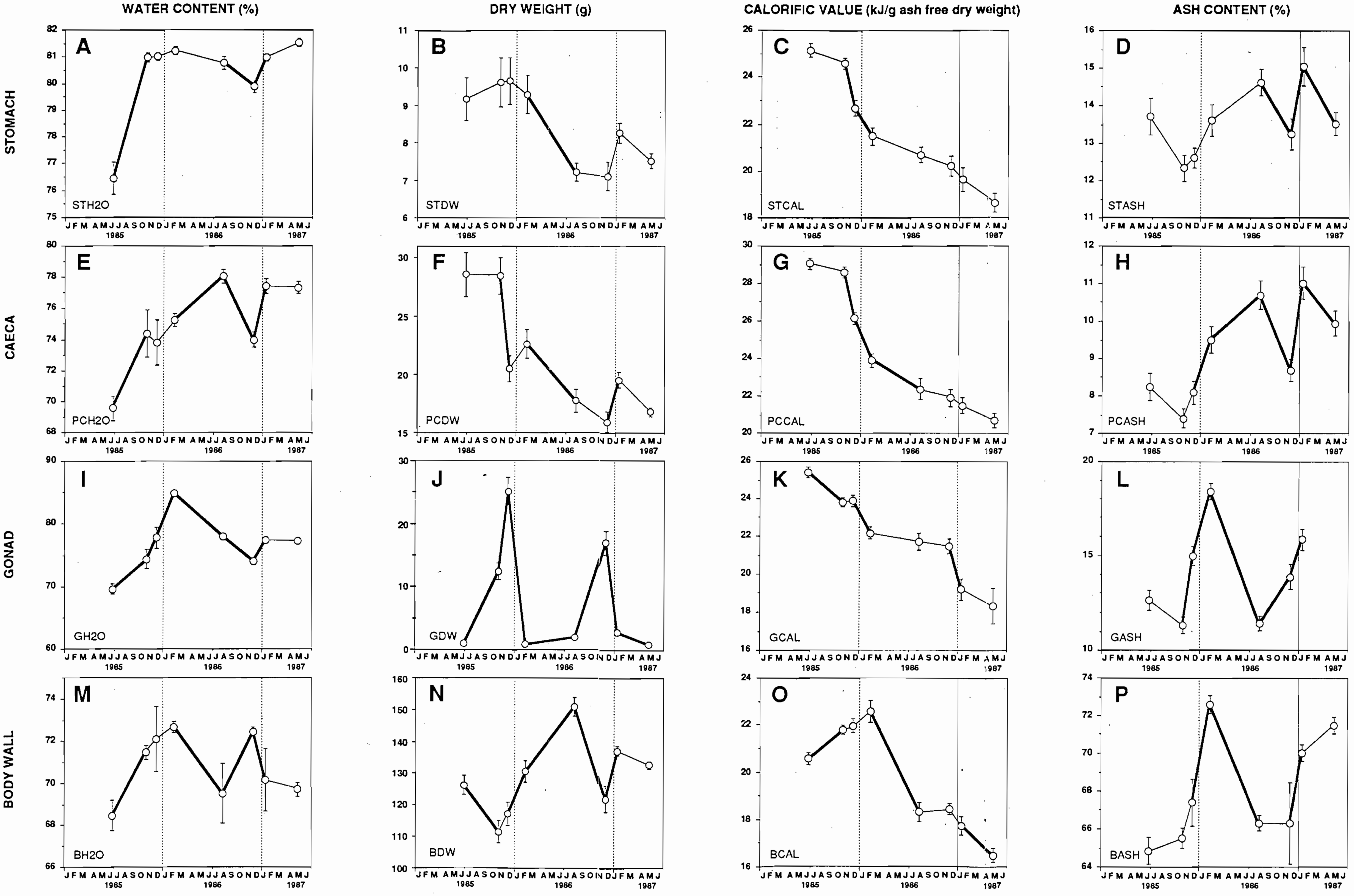


Figure 4.14 (A to D) Relationships between mean dry weight index (%) versus time for; (A) the stomach; (B) the caeca; (C) the gonad and; (D) the body wall compartments of *Acanthaster planci* from Helix Reef. Mean values (circles), standard errors (vertical bars) and significant differences between successive trips (bold lines joining points) are indicated.

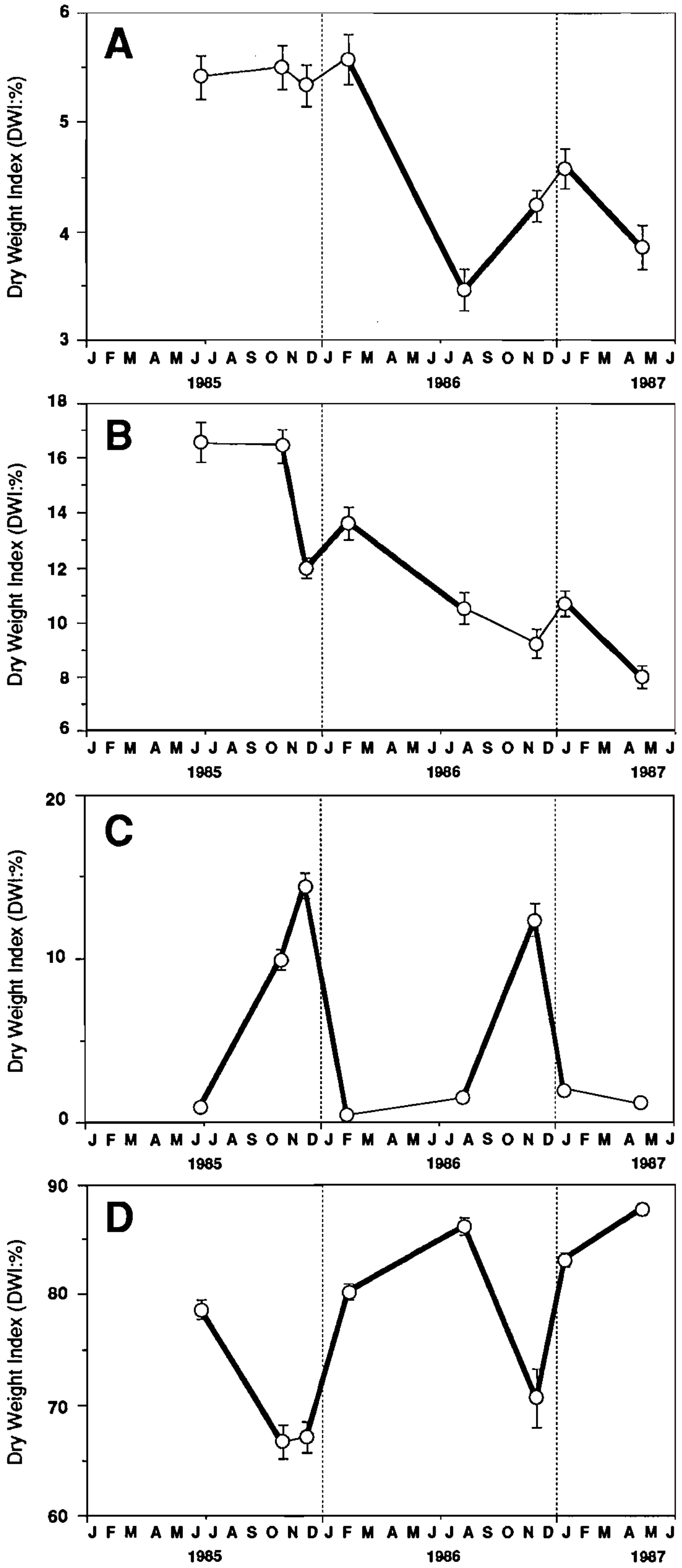


Figure 4.15 (A to D) Relationships between mean calorific index (%) versus time for; (A) the stomach; (B) the caeca; (C) the gonad and; (D) the body wall compartments of *Acanthaster planci* from Helix Reef. Mean values (circles), standard errors (vertical bars) and significant differences between successive trips (bold lines joining points) are indicated.

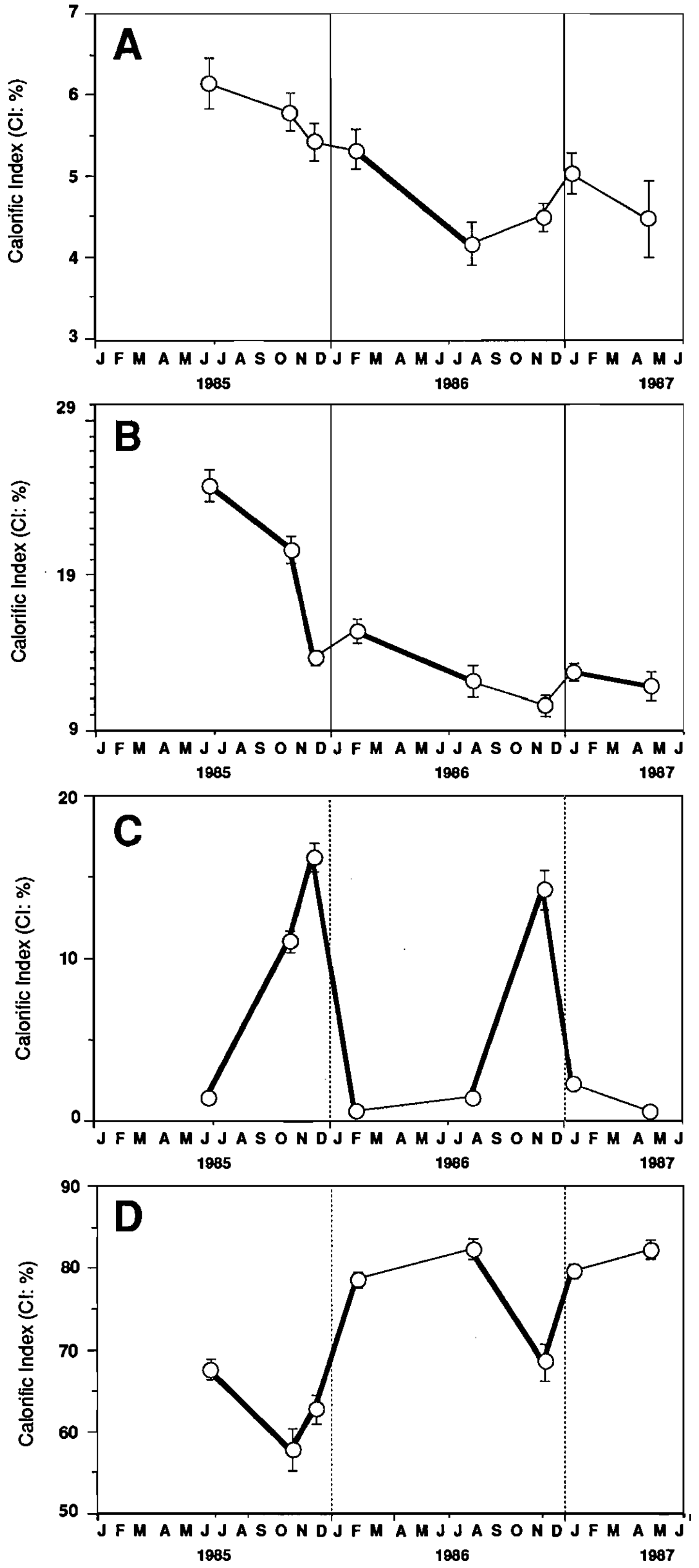


Figure 4.16 Variations in the macroscopic appearance of the stomach, caeca, gonad, body wall and spines of *Acanthaster planci* from Helix Reef.

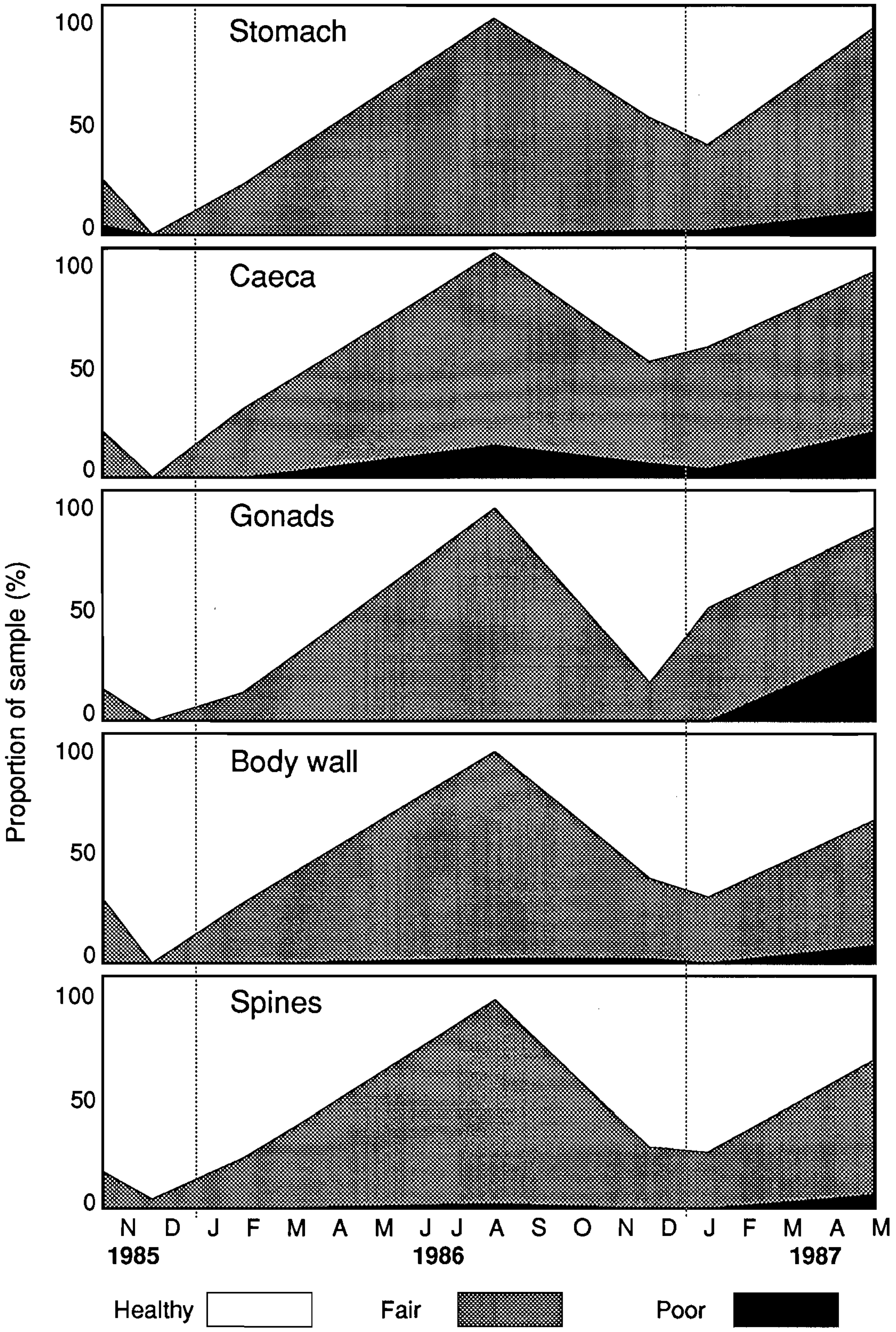


Figure 4.17 Presumed cohorts from the Helix Reef outbreak, interpreted on the basis of variations in underwater weight (based on Figure 4.8: U frequency distribution).

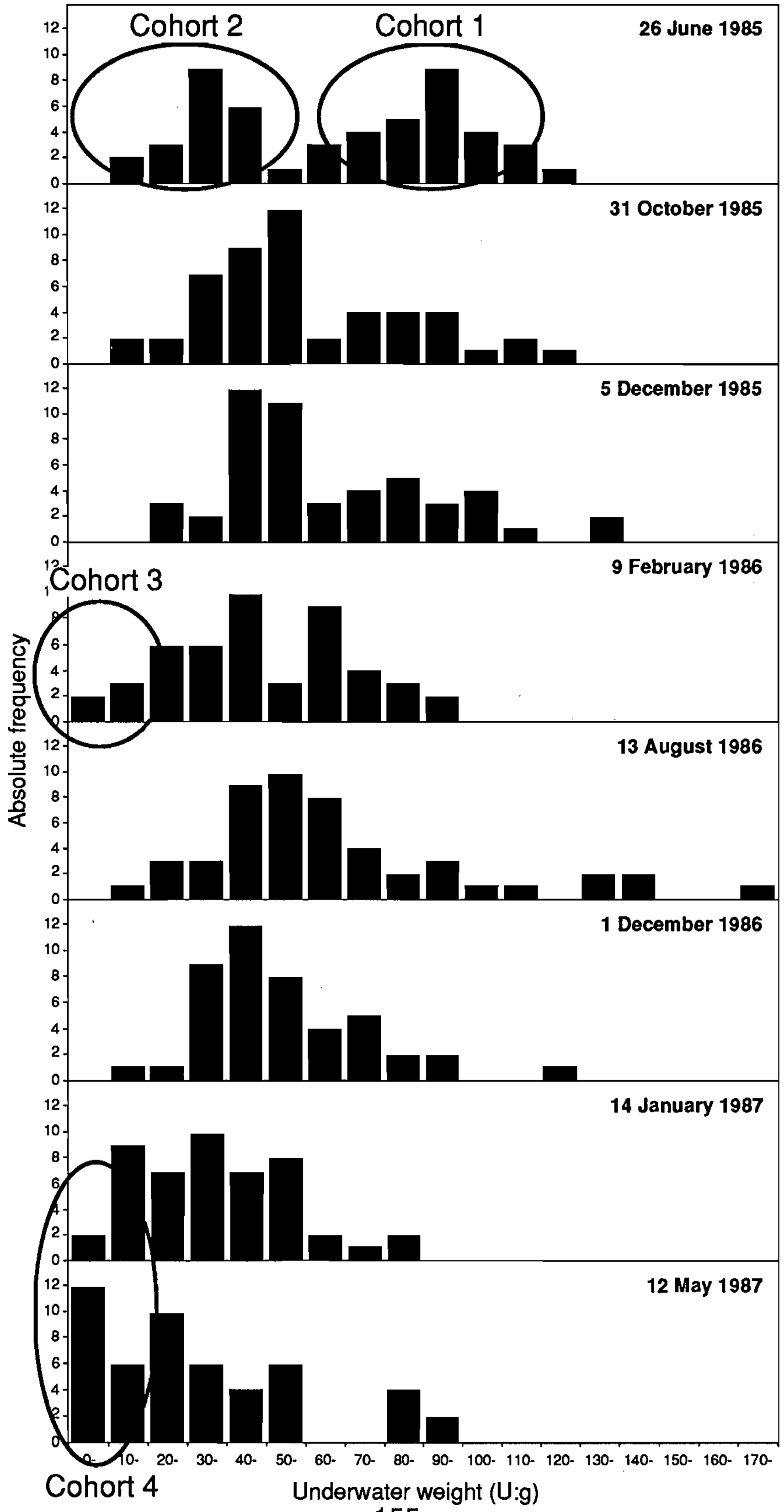
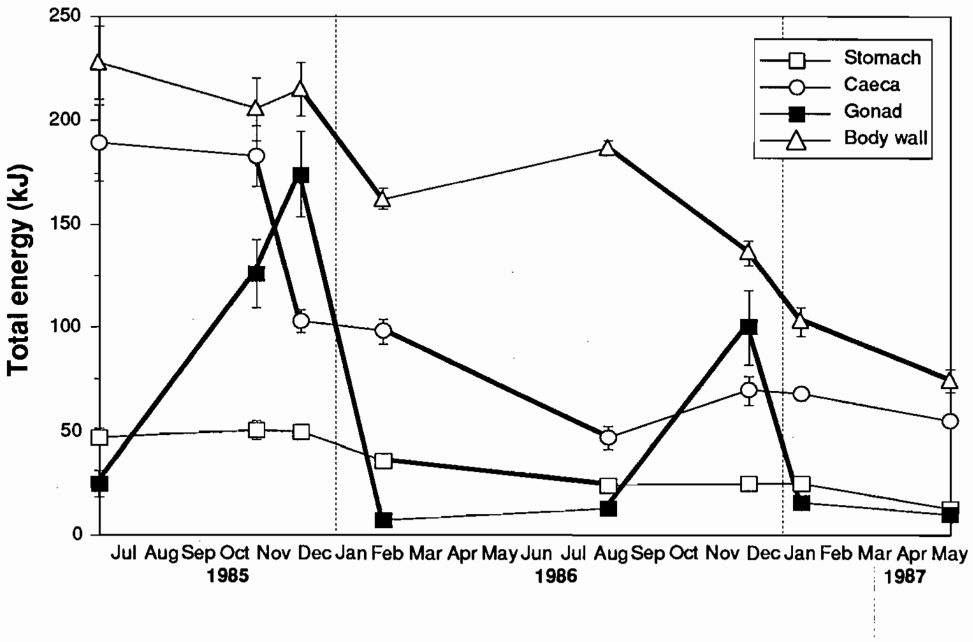


Figure 4.18 Variations in compartmental energy of the stomach, caeca, gonad and body wall versus time for a three ray sector of *Acanthaster planci* of W≈1100g from Helix Reef.



5. General discussion

5.1. Poly–cohort outbreaks and the "wave" theory

Kenchington (1977) proposed that the appearance of outbreaks on the Great Barrier Reef in the 1960s - 1970s could be described as a "wave" of successive recruitments being swept progressively further south each year from a primary outbreak as a result of south-moving water masses during the summer breeding season. The same hypothesis fits the pattern of outbreaks on the GBR in the 1980s equally well. Recent work by Dight *et al.* (1988) supports the validity of Kenchington's model.

A. planci larvae have been recorded as attaining late brachiolaria stage in as little as 12 days (Olson, 1987) or as long as 42+ days (Birkeland and Lucas, 1990), suggesting a protracted period in which they are competent to settle. As larval-carrying water masses move southward through the dispersed mid-shelf reef areas, the extended competency period produces a recruitment zone extending over a latitudinal range according to the velocity of southward currents and the competency period. The same process happens when these recruits grow to maturity, except that the recruitment zone extends from the earliest competency of larvae from the northernmost populations to the latest competency of larvae from the southernmost populations. The latitudinal range of recruitment therefore increases with each successive spawning. The interpretation that the Helix Reef outbreaks may have consisted of four successive cohorts is consistent with Kenchington's model. This interpretation forms the basis for the testable hypothesis that the number of cohorts in an outbreak will increase towards the south.

5.2. Responses of *Acanthaster planci* to starvation

A. planci, like many echinoderms, shrink in size when subject to starvation. Lawrence and Lane (1982) suggest that echinoderm biomass is, in general, limited by food, but that density is not. Shrinkage is consistent with this. However, if the degree and duration of starvation is severe enough, *A. planci* will die. *Acanthaster* is thus commonly density-limited and in this respect is an atypical echinoderm.

Food-limited density in outbreak populations is not surprising; *A. planci* is an efficient coral predator and the population densities achieved in outbreaks far exceed the carrying capacity of the environment – mortality from food limitation simply results from the same factors that lead to shrinkage, *in extremis*. Thus *A. planci* may provide an example of the postulated but undemonstrated (Lawrence, 1987b) trade-off between survival and reproduction in asteroids.

The level of the shrinkage / mortality response depends upon starfish size. Large starfish are more prone to mortality caused by food limitation than smaller conspecifics. This was evident in both the enforced starvation experiment and the Helix Reef population. There was no evidence from either the starvation studies or the Helix Reef population that a critical size existed below which starved starfish were able to grow and above which starfish shrank. On the contrary, it appears that shrinkage and mortality are manifest increasingly severely and in successively smaller starfish as the severity of food limitation increases.

As starvation progresses, the pattern of resorption of nutrients from various body compartments changes. When food availability is high, gonadal growth occurs without penalty to other compartments. As food availability declines, gonadal growth occurs at the expense of caecal reserves. Gonadal growth continues to occur under conditions of extreme starvation, but at the expense of the body wall. In these circumstances gonadal biomass does not appear to decline, although gonadal energy levels may do. Gonadal dry weights and indices were almost identical even when the body wall was being resorbed to enable gonadal growth. *Patiria miniata* and *Pisaster ochraceus* have been shown to exhibit gonadal growth while starvation decreased the size of the body wall (Nimitz, 1971). *Sclerasterias mollis* has shown concurrent shrinkage and gonadal development (albeit neither pronounced) in the first two months of a four month starvation period (Xu and Barker, 1990). The extent of gonadal development observed in *A. planci* from Helix Reef and Pelorus Island represents extreme reproductive effort.

5.3. Implications for population control

The propensity of A. *planci* for reproduction, even under conditions of extreme food-limitation, suggests that an outbreak population may continue to produce large quantities of gametes even when coral density is quite low. A small population of starfish, even with sub-optimal food availability, may reproduce over many years, remaining an effective larval source for infestation of other reefs in down-current areas. Starfish may only be able to reproduce for one year if they consume coral to the point where mortality results from starvation. Starfish may reproduce in several successive years if manual removal is incomplete and results in a lower predator / prey ratio. A "successful" control program may reduce *A. planci* density to the carrying capacity of the reef (as opposed to "background" levels), but could conceivably result in a remnant population that persisted through several subsequent spawning seasons.

If the object of the control program is to minimise coral mortality on the infested reef then spawning potential has no bearing. However, if the objective is to minimise the potential for subsequent outbreaks (either on the same reef via self-seeding or on down-current reefs) then consideration should be given to minimising the potential for subsequent spawning events. It may be better to allow the infested reef to be denuded, with the likelihood that starfish will starve, than to mount a partially successful control program, with the likelihood that a long term breeding population will remain. It is plausible that incomplete control exercises could favour the development of chronic situations as described by Birkeland and Lucas (1990).

5.4. Life strategies of *Acanthaster planci*

Lawrence (1990), categorised echinoderm life strategies according to Grime's model (Grime,1977) of the effects of stress and disturbance on biomass (Figure 5.1). **Competitors** are adapted to low stress (high productivity), low disturbance (long duration) environments, **stress-tolerators** to high stress (low productivity), low disturbance (long duration) environments and **ruderals** to low stress (high productivity), high disturbance (short duration) environments. High stress (low productivity), high disturbance (short duration) environments are described as the non-permissible fourth permutation of Grime's model (Lawrence, 1990). *Acanthaster planci* is ascribed to the competitor strategy on the basis of a suite of characteristics relating to the partitioning of resources between maintenance, protection and somatic and gonadal production. *A planci* is described as an active forager found in regions of high resource availability and long duration, being long-lived with a high potential for resource acquisition, and being iteroparous with high fecundity and a relatively ineffective protection against disturbance (predation). Other characteristics of competitive echinoderms include low reproductive effort.

In this study, resource availability was initially very high, but rapidly declined to well below maintenance levels. Although subject to neither physical disturbance nor a noticeable increase in predation, the extreme decline in food availability and the profound changes in community composition that resulted as a direct consequence of *Acanthaster* predation suggest a short habitat duration. The outbreak population likely consisted of several cohorts. Under these circumstances starfish are unlikely to have survived the 5 to 8 years commonly quoted as their life span (Birkeland and Lucas, 1990), but may have survived for only a few years. Reproductive output, at least in terms of biomass, remained high. Reproductive effort, judged by the accumulation of energy and biomass as gametes at the expense of the body wall and caeca during a period of low food availability, was very high. In the early stages of the outbreak (prior to food limitation in the summer of 1985-1986), the life strategy is best characterised as ruderal (large amounts of resources, longevity limited by food availability and sustained reproduction even under stress). The "impossible fourth permutation" (Lawrence, 1990) is briefly realised in the decline phase of the outbreak. In this situation, disturbance (loss of biomass related to shrinkage or mortality caused by extreme food shortage) and stress (limited or zero production, also related to extreme food shortage) are both maximised. The continuation of high reproductive effort by food-limited recruits during the decline phase (including resorption of the body wall to facilitate reproductive partitioning), rather than maintenance of the body wall at the expense of reproduction, favours only the potential offspring - the "impossible fourth permutation" for *A. planci* populations in the decline phase of an outbreak is a brief burst of altruism.

There is no all–encompassing life strategy for *A. planci.* At low densities relative to their food supply they may be long-lived, high reproductive output, low reproductive effort **competitors**. At higher densities they may be short duration, unstable, high reproductive effort **ruderals**, and as food runs out, their maintenance of reproductive output at the expense of functionality and structural integrity, a strategy presumed to lead to their eventual death, qualifies them briefly as **altruists**.

Figure 5.1 Life strategies of echinoderms classified according to stress and disturbance (after Lawrence, 1990).

Intensity of stress (Grime, 1979)
growth stress (Sibly and Calow, 1989)

Intensity of disturbance
(Grime, 1979)
mortality stress
(Sibly and Calow, 1989)

	low	high
low	competitor	stress-tolerator
high	ruderal	

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7. Appendix A

7.1. Data storage

Data are stored in and accessible from the following locations;

Original strip recordings, field observations and laboratory measurements

- Department of Zoology, James Cook University of North Queensland

Microcomputer data set

- Department of Zoology, James Cook University of North Queensland
- Dr J.S. Lucas c/- Department of Zoology, James Cook University of North Queensland
- the author, 22 Sallows St, Pallarenda, Qld. 4810

Microcomputer data sets are stored in the following dBase files;

OIRS.dbf
Contains raw and calculated data (with the exception of respiration measurements) from the starvation study (Chapter Three) conducted at Orpheus Island Research Station.

HELIX.dbf
Contains raw and calculated data from the long term study (Chapter Four) conducted at Helix Reef.

KEEPER.dbf
Contains raw and calculated data from a long term study conducted at Keeper Reef but not reported here.

Storage media include 5.25 inch floppy disks and 3.5inch floppy disks.

7.2. Data formats

The following data descriptions are included to facilitate the use of existing data sets by interested researchers.

```
Structure for database: D:helix.dbf
Number of data records:     393
Date of last update   : 08/24/90
Field  Field Name  Type       Width    Dec
    1  CODE        Character      4
    2  SEX         Character      1
    3  ST_PAN      Numeric        7      4
    4  ST_PAN_WET  Numeric        8      4
    5  ST_PAN_DRY  Numeric        8      4
    6  ST_BC       Numeric        7      4
    7  ST_BC_SAMP  Numeric        7      4
    8  ST_DEF1     Numeric        4      2
    9  ST_DEF2     Numeric        4      2
   10  ST_AC       Numeric        7      4
   11  ST_AC_SAMP  Numeric        7      4
   12  ST_ASHED    Numeric        7      4
   13  PC_PAN      Numeric        7      4
   14  PC_PAN_WET  Numeric        8      4
   15  PC_PAN_DRY  Numeric        8      4
   16  PC_BC       Numeric        7      4
   17  PC_BC_SAMP  Numeric        7      4
   18  PC_DEF1     Numeric        4      2
   19  PC_DEF2     Numeric        4      2
   20  PC_AC       Numeric        7      4
   21  PC_AC_SAMP  Numeric        7      4
   22  PC_ASHED    Numeric        7      4
   23  G_PAN       Numeric        7      4
   24  G_PAN_WET   Numeric        8      4
   25  G_PAN_DRY   Numeric        8      4
   26  G_BC        Numeric        7      4
   27  G_BC_SAMP   Numeric        7      4
   28  G_DEF1      Numeric        4      2
   29  G_DEF2      Numeric        4      2
   30  G_AC        Numeric        7      4
   31  G_AC_SAMP   Numeric        7      4
   32  G_ASHED     Numeric        7      4
   33  B_PAN       Numeric        7      4
   34  B_PAN_WET   Numeric        8      4
   35  B_PAN_DRY   Numeric        8      4
   36  B_BC        Numeric        7      4
   37  B_BC_SAMP   Numeric        7      4
   38  B_DEF1      Numeric        4      2
   39  B_DEF2      Numeric        4      2
   40  B_AC        Numeric        7      4
   41  B_AC_SAMP   Numeric        7      4
   42  B_ASHED     Numeric        7      4
   43  TRIPNUMB    Numeric        1
   44  DATE        Numeric        5      2
   45  CORALCOVER  Numeric        2
   46  COMBWETWT   Numeric        8      4
   47  COMBDRYWT   Numeric        8      4
   48  STWET       Numeric        8      4
   49  STDRY       Numeric        8      4
   50  STH2O       Numeric        4      1
```

```
   51  STCAL       Numeric        5      2
   52  STASH       Numeric        4      1
   53  PCWET       Numeric        8      4
   54  PCDRY       Numeric        8      4
   55  PCH2O       Numeric        4      1
   56  PCCAL       Numeric        5      2
   57  PCASH       Numeric        4      1
   58  GWET        Numeric        8      4
   59  GDRY        Numeric        8      4
   60  GH2O        Numeric        4      1
   61  GCAL        Numeric        5      2
   62  GASH        Numeric        4      1
   63  BWET        Numeric        8      4
   64  BDRY        Numeric        8      4
   65  BH2O        Numeric        4      1
   66  BCAL        Numeric        5      2
   67  BASH        Numeric        4      1
   68  DIAM        Numeric        2
   69  UWWT        Numeric        3
   70  WETWT       Numeric        4
   71  ASL         Numeric        2
   72  NUMARMS     Numeric        2
   73  N0          Numeric        1
   74  N1          Numeric        1
   75  N2          Numeric        1
   76  N3          Numeric        1
   77  ARMDAMAGE   Numeric        4      1
   78  PARTARMS    Numeric        5      2
   79  SPCOND      Numeric        1
   80  STCOND      Numeric        1
   81  PCCOND      Numeric        1
   82  GCOND       Numeric        1
   83  BCOND       Numeric        1
   84  HEALTH      Numeric        2
   85  NOTES       Character     20
   86  STDWI       Numeric        4      1
   87  PCDWI       Numeric        4      1
   88  GDWI        Numeric        4      1
   89  BDWI        Numeric        4      1
   90  STCVI       Numeric        4      1
   91  PCCVI       Numeric        4      1
   92  GCVI        Numeric        4      1
   93  BCVI        Numeric        4      1
   94  ASLRATIO    Numeric        4      1
   95  STCALTOT    Numeric       10      4
   96  PCCALTOT    Numeric       10      4
   97  GCALTOT     Numeric       10      4
   98  BCALTOT     Numeric       10      4
   99  COMBCALS    Numeric       10      4
** Total **                     549
```

Descriptions of field contents follow;

CODE:	Five character code to identify individual starfish from each trip
SEX:	Male, female or indeterminate
ST_PAN:	Weight of dish into which dissected stomach portion was placed
ST_PAN_WET:	Weight of above dish including freshly dissected stomach portion
ST_PAN_DRY:	Weight of dish plus dried stomach portion after drying to constant

	weight
ST_BC:	Weight of nickel crucible into which sample of stomach was placed for energetic determinations
ST_BC_SAMP:	Weight of above crucible including sample of dried stomach tissue
ST_DEF1:	Deflection of strip chart recorder prior to ballistic bomb calorimeter firing
ST_DEF2:	Deflection of strip chart recorder after ballistic bomb calorimeter firing
ST_AC:	Weight of porcelain crucible into which sample of stomach was placed for ash determinations
ST_AC_SAMP:	Weight of above crucible including sample of dried stomach tissue
ST_ASHED:	Weight of above crucible after ashing to a constant weight in a muffle furnace
PC_PAN:	Similar to ST_PAN above
PC_PAN_WET:	Similar to ST_PAN_WET above
PC_PAN_DRY:	Similar to ST_PAN_DRY above
PC_BC:	Similar to ST_BC above
PC_BC_SAMP:	Similar to ST_BC_SAMP above
PC_DEF1:	Similar to ST_DEF1 above
PC_DEF2:	Similar to ST_DEF2 above
PC_AC:	Similar to ST_AC above
PC_AC_SAMP:	Similar to ST_AC_SAMP above
PC_ASHED:	Similar to ST_ASHED above
G_PAN:	Similar to ST_PAN above
G_PAN_WET:	Similar to ST_PAN_WET above
G_PAN_DRY:	Similar to ST_PAN_DRY above
G_BC:	Similar to ST_BC above
G_BC_SAMP:	Similar to ST_BC_SAMP above
G_DEF1:	Similar to ST_DEF1 above
G_DEF2:	Similar to ST_DEF2 above
G_AC:	Similar to ST_AC above
G_AC_SAMP:	Similar to ST_AC_SAMP above
G_ASHED:	Similar to ST_ASHED above
B_PAN:	Similar to ST_PAN above
B_PAN_WET:	Similar to ST_PAN_WET above
B_PAN_DRY:	Similar to ST_PAN_DRY above
B_BC:	Similar to ST_BC above
B_BC_SAMP:	Similar to ST_BC_SAMP above
B_DEF1:	Similar to ST_DEF1 above
B_DEF2:	Similar to ST_DEF2 above
B_AC:	Similar to ST_AC above
B_AC_SAMP:	Similar to ST_AC_SAMP above
B_ASHED:	Similar to ST_ASHED above
TRIPNUMB:	Numeric value representing trip number for use in SYSTAT
DATE:	Start date of trip within which starfish was collected
CORALCOVER:	Estimated live coral cover
COMBWETWT:	Sum of wet weights of stomach, caeca, gonad and body wall portions
COMBDRYWT:	Sum of dry weights of stomach, caeca, gonad and body wall portions
STWET:	Wet weight of dissected stomach portion calculated as ST_PAN_WET – ST_PAN
STDRY:	Dry weight of dissected stomach portion calculated as ST_PAN_DRY – ST_PAN

STH2O:	Percentage water content of the stomach calculated as (STWET – STDRY) / (STWET) * 100
STCAL:	Calorific value (kJ .g^{-1} AFDW) of the stomach calculated from ballistic bomb calorimeter calibration as a function of deflection (ST_DEF1 – ST_DEF2) and bombing sample weight (ST_BC_SAMP – ST_BC). Includes endothermy correction for heat absorbed by salts (principally carbonate) present in sample (refer Methods)
STASH:	Percentage ash content of the stomach calculated as 1 – (ST_AC_SAMP – ST_ASHED) / (ST_AC_SAMP – ST_AC) * 100
PCWET:	Similar to STWET above
PCDRY:	Similar to STDRY above
PCH2O:	Similar to STH2O above
PCCAL:	Similar to STCAL above
PCASH:	Similar to STASH above
GWET:	Similar to STWET above
GDRY:	Similar to STDRY above
GH2O:	Similar to STH2O above
GCAL:	Similar to STCAL above
GASH:	Similar to STASH above
BWET:	Similar to STWET above
BDRY:	Similar to STDRY above
BH2O:	Similar to STH2O above
BCAL:	Similar to STCAL above
BASH:	Similar to STASH above
DIAM:	Starfish diameter in cm
UWWT:	Underwater weight in g
WETWT:	Whole wet weight in g
ASL:	Length of longest spines in mm
NUMARMS:	Total number of rays (damaged or intact)
N0:	Number of rays injured such that ray length = disc diameter (free ray length = 0)
N1:	Number of rays injured such that free ray length = 1/4 of ray length of an undamaged ray
N2:	Number of rays injured such that free ray length = 1/2 of ray length of an undamaged ray
N3:	Number of rays injured such that free ray length = 3/4 of ray length of an undamaged ray
ARMDAMAGE:	Percentage damage to total free ray length calculated as (sum of free ray lengths) / NUMARMS * 100
PARTARMS:	sum of free ray lengths
SPCOND:	Macroscopic classification of appearance of starfish spines; 1=poor, 2=mediocre, 3=good
STCOND:	Macroscopic classification of appearance of the dissected stomach portion; 1=poor, 2=mediocre, 3=good
PCCOND:	Similar to STCOND above
GCOND:	Similar to STCOND above
BCOND:	Similar to STCOND above
HEALTH:	Sum, for each compartment (including spines), of COND – 1 such that 0 is equivalent to all five compartments ranking POOR and 10 is equivalent to all compartments ranking GOOD
NOTES:	Note field for pertinent observations

STDWI:	Dry Weight Index (%) of the stomach calculated as STDRY / (sum of STDRY,PCDRY,GDRY,BDRY)*100
PCDWI:	Similar to STDWI above
GDWI:	Similar to STDWI above
BDWI:	Similar to STDWI above
STCVI:	Calorific Index (%) of the stomach calculated as STCALTOT / (sum of energy in stomach, caeca, gonad and body wall)
PCCVI :	Similar to STCVI above
GCVI:	Similar to STCVI above
BCVI:	Similar to STCVI above
ASLRATIO:	Arm spine length to diameter ratio calculated as a % according to ASL and DIAM
STCALTOT:	Total energy in the stomach, A function of STDRY, STCAL and STASH
PCCALTOT:	Similar to STCALTOT above
GCALTOT:	Similar to STCALTOT above
BCALTOT:	Similar to STCALTOT above
COMBCALS:	Sum of STCALTOT,PCCALTOT,GCALTOT,BCALTOT

```
Structure for database: D:oirs.dbf
Number of data records:      52
Date of last update   : 08/24/90
Field  Field Name  Type       Width    Dec
    1  CODE        Character      3
    2  TRIP        Numeric        1
    3  ANIMAL      Numeric        2
    4  ASL         Numeric        2
    5  ASLRATIO    Numeric        4      2
    6  DIAMETER    Numeric        2
    7  INIT_DIAM   Numeric        2
    8  WT          Numeric        4
    9  UW_WT       Numeric        3
   10  STWET       Numeric        6      3
   11  STDRY       Numeric        6      3
   12  STDWI       Numeric        4      1
   13  STBOMB      Numeric        5      3
   14  STCAL       Numeric        5      2
   15  STCVI       Numeric        4      1
   16  STASH       Numeric        5      3
   17  STAFDW      Numeric        5      3
   18  PCWET       Numeric        6      3
   19  PCDRY       Numeric        6      3
   20  PCDWI       Numeric        4      1
   21  PCBOMB      Numeric        5      3
   22  PCCAL       Numeric        5      2
   23  PCCVI       Numeric        4      1
   24  PCASH       Numeric        5      3
   25  PCAFDW      Numeric        5      3
   26  GWET        Numeric        6      3
   27  GDRY        Numeric        6      3
   28  GDWI        Numeric        4      1
   29  GBOMB       Numeric        5      3
   30  GCAL        Numeric        5      2
   31  GCVI        Numeric        4      1
   32  GASH        Numeric        5      3
```

```
   33  GAFDW       Numeric        5      3
   34  BWET        Numeric        6      3
   35  BDRY        Numeric        6      3
   36  BDWI        Numeric        4      1
   37  BBOMB       Numeric        5      3
   38  BCAL        Numeric        5      2
   39  BCVI        Numeric        4      1
   40  BASH        Numeric        5      3
   41  BAFDW       Numeric        5      3
** Total **                     184
```

Descriptions of field contents given below for fields of different name or contents to HELIX.dbf described above;

ANIMAL:	Code for individuals as recognised by morphologically distinct characters (refer Methods)
INIT_DIAM:	Diameter or positively re–identified starfish at the beginning of the study
WT:	Equivalent to WET_WT in HELIX.dbf
UW_WT:	Equivalent to WET_WT in HELIX.dbf
STBOMB:	Equivalent to (ST_BC_SAMP – ST_BC) in HELIX.dbf
STAFDW:	Equivalent to STASH in HELIX.dbf
PCBOMB:	Equivalent to (PC_BC_SAMP – PC_BC) in HELIX.dbf
PCAFDW:	Equivalent to PCASH in HELIX.dbf
GBOMB:	Equivalent to (G_BC_SAMP – G_BC) in HELIX.dbf
GAFDW:	Equivalent to GASH in HELIX.dbf
BBOMB:	Equivalent to (B_BC_SAMP – B_BC) in HELIX.dbf
BAFDW:	Equivalent to BASH in HELIX.dbf

7.3. Data examples

Sample data from main Helix Reef dataset (two records only)

```
DATA SUMMARY - HELIX REEF

RECORD #  1 - B051   24/6/1985   Coral cover approx. 36%


FIELD MEASUREMENTS

Diam: 24cm   Whole wet wt:  780g   Underwater wt:  45g   Sex: MALE

Spine length:   mm  Arms: 17  incl. 0 missing + 0 @1/4 + 0 @1/2 + 0 @3/4 length


CALCULATED FIELD VALUES

Arm damage:  0.0%   Equiv. arms: 17.00   Spine/Diam. ratio:  0.0%   Health:  0


LABORATORY MEASUREMENTS (3 arm sample)

    _______WET/DRY_WT_________ _______CALORIMETRY_______ ________ASH_WT_________
     PAN g   +WET g   +DRY g  CRUC. g +SAMP g def1 def2 CRUC. g +SAMP g ASHED g

ST: 46.6398  52.8629  47.8327  7.1735  7.4758 1.42 4.62 27.7509 28.3630 27.8213
PC: 46.6256  69.6440  51.8128  6.4035  6.6670 1.51 4.65 26.0169 28.0068 26.1805
G : 32.6667  33.1529  32.7679  7.1862  7.2890 1.50 2.60
B : 33.0277  84.6144  50.5346  6.2233  7.5072 0.75 4.70 26.6690 30.2299 29.0461


CALCULATED LABORATORY VALUES (3 arm sample)

          WET WT    DRY WT   WATER    DWI   CAL VAL     CALS     CI     ASH
            g         g      CONT%     %     kJ/g       kJ       %       %

ST:       6.2231    1.1929    80.8    5.0    23.92     25.25    5.6    11.5
PC:      23.0184    5.1872    77.5   21.6    25.94    123.52   26.3     8.2
G :       0.4862    0.1012    79.2    0.4    23.27                0.5
B :      51.5867   17.5069    66.1   73.0    19.77    114.91   67.7    66.8

TOTAL    81.3144   23.9882

NOTES:
```

DATA SUMMARY - HELIX REEF

RECORD # 6 - B056 24/6/1985 Coral cover approx. 36%

FIELD MEASUREMENTS

Diam: 43cm Whole wet wt: 2180g Underwater wt: 90g Sex: FEMALE

Spine length: mm Arms: 16 incl. 0 missing + 0 @1/4 + 0 @1/2 + 0 @3/4 length

CALCULATED FIELD VALUES

Arm damage: 0.0% Equiv. arms: 16.00 Spine/Diam. ratio: 0.0% Health: 0

LABORATORY MEASUREMENTS (3 arm sample)

	WET/DRY_WT			CALORIMETRY				ASH_WT		
	PAN g	+WET g	+DRY g	CRUC. g	+SAMP g	def1	def2	CRUC. g	+SAMP g	ASHED g
ST:	46.8393	60.7199	50.2108	6.3226	6.5459	0.09	2.74	21.9085	24.1122	22.2811
PC:	44.5474	74.1483	55.8067	9.3177	9.5878	0.99	4.93	21.6455	24.1903	21.8254
G :	32.3198	41.8869	34.7632	6.7218	6.8864	1.68	3.61	17.2285	18.3645	17.3829
B :	41.4110	196.4248	83.9965	7.3206	9.3960	1.30	8.41	26.5105	31.3822	29.8095

CALCULATED LABORATORY VALUES (3 arm sample)

	WET WT g	DRY WT g	WATER CONT%	DWI %	CAL VAL kJ/g	CALS kJ	CI %	ASH %
ST:	13.8806	3.3715	75.7	5.7	28.40	79.57	6.5	16.9
PC:	29.6009	11.2593	62.0	18.9	31.55	330.01	23.9	7.1
G :	9.5671	2.4434	74.5	4.1	26.67	56.30	4.4	13.6
B :	155.0138	42.5855	72.5	71.4	22.71	312.38	65.2	67.7
TOTAL	208.0624	59.6597				778.26		

NOTES: 5/6 g sa

8. Appendix B

8.1. Publication arising from this study

Kettle, B.T. and J.S. Lucas, (1987) Biometric relationships between organ indices, fecundity, oxygen consumption and body size in *Acanthaster planci* (L.) (Echinodermata; Asteroidea), Bulletin of Marine Science, 41(2). pp. 541-551.