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CHAPTER 5

REPRODUCTIVE MORPHOMETRY OF *A. planci* FROM THE WESTERN PACIFIC

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5.1. **Introduction**

5.1.1. Reproduction as the foundation of life histories

Life-history theory assumes that reproduction is always maximised (i.e. fitness) but constrained by the form of the organism (i.e. asymptotic size), its functions (i.e. physiological trade-offs) and its survival in the environment (see Stearns, 1992). Asymptotic size in animals is proximally determined by the schedule of reproduction (age-specific fecundity) and excess energy from resources (partitioned to growth). This ultimately reflects the constraints on the fitness maximising process involving mortality as well as resource acquisition and allocation (Jones and Johnson, 1977), often resulting in specific trade-offs in energy allocation among life-history characteristics (Stearns and Koella, 1986). Trade-offs between allocation of resources for maintenance activities, somatic growth and reproduction have not been studied in any detail in echinoderms (Lawrence, 1987b), although several authors have proposed that these mechanisms do exist (e.g., Menge, 1974; Ebert, 1975; 1982; Stearns; 1976; Kettle, 1990).

The parameters relating reproductive effort patterns to particular life-history characteristics are (Stearns, 1976);

(a) reproduce once or many times (semelparity vs. iteroparity).

(b) the amount of gametes produced (sperm and egg mass, and egg number i.e. fecundity).

(c) reproductive success (fertilization rate, recruitment and juvenile survival rate)

(d) age at first reproduction (size at maturity) i.e. changes in fecundity with age/size.

(e) the evolution of reproductive tactics as systems of coevolved adaptive traits.

There are two physiological thresholds related to reproduction in echinoderms (Lawrence, 1987a): (a) where a minimal amount of food is necessary for maintenance activities, below which gonadal growth does not occur, while above this level gonads develop with limited somatic growth (extrinsic limitation); and (b) where both gonad and somatic growth occur, to an extent, limited by the ability to acquire food (intrinsic limitation).

5.1.2. Physiological trade-offs involving reproduction

Theoretically, under selective pressure for fitness all individuals would be expected to maximise fecundity, mature immediately after birth, experience maximum longevity and grow as rapidly as its form, function and habitat would allow. The fact that organisms do not achieve these "demonic" extremes shows there are co-adapted physiological and life history trade-offs between these characteristics (Cole, 1954; Stearns, 1989b) which form the basis of life history studies. Trade-offs are caused by energy allocations between two or more functions competing for the same resources within an individual and lie at the heart of life-history theory (Stearns, 1992). Age-specific patterns of growth, survival and reproduction are produced by trade-offs from opposing selective forces on the individual (Stearns, 1982) and are optimised by the constraints of resource allocation (Smith, 1991). The trade-off assumption implies a negative genetic correlation between early and late life fitness traits, and has become an entrenched paradigm of life history studies (Giesel et al. 1982b). Therefore, life history trade-offs are governed over a large range of the continuum of various ratios of genotypic and phenotypic determination. For many types of organisms make phenotypic adjustments to various traits when encountering environmental stresses which often maintains fitness as high as possible (Stearns and Koella, 1986).

A range of predictable changes in the values of ecologically important phenotypic characters that are induced by environmental cues is called phenotypic plasticity, which can provide a selective advantage in a variable environment (Via, 1993). Where phenotypic expression optimises fitness over several different habitats, plastic life histories (Policansky, 1983) with variable life-history traits may be an adaptation of primary importance. This has also been specifically demonstrated by Stearns and Koella (1986) who graphically represented a range of independent responses, the reaction norm, in determining age at maturity in four diverse species as a function of environmental conditions. Kawecki and Stearns (1993) discussed the growing number of papers describing environmental heterogeneity and phenotypic plasticity, implying that habitat variation drives the evolution of plasticity, which reflects the significance of flexibility in the evolution of many, if not all, life histories.

Trade-offs among life-history characteristics have been proposed for several echinoderm species. Ebert (1975; 1982) suggested that reproduction influenced survival in echinoids indicating a trade-off between maintenance and reproduction because both reproduction and survival compete for the energy obtained from limited resources, a characteristic of high density populations of *A. planci*. This shows there are probably few essential interrelationships among growth, reproduction and mortality that determine the overall life-history characteristics of echinoderm species that develop within large aggregated populations.

Menge (1974) demonstrated a trade-off between reproductive effort (interpreted from fecundity) and the rate of adult mortality, caused primarily by winter storms in the intertidal starfish, *Leptasterias hexactis*, living in open coastal areas. This species exhibited several ***r*** - type characteristics which pointed to selective pressure for increased reproductive effort in areas exposed to seasonal wave action compared with populations in quieter habitats. However, linear regression analyses between whole wet weight and fecundity showed that the opposite response had occurred. Since the source of the mortality was density-independent (wave forces rolling shoreline boulders), the study demonstrated an exception to the predictions of both ***r*** - ***K*** selection and bet-hedging theory in populations with environmental fluctuation (see Stearns, 1976; Table 4). The study led Menge (1974) to caution that predictions on the causes of mortality from observations of putative life-history characteristics can sometimes lead to the wrong conclusions.

Trade-offs in reproductive characteristics have also been suggested for *A. planci.* Several asteroid species have a high variability in arm number, including multiarmed *A. planci* (7 - 23 arms; Kettle, 1990), where an increase in arm number (from the regular asteroid body plan) increases the biomass of the body wall which is intrinsically disadvantageous because increased resource allocation to the body wall slows potential growth rate and time to maturity (Lawrence, 1988). Internally there is a similar increase in the number of gonads and pyloric caeca but a decrease in the overall arm volume, because volume is associated with the square of the width of the arm base (Lawrence, 1988). Therefore, there is a greater resource allocation to body wall storage through development of a greater body surface area, the principal compartment of energy storage (Lawrence and Lane, 1982; Lawrence, 1984; Kettle, 1990). However, there may be a trade off with another function, possibly the capacity to feed and climb (Lawrence, 1987a; Birkeland, 1989), which allows the exploitation of the faster growing, widely branching acroporids; a unique resource among corallivorous asteroids. Just as homeothermy is advantageous, but only if the return is worth the cost, the development of the multiarmed condition should increase the capacity to obtain energy that meets the energy required to develop and maintain those additional arms (Lawrence and Moran, 1992).

Food limitation in high density populations of *A. planci* is an inevitable occurrence since the high densities achieved in outbreaks far exceed the carrying capacity of the environment. In these conditions, mortality caused by stress from food limitation simply results from the same factors that lead to shrinkage, *in extremis*, and provides an example of a potential trade-off between survival and reproduction (Kettle, 1990). The implementation of the SPBC method of age determination (Stump and Lucas, 1990; Stump, 1992) makes the testing of trade-offs in populations possible, both within and among the cohorts identified from this method. A first step in these analyses is to estimate the range of responses displayed in the natural environment by obtaining data from field populations which have developed under a range of conditions.

5.1.3. Reproductive characteristics in populations

In this chapter the reproductive characteristics of the five populations treated in Chapter 4 are described using morphometric analyses of gonad and whole body variables. The results are used to describe patterns of variation in life-history characteristics related to reproduction. These patterns are then discussed in terms of the environmental conditions of their habitats and their behaviour.

To compare gonad growth among the populations, the processes of gametogenesis (i.e. a seasonal gonad cycle) must be similar, and comparative data from each population need to be obtained at an equivalent late stage in the gametogenic cycle. A single measurement of gonad weight, just prior to the first seasonal spawning was employed by Conand (1983) and Kettle (1990) to represent potential annual fecundity and this approach is also used in the present study. The measurement assumes that any further gametogenic activity within the season, after the samples are collected, is of minor significance compared with the total annual production estimated at the time of sampling. Babcock and Mundy (1993) found that the majority of gametes are spawned in early summer in the Davies Reef population, and although there were multiple spawnings throughout the season, those in the later part of the season were relatively minor. Therefore, spawning probably occurs in a similar manner on Suva Reef which is approximately at the same latitude as Davies Reef and therefore, a similar seasonal pattern in seawater temperature variation.

In the Japanese *A. planci* populations a spawning period was reported between June and July around Okinawa Island when the water temperatures were above 25°C (Yokochi and Ogura, 1987; and Okaji, 1991). Okaji (1991) concluded that low density populations tended to spawn later in the season than high density populations due possibly to the reduced level of conspecific stimulation to spawn. Cheney (1972b; 1974) studied gonad indices in several populations around Guam and concluded there was not a definite annual spawning cycle in all individuals due to the lack of marked fluctuations in seawater temperature.

The present field study in Guam was undertaken in late June and early July which is well within the spawning season observed for the Western Pacific region in the northern hemisphere. Moran (1986; Table II) reported the spawning season in Guam (13.5°N) was between September and December, other studies have reported different timings of spawning in *A. planci* populations, north of the equator. Two distinct behavioural modes occurred among populations according to starfish density, a dispersed type with variable body sizes and gonad state, and aggregated groups exhibiting uniform body size and gonad state (Cheney, 1974). Cheney (1974) estimated gonad indices from three populations around Guam and showed there was no definite annual spawning cycle, but in one dispersed population (Piti) there was evidence of an annual trend in one year (1970) but not the next.

The evidence for a consistent timing for spawnings appears to be variable, however, from further sampling of a low density population (around Cocos Island), Cheney (1974) showed there was a sharply defined spawning period between September and October, with the likelihood of partial spawnings at other times. His data of mean surface seawater temperatures (Figure 2, Cheney, 1974) peaked during July and August. From Cheney's data, gonad indices declined in the spring-summer period coinciding with the highest water temperature, despite annual variation in surface seawater temperature being generally less than 2°C. Amesbury and Babin (1990) reported a peak in surface seawater temperature of approximately 29°C during July in the waters surrounding Guam. This shows that the collections for the present study were carried out at approximately the same time as the predicted major spawning period and therefore, morphometric comparisons made among the populations from the three regions are probably justified. However, there is still a possibility that there had been minor spawning events in at least two of the Guam populations (Hospital Point and South Tumon Bay) prior to the field study, which would have caused an increase in the significance of the differences found among the populations.

5.2. **Methods**

5.2.1. Population sample collections

Methods employed for field collections and processing of samples are as described in Chapter 4.

5.2.1.1. Davies Reef

Fecundity estimates from the Davies Reef *A. planci* population were obtained from whole gonad weights of specimens measured just prior to the seasonal spawning period. The relationship between fecundity and gonad mass has been described previously by Conand (1984) and applied to the study of Kettle (1990). Ripe *A. planci* were collected during four sampling trips to Davies Reef, Central GBR (Figure 3.1). These were; 27 - 29 November 1989; 24 - 30 November 1990, 22 - 25 November 1991, and 5 - 8 December 1991.

Whole wet weight (WET) and gonad weights (GWT (♂), GWO (♀)) were determined using a Thornton counter balance (10kg; ± 1g) in the 1990 and 1991 samples. Whole body weight was estimated from the relationship determined for whole wet weight and body diameter in the 1989 sample, and gonad weights were calculated from measured volumes (see Conand, 1983; Kettle, 1990). To obtain the entire gonad, the aboral body wall was removed after measuring body weights. Gonad lobules were detached with forceps, shaken to remove excess coelomic fluid, then weighed in a plastic bag.

5.2.1.2. Fiji and Guam

Following data collection for whole body morphometry (Chapter 4) the starfish were dissected and entire gonads removed, sexed and weighed. Gonad and whole wet weights were obtained using a portable digital balance (Murakami Co.).

5.2.2. Morphometric analyses of reproduction

The steps and analytical treatments are described in the **Methods** section of Chapter 4. Outliers were identified through inspection of plots of standardised residuals and fitted values. Where the magnitude of a small number of residuals were observed to be large (identifying the data as outliers) these data were omitted from further analyses.

5.2.2.1. Analyses of covariance (ANCOVA)

Fecundity, adjusted for whole body size, was estimated from gonad weights using ANCOVA techniques to remove the confounding influence of body size on fecundity, according to the methods of Packard and Boardman (1988). The scaled data were then used to determine the influence of estimated age on adjusted fecundity (with a level of significance of $\alpha = 0.01$). The methods recommended by Packard and Boardman (1988) are less susceptible to error when there is a reasonable overlap in size ranges between samples, as adjusted values are more sensitive to errors in slope estimates. A similar procedure was also used to obtain somatic weights, adjusted for mean body size.

Somatic storage tissue weight (SOM) is used to estimate the soft tissue weight of the body other than gonad weight, under the condition that the starfish are analysed just prior to the annual spawning period and gonad weight is at a maximum. When (SOM) is adjusted for the mean whole wet weight it is assumed to be an approximate measure of relative partitioning to stored reserves to the body wall, pyloric caeca and stomach (Equation 5.1).

$$(SOM) = (WET) - ((GW) + (UW)) \qquad (5.1)$$

where (SOM) = somatic tissue weight (g)
(WET) = whole wet weight (g)
(GW) = gonad weight (g)
(UW) = underwater weight, estimating skeletal weight (g)

5.3. **Results**

5.3.1 Sexual dimorphism

The ranges of the frequency distributions of whole ovary and testes weight for five populations demonstrate a general pattern of similar ovary weights compared with testes weights in *A. planci* within the same populations (Figure 5.1 a. - f.; Table 5.1) except in the Davies Reef PST group (all variables) and for gonad weights only in the Davies Reef PRE group.

Table 5.1. The morphometric characteristics of reproduction; mean body size, mean gonad weight and analyses of sexual dimorphism (t-tests for differences between sexes for each variable) in five adult *A. planci* populations.

Group	Sex	$(BD)_{mean}$ (SE)	$(WET)_{mean}$ (SE)	$(GW)_{mean}$ (SE)	(n)
DA PRE	♂	42.3 (1.1)	2436 (160)	245 (31.8)	16
	♀	42.6 (0.8)	2697 (141)	420 (48.7)	20
		t = 0.27; P = 0.79	t = 1.23; P = 0.47	t = 3.00; P = 0.01	
DA PST	♂	38.6 (0.5)	2071 (68.6)	221 (14.7)	78
	♀	40.5 (0.5)	2445 (75.1)	418 (24.6)	76
		t = 2.80; P < 0.01	t = 3.68; P < 0.01	t = 6.86; P < 0.01	
DO	♂	29.4 (0.6)	1163 (68.7)	40 (5.1)	19
	♀	30.5 (0.8)	1277 (85.7)	60 (12.7)	15
		t = 1.21; P = 0.23	t = 1.05; P = 0.30	t = 1.48; P = 0.16	
SU	♂	29.1 (0.8)	953 (77.7)	63.1 (8.6)	25
	♀	27.3 (1.1)	827 (95.4)	99.5 (25.5)	27
		t = -1.36; P = 0.18	t = -1.02; P = 0.31	t = 1.35; P = 0.19	
ST	♂	26.9 (0.5)	814 (52.0)	24 (2.9)	19
	♀	26.9 (0.6)	761 (52.4)	31 (4.5)	21
		t = -0.05; P = 0.96	t = -0.71; P = 0.48	t = 1.30; P = 0.20	
HP	♂	23.6 (0.4)	507 (24.7)	8 (1.6)	22
	♀	23.7 (0.7)	499 (37.1)	14 (4.2)	18
		t = 0.10; P = 0.92	t = -0.19; P = 0.85	t = 1.40; P = 0.18	

where $(BD)_{mean}$ = mean whole body diameter (cm) for estimated age > 3 years
$(WET)_{mean}$ = mean whole wet weight (g) for estimated age > 3 years
$(GW)_{mean}$ = mean gonad weight (g) for estimated age > 3 years
DA PRE = Davies Reef pre-outbreak group
DA PST = Davies Reef post-outbreak group
SU = Suva Reef
DO = Double Reef
ST = South Tumon Bay
HP = Hospital Point

The gonad weights ((GWT) = ♂, (GWO) = ♀) in each population appears to be related to body size. Body size variables and gonad weights were relatively low in the

Guam and Suva Reef populations, and high in the Davies Reef population. This pattern was also shown in the differences in mean body size and mean gonad weights estimated for age at full sexual maturity among the populations (Table 5.2).

Table 5.2. The morphometric characteristics of reproduction at full sexual maturity, mean body size and gonad weight at maturity (α) in five *A. planci* populations ((α) = estimated age at full sexual maturity, i.e. 3 years).

Group	Sex	$\mathbf{(BD)}_\alpha$ (SE)	$\mathbf{(WET)}_\alpha$ (SE)	$\mathbf{(GW)}_\alpha$ (SE)	(n)
DA PRE	♂	NA	NA	NA	0
	♀	NA	NA	NA	0
DA PST	♂	34 (2.3)	1389 (243)	142 (51)	4
	♀	34 (-)	1339 (-)	165 (-)	1
DO	♂	29 (1.0)	970 (137)	29 (9.0)	2
	♀	34 (2.5)	1240 (79)	145 (116)	2
SU	♂	26 (1.1)	588 (88)	28 (10.3)	7
	♀	24 (0.9)	520 (62)	32 (8.2)	14
ST	♂	26 (-)	641 (-)	41 (-)	1
	♀	23 (3)	571 (343)	12 (7.5)	2
HP	♂	22 (-)	339 (-)	5 (-)	1
	♀	22 (-)	506 (-)	17 (-)	1

where $\mathbf{(BD)}_\alpha$ = whole body diameter (cm) at maturity
$\mathbf{(WET)}_\alpha$ = whole wet weight (g) at maturity
$\mathbf{(GW)}_\alpha$ = gonad weight (g) at maturity
NA = no data available

There was a positive correlation between whole wet weight and gonad weight at the age of maturity using the combined data from all the populations, where ♂, $r = 0.918$; $\mathbf{F}_{(\mathrm{ratio})} = 23.2 > \mathbf{F}_{(\alpha 1;0.01;12,12)} = 4.91$; $P < 0.01$; and ♀, $r = 0.908$; $\mathbf{F}_{(\mathrm{ratio})} = 20.7 > \mathbf{F}_{(\alpha 1;0.01;18,18)} = 3.56$; $P < 0.01$. Body size strongly influenced ovary (fecundity) and testes weights in *A. planci*.

5.3.2. Allometry of gonad weight and whole wet weight

The relationships between whole wet weight and gonad weight are presented in Figure 5.2 (5.2a male starfish, 5.2b female starfish). The analyses of the relationships between gonad weight and whole wet weight were calculated using the power equation;

$$\mathbf{y = b \cdot X^a} \qquad (5.2)$$

The Student's t-test was used to determine the significance of differences between the hypothetical relationship (where the exponent **a** = 1) and the relationship of whole wet weight and gonad weight in fully mature individuals (> 3 years) (Tables 5.3 and 5.4).

5.3.2.1. Power analyses for whole testes weight and whole wet weight

Table 5.3. Power analyses and Student' t test for isometry of the relationship between whole testes weight and whole wet weight among five *A. planci* populations from the Western Pacific region.

Group	Power equation	Power analyses
DA PRE	$(GWT) = (6.85\text{x}10^{-4})\ (WET)^{1.628}$	$r^2 = 0.58$; $P < 0.01$; $n = 16$; MSE = 0.1628 S.t = 1.71; $t_{(0.01(1)14)} = 2.62$; $0.10 < P < 0.05$
DA PST	$(GWT) = (1.93\text{x}10^{-4})\ (WET)^{1.814}$	$r^2 = 0.76$; $P < 0.01$; $n = 78$; MSE = 0.103 S.t = 6.94; $t_{(0.01(1)76)} = 2.38$; $P < 0.01$
HP	NS	$r^2 = 0.20$; $P = 0.04$; $n = 22$
ST	NS	$r^2 = 0.18$; $P = 0.07$; $n = 19$
DO	$(GWT) = (2.64\text{x}10^{-3})\ (WET)^{1.352}$	$r^2 = 0.44$; $P < 0.01$; $n = 20$; MSE = 0.151 S.t = 1.78; $t_{(0.01(1)18)} = 2.55$; $0.25 < P < 0.10$
SU	$(GWT) = (2.51\text{x}10^{-4})\ (WET)^{1.783}$	$r^2 = 0.70$; $P < 0.01$; $n = 25$; MSE = 0.247 S.t = 3.26; $t_{(0.01(1)23)} = 2.50$; $P < 0.01$

where S.t = Student's t test
(GWT) = whole testes weight (g)
(WET) = whole wet weight (g)

Therefore, the Davies Reef PST group and the Suva Reef population showed a significantly different relationship to isometry for whole testes weight and whole wet weight. The relationships for Davies Reef PRE and Double Reef were not significantly different from isometry. The analyses for Hospital Point and South Tumon Bay were not significant (Table 5.3; Figure 5.2a).

5.3.2.2. Power analyses of whole ovary weight and whole wet weight.

The relationships between ovary weight and whole wet weight in each population were investigated using the power relationship (Equation 5.2; Table 5.4);

Table 5.4. Power analyses and Student' t test for isometry of the relationship between whole ovary weight and whole wet weight among five *A. planci* populations from the Western Pacific region.

Reef	Power equation	Power analyses
DA PRE	$(GWO) = (3.91\text{x}10^{-5}) \text{ x } (WET)^{2.0359}$	$r^2 = 0.62$; $P < 0.01$; $n = 20$; $MSE = 0.173$ $S.t = 2.76$; $t_{(0.01(1)18)} = 2.55$; $P < 0.01$
DA PST	$(GWO) = (1.016\text{x}10^{-5}) \text{ x } (WET)^{1.6418}$	$r^2 = 0.62$; $P < 0.01$; $n = 76$; $MSE = 0.143$ $S.t = 4.29$; $t_{(0.01(1)74)} \approx 2.376$; $P < 0.01$
HP	NS	$r^2 = 0.12$; $P = 0.15$; $n = 18$
ST	$(GWO) = (1.03\text{x}10^{-3}) \text{ x } (WET)^{1.530}$	$r^2 = 0.48$; $P < 0.01$; $n = 21$; $MSE = 0.370$ $S.t = 1.437$; $t_{(0.01(1)19)} = 2.539$; $0.10 < P < 0.05$
DO	$(GWO) = (7.40\text{x}10^{-5}) \text{ x } (WET)^{1.8774}$	$r^2 = 0.46$; $P < 0.01$; $n = 15$; $MSE = 0.293$ $S.t = 1.55$; $t_{(0.01(1)13)} = 2.65$; $0.05 < P < 0.10$
SU	$(GWO) = (1.31\text{x}10^{-4}) \text{ x } (WET)^{1.959}$	$r^2 = 0.89$; $P < 0.01$; $n = 27$; $MSE = 0.178$ $S.t = 7.04$; $t_{(0.01(1)25)} = 2.49$; $P < 0.01$

where (GWO) = whole ovary weight
(WET) = whole wet weight
S.t = Student's t test

The relationship between whole wet weight and ovary weight for the Hospital Point population was not significant. The exponents of the power relationships for Davies

Reef PRE and PST groups, and Suva Reef populations were significantly greater than isometry (where **a** = 1), while the exponents for the relationships from the Double Reef and South Tumon Bay populations were not significantly different from isometry (Figure 5.2b).

5.3.2.3. Linear regression analyses of whole testes weight and whole wet weight.

Data for regression analyses of testes weight and whole wet weight were first transformed by natural logs following inspection of a preliminary standardised residual plot. The plot of standardised residuals from the final model show no net trends (Figure 5.3a). The data from the Hospital Point and South Tumon Bay populations were omitted from the analyses. The significance of elevation and slopes were analysed in relation to the regression for Double Reef.

minimal model

Dependent Variable = ln (GWT)

Ind. V.	Coefficient	Std. Error	t-stat.	P
Constant	-8.1377	0.7247	-11.23	< 0.01
ln (WET)	1.6651	0.1037	16.06	< 0.01
DA PRE_{slope}	0.0726	0.0195	3.72	< 0.01
SU_{slope}	0.0956	0.0164	5.81	< 0.01
DA PST_{slope}	0.0942	0.0152	6.20	< 0.01

AOV of full regression model

	SS	df	MS	$F_{(ratio)}$	P
model	114.859	4	28.72	206.4	< 0.01
error	18.644	134	0.1391		
total	133.50	138			

summary of model

$\ln(GWT) = \ln WET + (SU)_{slope} + DA\ PRE_{slope} + DA\ PST_{slope}$
$r^2 = 0.86;\ P < 0.01;\ n = 139;\ MSE = 0.139$

analysis of mimimal model

$\mathbf{F}_{(ratio)} = 0.36 < \mathbf{F}_{(\alpha 1;0.01;3,136)} = 3.92;\ P > 0.25$

the regression analyses form 4 groups with significantly different slopes;

Population	Regression equation	Regression analyses
DO	$\ln(GWT) = (1.3525 \times \ln(WET)) - 5.9378$	$r^2 = 0.44;\ n = 20;\ P < 0.01;\ MSE = 0.151$
DA PRE	$\ln(GWT) = (1.6281 \times \ln(WET)) - 7.2861$	$r^2 = 0.58;\ n = 16;\ P < 0.01;\ MSE = 0.163$
SU	$\ln(GWT) = (1.7830 \times \ln(WET)) - 8.2898$	$r^2 = 0.70;\ n = 25;\ P < 0.01;\ MSE = 0.247$
DA PST	$\ln(GWT) = (1.8140 \times \ln(WET)) - 8.5532$	$r^2 = 0.76;\ n = 78;\ P < 0.01;\ MSE = 0.103$

The slopes of regressions for testes weight and whole wet weight in the Davies Reef PRE group, Suva Reef and Davies Reef PST group were significantly higher than the regression for Double Reef. The slope of the regression for Suva Reef was significantly lower than that for the Davies Reef PST group (Figure 5.3b).

5.3.2.4. Linear regression analyses of whole ovary weight versus whole wet weight.

The data from the Hospital Point population was omitted from the linear regression analyses. The data for the regression analyses of ovary weight and whole wet weight were first transformed by natural logs following inspection of a preliminary standardised residuals in the plot of the standardised residuals for the final model. There were no net trends in the log transformed standardised residuals plot (Figure 5.4a).

minimal model:

Dependent Variable = ln (GWO)

Ind. V.	Coefficient	Std. Error	t-stat.	P
Constant	-8.3656	0.6328	-13.22	< 0.01
ln (WET)	1.7385	0.0924	18.81	< 0.01
DA PREslope	0.0710	0.0202	3.52	< 0.01
DA PSTelev.	0.7512	0.1263	5.95	< 0.01
SUelev.	0.8727	0.1154	7.56	< 0.01

AOV of regression model

	SS	df	MS	$\mathbf{F}_{(\text{ratio})}$	P
model	263.34	4	65.83	334.0	< 0.01
error	30.35	154	0.1971		
total	293.7	158			

model:

$$\ln (GWO) = \ln WET + (DA\ PRE)_{slope} + (DA\ PST)_{elev.} + (SU)_{elev.}$$

$r^2 = 0.90$; $P < 0.01$; $n = 159$; $MSE = 0.197$

analysis for minimal model:

$$\mathbf{F}_{(\text{ratio})} = 1.40 < \mathbf{F}_{(\alpha 1;0.01;5,154)} \approx 3.13;\ 0.10 < P < 0.25$$

the regression analyses form 4 significantly different groups.

Group	Regression equation	Regression analyses
ST, DO	$\ln(GWO) = (1.4605 \times \ln(WET)) - 6.4724$	$r^2 = 0.54$; $P < 0.01$; $n = 36$; $MSE = 0.327$
DA PRE	$\ln(GWO) = (2.0359 \times \ln(WET)) - 10.1485$	$r^2 = 0.62$; $P < 0.01$; $n = 20$; $MSE = 0.173$
DA PST	$\ln(GWO) = (1.6418 \times \ln(WET)) - 6.8635$	$r^2 = 0.62$; $P < 0.01$; $n = 76$; $MSE = 0.143$
SU	$\ln(GWO) = (1.9592 \times \ln(WET)) - 8.9383$	$r^2 = 0.89$; $P < 0.01$; $n = 27$; $MSE = 0.178$

The regression between whole wet weight and ovary weight for Hospital Point was not significant. The slope of the regression for the Davies Reef PRE group was significantly greater than the combined slope for South Tumon Bay and Double Reef. The regressions for Davies Reef PST group and the Suva Reef population each had a significantly greater elevation than over the regression for the Davies Reef PRE group (Figure 5.4b).

5.3.2.5. Summary of allometric relationships for gonad weights and whole wet weight

The regression relationships for whole wet weight and ovary weight from the Hospital Point population (male and female) and the South Tumon Bay population (male only) were not significant. In the remaining populations there were significant increases in ovary and testes weight with increasing body size. However, only in some populations did gonad weight increase relative to whole wet weight at a rate with an exponent significantly greater than 1 (Table 5.5).

The groups demonstrating positive allometry in relation to gonad development are ranked in descending order in Table 5.5, i.e. where the exponent of whole wet weight in the power relationship with gonad weight was significantly greater than 1).

Table 5.5. Population samples which gonad growth demonstrated positive allometry (**a** > 1) in *A. planci* populations from the Western Pacific region.

Population	t-stat.	Exponent analyses
DA PRE (female)	2.036	$P < 0.01$; n = 20
SU (female)	1.959	$P < 0.01$; n = 27
DA PST (male)	1.814	$P < 0.01$; n = 78
SU (male)	1.783	$P < 0.01$; n = 25
DA PST (female)	1.642	$P < 0.01$; n = 76

In the Davies Reef PST group and the Suva Reef population, both male and female gonads developed with positive allometry (i.e. greater than isometric growth). In the low density Davies Reef PRE group only the female starfish developed gonads with a positive allometric rate. In the Guam populations gonad growth in both male and female starfish was relatively poor and did not differ significantly from isometry.

5.3.3. Analyses for gonad weights and estimated age

Linear regression analyses were determined for testes weight and estimated age within the five populations (Table 5.6).

Table 5.6. Linear regression analyses between testes weight and estimated age in five *A. planci* populations from the Western Pacific region.

Populations	Regression equations	Regression analyses
HP	NS	$r^2 = 0.03$; $n = 22$; $P = 0.41$
ST	NS	$r^2 = 0.06$; $n = 19$; $P = 0.30$
DO	NS	$r^2 = 0.04$; $n = 19$; $P = 0.44$
SU	$\ln(GWT) = (0.0386 \times (AGE)) + 1.7866$	$r^2 = 0.38$; $n = 25$; $P < 0.01$; $MSE = 0.518$
DA PRE	NS	$r^2 = 0.12$; $n = 16$; $P = 0.19$
DA PST	NS	$r^2 = 0.02$; $n = 78$; $P = 0.22$

In the regression analyses between testes weight and estimated age (Table 5.6; Figure 5.5a) there was only a significant positive relationship for the Suva Reef population. There was no significant change in testes weight over the range of estimated ages in the other populations.

Linear regression analyses were determined for ovary weight and estimated age within the five populations (Table 5.7).

Table 5.7. Linear regression analyses between whole ovary weight and estimated age in five *A. planci* populations from the Western Pacific region.

Reef	Regression equation	Regression analyses
HP	NS	$r^2 = 0.06$; $n = 18$; $P = 0.34$
ST	NS	$r^2 = 0.05$; $n = 21$; $P = 0.31$
DO	NS	$r^2 < 0.01$; $n = 15$; $P = 0.92$
SU	$\ln(GWO) = (0.0521 \times (AGE)) + 1.4273$	$r^2 = 0.48$; $n = 27$; $P < 0.01$; MSE = 0.851
DA PRE	NS	$r^2 = 0.01$; $n = 20$; $P = 0.69$
DA PST	NS	$r^2 = 0.02$; $n = 76$; $P = 0.20$

Regression analyses between ovary weight and estimated age (Table 5.7; Figure 5.5b) again show a significant positive relationship only in the Suva Reef populations.

5.3.4. Analyses of size-adjusted gonad weights and estimated age.

The analyses of adjusted gonad weights and estimated age were conducted using samples from the Davies Reef PRE and PST, Double Reef and Suva Reef *A. planci* populations. The Hospital Point and South Tumon Bay data was not analysed because the relationships between whole wet weight and gonad weights are not significant for both sexes. Gonad weights were adjusted using an approximate mean whole wet weight (1636g) estimated from the body size range overlap in the regressions from the five populations.

Table 5.8. Linear regression analyses for adjusted gonad weight and estimated age in three *A. planci* populations from the Western Pacific region; (a) male starfish, (b) female starfish.

(a)

Population	Regression equation	Regression analyses
DA PRE	NS	$r^2 = 0.08$; $n = 16$; $P = 0.29$
DA PST	NS	$r^2 = 0.03$; $n = 78$; $P = 0.12$
DO	NS	$r^2 = 0.01$; $n = 19$; $P = 0.74$
SU	NS	$r^2 = 0.01$; $n = 25$; $P = 0.67$

(b)

Population	Regression equation	Regression analyses
DA PRE	NS	$r^2 = 0.19$; $n = 20$; $P = 0.06$
DA PST	(AGO) = 6.1350 - (0.0130 x (AGE))	$r^2 = 0.10$; $n = 76$; $P < 0.01$
DO	NS	$r^2 = 0.08$; $n = 15$; $P = 0.29$
SU	NS	$r^2 = 0.02$; $n = 27$; $P = 0.44$

There were no significant relationships between adjusted testes weight and estimated age in the three populations (Figure 5.6a). However, there was a significant negative relationship between adjusted ovary weight and estimated age for the Davies Reef PST group. Therefore, there was a significant decline in fecundity with estimated age in the high density outbreak population.

There is a single maximum in the relationship between adjusted ovary weight and estimated age in the Davies Reef PST group at age 3+ years (Figure 5.6b). Since there were no samples obtained < 5+ years in the PRE group no maximum could be determined over the range of adult age classes from maturity. The Suva Reef population showed two maxima, the first was similar to the Davies Reef pattern occurring at 3 years and the second at 5+ years (Figure 5.6b).

5.3.4.1. Analyses of size-adjusted gonad weights in three populations.

The interpopulation comparisons of the differences in adjusted fecundities grouped for estimated age classes were determined using ANCOVA methods. Analyses of gonad weights adjusted for whole wet weight were not conducted with the data from the Hospital Point or Suva Reef populations as their regression analyses for whole wet weight and gonad weights are not significant. Gonad weights are adjusted for the approximate overall mean whole wet weight (1636g) (Table 5.9) and the tested for differences between populations. ANCOVA of testes weight (adjusted for (WET) = 1636g).

Table 5.9. Summary of mean adjusted gonad weights (adjusted for whole wet weight = 1636g) in three *A. planci* populations from the Western Pacific region: (a) adjusted testes weight (AGT), (b) adjusted ovary weight (AGO).

(a)

Group	$(AGT)_{mean}$	SE	(n)
DA PRE	125	11.4	16
DA PST	137	5.1	78
DO	63	5.1	20
SU	151	15.4	25

$F_{(ratio)} = 15.3 > F_{(\alpha 2;0.01;3,135)} \approx 4.47$; $P < 0.01$

(b)

Group	$(AGO)_{mean}$	SE	(n)
DA PRE	146	10.1	20
DA PST	210	7.8	76
DO	89	9.3	15
SU	280	20.1	27

$F_{(ratio)} = 31.5 > F_{(\alpha 2;0.01;3.134)} = 4.47$; $P < 0.01$

where (AGT) = adjusted testes weight (g)
(AGO) = adjusted ovary weight (g)

Using the Tukey HSD test (Zar, 1984) for comparison of means of adjusted testes weight there were two homogenous groups formed with no significant differences within groups (Q = 4.419; rejection level = 0.01) (Table 5.9a).

for adjusted testis weights

Group 1	DO
Group 2	PRE, PST and SU

where Group 2 > Group 1

Using the Tukey test for comparison of means of adjusted ovary weight (Q = 4.419, rejection level = 0.01) there are three homogenous groups formed with no significant differences within Group 1 (Table 5.9b).

for adjusted ovary weights

Group 1	PRE, DO
Group 2	PST
Group 3	SU

where Group 3 > Group 2 > Group 1.

5.3.4.2. Analyses of size-adjusted gonad weights between sexes

Analyses of adjusted gonad weights between sexes were undertaken for; Davies Reef PRE, PST and Suva Reef SU (regional mean whole wet weight = 1636g) (Table 5.10).

Table 5.10. ANOVA of adjusted gonad weights between sexes in three *A. planci* populations from the Western Pacific region.

Groups	ANOVA	Analysis
DA PRE	$\mathbf{F}_{(ratio)} = 1.82 < \mathbf{F}_{(\alpha2;0.01;1,34)} \approx 8.98$; $P = 0.19$	NS
DA PST	$\mathbf{F}_{(ratio)} = 62.2 > \mathbf{F}_{(\alpha2;0.01;1,152)} \approx 8.10$; $P < 0.01$	♀ > ♂
DO	$\mathbf{F}_{(ratio)} = 2.8 > \mathbf{F}_{(\alpha2;0.01;1,33)} \approx 8.98$; $0.10 < P < 0.25$	NS
SU	$\mathbf{F}_{(ratio)} = 25.4 > \mathbf{F}_{(\alpha2;0.01;1,29)} \approx 9.18$; $P < 0.01$	♀ > ♂

where NS = not significant

There was significant sexual dimorphism in adjusted gonad weights (adjusted for whole wet weight = 1636g) in the DA PST group and the SU population but not in the DA PRE group or the Double Reef population. There was a weakly significant difference in adjusted gonad weights between sexes in the DO population (Table 5.10).

5.3.5. Analyses of somatic weights in five populations.

Somatic weights were adjusted for the approximate regional mean of whole wet weight (1636g) and then tested for differences between populations (Table 5.11). ANCOVA of adjusted male somatic weights are determined for the five populations.

Table 5.11. Summary of mean adjusted male somatic weights in five *A. planci* populations from the Western Pacific region.

Group	$(AST)_{mean}$	SE	(n)
DA PRE	1389	14.2	12
DA PST	1395	8.9	39
HP*	1492	4.2	22
ST*	1511	6.2	19
DO	1498	4.5	20
SU	1424	10.5	25

where (AST) = male somatic weight, adjusted for mean whole wet weight = 1636g
* = weight adjusted beyond the range of whole wet weights obtained in the sample.

$\mathbf{F}_{(ratio)} = 37.8 > F_{(\alpha 2;0.01;5,133)} \approx 3.52$; $P < 0.01$

Using the Tukey HSD test (Zar, 1984) for comparison of means of adjusted male somatic weight there are two homogenous groups formed with no significant differences within groups (Q = 4.78, rejection level = 0.01).

Group	
Group 1	PRE, PST, SU
Group 2	HP, ST, DO

where Group 2 > Group 1

The Guam populations had significantly higher adjusted male somatic weights than the Davies Reef groups or the Suva Reef population (Table 5.11). The calculations of both adjusted male and female somatic weights in the Hospital Point and South Tumon Bay populations were achieved by extrapolation of the derived regressions for whole wet weight and somatic weight, although the adjusted weight were within in the range found in the Double Reef samples.

Table 5.12. Summary of mean adjusted female somatic weights in five *A. planci* populations from the Western Pacific region.

Group	$(ASO)_{mean}$	SE	Sample (n)
DA PRE	1404	12.2	8
DA PST	1280	16.4	30
HP*	1492	10.2	18
ST*	1466	8.8	21
DO	1464	8.2	15
SU	1295	12.9	27

where (AST) = male somatic weight, adjusted for mean whole wet weight = 1636g

* = weight adjusted beyond the range of whole wet weights obtained in the sample.

$$F_{(ratio)} = 53.5 > F_{(\alpha 2;0.01;5,113)} \approx 3.55;\ P < 0.01$$

Using the Tukey test for comparison of means of adjusted ovary weight there are two homogenous groups formed with no significant differences within each group (Q = 4.889, rejection level = 0.01).

Group	
Group 1	PST, SU
Group 2	PRE, HP, ST, DO

where Group 2 > Group 1.

The Guam populations and the cohorts which developed under pre-outbreak conditions on Davies Reef show significantly higher adjusted female somatic weights than the Davies Reef post-outbreak group and the Suva Reef population (Table 5.12). Adjusted somatic weights were also analysed for differences between sexes among populations (Table 5.13).

Table 5.13. Summary of analyses of adjusted somatic weights between sexes in five *A. planci* populations from the Western Pacific region.

Groups	ANOVA	Tukey (HSD) test
DA PRE	$\mathbf{F}_{(ratio)} = 0.63 < \mathbf{F}_{(\alpha 2;0.01;1,18)} = 10.2$; $P = 0.44$	NS
DA PST	$\mathbf{F}_{(ratio)} = 23.7 > \mathbf{F}_{(\alpha 2;0.01;1,67)} \approx 8.40$; $P < 0.01$	♂ > ♀
HP*	$\mathbf{F}_{(ratio)} < 0.01 < \mathbf{F}_{(\alpha 2;0.01;1,38)} \approx 8.83$; $P = 0.95$	NS
ST*	$\mathbf{F}_{(ratio)} = 17.1 > \mathbf{F}_{(\alpha 2;0.01;1,38)} \approx 8.83$; $P < 0.01$	♂ > ♀
DO	$\mathbf{F}_{(ratio)} = 16.3 < \mathbf{F}_{(\alpha 2;0.01;1,35)} = 8.98$; $P < 0.01$	♂ > ♀
SU	$\mathbf{F}_{(ratio)} = 58.6 > \mathbf{F}_{(\alpha 2;0.01;1,51)} \approx 8.49$; $P < 0.01$	♂ > ♀

where NS = not significant

There was significant sexual dimorphism in adjusted somatic weights (where male (AST) > female (ASO)), adjusted for whole wet weight = 1636g, in the Davies Reef PST group, South Tumon Bay, Double Reef and the Suva Reef populations, but not in the Davies Reef PRE group and the Hospital Point population (Table 5.13). The Davies Reef and Suva Reef populations show generally higher relative gonad weights and lower relative somatic weights compared with the populations from Guam. This was confirmed with a negative correlation (trade-off) between adjusted gonad weights and adjusted somatic weight using both sexes from the three populations combined ($\boldsymbol{r}_{male} = -0.899$; $\mathbf{F}_{(ratio)} = 18.8 > \mathbf{F}_{(\alpha 2;0.01;94,94)} \approx 1.68$; $P < 0.01$; $\boldsymbol{r}_{female} = -0.874$; $\mathbf{F}_{(ratio)} = 14.8 > \mathbf{F}_{(\alpha 2;0.01;79,79)} \approx 1.79$; $P < 0.01$).

5.3.6. Analyses for the Davies Reef pre and post-outbreak groups

Additional analyses within the Davies Reef population were conducted because of the higher ranges in body size of the PRE and PST groups in comparison with the ranges of the other populations. The analyses of adjusted values in the Davies Reef groups used a higher value of whole wet weight for adjusting gonad and somatic weights (2208g), which lies above the ranges of whole wet weights in the other populations.

Table 5.14. Summary of mean whole wet weights and ANOVA between sexes in: (a) PRE group and, (b) PST group for the Davies Reef *A. planci* population.

(a) PRE group

Group	$(\mathrm{WET})_{\mathrm{mean}}$ (g)	SE	(n)
PRE male	2436	159.8	16
PRE female	2697	140.6	20

ANOVA; $\mathbf{F}_{(\mathrm{ratio})} = 1.53 < \mathbf{F}_{(\alpha 2;0.01;1,34)} \approx 8.98$; $P > 0.20$

(b) PST group

Group	$(\mathrm{WET})_{\mathrm{mean}}$ (g)	SE	(n)
PST male	2071	68.6	78
PST female	2445	75.1	76

ANOVA; $\mathbf{F}_{(\mathrm{ratio})} = 13.5 > \mathbf{F}_{(\alpha 2;0.01;1,152)} \approx 8.10$; $P < 0.01$

There was no significant difference between the sexes for whole wet weight in the PRE group. However, there was a significant difference in whole wet weight between the sexes in the PST group, where female starfish were significantly larger than male starfish (Table 5.14).

Table 5.15. Summary of mean whole wet weights and ANOVA between the PRE and PST groups in (a) male starfish and, (b) female starfish from the Davies Reef *A. planci* population.

(a) male starfish

Group	$(\mathrm{WET})_{\mathrm{mean}}$ (g)	SE	(n)
DA PRE	2436	159.8	16
DA PST	2071	68.6	78

ANOVA; $\mathbf{F}_{(\mathbf{ratio})} = 8.36 > \mathbf{F}_{(\alpha 2;0.01;1,92)} \approx 8.24$; $P < 0.01$

(b) female starfish

Group	$(\mathrm{WET})_{\mathrm{mean}}$ (g)	SE	(n)
DA PRE	2697	140.6	20
DA PST	2445	75.1	76

ANOVA; $\mathbf{F}_{(\mathbf{ratio})} = 3.63 < \mathbf{F}_{(\alpha 2;0.01;1,94)} \approx 8.24$; $P = 0.06$

The mean whole wet weight of male PRE starfish is significantly higher than male PST starfish (equivalent to 0.15 decrease in whole wet weight). However, the mean whole wet weight of female PRE starfish is not significantly different from female PST starfish (equivalent to 0.09 decrease in whole wet weight) (Table 5.15). There was a significant response through a lowering of mean body size in male starfish from the younger cohorts which developed in higher densities, while under the same conditions female starfish maintained similar body sizes between the two groups.

Analyses of adjusted and unadjusted gonad weights were determined for the Davies Reef PRE and PST groups (Table 5.16).

Table 5.16. Summary of mean gonad weights and ANOVA between sexes in the Davies Reef PRE group, (a) unadjusted and, (b) adjusted for mean whole wet weight = 2208g.

(a) unadjusted gonad weights in the PRE group

Group	$(GW)_{mean}$ (g)	SE	(n)
DA PRE Male	245	31.8	16
DA PRE Female	420	48.7	20

$F_{(ratio)} = 8.14 < F_{(\alpha 2;0.01;1,34)} \approx 8.98$; $0.01 < P < 0.02$

(b) adjusted gonad weights in the PRE group

Group	$(AGW)_{mean}$ (g)	SE	(n)
DA PRE Male	204	18.5	16
DA PRE Female	268	18.7	20

$F_{(ratio)} = 5.86 < F_{(\alpha 2;0.01;1,34)} \approx 8.98$; $0.02 < P < 0.05$

where (GW) = unadjusted gonad weight (male or female)
(AGW) = adjusted gonad weight (male or female)

There is a weakly significant difference ($P < 0.02$) in adjusted gonad weights between sexes in the PRE group, where mean ovary weight was greater than mean testes weight (Table 5.16a). There was also a weakly significant difference ($P < 0.05$) in adjusted gonad weights between sexes in the PRE group. Since there was no significant difference in whole wet weight between the sexes in the PRE group the differences in gonad weights can be attributed to small but significant differences due to sex characteristics (Table 5.16b).

Table 5.17. Summary of mean gonad weights and ANOVA between sexes in the Davies Reef PST group: (a) unadjusted and (b) adjusted for mean whole wet weight = 2208g.

(a) unadjusted gonad weights in the PST group

Group	$(GW)_{mean}$ (g)	SE	(n)
DA PST Male	221	14.7	78
DA PST Female	418	24.6	76

$\mathbf{F}_{(ratio)} = 47.7 > \mathbf{F}_{(\alpha 2;0.01;1,152)} \approx 8.10$; $P < 0.01$

(b) adjusted gonad weights in the PST group

Group	$(AGW)_{mean}$ (g)	SE	(n)
DA PST Male	236	8.81	78
DA PST Female	344	12.7	76

$\mathbf{F}_{(ratio)} = 48.7 > \mathbf{F}_{(\alpha 2;0.01;1,152)} \approx 8.10$; $P < 0.01$

There was a significant difference in both unadjusted and adjusted gonad weights between sexes in the PST group, where ovary weight is greater than testes weight (Table 5.17a). The relative reproductive investment as determined by adjusted gonad weights is significantly higher in female PST group starfish than in male PST group starfish (Table 5.17b). The differences in adjusted gonad weights between sexes in the PST group can be primarily attributed to differences in the relative energy allocation to gametogenesis between the sexes.

Analyses of gonad weights, both unadjusted and adjusted (for mean whole wet weight = 2208g) are tested for differences between the PRE and PST groups (Table 5.18; Table 5.19).

Table 5.18. Summary of mean testes weights between Davies Reef PRE and PST groups; (a) unadjusted testes weights, (b) adjusted testes weights (adjusted for whole wet weight = 2208g).

(a) unadjusted testes weights (g)

Group	$(GWT)_{mean}$ (g)	SE	(n)
DA PRE male	245	31.8	16
DA PST male	221	14.7	78

$\mathbf{F}_{(ratio)} = 0.81 < F_{(\alpha 2;0.01;1,92)} \approx 8.24$; $P > 0.25$

(b) adjusted testes weights (g)

Group	$(AGT)_{mean}$ (g)	SE	(n)
DA PRE male	204	18.5	16
DA PST male	236	8.81	78

$\mathbf{F}_{(ratio)} = 4.11 < F_{(\alpha 2;0.01;1,94)} \approx 8.24$; $0.025 < P < 0.05$

where (GWT) = unadjusted testes weight
(AGT) = adjusted testes weight

There was no significant difference in unadjusted testes weights between groups. Since there was a significant difference in whole wet weight between male starfish in each group (♂ PRE > ♂ PST) (Table 5.15), the relative allocation to gametogenesis was lower in the PRE group. There was a weakly significant difference in adjusted testes weights between the PRE and PST groups,(♂ PST > ♂ PRE) (Table 5.18). In the higher density PST group, composed of younger estimated age classes, there was a weakly significant increase in relative allocation to gametogenesis in male starfish.

Table 5.19. Summary of mean ovary weights between Davies Reef PRE and PST groups; (a) unadjusted ovary weights, (b) adjusted ovary weights (adjusted for whole wet weight = 2208g).

(a) unadjusted ovary weights (g)

Group	$(GWO)_{mean}$ (g)	SE	(n)
DA PRE female	420	48.7	20
DA PST female	418	24.6	76

$F_{(ratio)} < 0.01 < F_{(\alpha 2;0.01;1,94)} \approx 8.24$; $P > 0.25$

(b) adjusted ovary weights (g)

Group	$(AGO)_{mean}$ (g)	SE	(n)
DA PRE female	268	18.7	20
DA PST female	344	12.7	76

$F_{(ratio)} = 12.2 < F_{(\alpha 2;0.01;1,94)} \approx 8.24$; $P < 0.01$

where (GWO) = unadjusted ovary weight
(AGO) = adjusted ovary weight

There was no significant difference in unadjusted ovary weights (Table 5.19) and female whole wet weight between groups (Table 5.15). However, there was a significant difference in adjusted ovary weights between the PRE and PST groups (Table 5.20). Therefore, the relative allocation to gametogenesis in female starfish from the PST group is greater than in the PRE group.

While in male and female starfish there was an increase in gametogenic activity (determined by adjusted gonad weights) in the higher density cohorts (PST group) the significance of differences was greater in female starfish than males.

5.3.7. Summary of reproductive characteristics in five populations from the Western Pacific region.

The results of morphometric analyses of variables related to reproduction show consistent differences between low (Davies Reef PRE) and high (Davies Reef PST) density populations, and between the Suva Reef and Guam low density populations. Therefore, four of the principal factors involved in the level of reproductive output are adult body size (whole body diameter), relative gonad mass (from adjusted gonad weight), relative somatic mass (from adjusted somatic weight) and population density (Table 5.20).

Table 5.20. Summary of population density and comparative mean morphometric characteristics of whole body diameter, adjusted body size and adjusted gonad weights (adjusted for whole wet weight = 1636g) among five *A. planci* populations from the Western Pacific region.

Site	Sex	BD (SE)	PD (ha.$^{-1}$)	GW(adj.)(SE)	SOM(adj.)	(SD)
DA PRE	m	42.3 (1.1)	[2,3] ~ 1 - 10	125 (11.3)	1389 (14.2)	
	f	42.6 (0.8)		146 (10.1)	1404 (12.2)	
DA PST	m	38.6 (0.5)	[4] ~ 420	137 (5.11)	1395 (8.94)	
	f	40.5 (0.5)		210 (7.75)	1306 (16.3)	
SU	m	29.1 (0.8)	[4] ~ 1 - 10	151 (15.4)	1424 (10.5)	
	f	27.3 (1.1)		280 (20.1)	1295 (12.9)	
DO	m	29.4 (0.6)	[4] ~ < 5	63 (5.1)	1497 (4.35)	
	f	30.9 (0.8)		97 (9.7)	1454 (8.20)	
HP	m	23.6 (0.4)	[4] ~ < 5	NA	1492 (4.18)	
	f	23.7 (0.7)		NA	1492 (10.2)	
ST	m	26.9 (0.5)	[4] ~ < 5	NA	1511 (6.16)	
	f	26.9 (0.6)		NA	1466 (8.78)	

where BD = body diameter
PD = *A. planci* population density
GW(adj.) = gonad weight (adjusted for whole wet weight = 1636g)
SOM(adj.) = somatic weight (adjusted for whole wet weight = 1636g)
using (SOM) = (WET) - ((GW) + (UW))

[2] = Keesing and Lucas (1992)

[3] = Ayling and Ayling (1992)

[4] = this study

Sexual dimorphism was significant in the Davies Reef PST group for gonad ($P < 0.01$) and whole wet weights between sexes ($P < 0.01$), and weakly significant between gonad weights in the Davies Reef PRE group ($P < 0.02$) (where female weights were greater than males).

5.4. **Discussion**

5.4.1. General reproductive characteristics

As in Chapter 4, the analyses among the five populations were conducted under the assumption that the SPBC method of age determination is widely applicable throughout the Western Pacific region. The age at full sexual maturity (3 years) is also assumed to be constant in these populations. The data needed to test the age at maturity hypothesis were not available from all the populations (i.e. from Davies Reef pre-outbreak group, Hospital Point and South Tumon Bay) therefore, the validity of an invariant age at maturity among these populations remains a critical assumption for the life history analyses.

Asymptotic size is proximally determined by reproductive investment and excess energy so that reproductive tactics ultimately reflect the constraints of a fitness maximising selection process involving mortality as well as energy acquisition and allocation (Jones and Johnson, 1977). They described the pattern of mortality rates in species with a planktonic larval stage as tending to be U - shaped, with a rapid decrease in mortality rate during the early life history which then flattens out and begins to rise at or soon after maturity. After a certain age, the mortality costs of reproduction increase when reproduction is delayed because mortality discounts the relative value of energy invested in growth by decreasing the probability of future reproduction (Dunbrack and Ware, 1987). Therefore, the age at maturity in *A. planci* may be more constrained by selection than other reproductive characteristics.

5.4.2. Body growth and fecundity

There was a large range in body size and gonad weight at full sexual maturity in the Guam populations (between Hospital Point and Double Reef (WET) ♂, 339 to 970g; ♀, 506 to 1240g and; (GW) ♂, 5 to 29g; ♀, 17 to 145g). The growth of gonads in the Guam populations show that testes and ovary growth do not differ significantly from isometry, in relation to body size, where the relationships were significant (Tables 5.3; 5.4). The relationships between whole wet weight and gonad weights were not significant for Hospital Point (♂, $P = 0.04$ and ♀, $P = 0.15$) and South Tumon Bay (♂ only, $P = 0.07$). If we assume the collections from all populations were made during similar stages of seasonal gametogenesis, there were lower gonad weights in the Guam populations compared with those from Suva Reef and Davies Reef (Figure 1a - f). This suggests that the priority of gametogenesis is not as high as the levels found in Davies Reef and Suva Reef populations. The abundance of food on the Guam reefs undoubtedly plays an important role in their reproductive development (Cheney, 1974).

If reproduction in the Guam populations involves processes which vary in relation to the other two regions, then other potential reproductive tactics in the Guam populations could produce similar levels of gametogenesis to those found in the Fiji and GBR populations. This might involve a protracted spawning period of a number of discrete events with gametogenesis continuing through most of the spawning period. Alternatively, a significant partial spawning may have already occurred prior to the Guam collections, such that the estimates obtained are significantly lower than the actual levels of annual gametogenesis. Cheney (1974) reported protracted spawning activity in the populations around Guam, however, the gonad indices (using a subjective four-point scale) remained high until late July or early August in the 1970 spawning season (Figure 5.1; Cheney, 1974). This shows that the timing of the collections in the present study probably took place prior to largest seasonal decline in gonad indices.

In the present study, it was noted that some gonads (in 1 - 3 arms) in several individuals from the Guam collections had the appearance of being partially spent, but this evidence was uncommon. There were no macroscopic signs of significant partial spawning in the starfish collected, although gonad lobule size did appear to be variable (where larger, mature lobules were generally found in the larger starfish). However, under the conditions of extrinsic resource limitation the Guam populations developed relatively higher adjusted somatic weights and lower adjusted gonad weights than the Suva Reef or Davies Reef populations (Tables 5.10 to 5.13). This alternative tactic can enhance reproductive success by promoting an iteroparous life history with a relatively lower reproductive output occurring in each spawning season.

Body wall thickness in *A. planci* from the GBR, was determined by the rigidity of the starfish when emersed (Kettle, 1990). Although this character is generally variable within populations (personal observation), body walls appear to become progressively thinner with increasing age and size in those starfish with a high reproductive effort (Kettle, 1990). The difference in thickness of the body walls was also made apparent by the frequent need to change scalpel blades during the processing of the Guam samples, which had not been necessary during the same procedure with *A. planci* from the GBR or Fiji populations. Kettle (1990) showed that the body wall was the largest storage compartment in *A. planci* and energy for somatic maintenance and reproduction in starfish from a high density population was derived from the body wall over the spawning season, and in conditions of limited food. An increasing allocation of energy to reproduction by large starfish contributes to a decline in caeca and body wall indices (Kettle and Lucas, 1987) resulting in a lower organic content in these body compartments, less available energy for maintenance or protection, inevitably reducing their lifespan. Similarly, Ebert (1982) found that longevity in echinoid species was related to the level of investment in body protection and maintenance mechanisms, supporting the "disposable soma" theory of senescence (Kirkwood and Holliday, 1979). In general, the characteristics of echinoid species with relatively long lifespans includes a more massive body wall among their adaptations (Ebert, 1982).

5.4.3. Reproductive allometry

The exponential increase in gonad size with increasing body size has been demonstrated in previous studies on *A. planci* from populations in several regions of the Indo-Pacific (e.g. Conand, 1984; Kettle and Lucas, 1987; Kettle, 1990) and the present analyses from the Davies Reef, Double Reef and Suva Reef populations. Maximum fecundity from the Davies Reef PST group was approximately 97 x 10^6 oocytes determined from an individual approximately 3900g whole wet weight (50cm whole body diameter). This is equivalent to 0.28 of body weight which is approximately 0.3 increase in gonad weight over an approximate 0.25 increase in wet weight from the previously reported maximum where gonad growth was found to be 0.20 of body mass at a whole wet weight of 3000g (approximately 40cm) (Kettle and Lucas, 1987).

The results from the analyses of ovary weights are similar to the extrapolated values from Kettle and Lucas' equation which predicts 119 x 10^6 eggs or 0.26 of the whole wet weight for a 50cm starfish (see Table 8, Birkeland and Lucas, 1990). In the 40cm starfish from Helix Reef, gonad growth represented 0.45 of the total body energy being devoted to reproduction (Kettle, 1990). By extrapolation of Kettle's calculation, the large ovary mass in the Davies Reef 50cm starfish contained in excess of 0.5 of total body energy.

The pattern of testes growth among the populations was different to the pattern in ovary growth derived from the power relationships using whole ovary weight and whole wet weight (Figure 5.2b). Positive allometry in ovary growth occurred in female starfish from the Davies Reef pre-outbreak group, Davies Reef post-outbreak group and the Suva Reef population. In the range of overlap of whole wet weights in these populations the elevation of the relationship with ovary weights for the Suva Reef population is significantly greater than that for the Davies Reef post-outbreak group (Figure 5.4b). This shows that ovary growth is not determined simply by individual body size. Since coral resources were comparatively more abundant on Davies Reef than Suva Reef, then factors other than simply food availability and body size were involved in determining the size of ovary. The differences in the relationships for testes and ovary growth among the populations reflects intrinsic differences in the reproductive tactics between sexes.

5.4.4. Population reproductive characteristics

The Davies Reef and Suva Reef populations showed generally higher relative gonad weight but lower relative somatic weight compared with individuals from the Guam populations. This was confirmed with a negative correlation (trade-off) between adjusted gonad weights and adjusted somatic weight, in both sexes from the three populations (Davies Reef, Double Reef and Suva Reef). Therefore, higher gonad weights such as those found in the Davies Reef post-outbreak group and the Suva Reef population were achieved at the expense of somatic weight, i.e. energy partitioning away from maintenance of somatic functioning and energy storage as previously shown by Kettle (1990). The Guam populations showed an alternate reproductive tactic with relatively higher partitioning to somatic reserves and relatively lower gonad growth.

A. planci from Suva Reef are estimated to have settled as early as 1986, using the results from the SPBC analyses. Massive recruitment was recorded in 1984 and another major episode in 1987 (Zann et al., 1990) which depleted the live coral cover over much of the reef. At the time of the present sampling exercise the reef was in the early stages of recovery with small colonies of acroporid species, interpreted as recent recruits, observed in most areas of the back reef during the collecting trips. All estimated age classes which settled between 1986 to 1991 were represented in the collections of samples obtained for this study. Larger numbers of juveniles (which settled in 1990 and 1991) than adults were collected (where juveniles comprised 56% of the collections) showing that recruitment to the adult population on Suva Reef was increasing at this time. Adjusted fecundity of *A. planci* showed no significant differences between estimated age classes (P = 0.31), despite a marked change in the pattern between estimated age classes 4+ and 5+ years, i.e. after settlement of the 1987 outbreak cohort (Figure 5.8).

Sexual maturity occurred at a smaller size on Suva Reef than in the Davies Reef population (Table 5.2) resulting in lower absolute gonad weights, although the relationships for testes and ovary growth were significantly greater than isometry in relation to body size in both populations. The pattern of a smaller adult size range implies there is a trade off between fecundity (related to size) and development time (growth rate), with size as the hidden intermediary (Sibly et al., 1985). An extended period of development in *A. planci* is demonstrated by the poor gonad growth in their second year (see Lucas, 1984; Zann et al., 1990), and this physiological delay allows a greater body size to be achieved prior to full sexual maturity (at 35months).

Fecundity has to increase exponentially with body size to maintain fitness over an extended period of development (Lewontin, 1965; Sibly et al., 1985). This pattern is found in both the Davies Reef and Suva Reef populations. Therefore, it is apparent that *A. planci* from the Guam populations prioritise somatic maintenance over gametogenesis which is in accord with previous observations made by Cheney (1974). He found that starved *A. planci* collected from around Guam resorbed gonad after 1 month, indicating that maintenance had a priority over reproduction. As Birkeland and Lucas (1990) pointed out, the results of the studies in Japan by Okaji (1989) and from the GBR by Kettle and Lucas (1987) oppose Cheney results, showing that gonad development has priority over somatic maintenance. If the differences in reproductive characteristics are due to selection from geographic or life-history variation (i.e. the bottleneck population effect), there may be some genetic basis. However, the regional proximity of Guam to Japan, where Okaji's study showed the alternative reproductive characteristics casts some doubt on a genetic argument. It would be worthwhile for Kettle and Lucas' analyses, including a similar study on the population dynamics as introduced here, be employed in a project on the Guam populations to address this issue.

The response to increased starfish density and lowered food availability in adult starfish from the Davies Reef population was a lowering of mean body size in the post-outbreak group (see Chapter 4), a significant increase in the slope of the regression between testes weight and whole wet weight ($P < 0.01$), and a significant increase in elevation of the regression for ovary weight and whole wet weight ($P < 0.01$) (Figures 5.3, 5.4; Sections 5.3.2.2, 5.3.2.3). The levels of gametogenic activity were maintained throughout the estimated adult lifespan in most populations (i.e. the regressions of adjusted gonad weights and estimated age in the adult age groups were not significant) except in the Davies Reef post-outbreak group where a negative relationship showed a significant decline in female fecundity after an estimated age of four years (Figure 5.8; Tables 5.9). Therefore, the significantly higher fecundities of the younger adult cohorts in the post-outbreak group, responsible for the outbreak, were not maintained with increasing estimated age indicating a tendency to semelparity.

Under the limiting conditions from increased starfish densities experienced in the Davies Reef population the gonad weights were maintained in both sexes, however, male starfish achieved this with a significantly lower mean body size. There were also significant differences according to sex in the adjusted gonad analyses with higher mean relative ovary weights in the post-outbreak group compared with the pre-outbreak group (Table 5.19b; $P < 0.01$), while the size difference in mean relative testes weight between groups was only weakly significant (Table 5. 18b; $0.025 < P < 0.05$). The physiological response to an increase in population density (density-dependent) involved a relative increase in gonad size, which was significantly stronger in female *A. planci*. The factors affecting the starfish after an increase in population density in the Davies Reef population stem from mass settlement, aggregative behaviour and nutrient demand (Tables 5.18, 5.19; Figures 5.3b, 5.4b). This resource stress contributed to the increased mortality rates in the adult phase (see Chapter 4), being partly dependent on the available levels of resource, body size (energy reserves) and the level of partitioning to reproduction. Therefore, relative reproductive effort can vary according to the influences associated with the level of cohort density.

Since the data for the two Davies Reef groups were obtained at the same time, living under similar limited resource conditions, the significant differences in body size and gonad weights are unlikely to be in response to the particular conditions at or near the time of the collections. Therefore, it is the conditions of the juvenile habitat during development, which are the primary influence on their life history and reproductive "tactics" in adult life. More comparative studies on lower density populations including an assessment of sex-specific behaviour, feeding rates of each sex and direct estimates of reproductive effort, i.e. the proportion of energy acquired that is allocated to reproduction (Lawrence, 1990), are necessary to identify the range of life-history characteristics which regulate the reproductive traits in each sex in *A. planci*.

5.4.5. Characteristics of sex

The results show that both extrinsic and intrinsic factors affect the observed variation in reproductive characteristics and have a greater influence on female *A. planci* than males. This is not surprising since the potential offspring number is related to the volume of oocytes released in a season. Where high fertilization rates are maintained, due to the high fertilizing capacity of *A. planci* sperm (Benzie, 1994), oogenesis is more closely linked to population growth than the amount of sperm produced. It therefore follows that selective pressure on resource partitioning from varying rates of mortality and recruitment density will influence fecundity more strongly than spermatogenesis.

Assuming there were similar rates of food intake in both sexes, the lower relative reproductive effort in male *A. planci* (in both gonad mass and the energy involved in gametogenesis) shows there is a difference in the allocation available to maintenance. This variation in allocation is used to predict that longevity, in general, will be greater in males than females under limiting conditions, as found in the Davies Reef outbreak. It is supported by the apparent increase in sex ratio towards male starfish found in collections towards the end of the Davies Reef outbreak. The ratio of female to male *A. planci* on Davies Reef in November 1992, one year after the termination of the field study for this project, of a sample of 46 starfish collected by Sweatman (personal communication) only 16 were female (H_0 = that the sex ratio is 1:1; $\chi^2 = 4.26$; $P < 0.05$). Therefore, there was a weakly significant difference from the predicted sex ratio in the late outbreak population. A similar pattern was also found in collections made during the decline of an outbreak (low coral cover, low density with small aggregations) on Lynch's Reef, nearby to Davies Reef, during 1990 (Butler, personal communication).

5.4.6. Resource demand in high density populations

Several studies have reported a positive correlation between the level of feeding behaviour and population density. In low densities and sufficient food availability *A. planci* is generally a nocturnal feeder (Chesher, 1969a; Pearson and Endean, 1969; Cheney, 1974; Endean, 1974; Yokochi et al., 1992) which implies they avoid visual predators (e.g. fish). However, feeding rates can be variable due to a complex of factors (Moran, 1986) including season (Keesing, 1990) and age (Lucas, 1984). Cheney (1974) described two behavioural modes, (a) dispersed, where individuals usually feed only at night and are cryptic by day, even when coral is abundant, and (b) aggregated, where feeding sites often involve groups of starfish and feeding continues during the day. In dispersed mode visual predators may be able to control populations of *A. planci* while high densities may "swamp" predators and reduce the risks involved in daytime feeding (see McCallum, Endean and Cameron, 1989). The increased activity such as movement and feeding suggests a possible source for at least part of the energy required for the development of the high reproductive effort found in outbreak population studies by Kettle and Lucas (1987) and Kettle (1990) as well as in the Davies Reef post-outbreak group.

Experimental manipulation of juvenile *A. planci* density and food availability was undertaken by Yokochi et al. (1992). They reared solitary starfish in aquaria with superabundant food and found they usually fed nocturnally yet, with increased starfish density or limited food supply, the feeding bouts extended through daytime due to their appetites. Although the experiment used small numbers of starfish in aquaria to simulate conditions of higher density (five and ten individuals with abundant food) and restricted access to coral food (five individuals), the results suggested that both population density and low food supply can influence feeding behaviour. The feeding activity of *A. planci* is strongly affected by nutritional demand (Yokochi et al., 1992), and movement (foraging activity) is significantly greater in higher densities than lower densities, even in areas of comparable coral cover (Keesing, 1990).

5.4.7. Reproduction and life-history characteristics

In a very high density population on Helix Reef, high reproductive effort was maintained by reducing the energy allocation to somatic processes and tending to a semelparous life history (see Kettle, 1990). Under those extreme outbreak conditions the coral cover was reduced from approximately 30 to 0% in one year (Kettle, 1990) and this resulted in a subsequent crash in population size from mortality attributed to a combination of a lack of food and high reproductive effort. His high density population studies and starvation experiments show that gametogenesis is consistently maintained at the expense of the main food storage compartments, so that structurally weakened and starving *A. planci* almost certainly died within the year (estimated maximum of six months starvation; Kettle, 1990). This reproductive tactic is more clearly associated with a semelparous life history. The pattern in high density populations with diminishing resources is that reproductive output is maintained at all costs in starfish at or soon after maturity (Kettle, 1990).

Table 5.21. Summary of reproductive characteristics of *A. planci* developed under various conditions.

Population type	(e.g.)	Resources	Reproductive effort	Lifespan (years)
Low density	DA PRE	high	high	9+
Low density	Suva Reef	low	high	7+
Low density	Guam*	low	moderate	6+
High density	DA PST	moderate	high	5+
High density	Helix Reef	diminishing	high	3-4+

where * = inferred reproductive characteristics assuming that the data collected from Guam were indicative of the annual development of gonads.

Apart from the Helix Reef case study, all other populations including the Davies Reef pre-outbreak group appeared to pursue an iteroparous life history (Table 5.22). By developing a simple model which ignored genetic and sex factors, Charnov and Schaffer (1973) showed that age specific mortality distributions are critical to the development of life histories, i.e. when juvenile exceeds adult mortality, an iteroparous life cycle is favoured irrespective of early or delayed maturation. In most marine invertebrates that broadcast spawn with planktotrophic larvae, juvenile mortality rates greatly exceed those of adults (i.e. *A. planci*, Keesing, 1990) which should, therefore, favour a longer reproductive (iteroparous) lifespan. Strathmann (1974) suggested that an iteroparous strategy promotes dispersal of larvae to test new habitats by sampling conditions many times which would be advantageous when survival is uncertain. Stearns (1976) summarised life-history theory, under both ***r*** - ***K*** and bet-hedging tactics, and suggested that variable adult mortality, rapid development, high reproductive effort, semelparity and short lifespan are selected in temporally fluctuating habitats (i.e. as occurs during outbreak episodes) while slow development, iteroparity, smaller reproductive effort and longer life are found in more stable habitats (i.e. low density persistent populations).

Production of a high reproductive output does not appear to affect lifespan in *A. planci* from the GBR and Suva Reef except when resources are limited (extrinsic limitation). This means that these starfish are capable of maintaining substantial energy reserves when up to 0.5 of the total body energy can be used in gametogenesis each reproductive season. *A. planci* has a much larger biomass in terms of kJ (energy) than the few other echinoderm species for which values have been reported (Lawrence and Moran, 1992). Their large body sizes can only be achieved by exploiting a reasonably high energy (animal) food resource that is plentiful and requires little effort to obtain; i.e., hard corals. Calow and Jennings (1977) suggested that the cost of high level reproduction may be offset by a super-abundant food supply so that food can be obtained with minimal effort from search and capture, reducing the metabolic demands which may affect lifespan and iteroparity.

In the Guam populations, gonad development was relatively poor and this was interpreted as a relatively lower reproductive effort. This was supported by the characteristic of relatively thick body walls in the Guam *A. planci*, and used as evidence of additional energy storage not found in adult starfish from other populations. Lawrence (1990) suggested that the development of a thick body wall occurred in some tropical valvatids as a consequence of stress from low resource availability and the advantage of allocating resources away from other compartments to increase longevity and promote an iteroparous life history. Using the data from the SPBC analyses the Guam starfish maintained an iteroparous life history (approximately three to four spawning seasons over their estimated lifespan) under poor food conditions. In the GBR and Suva Reef populations *A. planci* exhibited a "big bang iteroparity" (high reproductive output and a moderate to long lifespan), a life cycle which has been found in endoparasites and deep sea organisms (Calow, 1979). This physiologically unlikely combination of attributes is made possible by exploiting a high quality food resource, the hermatypic coral species, which generally comprise large percentages of the resources on tropical reefs.

FIGURES

Figure 5.1. Percentage frequency histograms of gonad weights (g) in five *A. planci* populations from the Western Pacific region; (a) Davies Reef pre-outbreak group, (b) Davies Reef post-outbreak group, (c) Suva Reef, (d) Hospital Point, Guam, (e) South Tumon Bay, Guam, (f) Double Reef, Guam.

Figure 5.2. Relationship between (GW) (g) and (WET) (g) for five *A. planci* populations from the Western Pacific region using the power equation, $(GW) = a \cdot (WET)^b$; for (a) testes weight, and (b) ovary weight; where (GW) = gonad weight (g); (WET) = whole wet weight; a and b are constants.

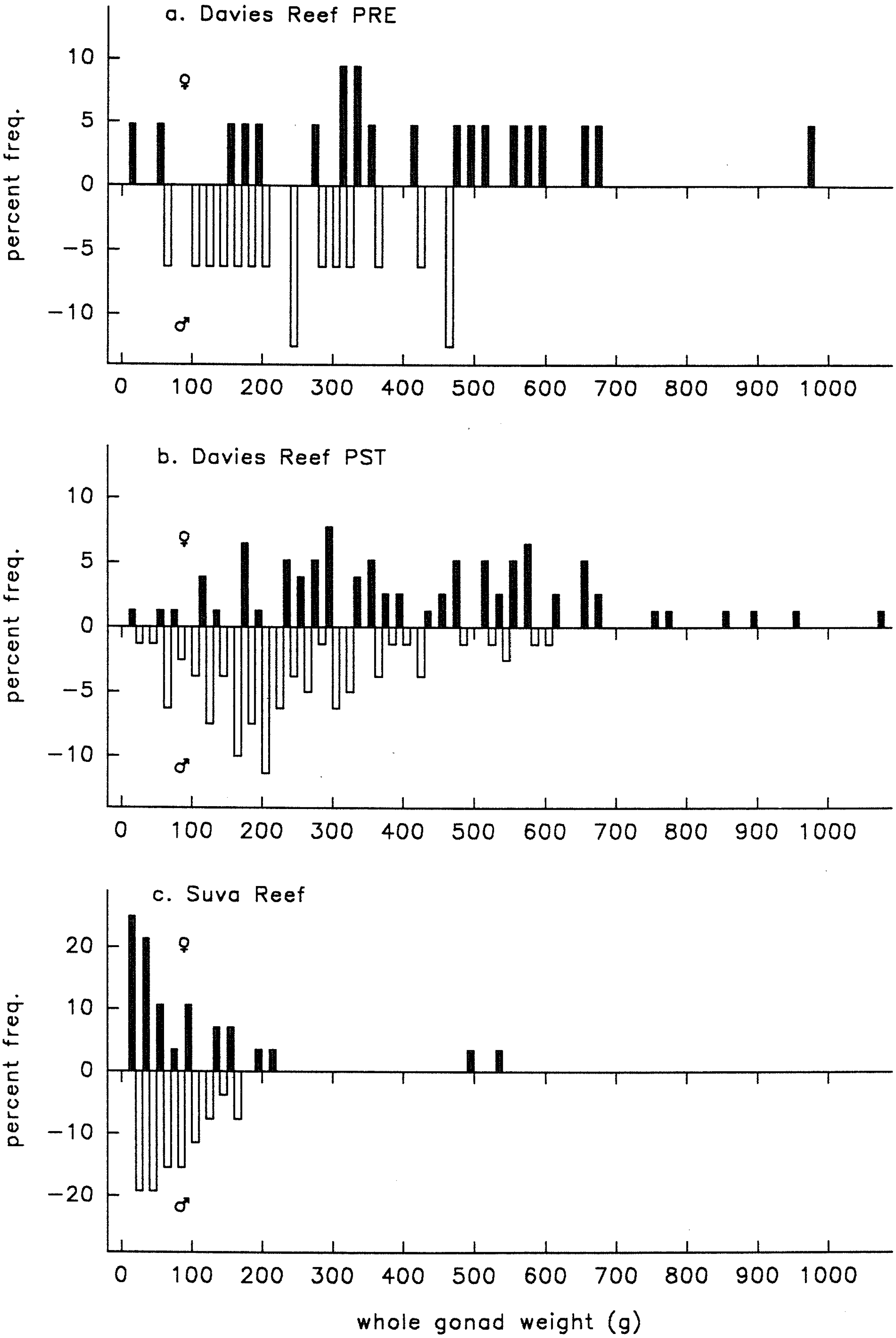
Figure 5.3. Linear regression analyses of ln (GWT) and ln (WET) for male starfish in five *A. planci* populations from the Western Pacific region; where (a) is the residual plot for fitted values, and (b) is the regression plot.

Figure 5.4. Linear regression analyses of ln (GWO) and ln (WET) for female starfish in five *A. planci* populations from the Western Pacific region; where (a) is the residual plot for fitted values, and (b) is the regression plot.

Figure 5.5. Relationships between ln (GW) and estimated age (AGE) in five *A. planci* populations from the Western Pacific region; where (a) testis weight, and (b) ovary weight.

Figure 5.6. Relationships between ln (AGWO) (ovary weight, adjusted for mean whole wet weight = 1636 g) and estimated age (AGE) in five *A. planci* populations from the Western Pacific region.

FIGURE 5.1



a. Davies Reef PRE

b. Davies Reef PST

c. Suva Reef

FIGURE 5.1

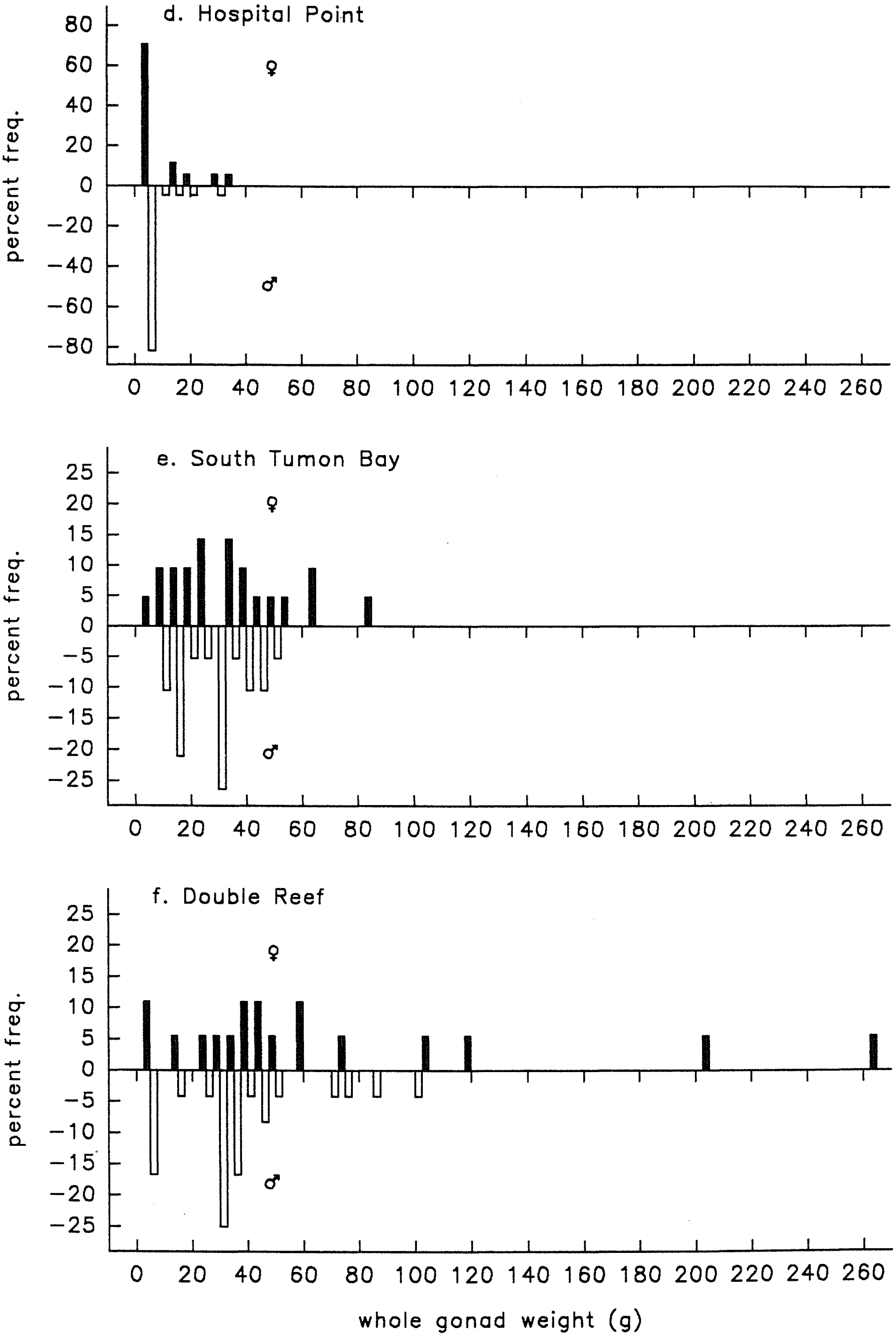
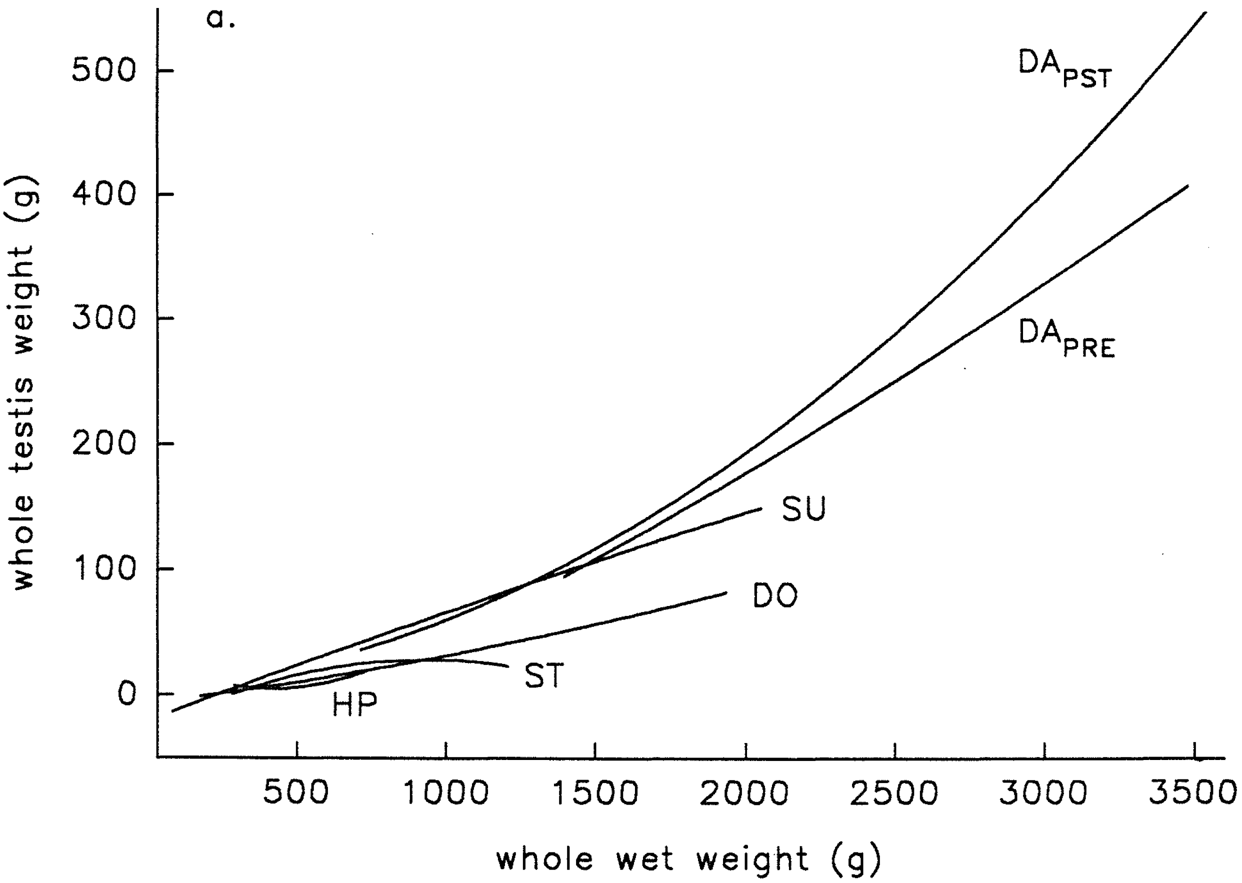

d. Hospital Point
e. South Tumon Bay
f. Double Reef
♀
♂
percent freq.
80
60
40
20
0
−20
−40
−60
−80
25
20
15
10
5
0
−5
−10
−15
−20
−25
0 20 40 60 80 100 120 140 160 180 200 220 240 260
whole gonad weight (g)

FIGURE 5.2


a.
whole testis weight (g)
500
400
300
200
100
0
500
1000
1500
2000
2500
3000
3500
whole wet weight (g)
DA$_{PST}$
DA$_{PRE}$
SU
DO
ST
HP

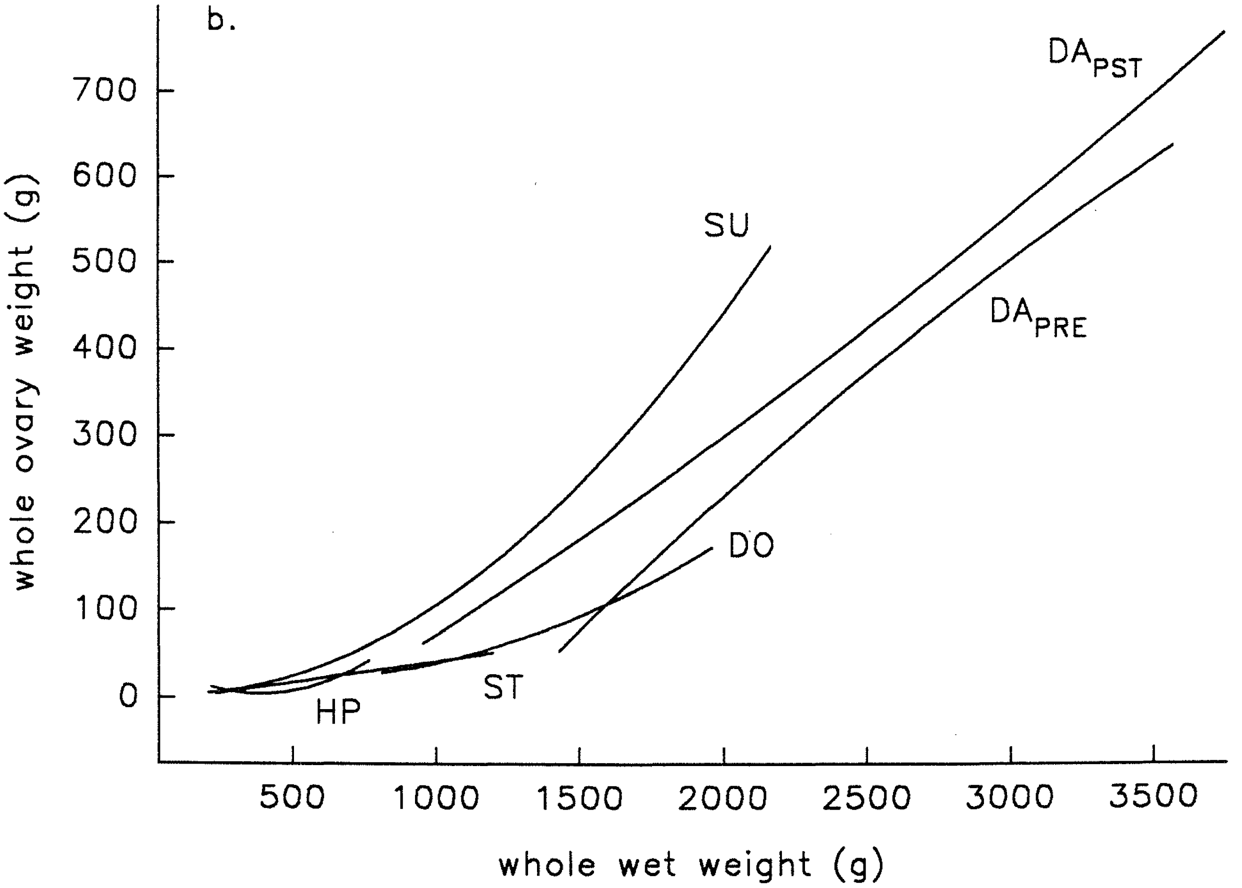

b.
whole ovary weight (g)
700
600
500
400
300
200
100
0
500
1000
1500
2000
2500
3000
3500
whole wet weight (g)
DA$_{PST}$
DA$_{PRE}$
SU
DO
ST
HP

FIGURE 5.3

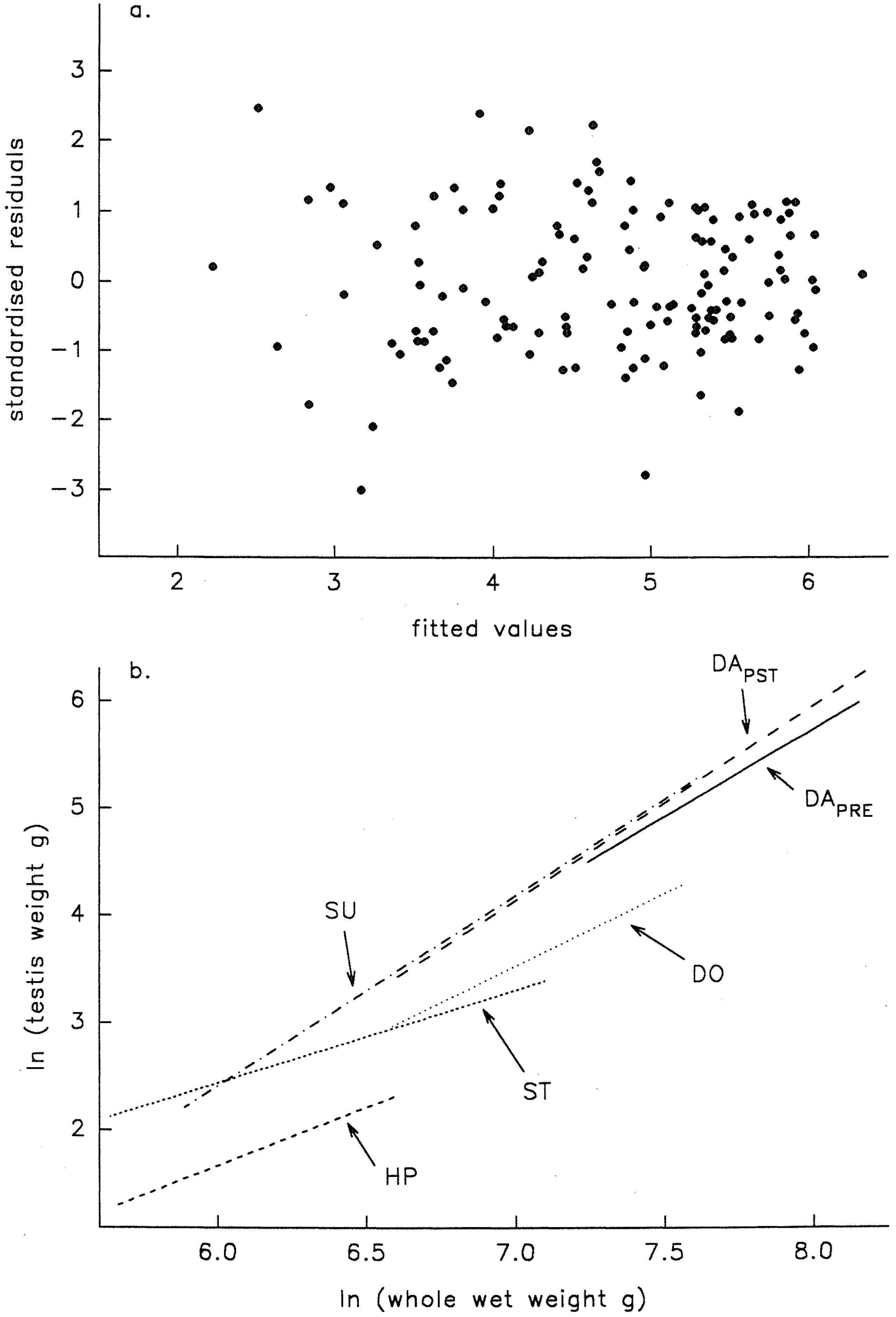
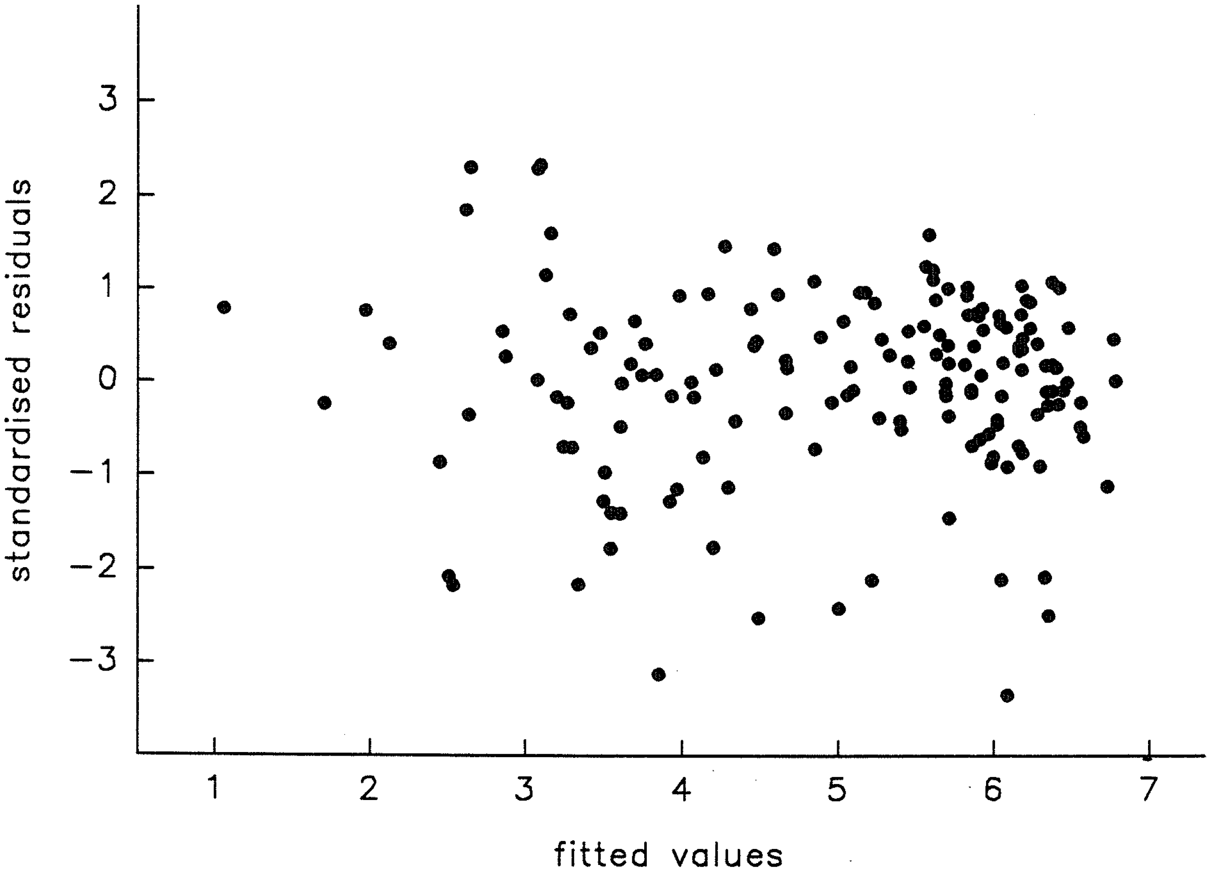
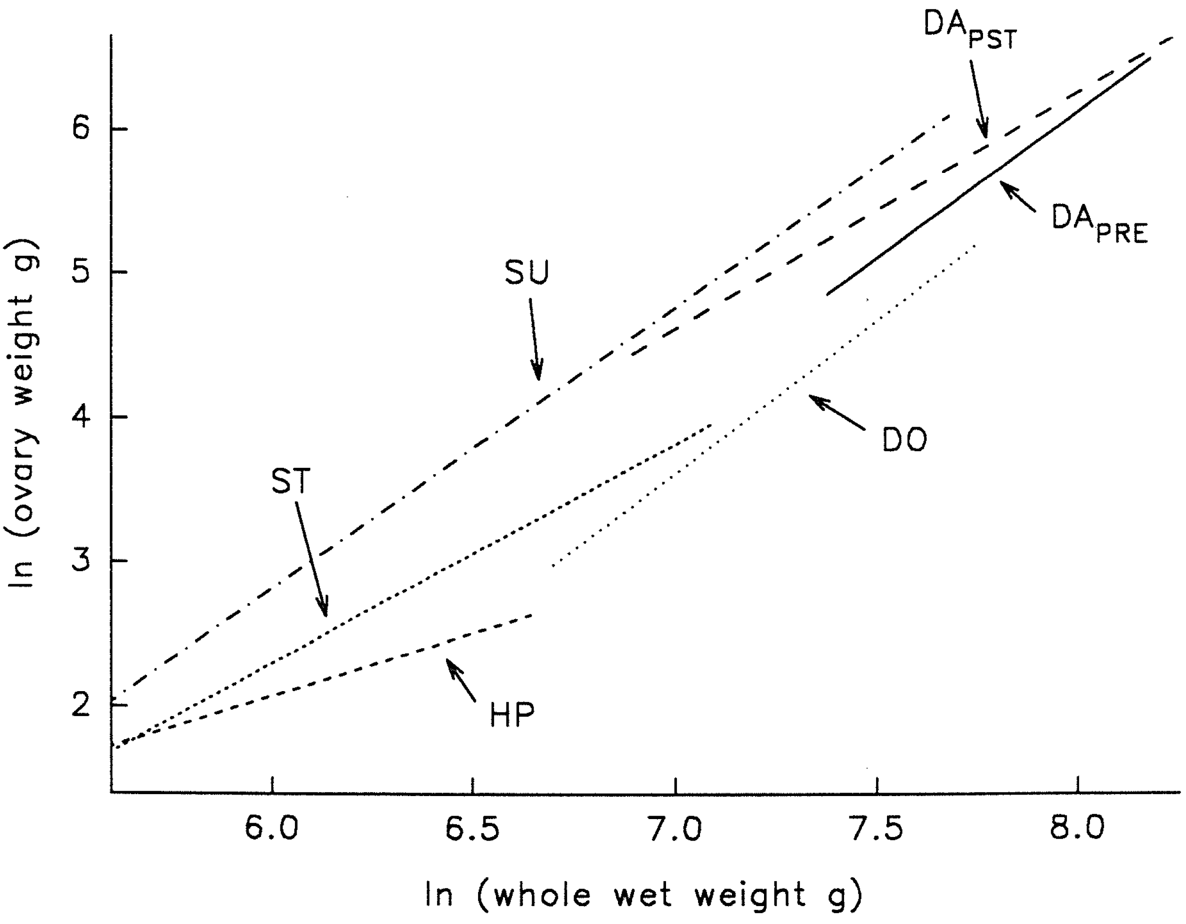

a.
standardised residuals
3
2
1
0
−1
−2
−3
2
3
4
5
6
fitted values
b.
ln (testis weight g)
6
5
4
3
2
6.0
6.5
7.0
7.5
8.0
ln (whole wet weight g)
DA$_{PST}$
DA$_{PRE}$
SU
DO
ST
HP

FIGURE 5.4



standardised residuals
3
2
1
0
−1
−2
−3
1
2
3
4
5
6
7
fitted values



ln (ovary weight g)
6
5
4
3
2
6.0
6.5
7.0
7.5
8.0
ln (whole wet weight g)
DA_{PST}
DA_{PRE}
SU
DO
ST
HP

FIGURE 5.5

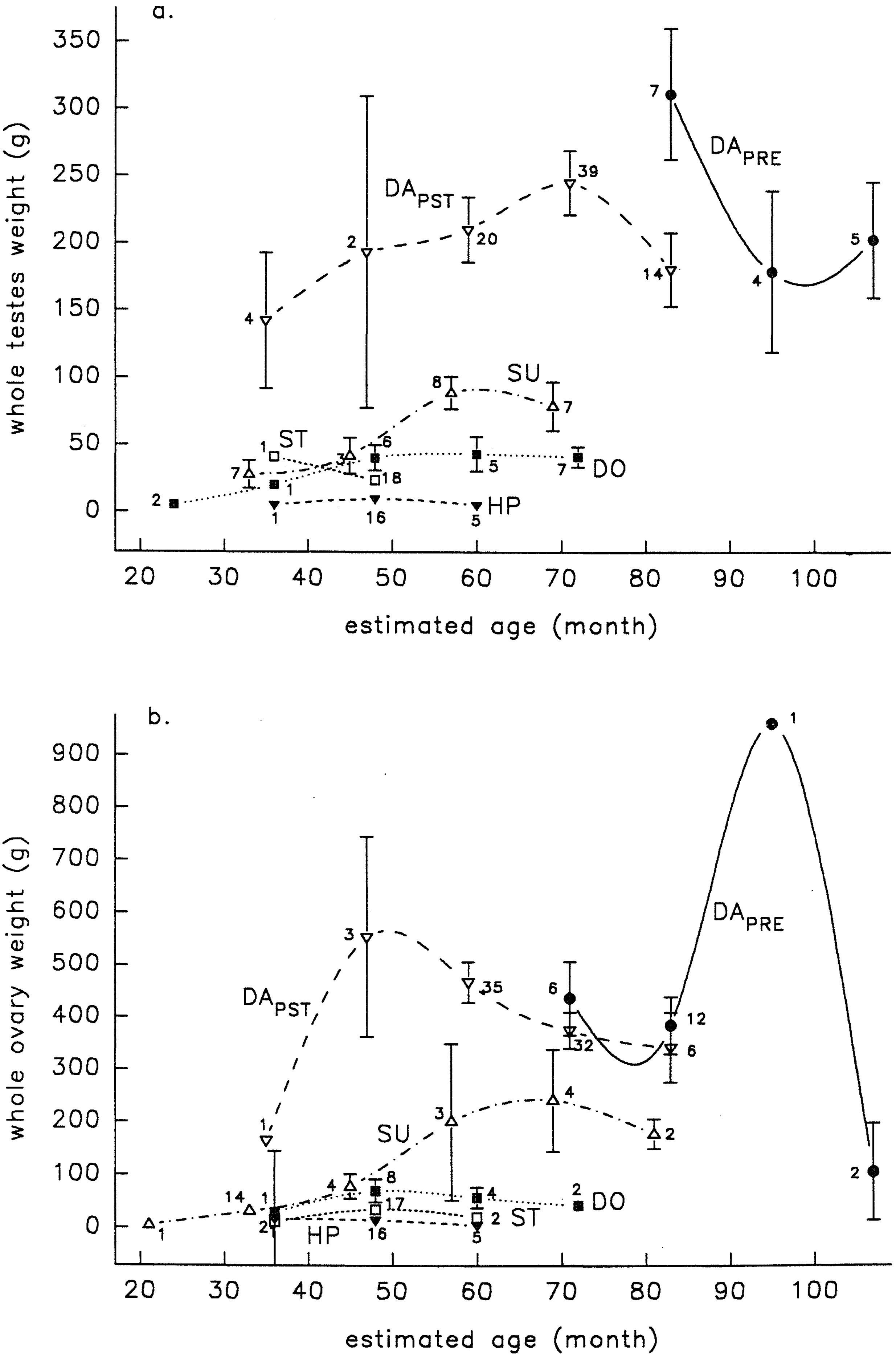
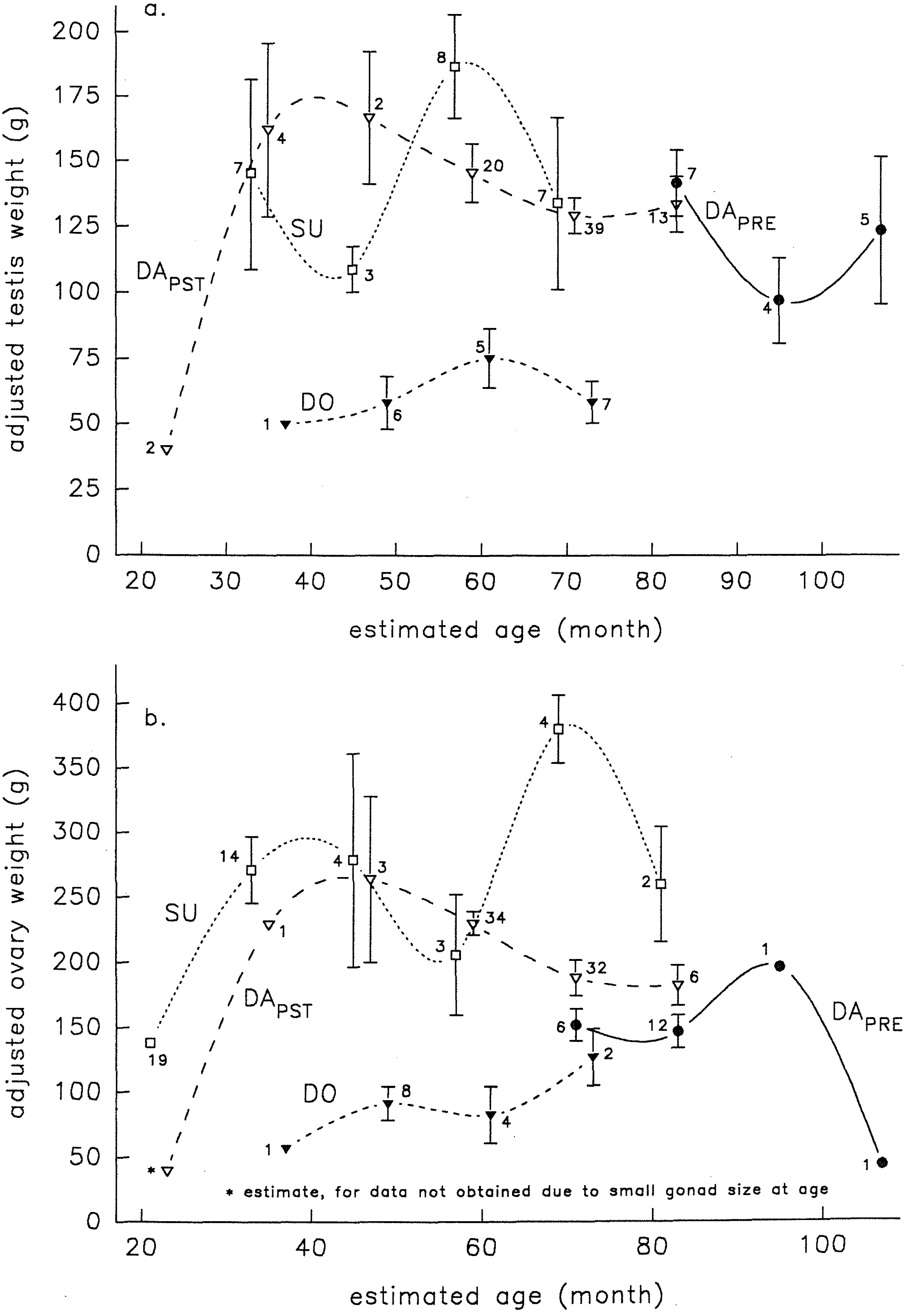

a.
whole testes weight (g)
350
300
250
200
150
100
50
0
20
30
40
50
60
70
80
90
100
estimated age (month)
DA$_{PRE}$
DA$_{PST}$
SU
ST
DO
HP
7
39
2
20
14
4
5
4
8
7
1
3
6
18
1
5
7
2
1
16
5
b.
whole ovary weight (g)
900
800
700
600
500
400
300
200
100
0
20
30
40
50
60
70
80
90
100
estimated age (month)
1
DA$_{PRE}$
3
35
DA$_{PST}$
6
12
32
6
1
SU
3
4
2
4
8
14
1
17
4
2
DO
2
2
ST
1
HP
16
5
2

FIGURE 5.6



* estimate, for data not obtained due to small gonad size at age

CHAPTER 6

A LIFE-HISTORY STRATEGY FOR *A. planci*

In the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient in directing available energy into channels favourable to the preservation of the species (Lotka, 1925). If a species is able to vary this channelling in relation to the environment it lives in, then its success and influence on communities has the potential to be of great significance.

◆

◆

6.1. The development of a life-history strategy for *A. planci*

Both Kettle (1990) and Moore (1990) suggested that *A. planci* has a variable life-history strategy depending on its habitat and/or population density. Moore (1990) proposed that the variation in life-history characteristics enables *A. planci* to persist in heterogenous reef ecosystems by being adapted to life in a range of habitats between two extremes; "permanent" (living in retentive hydrodynamic systems on reefs with low coral cover) and "temporary" (living on open-water reefs with high hydrodynamic flushing rates and rich coral resources). By occupying a wide range of reef types and developing characteristics favourable to the particular habitat, the chances of extinction are reduced (Moore, 1990). Therefore, a description of the life history of *A. planci* involves more complex theory than one specific strategy from a synthesis of factors involving *stress* and/or *disturbance*.

Kettle's population study of the Helix Reef outbreak and his experiments in aquaria showed that the characteristics of *A. planci* do not fit within the categories of the life history table developed by Lawrence (1990) (see Section 1.5.1.). In the early stages of the outbreak, prior to the impact of food limitation on the population (where aggregations typically form "feeding fronts", a tactic to optimise resource use), the species exhibited a *Ruderal* strategy (i.e. tolerates high mortality and low growth stresses), where longevity is limited by food availability and reproductive effort is sustained under resource stress (Kettle, 1990). As resources declined on Helix Reef the population continued to maintain high reproductive output and high reproductive effort.

In the decline phase following an outbreak, *A. planci* experiences peaks of both high *stress* (limited resources, low growth) and high *disturbance* (biomass is lost by starvation, sub-lethal predation or aboitic factors). Therefore, the "impossible fourth permutation" (i.e. a physiologically intolerable strategy; see Lawrence (1990) Figure 1) with high mortality and high growth stress may also be achieved but only for a short period as Lawrence (1991) noted, continued high stress would prevent recovery from high disturbance. According to Kettle (1990) in these conditions on Helix Reef a high reproductive effort was maintained as long as possible and resorption of the organic constituents of the body wall facilitated the energetic demands of the partitioning to reproduction. This was interpreted as an act of *Altruism* (Kettle, 1990), which promoted the survival of offspring when the resources of the adult population had been depleted. Therefore, Kettle concluded that there is no all encompassing life-history strategy for *A. planci*: *Competitors* at low density, *Ruderals* at higher densities, and *Altruists* favouring the spread of larval offspring over parental survival when resources are depleted.

The present study (summarised in Section 6.2.) has also shown there were varying patterns of life-history characteristics, both among populations and within the Davies Reef population (between the pre-outbreak and post-outbreak cohorts). Therefore, I proposed that *A. planci* can express variable life-history characteristics through phenotypic plasticity, both within and between populations (Stump, 1993). Variation in levels of estimated reproductive effort (as determined by relative gonad weight to body size relationships) occurred in relation to population (density) and habitat (food availability) characteristics where lower density populations express the iteroparous strategy (lower reproductive effort, low adult mortality), while high density populations tend towards a semelparous strategy (higher reproductive effort, high adult mortality) (Figure 6.1). Given the unavoidable constraints on the phenotypic plasticities of individual species, the patterns of longevity, iteroparity, and dispersal that promote coexistence (of polymorphisms), may themselves be life-history traits that evolved in part because they allow individuals to hedge their reproductive bets (Seger and Brockman, 1987). Therefore, this strategy alone, can account for large increases in their incidence as well as maintaining sparse populations within regions.

6.2. A summary of the principal results from this study

A variable life-history strategy is determined through the response of the characteristics of growth, mortality and reproduction in each population to their habitat conditions and each of these charcteristics were considered in this study. It was hypothesised that the history of individual growth is preserved in the growth increments of spine ossicles, reflecting the environmental conditions of their habitat during development. The analyses of spine ossicle growth in the four principal cohorts from the Davies Reef population showed a significant positive relationship between spine ossicle length and whole body diameter at the same age; i.e. within each cohort larger starfish tended to grow longer spines due to their relatively faster growth rates. The post-outbreak cohorts also had a pattern of attenuation in spine ossicle growth, at a younger estimated age than the pre-outbreak starfish, which was coincident with an increase in resource limitation (depletion of live corals) and mortality rates (apparent in cohort analyses of sequential field collections). Furthermore, there were generally smaller spine ossicle lengths at estimated age in starfish collected from aggregations compared with those collected in dispersed conditions (solitary and under less stress) in the post-outbreak group.

Estimates of lower body growth constants K_{BD}, assuming von Bertalanffy-type growth, were used to predict a smaller mean body size at maturity in the pre-outbreak cohorts from the Davies Reef population. Despite the weak significance of growth analyses using whole body diameter, the results suggested the mode of growth in low density populations tends to be indeterminate, given that they have a lower reproductive effort and the density is well below the carrying capacity of their habitat. Evidence for this in the Davies Reef population comes from the difference in predicted body sizes at maturity (where post- > pre-; from the VBGC analyses) and the small but significant difference in mean adult body sizes (pre- > post-; i.e. an estimated mean decrease of 0.12 in whole wet weight with the advent of the outbreak; Table 5.1).

A threefold increase in the spine ossicle growth constant K_S in the post-outbreak cohorts indicated those starfish developed with shorter asymptotic spine lengths (and demonstrated by curve analyses), shorter lifespan and higher mortality rates compared with the pre-outbreak cohorts. This response may have been caused by the behavioural tendency to form aggregations in the post-outbreak cohorts, promoting longer feeding bouts and higher levels of activity resulting from an increase in *stress* (after Pauly, 1991) on individuals. Given that several assumptions were extended to enable analyses of estimated age in other populations from the GBR region (Hook Island, Lady Musgrave Island) those results also supported the hypothesis of slower growth rates in low density populations, despite the availability of unlimited resources on the reefs, i.e. due to lower levels of activity and appetite.

The extent of influence from factors causing *stress* was reflected by the seasonal oscillation in the body wall reserves, opposed to the seasonal pattern of gametogenesis in the post-outbreak cohort which settled in 1986 on Davies Reef. Kettle (1990) also described an inverse cycle of energetic partitioning between the body wall and the seasonal demands of gametogenesis. He found that reduced amounts of soft tissues in the body wall occurred in response to competition for limited resources in aggregations and with a high estimated reproductive effort, a similar response was also interpreted from the morphometric analyses of the post-outbreak cohorts. Furthermore, under increased levels of food limitation (i.e. as experienced by the 1986 cohort) there was also a partial resorption of the somatic skeleton, giving rise to a seasonal oscillation in skeletal weight in this post-outbreak cohort. Skeletal resorption, interpreted from underwater weight measurements, was also found in *A. planci* held under experimental conditions of starvation over a six-month period. This decline in skeletal weight occurred predominantly in the ossicles within the body wall and the oral ossicle group. Resorption was less evident in the aboral spine ossicles since they retained the tetracycline marker introduced at the start of the experiment, for the analyses showed that the fluorescent stains occurred close to the spine ossicle base, indicating poor interim growth.

A. planci from five populations in the Western Pacific region; Davies Reef (GBR), Suva Reef (Fiji), Hospital Point (Guam), South Tumon Bay (Guam) and Double Reef (Guam) developed under a range of habitat conditions influencing the variation in their morphometric relationships. Multiple regression analyses showed that mean spine length was significantly longer at estimated age in the Davies Reef population compared with the others. This suggested either a more rapid rate of spine growth in the juvenile phase on Davies Reef, with high levels of resources or an extended juvenile growth phase allowing for longer spines to develop. As the age at maturity was assumed to be invariant (see Chapter 5), the results implicated either a genetic or a resource based difference in spine growth and hence, spine ossicle length at maturity among the populations. If spine ossicle growth reflects whole body growth in the juvenile phase, then its growth history can be used to develop theory on the differences in life-history characteristics between low and high density populations

The high fecundities among *A. planci* from the GBR and Suva Reef is offset by low larval and juvenile survival rates and therefore, is a characteristic of primary importance in the life history of this species throughout the Western Pacific region. Fecundity is tied to body size, through the exponential growth of gonads in populations where there were adequate resources (i.e. Davies Reef, Suva Reef and Double Reef). Therefore, lifetime fecundity may be maximised in relation to the variation in mortality rates among cohorts such that a longer lifespan is achieved in

A. planci through a lower reproductive effort spread over a number of years (i.e. an iteroparous life history, see Figure 6.1). The variation in estimated reproductive effort between pre- and post-outbreak cohorts from Davies Reef meant that lower reproductive effort occurred concomitantly with lower mortality rates and a predicted slower growth rate during the juvelile phase (i.e. a smaller body size at maturity). This is in accord with the predictions from the von Bertalanffy growth analyses and therefore, body growth may appear to be be determinate (i.e. expressed with higher reproductive effort and mortality rates) but under conditions of lower *stress* and *disturbance* the mode is indeterminate (i.e. lower reproductive effort and mortality rate). Therefore, growth is variable depending on the degree of plasticity in growth exhibited following maturity.

Growth in individual *A. planci* can only occur under an energy surplus from somatic maintenance, protection and reproduction, and hence depends on the level of resources held in the body storage tissues, the body wall and pyloric caeca. Adaptations for a long lifespan in many echinoderms include a more massive body wall, indicating a high level of energy storage for longevity and were related to the level of investment in body maintenance, low resource capture and protective mechanisms in echinoderms (Lawrence, 1990). *A. planci* from the GBR and Fiji exhibited negative allometric growth where the oral/aboral axis became thinner in larger and older starfish, reflecting reduced levels of energy storage. Therefore, the high reproductive effort determined from those individuals required high levels of energy to be partitioned from body reserves and resulted in the development of the thin body wall characteristic. Adult starfish from these populations were unable to maintain their body shape following emersion, since the tests often ruptured and collapsed under their own body weight.

By contrast, the Guam starfish showed a tendency to isometric body growth with relatively low fecundities. They developed thicker body walls which reflected a higher organic content, as determined from the lower elevations of the regressions for underwater weight and whole wet weight compared with the Davies Reef and Suva Reef populations, and were generally able to maintain their body shape for some time after emersion. By developing this physical condition in habitats of low resources implied that they had also developed a tactic of lower reproductive effort i.e. due to higher levels of partitioning resources to somatic maintenance. Therefore, in contrast with the other populations, somatic maintenance was prioritised over gametogenesis in the Guam populations, a tactic which would promote an iteroparous life history. Previous observations of *A. planci* from Guam also indicated that gametogenesis was not prioritised over somatic maintenance, as reported by Cheney (1974).

Application of life-history theory among populations of the Western Pacific region rests on the assumption of a constant age at maturity in all populations. Estimates of age-specific characteristics based on the SPBC method were assumed to commence at full sexual maturity. In previous studies describing age at maturity, gonad growth was found to be small at age 1+ years, and large at 2+ years when the first major spawning was assumed to occur. Therefore, full sexual maturity is apparently delayed, consistently, from the second to the third years through selective pressure from the exponential increase in fecundity with body size and an iteroparous life history. The development of this intermediate life-history phase involving postponement of maturation and body growth processes is only possible through the exploitation of a high energy food resource. This pattern of development was found in the GBR and Suva Reef populations but was not as well developed in the Guam populations. Smaller body sizes at maturity were found in the lower density populations (Suva Reef and Guam) implicating a trade-off between fecundity (related to body size) and development time under the conditions of limited resources. However, an iteroparous life history was apparent from estimated age structuring in all populations examined, except perhaps in very high density outbreaks, as described by Kettle (1990) from his Helix Reef study.

To compensate for the loss of iteroparous spawnings in short-lived, very high density populations there must be significant enhancement of reproductive success for an advantage to exist from the development of aggregations and smaller individual body size (lowering potential fecundity). Calow (1978) described a negative relationship between food ration and reproductive effort as "reproductive recklessness" due to the trade-off with increasing parental mortality. Recklessness will only be selected for when progeny have an equal or better chance of surviving through harsh nutritive conditions than parents (Calow, 1978). This tactic clearly describes the mechanism which has promoted so-called "Faustian" (Birkeland, 1989) and "fugitive" (Moore, 1990) traits in *A. planci* inhabiting temporary habitats and having a pelagic larval phase.

The relatively higher fecundities in the young adult cohorts from the post-outbreak group on Davies Reef were not sustained over the study period, under the conditions of diminishing resources, and an significant decline in fecundity occurred with estimated age soon after maturity. Both intrinsic and extrinsic factors influenced the reproductive characteristics of *A. planci* on Davies Reef and through sexual dimorphism probably had a more profound effect on females than males. The selective pressure on the pattern of resource partitioning influenced fecundity more than spermatogenesis, for energy costs involved in oogenesis are far greater (see Kettle, 1990) and therefore, contributes more to limiting population growth than by variation in spermatogenesis. It follows that under outbreak conditions the higher energy expenditure on fecundity promoted higher mortality rates in females than male starfish. This conclusion was supported by the deviation from the generally observed sex ratio of *A. planci* populations (i.e. 1:1), determined from collections made towards the end of the Davies Reef outbreak which contained significantly more males than females. If reproductive effort is relatively lower in male *A. planci* from high density populations then the pattern in life-history characteristics may well differ by sex. If males are able to participate in repeated spawning events by spawning small quantities of sperm repeatedly through the spawning period (see Babcock and Mundy, 1992) there would be an opportunity to gain a higher level of fitness, with an overall lower reproductive effort than females. In support of this hypothesis, Benzie (1994) found that male *A. planci* need only spawn relatively small quantities of sperm to enable high fertilization rates in aggregations which release relatively large quantities of spawned eggs.

Survival in echinoderms is affected by their reproductive energetics indicating a trade-off in allocation of resources between maintenance and reproduction (Ebert 1975; 1982). This implies that species with a very high reproductive effort have relatively short lifespans. Further studies by Ebert (1984) also found a trade-off between the growth constant ***K*** (from the von Bertalanffy growth equation) and long life in urchin species, such that a doubling of lifespan resulted in a halving of ***K*** (see Chapter 4). However, the four principal cohorts from the Davies Reef population were characterised by a positive correlation between the mortality rate ***M*** and the growth constant ***K*** and a negative correlation (trade-off) between asymptotic body size and ***K***. Among other factors the growth constant is related to the level of *stress*, as described by Pauly (1991), and therefore, is determined by various factors which increased mortality rates in the post-outbreak cohorts. The positive correlation between ***M*** and ***K*** occurred because of lower asymptotic body sizes in the post-outbreak cohorts and the physiological response to limited resource allocation to growth, reproduction, somatic maintenance and protection.

Life history analyses of the five populations from the Western Pacific region showed variations among several hypothesised life-history constants both within and among populations. The mode of body growth is apparently determined more by the plasticity in phenotypic responses to environmental conditions than differences in the genotypes, although small but significant differences in regional genotypes of *A. planci* have been shown elsewhere (see Benzie, 1992). The lack of correlation between ***K*** and ***M*** among the regional populations was probably due to different factors controlling ***K*** in each location, related to different levels of *stress* in populations. For a high growth constant can occur in individuals with low or high growth rates depending on intrinsic and extrinsic factors, i.e. water temperature, mode of growth, appetite, resource levels and population density.

6.3. A specific life-history strategy for *A. planci*.

I propose that the life history of *A. planci* involves a phenotypically polymorphic bet-hedging strategy. Seger and Brockman (1987) defined bet-hedging as a variable phenotypic expression of a single genotype which evolves as an adaptive response to population-wide temporal variation in fitness. A genotype with polymorphic phenotypes distributes itself over the available environments (genuine bet-hedging) and spreads the risk of local extinctions by maximising the geometric mean fitness of a panmictic population through varying migration rates (Gillespie, 1981; Seger and Brockman, 1987). Charnov (1993) reasoned that if a factor involved in juvenile condition such as size or growth rate can affect the reproductive success or fitness then it follows that the observed variations in life-history characteristics are "condition-dependent". He suggested that this mechanism for varying life histories is probably the most common form in nature.

In *A. planci* fitness is best described by maximising the lifetime offspring production $\boldsymbol{R}$, rather than the intrinsic rate of natural increase $\boldsymbol{r}$, (or similarly, the discounted offspring production $\boldsymbol{R}_0$ as was argued by Kozłowski (1993)). The advantage of a variable life-history strategy under temporal fluctuations of the environment is based on the argument that geometric mean fitness is increased by lowering between generation variance in fitness (Moran, 1992). By decreasing the variance between generations through the production of variable phenotypes within generations, Seger and Brockman (1987) showed that phenotypically polymorphic bet-hedgers can drive all other genotypes to extinction under conditions of temporal environmental variation (i.e. which influence migration rate, see above) because they have lower individual geometric-mean fitnesses (i.e. lifetime offspring production $\boldsymbol{R}$). The geometric mean is the natural measure of fitness under temporal variation because it is multiplicative, like population growth (Seger and Brockman, 1987).

To maintain polymorphic life-history characteristics in *A. planci* the proposed strategy can only develop from both spatial and temporal variation through migration (larval dispersal and variable recruitment) between reefs within, and to a lesser extent among, regions. The influence of variable recruitment on life history strategies in echinoderms has previously been proposed as a mechanism for selection of long life or a bet-hedging strategy (see Ebert, 1985). I suggest that bet-hedging is used by *A. planci* because it is rarely not found on reefs between outbreak episodes (i.e. where few individuals on reefs maintain panmixis among populations throughout particular regions). For these populations to persist, reproductive fitness must be maximised in extremely low densities as well as in high density populations through the use of variable reproductive tactics and mortality schedules (Figure 6.1). Schaffer (1974a) used models of life-history strategies to show that, under certain conditions of fertility, growth and adult survival, transient alternative life histories (i.e. more than one life-history strategy) could occur at the same time, including both semelparity and iteroparity. In *A. planci* semelparity is associated with very high reproductive effort and iteroparity with a lower reproductive effort. Selection for a high reproductive effort is an evolutionary consequence of rapid population expansion and decline events (Pianka and Parker, 1975), supporting the assertion that *A. planci* has a propensity to develop high density populations (Kettle, 1990) and, therefore, outbreaks can occur under natural environmental conditions.

The differences in the reproductive characteristics of the alternative life history strategies are reflected by the physical characteristics of the body wall among populations, and have been interpreted as the amount of stored energy available to the seasonal demand. The three principal patterns determined were:

(a) In high density populations starfish are resource limited, body size is constrained with high reproductive effort, the body wall is thin and fragile and there is a negative allometric relationship between whole body diameter and whole wet weight.

(b) In low density populations with abundant resources body size is not constrained, fecundity is high although reproductive effort is lower as body growth probably continues into adult life, storage of resources in the body wall increases with body growth maintaining isometric body relationships over a higher range of body sizes than those found in the higher density populations.

(c) In the low density Guam populations the starfish were also resource limited but the body walls were generally thicker and more robust, tending to isometric body size relationships, promoting iteroparity and a corresponding lower estimated reproductive effort.

Therefore, the conditioning factors affecting the populations in Guam promoted *Competitive* life-history characteristics under low resource levels, relative to the higher density populations. At the time of sampling, the Suva Reef population had sufficient resources for the *A. planci* population to remain within its carrying capacity, as evidenced by the regeneration of hard corals over the previous two year period while sustaining the population (personal observation). However, the generally small asymptotic body size and high estimated reproductive effort (particularly females) suggests there may have been other unidentified sources of *stress* promoting outbreak characteristics in the relatively low density population.

Lawrence (1990) stated that the criterion of longevity may be used to separate *Competitive* (5 to 15 years) and *Ruderal* (up to 5 years) species. Similarly, using the SPBC analyses on other GBR populations, *A. planci* from Lady Musgrave Reef were estimated to have survived for up to 12+ years and probably developed the competitive-type characteristics, although this has yet to be verified. In the high density outbreak populations maximum ages were estimated to be less than five years (Kettle, 1990; Chapter 3), which follows Stearns (1976) predictions of both bet-hedging with variable adult mortality and ***r* - *K*** selection. He stated that no distinction can be made between the two strategies, however, populations exhibiting "bet-hedging", have the capacity to modify life-history characteristics in ways that may be consistent with variation in environmental conditions. This capacity for variation within populations was determined from the Davies Reef studies of *A. planci*. Whether the expression of these types of variable traits result from expression of the same components of the genome or, from expressions of different segments of the genome cued to different environmental conditions awaits future investigations (Giesel et al., 1982b).

Several studies on life-history theory using models of age structure in populations have obtained general consensus among their results, finding that a decrease in adult survival rate leads to earlier maturity, larger reproductive effort earlier in life, and smaller adult body size (Taylor et al., 1974; Charlesworth and Leon, 1976; Michod, 1979). By using the effects of age structure in developing optimal life-history theory, more realistic fertility and growth survival functions can generate alternative reproductive strategies that are stable since each represents a local maximum in fitness (Schaffer, 1974a). Further analyses by Ricklefs (1981) showed that alternative reproductive strategies were only valid when trade-offs occur between life-history traits within age classes or when reproductive activities at one age have little affect on the future state of the organism (i.e. in species which have a determinate/asymptotic growth pattern).

The development of most life history models have used juvenile survival rate (including recruitment success) as one of the most important factors driving the evolution of age at maturity and reproductive investment (Stearns, 1980; Phillipi and Seger, 1989; Vøllestad et al., 1993). Therefore, the description of the life-history traits outlined are initially discussed in terms of this characteristic. The pattern of a constant age at maturity, as found in *A. planci*, has been interpreted by Stearns and Koella (1986) as a trade-off in potential fitness between postponing maturity for an increase in body size (decreasing juvenile mortality rates and increasing fecundity) and maturing earlier (decreasing generation time). Under the pressure of massive recruitments, aggregative behaviour and nutrient demand in the juvenile growth phase, varying patterns in growth, reproduction and mortality are developed in *A. planci* causing variation in their life-history characteristics.

More recent life-history theory has been used to predict norms of reaction (phenotypic plasticity) of life-history traits pertaining to age and size at maturity (i.e. Stearns and Koella, 1986; Kawecki and Stearns, 1993). The Stearns and Koella models were based on the assumptions of fitness defined by the Malthusian parameter ***r*** in the Euler-Lotka equation, a stable age distribution, no constraints (trade-offs) occur near local optima representing alternative phenotypes, fecundity increases with size and, delaying parental maturity reduces the juvenile mortality rate. Although these assumptions may not always be met, the predictions of reaction norms formed by Stearns and Koella (1986) were considered to be reasonably robust in application to real populations and remained valid when the models were tested under relaxation of individual assumptions. Kawecki and Stearns (1993) have advanced this theory to model natural populations in heterogeneous environments with a number of characteristics that are exhibited by *A. planci* populations. They predicted that the optimal age at maturity should not vary (as found in this study) with habitats that differ with respect to larval mortality, while the Stearns and Koella model predicted earlier maturation in populations subjeced to lowered levels of larval mortality.

Constant age at maturity was shown to be one of four possible patterns (the **L** shaped reaction norm) which described the theoretical relationship between body size and age at maturity (Stearns and Koella, 1986). A consistent delay in the age at maturity among populations (i.e. delayed from 1+ to 2+ years in *A. planci*) is promoted by both a high juvenile mortality rate and the exponential increase in fecundity with body size (Stearns and Koella, 1986), which conforms with the patterns described in *A. planci* populations in this study. To offset a high juvenile mortality rate in *A. planci*, high fecundities (i.e. through maximising body size prior to maturity) increases the absolute potential larval survival.

An **L** shaped trajectory describing body size and age at maturity showed that over a range of high growth rates the particular organism will appear to mature at a fixed age, changing only their size at maturity (Stearns and Koella, 1986). They found this pattern can also occur when adult mortality is independent of growth rate (see Chapter 4; i.e. where both high density and low resource habitats can influence mortality rates independently) or when adult mortality increases as growth rate decreases. Intrinsic factors are an important component of mortality in high density populations, as well as extrinsic sources such as competition for food, for increased fecundity in higher densities *A. planci* has the potential to compensate for a shorter reproductive period (i.e. lifespan). Therefore, the norm-of-reaction described for *A. planci* would contribute to maintaining relative fitness under the limiting conditions faced by outbreak populations (Figure 6.1).

A strategy of phenotypic plasticity in life-history characteristics allows for maximising reproductive fitness of *A. planci* in variable reef environments. Specific trade-offs between plastic life-history characteristics in *A. planci* have not previously been reported, however, the alternative expanation of genetic variation is unlikely, since calculated F_{ST} (standardised genetic variance for population differentiation) showed no significant variation among tested outbreak populations on the GBR, and further, the lack of genetic differentiation across the Pacific is consistent with gene flow of sufficient extent as to prevent local adaptations (Benzie, 1992). In populations where morphological variation exceeds electrophoretically detectable protein divergence, phenotypic plasticity may be present (Marcus, 1983) and therefore, is more likely to be the mechanism for the apparent variation in life-history characteristics of *A. planci*.

All species of echinoderms express some degree of phenotypic variability where the extent to which a character is variable may be indicative of its contribution to overall fitness (Marcus, 1983). Phenotypic plasticity expressed as a flexible life history indicates an adaptation to habitat unpredictability (Baird et al. 1986), and ensures the maximum survival of individuals over a range of conditions. Life history flexibility involves at least some life-history traits remaining sufficiently flexible to cope with changing circumstances that occur in an unpredictable environment (Baird et al., 1986).

An unpredictable habitat for *A. planci* can occur in various stages of the life cycle. In the adult stage large aggregations reduce coral cover to low levels in short periods which reduces their lifespan and transforms their habitat. When larval transport processes operate over a number of weeks (i.e. the estimated larval lifespan in *A. planci*) there is variable recruitment on reefs downstream from the parent population, i.e. larval density varies inversely with distance from the source and current patterns and mixing processes tend to promote a lottery for larval destination with time spent in the planktonic environment. Strathmann (1974) found there was selection pressure for the spread of sibling larvae as a fixed feature of life cycles and the extent of spread depends on survival and reproduction in the benthic phase of life as well as variation in duration of larval stages. Therefore, there is ample scope for potential selective pressure to maintain a flexible life strategy in *A. planci* in various phases of their life cycle.

6.4. Life-history variation and fitness

Examples of variability in life-history traits have been shown in a number of taxa and therefore, is used to maximise fitness under various physiological constraints. Kaitala (1991) found phenotype plasticity between populations and species of female waterstriders (*Gerris* spp.; Heteroptera) which were able to change reproductive allocation according to the food environment and high reproductive investment resulted in shortened lifespan. Different life history responses were also correlated with habitat characteristics in a study of three poecilid fish strains where resource allocation varied in response to high and low density treatments (Weeks, 1993). However, it was noted that some ambiguity occurred in relating the results of reproductive effort to the predictions from life-history theory due to problems associated with manipulating relatively long-lived species (Weeks, 1993).

Echinoderm species that reproduce by broadcasting larvae into the oceans at each spawning may increase the probability of successful colonisation by producing developmentally plastic individuals (Marcus, 1983). Therefore, a variable life-history strategy of *A. planci* is probably determined under the influence of conspecific density and food availability during the juvenile phase, well before maturity. Developmental plasticity uncouples the gene pool from the short-term selection pressures imposed by spatial and temporal heterogeneity (Stearns, 1980) and therefore, promotes the maintenance of the plastic response. Stearns (1980) speculated on the kinds of selective forces which operate in an unpredictable environment, favouring reduced reproductive effort, increased longevity and longer reproductive lifespan which permitted individuals to sample many environments with time and promoted the spread of offspring. To apply this argument to *A. planci* a definition of what is unpredictable about their environment is needed, and on coral reefs it is most likely to be the opportunity for successful fertilization in very low density populations or when high density populations significantly reduce resource levels over a short period of time. Resource limitation, whether it is "unpredictable" or not, is not only encountered by adult *A. planci* but also in the larval stages (Ayukai 1992) therefore, maintaining selective pressure for variability in the life-history strategy through various stages of the life-cycle.

If the variations in life-history strategy are caused by phenotypic plasticity then there must be environmental *stress* exerted on fitness which drives the life-history characteristics of *A. planci* between the various phenotypic states. Developmental mechanisms often produce dynamic patterns described as phenotype plasticity or constraint, where plasticity denotes the capacity of a single genotype to produce a range of environment dependent phenotypes and constraint occurs when the power of selection is limited by morpho-genetic design and ontogeny (Stearns, 1982). Evolutionary constraints on phenotypic expression can arise from inheritance, selection, development and design limits (Arnold, 1992). The best method for deciding that variable phenotypic responses are an adaptive advantage is to demonstrate that the consequences of the plastic response positively impact individual fitness although this has not been achieved in any studies so far (Reznick, 1990). However, the results of the *A. planci* population study from Davies Reef are interpreted as showing phenotypic plasticity in reproductive effort through increased levels of fecundity relative to body size in the post-outbreak cohorts. This demonstrates a tendency to maintain fitness under increased levels of *stress* and mortality. Adaptive life-history characteristics affect longevity by conferring fitness to:

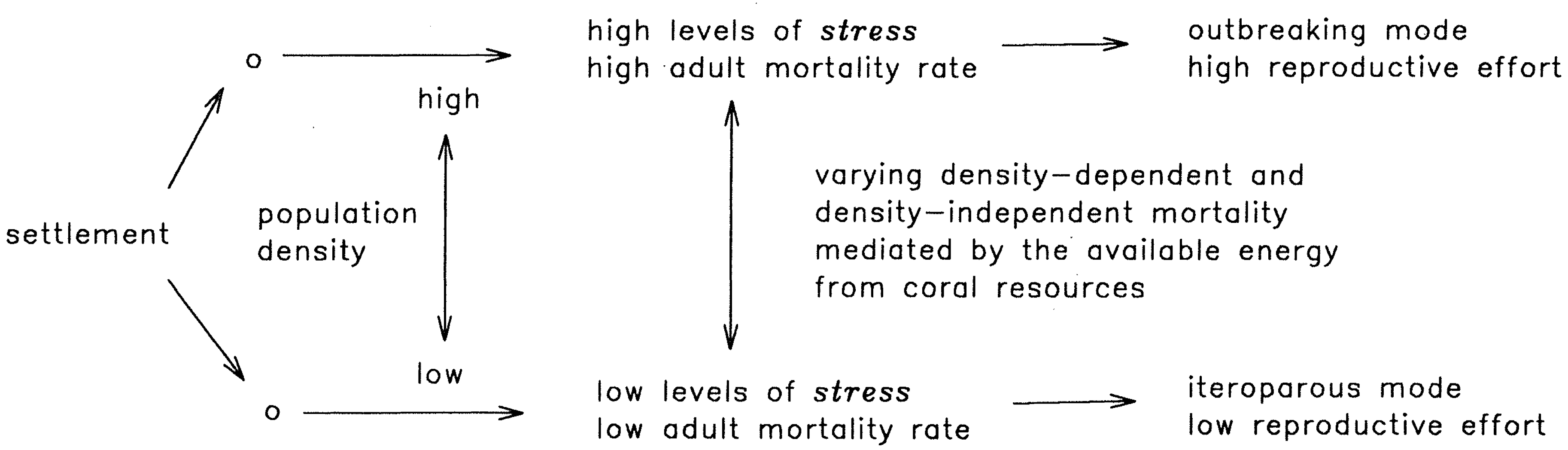
(a) achieve a smaller asymptotic body size and maximise early reproduction in individuals from high density populations with a shortened lifespan (i.e. the Davies Reef post-outbreak group).

(b) achieve a larger asymptotic body size through continued growth into the adult phase (where resource levels allow) and maximise reproductive success over a number of spawning seasons (iteroparity) (i.e. Davies Reef pre-outbreak group, the Suva Reef and Guam populations) or,

(c) achieve a very large body size by devoting more energy to growth throughout life in very low density populations with high resources and postponing spawning without conspecific stimulus (i.e. Lady Musgrave Reef, see Chapter 2).

Moran (1992) stated that to maintain the ability to develop alternative life-history characteristics the developmental cues in the juvenile environments must be matched with the environment in which the phenotype is selected (i.e. they must be reproductively successful). In *A. planci* this may be achieved when high density recruitment results in food limitation soon after maturity, where semelparous reproducers are more successful. By contrast, juveniles in low density populations do not receive the degree of stimulus from conspecific activity and reproductive effort is lower at maturity promoting reproductive success through iteroparity and longevity. The extent of longevity is determined by the availability of resources for the populations in their habitats. Further low density population studies and laboratory rearing experiments under controlled conditions are needed to confirm the predictions of the development of alternative life history strategies in *A. planci* populations.

FIGURE 6.1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from coral resources
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high reproductive effort
iteroparous mode
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